Contents lists available at ScienceDirect



Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

Biostratigraphy of acritarchs, chitinozoans, and miospores from Upper Ordovician sequences in Kuh-e Boghou, southwest of Kashmar, eastern central Iran: Stratigraphic and paleogeographic implications



Mohammad Ghavidel-Syooki*, Mohammad Hossein Piri-Kangarshahi

Institute of Petroleum Engineering, School of Chemical Engineering, College of Engineering, University of Tehran, P.O. Box: 11155/4563, Tehran, Iran

ARTICLE INFO

Article history: Received 7 January 2020 Received in revised form 20 September 2020 Accepted 27 October 2020 Available online 05 November 2020

Keywords: Biostratigraphy Acritarchs Chitinozoans Cryptospores Eastern-Central Iran Peri-Gondwana

$A \hspace{0.1in} B \hspace{0.1in} S \hspace{0.1in} T \hspace{0.1in} R \hspace{0.1in} A \hspace{0.1in} C \hspace{0.1in} T$

A siliciclastic succession is well exposed at Kuh-e Boghou, located in eastern-central Iran. To verify the exact age and paleogeographic position of this section of the Iranian Platform, a detailed, high-resolution palynological analysis of the Ghelli Formation was performed. Sixty-nine surface samples of the sedimentary succession were collected and analyzed. Most samples yielded abundant and well-preserved acritarchs (34 species of 24 genera), euglenids (3 species of a single genus), chitinozoans (36 species of 19 genera), and cryptospores (25 species of 10 genera). Based on the presence of well known chitinozoan species, a Late Ordovician (Katian-Hirnantian) age was assigned to this succession. The identified chitinozoan fauna allowed recognition of the Belonechitina robusta, Tanuchitina fistulosa, Armoricochitina nigerica, Ancyrochitina merga, Tanuchitina elongata, and Spinachitina oulebsiri biozones in ascending stratigraphic order as was previously established for the northern Gondwanan Domain. These results indicate that eastern-central Iran was part of the peri-Gondwana domain during the Late Ordovician. Seven morphotypes were recorded for the first time, and five of them were established as new species, namely Abditusdyadus khayyammii, Alhajrichitina spinifera, Dyadospora ferdowsii, Lophosphaeridium bulbosumensis and Moveria hafezii, and two were left in open nomenclature (e.g. Eisenackitina sp. and Moyeria sp. A). The abundant cryptospore taxa in the Late Ordovician might be related to land-derived sediments acquired during the global sea level fall in the Late Ordovician glaciation or to the adaptation of primitive land plants in a wide range of climatic conditions. The association of terrestrial miospores with marine palynomorphs suggests a nearshore marine environment.

© 2020 Elsevier B.V. All rights reserved.

1. Introduction

Iran consists of several tectonic blocks delineated by various types of faults established during the Paleozoic and Mesozoic which form several large terranes comprising Neoproterozoic–Paleozoic sequences with strong affinity to the northern margin of Gondwana (Domeier, 2018). The continental blocks of the northern margin of Gondwana is characterized by tectonism and magmatism associated with the Cadomian orogenic cycle of the Neoproterozoic–Early Cambrian (Motaghi et al., 2015). In the Early Paleozoic, these tectonic blocks were also characterized by the deposition of shallow marine platform-type successions, which were widely observed elsewhere along the Arabian margin of Gondwana, mostly during the Late Ordovician–Silurian (Heydari, 2008; Domeier, 2018). The Iranian Plate is subdivided into four principal terranes, including the Zagros, Sanandaj–Sirjan, Alborz, and central Iran terranes (Fig. 1), and it likely occupied the northeast margin of Gondwana at the beginning of the Paleozoic Era (Heydari,

* Corresponding author. *E-mail address:* mghavidel@ut.ac.ir (M. Ghavidel-Syooki). 2008; Motaghi et al., 2015; Domeier, 2018). Throughout the Neoproterozoic to the end of the Paleozoic, the Iranian Plate was part of the Arabian Plate, which, in turn, was located in the margin of the Gondwanan landmass: thus, hereafter, we refer to the Arabian margin of Gondwana. In fact, "Arabian Plate" is a tectonostratigraphic term widely used in Early Paleozoic paleogeographic reconstructions. This plate was formed in the Oligocene and since then, the rocks that comprise what is now the Arabian Peninsula, Syria, Jordan, Iraq, and Iran began separating from the African continent due to rifting along the margin of northeast Africa and the opening of the Red Sea and the Gulf of Aden (Heydari, 2008; Ghavidel-Syooki et al., 2011a). Furthermore, during the Neoproterozoic, the Iranian Plate (Zagros terrane) located near the Equator, moved southward (poleward) during the Cambrian-Ordovician and characterized the west and east Gondwana, reaching as far as ~60°S during the Silurian (Cocks and Torsvik, 2002; Heydari, 2008).

In the past decades, many geological investigations have been conducted on the Early Paleozoic rock units in both the Zagros and Alborz terranes to evaluate their relationships with the Gondwanan and Laurentia paleocontinents. Fortunately, these studies resulted in the



Fig. 1. Location of the study area (Kuh-e Boghou, eastern-central Iran) and its connections to the adjacent cities.

discovery of typical Gondwanan fauna and flora, as well as Late Ordovician glacial deposits, and have proven the relationships of the Alborz and Zagros terranes to the Gondwana landmass (Ghavidel-Syooki, 2000; Ghavidel-Syooki and Winchester-Seeto, 2002; Ghavidel-Syooki, 2003; Ghavidel-Syooki, 2006; Ghavidel-Syooki, 2008; Ghavidel-Syooki et al., 2011a, 2011b, 2014, 2015; Ghobadi Pour et al., 2015; Ghavidel-Syooki, 2016, 2017a, 2017b). Likewise, in the Early Paleozoic, the most voluminous example of magmatism is the Soltan Maidan volcanic complex from the east Alborz terrane, which is a sequence of mafic volcanic rocks interspersed with minor sedimentary horizons having a stratigraphic thickness that locally exceeds 1 km (Derakhshi et al., 2017). In addition, the Lut Block of central Iran, the Ordovician–Silurian transition is associated with transtensive extension and syn-rift volcanism, which resulted in flood basalts up to 500 m thick extending over 1000 km in areas near the Arabian margin, an integral part of Gondwana during the Ordovician (Berberian and King, 1981; Husseini, 1990; Bagheri and Stampfli, 2008; Torsvik and Cocks, 2009). In the present study, we focused on the relationships of the central Iranian terrane to Gondwana and Laurentia based on high-resolution palynological data. This terrane is considered a less deformed block surrounded by active margins, namely the Alborz-Binalud Mountains on the northern edge of central Iran and the Kopeh Dagh Mountains in the southern edge of the Eurasian Turan Plate (Motaghi et al., 2015).

2. Geological setting and previous studies

The study was conducted in Kuh-e Boghou, 46 km southwest of Kashmar, in the central Iranian terrane (Fig. 1). A paved road from Mashhad to the cities of Kashmar and Bardaskan is the main link to the study area. A thick Lower Paleozoic succession is well exposed and developed in Kuh-e Boghou. It has a thickness of 2230 m and has been assigned to the Devonian based on existing geological maps of the area (Eftekhar-nejad et al., 1976). The base of the study section is at 35° 05' 51.05" N and 58° 14' 59.03" E, 1084.7 m above sea level. This Paleozoic succession has not previously been identified in the area, and thus its detailed description is presented here to add the new paleontological data into the Iranian geological context.

Over the past few decades, several palynological investigations have been performed to determine the age relationship of the Lower Paleozoic succession of Kuh-e Boghou (Alavi, 1996; Esmaili-Suvary, 1996; Ruhizadeh, 1996; Ghavidel-Syooki, 2003; Ahmadi-Tabar, 2016; Piri-Kangarshahi, 2017). Based on the results of such investigations, this succession was divided into the Derenjal, Shirgesht, Ghelli, and Niur Formations, in ascending stratigraphic order, which are well known in the central Iranian terrane and have been allocated to the Upper Cambrian, Lower-Middle Ordovician, Upper Ordovician, and Lower-Middle Silurian, respectively (Ghavidel-Syooki, 2003). The Derenjal Formation primarily consists of cream-gray fossiliferous limestones with a few gray-black shale beds and its thickness varies because of a major fault in its basal part. The Shirgesht Formation is 700 m thick and has distinctive sedimentary facies, which mainly consist of dark gray shales, siltstones, and fine-grained sandstones. Although the Shirgesht Formation lacks marine fauna in Kuh-e Boghou, it contains trilobites and brachiopods in the type section of Shirgesht area in easterncentral Iran. In the study area, this formation contains well-preserved and abundant acritarch taxa, suggesting that it was deposited during the Early Ordovician (Tremadocian-Floian) (Ghavidel-Syooki, 2003). Further, the Ghelli Formation has a thickness of 664 m and primarily consists of olive-gray shales, micaceous siltstones, fine-grained arkosic sandstones, heterogeneous conglomerates (three horizons), cream fossiliferous limestones (two horizons), and three basaltic sills in its middle section (Fig. 2). In Kuh-e Boghou, the basal part of the Ghelli Formation begins with a few meters of highly fossiliferous, reddish-brown argillaceous limestones, which contain abundant trilobites and straight Orthoceras sp., comparable to the basal part of the Shale and Sandstone member of the Ghelli Formation in Ghelli village, where the reference section is located in the northeastern Alborz Mountains (56° 55' 51.80" E and 37° 11' 39.82" N; Ghavidel-Syooki, 2017b). Except for the basal part of the Ghelli Formation, brachiopod and trilobite fauna is rarely found throughout this formation. The macrofauna of the Ghelli Formation has not been studied in detail but has assigned to the Late Ordovician based on acritarch biostratigraphy (Ghavidel-Syooki, 2003). The thickness of the Niur Formation is approximately 1000 m in Kuhe Boghou and it is subdivided into shale, carbonate, white quartzite, and reefal members in ascending stratigraphic order. The lower contact of the Niur Formation is conformable with the Ghelli Formation, and its upper contact is disconformable with the Padeha Formation (Upper Devonian). The macrofauna of the Niur Formation has not been studied in detail, but has assigned to the Lower and Middle Silurian based on palynological data (Ghavidel-Syooki, 2003).

3. Materials and methods

Sixty-nine surface samples were collected along the entire Ghelli Formation in Kuh-e Boghou. Field and laboratory descriptions of the samples are shown in the stratigraphic column in Fig. 2. The collected samples which were designated by numbers (1–69) are preceded by prefixes referring to the collectors (MG, Mohammad Ghavidel-Syooki; MHP, Mohammad Hossein Piri). The palynomorphs were extracted from shale, siltstone, and fine-grained sandstone using the standard palynological technique of treatment in HCl and HF to remove carbonates and silicates, respectively, followed by neutralizing the residue in distilled water after each acid treatment. The samples were not oxidized and the resultant residues of each sample were treated with 30 mL saturated zinc bromide with a specific gravity of 1.95. Organic residues were then sieved through 10-20 µm nylon meshes to eliminate the finer debris and facilitate palynological analyses. The palynological residues were mounted on glass slides for optical and scanning electron microscopy examinations. All the samples were proved to be palyniferous and yielded well-preserved and abundant acritarchs, euglenids, chitinozoans, cryptospores, and scolecodonts, as well as rare graptolite remains. The palynomorph groups were counted, and their percentages were calculated accordingly (Tables 1-3). As samples MG-MHP 28 to MG-MHP 69 vielded relatively higher percentages of cryptospores than those of acritarchs and chitinozoans, we focused not only on marine palynomorph groups, but also on terrestrial cryptospores. The cryptospores and acritarchs ranged from yellow to orange-brown in color, indicating an intermediate degree of thermal maturity (Plates VI-IX). Their corresponding abundances are expressed semi-quantitatively (e.g., very rare = 1-2 identified specimens; rare =2-3 identified specimens; uncommon = 4-8 identified specimens; common = 9-20 identified specimens; abundant > 20 identified specimens). All the samples and slides related to the present study are deposited in the Iranian Natural History Museum, Department of Organization Environment under accessions MG-MHP 1 to MG-MHP 69.

4. Systematics and biostratigraphy of chitinozoans, acritarchs, and cryptospores

The 11019 palynomorph specimens have been investigated, which are mentioned in the following text: 6510 acritarch, 91 euglenid, 1918 chitinozoan, 1851 miospore, and 614 scolecodont specimens, as well as 35 graptolite remains (Tables 1-3). In total, 34 acritarch species (24 genera), three euglenid species (one genus), 36 chitinozoan species (19 genera), 27 miospore taxa (11 genera), and one scolecodont species (one genus), as well as some chitinous graptolite remains (Plates I–IX) were identified. The acritarch taxa are specified herein under the International Code of Botanical Nomenclature (Greuter et al., 1994) and are arranged alphabetically by genera under the incertae sedis "Acritarch" group. Furthermore, the identified chitinozoan taxa are well known elsewhere in the north Gondwana Domain and are listed according to the classification scheme of Paris et al. (1999). The term "miospore" refers to all fossil plant spores smaller than 200 µm (Steemans et al., 2000), including both cryptospores and trilete spores; these are listed according to the classification schemes of Richardson (1996a, 1996b) and Wellman and Richardson (1996). Detailed descriptions are provided for new taxa only, while stratigraphic and numerical distributions are presented for all taxa in Fig. 2 and Tables 1-3, respectively.

4.1. Chitinozoan systematics

Chitinozoans are an extinct group of enigmatic organic-walled microfossils widely distributed in Ordovician to Devonian marine sedimentary rocks (ca. 485–359 Myr) and are extensively used in highresolution biostratigraphy. The chitinozoan fauna of Kuh-e Boghou identified here allowed recognition of six biozones in the siliciclastic succession of the Ghelli Formation, all of which are well known in the north Gondwana Domain. These chitinozoan biozones and their biostratigraphic ages are discussed below in ascending stratigraphic order (Fig. 2). Detailed descriptions and biometric data are provided only for *Alhajrichitina spinifera* n. sp. and *Eisenackitina* sp. that were identified from the Upper Ordovician strata (Ghelli Formation) in Kuh-e Boghou (Plates I–V).



Table 1

Quantitative distributions of chitinozoan taxa throughout the Upper Ordovician (Ghelli Formation), Kuh-e Boghou, southwest of Kashmar, eastern-central Iran.

L	ist of encountered chitinozoan taxa	MG-MHP 1	MG-MHP 2	MG-MHP 3	MG-MHP 4	MG-MHP 5	MG-MHP 6	MG-MHP 7	MG-MHP 8	MG-MHP 9 MG-MHP 10	MG-MHP 11	MG-MHP 12	MG-MHP 13	MG-MHP 14	MG-MHP 16	MG-MHP 17	MG-MHP 18	MG-MHP 19	MG-MHP 20	MG-MHP 21	MG-MHP 22	MG-MHP 23	MG-MHP 24	MG-MHP 25	MG-MHP 26	MG-MHP 27	MG-MHP 28	MG-MHP 29	MG-MHP 30	MG-MHP 32	MG-MHP 33	MG-MHP 34	MG-MHP 35	MG-MHP 36 MG-MHP 37	MG-MHP 38	MG-MHP 39	MG-MHP 41	MG-MHP 42	MG-MHP 43	MG-MHP 44	MG-MHP 45 MG-MHP 46	MG-MHP 47	MG-MHP 48	MG-MHP 49	MG-MHP 51	MG-MHP 52	MG-MHP 53	MG-MHP 54	MG-MHP 55	MG-MHP 57	MG-MHP 58	MG-MHP 59	MG-MHP 60	Total
1	Belonechitina robusta	0	2	2	3	4	0	7	0	1 10) 13	2	0	0 0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0 0	0	0	0	0	0 0	0	0	0 0	0	0	0	0 0	0	0	0 0	5 0	0 0	0	0	0	5 0	0	0	0	44
2	Lagenochitina baltica	0	4	0	0	2	4	1	0	1 5	0	2	2	0 3	10	7	2	0	0	2	2	0	2	23	1	0	0	0	0 0	0	0	0	0	0 0	0	0	0 0	0	0	0	0 0	0	0	0 0	0 0) 0	0	0	0	0 0	0	0	0	73
3	Euconochitina lepta	0	1	1	0	0	0	2	5	1 0	1	1	2	0 0	24	1 3	3	5	7	24	49	26	0	41	0	14	0	0	0 0	0	0	0	0	0 0	0	0	0 0	0	0	0	0 0	0	0	0 0	0 0	1 0	0	0	0	0 0	0	0	0	210
4	Desmochitina erinacea	0	2	7	0	0	5	0	0	6 5	3	3	1	1 3	5	0	0	1	0	18	41	0	3	0	0	4	1	0	0 0	0	0	0	0	0 0	0	0	0 2	0	0	0	0 0	0	0	0 0	0 0	1 0	0	0	0	0 0	0	0	0	110
5	Calpichitina lenticularis	0	1	3	4	1	3	0	0	1 0	1	1	0	0 3	19	10	4	1	4	4	3	8	4	8	2	7	25	0	0 0	0	0	0	0	0 0	0	3	1 1	0	0	0	3 0	3	7	0 1	2 0	1 0	2	0	0	0 0	0	0	4	153
6	Desmochitina typica	0	2	0	6	3	0	3	0	1 7	6	0	0	3 (0	2	1	0	1	2	0	17	5	3	3	4	2	1	0 0	0	0	0	0	0 0	0	1	2 2	0	0	0	7 0	3	0	1 0	0 0	1 0	1	0	2	0 0	0	0	3	94
7	Rhabdochitina usitata	0	1	0	0	0	0	0	0	0 0	2	3	1	0 3	1	7	1	7	2	3	0	1	1	0	0	5	0	1	0 0	0	0	0	0	0 0	0	0	0 1	0	0	0	0 0	0	0	0 0	0 0	1 0	0	0	0	0 0	0	0	0	39
8	Cyathochitina kuckersiana	0	2	0	0	1	11	4	0	0 0	4	4	1	0 0	0	1	0	0	1	1	0	0	1	0	2	5	0	0	2 0	0	0	0	0	0 0	0	0	0 1	0	0	0	0 0	0	0	0 0	0 0	1 0	0	0	0	0 0	0	0	0	41
9	Cyathochitina campanulaeformis	0	1	1	0	0	1	1	2	0 0	5	3	5	0 1	0	2	2	0	0	0	3	0	1	1	0	3	1	0	0 0	0	0	0	0	0 0	0	0	0 1	0	0	0	0 0	0	0	0 0	0 0	0	0	0	0	0 0	0	0	0	34
10	Angochitina communis	0	1	0	0	1	0	1	0	0 0	1	4	1	0 0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0 0	0	0	0	0	0 0	0	0	0 0	0	0	0	0 0	0	0	0 0	0 0	0	0	0	0	0 0	0	0	0	9
11	1 Tanuchitina fistulosa	0	0	0	0	0	0	0	0	0 0	0	2	25	3 (0	0	0	0	0	0	0	0	0	0	0	0	0	0	0 0	0	0	0	0	0 0	0	0	0 0	0	0	0	0 0	0	0	0 0	0 0	1 0	0	0	0	0 0	0	0	0	30
12	2 Lagenochitina prussica	0	0	0	0	0	0	0	0	0 0	0	4	1	0 0	1	1	0	0	1	1	0	0	0	0	2	0	0	0	0 0	0	0	0	0	0 0	0	0	0 0	0	0	0	0 0	0	0	0 0	0 0	1 0	0	0	0	0 0	0	0	0	11
13	3 Pistillachitina pistillifrons	0	0	0	0	0	0	0	0	0 0	0	1	1	0 0	2	1	0	0	2	1	0	0	1	3	1	0	0	0	0 0	0	0	0	0	0 0	0	0	0 0	0	0	0	0 0	0	0	0 0	0 0	1 0	0	0	0	0 0	0	0	0	13
14	4 Desmochitina minor	0	0	0	0	0	0	0	0	0 0	0	2	2	9 3	8	7	5	5	11	16	1	8	1	10	3	6	2	2	0 3	1 0	0	0	0	0 0	0	1	0 3	0	0	0	2 3	0	0	0 0	0 0	1 0	1	6	2	0 0	0	0	1	123
15	5 Hyalochitina jajarmensis	0	0	0	0	0	0	0	0	0 0	0	5	0	1 (0	1	1	0	1	1	0	1	0	1	1	1	0	0	0 0	0	0	0	0	0 0	0	0	0 0	0	0	0	0 0	0	0	0 0	0 0	0	0	0	0	0 0	0	0	0	14
16	5 Armoricochitina nigerica	0	0	0	0	0	0	0	0	0 0	0	0	0	5 3	7	4	13	9	15	7	0	0	0	0	0	0	0	0	0 0	0	0	0	0	0 0	0	0	0 0	0	0	0	0 0	0	0	0 0	0 0	0	0	0	0	0 0	0	0	0	62
17	Fungochitina spinifera	0	0	0	0	0	0	0	0	0 0	0	0	0	1 1	0	1	2	0	1	1	0	0	1	0	1	4	1	1	0 0	0	0	1	0	0 0	0	3	1 2	0	0	0	3 0	0	0	0 0	0 0	1 0	0	0	0	0 0	0	0	0	25
18	8 Fungochitina actonica	0	0	0	0	0	0	0	0	0 0	0	0	0	1 (1	1	1	0	1	1	0	1	1	0	1	4	1	1	0 0	1	0	0	0	0 1	1	0	0 1	0	0	0	1 0	0	0	0 0	0 0	1 0	0	0	0	0 0	0	0	0	20
19	Belonechitina micracantha	0	0	0	0	0	0	0	0	0 0	0	0	0	4 2	14	10	34	11	15	18	15	4	5	145	2	33	2	0	0 3	0	0	0	4	0 0	0	0	0 3	0	0	0	0 0	0	0	0 0	0 0	1 0	0	0	0	0 0	0	0	0	324
20	Armoricochitina alborzensis	0	0	0	0	0	0	0	0	0 0	0	0	0	1 1	0	0	1	0	0	3	0	0	0	0	1	5	1	0	0 0	0	0	0	1	0 0	0	0	0 1	0	0	0	0 0	0	0	0 6	0 0	1 0	0	0	0	0 0	0	0	0	5
21	1 Desmochitina ovulum	0	0	0	0	0	0	0	0	0 0	0	0	0	1 0	1	1	0	0	1	2	8	0	0	0	1	3	1	0	1 0	0	0	0	0	0 0	1	0	0 1	0	0	0	0 0	0	0	0 0	0 0	, 0	0	0	0	0 C	0	0	0	22
22	2 Ancyrochitina merga	0	0	0	0	0	0	0	0	0 0	0	0	0	0 0	0	0	0	0	0	14	47	47	4	42	0	1	0	0	0 0	0	0	0	0	0 0	0	0	0 0	0	0	0	0 0	0	0	0 0	0 0) 0	0	0	0	0 0	0	0	0	155
23	3 Tanuchitina ontariensis	0	0	0	0	0	0	0	0	0 0	0	0	0	0 0	0	0	0	0	0	11	2	1	0	17	1	5	3	2	4 0	2	0	0	0	0 0	3	0	0 5	0	0	0	0 0	0	0	0 0	0 0) 0	0	0	0	0 0	0	0	0	56
24	4 Plectochitina sylvanica	0	0	0	0	0	0	0	0	0 0	0	0	0	0 0	0	0	0	0	0	1	0	2	0	0	1	4	2	0	0 0	0	0	0	0	0 0	0	0	0 0	0	0	0	0 0	0	0	0 0	0 0	1 0	0	0	0	0 0	0	0	0	10
25	5 Ancyrochitina ellisbayensis	0	0	0	0	0	0	0	0	0 0	0	0	0	0 0	0	0	0	0	0	1	1	0	1	0	0	1	0	0	0 0	0	0	0	0	0 0	0	0	0 0	0	0	0	0 0	0	0	0 0	0 0	1 0	0	0	0	0 0	0	0	0	4
26	5 Tanuchitina elongata	0	0	0	0	0	0	0	0	0 0	0	0	0	0 0	0	0	0	0	0	0	0	0	0	0	0	4	1	1	0 1	0	1	0	0	0 0	1	1	0 1	0	0	0	0 0	0	0	0 6	0 0	1 0	0	0	0	0 0	0	0	0	11
27	Eisenackitina sp.	0	0	0	0	0	0	0	0	0 0	0	0	0	0 0	0	0	0	0	0	0	0	0	0	0	0	2	0	1	0 0	0	0	0	0	0 0	0	0	1 0	0	0	0	0 0	0	0	0 0	0 0	1 0	0	0	0	0 0	0	0	0	4
28	Alhajrichitina adamantea	0	0	0	0	0	0	0	0	0 0	0	0	0	0 0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0 1	0	1	0	0	0 0	0	1	0 2	0	0	0	0 0	0	0	0 6	0 0	0	0	0	0	0 0	0	0	0	9
29	Alhajrichitina spinifera n. sp.	0	0	0	0	0	0	0	0	0 0	0	0	0	0 0	0	0	0	0	0	0	0	0	0	0	0	2	2	2	2 2	2	2	0	4	1 0	0	0	2 2	0	0	0	0 0	0	0	0 0	0 0) 0	0	0	0	0 0	0	0	0	23
30	Euconochitina moussegoudaensis	0	0	0	0	0	0	0	0	0 0	0	0	0	0 0	0	0	0	0	0	0	0	0	0	0	0	5	16	1	1 0	0	8	7	7 1	12 14	7	5 1	15 2	0	0	0	1 0	1	1	0 1	1 1	0	0	2	1 1	0 0	0	0	0	108
31	1 Rhabdochitina curvata	0	0	0	0	0	0	0	0	0 0	0	0	0	0 0	0	0	0	0	0	0	0	0	0	0	0	6	2	0	0 0	0	0	0	0	0 0	0	0	0 0	0	0	0	0 0	0	0	0 P	0 0	, 0	0	0	0	0 0	0	0	0	8
32	2 Spinachitina bulmani	0	0	0	0	0	0	0	0	0 0	0	0	0	0 0	0	0	0	0	0	0	0	0	0	0	0	7	5	0	0 0	0	0	0	0	0 0	0	0	0 0	0	0	0	0 0	0	0	0 0	0 0) 0	0	0	0	0 C	0	0	0	12
33	3 Spinachitina oulebsiri	0	0	0	0	0	0	0	0	0 0	0	0	0	0 0	0	0	0	0	0	0	0	0	0	0	0	0	3	2	0 0	1	0	2	0	0 0	0	0	0 0	0	0	0	62	0	0	1 2	2 0) 0	0	1	0	0 C	0	0	1	21
34	4 Conochitina rotundata	0	0	0	0	0	0	0	0	0 0	0	0	0	0 0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1 0	1	0	0	2	0 0	1	1	1 1	0	0	0	1 2	1	0	0 0	0 0	1 0	0	1	0	1 0	0	0	1	18
35	5 Pistillachitina comma	0	0	0	0	0	0	0	0	0 0	0	0	0	0 0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0 1	0	1	1	0	0 0	2	0	0 1	0	0	0	0 0	0	1	0 1	1 0	1 0	0	1	0	0 0	0	0	2	12
36	5 Cyathochitina caputoi	0	0	0	0	0	0	0	0	0 0	0	0	0	0 0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1 0	0	0	0	0	0 2	1	0	0 0	0	0	0	1 0	1	0	0 6	0 0	, 0	0	0	1	0 0	0	0	1	11
	Total	0	17	14	13	12	24	19	7 1	11 27	7 36	37	42	30 2	0 93	59	70	39	63	132	172	116	31	294	23	139	76	17 1	12 1	1 7	13	11	18 1	13 17	17	16 2	23 33	1 0	0	0 2	25 7	9	9	2 1	6 1	0	4	11	6	1 0	0	0	13	1918

