Colonial Palynomorphs from the Upper Ordovician of North-Eastern Iran: 'Thalli', Coenobial Chlorophyceae (Hydrodictyaceae) or Cyanobacteria?

Authors: Navidi-Izad, Navid, Hashemi, Hossein, Cascales-Miñana, Borja, Régnier, Sylvie, Wellman, Charles H., et al.

Source: Palynology, 44(4) : 575-585

Published By: AASP: The Palynological Society

URL: https://doi.org/10.1080/01916122.2019.1657197

PALYNOLOGY
2020, VOL. 44, NO. 4, 575–585
https://doi.org/10.1080/01916122.2019.1657197

Colonial palynomorphs from the Upper Ordovician of north-eastern Iran: ‘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] and Thomas Servais[b]

[a]Department of Geology, Faculty of Earth Sciences, Kharazmi University, Tehran, Iran; [b]CNRS, University of Lille, Lille, France; [c]Department of Animal and Plant Sciences, University of Sheffield, Sheffield, UK

ABSTRACT
This study documents ‘colonial’ palynomorphs from the Upper Ordovician Ghelli Formation of north-eastern Iran. The aggregates of organic-walled microfossils come from the Katian *Armoricochitina nigerica–Ancyrochitina merga* chitinozoan biozones of this formation. The ‘colonial’ microfossils 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 may suggest an affinity to green algal groups, in particular to colonial chlorophyceaen algae, most probably belonging to Hydrodictyaceae. Some specimens also show morphological similarities with cyanobacterial groups. There is so far no evidence to relate these ‘colonial’ palynomorphs to primitive land plants, but we hypothesise that they were possibly produced by ancient green algal lineages with some kind of subaerial existence.

KEYWORDS
acritarchs; cyanobacteria; embryophytes; green algae; spore

1. Introduction

Unraveling the origin of the earliest land plants (embryophytes) continues to be challenging (e.g. Graham 1993; Gray 1993; Kenrick and Crane 1997; Delwiche and Cooper 2015; Edwards and Kenrick 2015; Wellman and Strother 2015; Gerrienne et al. 2016). For a long time, it was considered that the mid-Silurian *Cooksonia* occurrence 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 embryophytes (see e.g. Strother et al. 2017; Morris et al. 2018). It is widely accepted 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 suggests a much earlier origin than the Silurian for the main land plant lineages, at least as far back as the Cambrian (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 from before the Ordovician (Kenrick et al. 2012; Wellman et al. 2013; Servais et al. 2019). The microfossil record identifies the earliest cryptospores in the Middle Ordovician (Strother et al. 1996; Rubinstein et al. 2010), while the first macrofossil records show the oldest sporangia and small plant fragments in the Late Ordovician (Wellman et al. 2003; Salamon et al. 2018). Similarly, organic geochemistry investigations of 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 (Spaak et al. 2017). In the 1990s, Gray introduced the term ‘Eoembryophytic evolutionary land flora’ to describe this Middle–Late Ordovician interval with the earliest liverwort-like plants (Gray 1993; Gerrienne et al. 2016 and references therein).

By far the most significant 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 in transition between ancient green algal lineages and embryophytes? 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 and Strother 2008).

Moreover, most authors agree that cryptospores from the early Middle Ordovician (Dapingian) described by Rubinstein et al. (2010) are derived from the earliest genuine embryophytes. To date, a large number of publications report such cryptospores from different palaeocontinents. So, for

CONTACT Hossein Hashemi h.hashemi@khu.ac.ir Department of Geology, Faculty of Earth Sciences, Kharazmi University, 49 Mofatteh Avenue, Tehran 15614, Iran.

instance, the microfossil record shows occurrences from most parts of Gondwana and its periphery (e.g. Gray et al. 1982; Vavrdová 1984; Richardson 1988; Steemans et al. 1996; Wellman et al. 2003; Rubinstein and Vaccari 2004; Le Hérissé et al. 2007; Steemans et al. 2009; Rubinstein et al. 2010; Mahmoudi et al. 2014; Spina 2015; Strother et al. 2015; Wellman et al. 2015; Ghavidel-Syooki 2016; Rubinstein et al. 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 the 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 do not indicate unambiguously the presence of vascular plants. The presence of a stem group of land plants 'at a bryophytic grade of organisation' since the middle part of the Middle Ordovician is thus established, whereas the presence of the first vascular plants possibly dates back to the Late Ordovician.

The Upper Ordovician (Katian–Hirnantian) Ghelli Formation of north-eastern Iran 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 also include acritarchs, chitinozoans and scolecodonts (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 (north-eastern Iran).

In addition to typical Upper Ordovician cryptospores, the Ghelli Formation also includes early trilete spores, as well as clusters of palynomorphs that resemble 'colonial' organisms, of possible algal, cyanobacterial or plant origin. The present study focuses on 'colonial' organisms; it does not redescribe the cryptospores and miospores, however. Some specimens of 'colonial' palynomorphs can be compared with the recently introduced Middle Ordovician spore 'thalli' of Strother et al. (2017) from the Kanosh Shale (Utah, USA). Vecoli et al. (2015) first published planar clusters of 'cryptospores' with thick and smooth walls from this section, before Strother et al. (2017) described them as the new genus *Grododowon*, interpreted as a post zygotic growth phase in the life cycle of an ancient charophytic alga. The question arises whether 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 potential biological affinities.

2. Geological setting

The studied section (37°12′69″N and 56°55′37″E) of the Upper Ordovician Ghelli Formation is located in north-eastern Iran, about 40 km south-west of Bojnurd and *ca.* 57 km north-east of Jajarm (Figure 1). Afshar-Harb (1979) designated 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 (Figure 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; it is attributed to the Early Ordovician, on the basis of trilobite, brachiopod and acritarch biostratigraphy (Ghavidel-Syooki 2006; Ghobadi Pour et al. 2011; Kebria-ee Zadeh et al. 2015). The overlying Ghelli Formation has a thickness of about 900 m. Afshar-Harb (1979) divided it into three members: in ascending stratigraphical order, these are volcanic rocks, shale and sandstone, and a syndeposited mélange (*sensu* Afshar-Harb 1979) of shales, siltstones and sandstones (Figure 3). The first palynological studies by Ghavidel-Syooki (2000) and Ghavidel-Syooki and Winchester-Seeto (2002) indicated that the Ghelli Formation can be attributed to the Upper Ordovician. More recently, Bayet-Goll and Neto de Carvalho (2016) investigated the ichnology and sedimentology of parts of the Ghelli Formation and recognised a tide-influenced deltaic succession including lower distributary channels, delta front and prodelta sedimentary facies. 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; 105 of these samples were selected and processed in the palynological laboratories of the Kharazmi University (Tehran, Iran) and the Unité Mixte de Recherche (UMR) 8198 Centre National de la Recherché Scientifique (CNRS) Evo-Eco-Paleo research unit of the University of Lille (France). Palynomorphs were extracted from fine-grained samples such as shale and siltstone, using standard palynological techniques. This involved cold hydrochloric acid (HCl), cold hydrofluoric acid (HF) and hot HCl maceration to remove carbonates, silicates and fluorosilicates, respectively. The organic residues were sieved through 15-μm and 20-μm nylon meshes at the universities of Lille and Kharazmi, respectively. No oxidation or alkali treatments were undertaken. All

