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## Virgatasporites and Attritasporites: the oldest land plant derived spores, cryptospores or acritarchs?

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### ABSTRACT

The oldest reported occurrence of cryptospores supposed to derive from land plants (embryophytes) is currently considered to be in the Middle Ordovician. The two genera *Virgatasporites* and *Attritasporites*, described in the 1960's from the Early Ordovician (Tremadocian) of Algeria, are morphologically close to the miospores, and therefore pose a dilemma, because these spore-like microfossils are recorded before the first appearance of the oldest land plant derived spores. Here the taxonomy, biostratigraphy and palaeobiogeography of the two genera and their species are revised. Both genera are found in many localities on the Gondwanan border between the late Cambrian and the Middle Ordovician. They have not been found at the margins of other palaeocontinents so far. The biological affinity of the taxa remains uncertain. Several authors considered the two genera to be spore-like microfossils, whereas other authors classified them as acritarchs, i.e. organic-walled microfossils of unknown biological affinity. As the relationship to the embryophyte lineage cannot be established clearly to date, the biological affiliation remains enigmatic. Therefore, in the absence of other evidence, the taxa *Virgatasporites* and *Attritasporites* should be temporarily classified as *incertae sedis*, i.e. as acritarchs, before their true biological affinity is known and they can be adequately placed into a biological group.

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Acritarchs; cryptospores; embryophyte origin; Gondwana; Cambrian; Ordovician

## 1. Introduction

For many decades the early Cambrian has been considered as the time interval when marine life appeared during the Cambrian “explosion” as recorded from Konservat-Lagerstätten like the Chenjiang Biota, China, or the Burgess Shale, Canada (Briggs 2015). Similarly, the Devonian was considered the geological time period when land plants appeared and rapidly diversified, with the Lower Devonian Rhynie Chert Lagerstätte (Scotland, UK) being one of the first complete terrestrial ecosystems with finely preserved details of early land plants (Edwards et al. 2017). Today, it is well understood that marine life developed much earlier, in the Precambrian, and, similarly, the first evidence of land plants is available from pre-Devonian intervals (Wellman et al. 2013). The oldest generally accepted plant fossils with *in situ* spores are from the middle Sheinwoodian, early Wenlock (middle Silurian) of the Barrandian area, Czech Republic (Libertín et al. 2018). Most of the claims of pre-Silurian plant megafossils can be discounted, and for many cases it has been proven that they are fragments of other organisms. However, there is now

abundant evidence from the microfossil record that land plants were already widespread even before the Silurian. An “Ordovician explosion” of land plants occurred during the Middle Ordovician (Servais et al. 2019), with geochemical and microfossil data confirming the presence of land plants on most continents during this time period. The oldest sporangia were described from the Upper Ordovician of Oman (Wellman et al. 2003), whereas the first trilete spores appeared in the Upper Ordovician of Saudi Arabia (Steemans et al. 2009). Putative land plants have been reported from the Upper Ordovician of Poland (Salamon et al. 2018). It is today clear that by the end of the Ordovician, land plants were distributed all over the globe (Wellman et al. 2013).

The oldest spore-like microfossils, named cryptospores, that are uncontroversially related to land plants, have been found in sediments of Middle Ordovician age (Rubinstein et al. 2010). Older records of “cryptospores”, such as those from the Cambrian (e.g. Strother and Beck 2000), are most probably derived from various algal groups. Similarly, the recent discovery of Early Ordovician “cryptospores” from Australia indicates that these microfossils derive

most probably from charophyte algae, but not from true land plants (Strother and Foster 2021).

The “spores” *Virgatasporites* and *Attritasporites* were described in the 1960’s from the Early Ordovician (Tremadocian) of Algeria (Combaz 1967). Their age poses a dilemma: the two genera and their species were recorded in palynological assemblages from sediments that are clearly older than the Middle Ordovician. If these taxa, described as spores, derive from land plants, they would be the oldest available evidence of embryophytes. The question about their biological affinity thus arises.

The objective of the present paper is to revise the available data from the literature and from our own palynological observations, in order to understand if *Virgatasporites* and *Attritasporites* are cryptospores from embryophytes or palynomorphs deriving from a particular algal group. It is beyond the scope of the present paper to fully revise the taxonomy of the two taxa, because it has so far not been possible to locate the type-material and to obtain large assemblages of material collected from the type locality. *Virgatasporites* and *Attritasporites* are herein compared with other cryptospores and acritarchs, and complete reviews of the biostratigraphic and palaeobiogeographical distributions of the two genera are presented.