Table 2

Distribution frequencies of miospore taxa throughout the Upper Ordovician (Ghelli Formation), Kuh-e Boghou, southwest of Kashmar, eastern-central Iran.

	List of encountered miospore taxa	MG-MHP 1	MC-MHP 9	MG-MHP 3	MG-MHP 4	MG-MHP 5	MG-MHP 6	MG-MHP 7	MG-MHP 8	MG-MHP 9	MC MHD 11	MG-MHP 19	MG-MHP 13	MG-MHP 14	MG-MHP 15	MG-MHP 16	MG-MHP 17	MG-MHP 18	MG-MHP 20	MG-MHP 21	MG-MHP 22	MG-MHP 23	MG-MHP 24	MG-MHP 25	MG-MHP 26	MG-MHP 98	MG-MHP 29	MG-MHP 30	MG-MHP 31	MG-MHP 32	MG-MHP 33	MG-MHP 34	MG-MHP 35 MG-MHP 36	MG-MHP 37	MG-MHP 38	MG-MHP 39	MG-MHP 40	MG-MHP 41	MG-MHP 42 MC-MHP 43	MG-MHP 44	MG-MHP 45	MG-MHP 46	MG-MHP 47 MC MHP 48	MG-MHP 49	MG-MHP 50	MG-MHP 51	MG-MHP 52	MG-MHP 53	MG-MHP 54	MG-MHP 55	MG-MHP 56	MG-MHP 57	MG-MHP 58	MG-MHP 59	MG-MHP 60 Total	I VIAI
1	Tetrahedraletes medinensis	0	0	0	0	0	0	0	0	0 0) 1	4	1	1	1	1	0	1 0	0	2	7	3	3	3	1 4	1 3	1	0	0	0	0	10	0 0	7	5	11	10	6	0 0	0	15	3	0 3	16	27	3	30	17	46	20	50	5	1	1	5 32	28
2	Velatitetras rugosa	0	0	0	0	0	0	0	0	0) (0	0	2	0	0	1	0 0	0	1	0	0	1	0	1 4	I 1	0	0	0	0	0	0	1 0	1	1	0	0	1	0 0	0	15	0	0 0	8	2	0	0	2	5	0	0	0	0	0	2 48	9
3	Retusotriletes sp. (as cluster)	0	0	0	0	0	0	0	0	0) (0	0	2	1	1	1	1 0	1	1	1	2	7	1	1 4	I 1	3	2	6	0	5	21	2 2	12	2 8	11	25	13	0 0	0	25	0	1 0	15	0	0	0	4	0	10	0	0	0	0	1 19	и
4	Dyadospora asymmetrica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0 0	0	0	0	0	0	0	0 0	6	1	0	1	0	2	5	0 0	4	1	0	0	1	0 0	0	20	2	1 0	5	13	0	12	5	6	9	7	0	0	0	1 10	12
5	Rimosotetras subspherica	0	0	0	0	0	0	0	0	0 1) (0	0	0	0	0	0	0 0	0	0	0	0	0	0	0 0) 15	54	5	1	0	0	17	1 8	25	5 10	21	15	5	0 0	0	35	12	10 5	15	8	13	0	8	1	1	10	0	0	0	0 24	15
6	Tetrahedraletes grayae	0	0	0	0	0	0	0	0	0 1) (0	0	0	0	0	0	0 0	0	0	0	0	0	0	0 0) 6	1	4	0	0	0	1	2 0	1	0	4	0	1	0 0	0	16	0	2 3	8	9	0	0	14	26	18	30	0	0	0	0 14	6
7	Segestrespora burgessii	0	0	0	0	0	0	0	0	0 1) (0	0	0	0	0	0	0 0	0	0	0	0	0	0	0 0) 0	0	0	0	0	0	3	0 0	0	1	1	0	0	0 0	0	6	1	0 0	5	1	0	3	1	0	0	0	0	0	0	0 27	2
8	Imperfectotriletes patinatus	0	0	0	0	0	0	0	0	0 1) (0	0	0	0	0	0	0 0	0	0	0	0	0	0	0 0) 0	0	0	0	0	0	1	0 0	0	0	0	2	0	0 0	0	1	0	0 0	1	0	0	0	0	1	0	0	0	0	0	1 7	ŗ
9	Rimosotetras punctata	0	0	0	0	0	0	0	0	0 1) (0	0	0	0	0	0	0 0	0	0	0	0	0	0	0 0) 0	0	0	0	0	0	1	0 0	1	0	0	0	0	0 0	0	10	0	0 0	0	2	0	0	0	15	1	10	0	0	0	1 41	1
10	Imperfectotriletes vavrdovae	0	0	0	0	0	0	0	0	0 1) (0	0	0	0	0	0	0 0	0	0	0	0	0	0	0 0) 0	0	0	0	0	0	2	0 0	1	0	2	0	1	0 0	0	1	0	2 1	0	0	0	0	0	0	1	0	0	0	0	0 11	1
11	Segestrespora iranense	0	0	0	0	0	0	0	0	0) (0	0	0	0	0	0	0 0	0	0	0	0	0	0	0 0	0	0	0	0	0	0	1	0 0	0	1	0	0	1	0 0	0	0	1	0 0	1	0	0	0	0	2	0	0	0	0	0	0 7	ł.
12	Imperfectotriletes persianense	0	0	0	0	0	0	0	0	0) (0	0	0	0	0	0	0 0	0	0	0	0	0	0	0 0) 0	0	0	0	0	0	1	0 0	0	0	0	0	1	0 0	0	0	0	0 0	3	6	0	0	1	5	1	0	0	0	0	1 19	9
13	Segestrespora laevigata	0	0	0	0	0	0	0	0	0) (0	0	0	0	0	0	0 0	0	0	0	0	0	0	0 0) 0	0	0	0	0	0	1	0 0	2	. 0	0	5	0	0 0	0	23	0	0 0	0	0	0	0	0	1	1	6	0	0	0	0 35	9
14	Velatitetras retimembrana	0	0	0	0	0	0	0	0	0) (0	0	0	0	0	0	0 0	0	0	0	0	0	0	0 0) 0	0	0	0	0	0	2	0 0	0	1	0	0	0	0 0	0	30	0	0 1	82	40	0	31	20	33	40	27	1	0	0	3 31	1
15	Dyadospora murusattenuata	0	0	0	0	0	0	0	0	0) (0	0	0	0	0	0	0 0	0	0	0	0	0	0	0 0) 0	0	0	0	0	0	0	0 0	0	0	0	0	1	0 0	0	15	1	0 0	15	15	0	3	7	10	3	11	1	0	0	1 83	3
16	Abditusdyadus laevigatus	0	0	0	0	0	0	0	0	0) (0	0	0	0	0	0	0 0	0	0	0	0	0	0	0 0	0	0	0	0	0	0	0	0 0	0	0	0	0	0	0 0	0	30	0	0 1	11	15	6	15	2	3	7	10	1	2	0	2 10)5
17	Cheilotetras caledonica	0	0	0	0	0	0	0	0	0) (0	0	0	0	0	0	0 0	0	0	0	0	0	0	0 0	0	0	0	0	0	0	0	0 0	0	0	0	0	0	0 0	0	10	0	0 1	0	0	5	0	0	0	2	1	0	0	0	2 21	1
18	Segestrespora membranifera	0	0	0	0	0	0	0	0	0) (0	0	0	0	0	0	0 0	0	0	0	0	0	0	0 0	0	0	0	0	0	0	0	0 0	0	0	0	0	0	0 0	0	10	0	3 (0	0	0	1	2	0	1	0	0	0	0	1 18	8
19	Rimosotetras problematica	0	0	0	0	0	0	0	0	0) (0	0	0	0	0	0	0 0	0	0	0	0	0	0	0 0	0	0	0	0	0	0	0	0 0	0	0	0	0	0	0 0	0	1	4	0 1	0	0	1	2	0	0	0	0	1	0	0	0 10	0
20	Abditusdyadus khayyammii n. sp.	0	0	0	0	0	0	0	0	0) (0	0	0	0	0	0	0 0	0	0	0	0	0	0	0 0	0	0	0	0	0	0	0	0 0	0	0	0	0	0	0 0	0	2	2	1 2	3	4	2	2	2	2	3	0	2	0	0	0 27	7
21	Rimosotetras granulata	0	0	0	0	0	0	0	0	0) (0	0	0	0	0	0	0 0	0	0	0	0	0	0	0 0	0	0	0	0	0	0	0	0 0	0	0	0	0	0	0 0	0	1	0	0 0	5	0	0	0	0	0	0	1	0	0	0	9 16	6
22	Dyadospora verrucata	0	0	0	0	0	0	0	0	0) (0	0	0	0	0	0	0 0	0	0	0	0	0	0	0 0	0	0	0	0	0	0	0	0 0	0	0	0	0	0	0 0	0	2	0	1 (0	0	0	1	3	0	0	15	1	1	0	2 26	6
23	Dyadospora ferdowsii n. sp.	0	0	0	0	0	0	0	0	0) (0	0	0	0	0	0	0 0	0	0	0	0	0	0	0 0	0	0	0	0	0	0	0	0 0	0	0	0	0	0	0 0	0	7	0	0 0	2	8	0	0	0	4	0	0	3	0	0	0 24	4
24	Tetraplanarisporites laevigatus	0	0	0	0	0	0	0	0	0) (0	0	0	0	0	0	0 0	0	0	0	0	0	0	0 0	0	0	0	0	0	0	0	0 0	0	0	0	0	0	0 0	0	1	0	0 0	1	1	0	0	1	0	0	0	1	0	0	0 5	;
25	Cryptotetras erugata	0	0	0	0	0	0	0	0	0 1) (0	0	0	0	0	0	0 0	0	0	0	0	0	0	0 0) 0	0	0	0	0	0	0	0 0	0	0	0	0	0	0 0	0	2	0	0 0	1	0	0	0	0	0	1	0	0	0	0	1 5	;
26	Cryptotetras mordacis	0	0	0	0	0	0	0	0	0 () (0	0	0	0	0	0	0 0	0	0	0	0	0	0	0 0) 0	0	0	0	0	0	0	0 0	0	0	0	0	0	0 0	0	1	0	0 0	1	2	0	0	1	0	0	0	1	0	0	1 7	r
	Total	0	0	0	0	0	0	0	0	0 1	1	4	1	5	2	2	2	2 0	1	4	8	5	11	4	3 1:	2 32	2 10	11	8	0	7	66	6 10	54	4 28	50	57	31	0 0	0	277	26	21 1	3 19(6 14	9 30	100	89	160	117	178	14	4	1	34 185	51

Fig. 2. Stratigraphic distributions of selected chitinozoan, acritarch, and cryptospore taxa from the Upper Ordovician (Ghelli Formation) of Kuh-e Boghou, southwest of Kashmar, easterncentral Iran. 1, Villosacapsula setosapellicula; 2, Acanthodiacrodium crassus; 3, Multiplicisphaeridium irregulare; 4, Veryhachium lairdii; 5, Veryhachium trispinosum; 6, Ordovicidium elegantulum; 7, Diexallophasis denticulata; 8, Leiofusa litotes; 9, Orthosphaeridium rectangulare; 10, Orthosphaeridium insculptum; 11, Dorsennidium hamii; 12, Baltisphaeridium trophirhapium; 13, Navifusa ancepsipuncta; 14, Dactylofusa platynetrella; 15, Lophosphaeridium acinatum; 16, Moyeria cabottii; 17, Neoveryhachium carminae; 18, Baltisphaeridium perclarum; 19, Dactylofusa cucurbita; 20, Dactylofusa striatifera; 21, Inflatarium trilobatum; 22, Tylotopalla caelamenicutis; 23, Tunisphaeridium eisenackii; 24, Safirotheca safira; 25, Estiastra iranicum; 26, Disparifusa perryi; 27, Moyeria hafezii n. sp.; 28, Moyeria sp. A; 29, Lophosphaeridium bulbosumensis n. sp.; 30, Excultibrachium concinnum; 31, Comasphaeridium lanugiferum; 32, Frankea breviuscula; 33, Cornuferifusa bifidipertica; 34, Baltisphaeridium sp.; 35, Belonechitina robusta; 36, Lagenochitina baltica; 37, Euconochitina lepta; 38, Desmochitina erinacea; 39, Calpichitina lenticularis; 40, Desmochitina typica; 41, Rhabdochitina usitata; 42, Cyathochitina kuckersiana; 43, Cyathochitina campanulaeformis; 44, Angochitina communis; 45, Tanuchitina fistulosa; 46, Lagenochitina prussica; 47, Pistillachitina pistillifrons; 48, Desmochitina minor; 49, Hyalochitina jajarmensis; 50, Armoricochitina nigerica; 51, Fungochitina spinifera; 52, Fungochitina actonica; 53, Belonechitina micracantha; 54, Armoricochitina alborzensis; 55, Desmochitina ovulum; 56, Ancyrochitina merga; 57, Tanuchitina ontariensis; 58, Plectochitina sylvanica; 59, Ancyrochitina ellisbayensis; 60, Tanuchitina elongata; 61, Eisenackitina sp.; 62, Alhajrichitina adamantea; 63, Alhajrichitina spinifera n. sp.; 64, Euconochitina moussegoudaensis; 65, Rhabdochitina curvata; 66, Spinachitina bulmani; 67, Spinachitina oulebsiri; 68, Conochitina rotundata; 69, Pistillachitina comma; 70, Cyathochitina caputoi; 71, Tetrahedraletes medinensis; 72, Velatitetras rugosa; 73, Retusotriletes sp. (as cluster); 74, Dyadospora asymmetrica; 75, Rimosotetras subspherica; 76, Tetrahedraletes grayae; 77, Segestrespora burgessii; 78, Imperfectotriletes patinatus; 79, Rimosotetras punctata; 80, Imperfectotriletes vavrdovae; 81, Segestrespora iranense; 82, Imperfectotriletes persianense; 83, Segestrespora laevigata; 84, Velatitetras retimembrana; 85, Dyadospora murusattenuata; 86, Abditusdyadus laevigatus; 87, Cheilotetras caledonica; 88, Segestrespora membranifera; 89, Rimosotetras problematica; 90, Abditusdyadus khayyammii n. sp.; 91, Rimosotetras granulata; 92, Dyadospora verrucata; 93, Dyadospora ferdowsii n. sp.; 94, Tetraplanarisporites laevigatus; 95, Cryptotetras erugata; 96, Cryptotetras mordacis.

Table 3

Quantitative distributions of acritarch and eugleind taxa throughout the Upper Ordovician (Ghelli Formation), Kuh-e Boghou, southwest of Kashmar, eastern-central Iran (*, euglenid taxa).

