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**Revision of the Middle–Upper Ordovician acritarch genus *Orthosphaeridium*
Eisenack 1968 nov. emend.**

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ABSTRACT

The acritarch genus *Orthosphaeridium* Eisenack, 1968 is one of the most frequently recorded acritarch taxa in the Ordovician. The taxonomy of this easily recognizable genus is revised herein based on a detailed literature review and on new investigations of palynological material from northeastern Iran and South China. The review confirms that *Baltisphaera* Burmann, 1970 is a junior synonym of *Orthosphaeridium* of which the diagnosis is here emended. Over 20 species have been described in literature, but many of them are apparently synonyms. The review

indicates that the following four species can be easily differentiated: *Orthosphaeridium bispinosum* Turner, 1984, *Orthosphaeridium ternatum* (Burmann, 1970) Eisenack, Cramer and Díez 1976, *Orthosphaeridium rectangulare* (Eisenack, 1963) Eisenack, 1968 (type species) and *Orthosphaeridium octospinosum* Eisenack, 1968. The taxonomical ranks of *Orthosphaeridium rectangulare* var. *quadricornis* Burmann, 1970 and *Orthosphaeridium octospinosum* var. *insculptum* Loeblich, 1970 are changed from the *species* to the *varietas* level. The review indicates that *Orthosphaeridium* first appeared in South China in the *Expansograptus hirundo* graptolite Biozone, i.e. in the early Dapingian (stage slice Dp1 and time slice 3a of the Middle Ordovician) and that it reached a global distribution during the Middle and Late Ordovician. The genus disappeared at the end of the Ordovician and has never been recorded from the Silurian. The genus is thus a stratigraphical index fossil for the Middle and Late Ordovician. *Orthosphaeridium* has been recorded from the margins of all palaeocontinents and palaeoecologically seems to be an eurythermic taxon.

Keywords: phytoplankton, Lower Palaeozoic, Palaeoecology, biostratigraphy, taxonomy.

1. Introduction

Graptolites and conodonts are traditionally two major groups of stratigraphic index fossils for the Ordovician. However, in successions where these fossils are absent, palynomorphs, such as acritarchs and chitinozoans, have a good biostratigraphic potential, including for long distance

correlations in Lower Palaeozoic strata. Some of the First Appearance Datums (FADs) of significant acritarch taxa have shown a great potential for the definition of Ordovician stage boundaries and long-distance correlation (Li et al., 2002; Molyneux et al., 2007; Li et al., 2010; Servais et al., 2018).

Some Ordovician acritarch taxa with biostratigraphic, but also palaeogeographical significance have been reviewed in recent years, for example, *Ampullula* (Yan et al., 2010), *Arbusculidium* (Fatka and Brocke, 1999), *Arkonía–Striatotheca* (Servais, 1997), *Aureotesta* (Brocke et al., 1997), *Barakella* (Yan et al., 2017), *Coryphidium* (Servais et al., 2008), *Dactylofusa velifera* (Wang et al., 2015), *Dicrodiacrodium* (Servais et al., 1996), *Frankea* (Servais, 1993; Fatka et al., 1997), *Pachysphaeridium* (Ribecai and Tongiorgi, 1999), *Peteinosphaeridium*, *Liliosphaeridium* and *Cycloposphaeridium* (Playford et al., 1995), *Rhopaliophora* (Li et al., 2014), *Sacculidium* (Ribecai et al., 2002) and *Veryhachium* (Servais et al., 2007). These revisions allow precise correlations that challenge graptolite and chitinozoan biostratigraphy (Servais et al., 2018) and provide detailed biostratigraphic information from strata where other fossils are absent (e.g., Kroeck et al., 2019).

The very common Ordovician genus *Orthosphaeridium* has not been revised to date. It has first been described by Eisenack (1968) and has subsequently been recorded widely in the Ordovician, also under different names, such as *Baltisphaera* Burmann, 1970. To date, over 20 species and one infraspecific taxon have been attributed to the genus *Orthosphaeridium*. This acanthomorph acritarch is easily distinguishable due to its large vesicle, and its long, simple and hollow processes that display a distinctive plug at their base. Several species have been described on the basis of a very limited number of specimens, and many of them appear to be synonyms and need a detailed revision. The aim of the present study is thus to revise the genus

Orthosphaeridium in detail, in terms of taxonomy and biostratigraphy. In addition, all occurrences of *Orthosphaeridium* are plotted on a palaeogeographical reconstruction map to show its palaeobiogeographical extension, the ecological distribution of the genus is also discussed.

2. Material and methods

The newly investigated material used in this study comes from a stratigraphic section in northeastern Iran, the type section for the Upper Ordovician Ghelli Formation, from which the genus *Orthosphaeridium* has been reported previously in many samples (e.g., Ghavidel-Syooki et al., 2000a, 2017c). In the frame of a PhD project by the first author more than 160 rock samples were collected for palynological analysis from the type section of the Ghelli Formation (Fig. 1). The Ghelli Formation in this area is about 900 meters thick and is subdivided into three members (Fig. 2). The basal part of this rock unit consists mainly of volcanic rocks and subordinate limestones, sandstones, siltstones, and shales, but the major part of the formation is composed of highly micaceous shales and sandstones. About 105 samples were treated in the palynology laboratory of Kharazmi University, Tehran, Iran, and in the palaeontology research unit of the Evo-Eco-Paleo research department at the University of Lille, France. Palynomorphs were extracted from fine-grained samples such as shales and siltstones following standard palynological techniques, involving cold hydrochloric (HCl), cold hydrofluoric (HF) and hot hydrochloric (HCl) acid maceration to remove carbonates, silicates and fluorosilicates, respectively. The organic residues were then passed through 15 and 20 μm nylon meshes,

respectively at Lille and Tehran. No oxidation or alkali treatments have been carried out. All processed samples contain palynomorphs, including acritarchs, chitinozoans, cryptospores and scolecodonts in varying abundance and states of preservation. Figure 2 indicates the stratigraphic column and the position of the investigated samples with the distribution of *Orthosphaeridium* specimens. All rock samples, palynological slides and residues are stored in the palaeontology collections of the Faculty of Earth Sciences, Kharazmi University, Tehran, Iran and of the UMR 8198 CNRS department of the University of Lille, respectively.

A few additional samples from the Dawan Formation (Huanghuachang section), Yichang, Hubei, South China, were also used. These latter samples were previously investigated by Li et al. (2010) and Yan et al. (2011, 2017). All relevant information about the Chinese material is provided in these latter publications.

3. The genus *Orthosphaeridium*

3.1. Historical overview

More than 20 species and one infraspecific taxon have been described so far (Table 1). The description of the individual taxa is presented here in chronological order.

Eisenack (1968) erected the genus *Orthosphaeridium* from erratic boulders derived from the Ordovician of Baltica. He created the new genus based on assemblages containing specimens with a more or less rectangular central body and long, simple, hollow processes that do not communicate with the vesicle cavity due to the existence of a plug at the base of the processes.

The name given by Eisenack (1968) derived from *ortho* (= straight), because of the approximately straight sides and edges of the central body, and *-sphaeridium*, because of the close relationship with the genus *Baltisphaeridium* Eisenack, 1958. The ending *-sphaeridium* indicates on the one hand the spherical outline of the genus, and on the other hand the classical ending *-idium* points out a supposed phytoplanktonic origin. The ending *-idium* is indeed traditionally used for dinoflagellate taxa, and Eisenack (1968) and many other authors considered these acritarch taxa to be the cysts of phytoplanktonic organisms, close to dinoflagellates.

At the time of the original description of the genus, *Baltisphaeridium rectangulare* Eisenack, 1963 was selected as the type species with a “rectangular vesicle and four hollow processes.” In addition, the new species *Orthosphaeridium octospinosum* Eisenack, 1968 was erected with a rectangular vesicle and 7 or 8 hollow processes.

Two years after the erection of *Orthosphaeridium*, Loeblich (1970) also recovered the genus from North America and described the two species *Orthosphaeridium inflatum* and *Orthosphaeridium insculptum* from the Upper Ordovician Sylvan Shale, Oklahoma, U.S.A. These two species subsequently became some of the most commonly recorded species of *Orthosphaeridium*. The species *Orthosphaeridium inflatum* is very similar to *Orthosphaeridium rectangulare* but Loeblich (1970) pointed out that the former has a less rectangular vesicle and that the sides of the body are more inflated. However, the central body shapes of both *O. rectangulare* and *O. inflatum* are very variable and it is impossible to distinguish different taxa in larger populations, which indicates that *Orthosphaeridium inflatum* can be considered as a junior synonym of *Orthosphaeridium rectangulare*. Similarly, the North American species *Orthosphaeridium insculptum* strongly resembles *Orthosphaeridium octospinosum* from Baltica,

although the species of Loeblich (1970) was described with a more varying number (4–12) of processes than that of Eisenack (1968) that only bears 7 or 8 processes. *O. insculptum* was also described to differ by having a greater central body and a less rectangular outline with a strongly granulate wall. All these morphological characteristics are highly variable and make it difficult to separate the two species, that are herein considered to belong to the same entity.

Not being aware of the description of Eisenack's (1968) new genus, Burmann (1970) created the new genus *Baltisphaera* with seven new species from Germany. However, *Baltisphaera* perfectly fits the diagnosis of Eisenack, and most authors follow Eisenack et al. (1976) and Turner (1984) who considered *Baltisphaera* as a junior synonym of *Orthosphaeridium*. Burmann (1970) described her seven new species on the basis of a very limited number of specimens observed in thin sections (not palynological slides). Only the species *Baltisphaera ternata* Burmann, 1970, illustrated by two specimens, can be considered as new. This species has a circular vesicle with a characteristic tri-radial arrangement of long processes, that has been identified subsequently in many palynological assemblages by different authors. The other taxa, *Baltisphaera quadrinata*, *B. transitoria*, *B. procera*, *B. quadricornis*, *B. abbreviata*, and *B. occultata*, have all been described on the basis of single specimens, and have rarely been reported after their original description. They are all poorly preserved (for most of them only line drawings were provided by Burmann, 1970) and they display either three (*B. procera*, considered to be a junior synonym of *B. ternata*), or four (or possibly five) processes (all of them are considered herein to be junior synonyms of *Orthosphaeridium rectangulare*).

Kjellström (1971a) emended the genus *Orthosphaeridium* based on new material from the Grötlingbo Borehole No.1, Gotland, Sweden, and erected the new species *Orthosphaeridium trabeculatum*. This species has a psilate rectangular vesicle and was described with nine

processes that have a “trabeculate interior structure.” However, the distal endings of the processes are trifurcate, which does not correspond to the genus *Orthosphaeridium*, although Kjellström (1971a) emended the genus diagnosis to include his new species. Such trifurcate terminations have never been reported from other specimens so far and it appears clear that the specimens do not belong to *Orthosphaeridium*, of which the emended diagnosis of Kjellström (1971a) cannot be retained. In the same year, Kjellström (1971b) described two further new species, *Orthosphaeridium densigranosum* and *O. densiverrucosum*, from the same borehole. While the first species is described with a sub–quadrate granulate vesicle and eight processes, the second species differs in having a verrucate ornamentation on both the vesicle and process wall. Both species fall in the range of morphological variation of *O. octospinosum*.

Subsequently, Loeblich and Tappan (1971) described two new species, *Orthosphaeridium chondrododora* and *O. vibrissiferum*, from the Upper Ordovician Eden Formation in Indiana, U.S.A. Both species have four long processes and ornamented vesicle and process walls, and they both fall within the morphological range of *O. rectangulare*. Most interestingly, Loeblich and Tappan (1971) indicated an “apparent phylogenetic trend” of the different *Orthosphaeridium* species.

Eisenack et al.(1976) was the first to consider *Baltisphaera* Burmann, 1970 to be a junior synonym of *Orthosphaeridium*. He therefore placed all of Burmann’s species of *Baltisphaera* in the genus *Orthosphaeridium*.

Martin (1980) introduced the new species *Orthosphaeridium gaspesianum* from the Upper Ordovician White Head Formation in the Gaspésie section, Québec, Canada. This species displays a sub–spherical vesicle with a reticulated surface and 6–8 processes and it appears to be clearly related to *O. octospinosum*.

Turner (1984) emended the diagnosis of *Orthosphaeridium* because he found another new species with only two processes, *Orthosphaeridium bispinosum*, in the assemblages of the upper Caradoc (Upper Ordovician) of Shropshire, United Kingdom. He therefore extended the definition of *Orthosphaeridium* to include also those species that display only two ‘polar’ processes.