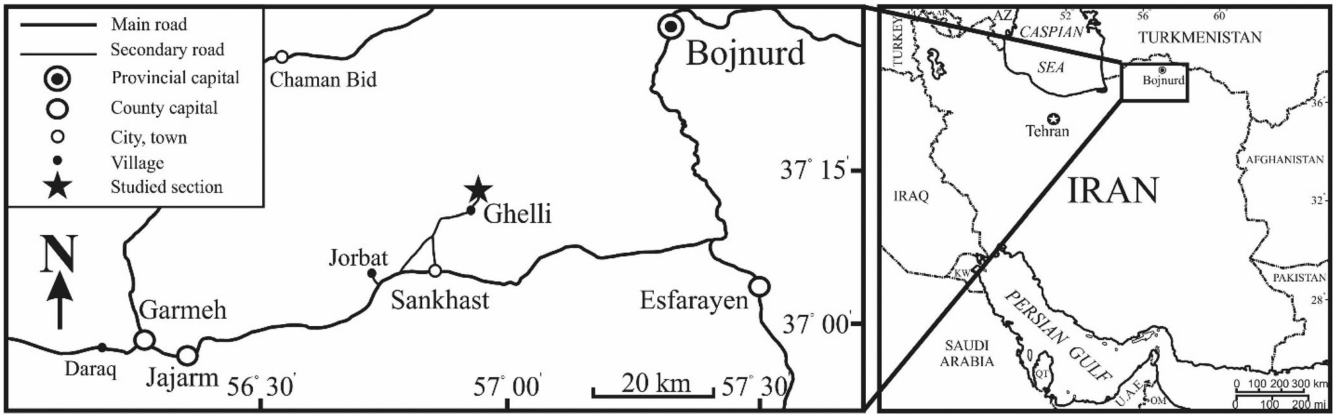

Figure 1. Geographical map of north-eastern Iran showing the location of the investigated section. Source: Authors.

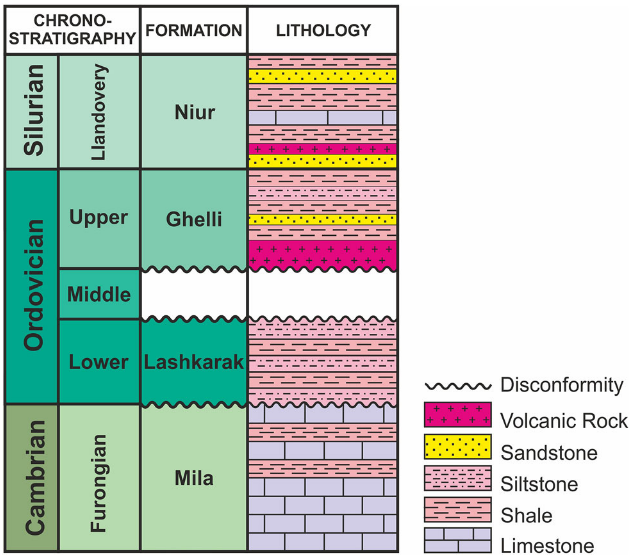

Figure 2. Simplified schematic lithostratigraphical sketch (not to scale) of the Lower Palaeozoic succession in the investigated area.

processed samples contained palynomorphs such as acritarchs, chitinozoans, scolecodonts and cryptospores, in varying abundances and states of preservation. Each palynological slide was observed using a Zeiss Axio Imager A2 optical microscope equipped with a Zeiss AxioCam ERc5s microscope camera. 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 and slides suffixed by '.s' which are deposited in the collections of the UMR 8198 CNRS of the University of Lille (France).

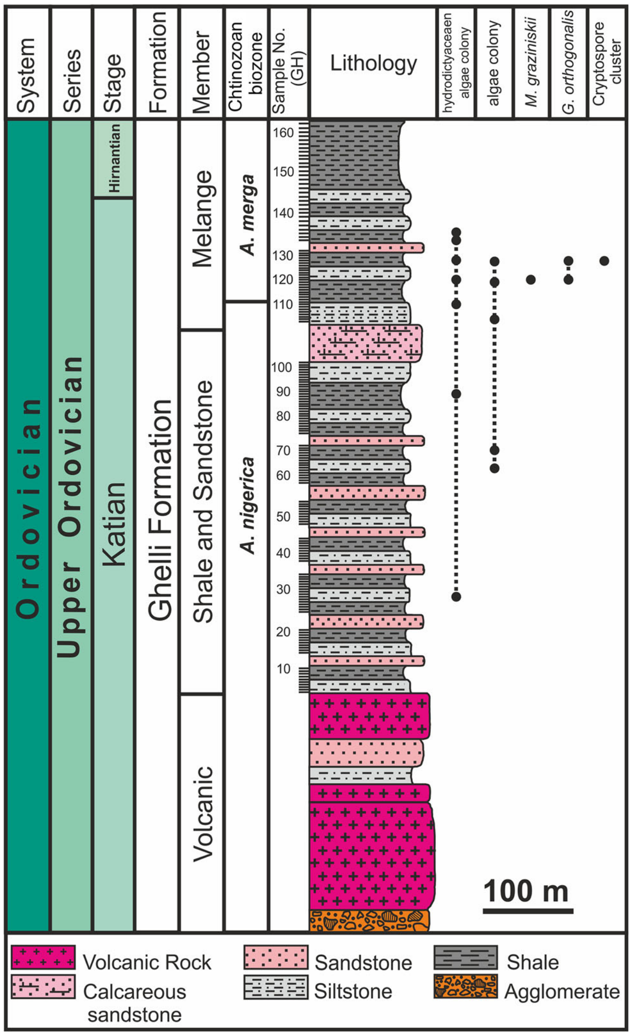

Figure 3. Stratigraphical column of the Upper Ordovician at the Ghelli section and stratigraphical distribution of the examined material. Chitinozoan biostratigraphy after Ghavidel-Syooki and Vecoli (2007), and Ghavidel-Syooki et al. (2011) and unpublished results from the authors.

