# The first report of cryptospore assemblages of Late Ordovician in Iran, Ghelli Formation, Eastern Alborz

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#### Abstract

For the first time, an assemblage of cryptospores, which includes 10 species belonging to nine genera, from the Upper Ordovician strata, is being reported, in Iran. These cryptospore assemblages were recovered from the upper part of Ghelli Formation., from the eastern Alborz Mountain range. These peri-Gondwanan cryptospores have been classified based on their morphology (monad, true dyad, pseudodyad, true attached, and loose tetrads). The results of the present study support previous findings that there are no significant differences between similar-aged cryptospore assemblages of the peri-Gondwanan, Baltic provinces and other parts of the world. Based on the presence of the chitinozoan index of the northern Gondwana (*Spinachitina oulebsiri*), the index acritarchs, and the present cryptospores, a late Hirnantian (Late Ordovician) age is proposed to the top of the Ghelli Formation. The cryptospores seem to be transported from an adjacent land area and the lack of land-derived elements in the up-section may indicate an increased distance offshore.

Keywords: Cryptospore, Late Ordovician, Ghelli Formation, Eastern Alborz, Iran.

## Introduction

The study area is located about 80 km north-east of the city of Shahroud and east of the Khosh-Yeilaghi village (N 36° 49' 24" to 36° 53' 04" and E 55° 14' 14" to 55° 24′ 12″) (Fig. 1). Ghavidel-Syooki et al. (2011a), studied the acritarchs and chitinozoans from this formation, but could identify only the cryptospore Tetrahedraletes sp. In this study, in addition to the investigations on acritarch and chitinozoan assemblages, we identified cryptospores following the morphological classification of Wellman and Richardson (1993). We focused only on the top part of the Ghelli Formation, that is, the beginning of the green shale (as a key bed), which was approximately equivalent to the first occurrence of the chitinozoan index S. oulebsiri of the late Katian age.

## Geological setting

The Khosh-Yeilaghi area is considered as a part of the eastern Alborz zone (Stocklin, 1968) and Alborz zone (Alavi, 1979, 1991). On the basis of Khosh-Yeilaghi geological map (Jafarian, 2004; scale 1:100000), the rock units of the Paleozoic and Mesozoic rocks comprise of Ghelli, Soltan-Meydan, Padeha, Khosh Yeilagh, Mobark, Doroud, Ruteh, Nesen, Elika and Shemshak formations (Fig. 1).

The Ghelli Formation (Abarsaj formation) was first introduced by Shahrabi (1990) in the Gorgan geological map (scale 1:250000). This formation comprises of alternate beds of gray and olive green shale and siltstones, having thin to moderate thickness, very thin and uncommon layers of grayish micaceous sandstone, and an interlayer of split basalts lying near the top (Figs. 2, 3). The lower part of the Ghelli Formation has been cut by a fault and is conformably overlain by the Soltan-Meydan volcanic Formation of the Silurian age (Ghavidel-Syooki et al., 2011a). A Late Ordovician age has been assigned to the Ghelli Formation, on the basis of palynological studies (Chateaneuf et al., 1978; Sabouri, 2003; Ghavidel-Syooki et al., 2011a; Mahmoudi et al., 2011; Mahmoudi, 2011). In the present study, the top (110 m) of the Ghelli Formation is sampled for a palynological study.

#### **Materials and Methods**

Twenty-three samples from the upper Ghelli Formation were collected and palynological slides were prepared as the standard processing methodology, at the palynological laboratory of the Geological Survey of Iran, and kept there as an archive. The slides were then subjected to an optical study. The blackish/opaque color of some of the cryptospores (especially monad forms) made it

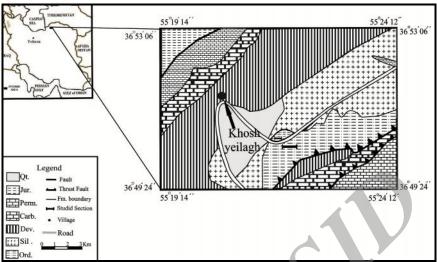


Figure 1. The sketch of geological map of the study area

difficult to identify them under light microscopy. For better brightness, we treated the samples with liquid bleach (NaClO+K<sub>2</sub>Cr<sub>2</sub>O<sub>7</sub>+DeIonized water), but the result was not useful. Therefore, Scanning Electron Microscopy (SEM) was applied to study these specimens. The SEM instrument, model Wegall Tescan, with High Vacuum, based at the Research Institute of Razi, has been used for identification of the palynomorphs.



Figure 2. Field photography of the studied section (by Mahmoudi, 2011)

The previous studies on cryptospores in the world Wellman & Gray (2000) proposed that these microfossils were derived from Bryophyte-like parental plants. The cryptospores and phytodebris were the first evidence of land plants that were recovered from the Llanvirnian (Darriwilian; Middle Ordovician) (Wellman & Gray, 2000). The first true spore (Embryophyte) was also reported

from the Middle Llanvirnian (Darriwilian; Middle Ordovician) of Saudi Arabia (Strother *et al.*, 1996).

In general, the cryptospores of Late Ordovician (Katian-Hirnantian) showed low diversity and abundance at the generic and species levels, and researchers were convinced that the glaciation of the Hirnantian age had no effect on these cryptospore assemblages (Vecoli et al., 2011). Recent findings revealed that the cryptospore assemblages of the Baltic and peri-Gondwana provinces (especially Turkey) were very similar to each other (Steemans, 2000; Vecoli et al., 2011). In some of the previous palynological articles on Late Ordovician of Iran, the cryptospores were considered as a whole or described only at the two generic and two species levels (Ghavidel-Syooki & Khosravi, 1994; Ghavidel-Syooki, 1995; Ghavidel-Syooki, 2006; Ghavidel-Syooki & Hosseinzadeh Moghadam, 2010; Ghavidel-Syooki et al., 2011a; Ghavidel-Syooki et al., 2011b). Also Ghavidel-Syooki et al., (2010) introduced an assemblage of cryptospores from the Silurian of north east of Iran, without any morphological classification.

## **Discussion and Results**

The cryptospores are moderately preserved and show moderate diversity and abundance (Table 1).

In this study, for the first time in Iran, an assemblage of cryptospores belonging to nine genera (10 species) have been identified from the Late Ordovician, Ghelli Fm., in north eastern Alborz, Iran. These are as follows:

Abditus Dydus laevigatus, Cheilotetras caledonica,

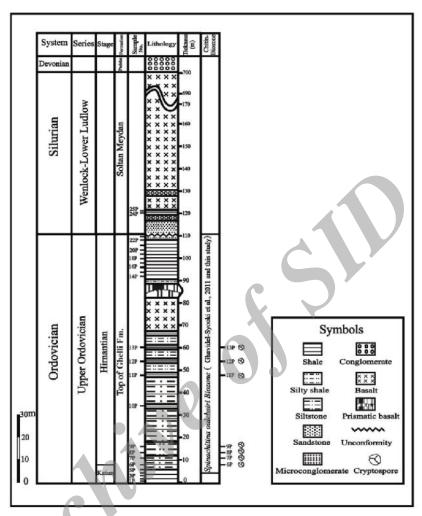


Figure 3. The stratigraphical column of the studied section

Table 1. The occurrence of cryptospores at the top of the Ghelli Fm. section

Abditusdyadus laevigatus	Tetrahedralete s medinensis	Rimosotetras problematica	Dyadospora murusdens	Segestrespora rogusa	Dyadospora murusattenuat	Hispanaediscu sp.	Gneudnaspora divellomedi	Rugosphaera cerebra	Cheilotetras caledonica	Sample
										Kh/6P/2011
										Kh/7P/2011
										Kh/8P/2011
										Kh/9P/2011
										Kh/11P/2011
										Kh/12P/2011
										Kh/13P/2011

Dyadospora murusdensa, D. murusattenuata, Gneudnaspora divellomedia, Hispanaediscus sp., Rimosotetras problematica, Rugosphaera cerebra,

Segestrespora rugosa, Segestrespora sp. cf. S. rugosa, Tetrahedraletes medinensis, Tetrahedraletes sp. cf. T. medinensis.