List of encountered acritarch taxa	MG-MHP 1	MG-MHP 2 MC MHP 2	MG-MHP 4	MG-MHP 5	9 dHM-DM	MG-MHP &	MG-MHP 9	MG-MHP 10	MG-MHP 15	MG-MHP 13	MG-MHP 1/	MC-MHP 10	MC-MHP 1	MG-MHP 18	MG-MHP 19	MG-MHP 20	MG-MHP 21	MG-MHP 23	MG-MHP 2	MG-MHP 20	MG-MHP 20	MG-MHP 27	MG-MHP 28	MG-MHP 29	MG-MHP 30	MG-MHP 32	MG-MHP 33	MG-MHP 34 MG-MHP 34	MG-MHP 30	MG-MHP 3: MG-MHP 35	MG-MHP 39	MG-MHP 40 MG-MHP 41	MG-MHP 45	MG-MHP 43 MG-MHP 44	MG-MHP 40	MG-MHP 46	MG-MHP 48	MG-MHP 49	MG-MHP 51 MG-MHP 51	MG-MHP 5	MG-MHF ac MG-MHP 5c	MG-MHP 5	MG-MHP at MG-MHP 57	MG-MHP 58	MG-MHP 59	Total
1 Villosacapsula setosapellicula	0	6 3	3 1	0	35 6	50 30	30	25 3	3 0	15	0 3	2	9 3	21	11	205	101	164 3	7 124	25	33	28	14	5	0 0	0 0	0	0 0	0	1 0	1	0 1	0	0 0	8	0 0	1 0	1 (6 0	0	1 5	5 1	10 0	0	0 3	1080
2 Acanthodiacrodium crassus	0	5 3	3 0	1	1 1	0 2	6	10 0	0 1	1	0 3	1 2	2) 49	22	48	41	56 1	6 18	70	123	74	18	3	1 1	1 0	0	1 0	1	0 0	2	0 0	0	0 0	6	1 0	1 0	0	0 0	0	0 0	0	0 0	0	0 5	611
3 Multiplicisphaeridium irregulare	0	5 1	16	3	20	9 7	17	27 0	0 1	7	8 2	9 1	8 9	18	2	48	34	31 1	1 89	55	47	84	7	5	0 0	0 0	0	0 0	0	0 0	0	0 0	0	0 0	6	0 0	1 0	0	0 0	0	0 0	0	0 0	0	0 0	604
4 Veryhachium lairdii	0	2 2	2 5	0	0	0 7	7	10 0	0 1	7	6 2	7 4	6 7	26	1	13	41	40 1	1 47	136	60	240	12	1	0 0	0 0	0	0 0	0	1 0	0	0 0	0	0 0	8	0 0	1 0	1 (0 0	0	0 2	0	0 0	0	0 1	768
5 Veryhachium trispinosum	0	12 1	9 25	0	5 1	11 15	0	30 0	D 1	2	7 2	2 4	9 21	29	10	15	11	15 1:	5 30	49	23	119	47	5	4 0	0 0	0	2 0	2	1 1	0	5 0	0	0 0	30	1 0	1 0	0 7	8 0	2 .	4 17	38 .	13 0	0	0 2	716
6 Ordovicidium elegantulum	0	1 6	5 15	5	5	1 0	3	0 1	1 7	2	0 2	: 3	1	16	0	37	41	60 2	2 27	15	3	11	1	1	1 1	1 0	0	0 0	0	0 0	1	0 0	0	0 0	2	0 0	1 0	1 1	0 0	0	0 0	1	0 0	0	0 0	283
7 Diexallophasis denticulata	0	2 5	54	3	20 1	10 6	25	3 .	1 1	4	4 1	0 34	8 23	3 25	9	13	10	6 1	3 51	58	25	52	4	4	2 0	0 0	0	1 0	0	2 0	0	1 2	0	0 0	7	0 0	1 0	0 0	0 0	0	0 0	5	1 0	0	0 6	456
8 Leiofusa litotes	0	2 (0	0	0 1	0 0	0	10 1	1 1	2	1 2	2	4 3	23	14	4	3	12 4	4 13	55	1	43	3	0	0 0	0 0	1	0 0	0	0 0	0	0 0	0	0 0	1	0 0	1 0	0 1	0 0	0	0 2	2	0 0	0	0 3	233
9 Orthosphaeridium rectangulare	0	1 2	2 5	7	1	1 2	0	0 2	2 11	1	0 1	2	: 5	3	0	6	5	16 1	1 0	1	5	6	5	0	0 0	0 0	0	0 0	2	0 0	2	0 0	0	0 0	1	0 0	1 0	0	1 0	0	0 1	1	0 0	0	0 0	97
10 Orthosphaeridium insculptum	0	0 0	0	0	0 1	0 0	0	0 0	0 0	0	4 4	1 2	4 18	3 24	10	74	31	40 1	0 71	24	31	48	27	1	1 3	3 0	1	0 0	1	1 1	5	0 0	0	0 0	15	1 1	. 0	6	3 3	0	0 6	9	8 0	0	0 3	509
11 Dorsennidium hamii	0	0 0	0	0	0	0 0	0	0 0	0 0	0	1 3	1 2	1	7	1	1	9	25 1	2 13	15	7	22	17	0	1 0	0 0	0	0 0	0	0 0	0	0 0	0	0 0	7	0 0	/ 0	0 1	0 0	0	0 0	0	0 0	0	0 0	153
12 Baltisphaeridium trophirhapium	0	0 0	0	0	0	0 0	0	0 0	0 0	0	1 0	1	0	0	1	0	1	0 0	5 0	0	0	2	1	0	0 0	0 0	2	0 0	0	0 0	0	0 1	0	0 0	0	0 0	/ 0	0 1	0 0	0	0 0	0	0 0	0	0 0	/ 10
13 Navifusa ancepsipuncta	0	0 0	0	0	0	0 0	0	0 0	0 0	0	1 0	1	0	1	0	0	1	0 2	2 1	1	0	0	2	0	0 0	0 0	0	0 0	0	1 0	0	0 0	0	0 0	0	0 0	/ 0	0 1	0 0	0	0 0	0	0 1	0	0 1	13
14 Dactylofusa platynetrella	0	0 0	0	0	0	0 0	0	0 0	0 0	0	1 0	0	6	6	0	7	0	0 1	1 1	11	3	23	5	0	0 0	0 0	0	0 0	0	0 0	3	1 0	0	0 0	0	0 0	/ 0	0 1	0 0	0	0 2	5	0 0	0	0 0	75
15 Lophosphaeridium acinatum	0	0 0	0	0	0	0 0	0	0 0	0 0	0	2 5	6 3	. 0	0	0	0	0	0 0	5 0	0	0	0	0	0	0 0	0 0	0	0 1	4	3 0	3	0 0	0	0 0	1	1 0	/ 0	0 1	0 0	0	0 2	0	1 0	0	0 0	26
16 Moyeria cabottii*	0	0 0	0 0	0	0	0 0	0	0 0	0 0	0	0 6	6 8	1 0	0	0	0	4	3 2	ž 14	2	2	12	6	0	0 0	0 0	0	0 0	1	1 0	0	0 0	0	0 0	0	0 0	1 0	0 1	0 0	0	0 0	0	0 0	0	0 0	61
17 Neoveryhachium carminae	0	0 0	0 0	0	0	0 0	0	0 0	0 0	0	0 1	6 5	4 9	8	0	0	8	12 4	4 12	10	4	75	0	0	0 0	0 0	0	0 0	0	0 0	0	0 1	0	0 0	0	0 0	1 0	0	1 0	0	0 0	1	0 0	0	0 0	215
18 Baltisphaeridium perclarum	0	0 0	0 0	0	0	0 0	0	0 0	0 0	0	0 1	0	3	0	0	1	6	3 2	2 5	1	4	11	2	0	0 0	0 0	0	0 0	0	0 0	0	0 1	0	0 0	0	0 0	1 0	0	0 0	0	0 0	0	0 0	0	0 0	40
19 Dactylofusa cucurbita	0	0 0	0 0	0	0	0 0	0	0 0	0 0	0	0 1	0	1	0	0	0	0	0 0	0 6	5	0	1	0	0	0 0	0 0	0	0 0	0	0 0	0	0 0	0	0 0	0	0 0	1 0	0	0 0	0	0 0	1	0 0	0	0 0	8
20 Dactylofusa striatifera	0	0 0	0 0	0	0	0 0	0	0 0	0 0	0	0 1	1	2	1	1	4	20	23 3	3 5	64	4	42	11	0	0 0	0 0	0	0 0	0	0 0	2	0 0	0	0 0	1	0 1	0	0	0 0	0	0 1	1	0 0	0	0 0	188
21 Inflatarium trilobatum	0	0 0	0 0	0	0 1	0 0	0	0 0	0 0	0	0 0	0	0	8	7	4	5	7 4	4 2	18	26	31	6	2	0 1	1 0	0	0 0	0	0 0	0	1 3	0	0 0	1	0 0	J O	0	1 0	1	0 0	0	3 0	0	0 0	131
22 Tylotopalla caelamenicutis	0	0 0	0 0	0	0 1	0 0	0	0 0	0 0	0	0 0	0	0	2	0	0	1	1 3	3 0	0	2	1	0	0	0 0	0 0	0	0 0	0	0 0	0	0 0	0	0 0	0	0 0	1 0	0	0 0	0	0 0	0	0 0	0	0 0	/ 10
23 Tunisphaeridium eisenackii	0	0 0	0	0	0 1	0 0	0	0 0	0 0	0	0 0	0	0	1	0	0	0	0 0) O	0	0	2	10	1	0 0	0 0	1	0 0	0	0 0	1	1 1	0	0 0	1	0 0	1 0	1	1 0	0	0 0	1	0 0	0	0 1	23
24 Safirotheca safira	0	0 0	0	0	0 1	0 0	0	0 0	0 0	0	0 0	0	0	2	0	1	1	0 0) O	0	0	0	1	0	0 0	0 0	0	0 0	0	0 0	0	0 0	0	0 0	1	0 0	1 0	0	0 0	0	0 1	1	0 0	0	0 1	9
25 Estiastra iranicum	0	0 0	0	0	0 1	0 0	0	0 0	0 0	0	0 0	0	0	1	1	0	0	0 0	3 0	0	0	0	0	0	1 0	0 0	0	0 0	0	0 0	0	0 0	0	0 0	1	0 0	1 0	0	0 0	0	0 0	0	0 0	0	0 1	5
26 Disparifusa perryi	0	0 0	0	0	0 1	0 0	0	0 0	0 0	0	0 0	0	0	6	0	0	1	0 0	1 1	5	1	1	0	0	0 0	0 0	0	0 0	0	0 0	0	1 0	0	0 0	1	0 0	/ 0	0	1 1	0	0 0	1	0 0	0	0 1	21
27 Moyeria hafezii n. sp.*	0	0 0	0	0	0 1	0 0	0	0 0	0 0	0	0 0	0	0	3	0	2	0	1 2	2 3	0	2	2	0	0	0 0	0 0	0	0 0	0	0 0	0	4 0	0	0 0	0	2 0	/ 0	0 /	0 0	0 3	3 0	0	0 0	0	0 0	24
28 Moyeria sp. A.*	0	0 0	0	0	0 1	0 0	0	0 0	0 0	0	0 0	0	0	1	0	0	0	0 1	1 0	1	1	1	1	0	0 0	0 0	0	0 0	0	0 0	0	0 0	0	0 0	0	0 0	/ 0	0 /	0 0	0	0 0	0	0 0	0	0 0	6
29 Lophosphaeridium bulbosumensis n. sp.	0	0 0	0 0	0	0 1	0 0	0	0 0	0 0	0	0 0	0	0	2	1	1	1	1 1	1 3	1	8	138	3	1	0 0	0 0	1	0 0	0	0 1	0	1 2	0	0 0	1	2 1	(1	2	1 1	0	0 0	1	0 0	0	0 1	177
30 Excultibrachium concinnum	0	0 0	0 0	0	0 1	0 0	0	0 0	0 0	0	0 0	0	0	0	0	0	0	1 0	1 1	1	1	3	0	0	0 0	0 0	0	0 0	0	0 0	0	0 0	0	0 0	0	0 0	/ 0	0 1	0 0	0	0 0	0	0 0	0	0 0	7
31 Comasphaeridium lanugiferum	0	0 0	0	0	0 1	0 0	0	0 0	0 0	0	0 0	0	0	0	0	0	0	3 0	1 1	2	0	5	0	0	0 0	0 0	3	2 0	1	1 0	2	0 1	0	0 0	1	0 0	/ 0	0 1	0 0	0	0 0	0	0 0	0	0 0	22
32 Frankea breviuscula	0	0 0	0	0	0 1	0 0	0	0 0	0 0	0	0 0	0	0	0	0	0	0	1 0	2	0	1	3	1	0	0 0	0 0	0	0 0	0	0 0	0	0 0	0	0 0	0	0 0	/ 0	0 1	0 0	0	0 0	0	0 0	0	0 0	8
33 Cornuferifusa bifidipertica	0	0 0	0 0	0	0	0 0	0	0 0	0 0	0	0 0	0	0	0	0	0	0	1 0	1	0	1	2	1	0	0 0	0 0	0	0 0	0	0 0	0	0 0	0	0 0	0	0 0	1 0	0	0 0	0	0 0	0	0 0	0	0 0	6
34 Baltisphaeridium sp.	0	0 0	0	0	0 1	0 0	0	0 0	0 0	0	0 0	0	0	0	0	0	0	1 1	1 0	1	0	1	0	0	0 0	0 0	0	0 0	0	0 0	0	0 0	0	0 0	1	0 0	1 0	0 /	0 0	0	0 0	1	0 0	0	0 0	6
Total	0	36 4	1 61	19	87 9	12 69	88 1	115 1	8 24	41	36 13	16 30	15 17	7 273	91	484	376	523 15	58 535	626	418	1083	205	29	11 6	3 0	9	6 1	12	12 3	22	15 13	0	0 0	101	8 3	\$ 1	12 2	23 5	3 1	8 39	74 :	36 1	0	0 2	9 6601

4.1.1. List of chitinozoan species Order: OPERCULIFERA Eisenack, 1931 Family: DESMOCHITINIDAE Eisenack, 1931 emend. Paris, 1981 Subfamily: DESMOCHITININAE Paris, 1981 Genus: Calpichitina Wilson and Hedlund, 1964 Calpichitina lenticularis (Bouché, 1965) (Plate I, 18; Plate V, 18) Eisenackitina sp. (Plate I, 20) Genus: Desmochitina Eisenack, 1931 Desmochitina minor Eisenack, 1931 (Plate I, 17, 19) Desmochitina erinacea Eisenack, 1931 (Plate I, 1, 2, 3, 4, 5, 6, 7, 8) Desmochitina typica Eisenack, 1931 (Plate I, 9, 10, 11, 12, 13, 14, 15) Desmochitina ovulum (Eisenack, 1962) (Plate I, 16) Subfamily: Pterochitininae Paris, 1981 Genus: Armoricochitina Paris, 1981 Armoricochitina alborzensis Ghavidel-Syooki and Winchester-Seeto, 2002 (Plate II, 11, 12) Armoricochitina nigerica (Bouché, 1965) (Plate II, 13, 14, 15, 16, 17, 18 19) Subfamily: ANCYROCHITININAE Paris, 1981 Genus: Ancyrochitina Eisenack, 1955 Ancyrochitina merga Jenkins, 1970 (Plate III, 11, 12) Ancyrochitina ellisbayensis Soufiane and Achab, 2000 (Plate III, 8, 9, 10) Genus: Angochitina Eisenack, 1931 Angochitina communis Jenkins, 1967 (Plate III, 6) Genus: Fungochitina Taugourdeau, 1966 restrict. Paris et al., 1999 Fungochitina actonica (Jenkins, 1967) (Plate IV, 10, 14) Fungochitina spinifera (Eisenack, 1962) (Plate IV, 11, 12, 15) Genus: Plectochitina Cramer, 1964 Plectochitina sylvanica Jenkins, 1970 (Plate III, 7) Subfamily: BELONECHITININAE Paris, 1981 Genus: Belonechitina Jansonius, 1964 Belonechitina robusta (Eisenack, 1959) (Plate III, 16, 20) Belonechitina micracantha (Eisenack, 1931) (Plate IV, 9) Order: PROSOMATIFERA Eisenack, 1972 Subfamily: CONOCHITININAE Paris, 1981 Genus: Euconochitina Taugourdeau, 1966 emend. Paris et al., 1999

Euconochitina moussegoudaensis Paris in Le Hérissé et al., 2013 (Plate V, 19) Euconochitina lepta (Jenkins, 1970) emend. Paris et al., 1999 (Plate

II. 20) Genus: Conochitina (Eisenack, 1931) emend. Paris et al., 1999 Conochitina rotundata Paris et al., 2015 (Plate III, 18) Genus: Pistillachitina Taugourdeau, 1966 Pistillachitina pistillifrons Eisenack, 1939 (Plate III, 14, 15) Pistillachitina comma (Eisenack, 1959) (Plate III, 13) Genus: Rhabdochitina Eisenack, 1931 Rhabdochitina usitata Jenkins, 1967 (Plate III, 19) Rhabdochitina curvata Al-Shawareb et al., 2017 (Plate IV, 16, 20) Subfamily: CYATHOCHITININAE Paris, 1981 Genus: Cyathochitina Eisenack, 1955 emend. Paris et al., 1999 Cyathochitina campanulaeformis (Eisenack, 1931) (Plate V, 16) Cyathochitina caputoi Da Costa, 1971 (Plate V, 12) Cyathochitina kuckersiana (Eisenack, 1934) (Plate V, 20) Family: LAGENOCHITINIDAE (Eisenack, 1931) Paris, 1981 Subfamily: LAGENOCHITINIDAE Eisenack, 1931 emend. Paris et al., 1999 Genus: Lagenochitina Eisenack, 1931 Lagenochitina baltica Eisenack, 1931 (Plate II, 7, 8, 9, 10) Lagenochitina prussica Eisenack, 1931 (Plate II, 1, 2, 3, 4, 5, 6) Genus: Alhajrichitina Al-Shawareb et al., 2017 Alhajrichitina adamantea Al-Shawareb et al., 2017 (Plate III, 3) Alhajrichitina spinifera n. sp. (Plate III, 1, 2, 4, 5) Subfamily: TANUCHITININAE Paris, 1981 Genus: Tanuchitina Jansonius, 1964 emend. Paris et al., 1999 Tanuchitina fistulosa Taugourdeau and de Jekhowsky, 1960 (Plate V, 4, 8) Tanuchitina elongata Bouché, 1965 (Plate IV, 18, 19) Tanuchitina ontariensis Jansonius, 1964 (Plate V, 1, 2, 3, 5, 6, 7) Genus: Hyalochitina Paris et al., 1999 Hyalochitina jajarmensis Ghavidel-Syooki, 2017b (Plate III, 17) Order: PROSOMATIFERA Eisenack, 1972 Subfamily: Spinachitininae Paris, 1981 Genus: Spinachitina Schallreuter, 1963 emend. Paris et al., 1999 Spinachitina bulmani (Jansonius, 1964) (Plate IV, 1, 2, 3, 4, 5, 6, 7, 8) Spinachitina oulebsiri Paris et al., 2000a (Plate V, 9, 10, 11, 13, 14, 15, 17)



Plate I. 1, 2, 3, 4, 5, 6, 7, 8. Desmochitina erinacea Eisenack, 1931; 9, 10, 11, 12, 13, 14, 15. Desmochitina typica Eisenack, 1931; 16. Desmochitina ovulum (Eisenack, 1962); 17, 19. Desmochitina minor Eisenack, 1931; 18. Calpichitina lenticularis (Bouché, 1965); 20. Eisenackitina sp.

4.1.2. Systematics of new chitinozoan taxa

Two chitinozoan species of *Alhajrichitina spinifera* n.sp. and *Eisenackitina* sp., are described and discussed below, wherein the

measurements are specified in micrometers (μ m). The proposed classification and terminology of Paris et al. (1999) are used, and the abbreviations defined by Paris (1981) are applied.

Review of Palaeobotany and Palynology 284 (2021) 104337



Plate II. 1, 2, 3, 4, 5, 6. Lagenochitina prussica Eisenack, 1931; 7, 8, 9, 10. Lagenochitna baltica Eisenack, 1931; 11, 12. Armoricochitina alborzensis Ghavidel-Syooki and Winchester-Seeto, 2002; 13, 14, 15, 16, 17, 18, 19. Armoricochitina nigerica (Bouché, 1965); 2 0. Euconochitina lepta (Jenkins, 1970)

Incertae sedis Group Chitinozoa Eisenack, 1931 Family: LAGENOCHITINIDAE Eisenack, 1931 emend. Paris, 1981 Subfamily: LAGENOCHITININAE Paris, 1981 *Genus*: **Alhajrichitina** Al-Shawareb et al., 2017 *Type species*: *Alhajrichitina adamantea* Al-Shawareb et al., 2017 *Alhajrichitina spinifera* n. sp. (Plate III, 1, 2, 4, 5)



Plate III. 1, 2, 4, 5. Alhajrichitina spinifera n. sp. 3. Alhajrichitina adamantea Al-Shawareb et al., 2017 6. Angochitina communis Jenkins, 1967 7. Plectochitina sylvanica Jenkins, 1970 8, 9, 10. Ancyrochitina ellisbayensis Soufiane and Achab, 2000 11, 12. Ancyrochitina merga Jenkins, 1970 13. Pistillachitina comma (Eisenack, 1959) 14, 15. Pistillachitina pistillifrons Eisenack, 1939 16, 20. Belonechitina robusta (Eisenack, 1959) 17. Hyalochitina jajarmensis Ghavidel-Syooki, 2017b 18. Conochitina rotundata Paris et al., 2015 19. Rhabdochitina usitata Jenkins, 1967

Holotype: Plate III, 2

Type stratum: Ghelli Formation (MG-MHP 27 to MG-MHP 41), Kuh-e Boghou, southwest of Kashmar, eastern-central Iran.

Name derivation: Refers to the spinous sculptures covering the entire vesicle surface.

Dimensions: L = 138.1 (129.7) 121.3 $\mu m;$ Dp = 99.3 (94.05) 88.8 $\mu m;$ Dc = 57.2 (55.65) 54.1 $\mu m;$ ln = 49.6 (48.4) 47.2 $\mu m;$ ls = 1.5 (1.7) 1.9 $\mu m;$ n = 10.