## 2. Early land plant evidence and the cryptospore debate

Molecular clock analyses place the origin of land plants, *i.e.* embryophytes, far earlier than that suggested by the fossil record, with dates spanning from c. 700 Ma to c. 450 Ma, indicating a high probability of a Precambrian or Cambrian origin, whereas the origin of vascular plants is dated to be Cambrian–Ordovician interval (*e.g.* Magallon et al. 2013; Gerrienne et al. 2016; Morris et al. 2018; Nie et al. 2020).

The first geochemical data became available recently too. There is still no clear evidence of biomarkers that can be linked to land plants during the Precambrian and Cambrian (see review in Servais et al. 2019), but Spaak et al. (2017) identified, for the first time, different biomarkers from the Middle Ordovician sediments of the Canning Basin, Australia, that can be related to typical bryophytes. Most interestingly, the sediments that delivered these biomarkers also provided cryptospores that can possibly be related to the same type of early bryophytic land plants (Spaak et al. 2017).

Phylogenetic analyses also made huge progress in recent years. For many years, the charophycean algae were considered to be paraphyletic to embryophytes (*e.g.* Mishler and Churchill 1984). Subsequently, three candidates for the closest living relatives to land plants were considered: the

Charophyceae, Coleochaetophyceae and the Zygnematophyceae (Gerrienne et al. 2016). The algal – land plant transition was considered to mirror the origin of subaerial land plants from the aquatic algal groups (Kenrick and Crane 1997; Gerrienne et al. 2016; Puttick et al. 2018). Different phylogenetic models exist, and the new plant group of the eophytes, described recently by Edwards et al. (2021) and delivering *in situ* cryptospores, may modify the models of earliest stem group embryophytes.

Most interestingly, the different algal groups and the first land plants produced organic-walled microfossils that can be recovered from palynological residues. Different groups of green algae produce acid-resistant microfossils that are described from the Palaeozoic, including the chlorophytes and the streptophytes. Whereas the first includes the classes Prasinophyceae and Chlorophyceae, the second includes the Zygnematophyceae and the Charophyceae. All these groups may produce palynomorphs, some of which have been reported from Palaeozoic palynological assemblages.

Many prasinophytes produce phycomata, that have also been found in the Palaeozoic, and that have often been classified among the acritarchs. The acritarch *Pterospermella* Eisenack 1972, for example, may correspond to the living prasinophyte phycomata *Pterosperma*, whereas *Tasmanites* Newton 1875 is related to the living prasinophyte *Pachysphaera* (Colbath and Grenfell 1995). Several early Palaeozoic acritarchs, in particular some leiospheres, may actually be related to prasinophycean algae (*e.g.* Le Hérisse 1989).

Among the chlorophycean algae, the hydrodictyaceans are recognized in the fossil record, for example, the Silurian–Devonian acritarch *Deflandrastrum* Combaz 1962, that is similar to the modern *Pediastrum* Meyen 1829. *Botryococcus* Kützing 1849 is another example of a colonial green alga, that can be found in the fossil record: the fossil equivalent, the colonial palynomorph *Gloeocapsomorpha* Zalesky 1917, is widely recorded, including from the Ordovician (Foster et al. 1989), and can thus be related to the chlorophytes. Of particular interest is the taxon *Grododowon orthogonalis* Strother 2017. This species was described by Strother et al. (2017) as “Ordovician spore ‘thalli’” which may suggest a land plant derived origin. Navidi-Izad et al. (2020) discussed the classification of this taxon and of similar colonial palynomorphs. The authors concluded that there is so far no evidence to relate these microfossil colonies to primitive land plants, but possibly to hydrodictyacean algae (Chlorophyceae).

The Zygnematophyceae are another of the algal groups that are possibly closely related to land plants. Some of these algae produce zygospores with acid-

resistant walls that can be found in the fossil record, including in the Palaeozoic, for example, *Paleoclosterium leptum* Baschnagel 1966 (Colbath and Grenfell 1995).

The Charophyceae also produce spores that have largely been recorded in the fossil record. Irregular clusters of dyads and polyad spores and spore packets have been described from the Cambrian and the Early Ordovician (e.g. Strother and Beck 2000; Strother and Foster 2021). These Cambrian and Early Ordovician “spores” possibly represent charophyte algal remains, and may thus indicate the transition from freshwater green algae to terrestrial land plants. However, these “spores” are clearly not derived from land plants. A recent publication by Wang et al. (2022) documents palynological assemblages from the Cambrian of China with such abundant spore-like palynomorphs that are attributed to the Cambrian “cryptospores” that are considered by the authors to derive from streptophytic algae.

