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3 **Colonial palynomorphs from the Upper Ordovician of northeastern Iran:**  
4 **spore “thalli”, coenobial Chlorophyceae (Hydrodictyaceae) or cyanobacteria?**

5  
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16  
17 ABSTRACT

18  
19 This study documents ‘colonial’ palynomorphs from the Upper Ordovician Ghelli Formation of  
20 northeastern Iran. The aggregates of organic–walled microfossils come from the Katian  
21 *Armoricochitina nigerica* and *Ancyrochitina merga* chitinozoan Biozones of this formation.  
22 They can be classified as acritarchs and/or cryptospores, but they cannot be attributed to a  
23 particular biological group. Some specimens resemble ‘thalli’ of putative spores, such as  
24 *Grododowon orthogonalis* Strother 2017. Other clusters suggest an affinity to green algal groups,  
25 in particular with colonial chlorophyceae algae, most probably of Hydrodictyaceae. Some  
26 specimens also show affinities with cyanobacterial groups. There are no arguments to relate  
27 these colonial palynomorphs to primitive land plants, but they are possibly produced by ancient  
28 green algal lineages that may have been experimenting with a subaerial existence.

29  
30 KEYWORDS: acritarchs; spores; green algae; land plants; cyanobacteria

1 **1. Introduction**

2

3 Unraveling the origin of the earliest land plants (embryophytes) and identifying their first fossil  
4 occurrence continues to be challenging (e.g. Gray 1993; Graham 1993; Kenrick & Crane 1997;  
5 Delwiche & Cooper 2015; Edwards & Kenrick 2015; Wellman & Strother 2015; Gerrienne et al.  
6 2016). For a long time, it was considered that mid–Silurian *Cooksonia* represented the oldest  
7 unequivocal microfossil evidence for land plants (Edwards et al. 1992). However, there are some  
8 recent claims, based on a variety of evidence, for an earlier origin of land plants (e.g. Strother et  
9 al. 2017; Morris et al. 2018). It is generally considered that land plants emerged from a  
10 charophycean lineage of aquatic multicellular green algae (e.g. Graham 1993; Karol et al. 2001).  
11 However, Harrison (2016) recently suggested that they may have originated from amongst a  
12 crust–forming terrestrial microbiome of bacteria, cyanobacteria, algae, lichens and fungi. Several  
13 green algal lineages have been proposed as the closest living relative to land plants, such as the  
14 Charophyceae, the Coleochaetophyceae and the Zygnematophyceae (see discussion in Gerrienne  
15 et al. 2016).

16 Molecular clock evidence indicates origins of the different land plant lineages much earlier  
17 than the Silurian, at least in the Cambrian and possibly in the Precambrian (Qiu et al. 2006;  
18 Clarke et al. 2011; Zhong et al. 2014; Morris et al. 2018). To date, however, no definite evidence  
19 of land plants exists before the Ordovician (Kenrick et al. 2012; Wellman et al. 2013; Servais et  
20 al. in press). The microfossil record identifies the earliest cryptospores in the Middle Ordovician  
21 (Strother et al. 1996; Rubinstein et al. 2010), while the first microfossil records the oldest  
22 sporangia and small plant fragments in the Late Ordovician (Wellman et al. 2003; Salamon et al.  
23 2018). Similarly, organic geochemistry investigations on biomarker compositions indicate a  
24 transition from green algae to land plants during the Early Palaeozoic, with the oldest reported  
25 biomarkers related to bryophytes from the Middle Ordovician of the Canning Basin, Australia  
26 (Spaak et al. 2017).

27 By far the most significant amount of data on Ordovician land plants is provided by  
28 microfossil evidence. However, there is an ongoing discussion on the precise biological affinities  
29 of the dispersed spores and spore-like microfossils. Were these produced by genuine  
30 embryophytes or by organisms on the transition between ancient green algal lineages and land  
31 plants? Some authors suggest that some Cambrian ‘cryptospores’ were probably the desiccation–

1 resistant spores of cryptogams belonging to the charophyte–embryophyte lineage (e.g. Strother  
2 1991; Strother et al. 2004; Taylor & Strother 2008).

3 On the other hand, most authors agree that cryptospores from the early Middle Ordovician  
4 (Dapingian) of Argentina described by Rubinstein et al. (2010) are derived from the earliest  
5 genuine land plants (embryophytes). To date, there is a large number of publications reporting  
6 such cryptospores from different palaeocontinents. So, for instance, the microfossil record shows  
7 occurrences from most parts of Gondwana and its periphery (e.g. Gray et al. 1982; Vavrdová  
8 1984; Richardson 1988; Wellman et al. 2003, 2015; Rubinstein and Vaccari 2004; Steemans et  
9 al. 1996, 2009; Le Hérissé et al. 2007; Rubinstein et al. 2010; Mahmoudi et al. 2014; Spina 2015;  
10 Strother et al. 2015; Rubinstein et al. 2016; Ghavidel–Syooki 2016; Vecoli et al. 2017), including  
11 South China (e.g. Wang et al. 1997), but also from Laurentia (e.g. Vecoli et al. 2015), Baltica  
12 (e.g. Vecoli et al. 2011; Badawy et al. 2014), Avalonia (Richardson 1988; Wellman 1996) and  
13 Siberia (e.g. Raevskaya et al. 2016). This indicates that a flora appeared in the Middle  
14 Ordovician and already displayed a world–wide distribution by the end of the Late Ordovician.

15 The oldest known trilete spores come from the Upper Ordovician (Katian) of Saudi Arabia  
16 (Steenmans et al. 2009), which have been interpreted as potentially an indication of the occurrence  
17 of earliest vascular plants (i.e. tracheophytes; Wellman et al. 2015). However, as these only  
18 occur in low numbers and some extant bryophytes may also produce trilete spores, the earliest  
19 occurrences of this type of spore in the Late Ordovician does not indicate unambiguously the  
20 presence of vascular plants. The presence of stem group land plants ‘at a bryophytic grade of  
21 organization’ (cryptophytes) since the Middle Ordovician is thus established, whereas the  
22 presence of the first vascular plants possibly dates back to the Upper Ordovician with such plants  
23 only becoming common in the Late Silurian.

