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Cryptospore and trilete spore assemblages from the Late Ordovician (Katian–Hirnantian) Ghelli Formation, Alborz Mountain Range, Northeastern Iran: Palaeophytogeographic and palaeoclimatic implications

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ABSTRACT

Well-preserved miospore assemblages are recorded from the Late Ordovician (Katian–Hirnantian) Ghelli Formation in the Pelmis Gorge, located in the Alborz Mountain Range, Northeastern Iran. The palynomorphs were extracted from siliciclastic deposits that are accurately dated using marine palynomorphs (acritarchs and chitinozoans). The spore assemblages consist of 14 genera and 28 species (26 cryptospores and 2 trilete spore species). Six new cryptospore species are described: *Rimosotetras punctata* n.sp., *Rimosotetras granulata* n.sp., *Dyadospora asymmetrica* n.sp., *Dyadospora verrucata* n.sp., *Segestrespora iranense* n.sp., and *Imperfectotriletes persianense* n.sp. The study furthers knowledge of the development of the vegetative cover during the Late Ordovician. Various and abundant cryptospores in the Late Ordovician (Katian–Hirnantian) Ghelli Formation are probably related to the augmentation of land-derived sediments either during the global sea-level fall linked to the Late Ordovician glaciation or adaptation of the primitive land plants in a wide range of climatic conditions. These miospore taxa were produced by the earliest primitive land plants, which probably grew close to the shoreline and were washed in from adjacent areas, producing a high volume of miospores. The associated marine palynomorphs consist of acritarchs (13 genera and 18 species), chitinozoans (9 genera and 10 species), prasinophycean algae, scolecodonts, and graptolite remains, which are not discussed in detail herein. The established chitinozoan biozones of this part of the Palaeozoic sequence are the *Armoricochitina nigerica* Biozone, the *Ancyrochitina merga* Biozone, the *Tanuchitina elongata* Biozone, and the *Spinachitina oulebsiri* Biozone, suggesting a Late Ordovician age (Katian–Hirnantian). These chitinozoan biozones are widely evidenced only in the peri-Gondwanan Domain, indicating that the study area was part of this palaeo-continent in the Late Ordovician.

1. Introduction

The investigation of terrestrial spores of Early Palaeozoic strata (cryptospores and trilete spores) has a long history beginning several decades ago. In fact, our current knowledge stems from research in this field of geology, ranging from Precambrian to Early Devonian strata (Combaz, 1967; Volkova, 1962, 1976, 1997, 1990; Taylor, 1995; Taylor and Strother, 2008; Taylor and Strother, 2009; Richardson, 1996b; Steemans et al., 1996; Steemans, 2000; Wellman and Gray, 2000; Strother et al., 1996, 2004, 2015; Le Hérissé et al., 2007; Rubinstein and Vaccari, 2004; Rubinstein et al., 2010, 2011; Wellman and Gray, 2000; Wellman et al., 2015; Vecoli et al., 2011; Thusu et al., 2013). The study of cryptospores is important because land plant macrofossils have not been found in sediments older than the Silurian, so cryptospores are the oldest witnesses of the earliest continental vegetation. It is now accepted that cryptospores were produced by early primitive land plants, which probably grew close to the shoreline and were washed in from adjacent areas. In the Middle East, cryptospores and trilete spores have been recorded from the Middle–Upper Ordovician Qasim Formation of the Arabian Peninsula (Strother et al., 1996, 2015; Steemans et al., 2009), from the Caradoc Series of the Hasirah Member Safiq Formation of Oman (Wellman et al., 2003), and from the Upper Ordovician–Silurian of Southeastern Turkey (Steemans et al., 1996). To date, however, only one published paper is available that discusses the record of cryptospore assemblages below the Devonian strata and is devoted to the well-dated Ghelli Formation of Iran (Mahmoudi et al., 2014). Therefore, the present paper is a complementary contribution to the knowledge of the taxonomy and palaeophytogeography of cryptospores and trilete spores from the Iranian Platform located at high palaeolatitudes (peri-Gondwanan Domain) in the Upper Ordovician (Katian–Hirnantian). The cryptospore and spore assemblages sampled herein were recorded from the well-dated Ghelli Formation using independent fossil evidence, such as acritarchs, chitinozoans, prasinophycean algae, conodonts, and brachiopods.

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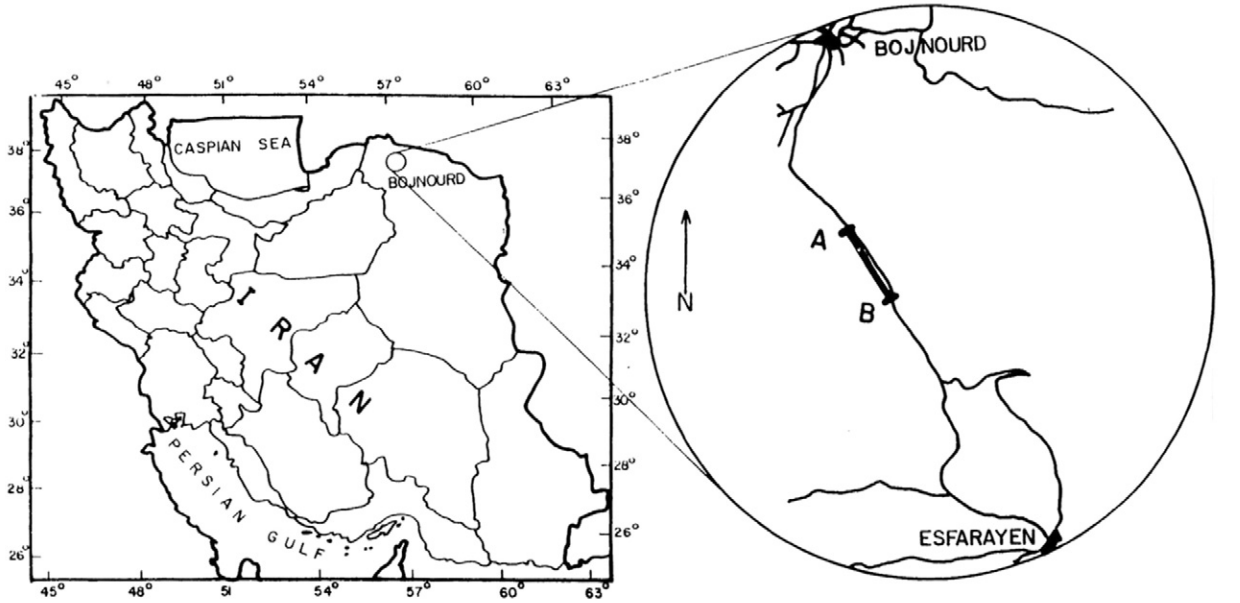

Fig. 1. Location map of the studied area (Ghavidel-Syooki, 2001).

2. Geological setting and previous studies

The study area is located approximately 32 km south of Bojnourd. The road from Bojnourd to Esfarayen is the main link to the region (Fig. 1). The measured and sampled stratigraphic section was chosen along this road (Fig. 2) because it cuts across the entire Palaeozoic strata and is easily accessible. In this area, the Lower Palaeozoic strata are 1200 m thick. They are divided in ascending stratigraphical order into the Mila (Cambrian), Lashkarak (Early–Middle Ordovician), Ghelli (Middle–Late Ordovician), and Niur (Early Silurian) formations (Afshar-Harb, 1979). The study area falls within the Kopeh–Dagh region (Northeastern Alborz Mountain Range), where the Lower Palaeozoic rock units extend toward the southern and eastern Caspian Sea. The Mila Formation consists mainly of medium to thick-bedded, cream reddish-brown limestones with poorly preserved megafossils (e.g., brachiopod and trilobites) that have not been identified at the level of genera and species. Therefore, based on stratigraphic position, the Mila Formation has been assigned to the Middle and Late Cambrian (Afshar-Harb, 1979). The Lashkarak Formation has a very unique sedimentary facies consisting of dark gray shales, siltstones, and fine-grained sandstones that are interbedded with thin-bedded fossiliferous limestones (Fig. 2). In the study area, the Lashkarak Formation contains conodonts, brachiopods, and acritarchs, which have been assigned to the Tremadocian–Darriwilian (Ahmadzadeh-Heravi, 1983; Ghavidel-Syooki, 2001). The Ghelli Formation consists mainly of olive gray silty shales, micaceous siltstones and fine-grained sandstones that are cut by a 44 m thick igneous sill. The lower and upper boundaries of the Ghelli Formation are conformable with overlying and underlying formations (Fig. 2). Some intervals of this formation contain brachiopods, conodonts, and well-preserved chitinozoans, which suggests a Late Ordovician age as its type section (Ghavidel-Syooki and Winchester-Seeto, 2002). The Niur Formation, although well-developed in Central Iran, was first described by Afshar-Harb (1979) from the Northeastern Alborz Mountain Range. In the Pelmis Gorge area, this formation consists mainly of black shales, siltstones, and sandstones with intercalations of fossiliferous limestones (Fig. 2). In the Pelmis Gorge area, the Niur Formation contains abundant corals, brachiopods, crinoids, and palynomorphs (acritarchs and chitinozoans), which suggest an Early Silurian age (Ghavidel-Syooki, 2001; Ghavidel-Syooki and Vecoli, 2007).

3. Materials and methods

A total of 140 surface samples were collected from the whole stratigraphic interval of the Lower Palaeozoic strata (Mila, Lashkarak, Ghelli, and Niur formations) in the Pelmis Gorge area at the eastern part of Kuh-e-Saluk. The collected samples are designated herein by the National Iranian Oil Company code numbers preceded by prefixes MG-1 to MG-140 (Fig. 2). Palynomorphs were extracted from shale, siltstone, and fine-grained sandstone samples using standard palynological procedures, which included the removal of carbonates and silicates by hydrochloric and hydrofluoric acids and density separation of the organic residues in 30 ml of saturated zinc bromide solution. Organic residues were then sieved through 15 μm nylon mesh sieves. Palynological residues were mounted on glass slides for optical and scanning electron microscopy examinations. All samples proved to be palyniferous and yielded well-preserved and abundant palynomorphs with dominating acritarch assemblages and rare algal clusters in the Mila Formation; however, chitinozoans, scolecodonts, and chitinous graptolite remain in the Lashkarak and Ghelli formations. It is worth mentioning here that cryptospores and rare trilete spores are present only in the Ghelli Formation (MG-90 to MG-130). The palynomorph groups mentioned earlier were counted, and their percentages were calculated. These calculations indicate that samples MG-90 to MG-100 bear miospores and that their percentage is fairly higher than that of acritarchs and chitinozoans (Table 1 and Fig. 3). The chitinozoan group is common in samples MG-90 to MG-104 and is very rare to rare in the rest of the samples (Table 1 and Fig. 3). The results of the palynological study of the area, consisting of acritarch and chitinozoan assemblages of Lower Palaeozoic rock units (Lashkarak, Ghelli and Niur formations) were previously published by Ghavidel-Syooki (2001), Ghavidel-Syooki and Winchester-Seeto (2002), and Ghavidel-Syooki and Vecoli (2007). Therefore, this paper focuses on the terrestrial palynomorph group of the Ghelli Formation (Katian–Hirnantian), although diagnostic acritarch and chitinozoan taxa are discussed briefly herein. The miospores and acritarchs range in color from yellow

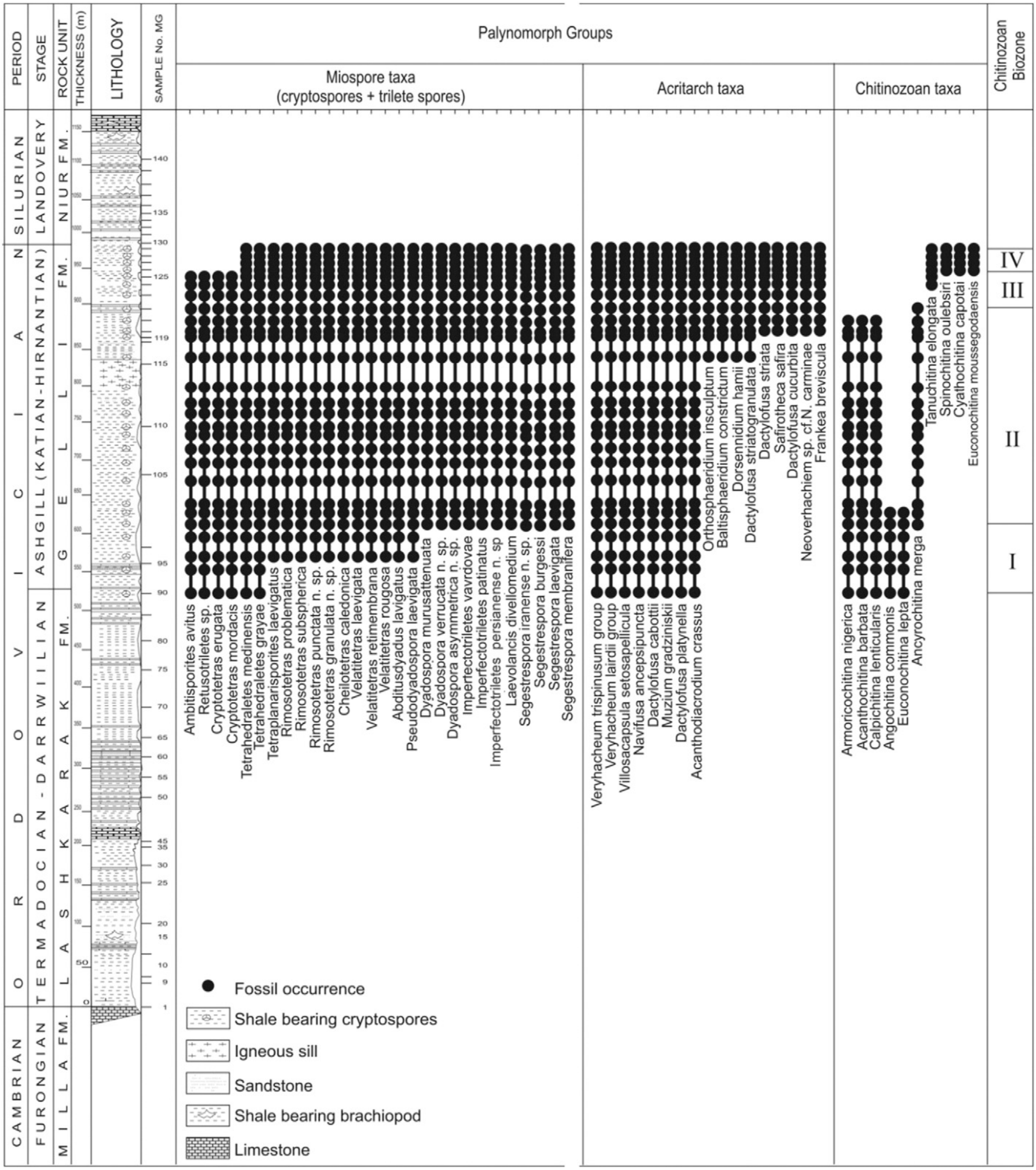

Fig. 2. Stratigraphic distribution of the different groups of palynomorphs within the Ghelli Formation in Pelmis Gorge, Northeastern Alborz Ranges.

to orange-brown, indicating an intermediate degree of thermal maturity (Plates I to VIII). All slides relating to this study are housed in the palaeontological collections of the Exploration Directorate of the National Iranian Oil Company under sample numbers MG-90 to MG-130.