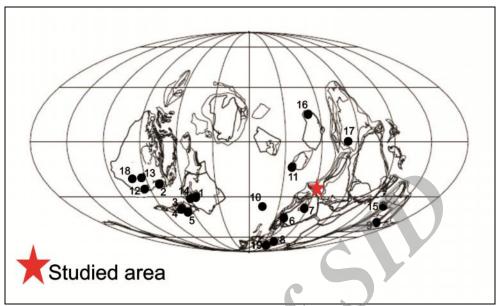


Figure 4. Location map of reported Late Ordovician (Katian- Hirnantian) cryptospore assemblages (Vecoli *et al.*, 2011) plotted on palaeogeographical reconsruction (Torsvik, 2009), at 445 My. 1. Valga-10 drillcore, Estonia (Vecoli *et al.*, 2011); 2. Anticosti Island (Vecoli *et al.* 2011); 3. Southwest Wales (Burgess, 1991); 4. Southern Britain (Wellman, 1996); 5. Belgium (Steemans, 2001); 6. Southeastern Turkey (Steemans *et al.*, 1996); 7. Saudi Arabia (Steemans *et al.*, 2009); 8. Northeast Libya (Richardson, 1988); 9. Northwest Argentina (Rubinstein, 2005; Rubinstein & Vaccari, 2004); 10. Czech Republic (Vavrdová, 1988, 1989); 11. South China (Wang *et al.*, 1997); 12. USA (Gray 1988); 13. Canada (Gray 1988); 14. Sweden (Gray, 1988); 15. South Africa (Gray *et al.*, 1986); 16. North China (Yin and He 2000); 17. Australia (Foster & Williams 1991); 18. USA (Strother, 1991); 19. Western Libya (Gray *et al.*, 1982). The star mark indicates the paleoposition of the study area assigned to the North Gondwana province.

The morphological classification of Wellman and Richardson (1993) has been applied to their classification.

In this classification, the cryptospores are divided into five groups: Unfused permanent tetrads, fused permanent tetrads, true dyad, pseudodyads, and hilate cryptospores, which include only monads.

Ghavidel-Syooki *et al.*, (2010) reported Silurian cryptospore assemblages from the northeast of Iran without any morphological classification.

Vecoli et al., (2011), concluded that there is no significant difference between cryptospore assemblages of the world in Late Ordovician and our data in this article are in agreement with them. With reference to the identified cryptospores (Plates 1 and 2), and the presence of biostratigraphy and palaeogeography indices, the chitinozoa species, Spinachitina oulebsiri (Paris, 1990; Paris et al., 2000, 2007), which is assigned to the Late Ordovician of northern Gondwana (Ghavidel-Syooki et al. 2011a; this study: Plate 3, Fig. 12), and also the reported index acritarchs of Late Ordovician (Ghavidel-Syooki et al., 2011a; this study: Plate 3, Figs. 1-11) a Late Ordovician age (late Hirnantian) is proposed for the top of the Ghelli Fm., (Fig. 5) (Ghavidel- Syooki *et al.* 2011a; this study).

The presence of peri- Gondwanan palaeobiogeographical index acritarchs (Delabroye *et al.*, 2010; Ghavidel-Syooki *et al.*, 2011a) and Plate 3, Figures 9-11 of this study, indicate that eastern Alborz was in the peri-Gondwanan province during the Late Ordovician (Mahmoudi *et al.*, 2011; Mahmoudi, 2011).

# Palaeoenvironment significance

In the studied samples, the Veryhachium tripinosom species appear to be abundant and the Baltisphaeridium, Villosocapsula, Leiofusa, Multiplicisphaeridium, Ordovicidium, Orthosphaeridium, Actinotodissus genera are common; Dorsennidium, Safirotecha, Peteinosphaeridium genera are rare and the Frankea, Navifusa, Pirea, Riptosocherma genera are very rare, respectively (Table 2b).

In general, the marine elements (acritarchs, prasinophytes and occasionally chitinozoans) are present throughout the section (110 m), but the



Figure 5. Stratigraphical distribution of some of the index acritarchs and chitinozoa at the top of the Ghelli Fm.

terrestrial elements (cryptospores), recovered only from samples No. 6 to 13 (8 to 60 m from the base of the section), constitute 7% (Table 2a) of the palynomorph assemblage. The admixture of land-derived and marine palynomorphs in the Ghelli Fm. materials (interval of 52 m), clearly indicate a continental influx. The cryptospores seem to be transported from an adjacent land area. The lack of land-derived elements in the up-section may indicate an increased distance offshore. This type of paleoenvironmental conclusion is well-explained

by Rubinstain & Vaccari 2004 and Le Herisse *et al.* 2013.

Nine genera (10 species) have been recovered from the Ghelli Formation of the Upper Ordovician strata of the eastern Alborz Mountain range, Iran. These cryptospores are classified morphologically and their assemblages have systematically revealed that there are no significant differences between similar-aged cryptospore assemblages of the peri-Gondwanan region, Baltic provinces, and other parts of the world.

The cryptospores seem to be transported from an adjacent land area, which is not so close-by. The lack of land-derived elements in the up-section may indicate an increased distance offshore

# Systematic cryptospores

The authors followed the subdivision and terminology proposed by Wellman and Richardson (1993, 1996) and Richardson (1996a, b) and for comprehensive synonymy listings Strother (1991), Wellman and Richardson (1996), and Vecoli *et al.* (2011) can be referred to Anteturma Cryptosporites Richardson, Ford & Parker 1984.

# True Tetrads

# Naked fused cryptospore tetrads

This group comprises of tetrads, where the spores are without outer envelopes and are fused together, and appear without lines of attachment that mark the position of the planes of attachment between the spores.

Genus *Cheilotetras* Wellman & Richardson1993 *Cheilotetras caledonica* Wellman & Richardson 1993

Pl. 1, Fig. 8; Pl. 2, Fig. 5

**Dimensions.** 30 (35) 40 µm.

**Description.** Fused permanent tetrads, outline circular, an individual 'spore' without an invaginated distal surface. The junction is entirely fused and no line of attachment is evident. The distal exine over the spores is laevigate.

Occurrence. Late Ordovician (Katian–Hirnantian), Anticosti Island, Québec, Canada, and Estonia (Vecoli *et al.*, 2011); Early Silurian (Llandovery): Scotland (Molyneux *et al.*, 2008); Middle Silurian (Wenlock): Scotland (Wellman & Richardson 1993; 1996; Molyneux *et al.*, 2008); Middle to Late Silurian (Wenlock– Ludlow): Scotland (Wellman, 1993); Middle to Late Silurian

(Wenlock– Peridoli): Southern Wales (Burgess & Richardson, 1995); Early Devonian (Lochkovian): Saudi Arabia (Steemans *et al.*, 2007).

