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Colonial palynomorphs from the Upper Ordovician of northeastern Iran: spore "thalli", coenobial Chlorophyceae (Hydrodictyaceae) or cyanobacteria?

Navid Navidi–Izad[a,b], Hossein Hashemi[a*], Borja Cascales–Miñana[b], Sylvie Régnier[b], Charles H. Wellman[c], Thomas Servais[b]

[a]Department of Geology, Faculty of Earth Sciences, Kharazmi University, 49 Mofatteh Avenue, Tehran 15614, Iran.
[b]CNRS, University of Lille, UMR 8198–Evo–Eco–Paleo, F–59000 Lille, France.
[c]University of Sheffield, Department of Animal and Plant Sciences, Alfred Denny Building, Western Bank, Sheffield S10 2TN, United Kingdom.

[*]Correspondng author h.hashemi@khu.ac.ir (Hossein Hashemi)

ABSTRACT

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

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

1. Introduction

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

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

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

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

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

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

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

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

2. Geological setting

The studied section (37° 21′ 69.12″ N and 56° 93′ 83.80″ E) of the Upper Ordovician Ghelli Formation is located in the northeastern Iran, about 40 km southwest of Bojnurd and *ca*. 57 km northeast of Jajarm (Fig. 1). Afshar–Harb (1979) introduced the type section of the Ghelli Formation approximately 2.5 km north of Ghelli. The Lower Palaeozoic successions in this area comprise four formations, in ascending order, the Mila, Lashkarak, Ghelli, and Niur formations (Fig. 2). The Mila Formation is mostly composed of limestones attributed to the Middle and Upper Cambrian (Stöcklin et al. 1964). It is partially exposed at the investigated section and is overlain by the Lashkarak Formation consisting of dark green–grey siltstone, shale and thin layers of limestone and sandstone; attributed to the Early Ordovician (Ghavidel–Syooki 2006; Ghobadi Pour et al. 2011; Kebria–ee Zadeh et al. 2015) on the basis of trilobite, brachiopod and acritarch biostratigraphy. The overlying Ghelli Formation has a thickness of about 900 meters. Afshar–Harb (1979) divided it into three members including, in ascending stratigraphic order, volcanic rocks, shale and sandstone, and syndeposited mélange (sensu Afshar-Harb, 1979) of shales, siltstones, and sandstones (Fig. 3). The first palynological studies by Ghavidel–Syooki (2000) and Ghavidel–Syooki & Winchester–Seeto (2002) indicated that the Ghelli Formation can be attributed to the Upper Ordovician. The overlying Niur Formation consists mainly of dark grey shale, siltstone, sandstone and limestone with abundant corals, brachiopods, crinoids, and palynomorphs providing evidence for an attribution to the lower Silurian (Afshar–Harb, 1979; Ghavidel–Syooki and Vecoli, 2007).

3. Material and methods

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

4. Observations and Comparison

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

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

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

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

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

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

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

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

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

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

Such aggregates have been largely reported in publications concerning Palaeozoic palynology, and their nomenclature remains inconsistent. Sometimes, such ‘clusters’ have been attributed to the acritarchs, i.e. to palynomorphs of unknown biological affinity. Evitt (1963) defined the informal group of the acritarchs to include small organic–walled microfossils of unknown biological affinity with various symmetries, shapes and structures. Evitt (1963) did not exclude colonial palynomorphs in his original definition. However, several authors specifically excluded colonial organisms from the acritarchs. For instance, Fensome et al. (1990) in the compilation of their catalogue of all acritarch taxa, did not include the colonial microfossils or aggregates of unknown organic–walled microfossils in their listings of taxa, and excluded them from their definition of the acritarchs. Subsequently some other authors further restricted the definition of the acritarchs to marine, single–celled microphytoplankton (see discussion in Servais 1996 for further details). This led to different concepts of the definition of the acritarchs. According to the restricted definitions after Evitt’s (1963) original diagnosis, the microfossils presented here would not be acritarchs, as they are colonial and probably not marine. However, by following the original definition of the acritarchs by Evitt (1963), all the colonial palynomorphs, including the specimens described in this study, can be classified as acritarchs, because their precise affiliation to a biological group is not proven. Additionally, Evitt (1963) never mentioned that acritarchs must be marine organisms. As a result, all the specimens illustrated and discussed here fit the original diagnosis of the acritarchs by Evitt (1963).