Ghavidel-Syooki (2016) provided relative percentages of the different palynomorph groups of the Upper Ordovician of the Ghelli Formation in the Pelmis Gorge area, with miospores (including cryptospores) being present in all samples in proportions varying between 15 and 80%, which indicates depositional areas that must have been close to land surfaces, from where the cryptospores originated. It is important to note that the proportions in the present study are rather different. The section investigated here comes from near the locality of Ghelli and lies about 40 km west of the section investigated by Ghavidel-Syooki (2016). Only 50 samples provided cryptospores, in proportions varying between 0.5 and 16.5%, but usually cryptospores are rare, and constitute less than 5% of the assemblage. Moreover, four samples yielded cryptospores with proportions higher than 10%, the marine palynomorphs (acritarchs and chitinozoans) being the dominant part of the assemblages. Scolecodonts are present in most of the samples and are also much more abundant than the cryptospores. This might indicate that the section investigated by Ghavidel-Syooki (2016) lies possibly in a more proximal part of the delta, whereas the section analysed herein is more distal.

The colonial palynomorphs from the Ghelli Formation are only moderately well-preserved. They are even less abundant than the cryptospores and were recovered in only 10 samples in very low proportions, usually between 1 and 2% (with an exceptionally high proportion of 8.6% in sample GH. 125). The few samples with higher abundances come from the upper part of the Ghelli Formation (Figure 3), i.e. from the strata that can be attributed to the *Armoricochitina nigerica–Ancyrochitina merga* chitinozoan biozones (Ghavidel-Syooki and Vecoli 2007; Ghavidel-Syooki et al. 2011).

4. Results

The palynological investigations in the Ghelli Formation confirm the presence of rich palynomorph assemblages containing acritarchs, chitinozoans, scolecodonts, cryptospores and trilete spores in various proportions, that have partly been described in previous studies (Ghavidel-Syooki 2000, 2016, 2017a, 2017b; Ghavidel-Syooki and Winchester-Seeto 2002; Ghavidel-Syooki and Vecoli 2007; Ghavidel-Syooki et al. 2011; Mahmoudi et al. 2014). The dominance of typical marine palynomorphs indicates that all samples are of marine origin. The varying proportion of cryptospores in the assemblages (Ghavidel-Syooki 2016; this study) suggests a terrestrial input in the deltaic environment of the Ghelli Formation.

Besides the classically studied palynomorph groups (acritarchs, chitinozoans, scolecodonts, cryptospores), the assemblages from the Ghelli Formation also contain other organic-walled microfossils, that are here named 'colonial palynomorphs'. These include 'thallus'-like structures (Plate 1) but also aggregates of mostly sphaeromorph forms, some of them forming colonies (Plate 2). The different types of colonial palynomorphs present in the studied assemblages (Plates 1 and 2) mostly resemble 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 attributes to *Muzivum graziniskii.* Ghavidel-Syooki (2016, fig. 2) classified this enigmatic palynomorph as an acritarch and identified its presence in all samples investigated from the Ghelli Formation and the uppermost part of the Lashkarak Formation, indicating that it is recovered from all intervals studied by Ghavidel-Syooki (2016). *Muzivum graziniskii* was originally described from the Devonian of Poland by Wood and Turnau (2001), who considered the taxon to belong to the hydrodictyacean algae. Here, the presence of palynomorphs similar to *Muzivum graziniskii* is confirmed. For instance, the specimen illustrated in Plate 1, figure 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 and Turnau 2001). However, we do not observe the specific geometry that is based on a very square set of 256 cells described in *Muzivum*, and therefore our identification remains questionable (as the specimen illustrated by Ghavidel-Syooki 2016). 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 (Plates 1 and 2). The presence of this type of colonial microfossil in the assemblages examined suggests a freshwater input into the marine environment, which is concordant with the high amount of cryptospores observed in the sediments.

Other specimens recovered herein resemble the recently described taxon *Grododowon orthogonalis* Strother 2017. Strother *in* 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 to belong to the 'cryptospores', i.e. spore-like microfossils *sensu* Strother (1991) and Strother and 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, Figure 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 partly fit the diagnosis of *Grododowon orthogonalis*, although for some specimens, the identification remains problematical and only tentative comparisons are possible. 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, were not recovered from the material examined. This is possibly due to the different laboratory techniques. A more delicate palynological processing technique, such as that used for 'small carbonaceous fossils' (SCFs; e.g. Harvey and Butterfield 2008), would potentially result in the recovery of larger sheets. However, it is also possible that larger 'thalli' are not present in the Ghelli Formation, as they have not been described in previous investigations, or recorded in this study.

Other clusters of spore-like microfossils ('cryptospores') are present in the same samples (e.g. Plate 1, Figure 6). Some resemble the cryptospores of unknown biologigal affinity found in the Cambrian (e.g. Strother et al. 2004). The individual cryptospores (not described in the present work, but extensively recovered by Ghavidel-Syooki 2016), display the typical morphology of cryptospores described from the Upper Ordovician (including the Ghelli Formation) and can be considered related to genuine land plants.

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 resemble neither cryptospores nor the spore 'thalli' described by Strother et al.