Uutela and Tynni (1991) introduced the new species *Orthosphaeridium latispinosum* from the Middle Ordovician of the Rapla borehole, Estonia. They considered that *O. latispinosum* has a sub-spherical vesicle with four stout and short processes. It is uncertain if this species belongs to *Orthosphaeridium* due to poor preservation and illustration. If it does, it should be considered a junior synonym of *O. rectangulare*. Uutela and Tynni (1991) also introduced the new forma *Orthosphaeridium insculptum* f. *erectum* from the upper Llanvirnian of Estonia, and they pointed out that this infraspecific taxon differs from *Orthosphaeridium insculptum* in having flagelliform processes. This ‘forma’ displays 8 processes of which the length is greater than the vesicle diameter. The processes are straight and have acuminate distal terminations with no clear constrictions at their proximal contacts. The surface of the vesicle is echinate, and the tubercles on the processes diminish in size from the base towards the distal termination. The vesicle has a median split. Uutela and Tynni (1991) described this forma based on three specimens and they only illustrated one microphotograph (plate XXVI, fig. 276). These specimens clearly fall within the range of *Orthosphaeridium insculptum*, i.e., *O. octospinosum*.

Parsons and Anderson (2000) described the two new species *Orthosphaeridium?* *extensum* and *Orthosphaeridium?* *triangulare* from the upper Cambrian of Random Island, Newfoundland. However, these two species do not belong to the genus *Orthosphaeridium*, but

are junior synonyms of *Lusatia dendroidea* Burmann, 1970 emend. Albani et al. 2007 that is a typical acritarch taxon of the upper Cambrian (Albani et al., 2006, 2007).

Finally, Le Hérisse et al. (2015) erected the new species *Orthosphaeridium orthogonium* from the Quwarah Member of the Qasim Formation, upperKatian–lowerHirnantian, Qusaiba, central Saudi Arabia. This species has a subrectangular vesicle with 10–12 processes. It has clearly a higher number of processes than all other species of *Orthosphaeridium*, and it possibly does not belong to the genus. Surprisingly, Le Hérisse et al. (2015, pl. IX, fig. 7) did not include *O. ternatum* in the genus *Orthosphaeridium*, but attributed it to *Baltisphaeridium*, following the classification by Rauscher (1974) that has usually not been followed.

3.2. Systematic paleontology

Group ACRITARCHA Evitt, 1963

Genus *Orthosphaeridium* Eisenack, 1968 emend. Turner, 1984 nov. emend.

Type species: Orthosphaeridium rectangulare (Eisenack, 1963) Eisenack, 1968, by original designation.

Original diagnosis (Eisenack, 1968, p. 91): “Central body when seen from the top more or less rectangular, in cross section oval to nearly rectangular, with long, hollow and tapering, unbranched processes, that lie preferably at the corners [of the vesicle] and of which the hollow

cavity is closed from the central vesicle. The opening of the vesicle occurs through a median transverse tear which is vertical to the long rectangle side.” (new translation).

Emended diagnosis (Turner, 1984): “Vesicle hollow, rectangular to circular in outline, bearing few (2–8) long, hollow, simple processes that taper to a sharp point; rarely a process may divide. Process interior is always separated from the vesicle cavity by a solid proximal plug. Excystment structure is an apparently straight split in a median or equatorial position.”

New emended diagnosis: Vesicle rectangular to circular in outline, with a single-layered and thick wall. Vesicle surface smooth to psilate to granulate, spinous or verrucate. Processes are hollow, long, simple with unbranched end and tapering to a sharp point. The processes do not communicate with the vesicle cavity and display a solid, basal plug. The number of processes varies from two to eight, or more (up to twelve), and their surface can be smooth or ornamented like the vesicle surface. The processes may be arranged in polar (if two), tri-radial (if three) position, or concentrated on each corner of the vesicle in quadrate forms, but may also be placed irregularly on the vesicle. A median split is commonly present.

Remarks: Eisenack’s (1968) original diagnosis was rather large and included a wide variation of morphologies. Kjellström’s (1971a) emended diagnosis is more restrictive and differs from the original diagnosis by adding trabeculate and trifurcate processes. These features were described on the basis of a few (seven) specimens only, of which one was illustrated (Kjellström, 1971a, plate 3, fig. 11). Such specimens with furcated processes were never recorded again and do not belong to *Orthosphaeridium*. For these reasons Kjellström’s (1971a) emendation cannot be retained. Turner (1984) enhanced the diagnosis of the genus because of his record of the species *Orthosphaeridium bispinosum* that displays two polar processes. Turner’s (1984) emended diagnosis was necessary at the time, and included that processes are 2–8 in

number. However, in some of the Iranian specimens, the number of the processes is clearly more than eight. Eisenack (1968) and Turner (1984) did not mention the ornamentation on the vesicle and process wall, that has been described in several species diagnoses. However, as many of the *Orthosphaeridium* species have a sculptured vesicle and process wall, the diagnosis is emended herein to take into account the great variety of number in processes (between 2 and 12) and of the surface wall ornamentation (smooth to psilate or verrucate).

Comparison: The variability between ‘baltisphaerid’ acritarchs (related to the genus *Baltisphaeridium*) is very high, and overlapping characteristics between different taxa may be observed. ‘Baltisphaerid’ acritarchs usually display more or less rounded vesicles and have unbranched processes, whereas ‘multiplicisphaerid’ acritarchs (related to the genus *Multiplicisphaeridium*) have branched processes. Several hundreds of species have been described within the ‘baltisphaerid’ and ‘multiplicisphaerid’ groups. From these, *Orthosphaeridium* is rather easy to recognize, because it is clearly distinguished from *Baltisphaeridium* due to its large, hollow processes that are closed at their base by a plug. Turner (1984) introduced the new genus *Baltisphaerosum*, and pointed out that this genus has a spherical to sub-spherical vesicle with hollow, simple or rarely branching processes, of which the bases are always plugged so that the processes do not communicate with the vesicle cavity. *Baltisphaerosum*, like *Orthosphaeridium*, displays a median split, interpreted as an excystment opening by many authors, whereas *Baltisphaeridium* usually displays a circular opening (pylome). Turner mentioned that “*Orthosphaeridium* is distinguished from *Baltisphaerosum* by its few, uniformly distributed processes.” This diagnosis is thus close to that of *Orthosphaeridium*, and Turner (1984) already indicated that “*Baltisphaerosum* gen. nov. and *Orthosphaeridium* clearly have close affinities and future research may show them to be

congeneric.” Turner (1984) assigned the forms with a pylome or without excystment structure to *Baltisphaeridium* and the other forms with a median split to *Baltisphaerosum*. However, Eiserhardt (1989) had a different view, when he emended *Baltisphaeridium* and considered the genus *Baltisphaerosum* as a junior synonym. The ‘baltisphaerid’ acritarchs, including several hundreds of species described, clearly need a detailed revision, including morphometrical studies to clarify the taxonomy.

Proposal of specific and infraspecific classification: The observation of a limited number of specimens resulted in the fact that some authors erected species with a very narrow description (e.g., Burmann, 1970). The analysis of larger populations of *Orthosphaeridium* indicates a broad morphological variability, mainly in the number of processes, but also in the presence of sculptural elements on the vesicle and process surface (from entirely smooth, to slightly psilate or coarsely granulate, including tubercule-like elements). Most taxa described fall within the range of a few distinguishable morphologies. Most specimens described in the literature, that are also found in the palynological assemblages investigated here, display either two, three, four, or more (usually around eight) processes.

Therefore, it is proposed here to retain four species that can easily be distinguished on the basis of the number of processes (Figure 3):

- *Orthosphaeridium bispinosum* Turner, 1984: two processes
- *Orthosphaeridium ternatum* (Burmann, 1970) Eisenack, Cramer and Díez, 1976: three processes
- *Orthosphaeridium rectangulare* (Eisenack, 1963) Eisenack, 1968: four processes
- *Orthosphaeridium octospinosum* Eisenack, 1968: more or less eight processes or more

The proposed new classification scheme with four distinctive species is illustrated in Table 1, that includes the list of all previously described taxa that are now considered as junior synonyms. Over 20 species and one infraspecific taxon have been described in the literature so far. The taxonomical revision allows to retain only the four above-mentioned, easily recognizable species.

In addition, a distinction can be made at an infraspecific level to classify specimens with smooth or ornamented vesicle and process walls:

- *Orthosphaeridium rectangulare* var. *quadricornis* var. nov. (psilate to verrucate vesicle surfaces)
- *Orthosphaeridium rectangulare* var. *rectangulare* Autonym (smooth vesicle)
- *Orthosphaeridium octospinosum* var. *insculptum* var. nov. (psilate to verrucate vesicle surfaces)
- *Orthosphaeridium octospinosum* var. *octospinosum* Autonym (smooth vesicle)

Orthosphaeridium rectangulare var. *quadricornis* var. nov. and *Orthosphaeridium octospinosum* var. *insculptum* var. nov. are two taxa of which the taxonomical status is changed here. *Orthosphaeridium rectangulare* var. *quadricornis* is based on the original description of *Baltisphaera quadricornis* Burmann 1970, the first taxon with four processes (thus belonging to *O. rectangulare*) described with a clearly distinctive ornamentation of the vesicle and process surface. *Orthosphaeridium octospinosum* var. *insculptum* is based on the original description of *Orthosphaeridium insculptum* Loeblich 1970, the first taxon with about eight processes (thus belonging to *O. octospinosum*) described with ornamented vesicle and process surfaces.

Orthosphaeridium bispinosum Turner, 1984

Plate I, figs. 1–4

1984 *Orthosphaeridium bispinosum* Turner, p.125, pl. 2, figs. 1–3; pl. 4, figs. 3, 5.

Original diagnosis (Turner, 1984, p. 126): “Vesicle very large, sub-spherical, hollow, thick walled (1.5–2.5 μm); wall bears a dense ornament of short, robust, solid spines with rounded tips. The two extremely long, slender, simple, homomorphic polar processes have acuminate distal terminations; they possess basal plugs of apparently solid wall material but have little or no proximal constriction; process interior separated from vesicle cavity; process walls ornamented with spines identical to those on vesicle wall.”

Original description (Turner, 1984, p. 126): “The dense ornamental spines of the vesicle and process surface appear to be echinate in bright field illumination but the scanning electron microscope shows them to be short, thick, solid, conical spines with broadly rounded tips. They cover the entire vesicle surface and extend onto the process walls, typically becoming sparser distally; rarely they may die away altogether, leaving the distal portion of the process walls smooth. The process wall is much thinner ($<0.5 \mu\text{m}$) and more delicate than the vesicle wall and frequently is folded; the distal tips of processes are infilled and solid. Excystment structure is a median split, with the vesicle often dividing completely (Pl. 4, fig. 5).”

Remarks: This species is easily distinguishable by its prominent two polar, long, slender and simple processes from all other species of *Orthosphaeridium*. Turner’s (1984) diagnosis and description are both very precise and can still be used at present.

Biostratigraphical and palaeogeographical distribution (quoting the original attributions, including the former British regional stages): This species has originally been recorded from the

Upper Ordovician (type–Caradoc) of England (Turner, 1984), and subsequently from many other localities: Caradoc–early Ashgill, Jordan (Keegan et al., 1990); Caradoc, Estonia (Uutela and Tynni, 1991); late Arenig, northwestern England (Cooper et al., 1995); Caradoc–Ashgill, Iran (Ghavidel–Syooki and Khosravi, 1995; Ghavidel–Syooki and Hoseinzadeh, 2010; Mahmoudi et al., 2014; Ghavidel–Syooki et al., 2014; Ghavidel–Syooki and Borji, 2018); late Caradoc, Saudi Arabia (Jachowicz, 1995); late Arenig, northwestern England (Molyneux, 1999); early Caradoc–Ashgill, ‘northern’ Gondwana (Vecoli and Le Hérissé, 2004); Middle Ordovician–Caradoc, Poland (Jachowicz, 2005); late Dapingian–early Darriwilian, northwestern England, (Molyneux, 2009); Caradoc–Ashgill, western Iraq (Al–Ameri, 2010); early late Katian, southwest Libya (Abuhamida, 2013); Katian–Hirnantian, northeastern Iran (Ghavidel–Syooki, 2017c).