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

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

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

6. Possible biological affinities

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

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

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

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

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

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

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

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

7. Conclusion

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

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

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

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

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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.

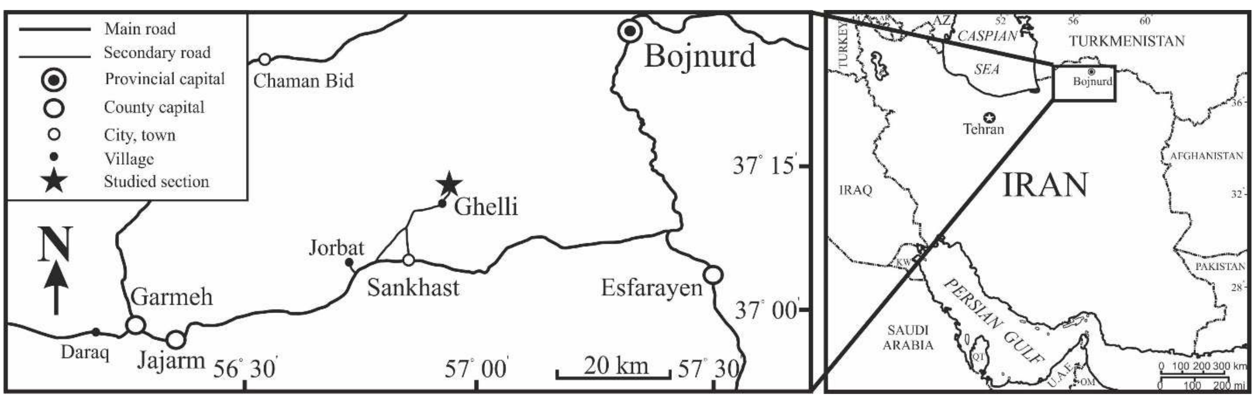

Figure 1

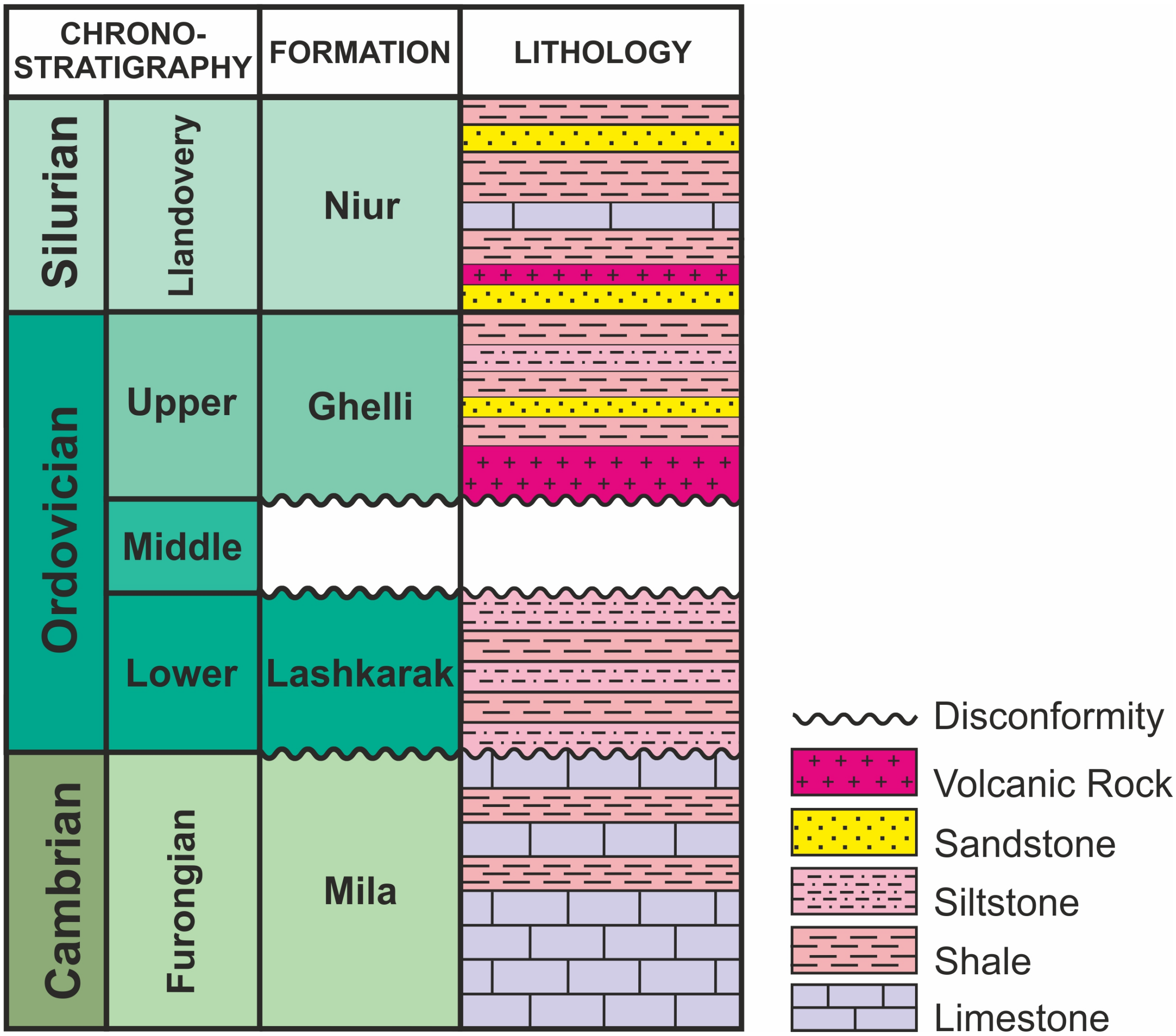
CHRONO-
STRATIGRAPHY
FORMATION
LITHOLOGY
Silurian
Llandovery
Niur
Ordovician
Upper
Ghelli
Middle
Lower
Lashkarak
Cambrian
Furongian
Mila
Disconformity
Volcanic Rock
Sandstone
Siltstone
Shale
Limestone