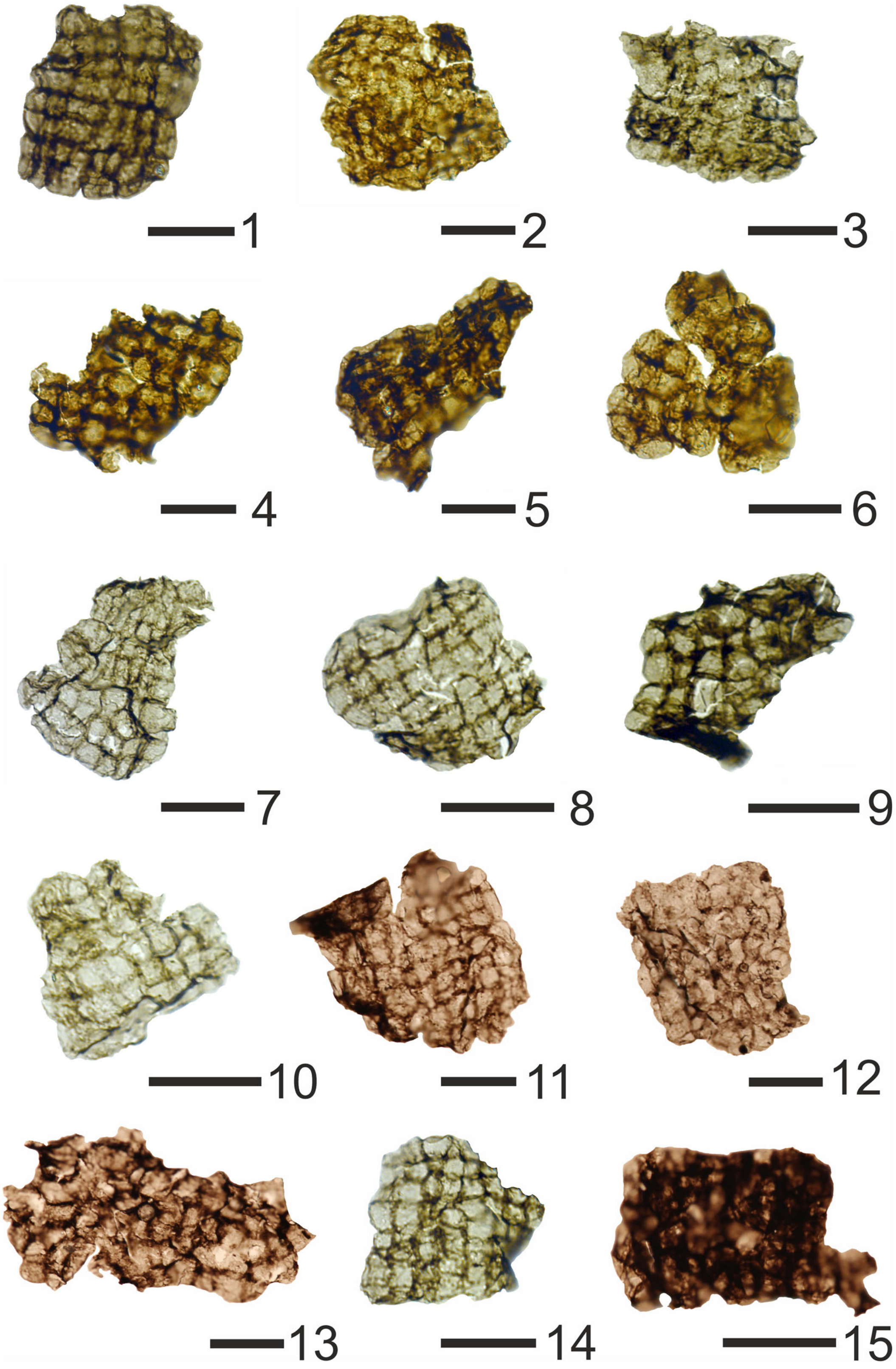

Plate 1. Selected specimens of colonial palynomorphs from the Upper Ordovician of north-eastern Iran, followed by slide number and England Finder (EF) coordinates. 1. ?*Grododowon orthogonalis* Strother 2017, slide GH.128.2, EF: P29/4; 2. hydrodictyaceaen algae colony, slide GH.128.1, EF: W48; 3. hydrodictyaceaen 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, 2001, 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 bars: 20 μm.

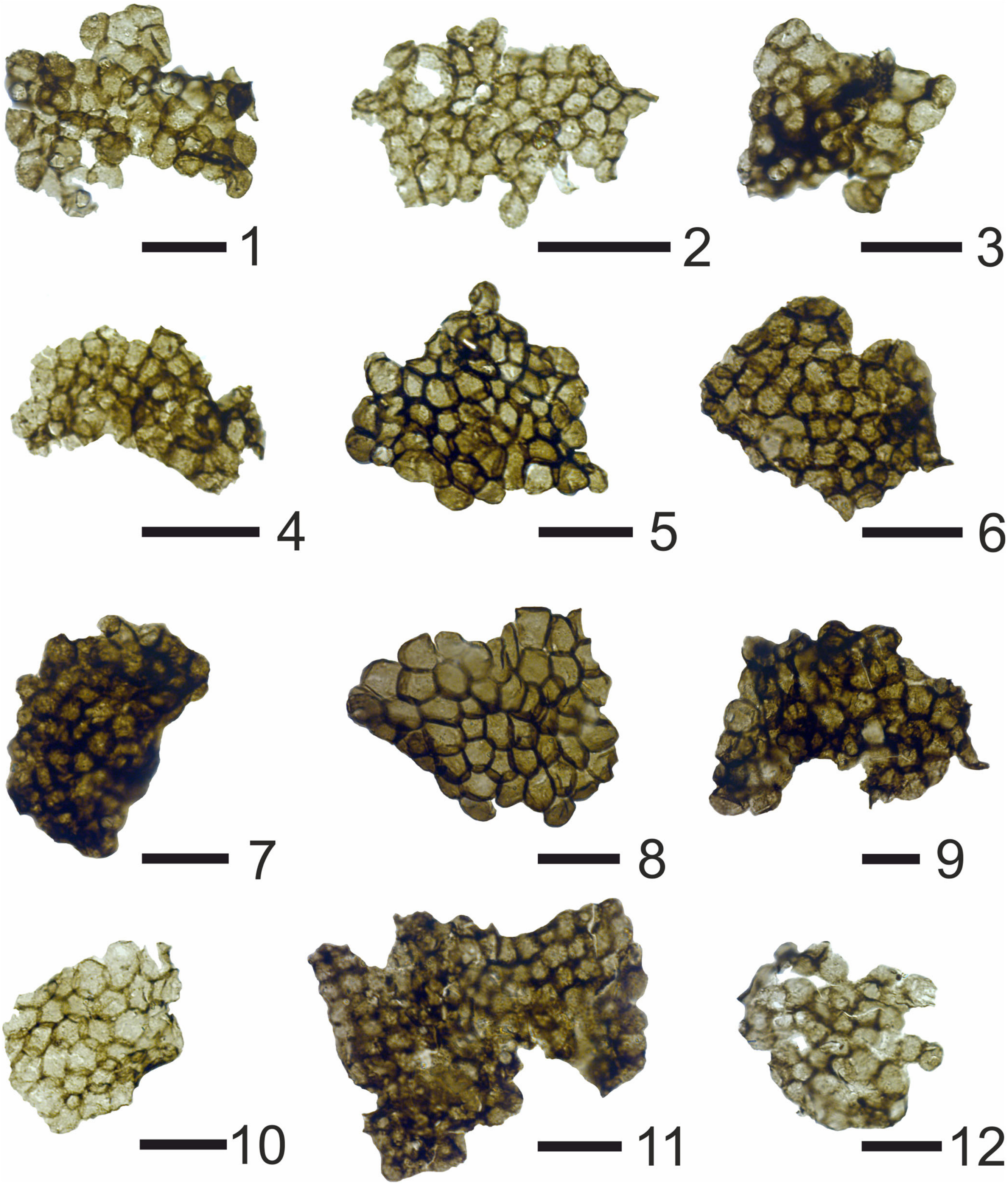

Plate 2. Selected specimens of colonial palynomorphs from the Upper Ordovician of north-eastern Iran, followed by slide number and England Finder (EF) coordinates. 1. Algae colony, slide GH.70.s, EF: O54/1; 2. algae colony, slide GH.70.s, EF: W53; 3. algae colony, slide GH.70.s, EF: S56/2; 4. algae colony, 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 bars: 20 µm.