24 The Upper Ordovician (Katian–Hirnantian) Ghelli Formation of northeastern Iran also  
25 includes a good representation of typical Late Ordovician cryptospores and trilete spores. These  
26 land plant derived spores are present within well–preserved palynomorph assemblages that  
27 include acritarchs and chitinozoans (Ghavidel–Syooki 2016). The first cryptospore assemblage  
28 from Iran was documented by Mahmoudi et al. (2014) from this formation in the Khosh Yeilagh  
29 area, eastern Alborz Ranges, Iran. More recently, Ghavidel–Syooki (2016) reported a well–  
30 preserved and diverse cryptospore assemblage from the Ghelli Formation in the Pelmis Gorge  
31 section in the Alborz Mountain Ranges, northeastern Iran.

1 In addition to typical Upper Ordovician cryptospores, the Ghelli Formation of northeastern  
2 Iran also includes early trilete spores, as well as clusters of palynomorphs that resemble colonial  
3 organisms, of possible algal or plant origin. The present study focuses on these organisms. Some  
4 specimens can be compared with the recently published spore ‘thalli’ of Strother et al. (2017)  
5 from the Middle Ordovician Kanosh Shale at Fossil Mountain, Utah. Vecoli et al. (2015) first  
6 published planar clusters of ‘cryptospores’ with thick and smooth walls from the Kanosh Shale,  
7 before Strother *in* Strother et al.(2017) described the new genus *Grododowon*, that the authors  
8 considered to represent a post zygotic growth phase in the life cycle of an ancient charophytic  
9 alga that was evolving in response to subaerial conditions. The question arises if the Iranian  
10 microfossils thus also indicate the presence of charophytic algae in the Upper Ordovician of the  
11 Gondwanan margin. Other specimens from Iran resemble material attributed to coenobial  
12 chlorococcales, in particular hydrodyctyacean algae, while others show morphologies that may  
13 relate them to cyanobacterial groups. Here, we aim to report the different morphotypes of  
14 ‘colonial’ microfossils from the Upper Ordovician Ghelli Formation and to discuss their  
15 nomenclature and possibly biological affinities.

16

## 17 **2. Geological setting**

18

19 The studied section (37° 21' 69.12" N and 56° 93' 83.80" E) of the Upper Ordovician Ghelli  
20 Formation is located in the northeastern Iran, about 40 km southwest of Bojnurd and *ca.* 57 km  
21 northeast of Jajarm (Fig. 1). Afshar–Harb (1979) introduced the type section of the Ghelli  
22 Formation approximately 2.5 km north of Ghelli. The Lower Palaeozoic successions in this area  
23 comprise four formations, in ascending order, the Mila, Lashkarak, Ghelli, and Niur formations  
24 (Fig. 2). The Mila Formation is mostly composed of limestones attributed to the Middle and  
25 Upper Cambrian (Stöcklin et al. 1964). It is partially exposed at the investigated section and is  
26 overlain by the Lashkarak Formation consisting of dark green–grey siltstone, shale and thin  
27 layers of limestone and sandstone; attributed to the Early Ordovician (Ghavidel–Syooki 2006;  
28 Ghobadi Pour et al. 2011; Kebria–ee Zadeh et al. 2015) on the basis of trilobite, brachiopod and  
29 acritarch biostratigraphy. The overlying Ghelli Formation has a thickness of about 900 meters.  
30 Afshar–Harb (1979) divided it into three members including, in ascending stratigraphic order,  
31 volcanic rocks, shale and sandstone, and syndeposited *mélange* (*sensu* Afshar-Harb, 1979) of

1 shales, siltstones, and sandstones (Fig. 3). The first palynological studies by Ghavidel–Syooki  
2 (2000) and Ghavidel–Syooki & Winchester–Seeto (2002) indicated that the Ghelli Formation  
3 can be attributed to the Upper Ordovician. The overlying Niur Formation consists mainly of dark  
4 grey shale, siltstone, sandstone and limestone with abundant corals, brachiopods, crinoids, and  
5 palynomorphs providing evidence for an attribution to the lower Silurian (Afshar–Harb, 1979;  
6 Ghavidel–Syooki and Vecoli, 2007).

### 8 **3. Material and methods**

9  
10 More than 160 surface samples were collected from the Ghelli Formation; of which 105 more  
11 palynologically promising ones were processed in the palynological laboratories of the Kharazmi  
12 University (Tehran, Iran) and the UMR 8198 CNRSEvo–Eco–Paleo research unit of the  
13 University of Lille (France). Following standard procedures, palynomorphs were extracted from  
14 fine–grained samples such as shale and siltstone, using standard palynological techniques. This  
15 involved cold hydrochloric (HCl), cold hydrofluoric (HF) and hot hydrochloric (HCl) acid  
16 maceration to remove carbonates, silicates, and fluorosilicates, respectively. The organic residues  
17 were sieved through 15 and 20µm nylon meshes, respectively, at the universities of Lille and  
18 Kharazmi. No oxidation or alkali treatments were undertaken. All processed samples contain  
19 palynomorphs such as acritarchs, chitinozoans, scolecodonts and cryptospores in varying  
20 abundances and states of preservation. The present study concerns the description of the colonial  
21 palynomorphs. Most of these were recovered from the upper part of the Ghelli Formation (Fig.  
22 3), i.e., the strata that can be attributed to the *A. nigerica* and *A. merga* chitinozoan Biozones  
23 (Ghavidel–Syooki & Vecoli, 2007; Ghavidel–Syooki et al., 2011; Navidi–Izad; personal  
24 observation). All rock samples, palynological slides and residues are stored in the  
25 palaeontological collections of the Faculty of Earth Sciences of Kharazmi University, Tehran,  
26 except for the residues suffixed by “.s” that deposited at the UMR 8198 CNRS of the University  
27 of Lille, France.