4. Systematic paleontology of palynomorphs

In this study, palynomorphs from the Ghelli Formation, especially miospores, were illustrated on Plates I through VII, index acritarchs on Plate VIII and chitinozoans on Plate IX. Detailed descriptions were

Table 1
Relative percentage of different palynomorph groups of Late Ordovician in the Ghelli Formation, in Pelmis Gorge area, Northeastern Alborz Mountain Range.

Sample number (MG)	Miospores (cryptospores + spores) %	Acritarchs %	Chitinozoans %	Scolecodonts %	Graptolite remains %
90	15	69	14	2	0
94	27	21.5	46	5.5	0
96	19	40	38	2.5	0.5
98	17	42.5	35.5	4.15	0.85
99	31	38	24	7	0
100	21.5	40	33	5.5	1
101	56	24	11	7	2
104	52	13.5	24.5	5.5	4.5
106	46.5	42	4.5	6.5	0.5
107	63	27.5	6	1	2.5
109	74	21	0	3	2
110	75	21.5	0.5	2	1
111	80	6	10	3	1
112	58	41	0	1	0
113	61.5	37.5	1	0	0
116	33	65.5	1	0.5	0
119	59.4	40.6	0	0	0
120	37.5	60.5	1	1	0
121	57.5	40	2	0.5	0
122	76.4	23.4	0.2	0	0
123	54	46	0	0	0
124	65	35	0	0	0
125	66.5	33	0	0.5	0
126	54	45.5	0.2	0.3	0
127	65	34.5	0.2	0.3	0
128	72	27	1	0	0
129	65	16	9	10	0

provided only for new taxa (Plate VII). Dimensions, stratigraphic, and palaeogeographic distributions are presented for all taxa (Table 2).

4.1. Miospore group (cryptospores and trilete spores)

Miospores have been treated as non-marine palynomorphs. The cryptospores are without trilete or monolete marks and are with or without contact features, consisting of tetrads, dyads, and monads (Richardson, 1996a,b; Wellman and Richardson, 1996; Strother, 1991; Steemans, 2000; Vecoli et al., 2011). The trilete spores are formed in tetrads but are dispersed separately with either a trilete or monolete mark on the proximal surfaces (Richardson, 1996a,b). The cryptospores can be divided into subgroups based on the presence/absence of morphological features, which have been proposed by Wellman and Richardson (1996) and Richardson (1996a,b). The term "miospore" is used herein as a general term indicating all fossil plant spores smaller than 200 μm (Steemans, 2000), including both cryptospores and trilete spores. Based on the presence or absence of morphological features proposed by Richardson (1996a,b), Wellman and Richardson (1996), and Vecoli et al. (2011), the systematic paleontology of miospores (cryptospores and trilete spores) is subsequently discussed.

4.1.1. Anteturma cryptosporites (Richardson, 1988)

4.1.1.1. Subgroup naked unfused tightly and loosely adherent cryptospore tetrads. This subgroup has adherent tetrads with lines separating the four spores of the tetrad and is without enclosing envelopes.

Genus ***Cryptotetras*** Strother et al. 2015.

Cryptotetras erugata Strother et al., 2015 (Plate I, 1–10).

Dimensions: 13 (19) 25 μm; 2 specimens were measured. The size range of the Iranian specimens is smaller than those of the Arabian Peninsula (Strother et al., 2015).

Occurrences: This species is present in the Ghelli Formation (samples MG-90 to MG-125), Northeastern Alborz Mountain Range.

Previous records: So far, there have been records of this species from the Hanadir Shale Member of the Qasim Formation, Ordovician (Darriwilian) of the Arabian Peninsula (Strother et al., 2015).

Cryptotetras mordacis Strother et al. 2015 (Plate I, 11, 12).

Dimensions: 21 (24) 27 μm; the Iranian specimens are smaller than those of the Arabian Peninsula (Strother et al., 2015).

Occurrences: This species is common in the Ghelli Formation (samples MG-90 to MG-125).

Previous records: There have been records of this species from the Hanadir Shale Member of the Qasim Formation, Ordovician (Darriwilian) of the Arabian Peninsula (Strother et al., 2015).

Genus ***Tetrahedraletes*** (Strother and Traverse, 1979) Wellman and Richardson, 1993.

Type species: *Tetrahedraletes medinensis* (Strother and Traverse, 1979) Wellman and Richardson, 1993.

Tetrahedraletes medinensis (Strother and Traverse, 1979) Wellman and Richardson, 1993 (Plate I, 13–20; Plate II, 1–8).

Synonymy: See Strother (1991, p. 122), Wellman and Richardson (1996, p. 165), and Vecoli et al. (2011, p. 83).

Dimensions: 15 (30) 45 μm; 20 specimens were measured. The size range of those from the Ghelli Formation is smaller than those from Turkey (Steemans et al., 1996), China (Wang et al., 1997), Canada and Estonia (Vecoli et al., 2011).

Occurrences: This species is present throughout the Ghelli Formation (samples MG-90 to MG-130), Northeastern Alborz Mountain Range (Fig. 2).

Previous records: So far, *Tetrahedraletes medinensis* has been recorded from the Caradoc type section, Shropshire, U.K. (Wellman, 1996); the Upper Ordovician at Hlásná Třebaň, Czechoslovakia (Vavrdová, 1988); the Upper Ordovician (Late Katian–Hirnantian) of the Bedinan Formation, Southeastern Turkey (Steemans et al., 1996); the Kalpintag Formation, South Xinjiang, China (Wang et al., 1997); the Ordovician/Silurian boundary from the upper member of the Salar del Rincon Formation in the Puna region, northwest Argentina (Rubinstein and Vaccari, 2004); the Hirnantian-Llandovery (*persculptus* graptolite Biozone–*turriculatus* graptolite Biozone) of southwest Wales (Burgess, 1991); the latest Ashgillian, or earliest Llandovery (Rhuddanian) of the Cedaberg Formation, South Africa; the Upper Ordovician (Katian–Hirnantian) strata of Anticosti Island, Québec, Canada, and Estonia (Vecoli et al., 2011); the Upper Ordovician (Katian–Hirnantian) of the Ghelli Formation, Khoshyeilagh area, Northeastern Iran (Ghavidel-Syooki et al., 2011b; Mahmoudi et al., 2014); and the Qusaiba-1 borehole, Sarah Formation, latest Ordovician (Hirnantian),

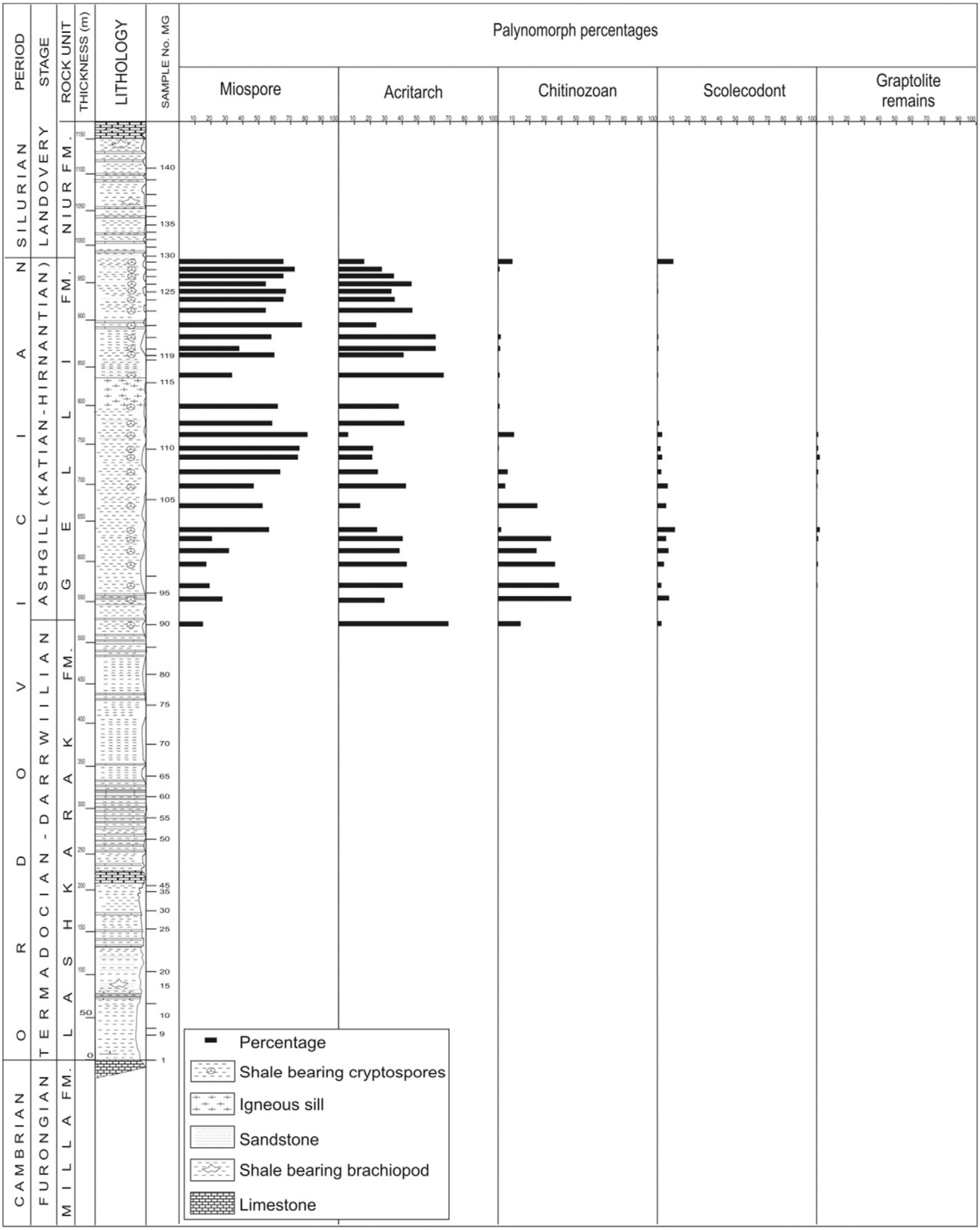

Fig. 3. Quantitative distribution of the different groups of palynomorphs throughout the Ghelli Formation.

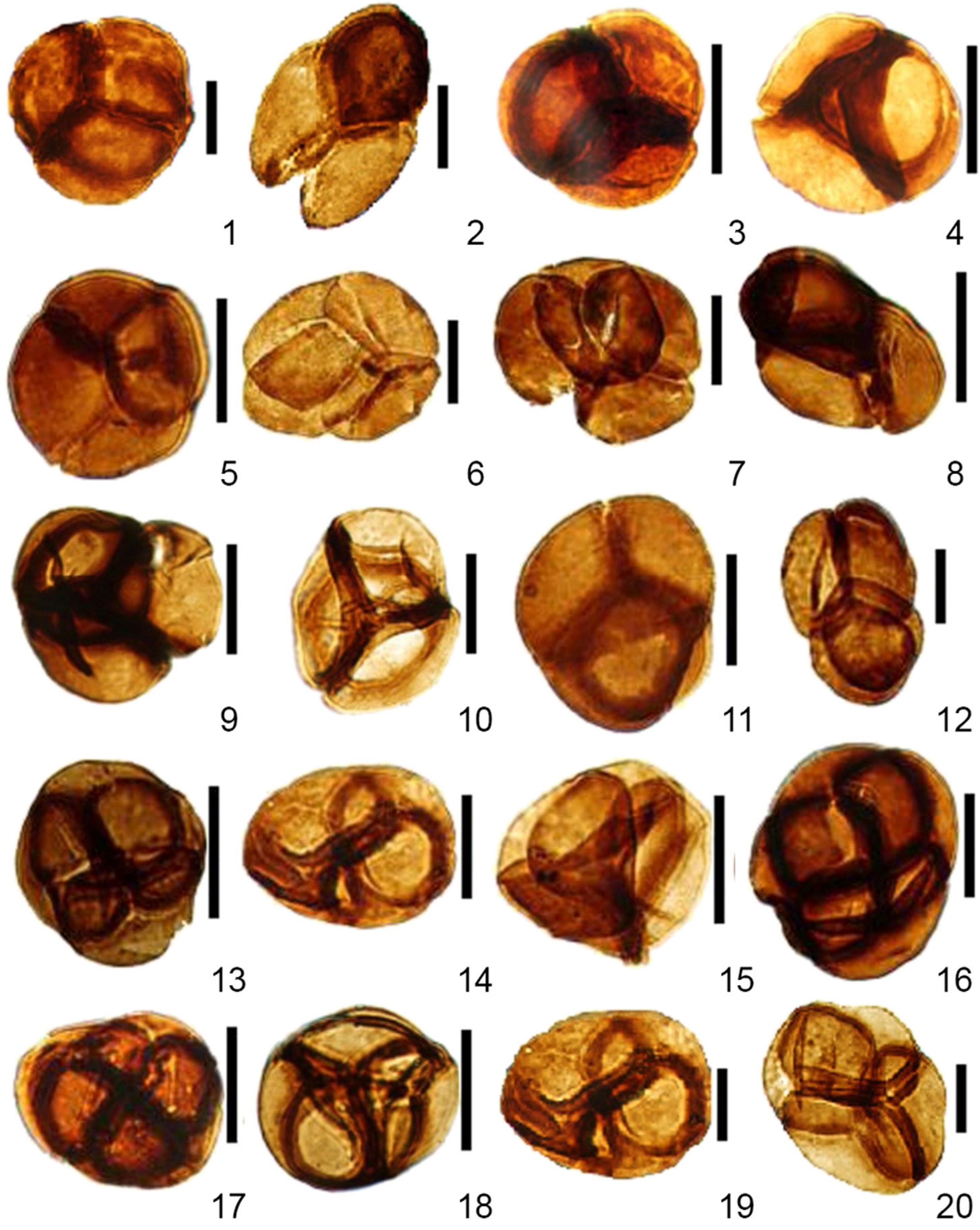

Plate I.