Figure 2

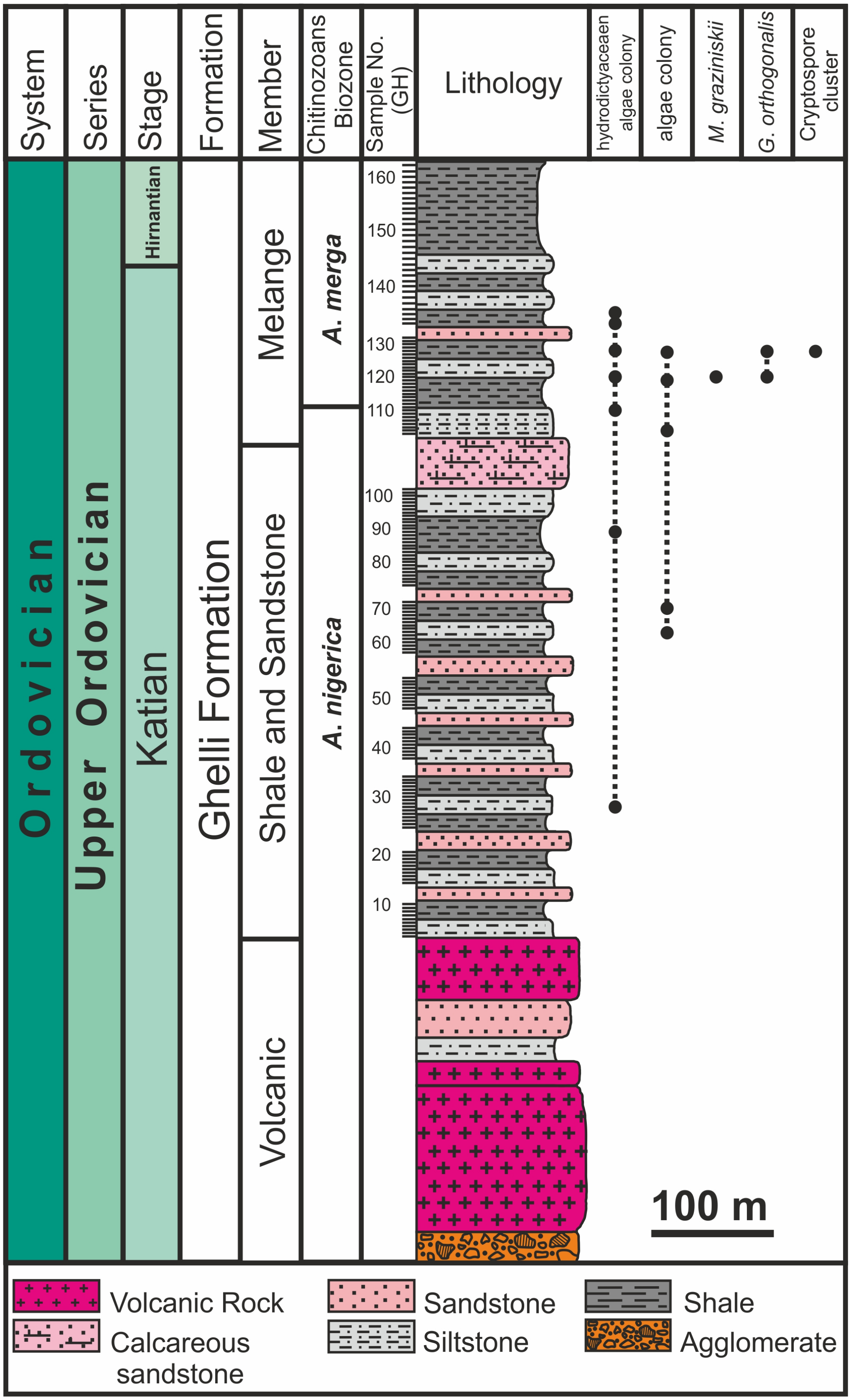
System
Series
Stage
Formation
Member
Chitinozoans Biozone
Sample No. (GH)
Lithology
hydrodictyaceaen algae colony
algae colony
M. graziniskii
G. orthogonalis
Cryptospore cluster
Ordovician
Upper Ordovician
Hirnantian
Katian
Ghelli Formation
Melange
Shale and Sandstone
Volcanic
A. merga
A. nigerica
160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
100 m
Volcanic Rock
Calcareous sandstone
Sandstone
Siltstone
Shale
Agglomerate

Figure 3

Plate legends

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

Plate 2. Selected specimens of colonial palynomorphs from the Upper Ordovician of northeastern Iran, followed by slide number and England Finder (EF) coordinates. 1. Algae colony, slide GH.70.s, EF:O54/1; 2. Algae colony, slide GH.70.s, EF:W53; 3. Algae colony, slide GH.70.s, EF:S56/2; 4. Algae colony, slide GH.70.s, EF:R74; 5. Algae colony, slide GH.120.s, EF:J54; 6. Algae colony, slide GH.127.1, EF:D28/2; 7. Algae colony, GH.128.2, EF:R50/1; 8. Algae colony, slide GH.119.3, EF:U44; 9. Algae colony, slide GH.104.3, EF:J16/3; 10. Algae colony, slide GH.63.s, EF:F73/1; 11. hydrodictyaceaen algae colony, slide GH.89.3, EF:J48/4; 12. Algae colony, slide GH.63.s, EF:L52/1. Scale bar is 20 μm.