28

### 29 **4. Observations and Comparison**

30

1 The palynological investigations in the Ghelli Formation confirm the presence of rich  
2 palynomorph assemblages containing acritarchs, chitinozoans, scolecodonts, cryptospores and  
3 trilete spores, that have partly been described in detail in previous studies (Ghavidel–Syooki  
4 2000; Ghavidel–Syooki & Winchester–Seeto 2002; Ghavidel–Syooki & Vecoli 2007; Ghavidel–  
5 Syooki et al. 2011; Mahmoudi et al. 2014; Ghavidel–Syooki 2016, 2017a, 2017b). The presence  
6 of typical marine palynomorphs indicates that all samples are of marine origin. The high  
7 proportion of cryptospores in the assemblages (Ghavidel\_Syooki, 2016; current study) suggests a  
8 terrestrial input from plants that inhabited land that was close by.

9 The assemblages from the Ghelli Formation also contain other palynomorphs, including  
10 aggregates of mostly sphaeromorph forms, some of them forming colonies (depicted in Plate 2)  
11 Importantly, different types of colonial palynomorphs are present in the studied assemblages  
12 (Plates 1, 2), most of them resembling microfossils attributed to colonial Hydrodictyaceae or  
13 cyanobacteria in the previously published literature.

14 Interestingly, Ghavidel–Syooki (2016, pl. VIII, fig. 12) illustrated a single specimen from the  
15 Ghelli Formation (re–figured in Ghavidel–Syooki 2017b, pl. I, fig. 12) of a colonial  
16 palynomorph that he attributed to *Muzivum graziniskii*. Ghavidel–Syooki (2016, fig. 2) classified  
17 this enigmatic palynomorph as an acritarch and indicated its presence in all samples investigated  
18 from the Ghelli Formation. *Muzivum graziniskii* was originally described from the Devonian of  
19 Poland by Wood & Turnau (2001), who considered the taxon to belong to the hydrodictyacean  
20 algae. In the present study, the presence in the Ghelli Formation of palynomorphs similar to  
21 *Muzivum graziniskii* is confirmed. For instance, the specimen illustrated in Plate 1, Fig. 8,  
22 typically resembles the planar, uni–layered coenobial sheets with a straight or undulatory outline,  
23 with the individual cells being thin–walled, primarily square and rarely rectangular, as described  
24 in the original diagnosis of *Muzivum graziniskii* (Wood & Turnau 2001). Other specimens are  
25 also very similar, but it remains difficult to attribute them to the same taxon with certainty, and  
26 they are here tentatively attributed to the hydrodictyacean algae or to algal clusters (Plate 1 and  
27 2). The presence of this type of colonial microfossil in the assemblages examined suggests a  
28 fresh–water input into the marine environment.

29 Other specimens recovered herein resemble the recently described taxon *Grododowon*  
30 *orthogonalis* Strother 2017. Strother et al. (2017) described the genus *Grododowon* as a cluster  
31 of thick–walled, tightly adherent, smooth–walled spore–like dyads forming planar sheets.

1 Strother et al. (2017) considered the taxon as ‘cryptospores’, i.e. spore-like microfossils *sensu*  
2 Strother (1991) and Strother & Beck (2000). The specimens from the Ghelli Formation include  
3 dyad-like ‘cryptospores’ with thick and smooth walls. The dyads are generally about 10 to 15  
4  $\mu\text{m}$  long and 5 to 8  $\mu\text{m}$  wide and they are arranged in orthogonal clusters similar to the type  
5 material from the Middle Ordovician of the USA (Strother et al. 2017). The specimen illustrated  
6 in Plate 1, Fig. 1 appears to approach the diagnosis of *Grododowon orthogonalis* Strother 2017.  
7 It displays a cluster with four dyad ‘cryptospores’ in one direction of the sheet and eight dyad  
8 cryptospores in the other direction. Other specimens (Plate 1) also fit in the diagnosis of  
9 *Grododowon orthogonalis*, although for some specimens, the identification remains  
10 problematical. It is interesting to note that the size of the planar sheets in the material  
11 investigated here is limited, ranging only from 45 to 55  $\mu\text{m}$ . Larger sheets of ‘thalli,’ as  
12 illustrated by Strother et al. (2017) from the Middle Ordovician of North America, are not  
13 retrieved from the material examined. A more delicate palynological processing technique, such  
14 as that used for ‘small carbonaceous fossils’ (SCF’s) (e.g. Harvey & Butterfield 2008) would  
15 potentially result in the recovery of larger sheets.

16 Other clusters of spore like microfossils (‘cryptospores’) are present in the same samples. The  
17 individual cryptospores display the typical morphology of cryptospores described from the  
18 Upper Ordovician (including from the Ghelli Formation) and can be considered as being related  
19 to genuine land plants (e.g. Plate 1, fig. 6).

20 On the other hand, several specimens of clusters of more or less spherical palynomorphs,  
21 usually between 5 and 10  $\mu\text{m}$  in diameter, are depicted in Plate 2. They neither resemble  
22 cryptospores nor the spore ‘thalli’ described by Strother et al. (2017). They are also clearly  
23 different from the normal, loosely arranged clusters of unornamented (sphaeromorph) acritarchs  
24 that are very common in the Palaeozoic, such as clusters of *Synsphaeridium* spp. or  
25 *Symplassosphaeridium* spp., that were usually attributed to prasinophycean algae (e.g. Le  
26 Hérissé et al. 2017). The clusters from the Ghelli Formation (Plate 2) are usually arranged in  
27 structured ‘colonies’, clearly attached to each other, in regular patterns, with either thick or thin  
28 walls. All these specimens are here tentatively attributed to algal colonies.

29 The presence of planar sheets and cryptospore clusters, in association with isolated  
30 cryptospores derived from primitive plants, thus indicates a variation of microfossils that might  
31 reflect the presence of different types of green algal groups.