# Naked unfused cryptospore tetrads

This group of permanent tetrads comprises of tetrads that remain permanently attached, with lines of attachment on the tetrads surface that mark the position of the planes of attachment between the spores. Unfused tetrads are naked, or enclosed within the laevigate or variously ornamented envelopes.

Genus *Rimosotetras* Burgess 1991 *Rimosotetras problematica* Burges 1991 Pl. 1, Fig. 9; Pl. 2, Figs. 6&7

**Dimensions.** 20 (25) 30 µm.

**Description.** Unfused permanent tetrads. Circularsub circular in outline, with lines of attachment on the tetrads surface that mark the position of the planes of attachment between the spores. The distal exine over the spores is laevigate.

**Occurrence.** Long stratigraphic range, having been frequently recorded in strata across the Late

Ordovician, through Silurian (Vecoli et al., 2011), such as in the: Late Ordovician (Katian-Hirnantian): Northwest Argentina (Rubinstein & 2004); Late Ordovician (Katian-Hirnantian): Anticosti Island, Québec, Canada, and Estonia (Vecoli et al., 2011); Late Ordovician to Early Silurian (Caradoc- late Llandovery): North Africa (Richardson, 1988); Late Ordovician to Early Silurian (late Ashgill- early Telychian): Libya (Hill et al., 1985); Late Ordovician to Middle Silurian (Caradoc- Ludlow): Southeast Turkey al., 1996); Early (Steemans etSilurian (Llandovery): Saudi Arabia (Steemans et al., 2000; Wellman et al., 2000; Steemans et al., 2007); Early Silurian (Llandovery): Brazil (Le Herisse et al., 2001): Middle Silurian (Wenlock): Shropshire. England (Burgess & Richardson, 1991); Middle Silurian (Wenlock): Scotland (Wellman & Richardson, 1993); Early to Late Silurian (Telychian- Ludfordian): Pennsylvania, USA (Beck & Strother 2008); Late Silurian (Ludlow): Southern Tunisia (Vecoli et al., 2009).

Table 2. Relative abundances of individual genera and species, derived from counts 23 specimens per sample from the top of the Ghelli Fm. in the studied area, based on the reported frequency of Playford & Wicander 2006, are specified as follows: V, very abundant (>25% of the total acritarch/ prasinophyte content); A, abundant (>10-25%); C, common (>5-10%); U, uncommon (1-5%); R, rare (<1%) and (-) barren.

a) Cryptospores and Chitinozoa; b) Acritarchs and Prasinophytes

Palynomorphs Taxa		Samples Number (Ord. Kh/1-23P)																						
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
	Abditusdyadus laevigatus	-	-	-	-	-	-	-	-	С	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cryptospores Taxa	Cheilotetras caledonica	-	-	-	-	-	С	-	-	-	-	-	-	-	-	_	_	-	-	-	-	-	_	-
	Dyadospora murusdensa	-	-	-	-	-	С	С	С	-	-	С	-	С	-	-	_	-	-	-	-	-	-	-
	Dyadospora murusattenuata	-	-	-	-	-	С	-	-	-	-	С	-	_	-	_		-	_	-	-	-	-	-
	Rimosotetras problematica	-	-	-	-	-	С	С	-	-	-	С	-	С	F	-	-	-	-	-	-	-	-	-
	Rugosphaera cerebra	-	-	-	-	-	С	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Tetrahedraletes medinensis	-	-	-	-	-	С	С	-	-	-	С	С	С	-	-	_	-	-	-	-	-	-	-
	Monads Cryptospores	-	-	-	-	-	С	С	С	С	-	С	С	С	-	-	-	-	-	-	-	-	-	-
	Ancyrochitina spp.	-	-	-	-	-		-	-	UC	-	UC	UC	UC	-	UC	-	-	-	-	-	-	-	-
Chitinozoa Taxa	Conochitina spp.	-	-	-	С	-	С	-	-	-	-	-	UC	-	-	-	-	-	-	-	-	-	UC	-
	Desmochitina minor	-	-	-	-	-	-	-	-	-	UC	-	-	-	-	-	-	-	-	-	-	-	-	-
	Rhabdochitina usitata	-	-	-	-	-	UC	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	Spinachitina oulebsiri	-	-	_	-	-	UC	-	-	UC	-	_	UC	-	-	-	_	-	-	_	-	-	-	
	Undetermined Chitinozoa	-	_	_	С	С	_	_	_	UC	_	_	UC	UC	-	UC	_	_	_	_	UC	-	_	