There is currently a largely semantic debate around the term cryptospore, because different groups of palynologists disagree about the definition of the term. Richardson et al. (1984) first used the “new spore Anteturma Cryptosporites” for non-marine spore-like microfossils. Strother (1991), on the other hand, defined the cryptospores as similar to spores of embryophytes but without a known biological affinity. Steemans (2000), in his emended definition, included in the cryptospores only spores that derive from embryophytes. Today, for most authors, cryptospores are related to land plants (*sensu* Steemans 2000) and are non-marine (*sensu* Richardson et al. 1984). But it is difficult to name a spore-like microfossil a cryptospore when the affinity to the land plants is not clear, and/or when the microfossil was found in marine sediments. It is important to consider that the largest majority of the cryptospores are not found *in situ*, i.e. in the sporangia of a land plant.

This debate may give rise to some misunderstandings. The Cambrian palynomorphs, most probably deriving from streptophytes, are not related to land plants (embryophytes), although they are termed “cryptospores” by some authors (e.g. Wang et al. 2022) following the concept of Strother (1991). For most palynologists, however, it is now clear that the cryptospores that derive from land plants (*sensu* Steemans 2000) only appeared in the Middle Ordovician (see summary in Servais et al. 2019). In addition, it is also relevant that none of the cryptospores described from sediments that predate the Silurian is proven to be of terrestrial (non-marine) origin, because terrestrial sediments are very rare, and most spores are found only in marine to nearshore sediments, together with organic-walled phytoplankton groups.

This ongoing debate also has an impact on the classification of the two genera revised in this study, *Attritasporites* and *Virgatasporites*, that could be classified either as cryptospores or acritarchs. In the latter case, they would be palynomorphs of unknown biological affinity, because acritarchs were originally defined by Evitt (1963) as a utilitarian category to classify all organic-walled microfossils and thus the group does not imply a biological affinity.

Similar to the term “cryptospores” the term “acritarch” also has different definitions (see Servais 1996). Evitt (1963) created the group primarily to classify all palynomorphs that could not be attributed to the dinoflagellates. Subsequently, some authors, in particular US scientists (e.g. Loeblich and Wicander 1976; Wicander and Wood 1997), replaced the term “acritarchs” by “organic-walled phytoplankton”, implying a biological affinity to phytoplanktonic microalgae, similar to the dinoflagellates.

So, what are *Attritasporites* and *Virgatasporites*? Spores, cryptospores or acritarchs? Palynomorphs derived from land plants, from phytoplanktonic organisms, or from a particular algal group?

### 3. Taxonomy of *Attritasporites* and *Virgatasporites*

#### 3.1. Original description

In the context of extensive palynological investigations covering all fossil groups, Combaz (1967) studied the Tremadocian palynomorphs of the Hassi Messaoud oil reservoir of the Algerian Sahara from different boreholes (from a selection of 170 wells drilled in total). From the borehole Oni 11, he described palynomorphs of the three main groups: spores, acritarchs and chitinozoa. Combaz (1967, fig. 4) provided a preliminary study of the palynofacies and reported the proportions of the major palynomorph groups, including “terrestrial spores” (“*spores terrestres*”), that were present, sometimes in high proportions (usually between 20 to 30%) in most of the 11 samples investigated.

Combaz (1967) placed a special emphasis on the “terrestrial spores”, describing them in detail. He clearly noted that he did not recognize a distinct trilete mark, as had been drawn in illustrations of several Precambrian and Cambrian taxa by Russian palynologists (e.g. *Leioligotriletes* Timofeev 1959), and that he considered these hand-drawn trilete marks to be artifacts. He mentioned, however, triradial thickenings in the spores, with a central part of the spores that is usually clearer. He also mentioned groupings of spores, looking like tetrads, considering them to be “tetraspores”, and comparing them to the Carboniferous spore *Crassispora*. Most interestingly,

two “tetrads” of *Attritasporites* were also illustrated (Combaz 1967, pl. 1, figs. 7–8).

Combaz (1967) noted that the distinction from the acritarchs in his assemblage was straightforward: the spores present a large envelope, sometimes ornamented, making some specimens look similar to *Densosporites*, a Carboniferous genus. Some of the illustrated specimens (pl. 1, figs. 27–28) were compared to the Devonian genus *Emphanisporites*.

He described two new spore genera, *Attritasporites*, resembling the Carboniferous spores, and *Virgatasporites*, that he compared to the Devonian *Emphanisporites*. Considering the age of the sediments, *i.e.* the Early Ordovician, Combaz (1967) was convinced that he had evidence for the first land plant vegetation.