1

2 **5. Sphaeromorph clusters, colonies, coenobia and ‘thalli’ in the Ordovician: acritarchs or**  
3 **cryptospores?**

4 Aggregates of several or numerous identical organic-walled microfossils have been attributed to  
5 simple clusters, colonies, coenobia or ‘thalli’ in the palynological literature. For example,  
6 Vavrdová (1990) mentioned ‘coenobial’ acritarchs in her Ordovician assemblages from  
7 Bohemia, as did Wood & Turnau (1996) by attributing their microfossils to ‘coenobial  
8 chlorococcales.’ Strother et al. (1996, fig. 3, 1) used the term ‘cluster of spore like cells’ for the  
9 problematic organisms of the Middle Ordovician of the USA. Foster et al. (2002) applied the  
10 term ‘colonial palynomorph’ to their microfossils from the Ordovician of Australia, whereas Le  
11 Hérissé et al. (2017, pl. 7), for example, used the terms cluster, colony, and coenobia to describe  
12 the different aggregates of palynomorphs from the Middle Ordovician of Saudi Arabia. Finally,  
13 Strother et al. (2017) used the term ‘thalli’ for the spore-like structures from the Middle  
14 Ordovician of Utah, USA.

15 Such aggregates have been largely reported in publications concerning Palaeozoic  
16 palynology, and their nomenclature remains inconsistent. Sometimes, such ‘clusters’ have been  
17 attributed to the acritarchs, i.e. to palynomorphs of unknown biological affinity. Evitt (1963)  
18 defined the informal group of the acritarchs to include small organic-walled microfossils of  
19 unknown biological affinity with various symmetries, shapes and structures. Evitt (1963) did not  
20 exclude colonial palynomorphs in his original definition. However, several authors specifically  
21 excluded colonial organisms from the acritarchs. For instance, Fensome et al. (1990) in the  
22 compilation of their catalogue of all acritarch taxa, did not include the colonial microfossils or  
23 aggregates of unknown organic-walled microfossils in their listings of taxa, and excluded them  
24 from their definition of the acritarchs. Subsequently some other authors further restricted the  
25 definition of the acritarchs to marine, single-celled microphytoplankton (see discussion in  
26 Servais 1996 for further details). This led to different concepts of the definition of the acritarchs.  
27 According to the restricted definitions after Evitt’s (1963) original diagnosis, the microfossils  
28 presented here would not be acritarchs, as they are colonial and probably not marine. However,  
29 by following the original definition of the acritarchs by Evitt (1963), all the colonial  
30 palynomorphs, including the specimens described in this study, can be classified as acritarchs,  
31 because their precise affiliation to a biological group is not proven. Additionally, Evitt (1963)

1 never mentioned that acritarchs must be marine organisms. As a result, all the specimens  
2 illustrated and discussed here fit the original diagnosis of the acritarchs by Evitt (1963).

3 On the other hand, some of the illustrated specimens could be attributed to the cryptospores  
4 (or to clusters of cryptospores), because they also fit in some of the diagnoses of this group, as  
5 some specimens have spore-like morphologies. The term cryptospore, like the term acritarch,  
6 has also different definitions and conceptions. Cryptospores are organic-walled microfossils that  
7 resemble spores ('sporomorphs'), but that do not display all the morphological criteria to allow  
8 them to be attributed to land plants. It is important to consider that Richardson et al. (1984) first  
9 defined the cryptospores as "non-marine sporomorphs (non-pollen grains) with no visible  
10 haptotypic features such as contact areas or tetrad marks. Single grains or monads, 'permanent'  
11 dyads and tetrads are included" (Richardson et al. 1984 p. 116). In this original definition, the  
12 cryptospores are thus considered as being of terrestrial origin ('non marine sporomorphs'). In  
13 addition, Richardson (1988) extended this definition to include single spores, naturally separated  
14 from dyads, which possess a circular contact area. Subsequently, Strother (1991) defined the  
15 cryptospores as "non-marine sporomorphs (non-pollen grains) without those typical visible  
16 haptotypic features such as trilete marks or furrows which characterized tracheophyte spores and  
17 pollen grains. Single grains or monad, 'permanent' dyads and tetrads are included as are  
18 sporomorphs separated from polyads which may or may not preserve contact area". Both  
19 Richardson (1988) and Strother (1991) consider thus the cryptospores as 'non-marine  
20 sporomorphs' with no clear biological affinity. However, Steemans (2000) emended Richardson  
21 et al.'s (1984) original definition by considering all cryptospores as derived from land plants:  
22 "Alete miospores (non-pollen grains) produced by primitive embryophytes. Single grains or  
23 monad, 'permanent' dyads and tetrads, and sporomorphs from polyads which may or may not  
24 preserve contact area". Steemans (2000) thus considered that the cryptospores are dispersed  
25 spores of the earliest land plants (embryophytic).

26 It appears evident that all of the specimens illustrated here do not fit the diagnosis of the  
27 cryptospores by Steemans (2000). Nevertheless, some of the specimens described in this study  
28 could be considered as cryptospores in the sense of Strother (1991) and Strother & Beck (2000),  
29 i.e. without a biological affiliation, and by accepting that the 'spores' can be assembled or  
30 colonial. It is also clear that the evidence that these microfossils are derived from land plants, and  
31 that they are non-marine, cannot be provided.

1 In summary, the specimens presented here could thus be classified as ‘acritarchs’ and, to  
2 some extent, as ‘cryptospores’ following the definition of the group by Strother (1991). They  
3 could be named aggregates, clusters, colonies, coenobia (a synonym of colonies). The  
4 terminology ‘thalli’ should be applied with care, because it may suggest a relation to  
5 thallophytes, an abandoned biological category to group algae, lichens and fungi, and thus  
6 implying a biological affinity.

7

## 8 **6. Possible biological affinities**

9

10 The most interesting question is not the classification in artificial groups used by palynologists,  
11 but that about the origin of these organisms: what is the biological affiliation of these coenobia  
12 and planar sheets from the Upper Ordovician of Iran? Do these microfossils represent spores and  
13 clusters of spores of various primitive land plants or of different green algal groups?