Orthosphaeridium ternatum (Burmman, 1970) Eisenack, Cramer and Díez, 1976

Plate I, figs. 5–10

1970 *Baltisphaera ternata* Burmann, p. 306, pl. 7, fig. 1; pl. 9, fig. 4.

1970 *Baltisphaera procera* Burmann, p. 307, pl. 8, fig. 1.

1974 *Baltisphaeridium ternatum* Rauscher, pp. 82, 96, pl. 10, figs. 1–4.

1975 *Baltisphaeridium ternata* Tynni, fig. 10.

1976 *Orthosphaeridium ternatum* Eisenack, Cramer and Díez, p. 529.

Original diagnosis: “Vesicle circular in outline with a tri–radial arrangement of long unbranched processes that are distinctly differentiated from the central body by a somewhat thinner basal constriction. The processes are hollow and taper more rapidly at the distal than at

the proximal end. They are placed regularly, about 120° apart. Processes and central body may be smooth or may be covered by verrucae. No pylome can be seen; the vesicle opens by splitting of the central body into two smooth-rimmed halves (translation from Eisenack et al., 1976).”

Remarks: This species is easily recognizable, because it shows a more or less rounded to circular vesicle with three regularly arranged processes. Burmann(1970) described the two new species *Baltisphaera ternata* and *Baltisphaera procera*, that are clearly belonging to the same unit, but that show slightly different shapes of the central body (due to compaction of the sediment), one having a more circular and the other a more oval to subspherical vesicle. Rauscher (1974) placed *B. ternata* in the genus *Baltisphaeridium*, but Eisenack et al.(1976) transferred all of Burmann’s *Baltisphaera* species to *Orthosphaeridium*. *Orthosphaeridium ternatum* has priority and *Orthosphaeridium procerum* is considered here as a junior synonym.

Biostratigraphical and palaeogeographical distribution (quoting the original attributions, including the former British regional stages): *Orthosphaeridium ternatum* has been reported from numerous localities around the world. After its original description from the late Llanvirn of Germany (Burmann, 1970, 1973) it has been recorded in the following localities: Arenig–Llanvirn, France (Martin, 1973); Llanvirn, France (Rauscher, 1974); Caradoc–Ashgill? of the Algerian Sahara (Jardiné et al., 1974); Middle Ordovician, Bothnian Sea, Finland (Tynni, 1975); early Llanvirn, Czech Republic (Vavrdová, 1976, 1977); early Arenig–late Llanvirn (Díez and Cramer, 1977); early Llanvirn, Shropshire, England (Booth, 1979); late Lanvirn, Lake District, NW England (Booth, 1979); Caradoc, England (Turner, 1984); early Llanvirn–early Ashgill, England (Downie, 1984); late Arenig–Llanvirn, Morocco (Elaouad–Debbaj, 1984); late Arenig, Wales (Molyneux, 1987, 1990); early Llanvirn, Belgium (Servais and Maletz, 1992); early Caradoc, Saudi Arabia (Jachowicz, 1995); Arenig, eastern Alps, Austria (Reitz and Höll, 1992);

Caradoc–Ashgill, Iran (Ghavidel–Syooki and Khosravi, 1995); Oretanian–Dobrotivian (Llanvirn–early Caradoc), northern Spain (Gutiérrez–Marco et al., 1996); Llanvirn, Algeria (Vecoli, 1999); Caradoc, southern Iran (Ghavidel–Syooki, 1997); early Caradoc, Zagros Basin, southern Iran (Ghavidel–Syooki, 2000b); early? Ordovician, southeastern Turkey, (Erkmen 1979); Llanvirn–Ashgill, northeastern Iran (Ghavidel–Syooki, 2001); Caradoc–Ashgill, northeastern Iran (Ghavidel–Syooki, 2000a); Darriwilian, Saudi Arabia (Le Hérisse et al., 2007); Darriwilian (4a–4b), southern and southeastern Turkey (Paris et al., 2007); Llanvirn–Llandeilo, western Iraq (Al–Ameri, 2010); early late Katian, southwestern Libya (Abuhamida, 2013); Katian, southeastern Iran (Ghavidel–Syooki et al., 2014); Ashgill, southeastern Caspian Sea (Ghavidel–Syooki, 2017b).

Orthosphaeridium rectangulare (Eisenack, 1963) Eisenack, 1968 (type species)

1963 *Baltisphaeridium rectangulare* Eisenack, p. 211, pl. 20, figs. 1–3, 10.

1968 *Orthosphaeridium rectangulare* Eisenack, p. 92, pl. 25. Fig. 1.

1970 *Orthosphaeridium inflatum* Loeblich, p. 733–734, figs. 29A–E.

1970 *Baltisphaera quadrinata* Burmann, p. 306, pl. 8, fig. 1.

1970 *Baltisphaera transitoria* Burmann, p. 306–307, pl. 12, fig. 1.

1970 *Baltisphaera quadricornis* Burmann, p. 307–308, pl. 13, fig. 2.

1970 *Baltisphaera abbreviata* Burmann, p. 308, pl. 14, figs. 7a, b.

? 1970 *Baltisphaera occultata* Burmann, p. 308, pl. 16, fig. 1.

1971 *Orthosphaeridium chondrodora* Loeblich and Tappan, p. 184–186, figs. 2–6

1971 *Orthosphaeridium vibrissiferum* Loeblich and Tappan, p. 186–188, figs. 7–12

? 1991 *Orthosphaeridium latispinosum* Uutela & Tynni, p. 103, pl. XXVI: 277, fig. 4 :
183.

Original diagnosis: Central body flattened, when seen from the top almost rectangular with more or less bulged sides, with four long, hollow processes that arise from the corner of the rectangle and that lie in a plane (new translation).

Remarks: This species is very easy to differentiate, because it displays a rectangular to sub-quadrangle vesicle with four major processes that are preferentially located at the corners of the vesicle. Several authors described the species under different new names, that are here considered as junior synonyms of *Orthosphaeridium*. Similar to the vesicle shape, the surface ornamentation is also highly variable. For species with an ornamented surface of the vesicle and the processes (psilate, granulate, verrucate ornamentation), the variety *Orthosphaeridium rectangulare* var. *quadricornis* var. nov. is proposed, based on the original description of the first ornamented specimen by Burmann (1970) as *Baltisphaera quadricornis*. All rectangular *Orthosphaeridium* specimens with four processes and smooth vesicle walls can be attributed to *Orthosphaeridium rectangulare* var. *rectangulare* (Autonym).

Biostratigraphical and palaeogeographical distribution (quoting the original attributions, including the former British regional stages): The species *Orthosphaeridium rectangulare* has been recorded under this identification from several localities around the world, in chronological order: from the Late Ordovician, Ashgill, Gotland, Sweden (Eisenack, 1963, 1968); Middle Ordovician, Llanvirn–Caradoc, Gotland, Sweden (Kjellström, 1971a); latest Ordovician, Oklahoma, U.S.A. (Loeblich, 1970); Llanvirn–Llandeilo (Díez and Cramer, 1974); Middle Ordovician, Bothnian Sea, Finland (Tynni, 1975); Caradoc–Ashgill, Portugal (Elaouad–Debbaj,

1978); late Ashgill, Morocco (Elaouad–Debbaj, 1988); Middle Ordovician, Sweden (Kjellström, 1971b); Ashgill, Québec, Canada (Martin, 1988); Ashgill, Jordan (Keegan et al., 1990); Ashgill, Estonia (Uutela and Tynni, 1991); middle–late Ashgill, southeastern Turkey (Stemans et al., 1996); Ashgill, northeastern Missouri, U.S.A. (Wicander et al., 1999); Ashgill, ‘northern’ Gondwana (Vecoli and Le Hérisse, 2004); Caradoc–Ashgill, southern Oklahoma, U.S.A. (Playford and Wicander, 2006); Ashgill, Michigan, U.S.A. (Wicander and Playford, 2008); Hirnantian, southern Tunisia (Vecoli et al., 2009); Katian–Hirnantian, southern Estonia (Delabroye et al., 2011a); Llandeilo–Caradoc, western Iraq (Al–Ameri, 2010); Hirnantian, Québec, Canada (Delabroye et al., 2011b); Katian–Hirnantian, southeastern Caspian Sea (Ghavidel–Syooki, 2008, 2017b); Hirnantian, Zagros Mountains, Iran (Ghavidel–Syooki et al., 2011b); Katian–Hirnantian, northern Iran (Ghavidel–Syooki et al., 2011a); late Hirnantian, eastern Alborz, Iran (Mahmoudi et al., 2014); Katian, southeastern Iran (Ghavidel–Syooki et al., 2014); Katian–Hirnantian, central Saudi–Arabia (Le Hérisse et al., 2015); Katian–Hirnantian, northeastern Alborz Mountains, Iran (Ghavidel–Syooki and Borji, 2018).

Orthosphaeridium rectangulare var. *quadricornis* var. nov. stat. nov.

Plate II, figs. 4–5

Basionym: *Baltisphaera quadricornis* Burmann, 1970, p. 307–308, pl. 13, fig. 2.

Diagnosis: A variety of *Orthosphaeridium rectangulare* with an ornamented surface of the central vesicle and/or the processes. Ornamentation variable, from psilate to granulate or verrucate.

Remarks: The name of this new variety is based on the name of the first rectangular specimens of *Orthosphaeridium* with a clearly ornamented surface described by Burmann (1970) as *Baltisphaera quadricornis*. The body shape and process morphology is similar to that of all *Orthosphaeridium rectangulare* morphotypes, but it differs from *O. rectangulare* var. *rectangulare* (Autonym) in having an ornamented central vesicle wall. This ornamentation may also be present on the wall of the processes.

The ornamentation of the wall of acritarch specimens is highly variable. Possibly ecological changes are responsible for these variations, but such assumptions remain speculative. However, it appears logical not to distinguish the different end members of this variation (from smooth to highly ornamented surfaces) as different species. Therefore, a classification into infraspecific entities, as varieties, is proposed. The identification at the species level is mostly straightforward. The identification at the variety level may sometimes be difficult, due to preservation or observation methods (optical microscopy *versus* scanning electron microscopy, SEM).

Discussion: *Baltisphaera quadricornis*, originally described by Burmann (1970), was placed by Eisenack et al. (1976) into *Orthosphaeridium* and retained as a separate species. It is here considered a variety of *Orthosphaeridium rectangulare* because it displays the same vesicle outline and process number and distribution as *Orthosphaeridium rectangulare* but the surfaces of the vesicle and of the processes have been described to be covered by tubercles. Burmann (1970) described another species, *Orthosphaeridium quadrinatum* (Burmann, 1970) Eisenack et al., 1976, with a vesicle wall being smooth or ornamented. Similarly, *Orthosphaeridium transitorium* (Burmann, 1970) Eisenack et al., 1976 was also described with the vesicle and processes walls being covered by tubercles. The two species *Orthosphaeridium chondrododora*

and *O. vibrissiferum* described by Loeblich and Tappan (1971) also correspond to ornamented morphotypes of *Orthosphaeridium rectangulare*. While *O. chondrododora* was described with an ornamentation by grana, *O. vibrissiferum* was described as displaying granulose spines. Loeblich and Tappan (1971, fig. 1) noted that these changes in the ornamentation were related to a phylogenetic trend (see also discussion below).

Biostratigraphical and palaeogeographical distribution (quoting the original attributions, including the former British regional stages): The species *Orthosphaeridium quadricornis* has been reported under this name from the late Llanvirn of Germany (Burmam, 1970, 1976), but also from the Ashgill–early Llandovery? of northern India (Prasad and Asher, 2001), as well as from the Ashgill of western Iraq (Al–Ameri, 2010).

Specimens identified as *Orthosphaeridium quadrinatum* have been reported after their initial description from the late Llanvirn of Germany by Burmann (1970, 1976) from the following localities: Caradoc, England (Turner, 1984); Caradoc, Czech Republic (Vavrdová, 1974); Caradoc, Britain (Downie, 1984); Ashgill, Jordan (Keegan et al., 1990); late Arenig (lower Darrivilian, stage slice Dw1) from the Griffelschiefer in the Schwarzburg Anticline, Germany (Heuse et al., 1994); early Caradoc, Saudi Arabia (Jachowicz, 1995); Arenig, China (Yin, 1995); Caradoc, western Iraq (Al–Ameri, 2010); Katian–Hirnantian, northeastern Iran (Ghavidel–Syooki, 2017c).