(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 attributed to prasinophycean algae by some authors (e.g. Le Hérissé et al. 2017), but for which the biological affinity remains questionable. 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, without further classification into a specific biological group.

The presence of planar sheets and cryptospore clusters, in association with isolated cryptospores derived from primitive plants, as well as the presence of aggregates or colonies of more or less spherical palynomorphs, thus indicates a variation of microfossils that might reflect the presence of different types of green algal groups in the investigated material.

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 and Turnau (2001) in 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 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, 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). 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 Evitt's (1963) definition, 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 stated 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 some diagnoses of this group, as some specimens have spore-like morphologies. The term 'cryptospore', like the term 'acritarch', has different definitions and conceptions. Cryptospores are organic-walled microfossils that resemble spores ('sporomorphs'), but 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, p. 116) 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'.

In this original definition, the cryptospores are thus considered to be of terrestrial origin ('non-marine sporomorphs'). Richardson (1988) extended this definition to include single spores, naturally separated from dyads, which possess a circular contact area. Subsequently, Strother (1991, p. 220-221) 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.

Thus, both Richardson (1988) and Strother (1991) consider the cryptospores to be 'non-marine sporomorphs' with no clear biological affinity. However, Steemans (2000, p. 190-191) emended Richardson et al.'s (1984) original definition by considering all cryptospores to be 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 embryophytes.

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

In summary, the specimens presented here can thus be classified as 'acritarchs' and, to some extent, a few of them could be classified as 'cryptospores' following the definition of the group *sensu* Strother (1991) but not *sensu* Steemans (2000). They could be named aggregates, clusters, colonies or coenobia (a synonym of colonies). The terminology 'thalli' can also be used for a descriptive purpose. However, it should not be in the sense that it may suggest a relation to 'thallophytes' (an abandoned biological category to group algae, lichens and fungi), thus implying a biological affinity.

6. Potential biological affinities

The most interesting questions are not about classification in artificial groups used by palynologists, but 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, '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: zygospores) 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, which can be single celled or colonial, and of either marine or freshwater origin.

Moreover, some of the microfossils that are spore like, but that do not display all the morphological characteristics that would allow them be classified as land plant miospores, can be named 'spores'. Such 'spores' (or, for some authors, 'cryptospores') could be affiliated with different algal groups (or even fungi), and may not be directly related to embryophyte land plants. Such spores correspond to the definition of cryptospores *sensu* Strother (1991), i.e. by excluding a biological affinity to embryophytes (*sensu* Steemans 2000). In this way, Strother et al. (2017, p. 67) considered that the taxon *Grododowon orthogonalis* Strother 2017 can be classified among the 'cryptospores'. Indeed, these 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 spherical acritarchs and clusters of such simple acritarchs to be 'prasinophycean phycomata' (e.g. Colbath and Grenfell 1995; Guy-Ohlson 1996; Le Hérissé et al. 2017), although modern prasinophycean phycomata do not occur in colonies.

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 exclusively freshwater (e.g. Colbath and 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 and Grenfell 1995).

The Upper Ordovician specimens of Iran mostly resemble different groups of green algae belonging to chlorophyceans, and some of them can be compared to the modern hydrodictyacean algae. The 'spore-like thalli' described by Strother et al. (2017) might be related to the class Charophyceae (and to a charophytic algal lineage), but equally they may belong simply to a group of green algae, for example of the class Chlorophyceae, and in particular to 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 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 *Eomerismopedia maureeniae*. This taxon was considered by these authors to be another cyanobacterium. Morphological comparisons with modern material, in particular with the genus *Merismopedia* Meyen 1839, allowed Foster et al. (2002) to attribute *Eomerismopedia* to the cyanobacterial family Chroococcaceae and in particular the order Chroococcales. Some of the material reported herein morphologically resembles members of this family, indicating that some of the recovered colonial palynomorphs may well be of cyanobacterial and not green algal origin, but comparisons remain so far only tentative.

7. Conclusions

In this paper, some 'colonial' palynomorphs from the Upper Ordovician Ghelli Formation (north-eastern Iran) are presented. The palynomorphs come from the *Armoricochitina nigerica–Ancyrochitina merga* chitinozoan biozones (Katian) 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 so far.

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 suggested to be 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 Hydrodictyaceae. Others, however, may represent cyanobacterial groups, as previously discussed by Foster et al. (2002).

Finally, the 'colonial' palynomorphs of the Ghelli Formation are most probably related to different groups of algae and possibly cyanobacteria, but they are not related to land plants. The assemblages from the Upper Ordovician of Iran fit in Gray's (1993) Eoembryophytic phase of earliest liverwort-like plants. They also correspond to Strother et al.'s (2010) thalloid bryophyte landscape and/or Gerrienne et al.'s (2016) proembryophytic interval that was proposed to characterise the long transition from green algae to liverworts. The 'colonial' palynomorphs were thus possibly produced by ancient green algal lineages with some kind of subaerial existence.

Acknowledgements

We thank the three reviewers of our manuscript, Reed Wicander (Mount Pleasant, USA), Paul Strother (Boston, USA) and an anonymous referee, for their valuable comments that greatly improved this paper. We also thank Managing Editor Jim Riding (Nottingham, UK), for the editorial work and useful comments. Navid Navidi-Izad acknowledges the palaeontological team of the Evo-Eco-Paleo unit (Lille University – CNRS) for making his research stay possible. He also acknowledges financial support received from the Iranian Ministry of Science, Research, and Technology (MSRT). Thomas Servais thanks Van Mildert College, University of Durham, for financing a Prowse research fellowship. Hamed Bouzari Nezhad is acknowledged for his invaluable assistance during field work in Iran. This is a contribution to IGCP no. 653, 'The onset of the Great Ordovician Biodiversification Event'.

Disclosure statement

No potential conflict of interest was reported by the authors.