1, 2, 3, 4, 5, 6, 7, 8, 9, 10.	*Cryptotetras erugata* Strother, Traverse and Vecoli, 2015
11, 12.	*Cryptotetras mordacis* Strother, Traverse, and Vecoli, 2015
13, 14, 15, 16, 17, 18, 19, 20.	*Tetrahedraletes medinensis* Strother and Traverse, 1979 emend. Wellman and Richardson, 1993

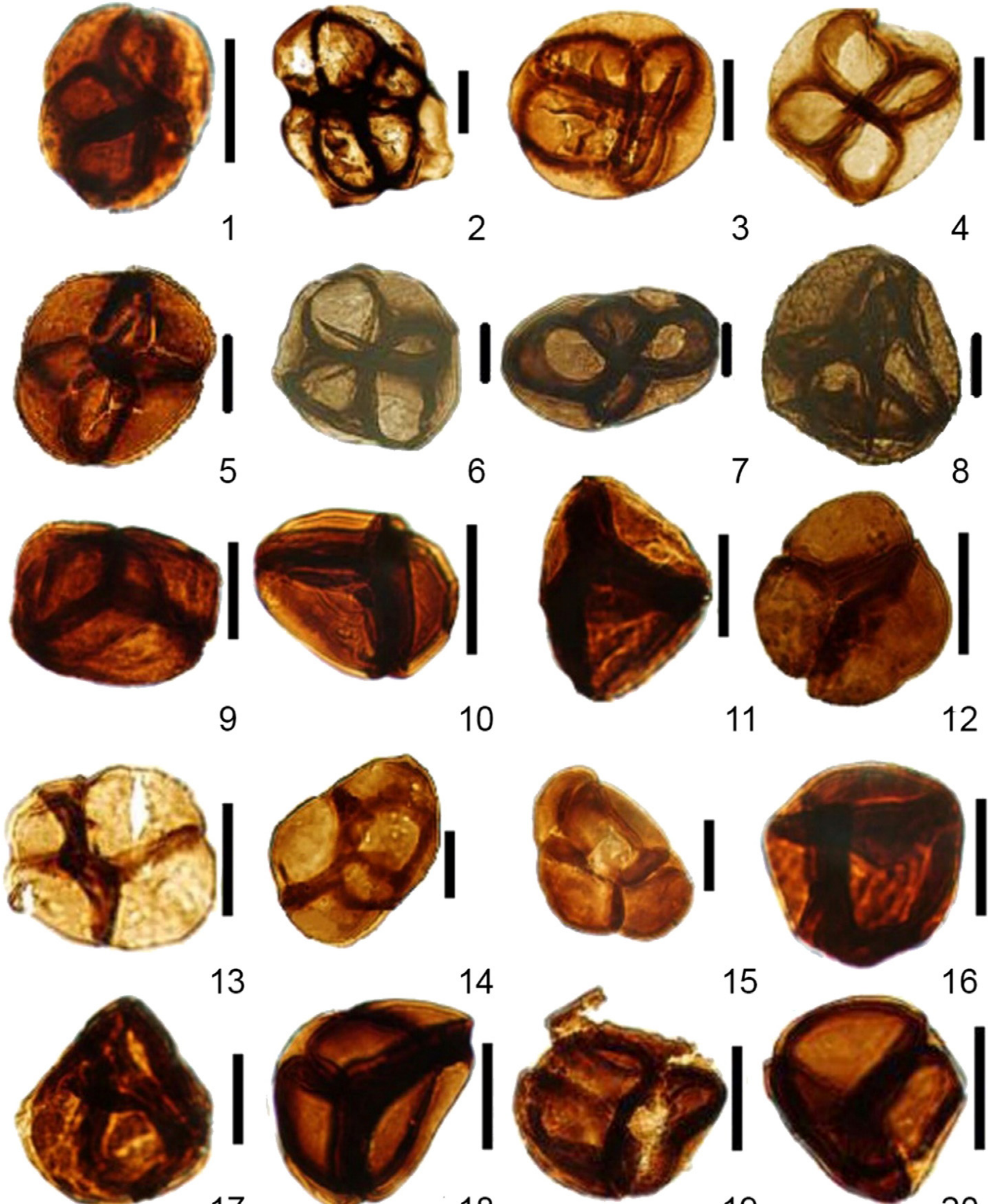

Plate II.

1, 2, 3, 4, 5, 6, 7, 8.	*Tetrahedraletes medinensis* Strother and Traverse, 1979 emend. Wellman and Richardson, 1993
9, 10, 11.	*Tetrahedraletes grayae* Strother, 1991
12, 13, 14, 15.	*Tetraplanarisporites laevigatus* Wellman et al., 2015
16, 17, 18, 19, 20.	*Rimosotetras problematica* Burgess 1991

the Arabian Peninsula, 488.3 ft. (Wellman et al., 2015), and the Hanadir Shale Member of the Qasim Formation, Ordovician (Darriwilian) of the Arabian Peninsula (Strother et al., 2015).

Tetrahedraletes grayae Strother, 1991 (Plate II, 9–11).
Dimensions: 16 (19.5) 23 μm; 3 specimens were measured. The size range of the Ghelli Formation's specimens is smaller than those of China, Canada, and Estonia (Wang et al., 1997; Vecoli et al., 2011).
Occurrences: *Tetrahedraletes grayae* is present in all studied samples of the Ghelli Formation (MG-90 to MG-125), Northeastern Alborz Mountain Range (Fig. 2).
Synonymy: See Vecoli et al. (2011, p. 83).
Previous records: Ashgill, Couches Fort Atkinson Dolomite, McQuokata Group, Illinois (Strother, 1991); Oostduinkerke borehole, Brabant Massif, Belgium (Steemans, 2001); Kosov Formation, Central Bohemia, Czech Republic; Upper Ordovician (Katian–Hirnantian) strata of Anticosti Island, Québec, Canada (Vecoli et al., 2011); the Hanadir Shale Member of the Qasim Formation, Ordovician (Darriwilian), the Arabian Peninsula (Strother et al., 2015); and Late Ordovician, Ghelli Formation, Khoshyeilagh area, Northeastern Alborz Mountains (Mahmoudi et al., 2014).

Genus ***Tetraplanarisporites*** Wellman et al. 2015.

Tetraplanarisporites laevigatus Wellman et al., 2015 (Plate II, 12-15).
Dimensions: 31 (44) 57 μm; 7 specimens were measured. The size range of the Iranian specimens is slightly larger than those from Saudi Arabia (Wellman et al., 2015).
Occurrence: This species is present throughout the Ghelli Formation (MG-98 to MG-130).
Synonymy: See Wellman et al. (2015).
Previous records: Qusaiba-1 borehole, Sarah Formation (Baqa Shale Member, Baqa Sandstone Member and Quwarah Member), Late Ordovician (Hirnantian) Saudi Arabia (Wellman et al., 2015).

Genus ***Rimosotetras*** Burgess, 1991.
Type species: *Rimosotetras problematica* Burgess, 1991.

Rimosotetras problematica Burgess, 1991 (Plate II, 16–20).
Synonymy: See Steemans et al. (1996) and Vecoli et al. (2011).
Dimensions: 17.5 (30) 42.5 μm; 10 specimens were measured. The size range of the Iranian specimens is smaller than those from Turkey (Steemans et al., 1996), Canada and Estonia (Vecoli et al., 2011), and Saudi Arabia (Strother et al., 2015).
Occurrences: This species is present in all of the studied samples of the Ghelli Formation (MG-98 to MG-130), Northeastern Alborz Mountain Range (Fig. 2).
Previous records: This species has a long stratigraphic range, from the Late Ordovician through the Silurian (Burgess, 1991; Steemans et al., 1996; Richardson, 1988; Rubinstein and Vaccari, 2004; Vecoli et al., 2011). Likewise, *Rimosotetras problematica* (Burgess, 1991) has been recorded from Silurian deposits elsewhere (Miller and Eames, 1982; Strother and Traverse, 1979; Steemans et al., 2000; Wellman et al., 2000; Le Hérissé et al., 2001; Burgess and Richardson, 1991; Wellman and Richardson, 1996; Spina and Vecoli, 2009). The species has also been recorded from the Early Devonian (Lochkovian) strata of the Tawil Formation in the Arabian Peninsula (Steemans et al., 2007). Likewise, this cryptospore species has been recorded from the Hanadir Shale Member of the Qasim Formation, Ordovician (Darriwilian), the Arabian Peninsula (Strother et al., 2015), and finally, this species has been recorded from the Upper Ordovician (Katian–Hirnantian), Ghelli Formation, Khoshyeilagh area, Northeastern Iran (Ghavidel-Syooki et al., 2011b; Mahmoudi et al., 2014).

Rimosotetras subspherica Strother et al., 2015 (Plate III, 1-6).
Dimensions: 19 (32) 45 μm; 11 specimens were measured. The size range of the Ghelli Formation's specimens is larger than those of the Hanadir Shale Member of the Qasim Formation of the Arabian Peninsula (Strother et al., 2015).
Occurrences: This species is present in the whole thickness of the Ghelli Formation (MG-98 to MG-129), Northeastern Alborz Mountain Range.
Previous records: This species has been recorded from the Hanadir Shale Member (Darriwilian) of the Arabian Peninsula (Strother et al., 2015).

***Rimosotetras punctata* n. sp.** (Plate III, 7–9).
Holotype: Plate III, 7.
Type stratum: Ghelli Formation, sample number MG-100, 32 km, southern Bojnourd, eastern flank of Kuh-e-Saluk, Northeastern Alborz Mountain Range.
Derivation of name: From the Greek punctatus, meaning bearing pores; the name is considered feminine.
Dimensions: 15 (16) 17 μm; 15 specimens were measured.
Occurrences: This species is present (MG-98 to MG-130) throughout the Ghelli Formation, Northeastern Alborz Mountain Range.
Description: Loosely permanent tetrads, individual spore members circular to subcircular in outline, walls of spore members uniformly thin, perforated with numerous pits that penetrate the entire walls.
Remarks: This species differs from other species of *Rimosotetras* in the perforated walls of spores.
Rimosotetras granulata n. sp. (Plate III, 10, 11).
Holotype: Plate III, 10.
Type stratum: Ghelli Formation, sample number MG-100, 32 km, southern Bojnourd, eastern flank of Kuh-e-Saluk, Northeastern Alborz Mountain Range.
Dimensions: 20 (24.5) 29 μm; 20 specimens were measured.
Occurrences: This species is present within the Ghelli Formation (MG-98 to MG-130), Northeastern Alborz Mountain Range.
Derivation of name: Refers to granulate–echinate ornamentation, which is distributed on the entire surface of each spore member of the tetrads.

4.1.1.2. Subgroup naked fused cryptospore tetrads.

Genus ***Cheilotetras*** Wellman and Richardson, 1993.
Type species: *Cheilotetras caledonica* Wellman and Richardson, 1993.
Cheilotetras caledonica Wellman and Richardson, 1993 (Plate III, 12, 13; Plate VII, 1, 2).
Synonymy: See Wellman and Richardson (1996).
Dimensions: 17 (24) 31 μm; 5 specimens were measured.
Occurrences: This species is present in the Ghelli Formation (MG-98 to MG-130), Northeastern Alborz Mountain Range.
Previous records: Based on the literature review, *Cheilotetras caledonica* has been previously reported mostly from the post-Ordovician strata worldwide, ranging from Early–Late Silurian strata (Wellman, 1993; Wellman and Richardson, 1996; Burgess and Richardson, 1991; Molyneux et al., 1996; Hagstrom, 1997; Molyneux et al., 2007; Molyneux et al., 2008) to Early Devonian strata (Burden et al., 2002; Steemans et al., 2007). This species has been described in Upper Ordovician (Katian–Hirnantian) strata of Canada and Estonia (Vecoli et al., 2011) and in the Upper Ordovician (Katian–Hirnantian), Ghelli Formation, Khoshyeilagh area, Northeastern Iran (Ghavidel-Syooki et al., 2011b; Mahmoudi et al., 2014).

4.1.1.3. Subgroup envelope-enclosed unfused cryptospore tetrads.

Genus ***Velatitetras*** Burgess, 1991.
Type species: *Velatitetras laevigata* (Burgess, 1991).

Velatitetras laevigata Burgess, 1991 (Plate III, 14).
Synonymy: See Steemans et al. (1996) and Vecoli et al. (2011).
Dimensions: 20 (22) 24 μm; 15 specimens were measured. The Iranian specimens are much larger than those from Turkey and are generally similar to those from Canada and Estonia (Vecoli et al., 2011).
Occurrences: This species is present in the Ghelli Formation (MG-98 to MG-130), Northeastern Alborz Mountain Range in Iran (Fig. 2).
Previous records: This species has been documented mainly in Ashgill (Late Katian–Hirnantian) to Llandovery worldwide. There is only one record from the Lochkovian of Saudi Arabia, which has been recorded by Steemans et al. (2007). Some relevant occurrences are reported here as follows: Caradoc-Ashgill, Bedinan Formation, Turkey (Steemans et al., 1996); Ashgill, Oostduinkerke borehole, Brabant Massif, Belgium

(Steemans, 2001); Upper Ordovician (Katian–Hirnantian) Canada and Estonia (Vecoli et al., 2011); Kalpintag Formation, Southern Xinjiang, China (Wang et al., 1997); Upper Caradoc–Lower Telychian: subsurface of Northeastern Libya (Richardson, 1988; Richardson and Ioannides, 1973); Llandovery, Salar del Rincón Formation, Puna Region, Argentina (Rubinstein and Vaccari, 2004); Qusaiba Mb., Nuayyim-2 and Hawiyah-152 boreholes, Saudi Arabia (Steemans et al., 2000; Wellman et al., 2000); Dadas Formation, Turkey (Steemans et al., 1996); Tanezzuft and Acacus formations, Tunisia (Spina and Vecoli, 2009); and Upper Ordovician-Lowermost Silurian of Qusiaba-1, the Arabian Peninsula (Wellman et al., 2015).

Velatitetras retimembrana (Miller & Eames) Steemans et al. 1996 (Plate III, 15-20; Plate IV, 1–9).
Synonymy: See Steemans et al. (1996).
Dimensions: 17 (27.5) 38 μm, width of envelope 3 to 4 μm with clear reticulation; 14 specimens were measured. The Iranian specimens are generally similar to those of Turkey (Steemans et al., 1996).
Occurrences: This species is present in the Ghelli Formation (MG-98 to MG-130), Northeastern Alborz Mountain Range of Iran (Fig. 2).
Previous records: *Velatitetras retimembrana* has previously been recorded from Late Ordovician, Bedinan Formation, Southeastern Turkey (Steemans et al., 1996); Ashgillian–Llandovery Wales area, UK (Burgess, 1991); Llandovery (Rhuddanian–Aeronian), Niagara Gorge, Lewiston, New York, USA (Miller and Eames, 1982); Llandovery (Rhuddanian), Tuscarora, Central Pennsylvania, USA (Johnson, 1985); Ashgillian, Drakes Formation, Ohio, USA (Gray, 1988); late Llandovery, Jupiter Formation, Anticosti Island, Quebec, Canada (Duffield, 1985); Llandovery (Rhuddanian–Aeronian), Northeast Libya (Richardson, 1988); and Late Ordovician, Kosov Formation, Hlásná Třebaň, Czech Republic (Vavrdová, 1988, 1989).

Velatitetras rugosa (Strother and Traverse) Steemans et al., 1996 (Plate IV, 10–20; Plate V, 1).
Synonymy: See Steemans et al. (1996) and Vecoli et al. (2011).
Dimensions: 20 (32.5) 45 μm; 15 specimens were measured. The Iranian specimens are smaller than those of Turkey and of Canada and Estonia (Vecoli et al., 2011).
Occurrences: This species is present in the Ghelli Formation (MG-96 to MG-130), Northeastern Alborz Mountain Range, in Iran (Fig. 2).
Previous records: This species has been recorded from Ashgillian (Hirnantian), Velleda Mb. of Ellis Bay Formation Anticosti Island (Richardson and Ausich, 2007). Other occurrences are as follows: Caradoc–Hirnantian, Bedinan Formation, Turkey (Steemans et al., 1996); Ashgillian, Oostduinkerke borehole, Brabant Massif, Belgium (Steemans, 2001); Ashgill–Early Llandovery: Hlásná Třebaň, Czechoslovakia (Vavrdová, 1988, 1989); Early Llandovery (Rhuddanian), Bronydd (Steemans et al., 2000; Wellman et al., 2000); Llandovery-Ludlow, Allenport, Pennsylvania, USA (Beck and Strother, 2008); Ludlow, uppermost Pitinga Formation, Urubu River area, western Amazon Basin, Brazil; Ludlow–Lochkovian, Tanezzuft, Acacus, Tadrart formations, Ghadamis basin, MG-1 borehole, Tunisia (Spina and Vecoli, 2009); and Upper Ordovician (Katian–Hirnantian) strata of Canada and Estonia (Vecoli et al., 2011).