Orthosphaeridium transitorium was only reported from the late Llanvirnian, Germany (Burmam, 1970, 1976) and not subsequently by other authors.

Orthosphaeridium chondrododora has been identified after its original description from the Late Ordovician of Indiana, U.S.A. (Loeblich and Tappan, 1971) from a number of localities: Middle Ordovician, Bothnian Sea, Finland (Tynni, 1975); Caradoc, Indiana, U.S.A. (Colbath,

1979); Ashgill, Morocco (Elaouad–Debbaj, 1988); Caradoc–Ashgill (Díez and Cramer, 1974); late Caradoc, United Kingdom (Downie, 1984); Caradoc, England (Turner, 1984); Ashgill, northeastern Libya (Hill and Molyneux, 1988); Ashgill, Scotland (Whelan, 1988); Ashgill, Estonia (Uutela and Tynni, 1991); Caradoc–Ashgill, Iran (Ghavidel–Syooki and Khosravi, 1995; Ghavidel–Syooki, 2000a); late Caradoc, Saudi Arabia (Jachowicz, 1995); middle–late Ashgill, southeastern Turkey (Stemans et al., 1996); Caradoc, England (Molyneux et al., 1996); late Ordovician, southeastern Turkey (Erkmen, 1979); early Caradoc–late Ashgill, ‘northern’ Gondwana (Vecoli and Le Hérissé, 2004); Katian, southeastern Turkey (Paris et al., 2007); Katian–Hirnantian, Québec, Canada (Delabroye et al., 2011b); Katian–Hirnantian, central Saudi Arabia (Le Hérissé et al., 2015).

Orthosphaeridium vibrissiferum has been identified after its first description from the Middle Ordovician, Indiana, U.S.A. (Loeblich and Tappan, 1971) from a few other localities: Caradoc, Poland (Górka, 1979); Middle–Late Ordovician (Llanvirn–Caradoc), Gotland, Sweden (Górka, 1987); Ashgill, Morocco (Elaouad–Debbaj, 1988); Llanvirn–Ashgill, Estonia (Uutela and Tynni, 1991); early Caradoc, Argentina (Ottone et al., 1999); early Caradoc–late Ashgill, ‘northern’ Gondwana (Vecoli and Le Hérissé, 2004); Katian, Estonia (Delabroye et al., 2011a).

Orthosphaeridium rectangulare var. *rectangulare* Autonym

Plate II, figs. 1–3, 6

Diagnosis: Same as that of the species.

Remarks: With the description of the new variety *Orthosphaeridium rectangulare* var. *quadricornis* all other specimens belonging to the species with a smooth surface of the vesicle and process wall can be assigned to *Orthosphaeridium rectangulare* var. *rectangulare* Autonym.

Discussion: *Orthosphaeridium inflatum* Loeblich, 1970 has been described with no ornamentation, but according to the present revision, no characteristic differences can be found between this species and *O. rectangulare*. Loeblich (1970) only pointed out that “*Orthosphaeridium inflatum* is very similar to *O. rectangulare* (Eisenack, 1963) Eisenack, 1968, but differs in having a less rectangular central body.” Most specimens identified as *Orthosphaeridium inflatum* could thus be attributed to *O. rectangulare* var. *rectangulare*. Similarly, *Baltisphaera abbreviata* Burmann, 1970 was described without ornamentation, and therefore corresponds to the same taxon.

Biostratigraphical and palaeogeographical distribution (quoting the original attributions, including the former British regional stages): Smooth specimens of *Orthosphaeridium rectangulare* have been recorded from different localities (see above), whereas *O. inflatum* has been identified as such from the Late Ordovician of Oklahoma, U.S.A. (Loeblich, 1970) and a few other localities: early and middle Ashgill, Québec, Canada (Jacobson and Achab, 1985); Ashgill, Jordan (Keegan et al., 1990); Caradoc–Ashgill, Iran (Ghavidel–Syooki and Khosravi, 1995; Ghavidel–Syooki, 1997, 2000a, 2001, 2003, 2006, 2017b); Katian, Québec, Canada (Delabroye et al., 2011b); late Katian, southern Sweden (Badawy, 2012).

A single identification corresponding to *Orthosphaeridium abbreviatum* (Burmann, 1970) Eisenack et al., 1976 is available from the Caradoc of western Iraq (Al–Ameri, 2010).

Orthosphaeridium octospinosum Eisenack, 1968

1968 *Orthosphaeridium octospinosum* Eisenack, p. 92, pl. 25, figs. 2–3.

1970 *Orthosphaeridium insculptum* Loeblich, p. 734–735, fig. 30 A–E.

1971b *Orthosphaeridium densigranosum* Kjellström, p. 28–30, fig. 19.

1971b *Orthosphaeridium densiverrucosum* Kjellström, p. 30, fig. 20.

? 1980 *Orthosphaeridium gaspesianum* Martin, p. 112, pl. 4, figs. 1, 2, 7, fig. 2.

1991 *Orthosphaeridium insculptum* f. *erectum* Uutela and Tynni, p. 103, pl. XXVI :
276, fig. 4: 140

? 2015 *Orthosphaeridium orthogonium* Le Hérisse, Molyneux and Miller, p. 51, pl. X,
figs. 1–2.

Original diagnosis (Eisenack, 1968, p. 92): Central body rectangular to square, generally throughout cuboid, with 8 or respectively 7 processes, that are similar to *O. rectangulare* originating and diverging from the corners [of the vesicle], so that they lay in the prolongation of a diagonal line of the [central body] surface. They correspond in their location and design type to those of the genus type (new translation).

Remarks: This distinctive species has clearly more than four processes, usually eight, or more. Most interestingly, Eisenack (1968) noted in his remarks that *O. octospinosum* could be a variant of *Orthosphaeridium* due to polyploidy, but that as a fossil it should be considered as a separate species. After the original description of this species by Eisenack (1968), several authors described almost the same morphology under different new species names. Loeblich (1970) created *O. insculptum* by noting simply that it was bigger than Eisenack's specimens and

that the American specimens showed an ornamented vesicle wall. Similarly, Kjellström (1971b) described the two almost identical species *O. densigranosum* and *O. densiverrucosum*, with the former taxon having smooth and the latter ornamented vesicle walls. Few of the authors, as it was usual at this time, mentioned variations between the individual morphotypes. However, Loeblich and Tappan (1971) noted a gradual change in their sections (see below). Here, all these taxa with more or less eight processes are considered to belong to the same species *O. octospinosum*.

Martin (1980) introduced *Orthosphaeridium gaspesianum* from the Late Ordovician of Québec and mentioned that it has a spherical central body with reticulated surface and 6 or 8 processes. Because the preservation of the specimens is poor and even with the SEM microphotographs it is not possible to observe the basal plug, the attribution of this species to *Orthosphaeridium* remains questionable. It could be that this reticulate ornamentation on the central body surface (illustrated in the drawing in Martin, 1980, fig. 2) might be the result of preservation or corrosion during maceration. This species has not been recorded from elsewhere so far.

The infraspecific taxon *Orthosphaeridium insculptum* f. *erectum* Uutela & Tynni, 1991 also falls within the range of variation of the species *O. octospinosum*, but it is not retained here as a separate *forma*.

The new species *O. orthogonium* Le Hérisse, Molyneux and Miller, 2015 is possibly related to the genus *Orthosphaeridium* and to the species *O. octospinosum*. This latter taxon has a higher number of processes and a clearly rectangular or trapezoidal central body that does not resemble the general morphology of *Orthosphaeridium*.

Discussion: *Orthosphaeridium octospinosum* is one of the four general morphotypes retained as separate species in the present study. It includes those specimens bearing clearly more than four processes. Following the original diagnosis by Eisenack (1968) this species has usually 8 processes with the main processes located in the corners of the vesicle and others arising from other parts of the central body.

Biostratigraphical and palaeogeographical distribution (quoting the original attributions, including the former British regional stages): Under its original name *O. octospinosum*, this species has been reported after its original description from the Late Ordovician of Baltica by Eisenack (1968) from other localities of the Middle and Late Ordovician: Late Ordovician (Ashgill), U.S.A. (Loeblich, 1970); Middle Ordovician, Gotland, Sweden (Górka, 1987); Ashgill, Morocco (Elaouad–Debbaj, 1988); Ashgill, Portugal (Elaouad–Debbaj, 1978); Middle Ordovician, Sweden (Kjellström, 1971b); Arenig, eastern Alps, Austria (Reitz and Höll, 1992); Ashgill, Turkey (Dean and Martin, 1992); Caradoc–Ashgill, Iran (Ghavidel–Syooki and Khosravi, 1995, Ghavidel–Syooki, 2000a, 2003); Caradoc, eastern Canada (Martin, 1983); Hirnantian, Saudi Arabia (Miller and Al–Ruwalli, 2007); early late Katian, southwestern Libya (Abuhamida, 2013); late Hirnantian, eastern Alborz, Iran (Mahmoudi et al., 2014); Katian–Hirnantian, northeastern Alborz Mountains, Iran (Ghavidel–Syooki, 2017c, Ghavidel–Syooki and Borji, 2018).

Orthosphaeridium octospinosum var. *insculptum* var. nov. stat. nov.

Plate II, figs. 7–9, 12

Basionym: *Orthosphaeridium insculptum* Loeblich 1971, p. 734–735, fig. 30 A–E.

Diagnosis: A variety of *Orthosphaeridium octospinosum* with an ornamented surface of the central vesicle and/or the processes. Ornamentation variable, from psilate to granulate or verrucate.

Remarks: In analogy with the proposed classification scheme of the species *O. rectangulare*, an infraspecific classification is also proposed for the species *O. octospinosum* to distinguish smooth and ornamented specimens. The name and conception of the new variety *Orthosphaeridium octospinosum* var. *insculptum* is adopted from the name and diagnosis of the first rectangular specimens bearing about eight processes (*O. octospinosum*) that have been described with an ornamented surface by Loeblich (1970) as *O. insculptum*. The body shape and process morphology is similar to that of all *O. octospinosum* morphotypes, but it differs from *O. octospinosum* var. *octospinosum* (Autonym) in having an ornamented central vesicle wall. This ornamentation may also be present on the wall of the processes.

Biostratigraphical and palaeogeographical distribution (quoting the original attributions, including the former British regional stages): Many authors identified specimens as *Orthosphaeridium insculptum* from numerous localities making this taxon one of the most widely recorded of the genus: Late Ordovician, Oklahoma U.S.A. (Loeblich, 1970; Tappan, 1980); Caradoc, Libya (Deunff and Massa, 1975); Ashgill, Portugal (Elaouad–Debbaj, 1978); Late Ordovician, southeastern Turkey (Erkmen 1979); Ashgill–Caradoc, Québec, Canada (Martin, 1980); Llandeilo–Caradoc, Ontario, Canada (Martin, 1983); early and middle Ashgill, Québec, Canada (Jacobson and Achab, 1985); Middle Ordovician (Llanvirn–Caradoc), Gotland, Sweden (Górka, 1987); Ashgill, Morocco (Elaouad–Debbaj, 1988); Ashgill, northeastern Libya (Hill and Molyneux, 1988); latest Ordovician, Czech Republic (Vavrdová,

1988); Ashgill, Québec, Canada (Martin, 1988); Llanvirn–Ashgill, Estonia (Uutela and Tynni, 1991); middle–late Ashgill, southeastern Turkey (Stemans et al., 1996); late Ashgill (Hirnantian), southern Norway (Smelror, et al., 1997); Ashgill, northeastern Missouri, U.S.A. (Wicander et al., 1999); early Caradoc–late Ashgill, ‘northern’ Gondwana (Vecoli and Le Hérisse, 2004); Ashgill, southern Oklahoma, U.S.A. (Playford and Wicander, 2006); Katian, southeastern Turkey (Paris et al., 2007); Hirnantian, southern Tunisia (Vecoli et al., 2009); Katian–Hirnantian, southern Estonia (Delabroye et al., 2011a); Hirnantian, Québec, Canada (Delabroye et al., 2011b); Katian–Hirnantian, southwestern Libya (Abuhamida, 2013); Caradoc–Ashgill, Iran (Ghavidel–Syooki, 1997, 2000a, 2001, 2003, 2006, 2008, 2016, 2017a, b, c); Hirnantian, Zagros Mountains, Iran (Ghavidel–Syooki et al., 2011b); Katian, northeastern Alborz Mountains, Iran (Ghavidel–Syooki and Borji, 2018).