	_					b																	- 10
Acritarchs & Prasinophyte Taxa		Sample Numbers (Ord. Kh/ 1-23P)  1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 22																					
i rasinopriyte raxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Actinotodissus crassus	С	С	-	-	1	1	-	1	-	С	С	-	R	1	-	R	-	-	1	1	-	-	-
Baltisphaeridium longispinosum	С	A	С	С	С	С	R	С	С	С	С	С	С	-	-	С	-	-	-	-	-	-	-
B. onniense	UC	UC	-	UC	С	UC	С	UC	UC	-	UC	-	-	1	-	-	-	-	-	1	-	-	-
B. perclarum	R	С	R	R	-	-	1	-	R	С	С	-	R	16	R	-	-	-	-	1	-	-	-
Dactylofusa cabottii	С	UC	-	UC	R	UC	R	UC	С	. 1	1	1	1	1	-	1	1	-	-	1	-	-	-
D. striata	С	С	-	С	С	-	1	С	С	1	-	ı	-	1	-	R	-	-	-	1	-	-	-
D. Striatifera	-	-	-	-	1	1	1	1	R	1	1	1	-	1	R	-	-	1	-	Y	-	-	-
Dorsennidium hamii	-	1	-	-	1	- 1	1	1	UC	1	R	1	UC	1	-	1	9	R	-	1	-	-	-
D. undosum	-	-	-	-	- 1	I		- 1	R		R	- 1	- 1	- 1	4		-	-1	-	1	-	-	-
Evittia denticulata denticulata	UC	UC	UC	С	1	С	1	UC	-	С	UC	С	С	1	UC	С	A	-	1		-	-	-
Frankea sartbernardensis	-	-	-	-	- 1	Т	1	1	-	-	-	-	-	16	-	-	-	VR	E	-	-	-	-
Leiofusa bispinosoides	-	1	-	-	1	1	1	R	-	R	R	1	- 1	1	ľ		T	-	-	1	-	1	-
L. fosiformis	UC	UC	UC	С	UC	С	1	UC	-	C	UC	1	С	UC	-	Ξ	1	-	-	1	-	UC	-
L. litotes	1	1	UC	-	1	1	1	1	UC	UC	С	1	1	1	-	1	1	1	-	1	-	-	-
Multiplicisphaeridium irregular	UC	С	UC	С	С	UC	-	С	С	c	C	C	UC	C	UC	С	ı	-	-	ı	-	-	R
Navifusa similis	-	-	-	R	R	- 1	1	-	-	ŀ	R	A	ī	- 1	-	-	1	-	-	1	-	-	-
Ordovicidium elegantulum	С	С	-	С	1	1	R	R	С	R	C	R	С	C	С	С	1	-	-	1	-	-	R
Orthosphaeridium bispinosum	R	-	-	Ē	4	-	1	1	-	Е	-	ı	-	1	1	-	R	-	-	н	-	-	-
O. octospinosum	R	C	R	C	-	t	1	R	С	С	R	1	-	1	-	-	1	-	-	- 1	-	-	-
O. rectangulare		R	E	4	R	R	-	Е	-	С	R	1	ı	ı	С	R	-	-	-	1	-	-	-
O. ternatum	1	1	-	-	1	1	1	1	-	R	R	1	R	1	1	-	1	-	-	1	-	-	-
Peteinosphaeridium accinctulum	-	-	-	R	1	1	- 1	16	-	Т	-	R	ı	R	-	- 1	-	-	-	-	-	-	-
P. septuosum	-	-	-	-	R	1	1	1	-	1	-	1	- 1	1	ī	-	-	-	-	1	-	-	-
Pirea capitulifera	-	ī	-	-	1	Ε	1	ī	-	Ι	-	1	1	ī	-	-	-	-	-	ī	-	-	VF
Polygonium gracile	R	R	R	-	-	UC	-	R	-	R	-	R	R	UC	-	-	R	-	UC	-	-	-	-
Riptosocherma improcera	-	1	-	-	1	1	1	1	-	VR	-	1	1	1	1	-	1	-	-	- 1	-	-	-
Safirotheca sp. cf. S. safira	-	-	R	-	- 1	1	1	-1	R	I	-	-	-	1	R	-	-	-	-	1	-	-	-
Stellechinatum uncinatum	UC	R	-	-	-	UC	1	1	-	1	UC	-	R	1	-	R	1	-	1	1	-	-	-
Sylvanidium paucibrachium	-	-	-	-	-	-	-	-	-	-	UC	UC	R	1	-	-	-	-	-	1	-	-	-
Tunisphaeridium eisenackii	-	-	-	-	-	VR	-	-	-	1	-	-	-	- 1	-	-	-	-	-	-	-	-	-
Veryhachium eurapaum	R	R	С	С	С	С	R	R	С	С	С	R	C	R	С	R	1	-	1	ı	-	-	R
V. oklahomens	R	UC	С	С	С	R	UC	R	С	R	UC	R	С	R	C	UC	-	-	-	-	С	С	С
V. reduatum	-	-	-	-	R	-	-	-	-	-	-	R	-	-	-	-	-	-	-	-	-	-	-
V. subglobosom	-	-	-	-	R	-	-	R	R	R	С	С	-	-	-	-	-	-	-	-	-	-	-
V. triangulatum	R	-	-	R	-	-	-	R	-	R	R	-	-	-	-	-	-	-	-	-	-	-	-
V. trispinosom	Α	A	С	A	A	A	A	A	A	A	A	A	A	A	A	A	-	-	-	-	-	A	A
Villosacapsula setosapellicula	С	-	C	С	С	-	С	C	С	С	С	С	-	С	С	С	С	-	-	-	-	-	С
Tylotopalla sp.	R	R	-	-	-	-	-	-	-	R	R	-	-	-	-	R	-	-	-	-	-	-	-

Genus Tetrahedraletes Strother & Traverse emend. Wellman & Richardson 1993 Tetrahedraletes medinensis Strother & Traverse

emend. Wellman & Richardson 1993 Pl. 1, Figs.11&12; Pl. 2, Figs. 9&11 **Dimensions.** 20 (25) 30 µm.

**Description.** Permanent tetrahedral tetrads, subcircular to subtriangular in outline. Within the tetrads, individual 'spores' have a subtriangular to subcircular equatorial outline. The walls are not very thick. The spores appear within the line of attachment, are clearly visible on the tetrad surface, and are without an enclosing envelope.

Occurrence. This species has been recorded worldwide and ranges from Ordovician (Caradoc) to Devonian (Vecoli et al., 2011). Some selected previous occurrences are as follows: Late Ordovician (Caradoc- Ashgill; late Katian-Hirnantian): Sudan (Gray, 1988; Le Herisse, 1989); Late Ordovician (Hirnantian): Wales (Burgess 1991); Late Ordovician (Caradoc- Ashgill; late Katian- Hirnantian): Australia (Forster & Williams 1991); Late Ordovician (Caradoc; late Katian): (Wellman, 1996); Late Ordovician (Caradoc-Ashgill; late Katian-Hirnantian): Southeast Turkey (Steemans et al., 1996); Late Ordovician (Katian-Hirnantian): Southern Xinjiang, China (Wang et al. 1997); Late Ordovician (Katian– Hirnantian): Pennsylvania (Taylor, 2002); Late Ordovician (Katian- Hirnantian): Anticosti Island, Québec, Canada, and Estonia (Vecoli et al. 2011); Late Ordovician to Early Silurian (late Asgill-ealy Llandovery): Saudi Arabia (Gray et al. 1986); Early Silurian (early Aeronian; middle Llandovery): North America (Miller & Eames 1982; Johnson 1985); Early Silurian (early Wenlock): Shropshire, England (Burgess & Richardson 1991); Early Silurian (Llandovery) Saudi Arabia (Steemans et al., 2007); Middle Silurian to Late Silurian (Sheinwoodian; early Wenlock)-(Ludfordian; late Ludlow): Pennsylvania, USA (Beck & Strother 2008) Late Silurian: South China; (Wang et al. 2005).

# **Tetrahedraletes grayae** Strother 1991 Pl. 2, Fig. 8

**Dimensions.** 25 (35) 40 µm.

**Description.** Three-dimensionally preserved permanent tetrad of alete sporomorphs in arranged tetrahedral configuration; individual spore bodies subtriangular to subspherical in outline; Walls thin, surfaces psilate to somewhat microgranular depending upon the preservation, sutures between spore bodies visible, but without a well-developed thickened ring in the margin.

**Occurrence.** Late Ordovician (Katian–Hirnantian): Belgium (Steemans, 2001); Late Ordovician

(Ashgill): Central Bohemia, Czech Republic (Vavrdová, 1989); Late Ordovician–Early Silurian (late Caradoc– early Telychian): northeastern Libya (Richardson, 1988); Early Silurian (Llandovery): Anticosti Island, Québec, Canada (Duffield, 1985); Early Silurian (Llandovery): Niagara Gorge, Lewiston, New York (Miller & Eames, 1982); Early Silurian: central Ohio, USA (Taylor, 2002).

# True dyad

This group comprises of dyads in which two distinct spores are present with a clear plane of attachment forming a line of attachment on the surface of the dyad. The true dyads are usually naked, or enclosed within an envelope.

*Unfused naked cryptospore dyads*This group comprises of dyads that readily separate into two alete spores.

Genus *Dyadospora* Strother & Traverse 1979 emend. Burgess & Richardson 1991 *Dyadospora murusdensa* Strother & Traverse 1979 emend. Burgess & Richardson 1991 Pl. 1, Fig. 5; Pl. 2. Figs. 1&4

**Dimensions.** 15 (22) 30 μm.

**Description.** Dyads, usually isomorphic, subcircular to elliptical in equatorial view, with an oblique compression. Individual 'spores' distally convex. A darkened equatorial crassitude,  $1-2~\mu m$  thick is present. Exine laevigate.