4.1.1.4. Subgroup envelope-enclosed unfused cryptospore dyads. This subgroup is characterized by true dyads enclosed within a smooth ornamented envelope.

Genus ***Abditusdyadus*** Wellman and Richardson, 1996.
Type species: *Abditusdyadus histosus* Wellman and Richardson, 1996.

Abditusdyadus laevigatus Wellman and Richardson, 1996 (Plate V, 2, 3, 4, 5).
Dimensions: 18 (23.5) 29 μm; 4 specimens were measured.
Occurrence: This species is present in the Ghelli Formation (MG-98 to MG-130).
Previous records: Ashgillian (late Katian–Hirnantian), Oostduinkerke Brabant Massif, Belgium (Steemans, 2001); Early Llandovery (Rhuddanian), Qusaiba member of Qalibah Formation, Saudi Arabia (Steemans et al., 2000; Wellman et al., 2000); Lochkovian, Lower Old Red Sandstone, Lorne, Scotland (Wellman and Richardson, 1996); Upper Ordovician (Katian–Hirnantian) strata of Canada and Estonia (Vecoli et al., 2011); and Upper Ordovician (Katian–Hirnantian), Ghelli Formation, Khoshyeilagh area, Northeastern Iran (Ghavidel-Syooki et al., 2011b; Mahmoudi et al., 2014).

4.1.1.5. Subgroup envelope-enclosed fused cryptospore dyads. This subgroup is characterized by pseudodyads within an envelope.

Genus ***Segestrespora*** Burgess, 1991.
Type species: *Segestrespora membranifera* (Johnson, 1985) Burgess 1991.

Segestrespora membranifera (Johnson, 1985) Burgess, 1991 (Plate V, 6).
Synonymy: See Steemans et al. (1996) and Vecoli et al. (2011).
Dimensions: 21 (27) 33 μm; 3 specimens were measured. The size range of the Iranian species is larger than those of Turkey (Steemans et al., 1996).
Occurrences: This species is rare to common and is present in the Ghelli Formation (MG-100 to MG-130).
Previous records: This species has a wide geographical distribution that stratigraphically ranges from Upper Ordovician to Lower Silurian (Llandovery). It has so far been recorded from Late Ordovician, Bedinan Formation, Southeastern Turkey (Steemans et al., 1996); Ashgillian, Oostduinkerke borehole, Brabant Massif, Belgium (Steemans, 2001); latest Ashgillian (Hirnantian)–earliest Silurian (Rhuddanian) from Scach to Bronydd Formation, Ashgillian–Rhuddanian type Llandovery area, southwestern Wales, U.K; *persculptus*–*acinaces* graptolite Biozone (Burgess, 1991); Ashgillian, Hlásná Třebaň, Kosov Formation, *bohemicus* graptolite biozone, Czechoslovakia (Vavrdová, 1989); Llandovery: Qusaiba Member of Qalibah Formation, Saudi Arabia (Steemans et al., 2000; Wellman et al., 2000); Upper Ordovician and Lowermost Silurian of Qusaiba-1, Qasim region, Central Saudi Arabia (Wellman et al., 2015); Upper Ordovician of Libya (Abuhmida, 2013); Salar del Rincón Formation, Puna Region, Argentina (Rubinstein and Vaccari, 2004); and Upper Ordovician (Katian–Hirnantian) strata of Anticosti Island, Québec, Canada, and Estonia (Vecoli et al., 2011).

Segestrespora laevigata Burgess, 1991 (Plate V, 7, 8; Plate VI, 12).
Synonymy: See Steemans et al. (1996) and Vecoli et al. (2011).
Dimensions: 12 (16.5) 21 μm; 3 specimens were measured (each spore is 13 μm long and 9 μm wide). The size range of the Iranian specimens is smaller than those of Turkey (Steemans et al., 1996).
Occurrences: This species is rare and is present in the Ghelli Formation (MG-100 to MG-130).
Previous records: This species has a wide geographical distribution and stratigraphically ranges from Late Ordovician to Rhuddanian. This species has so far been recorded from Late Ordovician (Caradoc–Hirnantian), Bedinan Formation, Southeastern Turkey (Steemans et al., 1996); Ashgillian, Oostduinkerke borehole, Brabant Massif, Belgium (Steemans, 2001); latest Ashgillian (Hirnantian)–earliest Silurian (Rhuddanian) from Scach to Bronydd Formation, type Llandovery area, southwestern Wales (Burgess, 1991); Llandovery, Qusaiba Member

Plate III.

1, 2, 3, 4, 5, 6.	*Rimosotetras punctata* n. sp.
10, 11.	*Rimosotetras granulata* n. sp.
12, 13.	*Cheilotetras caledonica* Wellman and Richardson 1993
14.	*Velatitetras laevigata* Burgess 1991
15, 16, 17, 18, 19, 20.	*Velatitetras retimembrana* (Miller & Eames) Steemans et al., 1996

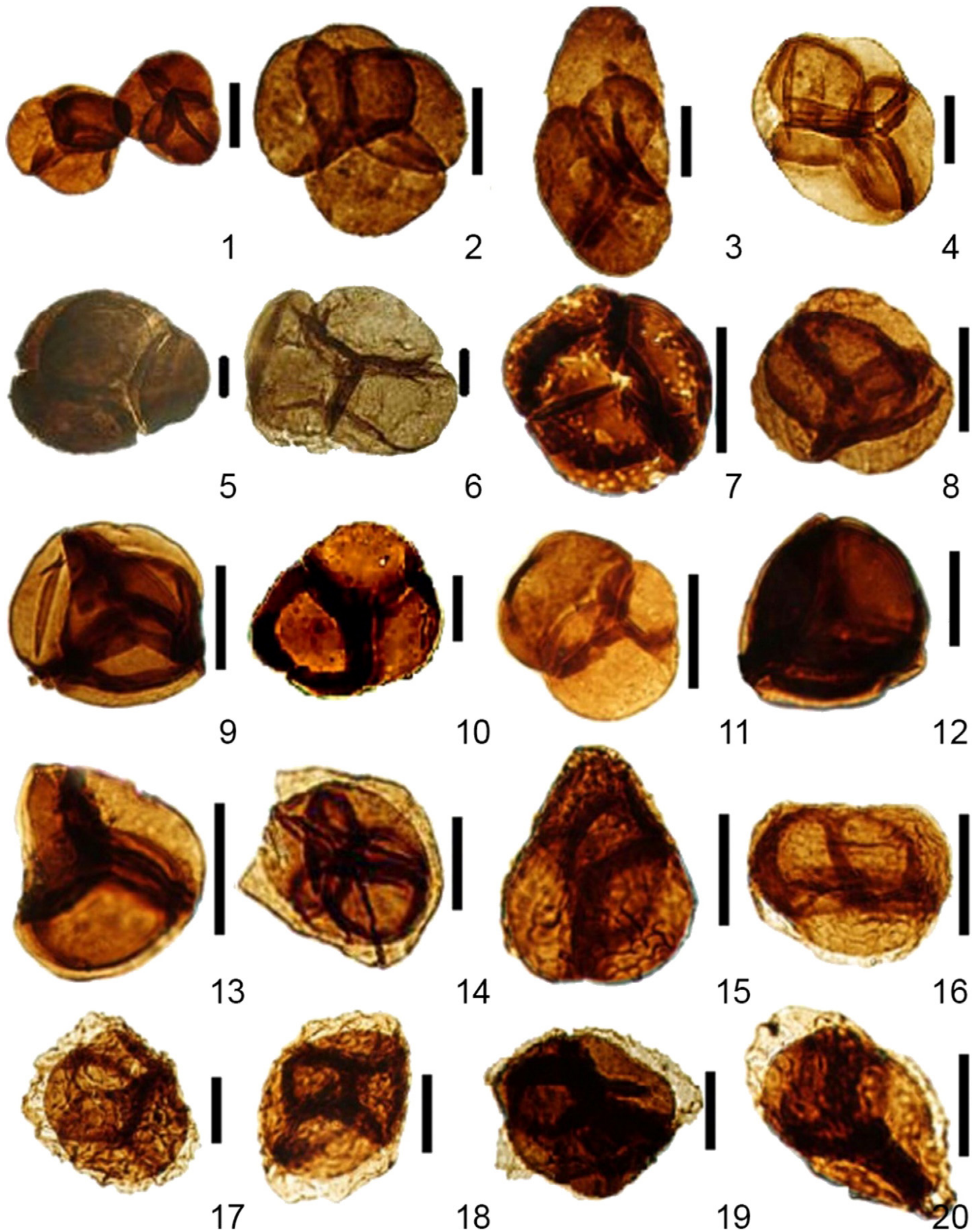

Plate III.

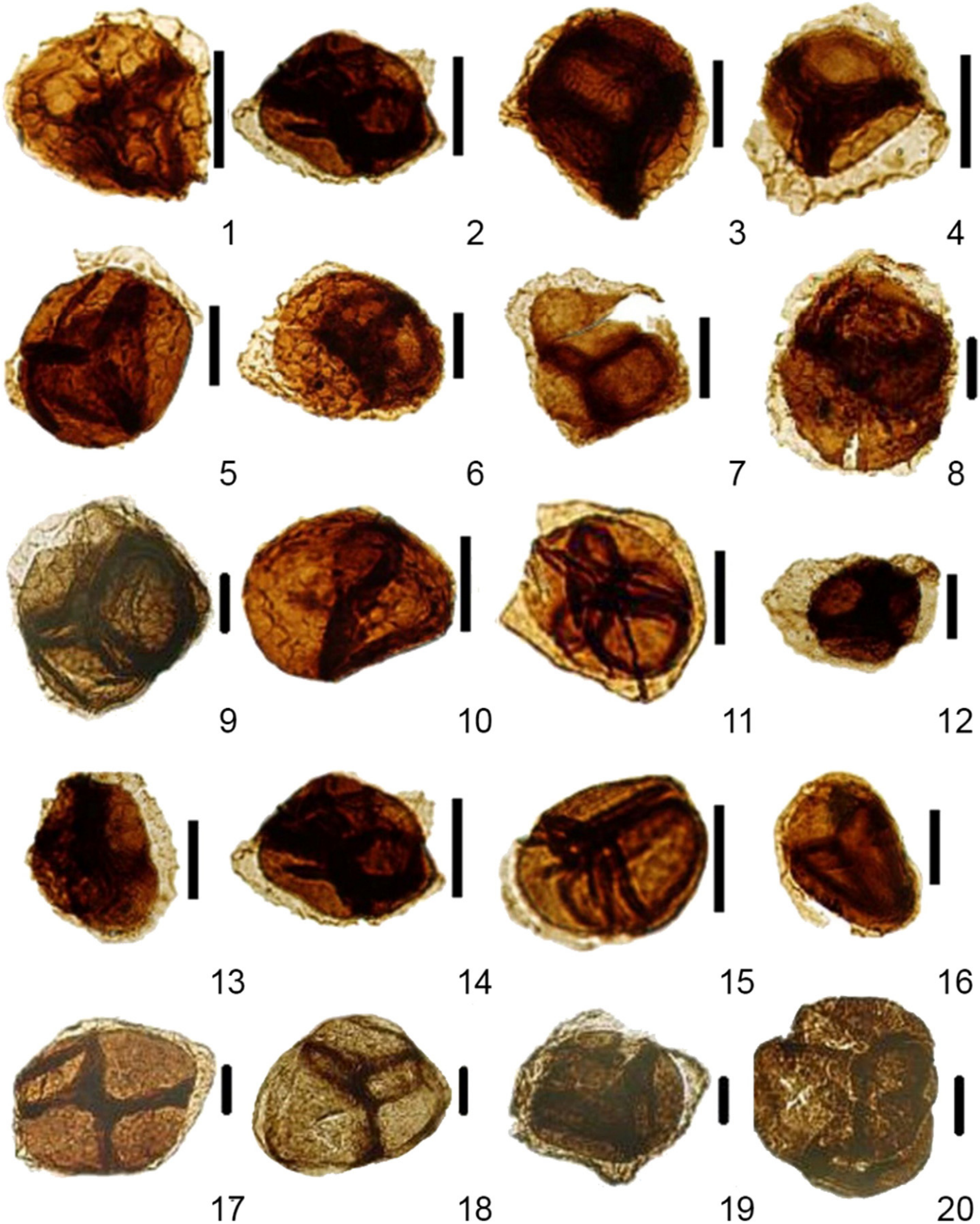

Plate IV.

1, 2, 3, 4, 5, 6, 7, 8, 9. *Velatitetras retimembrana* (Miller & Eames) Steemans et al., 1996

10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20. *Velatitetras rugosa* (Strother and Traverse) Steemans et al., 1996 of Qalibah Formation, Saudi Arabia (Steemans et al., 2000; Wellman et al., 2000); Upper Ordovician-Lowermost Silurian, Qusaiba-1, Qasim region, Central Saudi Arabia (Katian–Hirnantian) (Wellman et al., 2015); and Upper Ordovician (Katian–Hirnantian) age of Anticosti Island, Québec, Canada, and Estonia (Vecoli et al., 2011).

Segestrespora burgessii Steemans et al., 1996 (Plate V, 9, 10, 11).
Synonymy: See Burgess, 1991, *Segestrespora* sp. A, p. 589, pl. 2, (Fig. 6).
Dimensions: 19 (29) 39 μm; 4 specimens were measured (enclosed-envelope of 1 to 3 μm). The size range of the Ghelli Formation specimens is larger than those of Turkey (Steemans et al., 1996).
Occurrences: This species is rare but is present in the Ghelli Formation (MG-100 to MG-129).
Previous records: This species has so far been recorded from latest Ashgillian (Hirnantian)–earliest Silurian (Rhuddanian) from Scach to Bronydd Formation, type Llandovery area, Southwestern Wales (Burgess, 1991), and Late Ordovician, Bedinan Formation, South-eastern Turkey (Steemans et al., 1996).

***Segestrespora iranense* n. sp.** (Plate V, 12, 13).
Holotype: Plate V, 12.
Type stratum: Ghelli Formation, samples numbered MG-100 to MG-124, 32 km, southern Bojnourd, eastern flank of Kuh-e-Saluk, Northeastern Alborz Mountain Range.
Dimensions: 18 (20) 22 μm; 20 specimens were measured.
Occurrences: This species is present within the Ghelli Formation (MG-100 to MG-130), Northeastern Alborz Mountain Range.
Derivation of name: Refers to Iran, the country in which the species was first recorded.
Diagnosis: *Segestrespora iranense* n. sp. is a fairly small cryptospore species with an elliptical outline. The spore-like cells are ornamented by granules, or connate spinae. This cryptospore species is 30 μm long and 15 μm wide.
Description: *Segestrespora iranense* n. sp. is dyadic to pseudodyadic, with an elliptical outline that is entirely enclosed within a uniform envelope. The whole cryptospore is covered by granules, or connate spinae. Individual spore-like cells are kidney-shaped and are 30 μm long and 15 μm wide. The envelope firmly adheres to the enclosed spore-like cells. The annular ring is 2 to 3 μm wide and encircles the spore-like cells at their junction. *Segestrespora iranense* n. sp. is different from other species of *Segestrespora* in having granules throughout the entire cryptospore surface.

4.1.1.6. Subgroup unfused naked cryptospore dyads (true dyads). This subgroup comprises dyads, which readily separate into two alete spores (Burgess, 1991).