Under the taxonomic name *Orthosphaeridium densigranosum* the species has been reported from the Middle Ordovician (Lower Viruan) of Gotland, Sweden (Kjellström, 1971b), and from the Middle Ordovician, Bothnian Sea, Finland (Tynni, 1975), whereas a few reports were made of *Orthosphaeridium densiverrucosum* after its original description from the Middle Ordovician (Lower Viruan) Gotland, Sweden (Kjellström, 1971b): late Llanvirn, Poland (Górka, 1980); Middle Ordovician, southwestern Finland (Uutela, 1989); Llanvirn–Caradoc, Estonia (Uutela and Tynni, 1991); late Arenig–early Llanvirn, Sweden (Ribecai and Tongiorgi, 1995).

Orthosphaeridium octospinosum var. *octospinosum* Autonym

Plate II, figs. 10–11

Diagnosis: As for the species *Orthosphaeridium octospinosum*.

Remarks: With the description of the new variety *Orthosphaeridium octospinosum* var. *insculptum* all other specimens belonging to the species with a smooth surface of the vesicle and process wall can be assigned to *Orthosphaeridium octospinosum* var. *octospinosum* Autonym.

Discussion: As the specimens described previously under the identification of *O. insculptum*, *O. densigranosum*, *O. densiverrucosum* all display an ornamented vesicle wall, and because *O. gaspesianum* and *O. orthogonium* are not clearly attributable to *Orthosphaeridium*, the only smooth *Orthosphaeridium* with about eight processes have been identified in previous studies as *O. octospinosum*.

Biostratigraphical and palaeogeographical distribution: See that for the species *Orthosphaeridium octospinosum*.

4. Biostratigraphy of *Orthosphaeridium*

From the literature overview and from the taxonomical revision, it becomes clear that *Orthosphaeridium* is largely recorded from Middle and Late Ordovician strata. The late Cambrian records (as *O.?* *extensum* and *O.?* *triangulare*) are not corresponding to the genus, and Early Ordovician (Tremadocian and Floian) records have not yet been published. The only reports of possible Early Ordovician levels (Erkmen, 1979) are highly questionable.

The interesting question is thus if the genus displays distinctive biostratigraphical distributions depending on the individual taxa (species) or corresponding to different palaeocontinents. Therefore, the stratigraphical distribution from different palaeocontinents is revised, but also the First (FAD) and Last Appearance Datums (LAD) of the different taxa.

Figure 4 illustrates the biostratigraphical distribution of the four different species of *Orthosphaeridium*, based on all published occurrences. In the following paragraphs the stratigraphical range is indicated, as it was described by the authors in the original papers. Very often the traditional British stratigraphical terms were used (Arenig, Llanvirn, Llandeilo, Caradoc, Ashgill) that are now correlated with the current global chronostratigraphy (Fig. 4). The stratigraphical information is summarized below, and presented following different palaeobiogeographical areas.

4.1. Stratigraphical distribution in Iran

During the last decades, *Orthosphaeridium* has widely been recorded in a series of studies from several Sandbian–Hirnantian (Caradoc–Ashgill in terms of traditional British stratigraphy) sections in Iran (Fig. 4). Due to the general absence of palynological investigations of Middle Ordovician rocks, older occurrences are not yet reported from Iran. All of the four general morphotypes of *Orthosphaeridium* and the new varieties proposed in this study have been reported from previous investigations from Iran. All taxa have also been found in the material investigated in this work (Fig. 2).

Orthosphaeridium bispinosum has been found in several localities and the stratigraphical range of the species covers almost the entire Sandbian to Hirnantian interval: Seyahou Formation, Zagros basin, southern Iran (Ghavidel–Syooki and Khosravi, 1995); Abarsaj Formation, Kholin–Darreh, southeastern Caspian Sea (Ghavidel–Syooki and Hosseinzadeh Moghadam, 2010); Ghelli Formation, Khosh–Yeilagh section, eastern Alborz Mountains (Mahmoudi et al., 2014); Ghelli Formation, Ghelli type section, northeastern Iran (Ghavidel–

Syooki, 2017c); Ghelli Formation, Robat–e Gharabil area, northeastern Alborz Mountains (Ghavidel–Syooki and Borji, 2018). Similarly, *Orthosphaeridium ternatum* has been reported from several localities: Seyahou Formation, Zagros basin, southern Iran (Ghavidel–Syooki and Khosravi, 1995; Ghavidel–Syooki, 2000b); Ghelli Formation, northeastern Alborz Mountains (Ghavidel–Syooki, 2000a, 2001); Abarsaj Formation, southeastern Caspian Sea (Ghavidel–Syooki, 2017b). *Orthosphaeridium rectangulare* is recorded from several sections: the so–called Gorgan Schists, southeastern Caspian Sea (Ghavidel–Syooki, 2008); Ghelli Formation, Khoshyeilagh area (Ghavidel–Syooki et al., 2011a); Dargaz Formation, Zagros Mountains (Ghavidel–Syooki et al., 2011b); Ghelli Formation, Khosh–Yeilagh section, eastern Alborz Mountains (Mahmoudi et al., 2014); Abarsaj Formation, southeastern Caspian Sea, (Ghavidel–Syooki, 2017b); Ghelli Formation, Robat–e Gharabil area, northeastern Alborz Mountains (Ghavidel–Syooki and Borji, 2018). *Orthosphaeridium octospinosum* has been recorded from the following locations: Seyahou Formation, Zagros basin, southern Iran (Ghavidel–Syooki and Khosravi, 1995); Ghelli Formation, northeastern Alborz Mountains (Ghavidel–Syooki, 2000a, 2003); Ghelli Formation, Khosh–Yeilagh section, eastern Alborz Mountains (Mahmoudi et al., 2014); Ghelli Formation, Ghelli type section, northeastern Iran (Ghavidel–Syooki, 2017c); Ghelli Formation, Robat–e Gharabil area, northeastern Alborz Mountains (Ghavidel–Syooki and Borji, 2018).

All taxa show thus an almost uniform distribution over the entire Upper Ordovician of Iran, with no preferential distribution of individual species. Similarly, there is no particular trend in the section investigated here, with all species present at almost all intervals (Fig. 2).

4.2. Stratigraphical distribution in Baltica

The different species of *Orthosphaeridium* identified from the margins of the palaeocontinent Baltica have so far restricted ranges, which might result from insufficient sampling. Nevertheless, all four major morphotypes have been recorded from this palaeocontinent. Similarly to Iran, a preferential distribution of individual morphotypes is not clearly visible so far.

Orthosphaeridium bispinosum has so far only been recorded from the Viru Series in the Rapla borehole, Keila to Oandu regional stages, Estonia (Uutela and Tynni, 1991), and from the Middle Ordovician–Caradoc of Poland (Jachowicz, 2005), whereas *Orthosphaeridium ternatum* has only been reported from the Middle Ordovician, Bothnian Sea, Finland (Tynni, 1975). *Orthosphaeridium rectangulare* has been more widely recorded: Late Ordovician, Ashgill, Gotland, Sweden (Eisenack, 1963, 1968); Middle Ordovician, Llanvirn–Caradoc, Gotland, Sweden (Kjellström, 1971a); Middle Ordovician, Bothnian Sea, Finland (Tynni, 1975); Middle Ordovician, Sweden (Kjellström, 1971b); Ashgill, Estonia (Uutela and Tynni, 1991); Katian–Hirnantian, southern Estonia (Delabroye et al., 2011a). Under the name *Orthosphaeridium inflatum* the species was reported from the late Katian, southern Sweden (Badawy, 2012). Records as *Orthosphaeridium chondrododora* and *Orthosphaeridium vibrissiferum* are from the following intervals: Middle Ordovician, Bothnian Sea, Finland (Tynni, 1975); Caradoc, Poland (Górka, 1979); Middle Ordovician (Llanvirn–Caradoc), Gotland, Sweden (Górka, 1987); Ashgill, Estonia (Uutela and Tynni, 1991); Llanvirn–Ashgill, Estonia (Uutela and Tynni, 1991); Katian, Estonia (Delabroye et al., 2011a). *Orthosphaeridium octospinosum* has also been reported largely: from the Late Ordovician, Ashgill, Gotland, Sweden (Eisenack, 1968), the Middle Ordovician, Gotland, Sweden (Górka, 1987), and the Middle Ordovician of Sweden

(Kjellström, 1971b). *Orthosphaeridium octospinosum* var. *insculptum* var. nov. has been reported from the Middle Ordovician (Llanvirn–Caradoc), Gotland, Sweden (Górka, 1987); Llanvirn–Ashgill, Estonia (Uutela and Tynni, 1991); late Ashgill (Hirnantian), southern Norway (Smelror, et al., 1997); Katian–Hirnantian, southern Estonia (Delabroye et al., 2011a). The reports under the species names *Orthosphaeridium densigranosum* and *Orthosphaeridium densiverrucosum* have been reported from a series of localities: the Middle Ordovician (lower Viruan), Gotland, Sweden (Kjellström, 1971a, 1971b); Middle Ordovician, Bothnian Sea, Finland (Tynni, 1975), late Llanvirn, Poland (Górka, 1980); Middle Ordovician, southwestern Finland (Uutela, 1989); Llanvirn–Caradoc, Estonia (Uutela and Tynni, 1991); late Arenig–early Llanvirn, Sweden (Ribecai and Tongiorgi, 1995).

4.3. Stratigraphical distribution in Laurentia

Interestingly, *Orthosphaeridium bispinosum* and *O. ternatum* have not yet been recorded from this palaeocontinent. Only the species with four (*O. rectangulare*) and about eight processes (*O. octospinosum*) are reported from Laurentia. Similarly to Iran, Middle Ordovician studies are lacking so far, and therefore all occurrences from Laurentia are limited to the Late Ordovician. Although Loeblich and Tappan (1971) mentioned findings from samples of the Middle Ordovician, the investigated Bromide Formation is of early Sandbian (Late Ordovician) age. Thus there are so far no occurrences from the Middle Ordovician, most probably due to the lack of studies. Future palynological investigations of Middle Ordovician sediments will possibly report the presence of the genus and thus an earlier FAD in Laurentia.

Orthosphaeridium rectangulare has been found from the following localities: latest Ordovician, Oklahoma, U.S.A. (Loeblich, 1970); Ashgill, Québec, Canada (Martin, 1988); Ashgill, northeastern Missouri, U.S.A. (Wicander et al., 1999); Caradoc–Ashgill, southern Oklahoma, U.S.A. (Playford and Wicander, 2006); Ashgill, Michigan, U.S.A. (Wicander and Playford, 2008); Hirnantian, Québec, Canada (Delabroye et al., 2011b). *Orthosphaeridium inflatum* has been reported as such from the Late Ordovician, Oklahoma, U.S.A. (Loeblich, 1970), from the early and middle Ashgill, Québec, Canada (Jacobson and Achab, 1985) and the Katian, Québec, Canada (Delabroye et al., 2011b). Records with the identification as *Orthosphaeridium chondrodora* and *Orthosphaeridium vibrissiferum* are from the following localities: Middle–Late Ordovician, Indiana, U.S.A. (Loeblich and Tappan, 1971; but all corresponding to the Late Ordovician); Caradoc, Indiana, U.S.A. (Colbath, 1979); Katian–Hirnantian, Québec, Canada (Delabroye et al., 2011b). *Orthosphaeridium octospinosum* was reported under this identification from the Late Ordovician (Ashgill), U.S.A. (Loeblich, 1970) and the Caradoc of eastern Canada (Martin, 1983). *Orthosphaeridium insculptum* has been reported from the Late Ordovician, Oklahoma U.S.A. (Loeblich, 1970; Tappan, 1980); Ashgill–Caradoc, Québec, Canada (Martin, 1980); Llandeilo–Caradoc, Ontario, Canada (Martin, 1983); early and middle Ashgill, Québec, Canada (Jacobson and Achab, 1985); Ashgill, Québec, Canada (Martin, 1988); Ashgill, northeastern Missouri, U.S.A. (Wicander et al., 1999); Ashgill, southern Oklahoma, U.S.A. (Playford and Wicander, 2006); Hirnantian, Québec, Canada (Delabroye et al., 2011b).

No obvious discriminative trend for a biostratigraphical distribution of individual taxa is evident. However, it is noteworthy that Loeblich and Tappan (1971) proposed an evolutionary scenario with “a progressive increase in processes” between the Eden Shale Formation and the

Sylvain Shale Formation, which might correspond to ecological changes in the succession (see below).