14 In palaeobotany, the term miospore is a general term representing all fossil plant spores  
15 smaller than 200 µm, regardless of whether they are cryptospores, isospores, microspores, small  
16 megaspores, pre-pollen or pollen grains. However, not only land plants produce spores, but also  
17 many algal groups (for example zygnetacean algae produce spores) or fungal organisms  
18 (fungal spores), that all have been described from palynological assemblages. As long as the  
19 biological affinities of these ‘spores’ is unknown, they can be classified as acritarchs, that can be  
20 single celled or colonial, and either of marine or fresh-water origin.

21 Moreover, some of the microfossils that are spore-like, but that do not display all the  
22 morphological characteristics that allow them be classified as land plant miospores, can be  
23 named ‘spores.’ Such ‘spores’ (or for some authors ‘cryptospores’) could be affiliated to  
24 different algal groups (or even fungi), and not be directly related to embryophyte land plants.  
25 Such spores correspond to the definition of the cryptospores *sensu* Strother (1991), i.e. by  
26 excluding a biological affinity to embryophytes (*sensu* Steemans 2000). In this way, Strother et  
27 al. (2017) considered that the taxon *Grododowon orthogonalis* Strother 2017 can be classified  
28 among the ‘cryptospores.’ Indeed, the authors considered that these organisms are not produced  
29 by land plants but by algae close to the subphylum Charophyta, representing a “zygotic growth  
30 phase in the life cycle of an ancient charophytic alga.”

1 In terms of biological affinities, some of the colonial palynomorphs from the Palaeozoic,  
2 including those presented herein, have been attributed in the literature to different groups of  
3 green algae, including the chlorophyceae (Chlorophyta) and zygnemaphyceae (Charophyta)  
4 classes. For many years, several authors have considered featureless, simple sphaerical acritarchs  
5 and clusters of such simple acritarchs as ‘prasinophycean phycomata’(e.g. Colbath & Grenfell  
6 1995; Guy–Ohlson 1996; Le Hérissé et al. 2017).

7 Other simple, featureless palynomorphs arranged in regular colonies, with multiple numbers  
8 of regularly–arranged cells, have been compared, and sometimes attributed, to the  
9 Hydrodictyaceae, a family of the Chlorococcales, that belong to the Chlorophyceae (a class of  
10 the Chlorophyta). The colonial Hydrodictyaceae are considered to be exclusively fresh water  
11 (e.g. Colbath & Grenfell 1995; Batten 1996). They have been illustrated in many palynological  
12 studies, including from the Early Palaeozoic. Another enigmatic palynomorph is the brackish or  
13 freshwater colonial *Botryococcus*, a genus of green algae of the order Chlorococcales that is  
14 present in the fossil record since the Precambrian (e.g. Colbath & Grenfell 1995).

15 The specimens from the Upper Ordovician of Iran mostly resemble these different groups of  
16 green algae belonging to the chlorophyceans, and some of them can be compared to modern  
17 hydrodictyacean algae. The ‘spore–like thalli’ described by Strother et al. (2017) might be  
18 related to the class of the Charophyceae (and to a charophytic algal lineage), but they possibly  
19 also may belong simply to a group green algae, for example of the class of the Chlorophyceae,  
20 and in particular of the Order Chlorococcales.

21 In addition, other simple, colonial palynomorphs (acritarchs) have been related to the  
22 cyanobacteria. The problematic colonial palynomorph *Gloeocapsomorpha prisca* was described  
23 from the Ordovician Baltic Shale Basin of Estonia, where it is so abundant that it forms an ‘oil  
24 shale,’ exploited for its hydrocarbon content. *Gloeocapsamorpha* is currently considered to be an  
25 equivalent of the modern Entophysalidaceae “cyanobacteria”, which are mat–forming and  
26 stromatolite–forming microorganisms (Foster et al. 1989). Most interestingly, Foster et al. (2002)  
27 described other colonial microfossils from the Lower Ordovician of the Canning Basin,  
28 Australia, and attributed them to the new species *Eomerismopedia maureeniae*. This taxon was  
29 considered by the authors to be another cyanobacterium. Morphological comparisons with  
30 modern material, in particular with the genus *Merismopedia* Meyen 1839, allowed Foster et al.  
31 (2002) to consider that *Eomerismopedia* to belonging to the cyanobacterial family

1 Chroococcaceae and in particular the order Chroococcales. Some of the material recovered from  
2 the Upper Ordovician of Iran morphologically resemble this family of cyanobacteria, indicating  
3 that some of the recovered colonial palynomorphs may well be of cyanobacterial and not green  
4 algal origin.

## 6 **7. Conclusion**

8 In this paper, some colonial palynomorphs from the Upper Ordovician Ghelli Formation  
9 (northeastern Iran) are presented. The palynomorphs come from the *Armoricochitina nigerica*  
10 and *Ancyrochitina merga* chitinozoan Biozones (Katian in age) of this formation, of which the  
11 fossil content indicates typical marine environments, with a terrestrial input of cryptospores  
12 washed in from nearby land. The colonial (or coenobial) organic-walled microfossils can be  
13 attributed to the acritarchs, and some of them also to the cryptospores, depending on the  
14 definition used. However, they cannot be clearly attributed to any biological group with  
15 certainty.

16 Some specimens resemble the possible ‘thalli’ of spores, similar to *Grododowon*  
17 *orthogonalis* Strother 2017. Such specimens may indicate evidence for a transition between  
18 algae and plants. However, they are not unambiguously related to land plants, and have been  
19 related to charophytic algae by Strother et al. (2017).

20 Several other elements suggest an affinity to green algal groups, in particular with colonial  
21 chlorophyceae algae, most probably of Hydrodyctyaceae. Others, however, may represent  
22 cyanobacterial groups as previously discussed by Foster et al. (2002).

23 In summary, the assemblages from the Upper Ordovician of Iran fit in Gray’s (1993)  
24 Eoembryophytic phase (Middle–Upper Ordovician) of earliest liverworts–like plants. They also  
25 correspond to Strother et al.’s (2010) thalloid bryophyte landscape and/or the Gerrienne et al.’s  
26 (2016) Proembryophytic interval that was proposed to characterize the long transition from green  
27 algae to liverworts since the late Precambrian.

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6 contribution to IGCP n°653 ‘The onset of the Great Ordovician Biodiversification Event.’