Genus ***Dyadospora*** (Strother and Traverse, 1979 emended. Burgess and Richardson, 1991.
Type species: *Dyadospora murusattenuata* (Strother and Traverse, 1979; Burgess and Richardson, 1991).

Dyadospora murusattenuata (Strother and Traverse, 1979; Burgess and Richardson, 1991) (Plate V, 14; Plate VI, 1, 15; Plate VII, 3).
Synonymy: See Steemans et al. (1996), Wellman and Richardson (1996), and Vecoli et al. (2011).
Occurrences: This species is present in the Ghelli Formation, Northeastern Alborz Mountain Range of Iran (MG-100 to MG-130).
Dimensions: 19 (27) 35 μm; 4 specimens were measured. The size range of the Iranian specimens is smaller than those of Libya (Abuhmida, 2013).
Previous records: Based on the literature review, *Dyadospora murusattenuata* has a long stratigraphic range (Ordovician–Devonian) and has a common worldwide distribution. So far, this species has been recorded from Upper Caradoc-Upper Ashgill, E1-1 borehole, Libya (Richardson, 1988); Llandovery: Qusaiba Mb., Qalibah Formation, Saudi Arabia (Steemans et al., 2000); Ordovician and Silurian, Bedinan Formation, Southeastern Turkey (Steemans et al., 1996); Ashgillian, Kalpintag Formation, Southern Xinjiang, China (Wang et al., 1997); Ashgillian, Kosov Formation, Hlásná Třebaň, Czech Republic (Vavrdová, 1988, 1989); Hirnantian, Oostduinkerke borehole, Brabant Massif, Belgium (Steemans, 2001); Hirnantian, Salar del Rincón Formation, Puna Region, Argentina (Rubinstein and Vaccari, 2004); Upper Ordovician (Katian–Hirnantian) strata of Anticosti Island, Québec, Canada, and Estonia (Vecoli et al., 2011); and Upper Ordovician (Katian–Hirnantian), Ghelli Formation, Khoshyeilagh area, Northeastern Iran (Mahmoudi et al., 2014).

***Dyadospora asymmetrica* n. sp.** (Plate V, 15, 16, 17).
Holotype: Plate V, 15.
Type stratum: Ghelli Formation, sample number MG-100, 32 km, southern Bojnourd, eastern flank of Kuh-e-Saluk, Northeastern Alborz Mountain Range.
Derivation of name: Derived from two unequal spore cells.
Dimensions: 16 (22) 28 μm; 15 specimens were measured.
Occurrences: This species is present (MG-100 to MG-130) throughout the Ghelli Formation, eastern Alborz Mountain Range.
Description: Loose tetrads, individual spore members circular to subcircular in outline. The walls of each spore are granulate, or echinate. The walls of the spores are uniformly thick.
Remarks: This species differs from other species of *Dyadospora* in its thick wall, and loose attachment, and two unequal cells. The surface of the dyad is smooth and sometimes has one instance of shrunken cell contents (cytoplasm) in each spore member.

***Dyadospora verrucata* n. sp.** (Plate V, 18, 19, 20, VI, 14).
Holotype: Plate V, 18.
Type stratum: Ghelli Formation, from samples numbered MG-100 to MG-130, in 32 km, southern Bojnourd, eastern flank of Kuh-e-Saluk, Northeastern Alborz Mountain Range.
Derivation of name: From the verrucate ornamentation that covers both dyad spores.
Dimensions: 20 (22) 24 μm; 15 specimens were measured.
Occurrences: This species is present (MG-100 to MG-129) throughout the Ghelli Formation, Northeastern Alborz Mountain Range.
Description: Loosely attached dyads; dyads elliptical; consists of two unequal spores. The walls of the dyads are fairly thick and are covered by verrucate ornamentation.
Remarks: This species differs from other species of *Dyadospora* in its thick wall and verrucate ornamentation.

4.1.1.7. Subgroup naked fused cryptospore dyads (pseudodyads). This group consists of dyads that are not enclosed within an envelope, and they show a recognizable line of attachment.

Genus ***Pseudodyadospora*** Johnson, 1985.
Type species: *Pseudodyadospora laevigata* Johnson, 1985.

Pseudodyadospora laevigata Johnson, 1985 (Plate VII, 6, 7, 8, 16).
Synonymy: See Steemans et al. (1996) and Vecoli et al. (2011).
Dimensions: 22 (30) 38 μm; 4 specimens were measured. The size range of the Iranian specimens is smaller than those of Turkey (Steemans et al., 1996).
Occurrences: *Pseudodyadospora laevigata* is present within the Ghelli Formation at Pelmis Gorge, Northeastern Alborz Mountain Range (MG-100 to MG-130).
Previous record: So far, *Pseudodyadospora laevigata* has been recorded from the Ashgill–early Llandovery, Kosov Formation, Hlásná Třebaň, Czech Republic (Vavrdová, 1974, 1988, 1989); Ashgill, Kalpintag Formation, Southern Xinjiang, China (Wang et al., 1997); early Llandovery (Rhuddanian), Qalibah Formation and Qusaiba Mb., Saudi Arabia (Steemans et al., 2000; Wellman et al., 2000); Ordovician and Silurian, Bedinan Formation, Southeastern Turkey (Steemans et al., 1996); Hirnantian, the Velleda Member of the Ellis Bay Formation, Anticosti Island, Quebec, Canada (Richardson and Ausich, 2007); Ludlow–Pridoli, Dadas Formation, Southeastern Turkey (Steemans et al., 1996); Ludlow–Lochkovian, Tanezzuft, Acacus, Tadrart formations, Ghadames Basin, MG-1 borehole, southern Tunisia (Spina and Vecoli, 2009); Upper Ordovician (Katian–Hirnantian) strata of Anticosti Island,

Québec, Canada, and Estonia (Vecoli et al., 2011); and Upper Ordovician and Lowermost Silurian, Qusaiba-1, Qasim region, Central Saudi Arabia (Wellman et al., 2015).

4.1.1.8. Spores physically separated from cryptospore polyads.

Genus ***Imperfectotriletes*** Steemans et al. 2000.

Imperfectotriletes vavrdovae (Richardson) Steemans et al. 2000 (Plate VI, 2, 3; Plate VII, 4, 18).

Synonymy: See *Ambitisporites vavrdovii* Richardson, 2000, pp. 93, 97, pl. 20, (Figs. 4 to 6) and *Imperfectotriletes vavrdovae* Steemans et al. 2000, p. 99, pl. 2, fig. m.

Occurrence: *Imperfectotriletes vavrdovae* is present in Ghelli Formation, Northeastern Alborz Mountain Range (MG-100 to MG-130).

Dimensions: 16 (28) 40 µm; 20 specimens were measured. The size range of the Iranian specimens is smaller than that of Libya (Abuhmida, 2013).

Previous records: Ashgillian-lower Telychian, UK (Burgess, 1991), Czech Republic (Vavrdová, 1988), Southeastern Turkey (Steemans et al.,

Plate V.

1.	*Velatitetras rugosa* (Strother and Traverse) Steemans et al., 1996
2, 3, 4, 5.	*Velatitetras rugosa* (Strother and Traverse) Steemans et al., 1996
6.	*Segestrespora membranifera* (Johnson, 1985) Burgess, 1991
7, 8.	*Segestrespora laevigata* Burgess 1991
9, 10, 11.	*Segestrespora burgessii* Steemans et al., 1996
12, 13.	*Segestrespora iranense* n. sp.
14.	*Dyadospora murusattenuata* Strother and Traverse, 1979 emend. Burgess and Richardson 1991
15, 16, 17.	*Dyadospora asymmetrica* n. sp.
18, 19, 20.	*Dyadospora verrucata* n. sp.

Plate VI. (see on page 14)

1.	*Dyadospora murusattenuata* Strother and Traverse, 1979 emend. Burgess and Richardson 1991
2, 3.	*Imperfectotriletes vavrdovae* (Richardson) Steemans et al., 2000
4, 5, 6, 7.	*Imperfectotriletes patinatus* Steemans et al., 2000
8, 9, 10, 11.	*Imperfectotriletes persianense* n. sp.
12.	*Segestrespora laevigata* Burgess 1991
13.	*Retusotriletes* sp.
14.	*Dyadospora verrucata* n. sp.
15.	*Dyadospora murusattenuata* Strother and Traverse, 1979 emend. Burgess and Richardson 1991
16, 17.	*Ambitisporites avitus* Hoffmeister sensu Steemans et al. 1996
18, 19.	*Retusotriletes* sp.
20.	*Dactylofusa cucurbita* Jardiné et al. 1974

Plate VII. (see on page 15)

1, 2.	*Cheilotetras caledonica* Wellman and Richardson, 1993.
3.	*Dyadospora murusattenuata* Strother and Traverse, 1979 emend. Burgess and Richardson, 1991.
4, 18.	*Imperfectotriletes vavrdovae* (Richardson) Steemans et al. 2000.
5, 19.	*Laevolancis divellomedium* (Chibrikova) Burgess and Richardson, 1991.
6, 7, 8, 16.	*Pseudodyadospora laevigata* Johnson, 1985.
9, 15.	*Rimosotetras problematica* Burgess, 1991.
10, 11, 17.	*Tetraplanarisporites laevigatus* Wellman et al. 2015.
12.	*Segestrespora burgessii* Steemans et al., 1996.
13.	*Rimosotetras subspherica* Strother et al. 2015.
14.	*Tetrahedraletes medinensis* Strother and Traverse emend. Wellman and Richardson, 1993.
20.	*Velatitetras rugosa* (Strother and Traverse) Steemans et al., 1996

Plate VIII. (see on page 16)

1.	*Orthosphaeridium insculptum* Loeblich, 1970.
2.	*Veryhachium lairdii* group Servais et al., 2007.
3, 10.	*Baltisphaeridium constrictum* Kjellström, 1971.
4.	*Dorsennidium hamii* (Loeblich, 1970) and Stancliffe, 1994.
5.	*Dactylofusa platynetrella* (Loeblich & Tappan) Fensome, William. Barss, Freeman & Hill, 1990.
6.	*Villosacapsula setosapellicula* (Loeblich) Loeblich & Tappan, 1976.
7.	*Veryhachium* trispinosum group Servais et al., 2007.
8.	*Dactylofusa striatogranulata* Jardiné et al. 1974.
9.	*Dactylofusa cucurbita* Jardiné et al. 1974.
11.	*Acanthodiacrodium crassus* (Loeblich and Tappan, 1978) Vecoli, 1999.
12.	*Muzivum graziniskii* Wood & Turnau, 2001.
13.	*Neoveryhachium* sp. cf. N. carminae (Cramer) Cramer, 1970.
14.	*Frankea breviscula* Burmann, 1970 (reworked).
15.	*Dactylofusa cabottii* (Cramer, 1971) Fensome, Williams, Barss, Freeman and Hill, 1999).
16, 18, 19.	*Safirotheca safira* Vavrdová, 1989.
17.	*Dactylofusa striata* (Staplin et al., 1965) Fensome, et al. 1990.
20.	*Navifusa ancepsipuncta* Loeblich, 1970.

Plate IX. (see on page 17)

1, 3, 4, 5.	*Ancyrochitina merga* Jenkins, 1970.
2.	*Euconochitina lepta* (Jenkins, 1970) Bourahrouh, 2002.
6, 7.	*Armoricochitina nigerica* (Bouché, 1965).
8.	*Acanthochitina barbata* Eisenack, 1931.
9, 10.	*Cyathochitina caputoi* Da Costa, 1971.
21, 14, 15.	*Euconochitina moussegoudaensis* Paris, in Le Hérissé et al. 2013.
12, 13.	*Armoricochitina nigerica* (Bouché, 1965).
16, 17.	*Spinachitina oulebsiri* Paris et al., 2000a,b.
18.	*Calpichitina lenticularis* (Bouché, 1965).
19.	*Angochitina communis* Jenkins, 1967.
20.	*Tanuchitina elongata* (Bouché, 1965).

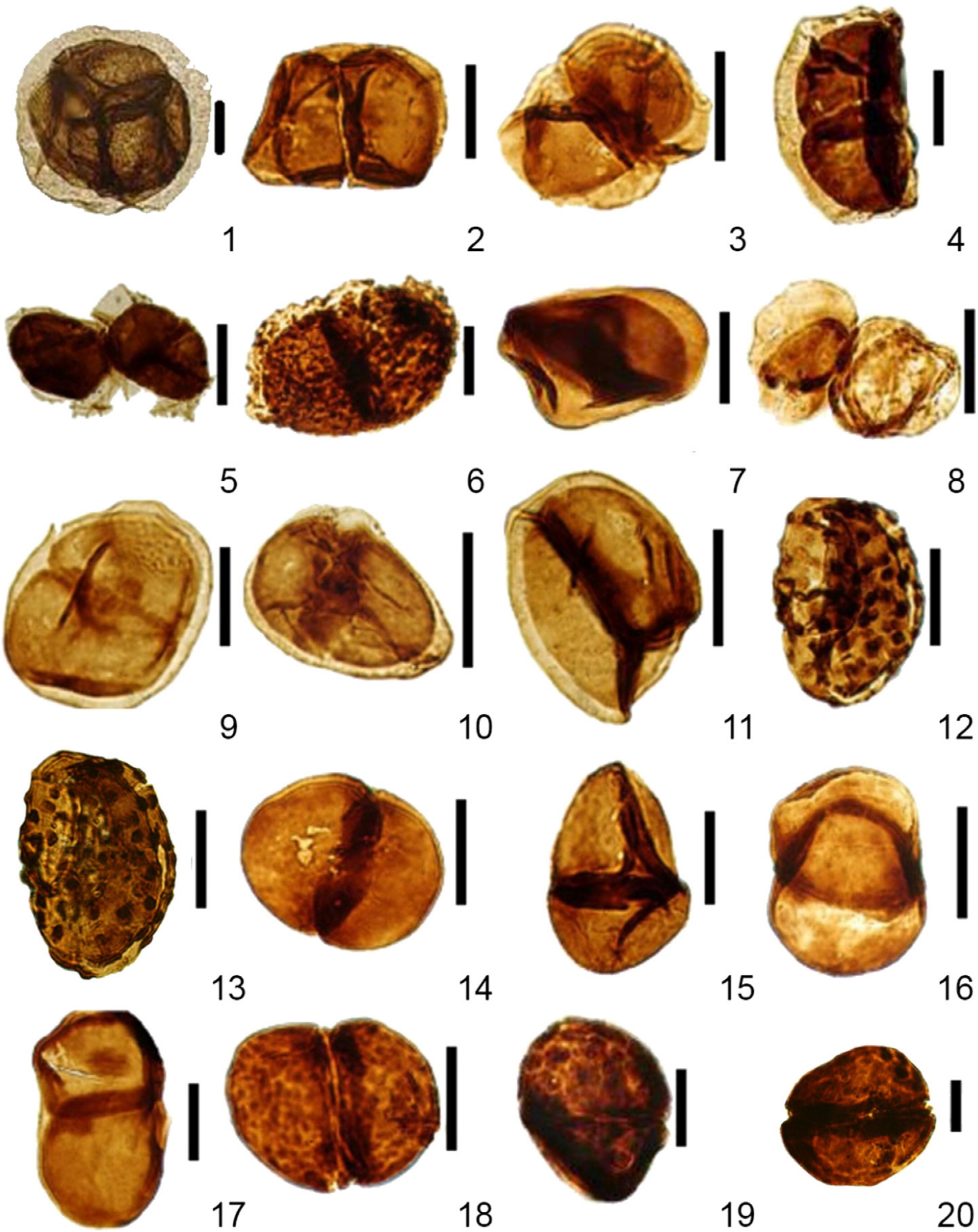

Plate V.