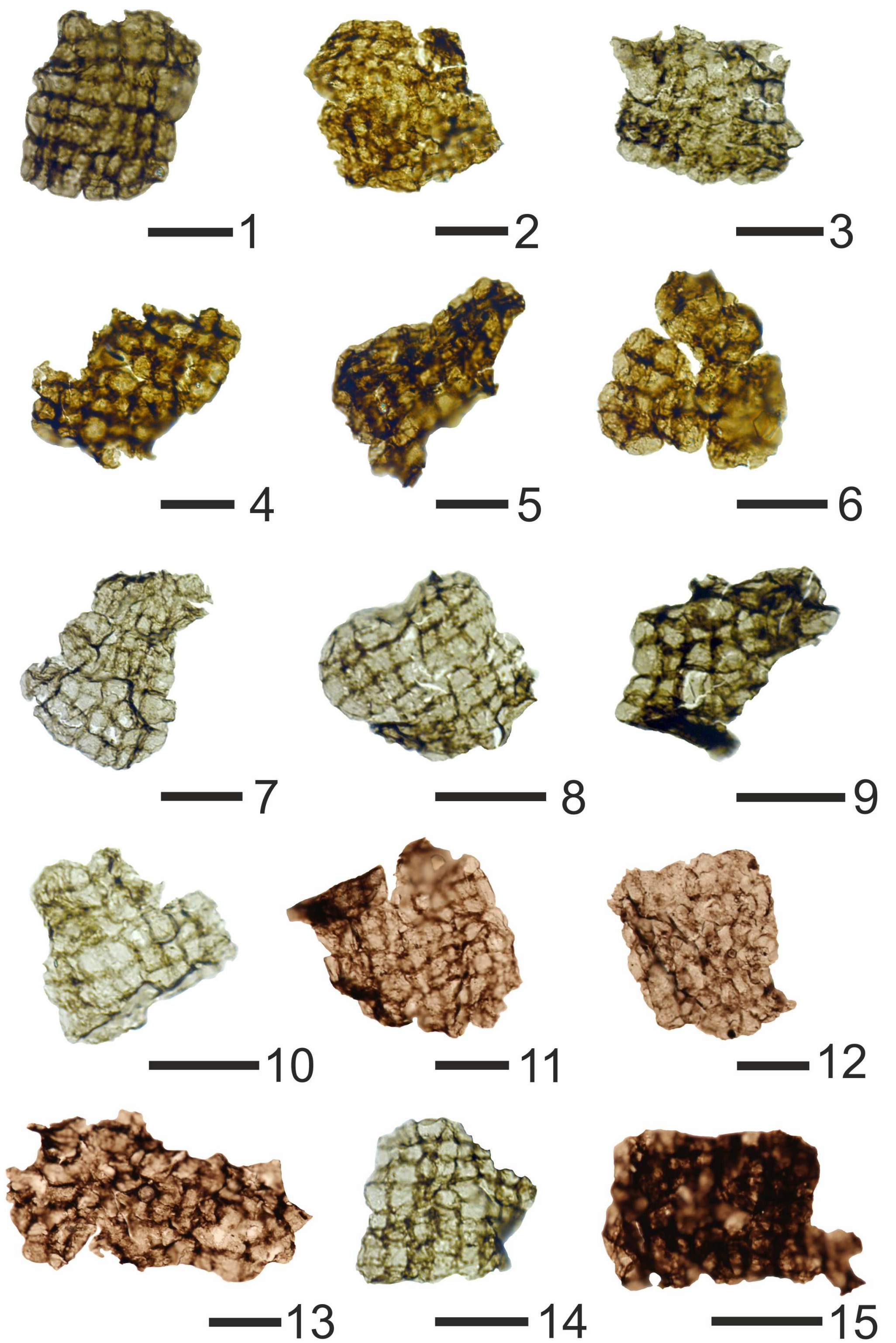

Plate 1