7

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**Figure legends**

**Figure 1:** Geographical map of northeastern Iran showing the location of the investigated section.

**Figure 2:** Simplified schematic lithostratigraphic sketch (not to scale) of the Lower Palaeozoic succession in the investigated area.

**Figure 3:** Stratigraphical column of the Upper Ordovician at the Ghelli section and stratigraphical distribution of the examined material. Chitinozoan biostratigraphy after Ghavidel–Syooki & Vecoli (2007), Ghavidel–Syooki et al. (2011) and unpublished results from the authors.

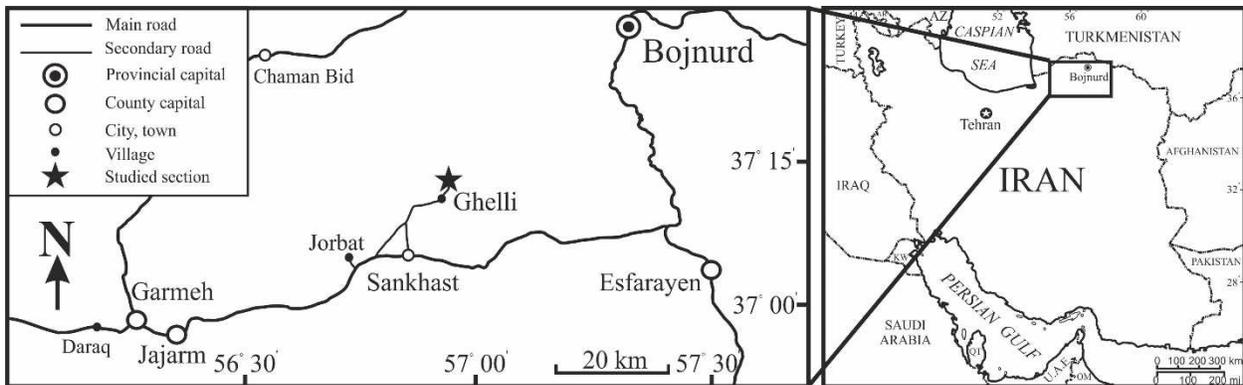


Figure 1

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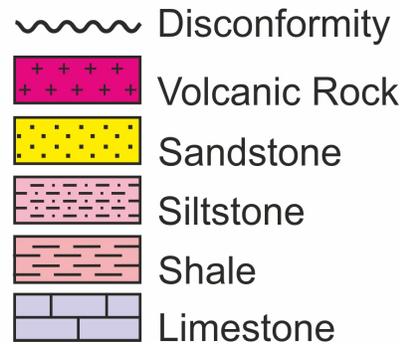
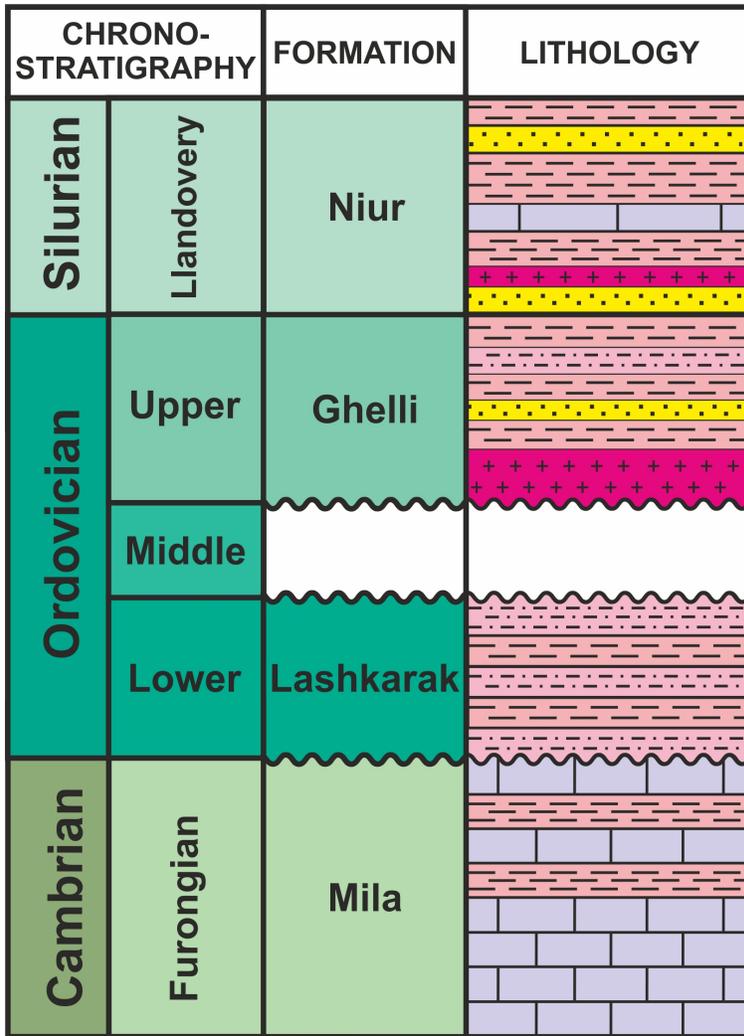
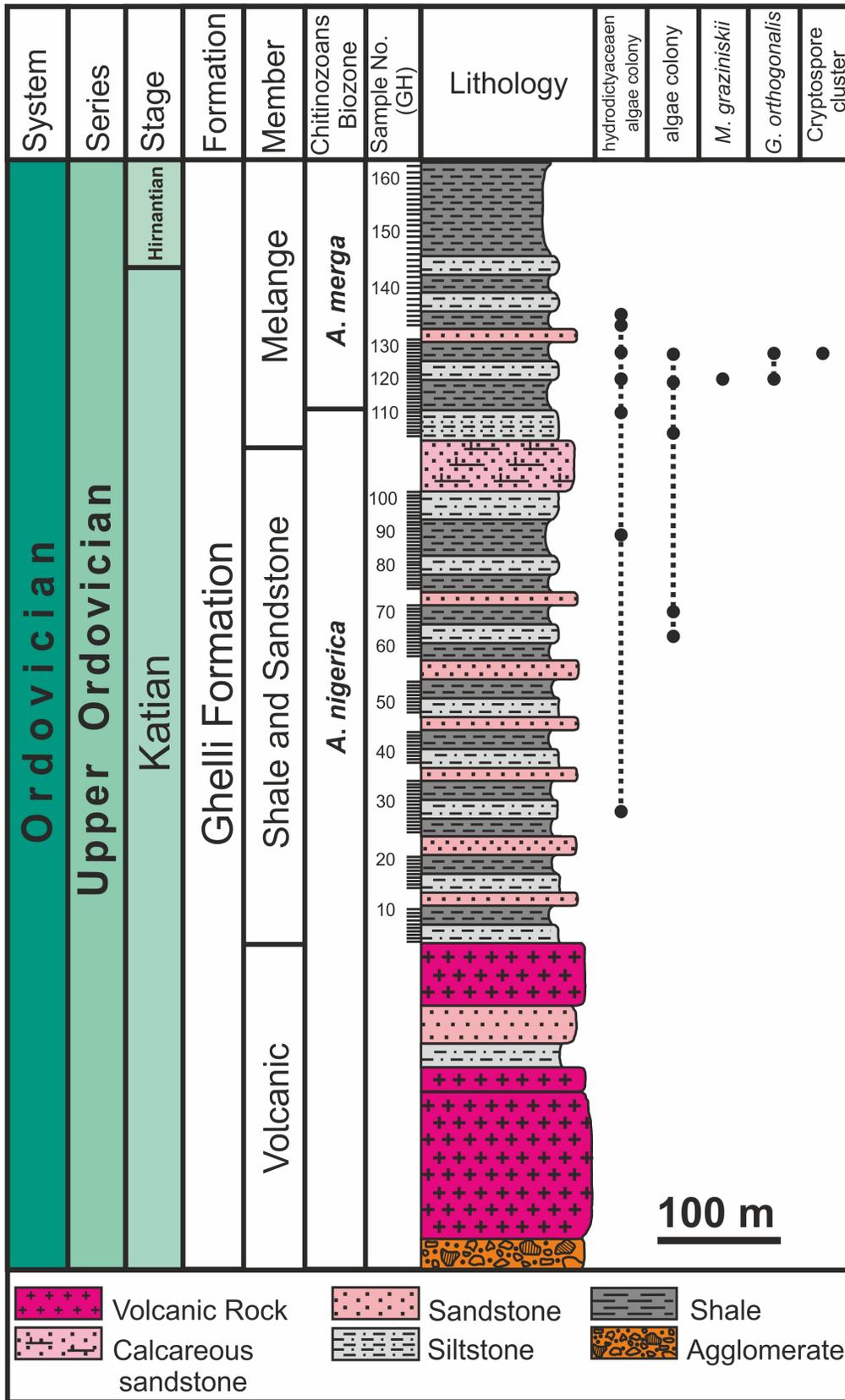