Description: Alhajrichitina spinifera n. sp. is a small chitinozoan with a diamond-shaped chamber and distinct cylindrical neck. Flexure is



Plate IV. 1, 2, 3, 4, 5, 6, 7, 8. Spinachitina bulmani (Jansonius, 1964); 9. Belonechitina micracantha (Eisenack, 1931); 10, 14. Fungochitina actonica (Jenkins, 1967); 11, 12, 15. Fungochitina spinifera (Eisenack, 1962); 13. Tetrahedraletes medinensis Strother and Traverse emend Wellman and Richardson, 1993; 16, 20. Rhabdochitina curvata Al-Shawareb et al., 2017; 17. Scolecodont (Kettnerite sp.); 18, 19. Tanuchitina elongata (Bouché, 1965).

observed, and shoulders are distinct. The chamber is divided into upper and lower parts. A sharp deflection in the outline of the chamber is indicated by a fold or thickening, which represents the maximum width of the vesicle and margin. The basal part of the chamber is rounded to ogival in shape with a basal scar. The vesicle surface is covered by abundant, simple, small spines and rarely granules. This species is quite



Plate V. 1, 2, 3, 4, 5, 6. Tanuchitina ontariensis Jansonius, 1964 4, 7. Tanuchitina fistulosa Taugourdeau and de Jekhowsky, 1960 9, 10, 11, 13, 14, 15 17. Spinachitina oulebsiri Paris et al., 2000 12. Cyathochitina caputoi Da Costa, 1971 16. Cyathochitina campanulaeformis (Eisenack, 1931) 18. Calpichitina lenticularis (Bouché, 1965) 19. Euconochitina moussegoudaensis Paris in Le Hérissé et al., 2013 20. Cyathochitina kuckersiana (Eisenack, 1934)

similar to *Alhajrichitina adamantea* (Al-Shawareb et al., 2017) but the Iranian specimens differ from those of the Arabian Peninsula by presenting smaller size and spinous ornamentation on the entire surface of the vesicle. Order: Operculatifera Eisenack, 1931 Family: Desmochttinidae Eisenack, 1931 emend. Paris, 1981 Subfamily: Eisenackininae Paris, 1981 Genus: **Eisenackitina** Jansonius, 1964 restrict. Paris, 1981

Review of Palaeobotany and Palynology 284 (2021) 104337



Plate VI. 1, 2. Tetrahedraletes grayae Strother, 1991; 3, 4. Dyadospora murusattenuata (Strother and Traverse, 1979) Burgess and Richardson, 1991; 5. Segestrespora membranifera (Johnson, 1985) Burgess, 1991; 6, 20. Abditusdyadus khayyammii n. sp. 7, 8. Rimosotetras problematica Burgess, 1991; 9. Rimosotetras punctata Ghavidel-Syooki, 2017a; 10. Dyadospora verrucata Ghavidel-Syooki, 2017a; 11, 12. Imperfectotriletes vavrdovae (Richardson) Steemans et al., 2000; 13. Imperfectotriletes persianense Ghavidel-Syooki, 2017a; 14. Cryptotetras erugata Strother et al., 2015; 15, 16. Rimosotetras subspherica Strother et al., 2015; 17. Velatitetras rugosa (Strother and Traverse) Steemans et al., 1996; 18, 19. Tetraplanarisporites laevigatus Wellman et al., 2015; 21. Tetrahedraletes medinensis Strother and Traverse emend Wellman and Richardson, 1993; 22, 23. Abditusdyadus laevigatus Wellman and Richardson, 1996; 24. Segestrespora burgessi Steemans et al., 1996.

Review of Palaeobotany and Palynology 284 (2021) 104337



Plate VII. 1, 2. Cryptotetras mordacis Strother et al., 2015; 3. Dyadospora asymmetrica Ghavidel-Syooki, 2017a; 4. Segestrespora iranense Ghavidel-Syooki, 2017a; 5, 6. Imperfectotriletes patinatus Steemans et al., 2000; 7, 8, 9, 10. Dyadospora ferdowsii n. sp.; 11, 12, 13. Velatitetras retimembrana (Miller & Eames) Steemans et al., 1996; 14. Tetrahedraletes medinensis Strother and Traverse emend Wellman and Richardson, 1993; 15. Rimosotetras granulata Ghavidel-Syooki, 2017a; 16. Segestrespora laevigata Burgess, 1991; 17. Segestrespora membranifera (Johnson, 1985) Burgess, 1991; 18, 19. Cheilotetras caledonica Wellman and Richardson, 1993; 20. Segestrespora burgessii Steemans et al., 1996; 21, 22, 23, 24. Abditusdyadus laevigatus Wellman and Richardson, 1996.



Plate VIII. 1. Navifusa ancepsipuncta Loeblich, 1970; 2. Dactylofusa striatifera (Cramer and Díez, 1972) Fensome et al., 1990; 3, 4. Dactylofusa cucurbita Jardiné et al., 1974; 5. Cornuferifusa bifidipertica Jacobson and Achab, 1985; 6, 7. Safirotheca safira Vavrdová, 1989; 8. Dactylofusa platynetrella (Loeblich and Tappan, 1978) Fensome et al., 1990; 9. Leiofusa litotes Loeblich and Tappan, 1978; 10. Lophosphaeridium acinatum Wicander and Playford, 1999; 11, 12, 13, 14. Moyeria hafezii n. sp.; 15. Comasphaeridium lanugiferum Jacobson and Achab, 1985; 16. Disparifusa perryi Loeblich and Tappan, 1978; 17. Moyeria cabottii (Cramer, 1971) Miller and Eames, 1982; 18. Moyeria sp. A.; 19. Acanthodiacrodium crassus (Loeblich and Tappan, 1978) Vecoli, 1999; 20, 21, 22, 23. Lophosphaeridium bulbosumensis n. sp.

Review of Palaeobotany and Palynology 284 (2021) 104337



Plate IX. 1, 2. Inflatarium trilobatum Le Hérissé et al., 2014; 3. Frankea breviuscula Burmann, 1970; 4. Villosacapsula setosapellicula (Loeblich, 1970) Loeblich and Tappan, 1976; 5. Tylotopalla caelamenicutis Loeblich, 1970; 6. Orthosphaeridium insculptum Loeblich, 1970; 7. Diexallophasis denticulata (Stockmans and Williére, 1963) Loeblich, 1970; 8. Veryhachium lairdii (Deflandre) Deunff, 1959; ex Downie, 1959; 9. Multiplicisphaeridium irregulare Staplin et al., 1965; 10. Neoveryhachium carminae (Cramer, 1964b) Cramer, 1970; 11. Baltisphaeridium trophirhapium Loeblich and Tappan, 1978; 12. Estiastra iranicum Ghavidel-Syooki, 2000; 13. Orthosphaeridium rectangulare (Eisenack, 1963) Eisenack, 1968; 14. Ordovicidium elegantulum Tappan and Loeblich, 1971; 15. Veryhachium trispinosum (Eisenack, 1938) Stockmans and Williére, 1963; 16. Excultibrachium concinnum Wicander and Playford, 1999; 17. Baltisphaeridium sp.; 18. Dorsennidium hamii (Loeblich, 1970) Sarjeant and Stancliffe, 1994; 19. Baltisphaeridium Loeblich and Tappan, 1978.

Eisenackitina sp. (Plate I, 20)

Dimensions: L = 52.5 μ m; Dp = 57.1 μ m; Dc = 30.3 μ m; ls = 4.2 (3.4) 2.6 μ m; width of spine = 1.5 (1.17) 0.84 μ m; n = 3.

Description: Small chitinozoan morphotype with ovoid to subcylindrical vesicles. The aboral pole is convex or straight with more or less parallel sides; the greatest width is at the middle part and the lower part of the chamber is sometimes convex. It has no flexure or shoulder, and the neck or lip is considerably reduced and usually absent. The external aperture is smooth with a diameter less than the maximum vesicle diameter. The vesicle surface is covered by dense spines. *Eisenackitina* sp. appeared rarely in samples MG-MHP 27, MG-MHP 29, and MG-MHP 40. It was only classified to the genus level because of this paucity of specimens. This species differs from other species of *Eisenackitina* in terms of biometric data and by presenting spines on the vesicle surface.

4.2. Chitinozoan biostratigraphy

Based on the presence and distribution of well known chitinozoan taxa (Fig. 2), six chitinozoan biozones were established in the Ghelli Formation of Kuh-e Boghou. These chitinozoan biozones, which are similar to those of the northern Gondwana Domain (Paris, 1990; Oulebsir and Paris, 1995; Paris et al., 2000b; Paris et al., 2007; Paris et al., 2015; Al-Shawareb et al., 2017; Ghavidel-Syooki, 2017b), are discussed in ascending stratigraphic order.

4.2.1. Belonechitina robusta Biozone

The base of this biozone is marked by the FAD of Belonechitina robusta (Eisenack, 1959). Its top corresponds to the FAD of Tanuchitina fistulosa (Taugourdeau and de Jekhowsky, 1960), which is the index species of the succeeding biozone. In the present material, Belonechitina robusta occurs with common frequency in the samples of MG-MHP 2 through MG-MHP 12 of the Ghelli Formation in Kuh-e Boghou, southwest of Kashmar City, east-central Iran (Fig. 2; Table 1). This biozone, which covers a 68-m thickness of the Ghelli Formation, consists of heterogeneous conglomerate followed by reddish-brown fossiliferous argillaceous limestone, and by an alternation of sandstone, siltstone, and shale toward the top. Belonechitina robusta has previously been reported from Late Ordovician (early to middle Sandbian) of Portugal (Paris, 1979, 1981), Spain (Robardet, 1980; Paris, 1981), France (Robardet et al., 1972; Paris, 1981), and the United Kingdom (Jansonius, 1964; Paris, 1979; Grahn, 1981, 1982); late Sandbian to early Katian of the United States (C. wilsoni-D. clingani graptolite biozones; see Ross, 1982); early Katian of Turkey (Paris et al., 2007); and early Katian of Iran (Ghavidel-Syooki, 2008). The other chitinozoan species occurring in this biozone include Lagenochitina baltica (Eisenack, 1931), Euconochitina lepta (Jenkins, 1970), Calpichitina lenticularis (Bouché, 1965), Desmochitina typica (Eisenack, 1931), Desmochitina erinacea (Eisenack, 1931), Angochitina communis (Jenkins, 1967), Cyathochitina kuckersiana (Eisenack, 1934), Cyathochitina campanulaeformis (Eisenack, 1931), and Rhabdochitina usitata (Jenkins, 1967). Cyathochitina campanulaeformis is a long-ranging (Middle to Upper Ordovician) and cosmopolitan species (Eisenack, 1931, 1959; Jenkins, 1967; Achab, 1978; Grahn, 1981, 1984; Al-Hajri, 1995; Al-Ghammari, 2010) while the others are classical components of Late Ordovician (Katian) in the northern Gondwana Domain (Molyneux and Paris, 1985; Al-Hajri, 1995; Oulebsir and Paris, 1995; Ghavidel-Syooki and Winchester-Seeto, 2002; Ghavidel-Syooki, 2008; Ghavidel-Syooki et al., 2011a; Ghavidel-Syooki et al., 2011b; Paris et al., 2015; Ghavidel-Syooki, 2016, 2017a, 2017b; Al-Shawareb et al., 2017). Based on the absence of ponceti-tanvillensis chitinozoan biozones along with a comparison to the chronostratigraphic chart of Videt et al. (2010), the basal part of the Ghelli Formation in Kuh-e Boghou is assigned to the middle Katian (an upper time slice Ka1) of Videt et al. (2010). Therefore, a hiatus exists between the Derenjal Formation (Late Cambrian) and the basal part of the Ghelli Formation, encompassing the Sandbian and earliest Katian (Jenchinochitina tanvillensis Biozone).

4.2.2. Tanuchitina fistulosa Biozone

The base of this biozone is marked by the FAD of Tanuchitina fistulosa (Taugourdeau and de Jekhowsky, 1960). Its top corresponds to the FAD of Armoricochitina nigerica (Bouché, 1965), which is the index species of the succeeding biozone. In this study, Tanuchitina fistulosa is present at rare to abundant frequencies in the samples MG-MHP 12 to MG-MHP 14 (Fig. 2; Table 1). In Kuh-e Boghou, this biozone, which includes a 247-m thickness of the Ghelli Formation, primarily consists of sandstone, siltstone, and shale. This species was selected as the index species of the chitinozoan biozones from the late Sandbian deposits in the Arabian Peninsula (Paris et al., 2000b) and the northern Gondwana Domain, immediately overlying the Belonechitina robusta Biozone (Webby et al., 2004; Paris, 2006; Videt et al., 2010). With the exception of Belonechitina robusta, which is the index species of the preceding biozone, all of the acritarch and associated chitinozoan taxa of the underling biozone continue into this chitinozoan biozone. The accompanying chitinozoan species of this biozone consist of Pistillachitina pistillifrons (Eisenack, 1939), Lagenochitina prussica (Eisenack, 1931), Desmochitina minor (Eisenack, 1931), and Hyalochitina jajarmensis (Ghavidel-Syooki, 2017b). Among these chitinozoan taxa, Desmochitina minor ranges from the Floian to Katian (Grahn, 1984; Ghavidel-Syooki and Winchester-Seeto, 2002; Ghavidel-Syooki, 2008, 2016, 2017b), while Pistillachitina pistillifrons, Lagenochitina prussica, and Hyalochitina jajarmensis are classical components of Late Ordovician in other locations such as Portugal (Paris, 1979), England (Vandenbroucke, 2008), Ukraine (Laufeld, 1971), Sweden (Laufeld, 1967), Estonia (Grahn, 1980; Nõlvak, 1980), Belgium (Vanmeirhaeghe, 2006), and Iran (Ghavidel-Syooki and Winchester-Seeto, 2002; Ghavidel-Syooki, 2008, 2017b). A comparison of Tanuchitina fistulosa Biozone and the chronostratigraphic chart of Videt et al. (2010) suggests middle Katian (uppermost time slice Ka1) of Videt et al. (2010) for this biozone of the Ghelli Formation in Kuh-e Boghou, southwestern Kashmar City, east-central Iran.

4.2.3. Armoricochitina nigerica Biozone

The base of this biozone is marked by the FAD of Armoricochitina nigerica (Bouché, 1965). Its top corresponds to the first FAD of Ancyrochitina merga (Jenkins, 1970), which is the index species of the succeeding biozone. In the present material, Armoricochiting nigerica oc-curs at rare to common frequencies in samples MG-MHP 14 to MG-MHP 21 (Fig. 2; Table 1). This biozone, which includes an 80-m thickness of the Ghelli Formation, mainly consists of shale, two igneous sills, a thin bed of cream fossiliferous limestone, and a microconglomerate. To date, Armoricochitina nigerica has only been recorded from Late Ordovician in the northern Gondwana Domain (Bouché, 1965; Molyneux and Paris, 1985; Al-Hajri, 1995; Oulebsir and Paris, 1995; Paris et al., 2000b; Ghavidel-Syooki and Winchester-Seeto, 2002; Bourahrouh et al., 2004; Paris et al., 2007; Ghavidel-Syooki, 2008; Le Heron and Craig, 2008; Ghavidel-Syooki et al., 2011a, 2011b; Abuhmida, 2013; Le Hérissé et al., 2013; Paris et al., 2015; Ghavidel-Syooki, 2016, 2017a, 2017b; Al-Shawareb et al., 2017; Oktay and Wellman, 2019). The Armoricochitina nigerica Biozone is correlatable with the upper part of the Dicellograptus complanatus graptolite zone of the British Standard (Paris, 1990, 1996, 2006; Webby et al., 2004) and corresponds to the upper Katian (the upper level of Ka3 time slice to the lower level of Ka4) of Videt et al. (2010). Armoricochitina nigerica has been reported from the Katian and Hirnantian strata of numerous localities in Northern Africa (Morocco, Algeria, Tunisia, Libya, Niger, and Chad); the Middle East (Iran, Arabian Peninsula, Syria, Iraq, and Turkey); and southern and central Europe (Spain, Portugal, France, Italy, and the Czech Republic). This species is one of the key chitinozoan taxa defining the northern Gondwana paleoprovince during Late Ordovician. Armoricochitina nigerica has not been observed in the United Kingdom and Belgium, indicating it did not extend to the northern margin of the Rheic Ocean (Paris et al., 2015). Indeed, Vandenbroucke et al. (2009) suggest that Armoricochitina nigerica could be regarded as a

polar taxon. Most species of the preceding biozones continue into the Armoricochitina nigerica Biozone; thus, Belonechitina micracantha, Fungochitina spinifera, Fungochitina actonica, Desmochitina ovulum, and Armoricochitina alborzensis are found in this biozone. Belonechitina micracantha is a long-ranging taxon as it is found in the Middle-Late Ordovician in many localities, including Floian to Katian in the Baltic region (Eisenack, 1931); Middle Ordovician of Algerian Sahara (Oulebsir and Paris, 1995); Early-Middle Ordovician of Morocco (Elaouad-Debbaj, 1984); Middle Ordovician of Turkey (Paris et al., 2007); Late Ordovician (Sandbian) of England (Van Nieuwenhove et al., 2006); France (Paris, 1981); Iran (Ghavidel-Syooki, 2008; Ghavidel-Syooki and Borji, 2018); and the Arabian Peninsula (Al-Hajri, 1995; Paris et al., 2015; Al-Shawareb et al., 2017). Other associated chitinozoan taxa such as Armoricochitina alborzensis, Desmochitina ovulum, Fungochitina spinifera, and Fungochitina actonica are characteristic components of Late Ordovician worldwide, including the United Kingdom (Jenkins, 1967; Vandenbroucke, 2005, 2008; Van Nieuwenhove et al., 2006), Iran (Ghavidel-Syooki and Winchester-Seeto, 2002; Ghavidel-Syooki, 2016, 2017a, 2017b; Ghavidel-Syooki and Borji, 2018), and the Arabian Peninsula (Paris et al., 2015; Al-Shawareb et al., 2017). A comparison of the Armoricochitina nigerica Biozone to the chronostratigraphic chart of Videt et al. (2010) indicates late Katian (uppermost part of time slice Ka3 to lower part of Ka4) for this biozone of Ghelli Formation.

4.2.4. Ancyrochitina merga Biozone

The base of this biozone is marked by the FAD of Ancyrochitina merga (Jenkins, 1970). Its top corresponds to the first FAD of Tanuchitina elongata (Bouché, 1965), which is the index species of the succeeding biozone. In the present material, Ancyrochitina merga occurs with abundant frequency in samples MG-MHP 21 to MG-MHP 27 (Fig. 2; Table 1). This biozone covers a thickness of 129-m, which consists mainly of shales and two igneous sills followed by an alternation of shale and sandstone. Ancyrochitina merga, a well known Upper Ordovician taxon (upper Katian), has been recorded in the United States (Jenkins, 1970), Libya (Molyneux and Paris, 1985; Paris, 1988; Abuhmida, 2013), Morocco (Elaouad-Debbaj, 1984; Bourahrouh et al., 2004), Algerian Sahara (Oulebsir and Paris, 1995), the Arabian Peninsula (Al-Hajri, 1995; Paris et al., 2000a; Paris et al., 2015; Al-Shawareb et al., 2017), Turkey (Oktay and Wellman, 2019), and Iran (Ghavidel-Syooki, 2000, 2008, 2016, 2017a, 2017b; Ghavidel-Syooki and Winchester-Seeto, 2002; Ghavidel-Syooki et al., 2011a, 2011b). The total range of this species was used by Paris (1990) and Bourahrouh et al. (2004) to define the Ancyrochitina merga Biozone in the northern Gondwana Domain. The associated chitinozoan species of this biozone include Plectochitina sylvanica (Jenkins, 1970), Tanuchitina ontariensis (Jansonius, 1964), and Ancyrochitina ellisbayensis (Soufiane and Achab, 2000). These taxa are characteristic components of Upper Ordovician worldwide, including the United States (Jenkins, 1970), Canada (Jansonius, 1964; Achab, 1984; Soufiane and Achab, 2000), Libya (Molyneux and Paris, 1985), Morocco (Elaouad-Debbaj, 1984, 1986; Bourahrouh et al., 2004), the Arabian Peninsula (Al-Hajri, 1995; Paris et al., 2015; Al-Shawareb et al., 2017), Iran (Ghavidel-Syooki and Winchester-Seeto, 2002; Ghavidel-Syooki et al., 2011a; Ghavidel-Syooki, 2008, 2016; Ghavidel-Syooki and Borji, 2018), and Turkey (Paris et al., 2007). A comparison of the Ancyrochitina merga Biozone to the chronostratigraphic chart of Videt et al. (2010) suggests the latest Katian (time slice Ka4) for this biozone of the Ghelli Formation in Kuh-e Boghou.

4.2.5. Tanuchitina elongata Biozone

The base of this biozone is marked by the FAD of *Tanuchitina elongata* (Bouché, 1965). Its top is distinguished by the first FAD of *Spinachitina oulebsiri* (Paris et al., 2000), which is the index species of the succeeding biozone. In this study, *Tanuchitina elongata* is present at rare to common frequencies in the samples MG-MHP 27 through MG-MHP 40 (Fig. 2; Table 1). This biozone, which covers a thickness of 104-m, primarily

consists of olive-gray shale, siltstone, and a limestone bed. The Tanuchitina elongata Biozone was originally defined by Paris et al. (2000a) and assigned to Late Ordovician (Late Ashgill). After the definition of the Spinachitina oulebsiri Biozone in Late Ordovician from the northeast Algerian Sahara (Paris et al., 2000a), the upper boundary of the Tanuchitina elongata Biozone was amended to be the FAD of Spinachitina oulebsiri (Paris et al., 2000a), the index species of the succeeding biozone. Herein, Tanuchitina elongata is regarded as a senior synonym of Tanuchitina bergstromi (Laufeld, 1967). This biozone has been well documented from Late Ordovician in Northern Africa including Morocco, Tunisia, Libya, and Algeria (Bouché, 1965; Elaouad-Debbaj, 1988; Paris, 1990; Oulebsir and Paris, 1995; Abuhmida, 2013); the Middle East including Iran (Ghavidel-Syooki and Winchester-Seeto, 2002; Ghavidel-Syooki, 2008, 2016, 2017a, 2017b), Turkey (Steemans et al., 1996; Paris et al., 2007; Oktay and Wellman, 2019), and the Arabian Peninsula (McClure, 1988; Al-Hajri, 1995; Paris et al., 2000b, 2015; Al-Shawareb et al., 2017). According to Paris (1990), at least the upper part of the Ra'an Shale member of the Qasim Formation in the Arabian Peninsula comprises the Tanuchitina elongata Biozone, which is associated with the Glyptograptus persculptus graptolite zone, indicating the early Hirnantian Stage (Webby et al., 2004). The Tanuchitina elongata Biozone has also been established in the upper part of the Halevikdere Formation (Hirnantian) in the Divarbakir area from southeastern Turkey (Steemans et al., 1996). However, subsequent studies by Paris et al. (2000a) also suggested the presence of a Spinachitina oulebsiri Biozone of the late Hirnantian in the uppermost part of the Halevikdere Formation of Turkey (Paris et al., 2007). The associated chitinozoan taxa in this biozone include Euconochitina moussegoudaensis (Paris in Le Hérissé et al., 2013), Alhajrichitina adamantea (Al-Shawareb et al., 2017), Alhajrichitina spinifera n. sp., Rhabdochitina curvata (Al-Shawareb et al., 2017), Spinachitina bulmani (Jansonius, 1964), and Eisenackitina sp. With the exception of Alhajrichitina spinifera and Eisenackitina sp., which are new records in our study area, the remaining species are characteristic components of the Upper Ordovician worldwide, including Iran (Ghavidel-Syooki and Winchester-Seeto, 2002; Ghavidel-Syooki, 2008, 2016, 2017b; Ghavidel-Syooki and Borji, 2018), Chad (Paris in Le Hérissé et al., 2013), Turkey (Oktay and Wellman, 2019), the Arabian Peninsula (Al-Hajri, 1995; Paris and Al-Hajri, 1995; Al-Shawareb et al., 2017), Morocco (Elaouad-Debbaj, 1986), Canada (Achab, 1978), Norway (Grahn et al., 1994), and Libya (Molyneux and Paris, 1985). A comparison of the Tanuchitina elongata Biozone to the chronostratigraphic chart of Videt et al. (2010) suggests early Hirnantian (time slice Hi1)) for this biozone of Ghelli Formation in Kuh-e Boghou.