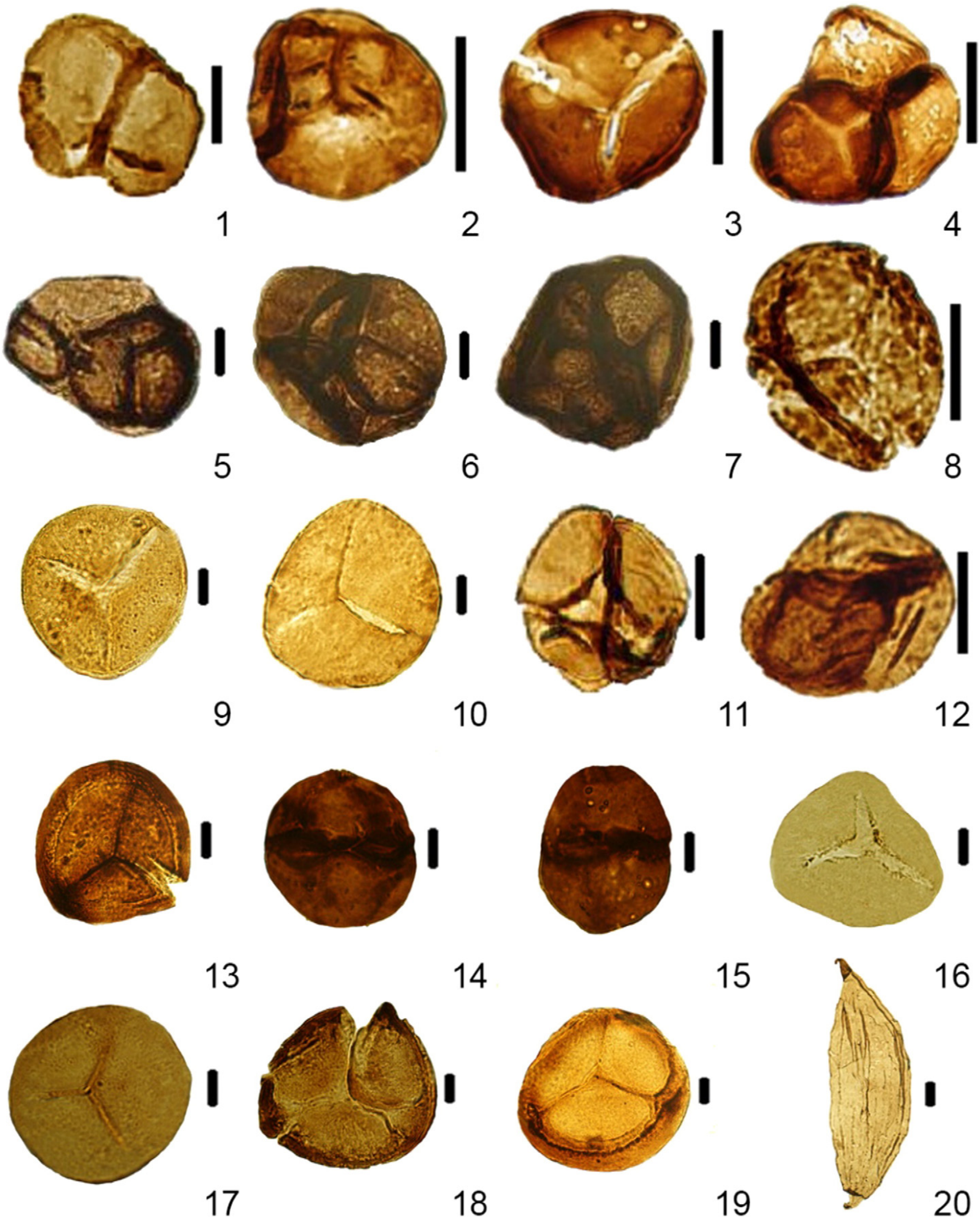

Plate VI (*caption on page 12*).

1996), Saudi Arabia (Steemans et al., 2000), Libya (Richardson, 1988), USA (Johnson, 1985), North-west Argentina (Rubinstein and Vaccari, 2004) and Upper Ordovician of Northern Chad and Southeastern Libya (Le Hérissé et al., 2013).

Imperfectotriletes patinatus Steemans et al., 2000 (Plate VI, 4, 5, 6, 7).
Type species: *Imperfectotriletes vavrdovae* (Richardson) Steemans et al., 2000.
Synonym: Steemans et al. (1996).

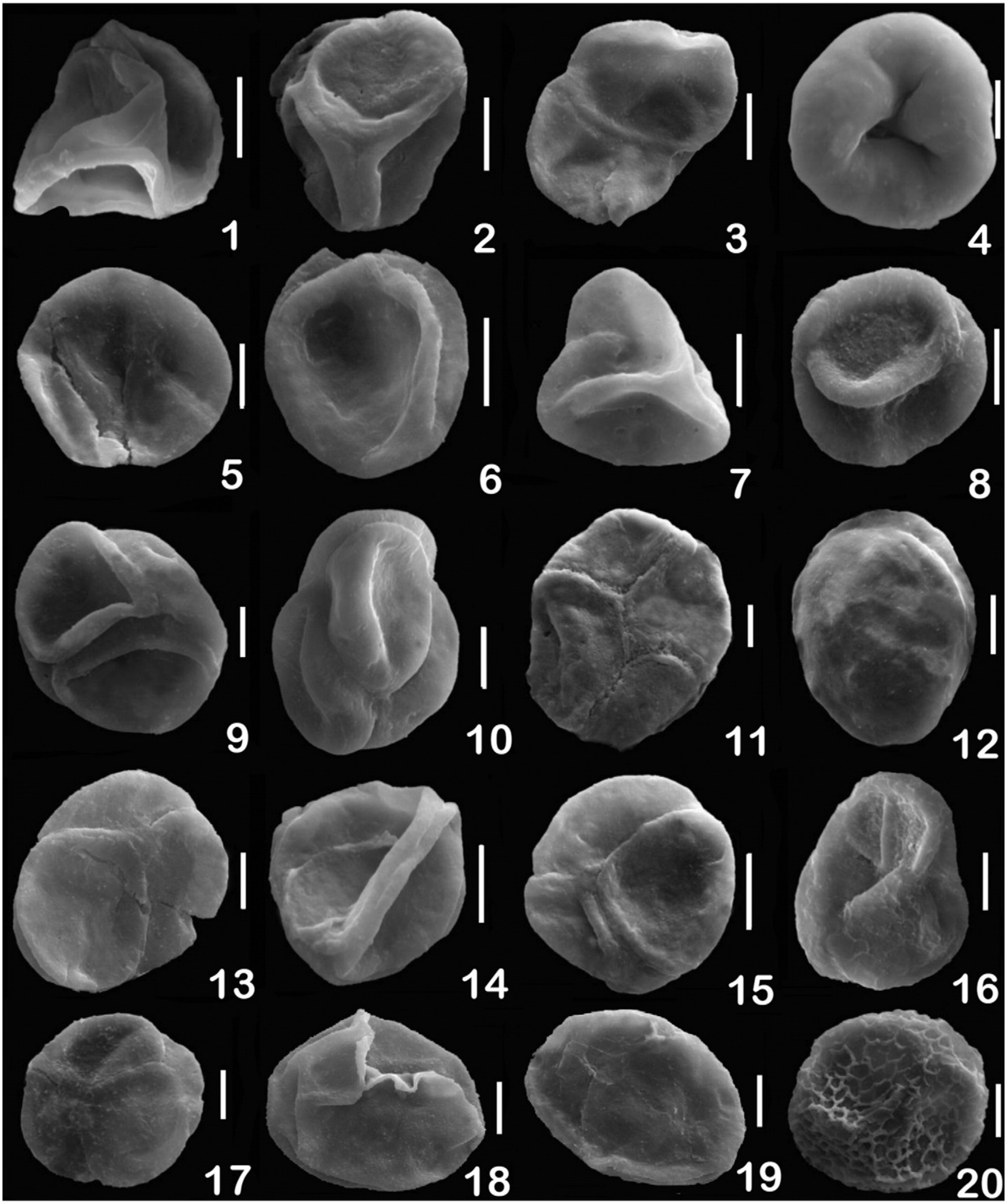

Plate VII (*caption on page 12*).

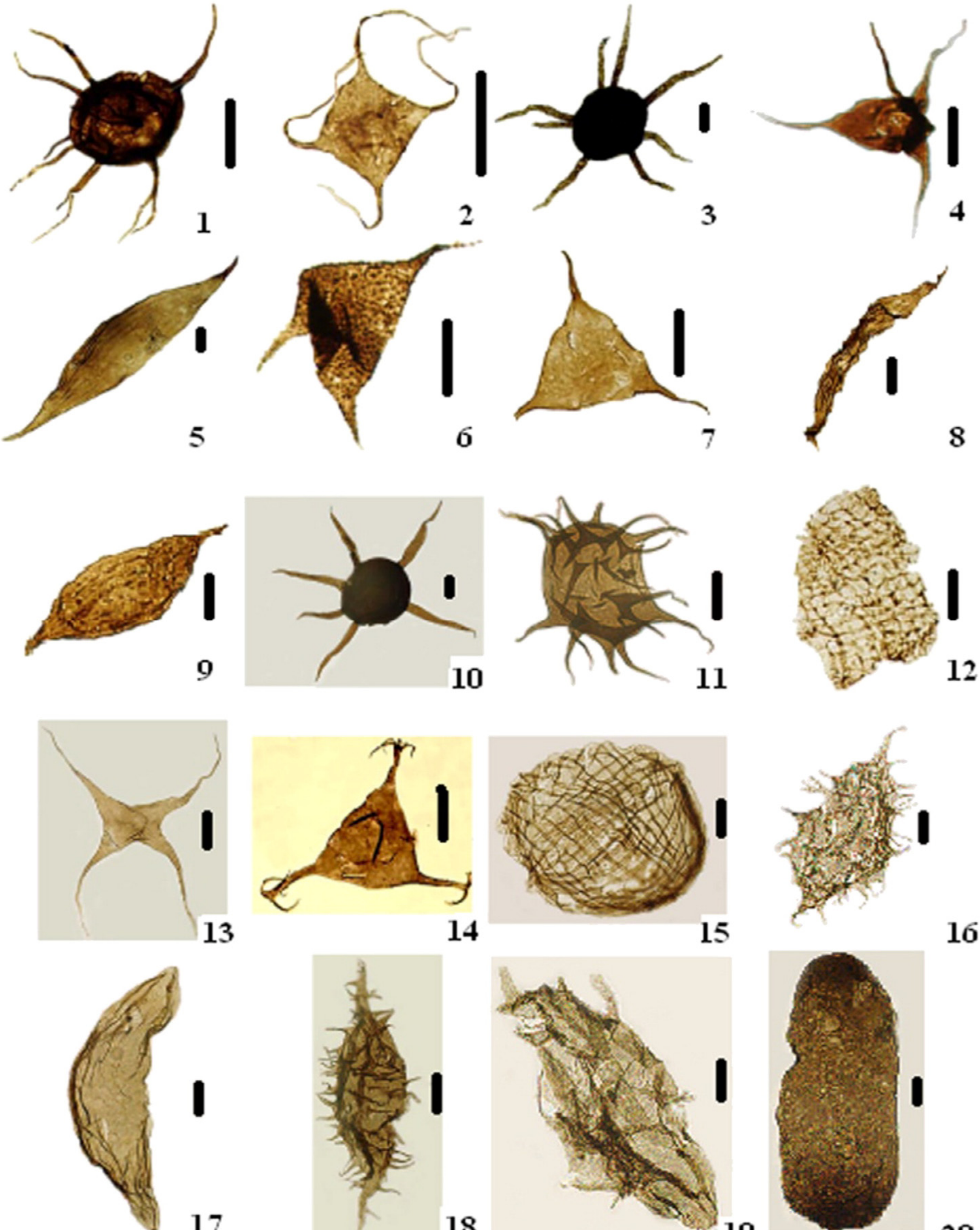

Plate VIII (*caption on page 12*).

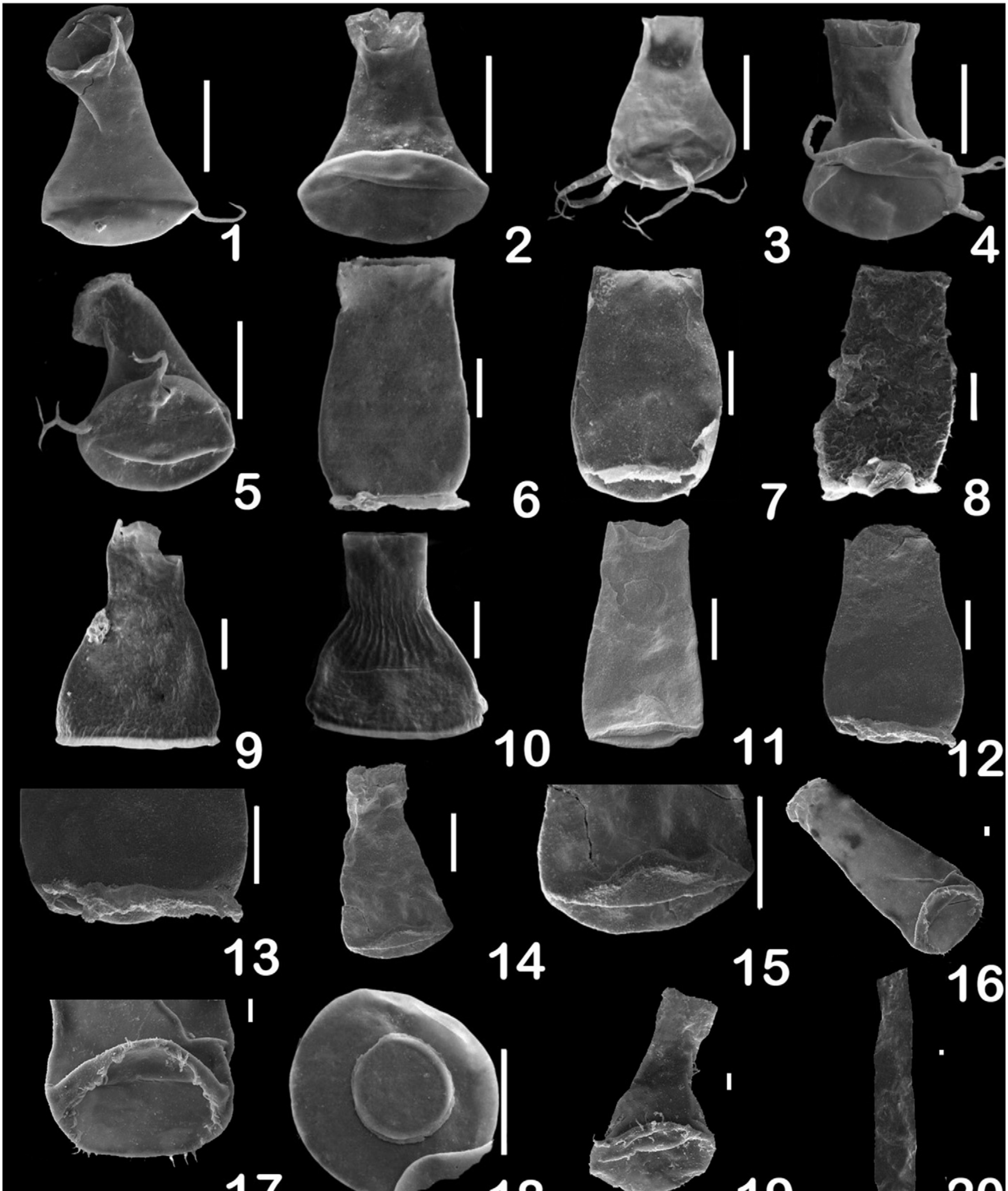

Plate IX (*caption on page 12*).