Notes on contributors

NAVID NAVIDI-IZAD is currently a PhD student at the Department of Earth Sciences, Kharazmi University, Tehran, Iran, working on the biostratigraphy, palaeoecology, and palaeobiogeography of the Lower Palaeozoic palynomorphs of northern Iran. He received his MSc in stratigraphy and palaeontology in 2013 from Tehran University, Iran. Navid visited the Evo-Eco-Paléo unit of University of Lille, France, for an 8-month sabbatical leave in 2018 and 2019.

HOSSEIN HASHEMI has been an associate professor in the Department of Geology, Faculty of Earth Sciences, Kharazmi University, Tehran, Iran since 1999. He obtained his MSc degree from Tehran University in 1990, working on Early Permian palynomorphs from the Alborz Ranges, northern Iran. Awarded a PhD scholarship by the Australian government, he continued research on Palaeozoic palynomorphs and received his doctoral degree from The University of Queensland in 1997. He is principally interested in the systematics and stratigraphic applications of Palaeozoic and Mesozoic palynomorphs.

THOMAS SERVAIS is a research director at the French Centre of Scientific Research (CNRS). He was trained as a geologist at the universities of Namur and Liege in Belgium, and received a PhD on Ordovician acritarchs in 1993. After postdoctoral studies in Belgium, Germany and the United Kingdom, Thomas was recruited as a CNRS research associate at the University of Lille in 1997. His research is focused on Lower Palaeozoic microphytoplankton. Thomas is currently vice-chairman of the International Subcommission of Ordovician Stratigraphy (ISOS) and co-leader of the International Geoscience Programme (IGCP) 653 'The onset of the Great Ordovician Biodiversification Event' (2016-2020).

BORJA CASCALES-MIÑANA After graduating in Spain and post-docs in France and Belgium, Borja Cascales-Miñana joined the CNRS as research fellow in 2017. He works on the early evolution of vascular plants and the Paleozoic floras. He has a special interest in the study of the first terrestrial ecosystems and the great biotic crises of vegetation. His activity involves the use of fossil-based data analysis to elucidate the plant dynamics through time, as well as regular fieldworks for the study of plant macrofossils and spore diversity.

SYLVIE REGNIER Graduated as a biotechnology technician and started working in the University Hospital Calmette at Lille (France) in the hematology lab (specializing in chemoresistance in Acute Myeloid Leukemia), before joining a private laboratory of soil, water and air analyses. She arrived in the Earth Science Department of the University of Lille in 2006. After training in the palynology laboratories of Lille and Liège (Belgium), she now specializes in palynomorph and microfossil extraction techniques, and currently works on optimizing the methods of palynomorph extraction (improving time and quality). She is also responsible for the SEM platform of the palaeontology research team of the Evo-Eco-Paleo CNRS research unit that she integrated in 2017.

CHARLES WELLMAN is Professor of Palaeobiology in the Department of Animal and, Plant Sciences of the University of Sheffield, UK. He received a B.Sc. from the University of Southampton in 1987 and a Ph.D. from Cardiff University in 1991 (A NERC CASE award with the Natural History Museum, London). Charles' Ph.D. research involved a study of early land plant microfossils from Scottish Silurian-Devonian 'Lower Old Red Sandstone' deposits. Subsequently Charles' research has diversified to investigate various aspects of the colonisation of the land, including work on both fossil and living plants, and a consideration of what lived on the land before the land plants.

ORCID

Charles H. Wellman http://orcid.org/0000-0001-7511-0464
Thomas Servais http://orcid.org/0000-0002-4089-7874

References

Afshar-Harb A. 1979. The stratigraphy, tectonic and petroleum geology of Kopet-Dagh region [dissertation]. London: Imperial College of Science and Technology, University of London.

Badawy AS, Mehlqvist K, Vajda V, Ahlberg P, Calner M. 2014. Late Ordovician (Katian) spores in Sweden: oldest land plant remains from Baltica. GFF. 136(1):16–21.

Bayet-Goll A, Neto de Carvalho C. 2016. Ichnology and sedimentology of a tide-influenced delta in the Ordovician from the northeastern Alborz range of Iran (Kopet Dagh region). Lethaia. 49(3):327–350.

Batten DJ. 1996. Green and blue-green algae. Colonial Chlorococcales. In: Jansonius J, McGregor DC, editors. Palynology: principles and applications American Association of Stratigraphic Palynologists Foundation. Vol. 1. Salt Lake City (UT): Publishers Press; p. 205–214.

Clarke JT, Warnock R, Donoghue PC. 2011. Establishing a time-scale for plant evolution. The New Phytologist. 192(1):266–301.

Colbath GK, Grenfell HR. 1995. Review of biological affinities of Paleozoic acid-resistant, organic-walled eukaryotic algal microfossils (including "acritarchs"). Review of Palaeobotany and Palynology. 86(3–4): 287–314.

Delwiche CF, Cooper ED. 2015. The evolutionary origin of a terrestrial flora. Current Biology. 19:899–910.

Edwards D, Kenrick P. 2015. The early evolution of land plants, from fossils to genomics: a commentary on Lang (1937) 'On the plant-remains from the Downtownian of Wales'. Philosophical Transactions of the Royal Society B: Biological Sciences. 370(1666):20140343.

Edwards D, Davies KL, Axe L. 1992. A vascular conducting strand in the early land plant *Cooksonia*. Nature. 357(6380):683–685.

Evitt WR. 1963. A discussion and proposals concerning fossil dinoflagellates, hystrichospheres, and acritarchs. I. Proceedings of the National Academy of Sciences of the United States of America. 49(2):158–164.

Fensome RA, Williams GL, Barss MS, Freeman JM, Hill JM. 1990. Acritarchs and fossil prasinophytes: an index to genera, species and intraspecific taxa. American Association of Stratigraphic Palynologists, Contribution Series. 154:1–771.

Foster CB, Reed JD, Wicander R. 1989. *Gloeocapsomorpha prisca* Zalessky, 1917: a new study: Part I: taxonomy, geochemistry, and paleoecology. Géobios. 22(6):735–759.

Foster CB, Wicander R, Playford G. 2002. *Eomerismopedia maureeniae* n.g. n.sp., a chroococcacean cyanobacterium from the lower Ordovician Coolibah Formation, Georgina Basin, Queensland, Australia. Neues Jahrbuch Für Geologie Und Paläontologie-Monatshefte. 2:65–74.

Gerrienne P, Servais T, Vecoli M. 2016. Plant evolution and terrestrialization during Palaeozoic times-The phylogenetic context. Review of Palaeobotany and Palynology. 227:4–18.