Figure 2

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Figure 3

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2 **Plate legends**

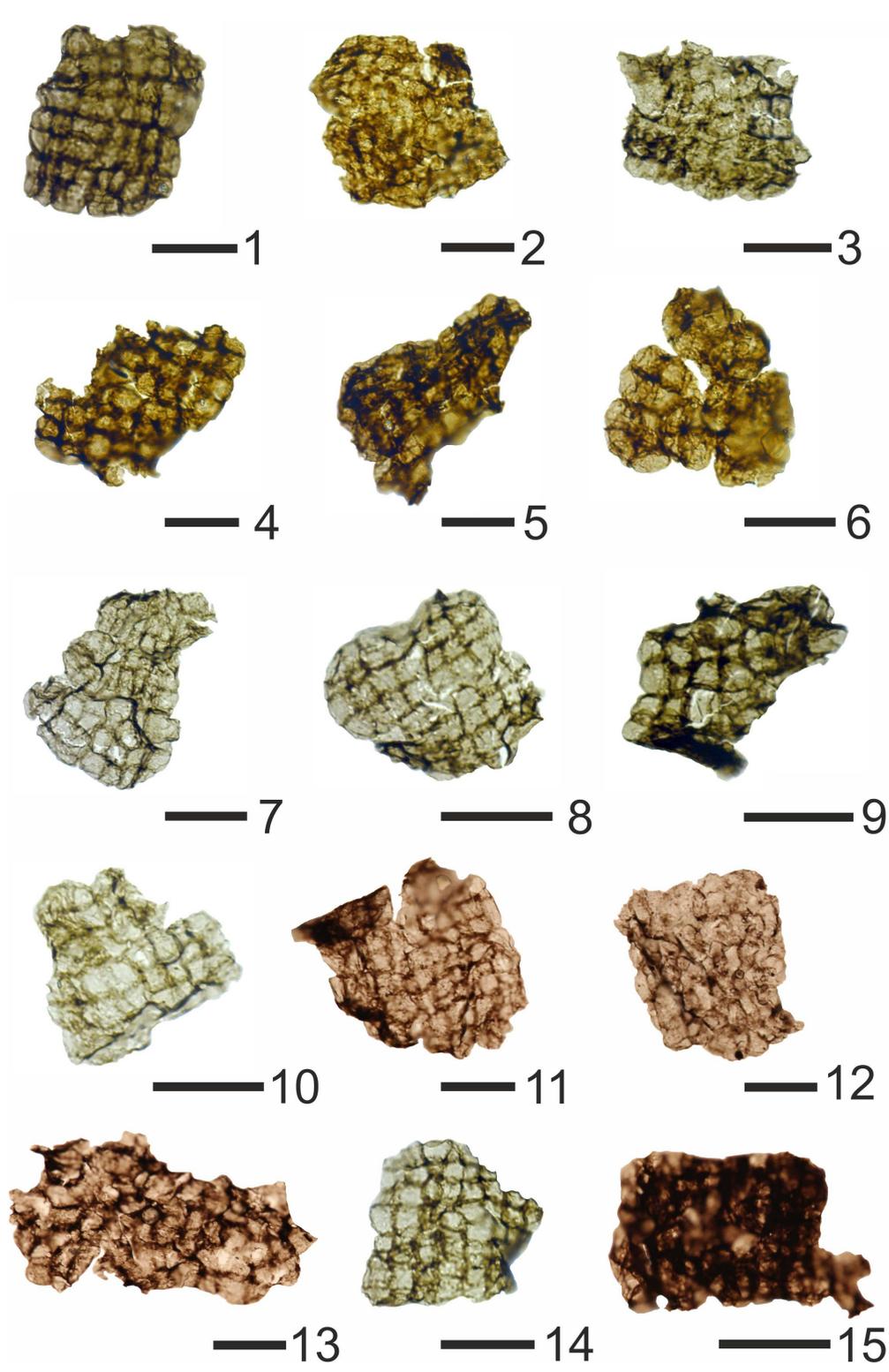
3 **Plate 1.** Selected specimens of colonial palynomorphs from the Upper Ordovician of  
4 northeastern Iran, followed by slide number and England Finder (EF) coordinates. 1.  
5 *Grododowon orthogonalis* Strother 2017, slide GH.128.2, EF: P29/4; 2. hydrodictyacean algae  
6 colony, slide GH.128.1, EF:W48; 3. hydrodictyacean algae colony, slide GH.110.s, EF: T55/1;  
7 4. *Grododowon orthogonalis* Strother 2017, slide GH.128.1, EF: T17/1; 5. *Grododowon*  
8 *orthogonalis* Strother 2017, slide GH.128.1, EF: Y23/1; 6. Cryptospore cluster, slide GH.128.1,  
9 EF: H39/1; 7. hydrodictyacean algae colony, slide GH.120.s, EF: M55/2; 8. *Muzivum*  
10 *graziniskii* Wood & Turnau, 1996, slide GH.120.s, EF: J53/4; 9. ? *Grododowon orthogonalis*  
11 Strother 2017, slide GH.120.s, EF: H66/1; 10. hydrodictyacean algae colony, slide GH.133.s,  
12 EF:W49/3; 11. hydrodictyacean algae colony, slide GH.135.2, EF: S37; 12. hydrodictyacean  
13 algae colony, slide GH.27.s, EF: F45/1; 13. hydrodictyacean algae colony, slide GH.27.s,  
14 EF:E57/2; 14.? *Grododowon orthogonalis* Strother 2017, slide GH.120.s, EF: X73/1; 15.  
15 hydrodictyacean algae colony, slide GH.135.2, EF: K15/4. Scale bar is 20  $\mu\text{m}$ .