4.4. Stratigraphical distribution in Gondwana

Orthosphaeridium specimens have been found from numerous localities from the peri-Gondwanan margin (Fig. 4) covering the entire Middle and Late Ordovician. All four species are recovered from different parts of this wide area, to which the localities in Iran also belong.

Orthosphaeridium bispinosum has been recorded from the following localities: Caradoc, England (Turner, 1984); Caradoc–early Ashgill, Jordan (Keegan et al., 1990); late Caradoc, Saudi Arabia (Jachowicz, 1995); early Caradoc–Ashgill, ‘northern’ Gondwana (Vecoli and Le Hérisse, 2004); early Katian southeastern Turkey (Paris et al., 2007); Caradoc–Ashgill, western Iraq (Al–Ameri, 2010); early late Katian, southwestern Libya (Abuhamida, 2013).

Orthosphaeridium ternatum has been recorded as follows: late Llanvirn, Germany (Burmans, 1970, 1973); Arenig–Llanvirn, France (Martin, 1973); Llanvirn, France (Rauscher, 1974); Caradoc–Ashgill?, Algerian Sahara (Jardiné et al., 1974); early Llanvirn, Czech Republic (Vavrdová, 1976, 1977); early Llanvirn, Shropshire, England (Booth, 1979); late Llanvirn, Lake District, northwestern England (Booth, 1979); Caradoc, England (Turner, 1984); early Llanvirn–early Ashgill, England (Downie, 1984); Arenig–Llanvirn, Morocco (Elaouad–Debbaj, 1984); early Caradoc, Saudi Arabia (Jachowicz, 1995); Arenig, eastern Alps, Austria (Reitz and Höll, 1992); Oretanian–Dobrotivian (Llanvirn–early Caradoc), northern Spain (Gutiérrez–Marco et al., 1996); Llanvirn, Algeria (Vecoli, 1999); Early? Ordovician, southeastern Turkey, (Erkmen 1979); Darriwilian (4a–4b), southern and southeastern Turkey (Paris et al., 2007); Llanvirn–

Llandeilo, western Iraq (Al–Ameri, 2010); early-late Katian, southwestern Libya (Abuhamida, 2013).

Orthosphaeridium rectangulare has been retrieved from: Caradoc–Ashgill, Portugal (Elaouad–Debbaj, 1978); late Ashgill, Morocco (Elaouad–Debbaj, 1988); Ashgill, Jordan (Keegan et al., 1990); middle –late Ashgill, southeastern Turkey (Stemans et al., 1996); Ashgill, ‘northern’ Gondwana (Vecoli and Le Hérissé, 2004); Hirnantian, southern Tunisia (Vecoli et al., 2009); Llandeilo–Caradoc, western Iraq (Al–Ameri, 2010). Records as *Orthosphaeridium inflatum* have been reported from the Ashgill of Jordan (Keegan et al., 1990), whereas taxa corresponding to *Orthosphaeridium rectangulare* var. *quadricornis* var. nov. have been mentioned from the following localities: late Llanvirn, Germany (Burmans, 1970, 1976); Caradoc, England (Turner, 1984); Caradoc, Czech Republic (Vavrdová, 1974); late Ordovician, southeastern Turkey (Erkmen 1979); Caradoc, Britain (Downie, 1984); Caradoc, England (Turner, 1984); Ashgill, northeastern Libya (Hill and Molyneux, 1988); Ashgill, Morocco (Elaouad–Debbaj, 1988); Ashgill, Jordan (Keegan et al., 1990); late Arenig, Germany (Heuse et al., 1994); late Caradoc, Saudi Arabia (Jachowicz, 1995); early Caradoc, Saudi Arabia (Jachowicz, 1995); Arenig, China (Yin, 1995); middle–late Ashgill, southeastern Turkey (Stemans et al., 1996); Caradoc, England (Molyneux et al., 1996); early Caradoc, Argentina (Ottone et al., 1999); Ashgill–early Llandovery, northern India (Prasad and Asher, 2001); early Caradoc–late Ashgill, ‘northern’ Gondwana (Vecoli and Le Hérissé, 2004); Katian, southeastern Turkey (Paris et al., 2007); Caradoc, western Iraq (Al–Ameri, 2010); Katian–Hirnantian, Saudi Arabia (Le Hérissé et al., 2015).

Finally, smooth specimens that are herein attributed to *Orthosphaeridium octospinosum* var. *octospinosum* have been found from the following localities: Ashgill, Morocco (Elaouad–

Debbaj, 1988); Ashgill, Portugal (Elaouad–Debbaj, 1978); Arenig, eastern Alps, Austria (Reitz and Höll, 1992); Ashgill, Turkey (Dean and Martin, 1992); Hirnantian, Saudi Arabia (Miller and Al–Ruwaili, 2007); early–late Katian, southwestern Libya (Abuhamida, 2013). The ornamented specimens attributable to *Orthosphaeridium octospinosum* var. *insculptum* have been reported from the following locations: Caradoc, Libya (Deunff and Massa, 1975); Ashgill, Portugal (Elaouad–Debbaj, 1978); late Ordovician, southeastern Turkey (Erkmen 1979); Ashgill, Morocco (Elaouad–Debbaj, 1988); Ashgill, northeastern Libya (Hill and Molyneux, 1988); latest Ordovician, Czech Republic (Vavrdová, 1988); middle–late Ashgill, southeastern Turkey (Stemans et al., 1996); early Caradoc–late Ashgill, ‘northern’ Gondwana (Vecoli and Le Hérissé, 2004); Katian, southeastern Turkey (Paris et al., 2007); Hirnantian, southern Tunisia (Vecoli et al., 2009); Katian–Hirnantian, southwestern Libya (Abuhamida, 2013).

Although the biostratigraphical control of many of these localities is not always precise, it clearly appears that some of the oldest occurrences are from the margin of the Gondwanan continent, where the genus was present until its last occurrence in the latest Ordovician.

4.5. *The stratigraphical distribution in China*

Although the Yangtze Platform (South China) is considered in most palaeogeographical reconstructions as being part of the Gondwanan margin, it is treated here separately, because some authors placed this area in the northern hemisphere, and the Chinese acritarch assemblages are usually considered as mixed, with peri–Gondwanan taxa, but also other elements (Li and Servais, 2002; Molyneux et al., 2013). Most Chinese data are from the Early–Middle Ordovician, with few studies in the Late Ordovician (Li et al., 2007; Yan et al., 2011). There are

very few reports of *Orthosphaeridium* from China, but they are particularly important, because the oldest *Orthosphaeridium* specimens so far recorded are from the early Dapingian, stage slice Dp1 and time slice 3a (Yan et al., 2011), i.e., from the earliest part of the Middle Ordovician. Two species are present in China (*O. ternatum* and *O. octospinosum*), but recordings remain sparse to date.

4.6. The stratigraphical distribution in Avalonia

During the Middle and Late Ordovician, Avalonia was an isolated microcontinent, first in the periphery of Gondwana, but docking with Baltica during the latest Ordovician. Therefore this microcontinent is here treated separately. Some of the oldest occurrences of *Orthosphaeridium* are from Avalonia, with occurrences in the stage slice Dp2: *Orthosphaeridium bispinosum* has been recorded from the late Arenigian of northwestern England (Cooper et al., 1995; Molyneux, 1999), but also from the late Dapingian–early Darriwilian of northwestern England (Molyneux, 2009), whereas *Orthosphaeridium ternatum* has been recorded from the late Arenig of Wales (Molyneux, 1987, 1990) and the early Llanvirn of Belgium (Servais and Maletz, 1992).

4.7. FAD of *Orthosphaeridium*

Many acritarch occurrences are not accurately dated. This is partly due to the fact that acritarchs are often the only fossil group present in poorly preserved sedimentary successions and that they are used themselves to provide first biostratigraphical data. This is, for example, the

case in the British Isles, where acritarchs were used to date the rocks when graptolites (or other fossils) were absent (e.g., Molyneux, 1990, 1999). Many occurrences in Figure 4 are therefore to be considered with some care. Very often, the age provided by the authors is also no longer valid. For example, the ‘Middle Ordovician’ in Loeblich and Tappan (1971) appears to be actually early Late Ordovician in age. Nevertheless, the stratigraphical overview (Fig. 4) indicates that all four major morphotypes have similar distributions, spanning the Middle and Late Ordovician.

Of particular interest are the first appearances. These have been analysed herein with care, in particular by searching for independent biostratigraphical control. As a result, it appears that the FAD of *Orthosphaeridium* is located in the early Dapingian in South China, i.e., at the base of the Middle Ordovician. Yan et al. (2011) reported this first occurrence of *Orthosphaeridium ternatum* (*Orthosphaeridium* sp. 1 in Yan et al., 2011) in the *Expansograptus hirundo* graptolite biozone, that can be correlated with the lower part of Dapingian stage slice Dp1, and with the upper part of timeslice 3a. From Avalonia, the first occurrence of *Orthosphaeridium bispinosum* has been reported by Molyneux (2009) from the Skiddaw Group of the English Lake District in northern England, from the *gibberulus–cucullus* graptolite biozone that corresponds to the later part of the Dapingian and the early part of the Darriwilian (timeslices 3b–4a). Cooper et al. (1995) recorded *Orthosphaeridium bispinosum* in the upper part of the *Frankea hamata–Striatotheca rarirrugulata* acritarch assemblage in northwestern England that corresponds to the late Arenig in terms of British regional stratigraphy, or the late Dapingian–early Darriwilian stages (stage slices Dp2–Dw1).

Although the precise location and origin of Burmann’s (1970) samples in eastern Germany is not known and attributed to the Llanvirn, Heuse et al. (1994) recorded *Baltisphaera*

quadrinata (now *Orthosphaeridium rectangulare* var. *quadricornis*) from the Griffelschiefer in the Schwarzburg Anticline, Germany, which they correlated with the late Arenig *D. hirundo* graptolite Biozone (*A. cucullus*biozone). This graptolite biozone can be correlated with the lower Darriwilian stage slice Dw1, and therefore the FAD on the peri-Gondwanan margin neighbouring Avalonia can be placed at the base of Dw1, which represents so far also the oldest occurrence of the *Orthosphaeridium rectangulare* morphotype.

The oldest occurrence of the *Orthosphaeridium octospinosum* morphotype is also reported from South China by Yan et al. (2011) who stated that the FAD of *Orthosphaeridium* sp. 2 (now *O. octospinosum* var. *insculptum*) is located in the *clavus–austrodentatus* graptolite biozone which correlates with the base of stage slice Dp3 to Dw1 (late Dapingian–early Darriwilian).

In conclusion, *Orthosphaeridium* clearly appears in the early part of the Middle Ordovician, with the currently oldest occurrence being recorded from South China (early Dapingian, time slice 3a). All other morphotypes are present in the Middle Ordovician and none of them appeared for the first time after the late Dapingian.

4.8. LAD of *Orthosphaeridium*

Orthosphaeridium specimens have never passed the Ordovician–Silurian boundary and it seems that they disappeared at the end of the Ordovician. *Orthosphaeridium ternatum* has not been recorded in the latest parts of the Ordovician, but it is too early to assume that it disappeared earlier than other morphotypes. *Orthosphaeridium bispinosum*, *O. rectangulare* and *O. octospinosum* all extended to the end of the Ordovician. Delabroye et al. (2011a) investigated

acritarchs from the Ordovician–Silurian boundary at southern Estonia and compared their assemblages with carbon isotope data. They indicated that some of the *Orthosphaeridium* specimens, recorded as *O. insculptum* and *O. rectangulare*, disappeared just before the Ordovician–Silurian boundary (stage slice Hi2 and time slice 6c).