Ghavidel-Syooki M. 2000. Palynostratigraphy and paleobiogeography of Lower Palaeozoic strata in the Ghelli area, northeastern Alborz Range of Iran (Kopet-Dagh region). Journal of Sciences Islamic Republic of Iran. 11:305–318.

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. Review of Palaeobotany and Palynology. 139(1–4):81–95.

Ghavidel-Syooki M. 2016. Cryptospore and trilete spore assemblages from the Late Ordovician (Katian-Hirnantian) Ghelli Formation, Alborz Mountain Range, Northeastern Iran: Palaeophytogeographic and palaeoclimatic implications. Review of Palaeobotany and Palynology. 231:48–71.

Ghavidel-Syooki M. 2017a. Stratigraphic evidence for Hirnantian glaciation in the Alborz Mountain Ranges, northeastern Iran. Palaeogeography, Palaeoclimatology, Palaeoecology. 485:879–898.

Ghavidel-Syooki M. 2017b. Biostratigraphy of acritarchs and chitinozoans in Ordovician Strata from the Fazel Abad area, Southeastern Caspian Sea, Alborz Mountains, Northern Iran: Stratigraphic Implications. Journal of Sciences Islamic Republic of Iran. 28:37–57.

Ghavidel-Syooki M, Hassanzadeh J, Vecoli M. 2011. Palynology and isotope geochronology of the Upper Ordovician-Silurian successions (Ghelli and Soltan Maidan Formations) in the Khoshyeilagh area, eastern Alborz Range, northern Iran; stratigraphic and palaeogeographic implications. Review of Palaeobotany and Palynology. 164(3–4): 251–271.

Ghavidel-Syooki M, Vecoli M. 2007. Latest Ordovician-Early Silurian chitinozoans from the eastern Alborz Mountain Range, Kopet-Dagh region, Northeastern Iran: biostratigraphy and paleobiogeography. Review of Palaeobotany and Palynology. 145(1–2):173–192.

Ghavidel-Syooki M, Winchester-Seeto T. 2002. Biostratigraphy and Palaeogeography of Late Ordovician chitinozoans from the northeastern Alborz Range, Iran. Review of Palaeobotany and Palynology. 118(1–4):77–99.

Ghobadi Pour M, Kebriaee-Zadeh MR, Popov LE. 2011. Early Ordovician (Tremadocian) brachiopods from the Eastern Alborz Mountains, Iran. Estonian Journal of Earth Sciences. 60(2):65–82.

Graham LE. 1993. Origin of land plants. New York (NY): Wiley.

Gray J, Massa D, Boucot AJ. 1982. Caradocian land plant microfossils from Libya. Geology. 10(4):197–201.

Guy-Ohlson D. 1996. Green and Blue-Green algae. 7B-Prasinophycean algae. In: Jansonius J, McGregor DC, editors. Palynology: principles and applications American Association of Stratigraphic Palynologists Foundation. Vol. 1. Salt Lake City (UT): Publishers Press; p. 181–189.

Harrison CJ. 2016. Development and genetics in the evolution of land plant body plans. Philosophical Transactions of the Royal Society B: Biological Sciences. 372:1–12.

Harvey THP, Butterfield NJ. 2008. Sophisticated particle-feeding in a large Early Cambrian crustacean. Nature. 452(7189):868–871.

Karol KG, McCourt RM, Cimino MT, Delwiche CF. 2001. The closest living relatives of land plants. Science (New York, N.Y.). 294(5550): 2351–2353.

Kebria-ee Zadeh MR, Ghobadi Pour M, Popov LE, Baars C, Jahangir H. 2015. First record of the Ordovician fauna in Mila-Kuh, eastern Alborz, northern Iran. Estonian Journal of Earth Sciences. 64:1–18.

Kenrick P, Crane PR. 1997. The origin and early evolution of plants on land. Nature. 389(6646):33–39.

Kenrick P, Wellman CH, Schneider H, Edgecombe GD. 2012. A timeline for terrestrialization: consequences for the carbon cycle in the Palaeozoic. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences. 367(1588):519–536.

Le Hérissé A, Al-Ruwaili M, Miller M, Vecoli M. 2007. Environmental changes reflected by palynomorphs in the early Middle Ordovician Hanadir Member of the Qasim Formation, Saudi Arabia. Revue de Micropaléontologie. 50(1):3–16.

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 Sag-Hanadir transitional beds in the QSIM-801 well, Saudi Arabia. Revue de Micropaléontologie. 60(3):289–318.

Mahmoudi M, Saburi J, Alimohammadian H, Majidifard MR. 2014. The first cryptospore assemblages of Late Ordovician in Iran, Ghelli Formation, eastern Alborz. Geopersia. 4:125–140.

Morris JL, Puttick MN, Clark JW, Edwards D, Kenrick P, Pressel S, Wellman CH, Yang Z, Schneider H, Donoghue PC. 2018. The timescale of early land plant evolution. Proceedings of the National Academy of Sciences. 115(10):E2274–E2283.

Qiu Y-L, Li L, Wang B, Chen Z, Knoop V, Groth-Malonek M, Dombrovska O, Lee J, Kent L, Rest J, et al. 2006. The deepest divergences in land plants inferred from phylogenomic evidence. Proceedings of the National Academy of Sciences of the United States of America. 103(42):15511–15516.

Raevskaya E, Dronov A, Servais T, Wellman CH. 2016. Cryptospores from the Katian (Upper Ordovician) of the Tungus basin: The first evidence for early land plants from the Siberian paleocontinent. Review of Palaeobotany and Palynology. 224:4–13.

Richardson JB. 1988. Late Ordovician and Early Silurian cryptospores and miospores from northeast Libya. In: El-Arnauti A, Owens B, Thusu B, editors. Subsurface palynostratigraphy of northeast Libya Benghazi: Garyounis University Publications; p. 89–109.

Richardson JB, Ford JH, Parker F. 1984. Miospores, correlation and age of some Scottish Lower Old Red Sandstone sediments from the Strathmore region (Fife and Angus). Journal of Micropalaeontology. 3(2):109–124.

Rubinstein CV, de la Puente GS, Delabroye A, Astini RA. 2016. The palynological record across the Ordovician/Silurian boundary in the Cordillera Oriental, Central Andean Basin, northwestern Argentina. Review of Palaeobotany and Palynology. 224:14–25.

Rubinstein CV, Gerrienne P, De La Puente GS, Astini RA, Steemans P. 2010. Early Middle Ordovician evidence for land plants in Argentina (eastern Gondwana). The New Phytologist. 188(2):365–369.