Occurrence. Late Ordovician (Katian– Hirnantian): Southern British (Wellman, 1996); Late Ordovician (Hirnantian): Turkey (Steemans et al., 1996); Late Ordovician (Ashgill; Middle Katian–Hirnantian): Southern Xinjiang, China (Wang et al., 1997); Late Ordovician (Hirnantian): Argentina (Rubinstein & Vaccari, 2004); Late Ordovician-Early Silurian (Caradoc-Rhuddanian): Northeast (Richardson 1988); Early Silurian (early Aeronian; middle Llandovery): North America (Miller & Eames, 1982); Early Silurian (Rhuddanian; early Silurian): North America (Johnson, 1985); Middle Silurian (Homerian; late Wenlock): Shropshire, England (Burgess & Richardson 1991); Early Silurian (Llandovery): Saudi Arabia (Steemans et al., 2000); Middle to Late Silurian (Late Wenlock-Early Ludlow): Peninsula (Taylor, 2002): Late Silurian: South China (Wang et al., 2005); Silurian: Sudan (Steemsns et al., 2010).

*Dyadospora murusattenuata* Strother & Traverse emend. Burgess and Richardson 1991

Pl. 2, Fig. 2

**Dimensions.** 15 (17) 20 μm.

**Description.** Dyads, usually isomorphic, subcircular in equatorial view, preserved in oblique compression. Individual "spores" distally convex. There is a crassitude at the point of contact between the two cryptospores. There is a cleft between the crassitudes of each 'spore'.

Occurrence. This species has a long stratigraphic range (Ordovician-Devonian) and common worldwide distribution (Vecoli et al., 2011). Some selected occurrences are as follows: Late Ordovician (late Caradoc- late Ashgil; Katian"Hirnantian): Libya (Richardson 1988); Late Ordovician (Ashgill; middle Katian): Czech Republic (Vavrdova, 1988; 1989); Late Ordovician (Katian-Hirnantian): Southeast Turkey (Steemans et al., 1996); Late Ordovician (Katian-Hirnantian): Southern Xinjiang, China (Wang et al., 1997); Late Ordovician (Katian– Hirnantian): Southwest Belgium (Rubinstein & Vaccari, 2004; Rubinstein, 2005); Late Ordocian (Katian-Hirnantian) Anticosti Island, Québec, Canada, and Estonia (Vecoli et al., 2011); Silurian: Sudan (Steemans etal., 2010); Early Silurian (Llandovery) Saudi Arabia (Steemans et al., 2007); Middle Silurian (Homerian; late Wenlock): Shropshire, England (Burgess & Richardson, 1991); Late Silurian: South China; (Wang et al., 2005).

Envelope-enclosed unfused cryptospore dyads Group characterized by true dyads enclosed within a variously ornamented envelope.

Genus *Abditusdyadus* Wellman & Richardson 1996 *Abditusdyadus laevigatus* Wellman & Richardson

1996 Pl. 2, Fig. 3

Dimensions. 15–20 µm.

**Description.** Dyads of two lavigate hilate cryptospores enveloped within thick walls.

Occurrence. Late Ordovician (Katian–Hirnantian): Belgium (Steemans, 2001); Late Ordovician (Katian–Hirnantian): Anticosti Island, Québec, Canada, and Estonia (Vecoli *et al.*, 2011); Early Silurian (Llandovery): Brazil (Mizusaki *et al.*, 2002); Early Silurian (Rodanian; early Llandovery): Saudi Arabia (Steemans *et al.*, 2000; Wellman *et al.*, 2000); Ealy Devonian

(Lochkovian): Scotland (Wellman & Richardson 1996).

## Pseudodyads

Envelope-enclosed fused cryptospore dyads

This group comprises of dyads in which two
permanently fused spores are joined by an

permanently fused spores are joined by an encircling thickened band without a plane of attachment and line of attachment. Pseudodyads occur in a naked form or enclosed within an envelope.

Genus *Segestrespora* Burgess 1991 *Segestrespora rugosa* (Johnson 1985) Burgess 1991

Pl. 1, Fig. 6

**Dimensions.** 30 (35) 40 µm.

**Description.** Pseudodyads, subcircular to elliptical in equatorial view, and totally enclosed within an envelope. Distal exine is ornamented with a closely spaced microrugulate.

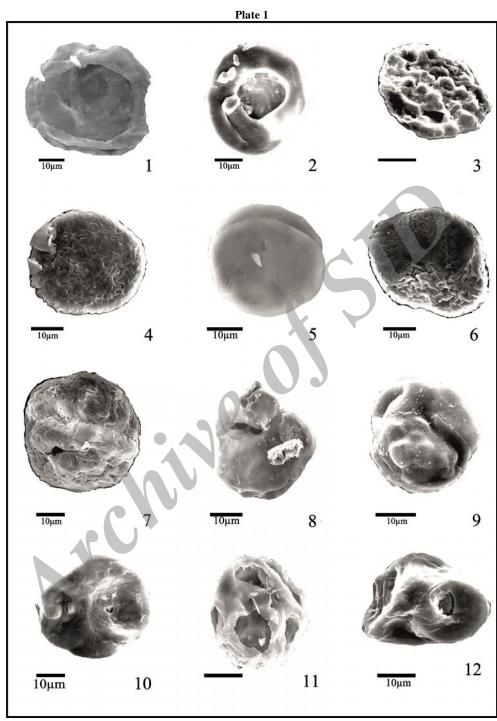
Occurrence. This species has a wide geographical distribution, stratigraphically ranging from the late Ordovician to the Llandovery (Vecoli et al. 2011). Some selected occurrences are as follows: Late Ordovician (Katian- Hirnantian): Northeast Libya (Richardson, 1988); Late Ordovician (Katian-Hirnantian): Southwest Wales (Burgess 1991); Late Ordovician (Katian- Hirnantian): Southeast Turkey (Steemans et al., 1996); Late Ordovician (Katian-Hirnantian): Belgium (Steemsns, 2001); Late Ordovician (Katian- Hirnantian): Anticosti Island, Québec, Canada, and Estonia (Vecoli et al., 2011); Early Silurian (Llandovery): SW Wales (Burgess 1991); Early Silurian (early Llandovery): Saudia Arabia (Steemans et al., 2000; Wellman et al., 2000).

# Hilate cryptospores

These forms consist of alete monad spores, hemispherical in longitudinal view, with a hilum, and an equatorial thickening. The exine may be laevigate or variously ornamented. Closely similar monads have been observed, partly united at the contact area as loose dyads.