5. Palaeoecology and palaeogeography

5.1. Palaeoecology

While during many years acritarch research was mostly focused on biostratigraphy, investigations on palaeoecological aspects became more important recently. It is now well established that acritarch assemblages change according to inshore–offshore conditions (e.g., Li et al., 2004; Lei et al., 2012). In addition, individual taxa also display morphological changes, in particular regarding process length, that seem to follow inshore–offshore trends, with morphotypes bearing shorter processes being more abundant in nearshore environments (e.g., Stricanne et al., 2004), although this observation can surely not be generalized. These distribution patterns are possibly related to palaeosalinity and palaeotemperature (e.g., Servais et al., 2004; Van Soelen and Kürchner, 2018). Several authors noted that acritarchs with large processes are typical of open marine environments. There have been no studies integrating *Orthosphaeridium* so far. The genus is absent in the sections investigated by Li et al. (2004). Jacobson (1979) recognized three classes of acritarchs on the basis of morphologic similarity corresponding to three marine palaeoenvironments in the Middle and Late Ordovician from the

United States. The three classes were defined as the leiosphaerid class, the peteinosphaerid–*Dicommopalla* class and the baltisphaerid–veryhachid–*Polygonium* class, corresponding to a near–shore shallow–water environment, a shoal environment, and an open–sea environment, respectively. Although Jacobson (1979) did not include *Orthosphaeridium* in his assemblages, the presence of ‘baltisphaerid’ acritarchs indicate an open–sea environment for this genus. The taxa of this acritarch class, including *Baltisphaeridium*, *Multiplicisphaeridium* and *Ordovicidium*, are usually found with *Orthosphaeridium*, which suggests that the genus *Orthosphaeridium* is probably characteristic of open marine environments.

Orthosphaeridium is an acritarch genus with prominent processes, that appear to have been hollow, and the basic plug was possibly important for gas exchange between the central vesicle and the process chambers, that possibly were used as floating devices. These assumptions remain speculative, as would be the interpretation of a changing ornamentation by granules or tubercles of the wall surface of *Orthosphaeridium*. There are so far no studies about the number of processes in acritarch taxa related to palaeoecological parameters. Nevertheless, the process length and the ornamentation of the vesicle and process walls were most probably related to palaeoenvironmental conditions. Possibly the changing morphologies were an ecophenotypic response to changing palaeoenvironments, although it is difficult, if not impossible to control this on the fossil material.

Loeblich and Tappan (1971) presented a different interpretation for the morphological trends of the genus *Orthosphaeridium*. These authors brought together their observations from the Late Ordovician of the United States (Bromide Formation, Eden Shale Formation, Sylvain Shale Formation) in relation to the morphologies published by Eisenack (1968) from the Baltic Ordovician (‘Borkholmer Stufe’, ‘Lyckholmer Stufe’). Loeblich and Tappan (1971) mentioned

‘evolutionary trends’ in the Ordovician with specimens of *Orthosphaeridium* having ‘decreased vesicle ornamentation, increased number of major processes, and decrease in vesicle inflation.’ Unfortunately, it is not possible to understand on how many samples these observations and interpretations were based. Loeblich and Tappan (1971, fig. 1) consider that these morphological changes show ‘apparent phylogenetic trends’. However, it seems that such changes could very well be ecophenotypic rather than genotypic. The analyses of all data at a global level (Fig. 4) does not confirm an increased number of processes over time. All four species of *Orthosphaeridium* with two, three, four, or more processes appear to be simultaneously present over the entire Middle and Late Ordovician. Similarly, a global trend is not evident regarding an increase or decrease of vesicle ornamentation over time. These morphological characteristics are possibly related to local palaeoenvironmental changes rather than to a phylogenetical trend that would be visible in successive time intervals. Future detailed studies on perfectly well preserved, larger assemblages could clarify these questions.

According to the palaeogeographical distribution of *Orthosphaeridium* (see below), the genus occurs widely in marine environments and is present in almost all climatic zones (divided by Boucot et al., 2009) during the Middle and Late Ordovician. This distribution pattern implies that *Orthosphaeridium* would derive from an eurythermic marine organism.

5.2. Palaeogeography

Figure 5 shows the palaeogeographical distribution of *Orthosphaeridium* on a global reconstruction. The genus and the four species show no preferential distribution pattern. The

palaeobiogeography of Palaeozoic acritarchs has been reviewed in several papers. Li and Servais (2002) listed a selection of Ordovician acritarch taxa that display different latitudinal distribution patterns that might be related to temperature. The genus *Orthosphaeridium* was not included in the study of Li and Servais (2002), but the genus would show the same distribution pattern as *Micrhystridium*, *Baltisphaeridium*, *Peteinosphaeridium* or *Polygonium*, that are all present at all palaeolatitudes (Li and Servais, 2002, fig. 2). Molyneux et al. (2013) discussed the distribution of Middle Ordovician acritarchs and mapped the ‘peri-Gondwana’, ‘Baltica’ and mixed provinces on a palaeogeographical reconstruction. *Orthosphaeridium* is clearly present in all these provinces, with no preferential distribution. During the Late Ordovician, *Orthosphaeridium rectangulare* was considered to be a cosmopolitan species by Molyneux et al. (2013).

The present review confirms this interpretation. *Orthosphaeridium* possibly has the highest diversity in peri-Gondwana and Baltica, with all of the species and varieties being described from these palaeocontinents. *Orthosphaeridium bispinosum* and *Orthosphaeridium ternatum* have not yet been reported from Laurentia and *Orthosphaeridium octospinosum* is not yet recorded from Avalonia. In South China, *Orthosphaeridium bispinosum* still needs to be discovered. The apparent absence of one species from a specific palaeocontinent does not seem to be a real evidence of the absence rather than a lack of investigations. Apparently, all taxa are cosmopolitan during the entire period of the Middle and Late Ordovician.

6. Conclusions

Orthosphaeridium is one of the most frequently recorded acritarch genera in the Middle and Late Ordovician with significance for biostratigraphy and palaeobiogeography.

The taxonomic revision based on a detailed literature review and on large assemblages from new material investigated from northeastern Iran and South China, revealed that most of the previously described species are based on limited numbers of specimens, and that many of them are synonyms. Four species belong to the genus: *Orthosphaeridium bispinosum*, *O. ternatum*, *O. rectangulare* (type species), and *O. octospinosum*. Two new subspecific taxa are erected at the *varietas* level. These are based on two previously described species of which the status has been modified: *Orthosphaeridium rectangulare* var. *quadricornis* and *O. octospinosum* var. *insculptum*.

The FAD of *Orthosphaeridium* is in the early Dapingian (stage slice Dp1 and time slice 3a), whereas the LAD of the genus is in the latest Ordovician (stage slice Hi2 and time slice 6c), as *Orthosphaeridium* has never been recorded beyond the Ordovician–Silurian boundary.

Orthosphaeridium has been described from many localities of the Gondwanan margin, Baltica, Laurentia and Avalonia. The genus and all species appear to be cosmopolitan with a global distribution. The easily recognizable genus is therefore a good palynological index fossil for the Middle and Late Ordovician at the global scale.

Orthosphaeridium seems to be derived from an eurythermic organism, because it has been found in several different climatic zones and palaeoenvironments.

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Figure Captions

Fig. 1. Geographical map of northeastern Iran showing the location of the study area and the investigated section.

Fig. 2. Synthetic view of the type section of the Ghelli Formation with the position of the investigated samples and the distribution of *Orthosphaeridium* species in the sequence. Chitinozoan biostratigraphy unpublished.

Fig. 3. Idealized line drawings of the four general morphotypes of *Orthosphaeridium* retained herein as species. 1. *Orthosphaeridium bispinosum*, 2. *Orthosphaeridium ternatum*, 3. *Orthosphaeridium rectangulare*, 4. *Orthosphaeridium octospinosum*. Scale bar=50 µm.

Fig. 4. Global stratigraphical distribution of the four species of *Orthosphaeridium*. Global Series and Stages, regional divisions, stage slices and time slices of the Ordovician, based on Webby et al. (2004) and Bergström et al. (2009). 1. Northern England (Booth, 1979; Downie, 1984; Turner, 1984; Whelan, 1988; Cooper et al., 1995; Molyneux et al., 1996; Molyneux, 1999, 2009); 2. southwestern England (Booth, 1979; Turner, 1984); 3. Jordan (Keegan et al., 1990); 4. Estonia (Uutela and Tynni, 1991; Delabroye et al., 2011a); 5. Iran (Ghavidel-Syooki and Khosravi, 1995; Ghavidel-Syooki, 1997, 2000a, 2000b, 2001, 2003, 2006, 2008; Ghavidel-Syooki et al., 2011a, 2011b; Mahmoudi et al., 2014; Ghavidel-Syooki et al., 2014; Ghavidel-Syooki and Borji, 2018); 6. Saudi Arabia (Jachowicz, 1995; Miller and Al-Ruwaili, 2007; Le Hérissé et al., 2007, 2015); 7. Libya (Hill and Molyneux, 1988; Abuhamida, 2013); 8. 'Northern Gondwana' (Vecoli and Le Hérissé, 2004); 9. Germany (Burmman, 1970, 1973, 1976; Heuse et al., 1994); 10. France (Martin, 1973; Rauscher, 1974); 11. Algerian Sahara (Jardiné et al., 1974); 12. Czechoslovakia (Vavrdová, 1974, 1976, 1977); 13. Morocco (Elaouad-Debbaj, 1984, 1988); 14. Wales (Molyneux, 1987, 1990); 15. Belgium (Servais and Maletz, 1992); 16. Spain (Gutiérrez-Marco et al., 1996); 17. Turkey (Erkmen 1979; Dean and Martin, 1992; Steemans et

al., 1996; Paris et al., 2007); 18. Sweden (Eisenack, 1963, 1968; Kjellström, 1971a, 1971b; Górká, 1987; Badawy, 2012); 19. United States (Loeblich, 1970; Loeblich and Tappan, 1971; Colbath, 1979; Tappan, 1980; Wicander et al., 1999; Playford and Wicander, 2006; Wicander and Playford, 2008); 20. Portugal (Elaouad–Debbaj, 1978); 21. Canada (Martin, 1980, 1983, 1988; Jacobson and Achab, 1985; Delabroye et al., 2011b); 22. Tunisia (Ottone et al., 1999; Vecoli et al., 2009); 23. Norway (Smelror, et al., 1997); 24. South China (Yan et al., 2011).

Fig. 5. Palaeogeographical distribution of *Orthosphaeridium* in the Middle–Late Ordovician. Palaeogeographical reconstruction modified from Boucot et al. (2009). *Orthosphaeridium bispinosum* ●; *Orthosphaeridium ternatum*??; *Orthosphaeridium rectangulare* ■; *Orthosphaeridium octospinosum* ★.

Table Caption

Table 1. New classification with four distinctive species of *Orthosphaeridium* with list of all previously described taxa that are now considered as junior synonyms.

Plates

Plate I. Microphotographs of Iranian (all except fig. 9) and South Chinese (fig. 9) material of *Orthosphaeridium bispinosum* and *Orthosphaeridium ternatum*. For each illustrated specimen the following information is given: sampled formation, sampled section, sample label, slide

label, England Finder coordinate (if available). For example, GH41–3, K45/1 refers to sample GH41, slide 3, England–Finder coordinates K45/1. Scale bar = 20 μm .

1–4. *Orthosphaeridium bispinosum* Turner, 1984

1. Ghelli Formation, Ghelli, GH41–3, K45/1

2. Ghelli Formation, Ghelli, GH9–2, O53/4

3. Ghelli Formation, Ghelli, GH22–3, U35

4. Ghelli Formation, Ghelli, GH51–2, O20/1

5–10. *Orthosphaeridium ternatum* (Burmann, 1970) Eisenack, Cramer and Díez, 1976

5. Ghelli Formation, Ghelli, GH123–3, K42

6. Ghelli Formation, Ghelli, GH115–2, O35

7. Ghelli Formation, Ghelli, GH57–1, M26/1

8. Ghelli Formation, Ghelli, GH107–2, O26

9. Dawan Formation, Daping, Yichang, Hubei, China AFI4016–1, K52/2

10. Ghelli Formation, Ghelli, GH40–S, F66/2

Plate II. Microphotographs of Iranian (all except fig. 12) and South Chinese (fig. 12) material of *Orthosphaeridium rectangulare* var. *rectangulare*, *Orthosphaeridium rectangulare* var. *quadricornis*, *Orthosphaeridium octospinosum* var. *octospinosum* and *Orthosphaeridium octospinosum* var. *insculptum*. For each illustrated specimen the following information is given: sampled formation, sampled section, sample label, slide label, England Finder coordinate (if available). For example, GH26–1, S60/1 refers to sample GH26, slide 1, England–Finder coordinates S60/1. Scale bar = 20 μm .