Rubinstein CV, Vaccari NE. 2004. Cryptospore assemblages from the Ordovician/Silurian boundary in the Puna region, north-west Argentina. Palaeontology. 47(4):1037–1061.

Salamon MA, Gerrienne P, Steemans P, Gorzelak P, Filipiak P, Le Hérissé A, Paris F, Cascales-Miñana B, Brachaniec T, Misz-Kennan M, et al. 2018. Putative Late Ordovician land plants. New Phytologist. 218(4): 1305–1305.

Servais T. 1996. Some considerations on acritarch classification. Review of Palaeobotany and Palynology. 93(1–4):9–22.

Servais T, Cascales-Miñana B, Cleal C, Gerrienne P, Harper DAT, Neumann M. 2019. Revisiting the great Ordovician diversification of land plants:

recent data and perspectives. Palaeogeography, Palaeoclimatology, Palaeoeocology 534.

Spaak G, Edwards DS, Foster CB, Pagès A, Summons RE, Sherwood N, Grice K. 2017. Environmental conditions and microbial community structure during the Great Ordovician Biodiversification Event; a multi-disciplinary study from the Canning Basin, Western Australia. Global and Planetary Change. 159:93–112.

Spina A. 2015. Latest Ordovician (Hirnantian) miospores from the NL-2 well, Algeria, North Africa, and their evolutionary significance. Palynology. 39(2):205–219.

Steemans P. 2000. Miospore evolution from the Ordovician to the Silurian. Review of Palaeobotany and Palynology. 113(1–3):189–196.

Steemans P, Le Hérissé A, Bozdogan N. 1996. Ordovician and Silurian cryptospores and miospores from Southeastern Turkey. Review of Palaeobotany and Palynology. 93(1–4):35–76.

Steemans P, Le Hérissé A, Melvin J, Miller MA, Paris F, Verniers J, Wellman CH. 2009. Origin and radiation of the earliest vascular land plants. Science (New York, N.Y.). 324(5925):353.

Stöcklin J, Ruttner A, Nabavi MH. 1964. New data on the Lower Palaeozoic and Precambrian of North Iran. Tehran: Geological Survey of Iran Report No. 1; p. 1–29.

Strother PK. 1991. A classification scheme for the cryptospores. Palynology. 15(1):219–236.

Strother PK, Al-Hajri S, Traverse A. 1996. New evidence for land plants from the lower Middle Ordovician of Saudi Arabia. Geology. 24(1): 55–90.

Strother PK, Beck JH. 2000. Spore-like microfossils from Middle Cambrian strata: expanding the meaning of the term cryptospore. In: Harley MM, Morton CM, Blackmore S, editors. Pollen and Spore London: The Royal Botanic Gardens Kew; p. 413–424.

Strother PK, Taylor WA, Beck JH, Vecoli M. 2017. Ordovician spore 'thalli' and the evolution of the plant sporophyte. Palynology. 41(sup1): 57–68.

Strother PK, Traverse A, Vecoli M. 2015. Cryptospores from the Hanadir Shale Member of the Qasim Formation, Ordovician (Darriwilian) of Saudi Arabia: taxonomy and systematics. Review of Palaeobotany and Palynology. 212:97–110.

Strother PK, Wood GD, Taylor WA, Beck JH. 2004. Middle Cambrian cryptospores and the origin of land plants. Australasian Palaeontological Association, Memoir. 29:99–113.

Strother PK, Servais T, Vecoli M. 2010. The effects of terrestrialization on marine ecosystems: the effects of the fall of CO_2. Geological Society, London, Special Publications. 339(1):37–48.

Taylor WA, Strother PK. 2008. Ultrastructure of some Cambrian palynomorphs from the Bright Angel Shale, Arizona, USA. Review of Palaeobotany and Palynology. 151(1-2):41–50.

Vavrdová M. 1984. Some plant microfossils of possible terrestrial origin from the Ordovician of Central Bohemia. Vestnik Ustredniho Ustavu Geologickeho. 3:165–170.

Vavrdová M. 1990. Coenobial acritarchs and other palynomorphs from the Arenig/Llanvirn boundary, Prague basin. Vestnik Ustredniho Ustavu Geologickeho. 65:237–242.

Vecoli M, Beck JH, Strother PK. 2015. Palynology of the Ordovician Kanosh Shale at Fossil Mountain, Utah. Journal of Paleontology. 98: 424–447.

Vecoli M, Delabroye A, Spina A, Hints O. 2011. Cryptospore assemblages from the Upper Ordovician (Katian-Hirnantian) strata of Anticosti Island, Quebec, Canada, and Estonia: palaeophytogeographic and palaeoclimatic implication. Review of Palaeobotany and Palynology. 166(1–2):76–93.

Vecoli M, Wellman CH, Gerrienne P, Le Hérissé A, Steemans P. 2017. Middle Ordovician cryptospores from the Saq-Hanadir transitional beds in the QSIM-801 well, Saudi Arabia. Revue de Micropaléontologie. 60(3):319–331.

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

Wellman CH. 1996. Cryptospores from the type area for the Caradoc Series (Ordovician) in southern Britain. Palaeontology. 55:103–136.

Wellman CH, Osterloff PL, Mohiuddin U. 2003. Fragments of the earliest land plants. Nature. 425(6955):282–285.

Wellman CH, Steemans P, Miller MA. 2015. Spore assemblages from Upper Ordovician and lowermost Silurian sediments recovered from the Qusaiba-1 shallow core hole, Qasim region, central Saudi Arabia. Review of Palaeobotany and Palynology. 212:111–126.

Wellman CH, Steemans P, Vecoli M. 2013. Palaeophytogeography of Ordovician-Silurian land plants. In: Harper D, Servais T, editors. Early Palaeozoic biogeography and palaeogeography Vol. 38. London: Memoirs of the Geological Society; p. 461–476.

Wellman CH, Strother PK. 2015. The terrestrial biota prior to the origin of land plants (embryophytes): a review of the evidence. Palaeontology. 58(4):601–627.

Wood GD, Turnau E. 2001. New Devonian coenobial chlorococcales (Hydrodictyaceae) from the Holy Cross Mountains and Radom-Lublin region of Poland: their palaeoenvironmental and sequence stratigraphic implications. In: Goodman DK, Clarke RT, editors. Proceedings of the IX International Palynological Congress, Houston, Texas, USA 1996: American Association of Stratigraphic Palynologists Foundation; p. 53–63.

Zhong B, Fong R, Collins LJ, McLenachan PA, Penny D. 2014. Two new fern chloroplasts and decelerated evolution linked to the long generation time in tree ferns. Genome Biology and Evolution. 6(5): 1166–1173.