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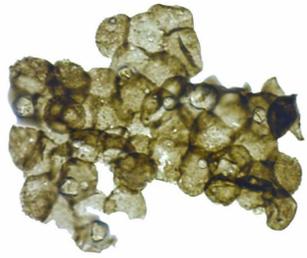
18 **Plate 2.** Selected specimens of colonial palynomorphs from the Upper Ordovician of  
19 northeastern Iran, followed by slide number and England Finder (EF) coordinates. 1. Algae  
20 colony, slide GH.70.s, EF:O54/1; 2. Algae colony, slide GH.70.s, EF:W53; 3. Algae colony,  
21 slide GH.70.s, EF:S56/2; 4. Algae colony, slide GH.70.s, EF:R74; 5. Algae colony, slide  
22 GH.120.s, EF:J54; 6. Algae colony, slide GH.127.1, EF:D28/2; 7. Algae colony, GH.128.2,  
23 EF:R50/1; 8. Algae colony, slide GH.119.3, EF:U44; 9. Algae colony, slide GH.104.3, EF:J16/3;  
24 10. Algae colony, slide GH.63.s, EF:F73/1; 11. hydrodictyacean algae colony, slide GH.89.3,  
25 EF:J48/4; 12. Algae colony, slide GH.63.s, EF:L52/1. Scale bar is 20  $\mu\text{m}$ .

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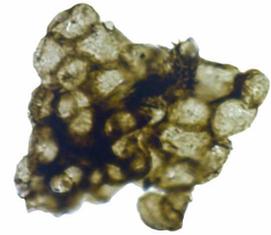
Plate 1



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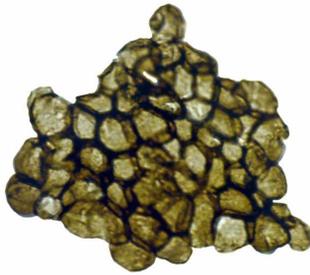
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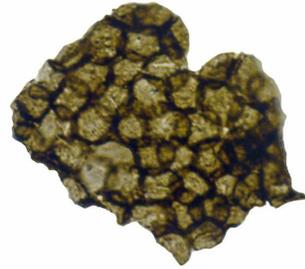
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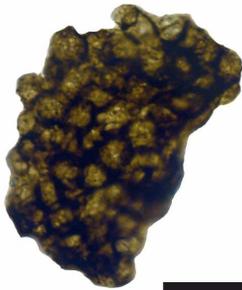
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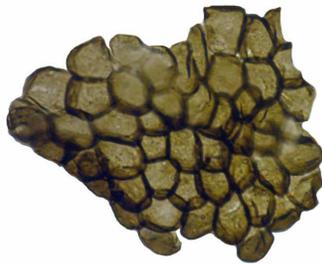
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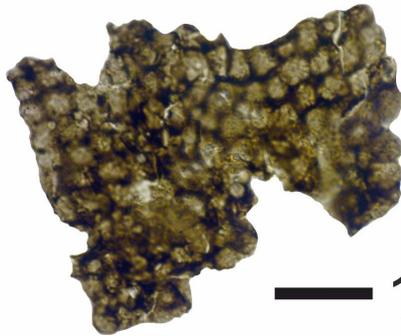
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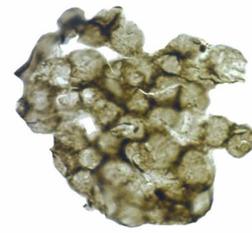
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Plate 2