In the systematic palaeontology part, Combaz (1967) classified the first genus *Attritasporites* under the heading *Anteturma Sporites* H. Potonié 1893 and *Turma incertae sedis*. The name of *Attritasporites* was chosen, because it derived from Latin *attrita*, rough. The name of the second genus, *Virgatasporites*, derived from the Latin *virgata*, striped, due to its radial striae.

The original diagnosis of *Attritasporites* reproduced here, “*Microspore à contour sub-circulaire à sub-triangulaire. Pas d’aperture nettement définie, cependant certains spécimens montrent une ébauche de marque triradiée. Épaississement annulaire peu régulier, situé en position proximale définissant une zone centrale claire, grossièrement circulaire ou triangulaire. Ornementation rudimentaire chagrinée, pseudo-vermiculée, infra-punctuée*”, can be translated into English: Microspore with subcircular to sub-triangular outline. No clearly defined aperture, however some specimens show an outline of a triradiate mark. Irregular annular thickening, located in a proximal position defining a clear central zone, roughly circular or triangular. Rudimentary chagrinated, pseudo-vermiculated, infra-punctate ornamentation.

The original diagnosis of the genus thus clearly included an interpretation of the biological affinity as a miospore.

Combaz (1967) described three species: *A. messaoudi* (type species, name corrected to *A. messaouensis*), *A. scabra* and *A. velata*. It is not possible to distinguish the three specific taxa, neither from their diagnoses, nor from the microphotographs (pl. 1, fig. 1–14). The description of different “species” and the absence of comparisons between them must be placed in the context of the pioneering years of palynology, when the color of the specimens was also used as a diagnostic feature.

The second, monospecific genus *Virgatasporites* was described with the following original diagnosis: “*Forme circulaire, aspect général d’une spore. Marque*

*trilète douteuse. La face proximale est caractérisée par un système de stries radiales peu saillantes et tendant à s’anastomoser*”, *i.e.*: Circular shape, general appearance of a spore. Dubious trilete mark. The proximal face is characterized by a system of slightly protruding radial striations which tend to anastomose.

A single species, *V. rudi* (corrected to *V. rudii*) was described. Most interestingly, Combaz (1967) mentioned a proximal side with narrow radial striae that are sometimes anastomosed.

It is important to note that it is not clear where the type-material is located, and if it is still available. For the present study, we were not able to restudy Combaz’ (1967) slides.

### 3.2. Subsequent descriptions and concepts

It would have been possible to disregard Combaz’ (1967) description, and consider the presence of these “spores” in the Tremadocian either as the result of contamination from younger sediments, or as being clearly of wrong age, with the other palynomorphs being reworked. However, the two genera have subsequently been recorded from many localities (see below). In addition, the ages of the investigated sediments providing these “spores” are all very similar, and sometimes even older, *i.e.* the late Cambrian.

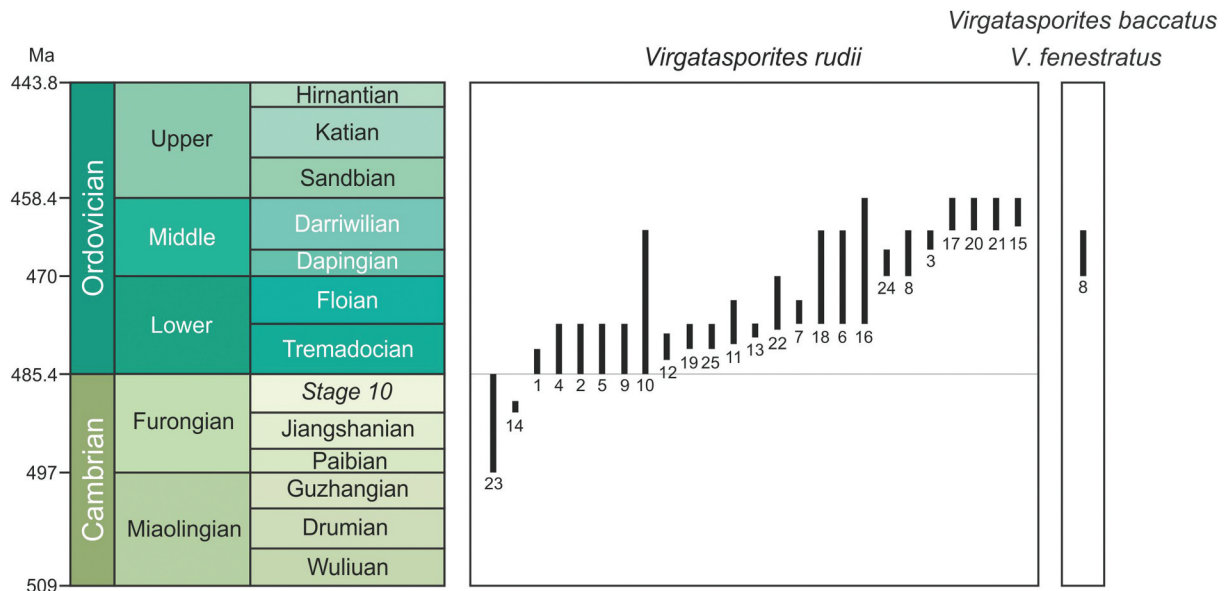
Furthermore, a literature review reveals that whereas the different species of *Attritasporites* were recovered from other areas, three additional species have been attributed to *Virgatasporites*: *V. baccatus* Vavrdová 1990, *V. fenestratus* Vavrdová 1992, and *V. normalis* (Fombella 1978) Fensome et al. 1990. Most of them were found in sediments together with the type-species *Virgatasporites rudii*.