4.2.6. Spinachitina oulebsiri Biozone

The base of this biozone is marked by the FAD of Spinachitina oulebsiri (Paris et al., 2000) in the Ghelli Formation. Its top corresponds to the first FAD of Spinachitina laevanensis (Nestor, 1980), which is the index species of the succeeding biozone in Early Silurian (Niur Formation; Ghavidel-Syooki and Vecoli, 2007). In this study, Spinachitina oulebsiri occurs at common frequency in samples MG-MHP 28 to MG-MHP 60 (Fig. 2; Table 1). This biozone, which includes a 36-m thickness of the Ghelli Formation in Kuh-e Boghou, mainly consists of siltstone with a 3-m heterogeneous conglomerate (Fig. 2). Spinachitina oulebsiri, which was originally established in the Upper Member of the M'Kratta Formation, northeast Algerian Sahara, Borj Nili area (Paris et al., 2000a), was indirectly correlated with the Normalograptus persculptus graptolite zone of the latest Hirnantian (Webby et al., 2004; Paris, 2006). This chitinozoan biozone is of particular interest regarding its correlation with Late Ordovician strata and its recognition of the Ordovician-Silurian boundary. Spinachitina oulebsiri has been recorded from the Hirnantian stage at numerous localities in Northern Africa (Le Heron and Craig, 2008; Abuhmida, 2013; Le Hérissé et al., 2013), Turkey (Steemans et al., 1996; Paris et al., 2007), and Iran (Ghavidel-Syooki, 2008; Ghavidel-Syooki et al., 2011b; Ghavidel-Syooki, 2016, 2017a, 2017b). This chitinozoan biozone is used to define the uppermost part of the chitinozoan biozones in the northern Gondwana Domain. However, Butcher (2009) guestioned the taxonomic validity of Spinachitina oulebsiri and the usefulness of this biozone, demonstrating that it is impossible to find quantitative criteria to clearly distinguish Spinachitina oulebsiri (Paris et al., 2000a) from Spinachitina fragilis (Nestor, 1980). The latter species was then considered by Butcher (2009) as a senior synonym of the former. According to Paris et al. (2000a), Spinachitina oulebsiri could be regarded as an early developmental stage of the Spinachitina fragilis lineage characterized by "the increase of the vesicle's length, by a progressive differentiation of the flexure, and by the development of a crown of spines on the margin while the diameter remains more or less stable" (Paris et al., 2000a, p. 101). Vandenbroucke et al. (2009) also recognized the objective difficulties in differentiating species within the Spinachitina oulebsiri-Spinachitina fragilis lineage, especially in poorly- or moderatelypreserved specimens. However, Vandenbroucke et al. (2009) decided to keep the two species until more detailed analyses were performed. They considered the split between the two morphotypes as being supported by subtle differences (conical vs. cylindrical basal spines, and overall stouter vs. slender chamber appearance in Spinachitina oulebsiri and Spinachitina fragilis, respectively).

Spinachitina oulebsiri has recently been reported from the Soom Shale of South Africa (Vandenbroucke et al., 2009), the Zapla Formation of northwestern Argentina (De La Puente, 2009; De La Puente and Rubinstein, 2013), and the Upper Ordovician (Hirnantian), Ghelli Formation, northeast of Alborz Mountains in Iran (Ghavidel-Syooki, 2008, 2016, 2017a, 2017b). Taxonomic revisions have differentiated Spinachitina oulebsiri from Spinachitina fragilis (Paris et al., 2000). The associated chitinozoan taxa of this biozone are Conochitina rotundata (Paris et al., 2015), Pistillachitina comma (Eisenack, 1959), and Cyathochitina caputoi (Da Costa, 1971), which are characteristic components of Late Ordovician (Hirnantian) in the northern-central Arabian Peninsula (Paris et al., 2015; Al-Shawareb et al., 2017), Iran (Ghavidel-Syooki, 2017b; Ghavidel-Syooki and Borji, 2018), and Chad (Le Hérissé et al., 2013). A comparison of the Spinachitina oulebsiri Biozone to the chronostratigraphic chart of Videt et al. (2010) reveals the late Hirnantian stage (time slice Hi2) for this biozone.

4.3. Acritarchs

Thirty-four acritarch species (24 genera) were identified from the Upper Ordovician, Ghelli Formation, Kuh-e Boghou (Plates VIII–IX).

4.3.1. List of acritarch taxa

Genus: Acanthodiacrodium Timofeev, 1958 emend. Deflandre and Deflandre-Rigaud, 1962

Acanthodiacrodium crassus (Loeblich and Tappan, 1978) Vecoli, 1999 (Plate VIII, 19)

Genus: **Baltisphaeridium** Eisenack, 1958 ex. Eisenack, 1959 emend. Eiserhart, 1989

Baltisphaeridium trophirhapium Loeblich and Tappan, 1978 (Plate IX, 11)

Baltisphaeridium perclarum Loeblich and Tappan, 1978 (Plate IX, 19) *Baltisphaeridium* sp. (Plate IX, 17)

Genus: Cornuferifusa Jacobson and Achab, 1985

Cornuferifusa bifidipertica Jacobson and Achab, 1985 (Plate VIII, 5) *Genus:* **Comasphaeridium** Staplin et al., 1965

Comasphaeridium lanugiferum Jacobson and Achab, 1985 (Plate VIII, 15)

Genus: **Dactylofusa** Brito and Santos, 1965 emend. Cramer, 1971 *Dactylofusa cucurbita* Jardiné et al., 1974 (Plate VIII, 3, 4)

Dactylofusa striatifera (Cramer and Díez, 1972) Fensome et al., 1990 (Plate VIII, 2)

Dactylofusa platynetrella (Loeblich and Tappan) Fensome et al., 1990 (Plate VIII, 8)

Genus: Diexallophasis Loeblich, 1970

Diexallophasis denticulata (Stockmans and Williére) Loeblich, 1970 (Plate IX, 7)

Genus: Disparifusa Loeblich, 1970

Disparifusa perryi Loeblich and Tappan, 1978 (Plate VIII, 16)

Genus: Dorsennidium Wicander, 1974 emend. Sarjeant and Stancliffe, 1994

Dorsennidium hamii (Loeblich, 1970) Sarjeant and Stancliffe, 1994 (Plate IX, 18)

Genus: Estiastra Eisenack, 1959

Estiastra iranicum Ghavidel-Syooki, 2000 (Plate IX, 12)

Genus: **Excultibrachium** Loeblich and Tappan, 1978 emend. Turner, 1984

Excultibrachium concinnum Wicander et al., 1999 (Plate IX, P) Genus: Frankea Burmann, 1970 emend. Servais, 1993 Frankea breviuscula Burmann, 1970 (Plate IX, C) Genus: Leiofusa Eisenack, 1938 emend. Combaz et al., 1967 Leiofusa litotes Loeblich and Tappan, 1978 (Plate VIII, 9) Genus: Lophosphaeridium Timofeev, 1959 ex. Downie, 1963 Lophosphaeridium acinatum Wicander et al., 1999 (Plate VIII, 10) Lophosphaeridium bulbosumensis n. sp. (Plate VIII, 20, 21, 22, 23) Genus: Multiplicisphaeridium Staplin, 1961 emend. Turner, 1984 Multiplicisphaeridium irregulare Staplin et al., 1965 (Plate IX, I) Genus: Navifusa Combaz et al., 1967 ex. Eisenack et al., 1976 Navifusa ancepsipuncta Loeblich, 1970 ex. Eisenack et al., 1979

(Plate VIII, 1)

Genus: Neoveryhachium Cramer, 1971

Neoveryhachium carminae Cramer, 1970 (Plate IX, 10)

Genus: Inflatarium Le Hérissé et al., 2014

Inflatarium trilobatum Le Hérissé et al., 2014 (Plate IX, 1, 2)

Genus: Ordovicidium Tappan and Loeblich, 1971

Ordovicidium elegantulum Tappan and Loeblich, 1971 (Plate IX, 14) Genus: **Orthosphaeridium** Eisenack, 1968 emend. Kjellström, 1971

Orthosphaeridium rectangulare (Eisenack, 1963) Eisenack, 1968 (Plate IX, 13)

Orthosphaeridium insculptum Loeblich, 1970 (Plate IX, 6) Genus: **Safirotheca** Vavrdová, 1989

Safirotheca safira Vavrdová, 1989 (Plate VIII, F, G)

Genus: **Tunisphaeridium** Deunff and Evitt, 1968

Tunisphaeridium eisenackii Loeblich and Tappan, 1978 (Plate IX, 20)

Genus: **Tylotopalla** Loeblich, 1970

Tylotopalla caelamenicutis Loeblich, 1970 (Plate IX, 5)

Genus: Veryhachium Deunff, 1954 emend. Sarjeant and Stancliffe, 1994

Veryhachium trispinosum (Eisenack, 1938) Stockmans and Williére, 1963 (Plate IX, 15)

Veryhachium lairdii (Deflandre) Deunff, 1959 ex. Downie, 1959 (Plate IX, 8)

Genus: **Villosacapsula** Loeblich and Tappan, 1976 *Villosacapsula setosapellicula* (Loeblich, 1970) Loeblich and Tappan, 1976 (Plate IX, 4)

4.3.2. Unranked group EUGLENIDA Büschli 1884, emend. Simpson 1997 Genus: **Moyeria** Thusu, 1973 Type species: Moyeria uticana Thusu, 1973 Moyeria cabottii (Cramer, 1971) Miller and Eames, 1982 (Plate

VIII, 17)

Moyeria hafezii n. sp. (Plate VIII, 11, 12, 13, 14) Moyeria sp. A. (Plate VIII, 18)

4.3.3. Systematic paleontology of the newly identified acritarch taxa *Incertae sedis* Group Acritarcha Evitt, 1963.

Genus: **Baltisphaeridium** Eisenack, 1958 ex. Eisenack, 1959 emend. Eisenack, 1959

Type species: Baltisphaeridium longispinosum (Eisenack, 1931 ex. Wetzel, 1933) Eisenack, 1959

Baltisphaeridium sp. (Plate IX, 17)

Type stratum: Upper Ordovician, Ghelli Formation (samples MG-MHP 22 to MG-MHP 55), Kuh-e Boghou, southwest of Kashmar, eastern-central Iran.

Dimensions: Vesicle diameter without processes, $42 \mu m$; vesicle diameter with processes, $92 \mu m$; length of process, $25.5 \mu m$; width of process, $2.5 \mu m$. One specimen was measured.

Description: Vesicles circular to subcircular in outline. Eilyma thick and psilate with numerous arcuate compression folds. Processes discrete, heteromorphic, and straight to slightly bent, freely communicating with the vesicle cavity. Proximal contacts of the processes orthogonal, tapering slightly to a distal point. Processes covered by thread-like ornamentations from the base to top. In some wellpreserved processes, distal points are fensate and associated with thread sculptures.

Genus: **Lophosphaeridium** Timofeev, 1959 ex. Downie, 1963 emend. Lister, 1970

Type species: Lophosphaeridium rarum Timofeev, 1959 ex. Downie, 1963.

Lophosphaeridium bulbosumensis n. sp. (Plate VIII, 20, 21, 22, 23)

Holotype: Plate VIII, 21

Type stratum: Upper Ordovician (Ghelli Formation), Kuh-e Boghou, southwest of Kashmar, eastern-central Iran.

Name derivation: Refers to its bulbous or tubercle-like vesicle ornamentations.

Dimensions: Diameter, 30.7 (36.6) 43.5 μ m; diameter of vesicle, 3.5 (4) 4.8 μ m; number of bulbous ornamentations, 26 (37.5) 43. Four specimens were measured.

Description: Vesicles circular to subcircular in outline and commonly present compression folds. Eilyma perforate with numerous, discrete, separate, solid tubercle-like or irregular bulbous ornamentations that are rounded in polar view and arcuate in lateral view. Tubercles range in size from 3.5 µm to 4.8 µm. This species differs from other *Lophosphaeridium* species in their bulbous or tubercle ornamentations.

Occurrence: Samples MG-MHP 18 to MG-MHP 60 of the Ghelli Formation.

Unranked group EUGLENIDA Büschli 1884, emend. Simpson 1997.

Genus: Moyeria Thusu, 1973

Type species: Moyeria uticana Thusu, 1973

Moyeria hafezii n. sp. (Plate VIII, 11, 12, 13, 14)

Holotype: Plate VIII, 12. Type stratum: Upper Ordovician strata (Ghelli Formation), Kuh-e Boghou, southwest of Kashmar, eastern-central Iran.

Name derivation: Refers to Khwāja Shams-ud-Dīn Muḥammad Hāfeẓ-e Shīrāzī, the Persian poet known as Hafez and as "Hafiz" (born in 1315 ACE in Shiraz; died in 1390 ACE in the same city; buried in Tomb Hafez, Shiraz). He is famous for his lyrical poems, and his major work is "Divan of Hafez."

Dimensions: Vesicle length, 29.2 (56.6) 64.5 μm; vesicle width, 18.5 (28.5) 35.3 μm; number of muri, 5 (6.5) 7; width, 1.1 (1.5) 1.8 μm.

Description: Hollow vesicles, naviform in outline with rounded polar regions. Thin, psilate eilyma ornamented with 5–7 solid, psilate, parallel muri, forming a helicoidal pattern. No excystment structure observed.

Occurrence: Samples MG-MHP 18 to MG-MHP 53 from the Ghelli Formation.

Remarks: Moyeria hafezii n. sp. superficially resembles Spurimoyeria facilaculata (Wicander and Loeblich, 1977) and Spurimoyeria iranica (Hashemi and Playford, 1998). Moyeria hafezii differs from Spurimoyeria species in its helicoidal or spiral patterns of ribs, contrasting to the linear muri of the latter. Moyeria hafezii n. sp. is older than the Spurimoyeria facilaculata and Spurimoyeria iranica reported by Wicander and Loeblich (1977) and Hashemi and Playford (1998), and it is also larger in size and presents more muri than Spurimoyeria facilaculata and Spurimoyeria iranica.

Moyeria sp. A (Plate VIII, 18)

Type stratum: Moyeria sp. is rarely present in the Ghelli Formation from samples MG-MHP 18 to MG-MHP27.

Dimensions: Total length with membrane, 68 μ m; total length without membrane, 58 μ m; membrane thickness, 2.5–10 μ m; length of upper cell, 27 μ m; length of lower cell, 29.3 μ m.

Description: This species has two separated vesicles that distinctively contact and are surrounded by a membrane. Muri are psilate and range in number from 7 to 10 with a width of 1.1–1.3 µm. This species differs from other Moyeria species in the dyad–shaped pattern enclosed in an enveloped membrane and helicoidal muri pattern. It could not be identified to the specific level because of insufficient specimens.

4.3.4. Acritarch biostratigraphy

In the study area, acritarchs first appeared in the lowermost part of the Ghelli Formation, including Villosacapsula setosapellicula (Loeblich, 1970; Loeblich and Tappan, 1976), Acanthodiacrodium crassus (Loeblich and Tappan, 1978; Vecoli, 1999), Multiplicisphaeridium irregulare (Staplin et al., 1965), Diexallophasis denticulata (Stockmans and Willière) Loeblich, 1970), Leiofusa litotes (Loeblich and Tappan, 1978), Ordovicidium elegantulum (Tappan and Loeblich, 1971), Veryhachium trispinosum (Eisenack) Deunff, 1954 ex Downie, 1954, and Veryhachium lairdii (Deflandre) Deunff, 1959 ex Downie, 1959 (Table 3). These acritarch taxa first occurred in sample MG-MHP 2 and persisted in the succeeding chitinozoan biozones (Fig. 2). Veryhachium trispinosum, Veryhachium lairdii, and Diexallophasis denticulata are long-ranging taxa occurring throughout the Paleozoic Era in Sweden (Kjellström, 1971; Górka, 1987), United Kingdom (Turner, 1985), United States (Loeblich and Tappan, 1978; Wicander et al., 1999; Playford and Wicander, 2006), Czech Republic (Vavrdová, 1988), the Arabian Peninsula (Jachowicz, 1995; Le Hérissé et al., 2014; Le Hérissé et al., 2017), and Iran (Ghavidel-Syooki, 2008, 2016, 2017a). Other acritarch species, such as Villosacapsula setosapellicula, Leiofusa litotes, Acanthodiacrodium crassus, Multiplicisphaeridium irregulare, and Ordovicidium elegantulum have only been recorded from the Late Ordovician (Katian) in the United States (Loeblich, 1970; Miller, 1991; Wicander et al., 1999; Playford and Wicander, 2006), Canada (Jacobson and Achab, 1985), Algerian Sahara (Jardiné et al., 1974), Libya (Molyneux and Paris, 1985; Hill and Molyneux, 1988; Abuhmida, 2013), Morocco (Elaouad-Debbaj, 1988), Portugal (Elaouad-Debbaj, 1981), the Arabian Peninsula (Jachowicz, 1995; Le Hérissé et al., 2014; Le Hérissé et al., 2017), Jordan (Keegan et al., 1990), and the Iranian Platform (Ghavidel-Syooki et al., 2011a, 2011b; Ghavidel-Syooki, 2008, 2016, 2017a, 2017b). The second, third, and fourth appearances of acritarch taxa were observed in samples MG-MHP 14 to MG-MHP 18, and consisted of Dactylofusa platynetrella (Loeblich and Tappan, 1978) Fensome et al., 1990, Dactylofusa striatifera (Cramer and Díez, 1972) Fensome et al., 1990, Orthosphaeridium insculptum (Loeblich, 1970), Dactylofusa striata (Staplin et al., 1965) Fensome et al., 1990, Moyeria cabottii (Cramer, 1971) Miller and Eames, 1982, Dactylofusa cucurbita Jardiné et al., 1974, Tunisphaeridium eisenackii (Loeblich and Tappan, 1978), Inflatarium trilobatum Le Hérissé et al., 2014, Estiastra iranicum Ghavidel-Syooki, 2000, Baltisphaeridium perclarum Loeblich and Tappan, 1978, Lophosphaeridium acinatum Wicander and Playford, 1999, Lophosphaeridium bulbosumensis n. sp., Dorsennidium hamii (Loeblich) Sarjeant and Stancliffe, 1994, Tylotopalla caelamenicutis Loeblich, 1970, Safirotheca safira Vavrdová, 1989, Neoveryhachium carminae Cramer, 1971, Navifusa ancepsipuncta Loeblich, 1970, Disparifusa perryi Loeblich and Tappan, 1978, and Moyeria hafezii n. sp. (Fig. 2). Lophosphaeridium bulbosumensis n. sp. and Moyeria hafezii n. sp. were recorded for the first time. Orthosphaeridium insculptum, Navifusa ancepsipuncta, Dorsennidium hamii, Baltisphaeridium perclarum, Lophosphaeridium acinatum, Tunisphaeridium eisenackii, Moyeria cabottii, Dactylofusa platynetrella, Dactylofusa striata, Dactylofusa striatifera, Dactylofusa cucurbita, and Safirotheca safira have only been

recorded from the Upper Ordovician of north America (Loeblich and Tappan, 1978; Jacobson and Achab, 1985; Robertson, 1997; Wicander and Playford, 2008), Northern Africa (Jardiné et al., 1974; Hill and Molyneux, 1988; Vecoli, 1999), Jordan (Keegan et al., 1990), the Arabian Peninsula (Jachowicz, 1995; Le Hérissé et al., 2014), and Iran (Ghavidel-Syooki, 2000, 2003, 2008, 2016, 2017a, 2017b). Dactylofusa cucurbita and Safirotheca safira are restricted to the peri-Gondwanan paleoprovince (Jardiné et al., 1974; Vavrdová, 1988, 1989; Vecoli, 1999; Le Hérissé et al., 2014; Ghavidel-Syooki, 2016, 2017a, 2017b). Moreover, it should be noted that the presence of Moyeria cabottii in samples MG-MHP 15 to MG-MHP 37 (Fig. 2; Table 1) has been recorded in the Middle–Upper Ordovician strata of Sweden (Kjellström, 1971; Górka, 1987), England (Turner, 1985), the United States (Loeblich and Tappan, 1978; Colbath, 1979), Czech Republic (Vavrdová, 1988), China (Li et al., 2006), and Iran (Ghavidel-Syooki, 2017a, 2017b). It is worth noting that Moyeria cabottii (Cramer, 1971) Miller and Eames, 1982 is a common palynomorph in the Ordovician–Silurian shallow-water, nearshore marine environment (Gray and Boucot, 1989) but also from various nonmarine deposits. Genus Moyeria has recently been transferred from the incertae sedis group Acritarcha to the Euglenida which comprise the oldest freshwater protozoans (Strother et al., 2019). As so, there is no ambiguity regarding the affinity of this taxon. Although Neoveryhachium carminae was originally described and introduced from the Middle Silurian of north America (Cramer, 1971), it has been recorded from the Upper Ordovician elsewhere, such as Northern Africa (Vecoli, 1999), Iran (Ghavidel-Syooki, 2008; Ghavidel-Syooki et al., 2011b; Ghavidel-Syooki, 2016, 2017a, 2017b), the Arabian Peninsula (Le Hérissé et al., 2014), and China (Li et al., 2006). Therefore, this species stratigraphic range is from the Upper Ordovician to the Middle Silurian. The fifth appearance of acritarchs is characterized by the presence of Excultibrachium concinnum (Wicander and Playford, 1999), Cornuferifusa bifidipertica (Jacobson and Achab, 1985), Comasphaeridium lanugiferum (Jacobson and Achab, 1985), Baltisphaeridium sp., and Frankea breviuscula (Burmann, 1970). Excultibrachium concinnum, Comasphaeridium lanugiferum, and Cornuferifusa bifidipertica have been recorded from the Late Ordovician (Sandbian) of the United States (Loeblich and Tappan, 1978; Colbath, 1979; Wicander et al., 1999; Playford and Wicander, 2006), Late Ordovician (Sandbian-Katian) of Canada (Legault, 1982; Jacobson and Achab, 1985), Late Ordovician (Sandbian) of England (Turner, 1984), and Darriwilian-Sandbian of Gotland, Sweden (Górka, 1987). Frankea breviuscula has also been recorded from the Darriwilian of eastern Germany (Burmann, 1970) and Czech Republic (Vavrdová, 1977), and from the Sandbian, Shropshire, England (Turner, 1982).