Genus *Gneudnaspora* Balme emend. Breuer, Al-Ghazi, Al-Ruwaili, Higgs, Steemans & Wellman 2007

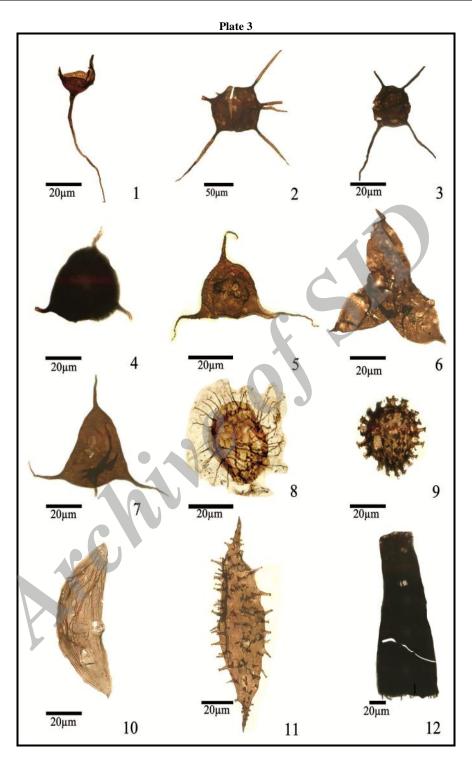
*Gneudnaspora divellomedia* (Chibrikova) Balme 1988 var. minor Breuer, Al-Ghazi, Al-Ruwaili,



1&2. Gneudnaspora divellomedia (Chibrikova) Balme 1988 var. Breuer, Al-Ghazi, Al-Ruwaili, Higgs, Steemans & Wellman 2007. 3) Hispanaediscus sp.. 4. Rugosphaera cerebra Miller & Eames 1979. 5. Dyadospora murusdensa Strother & Traverse 1979 emend. Burgess & Richardson 1991. 6. Segestrespora rugosa (Johnson) Burgess 1991. 7) Segestrespora sp. cf. S. rugosa (Johnson) Burgess 1991. (Surfacial Granular sculptures are probably due to pyritization). 8. Cheilotetras caledonica Wellman & Richardson 1993. 9. Rimosotetras problematica Burgess 1991. 10. Tetrahedraletes sp. cf. T. medinensis Strother & Traverse 1979 emend. Wellman & Richardson 1993. 11&12. Tetrahedraletes medinensis Strother & Traverse 1979 emend. Wellman & Richardson 1993



1&4. Dyadospora murusdensa Strother & Traverse 1979 emend. Burgess & Richardson 1991. 2. Dyadospora murusattenuata Strother & Traverse 1979 emend. Steemans, Le Herisse & Bozdogan 1996. 3. Abditusdydus laevigatus Wellman & Richardson 1996. 5. Cheilotetras caledonica Wellman & Richardson 1993. 6&7. Rimosotetras problematica Burgess 1991. 8. Tetrahedraletes grayae Strother 1991. 9&11. Tetrahedraletes medinensis Strother & Traverse 1979 emend. Wellman & Richardson 1993. 10. Tetrahedraletes sp. cf. T. medinensis Strother & Traverse 1979 emend. Wellman & Richardson 1993. 12. Cryptospores cluster



1. Orthosphaeridium bispinosum Turner 1984. 2. Orthosphaeridium octospinosum Eisenack 1968. 3. Orthosphaeridium rectangulare (Eisenack, 1963) Eisenack 1968. 4. Veryhachium subglobosum Jardin, Combaz, Magloire & Peniguel 1974. 5. Villosacapsula sp. cf. setosapellicula (Loeblich, 1970) Loeblich & Tappan 1976. 6. Veryhachium triangulatum Konzolava-Mazancova 1969. 7. Sylvanidium paucibrachium Loeblich 1970. 8. Tunisphaeridium eisenackii Loeblich & Tappan 1978. 9. Tylotopalla sp. 10. Dactylofusa striatifera (Cramer & Diez 1972) Fensome, Williams, Barss, Freeman & Hill 1990. 11. Safirotheca sp. cf. S. safira Vavrdová 1989. 12. Spinachitina oulebsiri Paris et al. 2000

Higgs, Steemans & Wellman 2007 Pl. 1, Figs. 1–2

**Dimensions.** 30 (45) 55 μm.

**Description.** Monad spores, hemispherical in longitudinal view, with a hilum and an equatorial thickening.

Occurrence. Middle Ordovician (Dapingian-Darwilian): Argentina (Rubinstein et al., 2010; 2011); Late Ordovician (Katian–Hirnantian): Southern British (Wellman, 1996); Late Ordovician (Katian-Hirnantian): Southeast Turkey (Steemans et al. 1996); Late Ordovician (Katian–Hirnantian): Southern Xinjiang, China (Wang et al., 1997); Late Ordovician (Katian-Hirnantian): Belgium (Steemans, 2001); Late Ordovician: Saudi Arabia (Miller et al., 2007): Late Ordovician (Katian-Hirnantian): Southern Saudi Arabia (Steemans et al., 2009); Late Ordovician (Katian- Hirnantian): Anticosti Island, Québec, Canada, and Estonia (Vecoli et al., 2011); Middle Silurian (Wenlock): Shropshire, England (Burgess & Richardson, 1991); Late Silurian (Ludlow): Southern Tunisia (Vecoli et al., 2009); Early- Late Devonian: Northern Saudi Arabia (Bureuer et al., 2007).

Genus *Hispanaediscus* Cramer 1966 emend. Burgess & Richardson 1991

Hispanaediscus sp. Pl. 1, Fig. 3

**Dimensions.** 17 (23) 30 µm.

**Description.** Amb subrounded, distal exine ornamented, with closely spaced verrucae, in part coalescing to form muri  $1-2~\mu m$  wide and about  $1~\mu m$  high; Hilum very thin and transparent.

Occurrence. This genus is very similar to the reported genus of Katian–Hirnantian Anticosti Island, Québec, Canada, and Estonia (Vecoli *et al.*, 2011). For precise determination of this species, there should be a hilum on the proximal face, and also, the ornamentations should be real not pyrite damaged (personal communication of Prof. Wellman). We found a taxa similar to this form and to a genus reported by Vecoli *et al.*, (2011) from the Upper Ordovician strata of the Zagros basin,

South of Iran (unpublished data, National Oil Company of Iran).

Genus *Rugosphaera* Strother & Traverse 1979 *Rugosphaera cerebra* Miller & Eames 1979 Pl. 1, Fig. 4

**Dimensions.** 35 (40) 45 μm.

**Description.** Laevigate subcircular monads enclosed in rugulate envelopes. The ornamentation of the envelope consists of closely spaced sinuous muri.

Occurrence. Late Ordovician (late Caradoc; early Katian): Shropshire, England (Richardson, 1988); Late Ordovician (late Caradoc; early Katian): Wales (Richardson, 1988); Late Ordovician: Southeast Turkey (Steemans *et al.*, 1996).

List of cryptospores taxa

Abditusdydus laevigatus Wellman & Richardson 1996.

Cheilotetras caledonica Wellman & Richardson

*Dyadospora murusdensa* Strother & Traverse 1979 emend. Burgess & Richardson 1991.

*Dyadospora murusattenuata* Strother & Traverse 1979 emend. Steemans, Le Herisse & Bozdogan 1996.

*Gneudnaspora divellomedia* (Chibrikova) Balme 1988 var. Breuer, Al-Ghazi, Al-Ruwaili, Higgs, Steemans & Wellman 2007.

Hispanaediscus sp.

Rimosotetras problematica Burgess 1991.

Rugosphaera cerebra Miller & Eames 1979.

Segestrespora rugosa (Johnson) Burgess 1991.

Segestrespora sp. cf. S. rugosa (Johnson) Burgess 1991.

Tetrahedraletes grayae Strother 1991.

Tetrahedraletes medinensis Strother & Traverse 1979 emend. Wellman & Richardson 1993.

*Tetrahedraletes* sp. cf. *T. medinensis* Strother & Traverse 1979 emend. Wellman & Richardson 1993.

#### References

Alavi, M., 1979. The virani ophiolite and surrounding rocks. Gol. Rundsch. 68 (1): 334-341.

Alavi, M., 1991. Sedimentary and structural characteristics of the Paleo-Tethys remnants in northeastrern Iran. American Association of Petroleum Geologists Bulletin. 103 (8): 938-992.