Table 2
Comparison of Late Ordovician (Katian–Hirnantian) miospore (cryptospores + trilete spores) taxa from the Ghelli Formation with other localities that contain a significant number of cryptospores in coeval geological time.

List of selected miospore species (in this study)	Saudi Arabia	Belgium	Turkey	Czech Republic	North Africa (Libya)	China	South America (Argentina)	UK	North America & Canada
Tetrahedraletes medinensis	+	+	+	+	+	+	+	+	+
Tetrahedraletes grayae	+	+	−	−	−	+	+	−	+
Tetraplanarisporites laevigatus	+	−	−	−	−	−	−	−	−
Rimosotetras problematica	+	+	+	+	−	+	−	+	−
Rimosotetras subspharica	+	−	−	−	−	−	−	+	−
Rimosotetras punctata n. sp.	−	−	−	−	−	−	−	−	−
Rimosotetras granulata n. sp.	−	−	−	−	−	−	−	−	−
Cheilotetras caledonica	+	+	−	−	−	−	−	−	−
Velatitetras laevigata	+	+	+	+	+	+	−	+	+
Velatitetras retimembrana	−	−	−	+	−	−	+	+	+
Velatitetras rugosa	+	+	+	+	+	+	+	+	+
Abditusdyadus laevigatus	+	+	+	+	−	−	−	−	+
Segestrespora membranifera	+	+	+	+	−	−	+	+	+
Segestrespora laevigata	+	+	+	+	−	+	−	+	+
Segestrespora burgessii	−	−	−	−	−	−	−	+	−
Segestrespora iranense n.sp.	−	−	−	−	−	−	−	−	+
Dyadospora murusattenuata	+	+	−	+	+	+	+	+	+
Dyadospora verrucata n. sp.	−	−		−	−	−	−	−	−
Dyadospora asymetrica n. sp.	−	−		−	−	−	−	−	−
Pseudodyadospora laevigata	+	+	+	+	+	+	+	+	+
Imperfectotriletes vavrdovae	+	−	+	+	−	+	+	+	+
Imperfectotriletes persianense n. sp.	−	−	−	−	−	−	−	−	−
Imperfectotriletes patinatus	+	−	−	−	−	−	−	−	+
Cryptotetras erugata	+	−	−	−	−	−	−	−	−
Cryptotetras mordacis	+	−	−	−	−	−	−	−	−
Laevolancis divellomedium	+	+	+	+	+	+	−	+	+
Ambitisporites avitus	+	−	+	−	−	+	−	+	+
Retusotriletes sp. A.	+	−	−	−	−	−	−	−	−

Occurrences: This cryptospore species is present in the Ghelli Formation, Northeastern Alborz Mountain Range (MG-100 to MG-130).
Dimensions: 21 (32.5) 44 μm; 3 specimens were measured. The size range of the Ghelli Formation specimens is nearly the same as that of Turkey (Steemans et al., 1996).
Previous records: Ashgillian from the Oostduinkerke borehole, Brabant Massif, Belgium; Upper Ordovician and Lowermost Silurian of Qusaiba-1, shallow core hole, Qasim region, Central Saudi Arabia (Wellman et al., 2015).

***Imperfectotriletes persianense* n. sp.** (Plate VI, 8, 9, 10, 11).
Holotype: Plate VI, 9.
Type stratum: Ghelli Formation, sample number MG-100, 32 km, southern Bojnourd, eastern flank of Kuh-e-Saluk, Northeastern Alborz Mountain Range.
Derivation of name: From the Latin word *Persia*, which refers to the ancient name of Iran.
Dimensions: 18 (19) 20 μm; 10 specimens were measured.
Occurrences: This species is present (MG-100 to MG-130) in the Ghelli Formation, Northeastern Alborz Mountain Range.
Description: Amb subtriangular to elliptical with rounded apices. Exine of spore is usually folded and irregularly covered by verrucate ornamentation. The trilete mark is distinct, with an opening on the proximal pole.
Remarks: This species is different from other species of *Imperfectotriletes* due to its verrucate ornamentation.

4.1.1.9. Subgroup Hilate cryptospores.

Genus ***Laevolancis*** Burgess and Richardson, 1991.
Type species: *Laevolancis divellomedium* (Chibrikova) Burgess and Richardson, 1991.

Laevolancis divellomedium (Chibrikova) Steemans et al., 2000.
Synonymy: See Steemans et al. (1996) and Rubinstein and Vaccari (2004).
Dimensions: 30 (35.5) 41 μm; 5 specimens were measured. The size range of the Ghelli Formation specimens is larger than that of Libya (Abuhmida, 2013).
Occurrences: *Laevolancis divellomedium* is present within the Ghelli Formation, Northeastern Alborz Range (MG-98 to MG-125).
Previous records: Caradoc in Southern Britain (Wellman, 1996); Rhuddanian in Saudi Arabia (Steemans et al., 2000; Wellman et al., 2000; Molyneux and Al-Hajri, 2000); uppermost Ordovician in southern Xinjiang, China (Wang et al., 1997); and Upper Ordovician/Silurian of northwest Argentina (Rubinstein and Vaccari, 2004).

4.1.2. Anteturma SPORITES Potonié, 1893

Turma TRILETES Reinsch, 1891.
Subturma ZONOTRILETES Waltz, 1935.
Infraturma CRASSITI Bharadwaj and Venkatachala, 1961.
Genus ***Ambitisporites*** Hoffmeister, 1959.
Type species: *Ambitisporites avitus* Hoffmeister, 1959.

Ambitisporites avitus Hoffmeister sensu Steemans et al. 1996 (Plate VI, 16, 17).
Synonymy: See Steemans et al. (1996).
Occurrences: This species is present within the Ghelli Formation, Northeastern Alborz Mountain Range of Iran (MG-90 to MG-125).
Dimensions: 14 (15) 16 μm; 5 specimens were measured. The specimens of the Ghelli Formation are smaller than that of the type species (Burgess and Richardson, 1991).
Previous records: This species is known throughout the Silurian (Richardson and McGregor, 1986) and is widely distributed all over the world. So far, it has been recorded from the Late Ordovician and Late Silurian, Bedinan and Dadas formations, Turkey (Steemans et al., 1996); and Lower Silurian (Aeronian) from the *sedgwickii* graptolite Biozone, Southwestern Wales (Burgess, 1991). However, based on Steemans et al. (1996), it could have appeared in the latest Ordovician.

Genus ***Retusotriletes*** (Naumova) Streel, 1964.
Type species: *Retusotriletes warringtonii* Richardson and Lister, 1969.

***Retusotriletes* sp.** (Plate VI, 13, 18, 19).

Description: This species occurs in the Ghelli Formation and extends from samples MG-90 to MG-125. The size range of this species is 12 to 16 μm (with distinct curvature perfectae). Amb subcircular to triangular with convex sides and rounded apices. The exine is smooth and homogenous. The trilete mark is distinct, and each spore radius merges into curvature perfectae and sometimes coincides with the equatorial outline. This species is similar to *Retusotriletes* cf. *minor*, but the latter differs from the Iranian specimens by the presence of a thinner area at the proximal pole and by its larger size.

4.1.2.1. Cryptospore biostratigraphy.

The recovery of miospores provides another opportunity for independent age assessment of the Ghelli Formation within the study area. The encountered cryptospores are critical because they have a limited stratigraphic range from the Middle Ordovician to the Lower Silurian interval elsewhere. This study's cryptospore findings are important in this formation because marine palynomorph assemblages suggest an Ashgillian (Katian–Hirnantian) age for the Ghelli Formation. The outcrop samples of the Ghelli Formation (MG-90 to MG-130) resulted in 14 genera (28 miospore species: 26 cryptospores and 2 trilete spores), consisting of *Abditusdyadus laevigatus*, *Cryptotetras erugata*, *Cryptotetras mordacis*, *Tetrahedraletes medinensis*, *Tetrahedraletes grayae*, *Cheilotetras caledonica*, *Dyadospora murusattenuata*, *Dyadospora verrucata* n. sp., *Dyadospora asymmetrica* n. sp., *Laevolancis divellomedium*, *Pseudodyadospora laevigata*, *Rimosotetras problematica*, *Rimosotetras subspherica*, *Rimosotetras punctata* n. sp., *Rimosotetras granulata* n. sp., *Segestrespora* (*Dyadospora*) *burgessii*, *Segestrespora membranifera*, *Segestrespora iranense* n. sp., *Segestrespora laevigata*, *Tetraplanarisporites laevigatus*, *Velatitetras retimembrana*, *Velatitetras* (*Nodospora*) *rugose*, *Velatitetras laevigata*, *Imperfectotriles vavrdovae*, *Imperfectotriletes patinatus*, *Imperfectotriletes persianense* n. sp., *Ambitisporites avitus*, and *Retusotriletes* sp. A. (Plates I-VII and Table 2). There are several proposals for cryptospore biozonations (Wellman, 1996; Steemans, 2000; Wellman and Gray, 2000; Wellman et al., 2013; Gray, 1985, 1988; Richardson, 1988, 1996b; Vecoli et al., 2011), but one cannot see any agreement in this respect, either because of the paucity of cryptospore data or the heterogeneity of data on assemblages of a time interval. For instance, there are a few papers that concern only the Late Ordovician (Katian–Hirnantian), and the majority of contributions are on the Ordovician/Silurian boundary. However, as illustrated in Fig. 2, three local events can be marked by miospores within the Ghelli Formation. The first event is characterized by the appearance of *Ambitisporites avitus*, *Retusotriletes* sp. A, *Cryptotetras erugata*, *Cryptotetras mordacis*, *Tetrahedraletes medinensis*, and *Tetrahedraletes grayae*, corresponding to sample MG-90 and their presence in succeeding events of the Ghelli Formation (Fig. 2). The occurrences of these miospores are correlatable with the appearance of diagnostic chitinozoan taxa, such as *Armoricochitina nigerica*, *Acanthochitina barbata*, *Calpichitina lenticularis*, *Angochitina communis*, and *Euconochitina lepta*, suggesting early to middle Katian for this event/assemblage (Fig. 2). The second event corresponds to sample MG-98 and is defined by the onset of many cryptospore taxa, such as *Tetraplanarisporites laevigatus*, *Abditusdyadus laevigatus*, *Rimosotetras subspherica*, *Rimosotetras punctata* n. sp., *Rimosotetras granulata* n. sp., *Rimosotetras problematica*, *Cheilotetras caledonica*, *Velatitetras retimembrana*, *Velatitetras* (*Nodospora*) *rugosa*, *Velatitetras laevigata*, and *Pseudodyadospora laevigata*, correlating with the first appearance of *Ancyrochitina merga*, suggesting a late Katian age for this event (Fig. 2). The third event is marked by the first appearance of cryptospore taxa, such as *Imperfectotriletes vavrdovae*, *Imperfectotriletes patinatus*, *Dyadospora murusattenuata*, *Dyadospora verrucata* n. sp., *Dyadospora asymmetrica* n. sp., *Laevolancis divellomedium*, *Segestrespora burgessii*, *Segestrespora laevigata*, *Segestrespora membranifera*, and *Segestrespora iranense* n. sp. at MG-100 of the Ghelli Formation, corresponding to the *Ancyrochina merga* Biozone and their continuation within the *Tanuchitina elongata* and *Spinachitina oulebsiri* chitinozoan biozones, representing Hirnantian age (Fig. 2). For palaeobiographic evaluations of cryptospores, the author has selected the Coefficient Similarity (CS) of Clark and Hartleberg (1983) because it was successfully used by Bergström (1990) when he evaluated the provincialism of Lower Palaeozoic conodonts. This coefficient of similarity is expressed as $CS = 2v / a + b$, where v is the number of species in common between the two compared areas, and a and b are, respectively, the total number of species recorded in each area. This CS was applied for the miospores encountered in this study and previously published assemblages of coeval age from elsewhere (e.g., Belgium, Turkey, Czech Republic, Libya, China, Argentina, the United Kingdom, Estonia, and Canada) (Table 2). By using the coefficient of similarity, the identified cryptospore species of the Ghelli Formation are 83% in common with Saudi Arabia, 67% in common with Turkey, 70% in common with Belgium, 60% in common with Argentina, 56% in common with the UK, 56% in common with Libya, 60% in common with Estonia and Canada, 44% in common with the Czech Republic, and 35% in common with China. The CS values show a marked similarity between the studied area and selected assemblages of other countries, representing primitive land plants that produced cryptospores, were cosmopolitan and tolerated a wide range of climatic conditions during the global sea-level fall linked to the Late Ordovician glaciation. Herein, the Ghelli Formation is considered to be deposited in a shallow marine environment (littoral) because the high amount of terrestrial miospores and low amount of marine palynomorphs (acritarchs and chitinozoans and marine algae) indicate that the earliest land plants that produced cryptospores grew on adjacent areas that were then inundated. The percentages are 15% in MG-90, 72% in MG-128, and 80% in MG-111 (Table 1). Such high proportions of land-derived palynomorphs indicates that primitive land plants were close to the depositional environment. It should be mentioned that the relative percentages of different palynomorphs alternate between MG-90 and MG-130 (Table 1), but generally, the terrestrial palynomorph content increases from the bottom to the top of this formation (Table 1), possibly indicating a decrease in distance from onshore. This is consistent with the presence of *Dactylofusa cabottii* as well as *Musivium gradzinskii* (Wood and Turnau, 2001) in the Ghelli Formation, which suggests shallow-water, nearshore, marine conditions.

4.2. Acritarchs

The following acritarch taxa were identified (Plate VIII):

Group Acritarcha Evitt, 1963.

Genus *Acanthodiacrodium* (Timofeev, 1958; Deflandre and Deflandre-Rigaud, 1962).

Acanthodiacrodium crassus (Loeblich and Tappan, 1978) Vecoli, 1999 (Plate VIII, 11).

Genus *Baltisphaeridium Eisenack*, 1958 ex (Eisenack, 1959) Eiserhardt, 1989.

Baltisphaeridium constrictum Kjellström, 1971 (Plate VIII, 3, 10).

Genus *Dactylofusa* (Brito and Santos, 1965) Cramer, 1971.

Dactylofusa cucurbita Jardiné et al. 1974 (Plate VIII, 9; Plate VI, 20).

Dactylofusa striata (Staplin et al. 1965) Fensome et al. 1990 (Plate VIII, 17).

Dactylofusa platynetrella (Loeblich & Tappan) Fensome et al. 1990 (Plate VIII, 5).

Dactylofusa cabottii (Cramer, 1971) Fensome et al. 1990 (Plate VIII, 15).

Dactylofusa striatogranulata Jardiné et al. 1974 (Plate VIII, 8).

Genus *Dorsennidium* (Wicander, 1974) Sarjeant and Stancliffe, 1994.

Dorsennidium hamii (Loeblich, 1970) Sarjeant and Stancliffe, 1994 (Plate VIII, 4).

Genus *Frankea* Burmann, 1970 emended. Servais, 1993.