4.4. List of cryptospore taxa

4.4.1. Naked unfused tightly and loosely adherent cryptospore tetrads subgroup

Genus: Cryptotetras Strother et al., 2015

Cryptotetras erugata Strother et al., 2015 (Plate VI, 14)

Cryptotetras mordacis Strother et al., 2015 (Plate VII, 1, 2)

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

Tetrahedraletes medinensis Strother & Traverse emend Wellman and Richardson, 1993. (Plate IV, 13; Plate VI, 21; Plate VII, 14)

Tetrahedraletes grayae Strother, 1991 (Plate VI, 1, 2)

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

Tetraplanarisporites laevigatus Wellman et al., 2015 (Plate VI, 18, 19, 20)

Genus: Rimosotetras Burgess, 1991 Rimosotetras problematica Burgess, 1991 (Plate VI, 7, 8) Rimosotetras subspherica Strother et al., 2015 (Plate VI, 15, 16) Rimosotetras punctata Ghavidel-Syooki, 2017a (Plate VI, 9) Rimosotetras granulata Ghavidel-Syooki, 2017a (Plate VI, 15) 4.4.2. Naked fused cryptospore tetrads subgroup Genus: Cheilotetras Wellman and Richardson, 1993 Cheilotetras caledonica Wellman and Richardson, 1993 (Plate VII, 18, 19)

4.4.3. Envelope-enclosed unfused cryptospore tetrads subgroup Genus: Velatitetras Burgess, 1991 Velatitetras retimembrana (Miller and Eames) Steemans et al., 1996

(Plate VII, 11, 12, 13)

Velatitetras rugosa (Strother and Traverse) Steemans et al., 1996 (Plate VI, 17)

4.4.4. Envelope-enclosed unfused cryptospore dyads subgroup Genus: Abditusdyadus Wellman and Richardson, 1996 Abditusdyadus laevigatus Wellman and Richardson, 1996 (Plate VI, 22, 23; Plate VII, 21, 22, 23, 24)

Abditusdyadus khayyammii n. sp. (Plate VI, 6, 20)

4.4.5. Envelope-enclosed fused cryptospore dyads subgroup Genus: Segestrespora Burgess, 1991 Segestrespora membranifera (Johnson, 1985) Burgess, 1991 (Plate VI, 5; Plate VII, 17)

Segestrespora laevigata Burgess, 1991 (Plate VII, 16) Segestrespora burgessii Steemans et al., 1996 (Plate VII, 20) Segestrespora iranense Ghavidel-Syooki, 2017a (Plate VII, 4)

4.4.6. Unfused naked cryptospore dyads (true dyads) subgroup Genus: Dyadospora (Strother and Traverse, 1979) emend. Burgess and Richardson, 1991

Dyadospora murusattenuata (Strother and Traverse, 1979) Burgess and Richardson, 1991 (Plate VI, 3, 4)

Dyadospora asymmetrica Ghavidel-Syooki, 2017a (Plate VII, 3) Dyadospora verrucata Ghavidel-Syooki, 2017a (Plate VI, 10) Dyadospora ferdowsii n. sp. (Plate VII, 7, 8, 9, 10

4.4.7. Spores physically separated from cryptospore polyads Genus: Imperfectotriletes Steemans et al., 2000 Imperfectotriletes vavrdovae (Richardson) Steemans et al., 2000 (Plate VI, 12)

Imperfectotriletes patinatus Steemans et al., 2000 (Plate VII, 5, 6) *Imperfectotriletes persianense* Ghavidel-Syooki, 2017a (Plate VI, 13)

4.4.8. Systematics of new cryptospore taxa Anteturma cryptosporites (Richardson, 1988) Subgroup envelope-enclosed unfused cryptospore dyads Genus: Abditusdyadus Wellman and Richardson, 1996 Type species: Abditusdyadus histosus Wellman and Richardson, 1996 Abditusdyadus khayyammii n. sp. (Plate VI, 6, 20) Holotype: Plate VI, 6

Type stratum: Upper Ordovician, Ghelli Formation, Kuh-e Boghou, 46 km southwest of Kashmar, eastern-central Iran.

Name derivation: Refers to Omar Khayyam Neyshaburi, a Persian mathematician, astronomer, and poet (born on May 18, 1048 ACE in Neyshabur; died on December 4, 1131 ACE in the same city).

Dimensions: Length, 48.7 (50.6) 52.5 μ m; width, 35.8 (39.15) 42.5 μ m; thickness of envelope-enclosed unfused cryptospore dyads, 2.7 (3.6) 4.5 μ m; number of pores, 76. Fifteen specimens were measured.

Description: Cryptospore consisting of a dyad with levigate ornamentations and hilate with thick-wall enveloped membrane. Dyad with two attached prominent spores enclosed by a tightly complete or incomplete levigate membrane. Spores levigate with many visible pores. This species differs from other species of *Abditusdyadus* in its perorate sculpture and thin tight membrane.

Occurrence: Samples MG-MHP 45 to MG-MHP 57.

Remarks: This taxon differs from other species of *Abditusdyadus* in having punctate sculptures.

Subgroup unfused naked cryptospore dyads (true dyads)

Genus: **Dyadospora** (Strother and Traverse, 1979) emend. Burgess and Richardson, 1991

Type species: Dyadospora murusattenuata Strother and Traverse, 1979 emend. Wellman and Richardson, 1993

Dyadospora ferdowsii n. sp. (Plate VII, 7, 8, 9, 10) *Holotype*: Plate VII, 9

Type stratum: Upper Ordovician, Ghelli Formation, Kuh-e Boghou, 46 km southwest of Kashmar, eastern-central Iran.

Name derivation: Refers to Abul-Qâsem Ferdowsi Tusi, a Persian poet and the author of the Shahnameh book, the longest epic poem in the world created by a single poet, and the national epic of Greater Iran (born in 940 ACE in Tus, near Mashhad; died in 1020 ACE in the same place).

Dimensions: Length, 27 (35.8) 49.5 μm; width, 17.8 (29.9) 34 μm; number of pores, 30–65. Fifteen specimens were measured.

Description: Terrestrial dyad cryptospore consisting of two loosely attached prominent spores. This species includes two spores with heteromorphic sizes; in equatorial view, the contact of individual spores is usually tight but loose occasionally. Surfaces of both spores punctate and the number of pores in each dyad range from 30 to 76.

Occurrence: Samples MG-MHP 45 to MG-MHP 57 of the Upper Ordovician (Ghelli Formation).

Remarks: This taxon differs from other species of *Dyadospora* in having punctate sculptures.

4.5. Biostratigraphy of cryptospores

The cryptospores identified in the study area are critical because they have a limited stratigraphic range from the Middle Ordovician to the Lower Silurian (Vecoli et al., 2017). The surface samples of the Ghelli Formation contained 25 cryptospore species (10 genera) and 1 trilete spore species (1 genera). Three local events can be marked by cryptospores within the Ghelli Formation of Kuh-e Boghou. The first event of cryptospores is marked by Tetrahedraletes medinensis Strother and Traverse emend. Wellman and Richardson, 1993 in sample MG-MHP 11 of the Ghelli Formation and by its continuation through the succeeding chitinozoan biozones (Fig. 2). This taxon is a long-ranging cryptospore and has been recorded from the Middle Ordovician (Darriwilian) to Lower Silurian (Rhuddanian) elsewhere (Vavrdová, 1988; Burgess, 1991; Wellman, 1996; Steemans et al., 1996; Vecoli et al., 2011; Mahmoudi et al., 2014; Strother et al., 2015; Wellman et al., 2015; Ghavidel-Syooki, 2017a; Rubinstein and Vajda, 2019). The second event is marked by the occurrence of Velatitetras rugosa, which corresponds to the basal part of Armoricochitina nigerica, persisting into the succeeding chitinozoan biozones (Fig. 2). Velatitetras rugosa is present with very rare to common frequencies (Table 1) within the Ghelli Formation (MG-MHP 14 to MG-MHP 60) of Kuh-e Boghou. To date, this species has been recorded from the Ashgillian (Hirnantian) of Canada (Richardson and Ausich, 2007), the Silurian of United States (Beck and Strother, 2008), the Ashgillian of Belgium (Steemans, 2001), the Ashgill-Early Llandovery of the Czech Republic and Slovakia (Vavrdová, 1988, 1989), the Early Llandovery (Steemans et al., 2000; Wellman et al., 2000), the Late Ordovician (Katian-Hirnantian) of Canada and Estonia (Vecoli et al., 2011), the Late Ordovician (Sandbian-Hirnantian) of Turkey (Steemans et al., 1996), and the Upper Ordovician (Katian) of Iran (Ghavidel-Syooki, 2017a). The third event appears below and above a conglomerate horizon (3 m) in the upper part of the Ghelli Formation (Fig. 2). This event is characterized by the appearance of many cryptospore taxa (Fig. 2), including Tetrahedraletes grayae (Strother, 1991), Dyadospora murusattenuata (Strother and Traverse, 1979) Burgess and Richardson, 1991, Abditusdyadus khayyammii n. sp., Rimosotetras problematica (Burgess, 1991), Rimosotetras punctata (Ghavidel-Syooki, 2017a), Dyadospora verrucata (Ghavidel-Syooki, 2017a), Imperfectotriletes vavrdovae (Richardson) Steemans et al., 2000, Imperfectotriletes persianense (Ghavidel-Syooki, 2017a), Cryptotetras erugata (Strother et al., 2015), Rimosotetras subspherica (Strother et al., 2015), Tetraplanarisporites laevigatus (Wellman et al., 2015), Abditusdyadus laevigatus (Wellman and Richardson, 1996), Segestrespora burgessii (Steemans et al., 1996), Cryptotetras mordacis (Strother et al., 2015), Dyadospora asymmetrica (Ghavidel-Syooki, 2017a), Segestrespora iranense (Ghavidel-Syooki, 2017a), Imperfectotriletes patinatus (Steemans et al., 2000), Dyadospora ferdowsii n. sp., Velatitetras retimembrana (Miller and Eames) Steemans et al., 1996, Rimosotetras granulata (Ghavidel-Syooki, 2017a), Segestrespora laevigata (Burgess, 1991), Segestrespora membranifera (Johnson, 1985) Burgess, 1991, and Cheilotetras caledonica (Wellman and Richardson, 1993). This event corresponds to the appearance of Spinachitina oulebsiri in the study area (Fig. 2). Most of the aforementioned cryptospore species of the Ghelli Formation are typical of the interval ranging from the Middle Ordovician (Darriwilian) to the Early Silurian (Llandovery; Edwards and Wellman, 2001). To date, the aforementioned cryptospore taxa have been reported from Brazil and Paraguay (Gray et al., 1992; Melo and Steemans, 1997; Steemans, 2000; Steemans and Pereira, 2002), north America (Strother and Traverse, 1979; Miller and Eames, 1982; Duffield, 1985; Johnson, 1985), Belgium (Steemans, 2001), Bulgaria (Lakova et al., 1992), the Czech Republic (Vavrdová, 1984, 1988, 1989), the United Kingdom (Burgess, 1991; Wellman, 1996), China (Wang et al., 1997), Russia (Siberia) (Raevskaya et al., 2016), Turkey (Steemans et al., 1996), Iran (Mahmoudi et al., 2014; Ghavidel-Syooki, 2017a), the Arabian Peninsula (Steemans et al., 2000; Wellman et al., 2000; Strother et al., 2015; Vecoli et al., 2017), and Libya (Richardson, 1988; Le Hérissé et al., 2013; Abuhmida and Wellman, 2017). There is very limited palynostratigraphic evidence to distinguish Late Ordovician miospore assemblages from Early Silurian ones. The miospore biostratigraphy across the Ordovician-Silurian boundary was revised by Steemans et al. (2000). The authors stated that the primary criteria for this distinction include: (i) the first occurrence and proliferation of true trilete spores (e.g., Ambitisporites avitus Steemans et al., 1996), (ii) the first occurrence of Laevolancis divellomedia, and (iii) the progressive decline of cryptospores enclosed in membranous envelopes. In the present study, Iranian cryptospore assemblages were characterized by a high abundance of cryptospores enclosed in an outer envelope, numerous specimens of Imperfectotriletes sp., and absence of Laevolancis divellomedia. Furthermore, in our study area, there is a trend of increasing cryptospore diversity within the Late Ordovician, especially from the Katian to the Hirnantian. More than 25 cryptospore species were present in the Hirnantian strata of Kuh-e Boghou, which contain all basic morphologies of cryptospores, such as monads, naked or envelopeenclosed, and fused and unfused dyads and tetrads (Fig. 2). Similar results were found for Algerian (Spina, 2015), Argentina (Rubinstein and Vaccari, 2004; Rubinstein et al., 2016), Turkey (Steemans et al., 1996), and Arabian Peninsula (Wellman et al., 2015; Vecoli et al., 2017) assemblages. In addition, it is now well established that trilete spores consistently occur in Late Ordovician (Hirnantian) strata worldwide, as shown by the records of trilete spore assemblages (Steemans et al., 1996; Wellman et al., 2015; Rubinstein et al., 2016).

5. Discussion and conclusions

The present study was restricted to the Upper Ordovician strata, i.e., the Ghelli Formation. The investigated palynomorph was obtained from 69 samples collected from an outcrop section in Kuh-e Boghou, 46 km southwest of Kashmar in eastern-central Iran. Most of the samples yielded abundant and well-preserved acritarchs (34 species allocated to 24 genera), euglenid (3 species allocated to one genus), chitinozoans (36 species assigned to 19 genera), miospores (26 species belonging to 11 genera), and scolecodont (one species allocated to one genus), as well as some graptolite remains. Of the ninety-eight observed

palynomorph taxa, seven morphotypes were recorded for the first time and five of them were established as new species, namely, *Moyeria hafezii* n. sp., *Lophosphaeridium bulbosumensis* n. sp., *Alhajrichitina spinifera* n. sp., *Dyadospora ferdowsii* n. sp., and *Abditusdyadus khayyammii* n. sp.; two taxa were only identified to the genus level (*Moyeria* sp. A and *Eisenackitina* sp.). Among the identified palynomorph taxa of this formation, the chitinozoan taxa showed strong affinity to the Late Ordovician (Katian–Hirnantian) of the peri-Gondwanan Paleoprovince, including records from Northern Africa (Morocco, Algeria, Tunisia, Libya, and Nigeria), the Middle East (Turkey, the Arabian Peninsula, Syria, Jordan, and Iran), southwestern Europe (Italy, France, Spain, and Portugal), and central Europe (Czech Republic).

The known chitinozoan taxa allowed defining the *Belonechitina robusta, Tanuchitina fistulosa, Armoricochitina nigerica, Ancyrochitina merga, Tanuchitina elongata*, and *Spinachitina oulebsiri* biozones, which have been previously established in the north Gondwanan Domain but have never been recorded outside the Gondwanan Paleocontinent. On the contrary, based on the presence of these well known chitinozoan biozones, a Late Ordovician (Katian–Hirnantian) age has been assigned to the Ghelli Formation in Kuh-e Boghou. Moreover, comparison of these chitinozoan biozones with the chronostratigraphic charts of Webby et al. (2004), Paris (2006) and Videt et al. (2010), suggests a hiatus between the Ghelli Formation (Katian–Hirnantian) and the Derenjal Formation (Late Cambrian), spanning the Tremadocian– Sandbian interval, which corresponds to the absence of *Destombesi– Tanvillensis* chitinozoan biozones probably related to the initial stage of the Paleo-Tethys rifting.

Most acritarch taxa of the Ghelli Formation in Kuh-e Boghou have cosmopolitan distributions, with records from the Middle–Upper Ordovician strata of Sweden, England, Portugal, Czech Republic, the United States, China, Libya, Morocco, Algeria, the Arabian Peninsula, Turkey, and Iran. It should be mentioned that a few acritarch species of the Ghelli Formation, such as *Dactylofusa cucurbita*, *Safirotheca safira* and *Inflatarium trilobatum* are restricted to the peri-Gondwanan Paleoprovince. Furthermore, *Moyeria cabottii* (= *Dactylofusa cabottii*) was transferred from the *incertae sedis* group Acritarcha into the Euglenida based on new data (e.g. affinity, morphology, pellicle component, type species).

In the present study, the identified miospores were characterized by a trend of increasing cryptospore diversity from the Katian to Hirnantian, which represent all basic morphologies of cryptospores, including naked and enveloped-enclosed monads, dyads, tetrads, and polyads. These cryptospores are considered to represent the earliest evidence of continental vegetation and thus document a fundamental phase of land plants' evolution, confirming the worldwide uniformity of cryptospore assemblages during the Late Ordovician. The presence of miospores is most likely related to the global sea level fall which resulted in the earliest primitive land plants growing close to shoreline being washed in from adjacent areas and producing a high volume of miospores.

The Ghelli Formation mainly consists of siliciclastic sediments, containing a considerably high amount of detrital quartz, few feldspar grains, and high amounts of clay minerals. The lithofacies of this formation from base to top include lonestones, structureless mudstones, crudely laminated layers, finely laminated mudstones, and clast-poor muddy to sandy varieties. Other textural components of the Ghelli Formation include turbidite structures, grain lineations, and a soft sediment deformation of the matrix below larger grains. These sedimentological data suggest that deposition probably occurred in an ice-intermediate to ice-distal state with a low-agitation shelf environment in which materials were supplied by meltwater and run-off of ice-rafted debris. The debris flows and slumps were two important factors, particularly for mass flow and for the formation of massive diamictites by remobilization. The glaciomarine deposits of the Ghelli Formation represent a typical deglaciation sequence reflecting retreat of the ice front. The siliciclastic sediments of the Ghelli Formation can be correlated with similar glaciomarine deposits known from the peri-Gondwanan terranes elsewhere.

Declaration of Competing Interest

I wish to re-submit an original research article for publication in Review of Palaeobotany and Palynology, titled "Biostratigraphy of Acritarchs, Chitinozoans, and Miospores from Upper Ordovician Stratal Sequences in Kuh-e Boghou, Southwest of Kashmar, Eastern Central Iran: Stratigraphic and Palaeogeographic Implications." The paper was coauthored by Mohammad Hossein Piri-Kangarshahi.

This manuscript has not been published or presented elsewhere in part or in its entirety and is not under consideration by any other journal. We have read and understood your journal's policies, and we believe that neither the manuscript nor the study violates any of these. There are no conflicts of interest to declare.

Acknowledgments

We gratefully acknowledge Prof. Florentin Paris for checking our chitinozoan identifications and two anonymous reviewers for their helpful comments and suggestions to improve this manuscript. The authors also wish to thank Mrs. Zahra Orak for palynological treatment of the samples and specially thank Mrs. Hedieh Ghavidel-Syooki for providing thorough and constructive suggestions.