Balme, B.E., 1988. Miospores from Late Devonian (Early Frasnian) strata, Carnarvon Basin, Western Australia. Paläeontographica, Abteilung B. 209 (4): 109–166.

Beck, J.H., Strother, P.K., 2008. Miospores and cryptospores from the Silurian section at Allenport, Pennsylvania, USA.

- Journal of Palaeontology. 82: 857-883.
- Breuer, P., Al-Ghazi, A., Al-Ruwaili, M., Higgs, K.T., Steemans, P., Wellman, C.H., 2007. Early to Middle Devonian miospores from northern Saudi Arabia Miospores. Revue de micropaleontology. 50: 27–57.
- Burgess, N.D., 1991. Silurian cryptospores and miospores from the type Llandovery area, southwest Wales. Palaeontology. 34 (3): 575-599.
- Burgess, N.D., Richardson, J.B., 1991. Silurian cryptospores and miospores from the type Wenlock area, Shropshire England. Palaeontology. 34 (3): 601–628.
- Burgess, N.D., Richardson, J.B., 1995. Late Wenlock to early Pridoli cryptospores and miospores from south and southwest Wales, Great Britain. Palaeontographica Abteilung. B, 236 (1/3): 1-44.
- Chateauneuf J.J., Jenny J., Stampfli G., 1978. L'Ordovician de l'Elbourz oriental. Stratigraphie et palynologie. Note du laboratoire de Paleontologie de l'uriuersite de Geneveg, 2 (1-13): 55-61.
- Delabroye, A., Vecoli, M., Hints, O., Servais, T., 2010. Acritarchs from the Ordovician–Silurian boundary beds of the Valga-10 drill core, southern Estonia (Baltica), and their stratigraphic and palaeobiogeographic implications. 35 (1): 4-45.
- Foster, C.B., Williams, G.E., 1991. Late Ordovician–Early Silurian age for the Mallowa Salt of the Carribuddy Group, Canning Basin, Western Australia, based on occurrences of Tetrahedraletes medinensis Strother and Traverse 1979. Australian Journal of Earh Sciences. 38: 223–228.
- Ghavidel-Syooki, M., Khosravi, M. B., 1994. The study of lower Paleozoic sediment in Tang-e-Zakin, Kuh-e-Faraghan and introducing Seyahou and Sarchahan Formations in Zagros basin. Quaterly Geoscieince Jornal. 4 (14): 202-210.
- Ghavidel-Syooki, M., 1995. The Sarchahan Formation, Quaterly Geosience Jornal. 4 (15-16): 74-89.
- Ghavidel-syooki, M., 2006. Chitinozoan Biostratigraphy and Palaeogeography of Silurian Strata (Niur Formation) at Eastern Alborz Range (Kopet-Dagh Region) Northeastern Iran. JUST. 32 (3): 127-146.
- Ghavidel-Syooki, M., Hosseinzadeh Moghadam, M., 2010. Palynostratigraphy of early Paleozoic sediments in south of Fazel abad area, Kholin Darreh (South east of Gorgan), Stratigraphy and Sedimentology researches. 26 (38): 1-24, (in Persian).
- Ghavidel-Syooki, M., Hassanzadeh, J., Vecoli, M., 2011a. Palynology and isotope geochronology of the Upper Ordovician–Silurian successions (Ghelli and Soltan Maidan Formations) in the Khoshyeilagh area, eastern Alborz Range, northern Iran; stratigraphic and palaeogeographic implications. Review of Palaeobotany and Palynology. 164 (3-4): 251–271.
- Ghavidel-syooki, M., Álvaro J., Popov, L., Ghobadi Pour, M., Ehsani, M. H., Suyarkova, A., 2011b. Stratigraphic evidence for the Hirnantian (latest Ordovician) glaciation in the Zagros Mountains, Iran. Palaeogeography, Palaeoclimatology, Palaeoecology, 307 (1-4): 1–16.
- Gray, J., 1988. Land plant spores and the Ordovician–Silurian boundary. Bulletin of the British Museum of Natural History (Geology), 43: 351–358.
- Gray, J., Massa, D., Boucot, A.J., 1982. Caradocian land plant microfossils from Libya. Geology. 10: 197–201.
- Gray J., Theron J.H., Boucot A.J., 1986. Age of the Cedarberg Formation, South Africa and early land plant evolution. Geological Magazine. 123 (4): 445-454.
- Johnson, N.G., 1985. Early Silurian palynomorphs from the Tuscarora Formation in Central Pennsylvanian and their paleobotanical and geological significance. Review of Palaeobotany and Palynology. 45: 307–360.
- Le Herisse, A, Paris, F, Steemans, P., 2013. Late Ordovician-earliest Silurian palynomorphs from northern Chad and correlation with contemporaneous deposits of southeastern Libya. Bulletin of Geosciences. 88 (3): 483-504.
- Mahmoudi M., Alimohammadian H., Sabouri J., Majidifard M. R., 2011. The investigation of magnetical and biological palaeogeography of Abarsaj fm., (Gelli Fm.) and Soltan Meydan in north east of Shahroud. 30<sup>th</sup> Geological Survey of Iran, Tehran, Iran (in Persian).
- Mahmoudi M., 2011. Investigation of palaeomagnetogeography of volcanic beds of Abarsaj fm. (Ghelli Fm.) and Soltan Meydan Formations and palynological study of in encompassing strata of them at northeast of Shahroud city, Iran. Research institute of geosciences, Geological Survey of Iran, (Un published M Sc. Thesis, in Persian); 350p.
- Miller, M.A., Eames L.E., 1982. Palynomorphs from the Silurian Medina Group (Lower Llandovery) of the Niagara Gorge, Lewiston, New York, USA. Palynology. 6: 221–254.
- Miller, M. A., Al-Ruwaili, M. H., 2007. Preliminary palynological investigation of Saudi Arabian Upper Ordovician glacial sediments. Revue de Micropaléontologie. 50 (1): 17-26.
- Mizusaki, A.M., Melo, J.H.G., Lelarge M.L., Steemans P., 2002. Vila Maria Formation, Paranà Basin, Brazil— an example of integrated geochronological and palynological datings. Geological Magazine. 139: 453–463.
- Molyneux, S.G., Barron, H.F., Smith R.A., 2008. Upper Llandovery–Wenlock (Silurian) palynology of the Pentland Hills inliers, Midland Valley of Scotland. Scottish Journal of Geology. 44: 151–168.
- Paris, F., 1990. The Ordovician biozones of the North Gondwana domain. Review of Paleobotany and Palynology. 66 (3-4): 181–209.