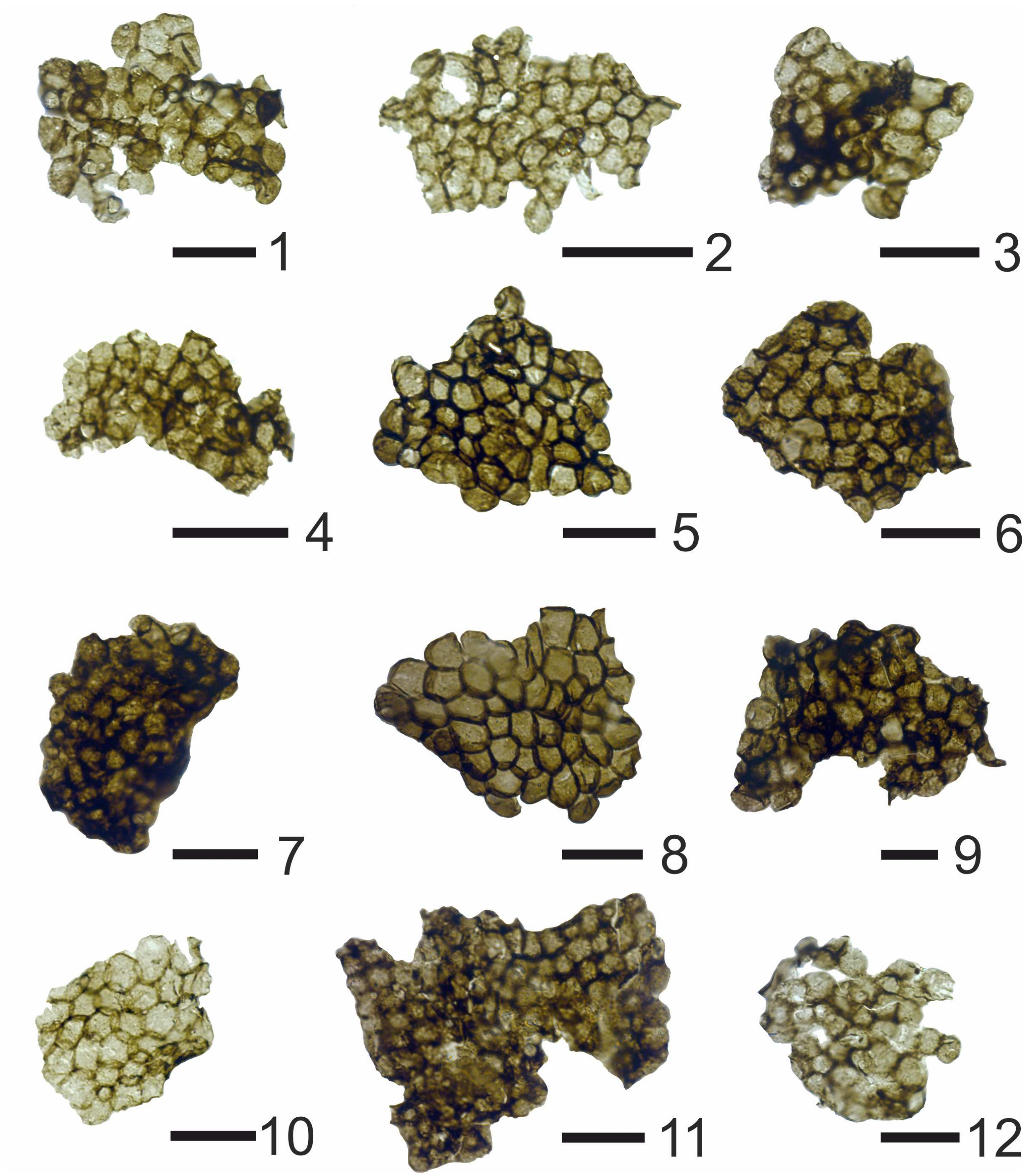

Plate 2