References

- Abuhmida, F., 2013. Palynological analysis of the Ordovician to Lower Silurian sediments from the Marzuq Basin, southwest Libya. Ph.D. thesis. University of Sheffield Department of Animal and Plant Sciences, p. 641.
- Abuhmida, F.H., Wellman, C.H., 2017. Palynology of the Middle Ordovician Hawaz Formation in theMurzuq Basin, south-west Libya. Palynology 41 (suppl.1), 31–56.
- Achab, A., 1978. Sur quelques chitinozoaires de la formation de vauréal et de la formation macasty (Ordovicien supérieur); ile d'anticosti, Québec, Canada. Rev. Palaeobot. Palynol. 25, 295–314.
- Achab, A., 1984. Chitinozoaires de l'ordovicien moyen de subsurface de l'ile anticosti. Rev. Palaeobot. Palynol. 43, 123–143.
- Ahmadi-Tabar, L., 2016. Palynostratigraphy and palaeogeography of the Upper Ordovician strata in Kashmar region with emphasis on chitinozoan fauna. Thesis for M. Sc degree in Stratigraphy and Palaeontology. Islamic Azad University, north Tehran branch, p. 117 (in Persian).
- Alavi, S.M., 1996. Palynostratigraphy and Palaeogeography of Late Ordovician Strata in Southwest of Kashmar City. Unpubl. M.Sc. Thesis. Ferdowsi University, p. 119 (in Persian).
- Al-Ghammari, M., 2010. Ordovician- Silurian Palynology of Oman. Ph.D. thesis. University of Sheffield, pp. 1–347 unpublished.
- Al-Hajri, S., 1995. Biostratigraphy of the Ordovician chitinozoa of northwestern Saudi Arabia. Rev. Palaeobot. Palynol. 89, 27–48.
- Al-Shawareb, A., Miller, M., Vecoli, M., 2017. Late Ordovician (Katian) chitinozoans from northwest Saudi Arabia: Biostratigraphic and paleoenvironmental implications. Rev. Micropaleontol. 60 (3), 333–369.
- Bagheri, S., Stampfli, G.M., 2008. The Anarak, Jandaq and Posht-e-Badam metamorphic complexes in central Iran: New geological data, relationships and tectonic implications. Tectonophysics 451, 123–155.
- Beck, J.H., Strother, P.K., 2008. Miospores and cryptospores from the Silurian section at Allenport, Pennsylvania, USA. J. Palaeontol. 82 (5), 857–883.
- Berberian, M., King, G.C.P., 1981. Towards a paleogeography and tectonic evolution of Iran. Can. J. Earth Sci. 18 (2), 210–265.
- Bouché, P.M., 1965. Chitinozoaires du Silurien sl du Djado (Sahara nigérien). Rev. Micropaleontol. 8 (3), 151–164.
- Bourahrouh, A., Paris, F., Elaouad-Debbaj, Z., 2004. Biostratigraphy, biodiversity and paleoenvironment of the chitinozoans and associated palynomorphs from the Upper Ordovician of the Central Anti-Atlas, Morocco. Rev. Palaeobot. Palynol. 130, 17–40.
- Brito, I.M., Santos, A.S., 1965. Contribuição ao conhecimento dos microfósseis silurianos e devonianos da Bacia do Maranhão. I – Os Netromorphitae (Leiofusidae). Not. Prelim. Est. Div. Geol. Mineral. 129, 1–23.
- Burgess, N.D., 1991. Silurian cryptospores and miospores from the type Llandovery area, south-west Wales. Palaeontology 34, 575–599.
- Burgess, N.D., Richardson, J.B., 1991. Silurian cryptospores and miospores from type Wenlock area, Shropshire, England. Palaeontology 34, 601–628.
- Burmann, G., 1970. Weitere organische Mikrofossilien aus dem unteren Ordovizium. Paläontologische Abhandlungen, Abt. B 3, 289–332.

Butcher, A., 2009. Early Llandovery chitinozoans from Jordan. Palaeontology 52 (3), 593–629.

Cocks, L.R.M., Torsvik, T.H., 2002. Earth geography from 500 to 400 million years ago: A faunal and palaeomagnetic review. J. Geol. Soc. 159 (6), 631–644.

- Colbath, G.K., 1979. Organic-walled microphytoplankton from the Eden Shale (Upper Ordovician), Indiana, U.S.A. Palaeontogr. Abt. B 171, 1–38.
- Combaz, A., Lange, F.W., Pansart, J., 1967. Les "Leiofusidae" Eisenack, 1938. Rev. Palaeobot. Palynol. 1, 291–307.
- Cramer, F.H., 1964. Microplankton from three Palaeozoic formations in the Province of León, NW-Spain. Leidse. Geol. Meded. 30 (1), 253–361.
- **Cramer, F.H., 1970.** Distribution of selected Silurian Acritarchs. An account of the palynostratigraphy and paleogeography of selected Silurian acritarch taxa. Revista Española de Micropaleontología Número Extraordinario, pp. 1–203.
- Cramer, F.H., 1971. Distribution of selected Silurian acritarchs. Rev. española Micropaleontol. Númer. Extraordinario 1, 1–203.
- Cramer, F.H., Díez, M., 1972. North America Silurian palynofacies and their spatial arrangement: Acritarchs. Palaeontogr. Abt. B 138, 107–180.
- Da Costa, N.M., 1971. Quitinozoários silurianos do Igarapé da Rainha, Estado do Pará. Divisão de Geologia e Mineralogia. Boletim. 255. Departamento Nacional da Produção Mineral, Belém, pp. 1–101.
- De La Puente, G.S., 2009. Quitinozoos del Ordovicico de la Cuenca Andina central (noroeste Argentino) y su aplicacion a la bioestratigrafia, paleobiologeigrafia y Paleoambientes. (Doctoral thesis). University of Cordoba, p. 246 unpublished.
- De La Puente, G.S., Rubinstein, C.V., 2013. Ordovician chitinozoans and marine phytoplankton of the Central Andean Basin, northwestern Argentina: A biostratigraphic and paleogeographic approach. Rev. Palaeobot. Palynol. 198, 14–46.
- Deflandre, G., Deflandre-Rigaud, M., 1962. Nomenclature et systématique des hystrichospheres (sens. lat.), Observations et rectifications. Rev. Micropaléontol. 4, 190–196.
- Derakhshi, M., Ghasemi, H., Miao, L., 2017. Geochemistry and petrogenesis of Soltan Maidan basalts (E Alborz, Iran): Implications for asthenosphere-lithosphere interaction and rifting along the N margin of Gondwana. Geochemistry 77 (1), 131–145.
- Deunff, J., 1954. Veryhachium, genre nouveau d'Hystrichosphères du Primaire. Compte rendu sommaire des Seances de la Société géologique 13, 305–307.
- Deunff, J., 1959. Microorganismes planctoniques du primaire Armoricain. I Ordovician du Veryhac'h (presqu'île de Crozon). Bulletin de la Société géologique et minéralogique de Bretagne, nouvelle série 2, 1–41 [For 1958].
- Deunff, J., Evitt, W.R., 1968. Tunisphaeridium, a new acritarch genus from the Silurian and Devonian. Stanford University Publications, Geological Sciences 12 (1), 1–13.
- Domeier, M., 2018. Early Paleozoic tectonics of Asia: Towards a full-plate model. Geosci. Front. 9 (3), 789–862.
- Downie, C., 1959. Hystrichospheres from the Silurian Wenlock Shale of England. Palaeontology 2, 56–71.
- Downie, C., 1963. Hystrichospheres (acritarchs) and spores of the Wenlock Shales (Silurian) of Wenlock, England. Palaeontology 6, 625–652.
- Duffield, S.L., 1985. Land-derived microfossils from the Jupiter Formation (Upper Llandoverian), Anticosti Island, Quebec. Palaeontology 59, 1005–1010.
- Edwards, D., Wellman, C.H., 2001. Embryophytes on land: the Ordovician to Lochkovian (Lower Devonian) record. In: Gensel, P.G., Edwards, D. (Eds.), Plants Invade the Land. Columbia University Press, New York, pp. 3–28.
- Eftekhar-nejad, J., Aghanabati, A., Hamzehpour, B., 1976. Geological map of Kashmar. Geological Survey of Iran, Geological map of Iran 1:250,000 Series, no J5 http://gsi.ir/fa/ map/762.
- Eisenack, A., 1931. Neue Mikrofossilien des Baltischen Silurs. I. Paläontologische Zeitschrift 13, 74–118.
- Eisenack, A., 1934. Neue Mikrofossilien des baltischen Silurs. III. und neue Mikrofossilien des böhmischen Silurs. I. Paläontologische Zeitschrift 16, 52–76.
- Eisenack, A., 1938. Hystrichosphaerideen und verwandte Formen im baltischen Silur. Zeitschrift für Geschiebeforschung und Flachlandsgeologie 14 (1), 1–30.
- Eisenack, A., 1939. Chitinozoen und Hystichosphaerideen im Ordovizium des Rheinischhen Schiefergebirges. Senckenbergiana 21, 135–152.
- Eisenack, A., 1955. Neue Chitinozoen aus dem Silur des Baltikums und dem Devon der Eifel. Sencknbergiana lethaea 36, 311–319.
- Eisenack, A., 1958. Tasmanites Newton 1875 and Leiosphaeridia n.gen als Gattungen der Hystrichosphaeridea. Palaeontogr. Abt. A 110, 1–19.
- Eisenack, A., 1959. Neotypen baltischer Silur-Chitinozoen und neue Arten. Neues Jahrbuch für Geologie und Paläontologie, Abh. 108, 1–20.
- Eisenack, A., 1962. Neotypen baltischer Silur-Chitinozoen und neue Arten. Neues Jahrbuch für Geologie und Paläontologie, Abh. 114, 291–316.
- Eisenack, A., 1963. Mitteilungen zur Biologie der Hystrichosphären und über neue Arten. Neues Jahrbuch für Geologie und Paläontologie, Abh. 118 (2), 207–216.
- Eisenack, A., 1968. Mikrofossilien eines Geschiebes der Borkholmer Stufe, baltisches Ordovizium, F2. Mitteilungen aus dem Geologischen Staatsinstitut in Hamburg 37, 81–94.
- Eisenack, A., 1972. Beiträge zur Chitinozoen-Forschung. Palaeontgr. A 140, 117–130.
- Eisenack, A., Cramer, F.H., Díez, M., 1976. Katalog der fossilen Dinoflagellaten, Hystrichosphä- ren und verwandten Mikrofossilien. Band IV Acritarcha 2, Teil 3, E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, p. 863.
- Eisenack, A., Cramer, F.H., Díez, M., 1979. Katalog der Fossilen Dinoflagellaten, Hystrichosphären und Verwandten Mikrofossilien. Band V: Acritarcha Part 3. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, Germany, p. 532.
- Eiserhart, K.H., 1989. Baltisphären aus Gotländer Öjlemyrflint (Acritarcha, Oberordoviz Geschiebe, Schweden). Mitteilungen des Geologischen und Paläontologischen Institut der Universität Hamburg 68, 79–129.

- Elaouad-Debbaj, Z., 1981. Acritarches de l'Ordovicien Supérieur du synclinal de Buçaco (Portugal). Systématique, Biostratigraphie, Intérêt paléogéographique. Bulletin de la Société Géologique et Minéralogique de Bretagne, série C 3, 83–88.
- Elaouad-Debbaj, Z., 1984. Chitinozoaires Ashgilliens de l'Anti-Atlas (Maroc). Geobios 17, 45–68.
- Elaouad-Debbaj, Z., 1986. Chitinozoaires de la Formation Inférieure du Ktaoua, Ordovicien supérieur de l'Anti-Atlas (Maroc). Hercynica 2, 35–55.
- Elaouad-Debbaj, Z., 1988. Acritarches et Chitinozoaires du Trémadoc de l'Anti-Atlas Central (Maroc). Rev. Micropaléontol. 31, 85–128.
- Esmaili-Suvary, A., 1996. Palynostratigraphy and palaeogeography of lower part of Niur Formation in southwest of Kashmar City. Unpubl. M.Sc. Thesis. Ferdowsi University, p. 132 (in Persian).
- Evitt, W.R., 1963. A discussion and proposals concerning fossil dinoflagellates, hystrichospheres, and acritarchs, I and II. Proc. Natl Acad. Sci. Washington 49 (158–164), 298–302.
- Fensome, R.A., Williams, G.L., Barss, M.S., Freeman, J.M., Hill, J.M., 1990. Acritarchs and fossil prasinophytes, an index to genera, species, and infraspecific taxa. American Association of Stratigraphic Palynologists, Contribution Series 25, 1–771.
- Ghavidel-Syooki, M., 2000. Palynostratigraphy and Palaeobiogeography of Lower Palaeozoic strata in the Ghelli area, Northeastern Alborz Range (Kopeh-Dagh Region). J. Sci. Islam. Repub. Iran. 11, 305–318.
- Ghavidel-Syooki, M., 2003. Palynostratigraphy and paleoecology of lower Paleozoic strata at Kuh-e Boghou, southwest of Kashmar City, at Eastern Central Iran. Iran. Int. J. Sci. 4, 181–207.
- Ghavidel-Syooki, M., 2006. Palynostratigraphy and palaeogeography of the Cambro– Ordovician strata in southwest of Shahrud City (Kuh-e Kharbash near Deh–Molla), Central Alborz Range, northern Iran. Rev. Palaeobot. Palynol. 139, 81–95.
- Ghavidel-Syooki, M., 2008. Palynostratigraphy and Palaeogeography of the Upper Ordovician Gorgan Schists (Southeastern Caspian Sea), Eastern Alborz Mountain Ranges, northern Iran. Comun. Geol. 95, 123–155.
- Ghavidel-Syooki, M., 2016. Biostratigraphy of acritarchs and chitinozoans in Ordovician strata from the Fazel Abad area, southeastern Caspian Sea, Alborz Mountains, northern Iran: stratigraphic and paleogeographic implications. In: Sorkhabi, R. (Ed.), Tectonic Evolution, Collision, and Seismicity of Southwest Asia: In Honor of Manuel Berberian's Forty-five Years of Research Contributions. Geological Society of America, Special Paper 525, pp. 1–32.
- Ghavidel-Syooki, M., 2017a. Cryptospore and trilete spore assemblages from the Late Ordovician (Katian–Hirnantian) Ghelli Formation, Alborz Mountain Range, Northeastern Iran: Palaeophytogeographic and palaeoclimatic implications. Rev. Palaeobot. Palynol. 244, 217–240.
- Ghavidel-Syooki, M., 2017b. Stratigraphic evidence for Hirnantian glaciation in the Alborz Mountain Ranges, northeastern Iran. Palaeogeogr. Palaeoclimat. Palaeoecol. 485, 879–898.
- Ghavidel-Syooki, M., Borji, S., 2018. Chronostratigraphy of Acritarchs and Chitinozoans from upper Ordovician Strata from the Robat-e Gharabil Area, NE Alborz Mountains, northern Khorassan Province: Stratigraphic and Paleogeographic Implications. J. Sci. Islam. Repub. Iran. 29, 35–51.
- Ghavidel-Syooki, M., Vecoli, M., 2007. Latest Ordovician-early Silurian chitinozoans from the eastern Alborz Mountain Range, Kopeh-Dagh region, northeastern Iran: Biostratigraphy and palaeobiogeography. Rev. Palaeobot. Palynol. 145, 173–192.
- Ghavidel-Syooki, M., Winchester-Seeto, T., 2002. Biostratigraphy and palaeogeography of Late Ordovician chitinozoans from the northeastern Alborz Range. Iran. Rev. Palaeobot. Palynol. 118, 77–99.
- 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. Rev. Palaeobot. Palynol. 164, 251–271.
- Ghavidel-Syooki, M., Álvaro, J.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. Palaeogeogr. Palaeoclimatol. Palaeoecol. 307, 1–16.
- Ghavidel-Syooki, M., Popov, L.E., Álvaro, J.J., Ghobadi Pour, M., Tolmacheva, T.Y., Ehsani, M.H., 2014. Dapingian-lower Darriwilian (Ordovician) stratigraphic gap in the Faraghan Mountains, Zagros Ranges, south-eastern Iran. Bull. Geosci. 89 (4), 679–706.
- Ghavidel-Syooki, M., Evans, D.H., Ghobadi Pour, M., Popov, L.E., Álvaro, J.J., Rakhmonov, U., Klishevich, I.A., Ehsani, M.H., 2015. Late Ordovician cephalopods, tentaculitides, machaeridians and echinoderms from Kuh-e Faraghan, High Zagros, Iran. Alcheringa 39 (4), 530–549.
- Ghobadi Pour, M., Ghavidel-Syooki, M., Álvaro, J.J., Popov, L.E., Ehsani, M.H., 2015. First reported Late Ordovician trilobites from the High Zagros Ranges, Iran: A biogeographic link between Gondwanan Chinese and Mediterranean faunas. Geobios 48 (5), 351–369.
- Górka, H., 1987. Acritarches et prasinophycean de ľordovicien moyen (viruen) de sondage de smedsby gård no. 1 (Gotland, Suède). Rev. Palaeobot. Palynol. 52, 257–283 287–297.
- Grahn, Y., 1980. Early Ordovician Chitinozoa from Öland. Sveriges Geologiska Undersökning, Serie C 775, 1–41.
- Grahn, Y., 1981. Middle Ordovician Chitinozoa from Öland. Sveriges Geologiska Undersökning, Serie C 784, 1–51.
- Grahn, Y., 1982. Caradocian and Ashgillian Chitinozoa from the Subsurface of Gotland. Sveriges Geologiska Undersökning, Serie C 788, 1–66.
- Grahn, Y., 1984. Ordovician chitinozoa from Tallinn, northern Estonia. Rev. Palaeobot. Palynol. 43, 5–31.
- Grahn, Y., Idil, S., Østvedt, A.M., 1994. Caradocian and ashgillian chitinozoan biostratigraphy of the Olso-asker and ringerike districts, Oslo region, Norway. GFF (Geologiska Föreningens Förhandlingar) J. Geol. Soc. Sweden 116, 147–160.

Gray, J., Boucot, A.J., 1989. Is Moyeria a euglenoid? Lethaia 22, 447-456.

- Gray, J., Boucot, A.J., Grahn, Y., Himes, G., 1992. A new record of early Silurian land plant spores from the Paraná Basin, Paraguay (Malvinokaffric Realm). Geol. Mag. 129, 741–752.
- Greuter, W., Barrie, F.R., Burdet, H.M., Chaloner, W.G., Demoulin, V., Hawksworth, D.L., Jørgensen, P.M., Nicolson, D.H., Silva, P.C., Trehane, P., McNeill, J., 1994. International Code of Botanical Nomenclature (Tokyo Code) Adopted by The Fifteenth International Botanical Congress, Yokohama, August–September 1993. 131. Koeltz Scientific Books, Königstein, pp. 1–389.
- Hashemi, H., Playford, G., 1998. Upper Devonian palynomorphs of the Shishtu Formation, Central Iran Basin, east central Iran. Palaeontogr. Abt. B 246, 115–212.
- Heydari, E., 2008. Tectonic versus eustatic controls on supersequences of the Zagros Mountains of Iran. Tectonophysics 451, 56–70.
- Hill, P.J., Molyneux, S.G., 1988. Biostratigraphy, palynofacies and provincialism of Late Ordovician-Early Silurian acritarchs from northeast Libya. Printed in. In: El-Arnauti, A., Owens, B., Thusu, B. (Eds.), Subsurface Palynostratigraphy of northeast Libya, Garyounis University Publications, Benghazi, Libya, pp. 27–43.
- Husseini, M.I., 1990. The Cambro-Ordovician Arabian and adjoining plates: A glacioeustatic model. J. Petrol. Geol. 13, 267–288.
- Jachowicz, M., 1995. Ordovician acritarch assemblages from central and northwestern Saudi Arabia. Rev. Palaeobot. Palynol. 89, 19–25.
- Jacobson, S.R., Achab, A., 1985. Acritarch biostratigraphy of the Dicellograptus complanatus graptolite zone from the Vaureal formation (Ashgillian), Anticosti Island, Quebec, Canada. Palynology 9, 165–198.
- Jansonius, J., 1964. Morphology and classification of some Chitinozoa. Bull. Can. Petrol. Geol. 12, 901–918.
- Jardiné, S., Combaz, A., Magloire, L., Peniguel, G., Vachey, G., 1974. Distribution stratigraphique des acritarches dans le Paléozoïque du Sahara algérien. Rev. Palaeobot. Palynol. 18, 99–129.
- Jenkins, W.A.M., 1967. Ordovician chitinozoa from Shropshire. Palaeontology 10, 436–488.
- Jenkins, W.A.M., 1970. Chitinozoa from the Ordovician Sylvan Shale of the Arbuckle Mountains, Oklahoma. Palaeontology 13, 261–288.
- Johnson, N.G., 1985. Early Silurian palynomorphs from the Tuscarora Formation in central Pennsylvania and their paleobotanical and geological signification. Rev. Palaeobot. Palynol. 45, 307–359.
- Keegan, J.B., Rasul, S.M., Shaheen, Y., 1990. Palynostratigraphy of lower Palaeozoic, Cambrian to Silurian, sediments of the Hashemite Kingdom of Jordan. Rev. Palaeobot. Palynol. 66, 167–180.
- Kjellström, G., 1971. Middle Ordovician Microplanktonn from the Grötlingbo, Borehole No. 1 in Gotland, Sweden. Sveriges Geologiska Undersökning, Serie C 669 (65), 1–35.
- Lakova, I., Gocev, P.M., Yanev, S., 1992. Palynostratigraphy and geological setting of the Lower Paleozoic allochthon of the Dervent Heights, SE Bulgaria. Geol. Balcanica 22 (6), 71–88.
- Laufeld, S., 1967. Caradocian Chitinozoa from Dalarna, Sweden. GFF (Geologiska Föreningen i Stockholm Förhandlingar): J. Geol. Soc. Sweden 89, 275–349.
- Laufeld, S., 1971. Chitinozoa and correlation of the Molodova and Restevo Beds of Podolia, U.S.S.R. Mémoires Bureau Recherche Géologique et Minieres 73, 291–300.
- Le Hérissé, A., Paris, F., Steemans, P., 2013. Late Ordovician–earliest Silurian palynomorphs from northern Chad and correlation with contemporaneous deposits of southeastern Libya, Bull. Geosci. 88 (3), 483–504.
- Le Hérissé, A., Molyneux, S.G., Miller, M., 2014. Late Ordovician to early Silurian acritarchs from the Qusaiba-1 shallow core hole, central Saudi Arabia. Rev. Palaeobot. Palynol. 212, 22–59.
- Le Hérissé, A., Vecoli, M., Guidat, C., Not, F., Breuer, P., Wellman, C., Steemans, P., 2017. Middle Ordovician acritarchs and problematic organic-walled microfossils from the Saq-Hanadir transitional beds in the QSIM-801 well, Saudi Arabia. Rev. Micropaléontol. 60, 289–318.
- Le Heron, D.P., Craig, J., 2008. First-order reconstructions of a Late Ordovician Saharan ice sheet. J. Geol. Soc. 165 (1), 19–29.
- Legault, J.A., 1982. First report of Ordovician (Caradoc-Ashgill) palynomorph from Orphan Knoll, Labrador Sea. Can. J. Earth Sci. 19, 1851–1856.
- Li, J., Wicander, R., Yan, K., Zhu, H., 2006. An Upper Ordovician acritarch and prasinophyte assemblage from Dawangou, Xinjiang, northwestern China: Biostratigraphic and paleogeographic implications. Rev. Palaeobot.Palynol. 139, 97–128.
- Lister, T.R., 1970. The acritarchs and chitinozoa from the Wenlock and Ludlow Series of the Ludlow and Millichope areas, Shropshire. Palaeontogr. Soc. Monogr. 124 (1), 1–100.
- Loeblich, A.R., 1970. Morphology, ultrastructure and distribution of Paleozoic acritarchs. Proceedings of the North American Paleontological Convention, Chicago, 1969, part G. 2, pp. 705–788.
- Loeblich, A.R., Tappan, H., 1976. Some new and revised organic-walled phytoplankton microfossil genera. J. Paleontol. 50 (2), 301–308.
- Loeblich, A.R., Tappan, H., 1978. Some Middle and Late Ordovician microphytoplankton from central North America. J. Paleontol. 52 (6), 1233–1287.
- Mahmoudi, M., Saburi, J., Alimohammadian, H., Majidifard, M.R., 2014. The first cryptospore assemblages of Late Ordovician in Iran, Ghelli Formation, Eastern Alborz. Geopersia 4, 125–140.
- McClure, H.A., 1988. Chitinozoan and acritarch assemblages, stratigraphy and biogeography of the early Palaeozoic of Northwest Arabia. Rev. Palaeobot. Palynol. 56, 41–60.
- Melo, J.H.G., Steemans, P., 1997. Resultados de investigações palinoestratigráficas em Amostras de superficie de região de Presidente Figueiredo (AM), Bacia do Amazonas. Petrobras/CENPES (External report), pp. 1–11.
- Miller, M.A., 1991. Paniculaferum missouriensis gen. et sp. nov. a new Upper Ordovician acritarch from Missouri, U. S. A. Rev. Palaeobot. Palynol. 70, 217–223.