Frankea breviuscula Burmann, 1970 (Plate VIII, 14).

Genus *Musivium* Wood and Turnau, 2001.

Musivium gradzinskii Wood and Turnau, 2001 (Plate VIII, 12).

Genus *Navifusa* (Combaz et al. 1967; Eisenack, 1976).

Navifusa ancepsipuncta (Loeblich, 1970) Eisenack et al. 1979 (Plate VIII, 20).

Genus *Neoveryhachium* Cramer, 1970.

Neoveryhachium carminae (Cramer) Cramer, 1971 (Plate VIII, 13).

Genus *Orthosphaeridium* Eisenack, 1968 emended. Kjellström, 1971.

Orthosphaeridium insculptum Loeblich, 1970 (Plate VIII, 1).

Genus *Safirotheca* Vavrdova´, 1989.

Safirotheca safira Vavrdova´, 1989 (Plate VIII, 16, 18, 19).

Genus *Veryhachium* Deunff, 1954 emended. Sarjeant and Stancliffe, 1994.

Veryhachium lairdii group (Plate VIII, 2).

Veryhachium trispinosum group (Plate VIII, 7).

Genus *Villosacapsula* Loeblich and Tappan, 1976.

Villosacapsula setosapellicula (Loeblich) Loeblich and Tappan, 1976 (Plate VIII, 6).

4.3. Acritarch biostratigraphy

In this study, a total of 13 genera (18 species) of Late Ordovician acritarch taxa were identified. These are associated with reworked Early-Middle Ordovician acritarch taxa (e.g., *Frankea breviuscula*) that probably originated from neighboring areas having a short transport distance because they evidence a good state of preservation. Among the aforementioned acritarch taxa, the Late Ordovician acritarch species *Villosacapsula setosapellicula* has been recorded from the Richmondian (Katian) of Oklahoma, Missouri, Algerian Sahara (Paris et al., 2000a), and Libya (Molyneux and Paris, 1985; Hill and Molyneux, 1988); the Katian of Canada (Jacobson and Achab, 1985); and the Upper Ordovician of Morocco and Jordan. *Orthosphaeridium insculptum* has also been recorded from the Katian Sylvan Shale of Oklahoma, USA; the Katian Maquoketa Shale, Northeastern Missouri, USA (Wicander et al., 1999); the Katian Vaureal Formation of Anticosti Island, Québec, Canada (Jacobson and Achab, 1985; Vecoli, 2008); the Upper Ordovician of the Czech Republic (Vavrdová, 1988); the Ashgill deposits of Portugal and Morocco; the Upper Ordovician (Katian – Hirnantian) Seyahou Formation of the Zagros Mountains, southern Iran (Ghavidel-Syooki, 2011a); and the Upper Ordovician (Katian–Hirnantian), Ghelli Formation, Kopeh-Dagh Region, Northeastern Alborz Mountain Range of Iran (Ghavidel-Syooki, 2001; Ghavidel-Syooki et al., 2011b). The acritarch species of *Baltisphaeridium constrictum*, *Navifusa ancepsipuncta*, *Dactylofusa striatogranulata*, *Dactylofusa platynetrella* and *Acanthodiacrodium crassus* are typical acritarch taxa that have been recorded from the Late Ordovician of the Czech Republic (Vavrdová, 1988), North America (Jacobson and Achab, 1985), Portugal and North Africa (Vecoli, 1999), Iran (Ghavidel-Syooki et al., 2011a) and Iraq (Al-Ameri and Wicander, 2008). The acritarch species of *Dactylofusa cucurbita* is recorded for the first time from the Ghelli Formation in Iran. It has previously been recorded from the Late Ordovician of the Algerian Sahara (Jardiné et al., 1974; Vecoli, 1999), Libya (Abuhmida, 2013), and the Czech Republic (Vavrdová, 1988). Likewise, the acritarch species of *Safirotheca safira* has so far been reported from the Late Ordovician of the Czech Republic (Vavrdová, 1989) and the Iranian platform (Ghavidel-Syooki et al., 2011a). Furthermore, some of the acritarch species of the Ghelli Formation, such as the *Veryhachium lairdii* group, the *Veryhachium trispinosum* group, *Dactylofusa cabottii* and *Frankea breviuscula* have been recorded from the Middle-Upper Ordovician strata of Sweden (Kjellström, 1971), England, the United States (Tappan and Loeblich, 1971), the Czech Republic (Vavrdová, 1988), North Africa (Vecoli, 1999), Saudi Arabia (Paris et al., 2000b), China (Li et al., 2006; Li, 1987) and Iran (Ghavidel-Syooki, 2000, 2001, 2003, 2006, 2008). *Dactylofusa cabottii* has widespread distribution and ranges from Caradocian (Turner, 1984) to Ludlow (Hagstrom, 1997). It should be mentioned that *Dactylofusa cabottii* is a common palynomorph in the Late Ordovician-Silurian shallow-water, nearshore, marine strata. It was considered a possible euglenoid that represented the oldest freshwater protozoan because of its occurrence in various non-marine deposits. Determining whether *Dactylofusa cabottii* is euglenoid is beyond the scope of this paper. However, because we are uncertain about the biological affinity of *D. cabottii* and based on its widespread occurrence in nearshore marine strata, it is placed in the acritarch group. *Musivium gradzinskii* (Wood and Turnau, 2001) is another common palynomorph in the Ghelli Formation. This species has been recorded from the Devonian, the Holy Cross Mountain and Radom-Lublin region of Poland, and has been assigned to the family Hydrodictyaceae of the Chlorophyta based on its coenobial habit and comparison with extant Hydrodictyaceae, which are found only in fresh to brackish water. The depositional environment of *Musivium gradzinskii* is interpreted as a very nearshore to offshore shelf (Wood and Turnau, 2001). On the other hand, based on the acritarch biostratigraphy of the *Dicellograptus complanatus* graptolite zone from the Katian Vaureal Formation of Anticosti Island, Québec Canada (Jacobson and Achab, 1985), and the Katian, Maquoketa Shale of Northeastern Missouri (Playford and Wicander, 2006; Wicander and Playford, 2008), all are acritarch species of the Ghelli Formation, indicating Late Ordovician age (Katian–Hirnantian). Finally, the reworked acritarch taxa of Upper Ordovician (Katian–Hirnantian) sediments found in the Ghelli Formation are similar to those found in Saudi Arabia, Libya, Morocco, Algeria, Turkey and the Zagros basin of Iran (Ghavidel-Syooki et al., 2011b; Al-Hajri, 1995). Herein, it should be mentioned that a few acritarch species, such as *Dactylofusa cucurbita* and *Safirotheca safira*, are restricted to peri-Gondwanan palaeoprovinces, and the remaining acritarchs are cosmopolitan.

4.4. Chitinozoans

The following chitinozoan taxa were identified (Plate IX):

Order Operculifera Eisenack, 1931.

Family Desmochitinidae (Eisenack, 1931) Paris, 1981.

Subfamily Desmochitinidae Paris, 1981.

Genus *Calpichitina* Wilson and Hedland, 1964.

Type species: *Calpichitina scabiosa* Wilson and Hedland, 1964.

Calpichitina lenticularis Bouché, 1965 (Plate IX, 18).

Subfamily Pterochitininae Paris, 1981.

Genus *Armoricochitina* Paris, 1981.

Armoricochitina nigerica Bouché, 1965 (Plate IX, 6, 7, 12, 13).

Subfamily Ancyrochitininae Paris, 1981.

Genus *Ancyrochitina* Eisenack, 1955.

Ancyrochitina merga Jenkins, 1970 (Plate IX, 1, 3, 4, 5).

Genus *Angochitina* Eisenack, 1931.

Angochitina communis Jenkins, 1967 (Plate IX, 19).

Subfamily Belonechitininae Paris, 1981.

Genus *Acanthochitina* (Eisenack, 1931) Jenkins, 1967.

Acanthochitina barbata Eisenack, 1931 (Plate IX, 8).

Order Prosomatifera Eisenack, 1972.

Subfamily Conochitininae Paris, 1981.

Genus *Euconochitina* Taugourdeau, 1966 emended. Paris et al. 1999.

Euconochitina moussegoudaensis Paris in Le Herissé et al. 2013 (Plate IX, 11, 14, 15).

Euconochitina lepta Jenkins, 1970 emended. Paris et al. 1999 (Plate IX, 2).

Subfamily Tanuchitininae Paris, 1981.

Genus *Tanuchitina* Jansonius, 1964 emended. Paris et al. 1999.

Tanuchitina elongata Bouché, 1965 (Plate IX, 20).

Order Prosomatifera Eisenack, 1972.

Subfamily Spinachitininae Paris, 1981

Genus *Spinachitina* Schallreuter, 1963 emended. Paris et al. 1999.

Spinachitina oulebsiri Paris et al. 2000 (Plate IX, 16, 17).

Subfamily Cyathochitininae Paris, 1981.

Genus *Cyathochitina* Eisenack, 1955 emended. Paris et al. 1999.

Type species: *Conochitina campanulaeformis* Eisenack, 1931.

Cyathochitina caputoi Da Costa, 1971 (Plate IX, 9, 10).

The distribution of the aforementioned chitinozoan taxa in the study section (Fig. 2) allows the identification of four well-known chitinozoan biozones which are discussed briefly herein.

4.5. Chitinozoan biostratigraphy

Although some samples of the Ghelli Formation contain a good percentage of chitinozoans among other palynomorphs (MG-90 to MG-100), the remaining samples contain a very rare percentage of this group (Table 1). In this study, nine chitinozoan genera (ten species) were recognized that are well-known both biostratigraphically and palaeogeographically. Based on the presence of these diagnostic chitinozoan taxa, the Ghelli Formation is assigned to the *Armoricochitina nigerica*, *Ancyrochitina merga*, *Tanuchitina elongata*, and *Spinachitina oulebsiri* chitinozoan biozones, suggesting Late Ordovician age (Katian–Hirnantian; Fig. 2). All chitinozoan species found in the Late Ordovician of the Pelmis Gorge area have been recorded from the North Gondwana domain, including North Africa (Morocco, Algeria, Tunisia, Libya, and Nigeria), the Middle East (Saudi Arabia, Syria, Jordan, and Iran), Southwestern Europe (Italy, France, Spain, and Portugal), and Central Europe (Czech Republic). In particular, *Armoricochitina nigerica*, *Ancyrochitina merga*, *Tanuchitina elongata*, and *Spinachitina oulebsiri* have never been recorded outside the North Gondwana domain (Paris, 1981, 1990, 1996; Webby et al., 2004; Servais et al., 2004). Accordingly, the study area belongs to the peri-Gondwanan palaeo-continent during the Late Ordovician age.

5. Discussion and conclusions

The present study is restricted to the Ghelli Formation. The investigated palynomorph assemblages come from 27 samples collected from an outcrop section at Pelmis Gorge, 32 km south of the city of Bojnourd, Northeastern Iran. All samples yielded abundant and well-preserved acritarchs, chitinozoans, and miospores. The acritarch and chitinozoan taxa are characteristic of the Late Ordovician, being associated with reworked acritarch species of the Lower and Middle Ordovician, probably derived from adjacent areas. The identified acritarch and chitinozoan taxa of the Ghelli Formation show strong affinity with Ashgillian assemblages from the peri-Gondwanan landmass, including North Africa (Morocco, Algeria, Tunisia, Libya, and Nigeria), the Middle East (Saudi Arabia, Syria, Jordan, and Iran), Southwestern Europe, (Italy, France, Spain, Portugal), Central Europe (Czech Republic) and, to some extent, China. Several acritarch and chitinozoan species are known from different palaeogeographic realms. However, only local biozonations have been established with acritarchs for the Upper Ordovician North Gondwanan domain (Jardiné et al., 1974; Hill and Molyneux, 1988; Keegan et al., 1990; Ghavidel-Syooki, 2001; Ghavidel-Syooki et al., 2011a,b; Vandenbroucke et al., 2009). In contrast, chitinozoan assemblages have been well documented from North Africa, particularly in Morocco (Oulebsir and Paris, 1995; Bourahrouh, 2002; Bourahrouh et al., 2004). A standard biozonation established for the region by Paris (1990) was used in the present work. The significant acritarch taxa of this study from the Ghelli Formation consist of *Orthosphaeridium insculptum*, *Dorsennidium hamii*, *Dactylofusa striatogranulata*, *Dactylofusa cucurbita*, *Dactylofusa platynetrella*, *Baltisphaeridium constrictum*, *Dactylofusa striata*, *Acanthodiacrodium crassus*, *Navifusa ancepsipuncta*, *Safirotheca safira*, *Villosacapsula setosapellicula*, and *Neoveryhachium carminae*. Some of these acritarch taxa are long-ranging species extending from the Ordovician through the Silurian (e.g., *Frankea breviscula*; *Neoveryhachium carminae*), but the remaining acritarch taxa are indicative of the Late Ordovician (Vecoli and Le Hérissé, 2004). A few acritarch species of the Ghelli Formation, namely, *Dactylofusa striata*, *Dactylofusa platynetrella*, *Safirotheca safira*, *Dactylofusa striatogranulata*, and *Dactylofusa cucurbita*, are diagnostic acritarch taxa for the Late Ordovician and are restricted to Ashgill (Jacobson, 1987; Molyneux et al., 1995; Jardiné et al., 1974; Vecoli and Le Hérissé, 2004). Likewise, the acritarch species of *Dactylofusa striatogranulata*, *Dactylofusa cucurbita* and *Safirotheca safira* seem to be restricted to the peri-Gondwanan landmass. Thus, these species have been described from the Upper Ordovician glacial marine deposits of the Algerian Sahara biozone F (Jardiné et al., 1974; Vecoli, 2000), Bohemia (Vavrdová, 1974), Libya (Molyneux and Paris, 1985; Vecoli et al., 2009; Abuhmida, 2013) and Iran (Ghavidel-Syooki et al., 2011b). *Neoveryhachium carminae* is well represented in the samples of the Ghelli Formation. This species is characteristic of the Silurian and has been primarily recorded from fragments formation in Normandy (Rauscher, 1973), which is now assigned to the upper Ashgillian (Paris, 1990). Furthermore, this species has been recorded from the Upper Ordovician deposits of Tunisia (Vecoli, 1999, 2004) and the Late Ordovician marine glacial deposits of the Dargaz Formation in the Zagros Mountains (Ghavidel-Syooki et al., 2011a). Of the chitinozoans of the productive samples of the Ghelli Formation (MG-90 to MG-130), the most important identified species are *Armoricochitina nigerica*, *Ancyrochitina merga*, *Tanuchitina elongata*, *Angochitina communis*, *Euconochitina moussegoudaensis*, *Euconochitina lepta*, *Calpichitina lenticularis*, and *Spinachitina oulebsiri*. Based on the presence of these diagnostic chitinozoan taxa, the siliciclastic sequence of the Rauscher biozones, suggesting Late Ordovician age (Katian–Hirnantian; Fig. 2). All chitinozoan species found in the Ghelli Formation of the Pelmis Gorge area have been recorded from the North Gondwanan domain. Therefore, the study area was part of the peri-Gondwanan palaeo-continent during the Late Ordovician. Hence, the stratigraphic position of the cryptospore assemblages of the Ghelli Formation and the level of the oldest trilete spores of *Ambitisporites avitus* can be assigned to the Ashgillian (Katian–Hirnantian).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at http://dx.doi.org/10.1016/j.revpalbo.2016.04.006. These data include the Google maps of the most important areas described in this article.

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