1–3, 6. *Orthosphaeridium rectangulare* var. *rectangulare*

1. Ghelli Formation, Ghelli, GH26–1, S60/1
2. Ghelli Formation, Ghelli, GH32–2, N52/1
3. Ghelli Formation, Ghelli, GH115–2, O50/1
6. Ghelli Formation, Ghelli, GH1–2, V45/1

4–5. *Orthosphaeridium rectangulare* var. *quadricornis*

4. Ghelli Formation, Ghelli, GH7–1, M53/4
5. Ghelli Formation, Ghelli, GH105–2, R62/3

7–9, 12. *Orthosphaeridium octospinosum* var. *insculptum*

7. Ghelli Formation, Ghelli, GH134–3, N22/3
8. Ghelli Formation, Ghelli, GH115–2, G54
9. Ghelli Formation, Ghelli, GH30–S, O60/2
12. Dawan Formation, Huanghuachang, Yichang, Hubei, China HHDW28–2, M40

10–11. *Orthosphaeridium octospinosum* var. *octospinosum*

10. Ghelli Formation, Ghelli, GH65–2, N57
11. Ghelli Formation, Ghelli, GH133–S, R50/2

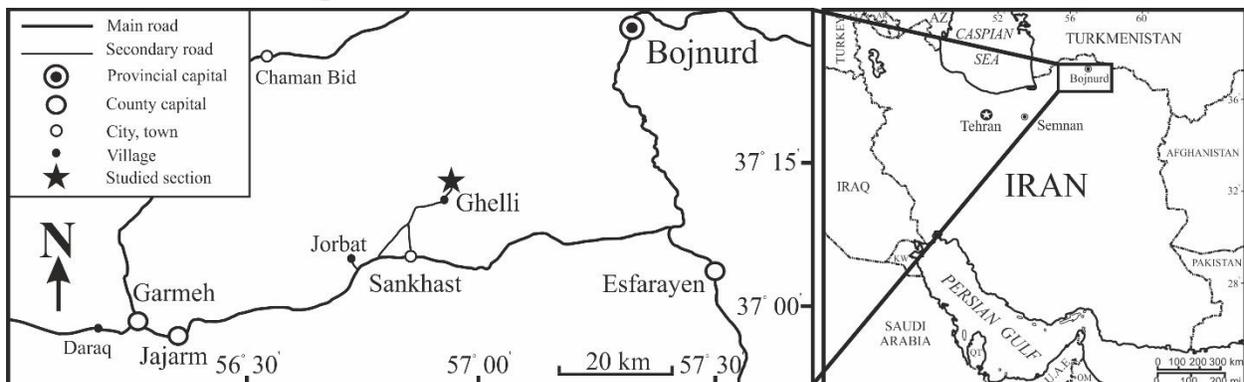


Figure 1

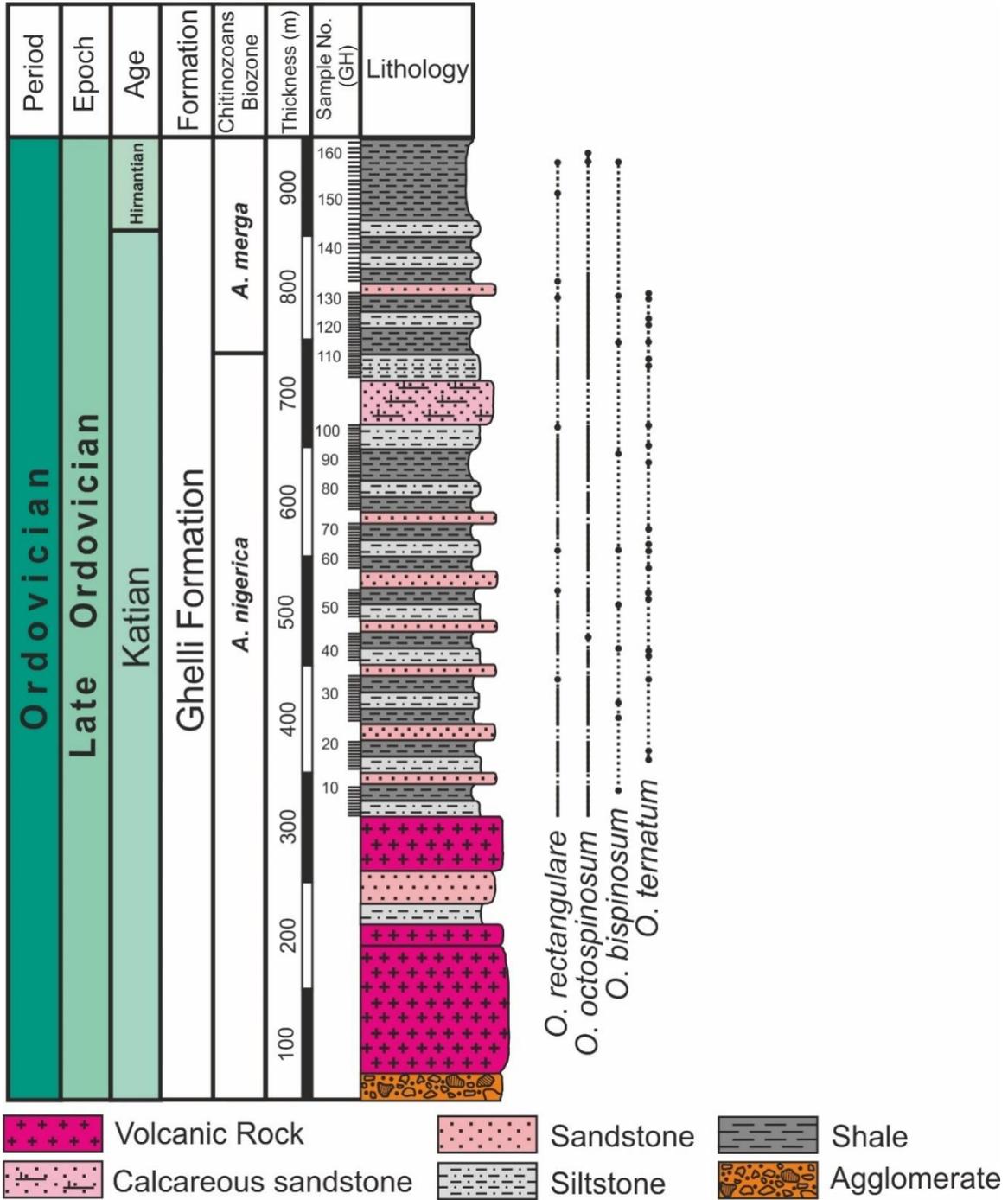


Figure 2

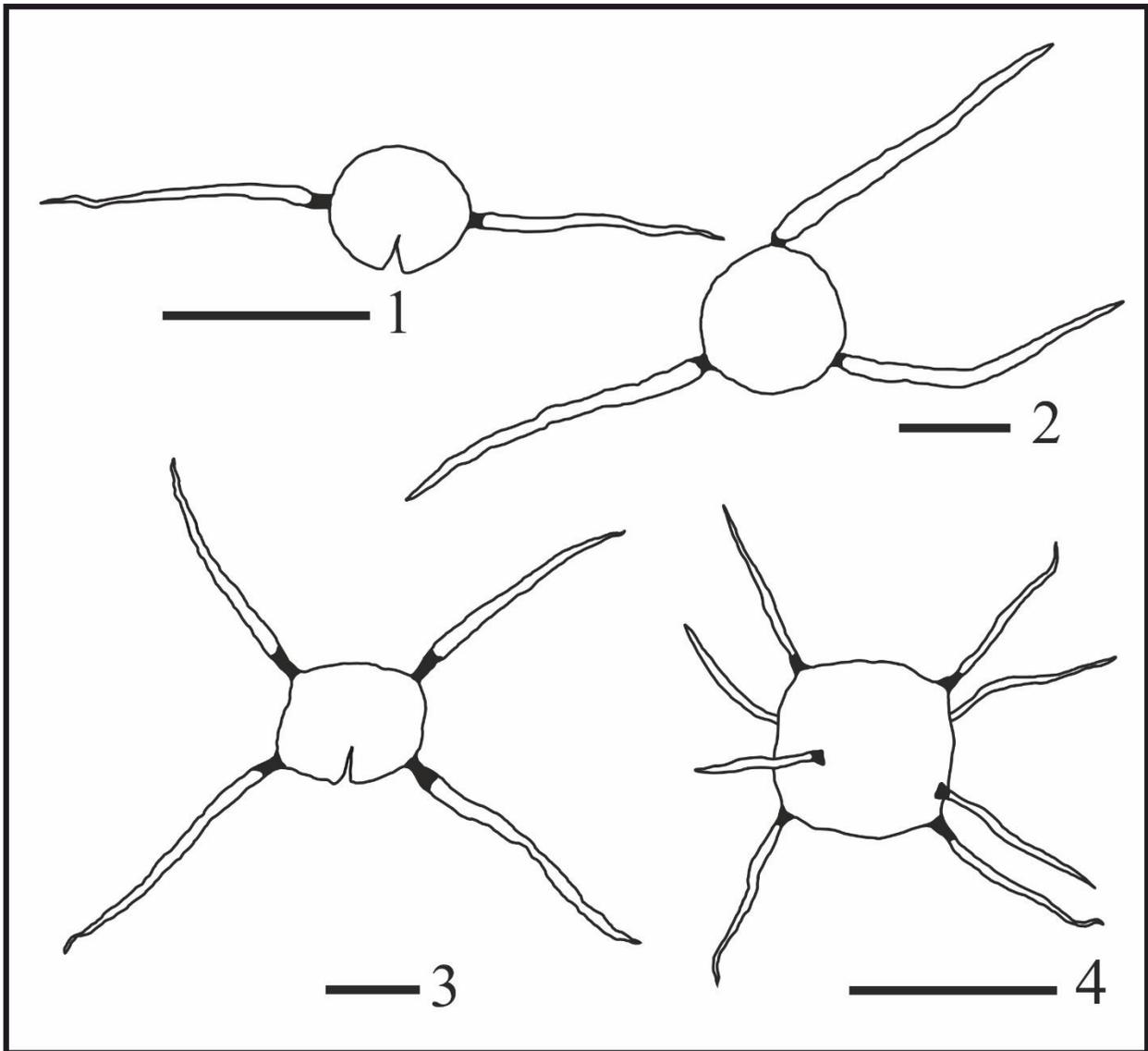


Figure 3

Current classification	Original name and junior synonyms	Author
<i>Orthosphaeridium bispinosum</i>	<i>Orthosphaeridium bispinosum</i>	Turner 1984
<i>Orthosphaeridium ternatum</i>	<i>Baltisphaera ternata</i> <i>Baltisphaera procera</i>	Burmans 1970 Burmans 1970
<i>Orthosphaeridium rectangulare</i>	<i>Baltisphaeridium rectangulare</i> <i>Orthosphaeridium inflatum</i> <i>Baltisphaera quadrinata</i> <i>Baltisphaera transitoria</i> <i>Baltisphaera quadricornis</i> <i>Baltisphaera abbreviata</i> ? <i>Baltisphaera oculata</i> <i>Orthosphaeridium chondrodora</i> <i>Orthosphaeridium vibrissiferum</i> ? <i>Orthosphaeridium latispinosum</i>	Eisenack 1958 Loeblich 1970 Burmans 1970 Burmans 1970 Burmans 1970 Burmans 1970 Burmans 1970 Burmans 1970 Loeblich and Tappan 1971 Loeblich and Tappan 1971 Uutela and Tynni 1991

<i>Orthosphaeridium octospinosum</i>	<i>Orthosphaeridium octospinosum</i> <i>Orthosphaeridium insculptum</i> <i>Orthosphaeridium densigranosum</i> <i>Orthosphaeridium densiverrucosum</i> ? <i>Orthosphaeridium gaspesianum</i> <i>Orthosphaeridium insculptum</i> forma <i>erectum</i> ? <i>Orthosphaeridium orthogonium</i>	Eisenack 1962 Loeblich 1970 Kjellström 1971b Kjellström 1971b Martin 1980 Uutela & Tynni 1991 Le Hérisse et al. 2015
Unknown genus	<i>Orthosphaeridium trabeculatum</i>	Kjellström 1971a
<i>Lusatia dendroidea</i>	<i>Orthosphaeridium</i> ? <i>extensum</i> <i>Orthosphaeridium</i> ? <i>triangulare</i>	Parsons and Anderson 2000 Parsons and Anderson 2000

Table 1

- The complete literature of *Orthosphaeridium* is revised.
- New material from Iran and China allows for emendation of the genus.
- *Orthosphaeridium* is an excellent index tool for the Middle-Upper Ordovician biostratigraphy.
- *Orthosphaeridium* apparently represents an eurythermic organism.

Journal Pre-proof