Miller, A., Eames, L., 1982. Palynomorphs from the Silurian medina group (lower llandovery) of the Niagara Gorge, Lewiston, New York, U.S.A. Palynology 6, 221–254.

- Molyneux, S.G., Paris, F., 1985. Late Ordovician Palynomorphs. In: Thusu, B., Owens, B. (Eds.), Palynostratigraphy of Northeast Libya. J. Micropalaeontol. 4, pp. 11–26.
- Motaghi, K., Tatar, M., Priestley, K., Romanelli, F., Doglioni, C., Panza, G.F., 2015. The deep structure of the Iranian Plateau. Gondwana Res. 28, 407–418.
- Nestor, V., 1980. New chitinozoans species from the Lower Llandovery of Estonia. Eesti NSV Teaduste Akadeemia Toimedised Koide Geoloogia 29 (3), 98–106 (in Russia with English summary).
- Nõlvak, J., 1980. Chitinozoans in biostratigraphy of the Northern East Baltic Ashgillian. A preliminary report. Act. Palaeontol. Polonica 25, 253–260.
- Oktay, B., Wellman, C.H., 2019. Palynological analysis of Upper Ordovician to Lower Silurian sediments from the Diyarbakir Basin, southeastern Turkey. Rev. Palaeobot. Palynol. 263, 28–46.
- Oulebsir, L., Paris, F., 1995. Chitinozoa ordoviciens du Sahara algérien: biostratigraphie et affinités paléogéographiques. Rev. Palaeobot. Palynol. 86, 49–68.
- Paris, F., 1979. Les Chitinozoaires de la Formation de Louredo, Ordovicien supérieur du Synclinal de Buçaco (Portugal). Palaeontogr. Abt. A 164, 24–51.
- Paris, F., 1981. Les Chitinozoaires dans le Paléozoïque du Sud-Ouest de Ì Europe. Mémoires de la Société géologique et minéralogique de Bretagne 26, 1–496.
- Paris, F., 1988. Late Ordovician and Early Silurian chitinozoans from central and southern Cyrenaica. In: El-Arnauti, A., Owens, B., Thusu, B. (Eds.), Subsurface Palynostratigraphy of Northeast Libya. Garyounis University Publication, Benghazi (SPLAJ), pp. 61–71.
- Paris, F., 1990. The Ordovician biozones of the Northern Gondwana Domain. Rev. Palaeobot. Palynol. 66, 181–209.
- Paris, F., 1996. Chitinozoan biostratigraphy and palaeoecology. In: Jansonius, J., McGregor, D.C. (Eds.), Palynology: Principles and Applications. American Association of Stratigraphic Palynologists Foundation 2, pp. 531–552.
- Paris, F., 2006. Chitinozoans a fascinating and mysterious microfossil group. Géosciences-Rennes. UMR 6118 du CNRS, Université de Rennes I, Campus de Beaulieu, 35,042 Rennes-cedex, France, p. 81.
- Paris, F., Al-Hajri, S., 1995. New chitinozoan species from the Llandovery of Saudi Arabia. Rev. Micropaleontol. 38, 311–328.
- Paris, F., Grahn, Y., Nestor, Y., Lakova, I., 1999. A revised chitinozoan classification. J. Paleontol. 73, 549–570.
- Paris, F., Bourahrouh, A., Le Hérissé, A., 2000a. The effects of the final stages of the Late Ordovician glaciation on marine palynomorphs (chitinozoans, acritarchs, leiospheres) in well NI-2 (NE Algerian Sahara). Rev. Palaeobot. Palynol. 113, 87–104.
- Paris, F., Verniers, J., Al-Hajri, S., 2000b. Ordovician chitinozoans from central Saudi Arabia. In. In: Al-Hajri, S., Owens, B. (Eds.), Palaeozoic Palynostratigraphy of Saudi Arabia. GeoArabia, special publication n°1, pp. 42–56.
- Paris, F., Le Hérissé, A., Monod, O., Kozlu, H., Ghienne, J.F., Dean, W.T., Vecoli, M., Gunay, Y., 2007. Ordovician chitinozoans and acritarchs from southern and southeastern Turkey Chitinozoaires et acritarches ordoviciens du sud et du sud-est de la Turquie. Rev. Micropaléontol. 50, 81–107.
- Paris, F., Verniers, J., Miller, M.A., Al-Hajri, S., Melvin, J., Wellman, C.H., 2015. Late Ordovician–earliest Silurian chitinozoans from the Qusaiba-1 core hole (North Central Saudi Arabia) and their relation to the Hirnantian glaciation. Rev. Palaeobot. Palynol. 212, 60–84.
- Piri-Kangarshahi, M.H., 2017. Palynostratigraphy and Palaeogeography of Palynomorphs (Cryptospores, Acritarchs and Chitinozoans) at Ordovician - Silurian boundary in Kuh-e Boghou, southwest of Kashmar City, Central Iran Basin. Thesis for M.Sc. degree in: Stratigraphy and Paleontology. Payame Noor University, Branch East Tehran, p. 266 (in Persian).
- Playford, G., Wicander, R., 2006. Organic-walled microphytoplankton of the Sylvan Shale (Richmondian: Upper Ordovician), Arbuckle Mountains, Southern Oklahoma, U. S. A. Oklahoma Geol. Surv. 148, 1–116.
- Raevskaya, E., Dronov, A., Servais, T., Wellmans, C.H., 2016. Cryptospores from the Katian (Upper Ordovician) of the Tungus basin: The first evidence for early land plants from the Siberian paleocontinent. Rev. Palaeobot. Palynol. 224, 4–13.
- Richardson, J.B., 1988. Late Ordovician and Early Silurian cryptospores and miospores from northeast Libya. In: El-Arnaulti, A., Owens, B., Thusu, B. (Eds.), Subsurface palynostratigraphy of northeast Libya. Garyounis University Publications, Benghazi, pp. 89–109.
- Richardson, J.B., 1996a. Taxonomy and classification of some new Early Devonian cryptospores from England. In: Cleal, C.J. (Ed.), Studies on Early Land Plant Spores from Britain. Spec. Pap. Palaeont. 55, pp. 7–40.
- Richardson, J.B., 1996b. Palaeozoic spores and pollen: Chapter 18A Lower and Middle Palaeozoic records of terrestrial palynomorphs. In: Jansonius, J., McGregor, D.C. (Eds.), Palynology: Principles and Applications. American Association of Stratigraphic Palynologists Foundation, Houston, pp. 555–574.
- Richardson, J.G., Ausich, W.I., 2007. Late Ordovician–Early Silurian cryptospore occurrences on Anticosti Island (Île d'Anticosti), Quebec, Canada. Can. J. Earth Sci. 44, 1–7.
- Robardet, M., 1980. Evolution géodynamique de Nort-Est du Massif armoricain au Paléozoique. Thèse (no, d' enregistrement au C.N. R. S.: AO 8533). Memoires de la Societe geologique et mineralogique de Bretagne 20, 1–350.
- Robardet, M., Jenny, J.L., Nion, J., Paris, F., Pillet, J., 1972. La Formation du Pont-de-Caen (Caradocianien) dans les synclinaux de Domfrontet de Sées (Normandie). Ann. Soc. Géol. Nord, 92, 117–137.
- Robertson, E.B., 1997. Fossil microplankton from the upper Ordovician Maquoketa Formation exposed in Pike County, Missouri. Georgia. J. Sci. 55, 76–99.
- Ross, R.J., 1982. The Ordovician system in the United States: Correlation Chart and Explanatory Notes. Publication 12. International Union Geological Sciences, Paris, p. 73.
- Rubinstein, C.V., Vaccari, N.E., 2004. Cryptospore Assemblages from the Ordovician/Silurian boundary in the Puna Region, North-west Argentina. Palaeontol. 47, 1037–1061.

- Rubinstein, C.V., Vajda, V., 2019. Baltica cradle of early land plants? Oldest record of trilete spores and diverse cryptospore assemblages; evidence from Ordovician successions of Sweden Gff 141, pp. 181–190
- Rubinstein, C.V., de la Puente, G.S., Delabroye, A., Astini, R.A., 2016. The palynological record across the Ordovician/Silurian boundary in the Cordillera Oriental, Central Andean Basin, northwestern Argentina. Rev. Palaeobot. Palynol. 224, 14–25.
- Ruhizadeh, Z., 1996. Palynostratigraphy and palaeogeography of upper part of Niur Formation in southwest of Kashmar City. Unpubl. M.Sc. Thesis. Ferdowsi University, p. 107 (in Persian).
- Sarjeant, W.A.S., Stancliffe, R.P.W., 1994. The Micrhystridium and Veryhachium Complexes (Acritarcha: Acanthomorphitae and Polygonomorphitae): A taxonomic reconsideration. Micropaleontol. 40, 1–77.
- Schallreuter, R., 1963. Neue Chitinozoen aus ordovizischen Geschieben und Bemerkungen Zur Gattung Illichitina. Paläontol. Abh. 1, 391–405.
- Servais, T., 1993. The Ordovician acritarch Frankea. Spec. Pap. Palaeont. 48, 79–95.
- Soufiane, A., Achab, A., 2000. Chitinozoan zonation of the Late Ordovician and the Early Silurian of the island of Anticosti, Quebec, Canada. Rev. Palaeobot. Palynol. 109, 85–111.
- Spina, A., 2015. Latest Ordovician (Hirnantian) miospores from the NI-2 well, Algeria, North Africa, and their evolutionary significance. Palynology 39, 205–219.
- Staplin, F.L., 1961. Reef-controlled distribution of Devonian microplankton in Alberta. Paleontol. 4, 392–424.
- Staplin, F.L., Jansonius, J., Pocock, S.A.J., 1965. Evaluation of Some Acritarcheous Hystrichosphere Genera. Neues Jahrbuch f
 ür Geologie und Pal
 äontologie, Abh. 123 (2), 167–201.
- Steemans, P., 2000. Miospore evolution from the Ordovician to the Silurian. Rev. Palaeobot. Palynol. 113, 189–196.
- Steemans, P., 2001. Ordovician cryptospores from the Oostduinkerke borehole, Brabant Massif, Belgium. Geobios 34, 3–12.
- Steemans, P., Pereira, E., 2002. Llandovery miospore biostratigraphy and stratigraphic evolution of the Paraná Basin, Paraguay – Palaeogeographic implications. Bull. Soc. Géolog. 173, 407–414.
- Steemans, P., Le Hérissé, A., Bozdogan, N., 1996. Ordovician and Silurian cryptospores and miospores from Southeastern Turkey. Rev. Palaeobot. Palynol. 93, 35–76.
- Steemans, P., Higgs, K.T., Wellmans, C.H., 2000. Cryptospores and trilete spores from the Llandovery, Nuayyin-2 Borehole, Saudi Arabia. In. In: Al-Hajri, S., Owens, B. (Eds.), Stratigraphic Palynology of the Palaeozoic of Saudi Arabia, pp. 92–115.
- Stockmans, F., Williére, Y., 1963. Les Hystrichosphéres ou mieux les Acritarches du Silurien Belge. Sondage de la Brasserie Lust à Courtrai (Kortrijk). Bull. Soc. Belg. Géolog. Paléontol.et d'hydrologie 71, 450–481.
- Strother, P.K., 1991. A classification scheme for the cryptospores. Palynology 15 (1), 219–236.
- Strother, P.K., Traverse, A., 1979. Plant microfossils from the Llandoverian and Wenlockian rocks of Pennsylvania. Palynology 3, 1–21.
- Strother, P.K., Traverse, A., Vecoli, M., 2015. Cryptospores from the Hanadir Shale Member of the Qasim Formation, Ordovician (Darriwilian) Saudi Arabia. Rev. Palaeobot. Palynol. 212, 97–110.
- Strother, P.K., Taylor, W.A., Van de Schootbruggec, B., Leanderd, B.S., Wellman, C.H., 2019. Pellicle ultrastructure demonstrates that Moyeria is a fossil euglenid. Palynology 1–12.
- Tappan, H., Loeblich, A.R., 1971. Surface sculpture of the wall in Lower Paleozoic Acritarchs. Micropaleontol. 17, 385–410.
- Taugourdeau, P., 1966. Les Chitinozoaires. Techniques d'Études, morphologies et classification. Mem. Soc. Geol. 104, 64.
- Taugourdeau, P., de Jekhowsky, B., 1960. Répartition de description des Chitinozoaires siluro-dévoniens de quelques sondage de la C.R.E.P.S., del la C.F.P.A. et de la S.N. Repal au Sahara. Revue de l'Institut Francais du Pétrole 15 (9), 1199–1260.
- Thusu, B., 1973. Acritarches provenant de l'Ilion Shale (Wenlockien), Utica, New York. Rev. Micropaléontol. 16, 137–146.
- Timofeev, B.V., 1958. Über das Alter Sächsischer Grauwacken Mikropaläophytologische Untersuchungen von Proben aus der Weesensteiner und Lausitzer Grauwacke. Géolog. 7, 826–845.
- Timofeev, B.V., 1959. Drevneishaja flora Pribaltici i ee stratigraficheskoe znachenie. (The oldest flora of the Baltic Provinces and its stratigraphical significance). Tr. VNIGRI. 129, 1–136.
- Torsvik, T.H., Cocks, L.R.M., 2009. The Lower Palaeozoic palaeogeographical evolution of the northeastern and eastern peri-Gondwanan margin from Turkey to New Zealand. In. In: Bassett, M.G. (Ed.), Early Palaeozoic Peri-Gondwana Terranes: New Insights from Tectonics and Biogeography. Geol. Soc., London, Spec. Publ 325, pp. 3–21.
- Turner, R.E., 1982. Reworked acritarchs from the type section of the Ordovician Caradoc Series, Shropshire. Palaeontology 25, 119–143.
- Turner, R.E., 1984. Acritarchs from the type area of the Ordovician Caradoc Series, Shropshire, England. Palaeontogr. Abt. B 190, 87–157.
- Turner, R.E., 1985. Acritarchs from the type area of the Ordovician Llandeilo Series, South Wales. Palynology 9 (1), 211–234.

- Van Nieuwenhove, N., Vanderbroucke, T.R.A., Verniers, J., 2006. Chitinozoan biostratigraphy of the Upper Ordovician Greenscoe section, southern Lake District, UK. Rev. Palaeobot. Palvnol. 139, 151–169.
- Vandenbroucke, T.R.A., 2005. Upper Ordovician Global Stratotype Section and points and British historical type area: A chitinozoan point of view. Unpublished Ph.D. thesis. Ghent University, Belgium 33 pls.
- Vandenbroucke, T.R.A., 2008. Upper Ordovician Chitinozoans From the British Historical Type Area and adjacent key sections. Monograph Palaeontological society 161 (628), 1–113.
- Vandenbroucke, T., Gabbot, S.E., Paris, F., Aldridge, R.J., Theron, J.N., 2009. Chitinozoans and the age of the Soom Shale, an Ordovician black shale Lagerstätte, South Africa. J. Micropalaeontol. 28, 53–66.
- Vanmeirhaeghe, J., 2006. Chitinozoan biostratigraphy of the Upper Ordovician of Faulxles-Tombes (central Condroz Inlier, Belgium). Rev. Palaeobot. Palvnol. 139, 171–188.
- Vavrdová, M., 1977. Acritarchs from the Sárka Formation (Llanvirnian). Vestnik Ústred. ústavu geol. 52, 109–118.
- Vavrdová, M., 1984. Some plant microfossils of possible terrestrial origin from the Ordovician of central Bohemia. Věstník Ústředního ústavu geologického 59 (3), 165–170.
- Vavrdová, M., 1988. Further acritarchs and terrestrial plant remains from the Late Ordovician at Hlásná Třebaň (Czesoslovakia). Časopis pro mineralogii a geologii 33 (1), 1–10.
- Vavrdová, M., 1989. New acritarchs and miospores from the Late Ordovician of Hlásná Treban, Czechoslovakia. Časopis pro mineralogii a geologii 34 (4), 403–419.
- Vecoli, M., 1999. Cambro-Ordovician palynostratigraphy (acritarchs and prasinophytes) of the Hassi-R'Mel area and northern Rhadames Basin, North Africa. Palaeontogr. Ital. 86, 1–112.
- Vecoli, M., Delabroye, A., Spina, A., Hints, O., 2011. Cryptospore assemblages from Upper Ordovician (Katian-Hirnantian) strata of Anticosti Island, Quebec, Canada, and Estonia: Palaeophytogeographic and palaeoclimatic implications. Rev. Palaeobot. Palynol. 166, 76–93.
- Vecoli, M., Wellman, C.H., Gerrienne, P., Le Hérissé, A., Steemans, P., 2017. Middle Ordovician cryptospores from the Saq-Hanadir transitional beds in the QSIM-801 well, Saudi Arabia. Rev. Micropaléontol. 60, 319–331.
- Videt, B., Paris, F., Rubino, J.L., Boumendjel, K., Dabard, M.P., Loi, A., Ghienne, J.F., Marante, A., Gorini, A., 2010. Biostratigraphical calibration of third order Ordovician sequences on the northern Gondwana platform. Palaeogeogr. Palaeoclimatol. Palaeoecol. 296, 359–375.
- Wang, Y., Li, J., Wang, R., 1997. Latest Ordovician cryptospores from southern Xinjiang, China. Rev. Palaeobot. Palynol. 99, 61–74.
- Webby, B.D., Cooper, R.A., Bergström, S.M., Paris, F., 2004. Stratigraphic framework and time slices. In: Webby, B.D., Paris, F., Droser, M.L., Percival, I.G. (Eds.), The Great Ordovician Biodiversification Event. Columbia University Press, New York, pp. 41–47.
- 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. Spec. Pap. Palaeontol. 55, pp. 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: Spec. Pap. Palaeontol. 55, pp. 41–101.
- Wellman, C.H., Higgs, K.T., Steemans, P., Al-Hajri, S., Owens, B., 2000. Spore assemblages from a Silurian sequence in Borehole Hawiyah-151 from Saudi Arabia. In: Al-Hajri, S., Owens, B. (Eds.), Stratigraphic Palynology of the Palaeozoic of Saudi Arabia. GeoArabia, Special Publications 1, pp. 116–133.
- Wellman, C.H., Steemans, P., Miller, M.A., 2015. Spore assemblages from Upper Ordovician and lowermost Silurian sediments recovered from Qusaiba-1 shallow core hole, Qasim region, central Saudi Arabia. Rev. Palaeobot. Palynol. 212, 111–126.
- Wetzel, O., 1933. Die in organischer Substanz erhaltenen Mikrofossilien des baltischen Kreide-Feuersteins mit einem sedimentpetrographischen und stratigraphischen Anhang. Palaeontogr. Abt. A 78, 1–110.
- Wicander, R., 1974. Upper Devonian–Lower Mississippian Acritarchs and Parasinophycean Algae from Ohio, USA. Palaeontogr. Abt. B 148, 9–43.
- Wicander, R., Loeblich, A.R., 1977. Organic-walled microphytoplankton and its stratigraphic significance from the Upper Devonian Antrim Shale, Indiana, U.S.A. Palaeontogr. Abt. B 160, 129–165.
- Wicander, R., Playford, G., 2008. Upper Ordovician microphytoplankton of the Bill's Creek Shale and Stonington Formation, Upper Peninsula of Michigan, U.S.A.: Biostratigraphy and paleogeographic significance. Rev. Micropaléontol. 51, 39–66.
- Wicander, R., Playford, G., Robertson, E.B., 1999. Stratigraphic and paleogeographic significance of an Upper Ordovician Acritarch Flora from the Maquoketa Shale, Northeastern Missouri, U.S.A. Memoir J. Paleontol. 51, Suppl. 73 (6), 1–38.
- Wilson, L.R., Hedlund, R.W., 1964. Calpichitina scabiosa, a new Chitinozoan from the Sylvan Shale (Ordovician) of Oklahoma. Oklahoma Geol. Notes 24, 161–164.