- Paris F., Bourahrouh A., Le Herissé, A., 2000. The effects of the final stages of the Late Ordovician glaciation on marine palynomorphs (chitinozoans, acritarchs, leiospheres) in well Nl-2 (NE Algerian Sahara). Review of Palaeobotany and Palynology. 113: 87-104.
- Richardson, J.B., 1988. Late Ordovician and Early Silurian cryptospores and miospores from northeast Libya. In: El-Arnauti, A., Owens, B., Thusu, B. (Eds.), Subsurface Palynostratigraphy of Northeast Libya. Garyounis University Press, Benghazi. 89-109 pp.
- Richardson, J.B., 1996. Chapter 18A, Lower and Middle Palaeozoic records of terrestrial palynomorphs. In: Jansonius, J., and McGregor, D.C. (Eds.), Palynology: Principles and Applications. American Association of Stratigraphic Palynologists Foundation, Houston. 555–574 pp.
- Richardson, J. B., Ford, J. H., Parker, F., 1984. Miospores, correlation and age of some Scottish Lower Old Red Sandstone sediments from the Strathmore region (Fife and Angus). Journal of Micropalaeontology. 3: 109-124.
- Rubinstein, C.V., 2005. Ordovician to Lower Silurian palynomorphs from the Sierras subandinas (Subandean ranges), northwestern Argentina: a preliminary report. In: Steemans, P., Javaux, E. (Eds.), Pre-Cambrian to Palaeozoic Palaeopalynology and Palaeobotany- Carnets de Géologie / Notebooks on Geology, Brest, Memoir.
- Rubinstein, C.V., Vaccari, N.E., 2004. Cryptospores assemblages from the Ordovician/ Silurian boundary in the Puna Region, NW Argentina. Palaeontology. 47: 1037-1061.
- Rubinstein, C.V., Gerrienne, P., De la Puente, G.S., Astini, R.A., Steemans P., 2010. Early-Middle Ordovician evidence for land plants in Argentina (eastern Gondwana). The New Phytologist. 188: 365–369.
- Rubinstein, C.V., Vecoli, M., Astini, R.A., 2011. Biostratigraphy and palaeoenvironmental characterization of the Middle Ordovician from the Sierras Subandinas (NW Argentina) based on organic-walled microfossils and sequence stratigraphy. Journal of South American Earth Sciences. 31: 124–138.
- Sabouri, J., 2003. Palynostratigraphy and Palaeogeography of Ordovician in north of Iran, 22th Geoscience conference, Geological Survey of Iran, Tehran, Iran, Abstract book, 147-148 pp. (in Persian).
- Shahrabi, M., 1990. 1:250000 scale geological map of Gorgan Geological Survey of Iran-Tehran, Iran (in Persian).
- Steemans, P., 2000. Miospore evolution from the Ordovician to Silurian. Review of Palaeobotany and Palynology. 113 (1-3): 189-196.
- Steemans, P., 2001. Ordovician cryptospores from the Oostduinkerke borehole, Brabant Massif, Belgium. Geobios. 34 (1): 3-12.
- Steemans, P., Le Hèrisse, A., Bozdogan, N. 1996. Ordovician and Silurian cryptospores and miospores from southeatern Turkey. Review of Palaeobotany and Palynology. 93 (1-4): pp. 35–76.
- Steemans, P., Higgs, K.T., Wellman, C.H., 2000. Cryptospores and trilete spores from the Llandovery, Nuavyim-2 Borehole, Saudi Arabia. In: Al-Hajri, S., Owens, B. (Eds.), Stratigraphic Palynology of the Palaeozoic of Saudi Arabia. GeoArabia, Bahrain, Special. 1: 92–115.
- Steemans, P., Wellman C.H., Filatoff J., 2007. Palaeophytogeographical and palaeoecological implications of a miospore assemblage of earliest Devonian (Lochkovian) age from Saudi Arabia. Palaeogeography, Palaeoclimatology, Palaeoecology. 250 (1-4): 237–254. Steemans, P., Le Hérissé, A., Melvin, J., Miller, M., Paris, F., Verniers, J., Wellman, C. H., 2009. Origin and Radiation of
- the Earliest Vascular Land Plants. Scienc. 324 (5925): 353-353.
- Stocklin, J., 1968. Structural history and tectonics of Iran, A Review Bulletin American Association of Petroleum Geologists. 52 (7): 1229-1258.
- Strother, P.K., 1991. A classification scheme for the cryptospores. Palynology. 15: 219-236.
- Strother, P.K., 1996. Acritarchs. In: Jansonius J., McGregor D.C., (eds.), Palynology: Principles and Applications. Principles. American Association of Stratigraphic Palynologists Foundation, Dallas. 1: 81-106.
- Strother, P.K., Al-Hajri, S.A., Traverse A., 1996. New evidence for land plants from the lower Middle Ordovician of Saudi Arabia. Geology. 24 (1): 55-58.
- Taylor, W.A., 2002. Studies in cryptospore ultrastructure: variability in the tetrad genus Tetrahedraletes and type material of the dvad Dvadospora murusattenuata, Review of Palaeobotany and Palynology, 119 (1-2): 325–334.
- Torsvik T.H., 2009. BugPlates: Linking Biogeography and Palaeogeography. www. geodynamics.no.
- Vavrdová M., 1988. Further acritarchs and terrestrial plant remains from the late Ordovician at Hlásná Treban (Czechoslovakia). Casopis pro Mineralogii a Geologii. 33: 1-10.
- Vavrdová, M., 1989. New acritarchs and miospores from the late Ordovician at Hlásná Treban, Czechoslovakia. Casopis pro Mineralogii a Geologii. 34: 403-419.
- Vecoli, M., Riboulleau, A., Versteegh, G.J.M., 2009. Palynology, organic geochemistry and carbon isotope analysis of a latest Ordovician through Silurian clastic succession from borehole Tt1, Ghadamis Basin, southern Tunisia, North Africa: Palaeoenvironmental interpretation. Palaeogeography, Palaeoclimatology, Palaeoecology. 272 (1-2): 378-394.
- Vecoli, M., Delabroye, A., Spina, A., Hints, O., 2011. Cryptospore assemblages from Upper Ordovician (Katian-Hirnantian) strata of Anticosti Island, Québec, Canada, and Estonia: Palaeophytogeographic and palaeoclimatic

implications. Review of Palaeobotany and Palynology. 166 (1-2): 76-93.

Wang Y., Li J., Wang R., 1997. Latest Ordovician cryptospores from southern Xinjiang, China. Review of Palaeobotany and Palynology. 99 (1): 61–74.

Wang Y., Huai-cheng Z., Jun L., 2005. Late Silurian plant microfossil assemblage from Guangyuan, Sichuan, China. Review of Palaeobotany and Palynology. 133 (3-4): 153- 168.

Wellman C.H., 1993. A land plant microfossil assemblage of Mid Silurian age from the Stonehaven Group, Scotland. Journal of Micropalaeontology. 12 (3-4): 47–66.

Wellman C.H., 1996. Cryptospores from the type area of the Caradoc Series in southern Britain. In: Cleal, C.J. (Ed.), Studies on Early Land Plant Spores from Britain: Special Papers in Palaeontology, 55: 103–136.

Wellman C.H., Richardson J.B., 1993. Terrestrial plant microfossils from Silurian inliers of the Midland valley of Scotland. Palaeontology. 36: 155-193.

Wellman C.H., Richardson J.B., 1996, Sporomorph assemblages from the 'Lower Old red Sandstone' of Lorne, Scotland., In: Cleal, C.J. (Ed.), Studies on Early Land Plant Spores from Britain: Special Papers in Palaeontology. 55: 41–101.

Wellman C.H., Gray J., 2000. The microfossil record of early land plants. Philosophical Transactions Royal Society of London. 355 (1398): 717-732.

Wellman C.H., Higgs K.T., Steemans P., 2000. Spore assemblages from a Silurian sequence in Borehole Hawiyah-151 from Saudi Arabia. In: Al-Hajri, S., and Owens, B. (Eds.), Stratigraphic Palynology of the Palaeozoic of Saudi Arabia: GeoArabia, Bahrain, Special. 1: 116-133,