Most interestingly, Fombella (1978) described the new acritarch genus *Abacum* that is very similar to *Virgatasporites*. This genus was reported from the middle Cambrian to Lower Ordovician Oville Formation in northern Spain. Pittau (1985) erroneously transferred *V. rudii* to *Abacum* but *Virgatasporites* has priority over *Abacum* and therefore the latter genus is considered a junior synonym of the former.

## 4. Biostratigraphy of *Attritasporites* and *Virgatasporites*

### 4.1. Biostratigraphic distribution of *Virgatasporites rudii*

The most frequently recorded species of Combaz’ (1967) original publication is *Virgatasporites rudii*. The biostratigraphic distribution of this species is illustrated in Figure 1. After the original description from the early Tremadocian sediments of the Hassi Messaoud region, Algerian Sahara, Rasul and



**Figure 1.** Stratigraphic distribution of *Virgatasporites* species. 1. Combaz (1967), Algeria. 2. Rasul and Downie (1974), England. 3. Cramer and Díez (1977), Morocco. 4. Volkheimer et al. (1980), Argentina. 5. Fombella (1983), Spain. 6. Fang (1987), Gao (1991) South China. 7. Albani (1989), Sardinia, Italy. 8. Vavrdová (1990, 1993), the Czech Republic. 9. Herbosch et al. (1991), Belgium. 10. Jachowicz (1995), Saudi Arabia. 11. Servais and Molyneux (1997), Germany. 12. Vecoli (1999), southern Tunisia. 13. Breuer and Vanguetaine (2004), Belgium. 14. Albani et al. (2006), Spain. 15. Paris et al. (2007), Turkey. 16. Al-Husseini (2010), Saudi Arabia. 17. Rickards et al. (2010), Oman. 18. Piçarra et al. (2011), Portugal. 19. White et al. (2012), Nova Scotia, Canada. 20. Le Hérisse et al. (2017), Saudi Arabia. 21. Abuhmida and Wellman (2017), Libya. 22. Rubinstein et al. (2019), Colombia. 23. Ghavidel-Syooki (2019), Zagros Basin, southern Iran. 24. Vecoli and Cesari (2019), Saudi Arabia. 25. This study, Alborz Mountains, northern Iran.

Downie (1974) recorded *V. rudii* from the Tremadocian Shineton Shales succession of Shropshire, England, but without illustrating specimens. Cramer and Díez (1977) reported *Virgatasporites* sp. from the late Arenigian of Morocco with a single illustrated specimen roughly resembling *V. rudii*. Subsequently, Volkheimer et al. (1980) described the first Ordovician acritarch assemblage in South America and identified *Virgatasporites* sp. with high morphological similarity to *V. rudii* from Dapingian sediments of the Mojotoro Formation in northern Argentina. Fombella (1983) recorded the taxon from the Tremadocian of northern Spain. Albani (1989) recorded relatively well-preserved specimens as *Abacum* sp. from the Arenigian of Sardinia, Italy. However, as aforementioned *Abacum* is considered a junior synonym of *Virgatasporites* and the Sardinian specimens should be classified as *V. rudii*. Vavrdová (1990, 1993) also described this species from the late Arenigian of Bohemia, Czech Republic. Herbosch et al. (1991) recorded *V. rudii* from the Tremadocian of the southern border of the Brabant Massif in Belgium, but the species was not illustrated. Jachowicz (1995) described *V. rudii* and *V. sp.* from the Tremadoc-Arenig interval of the exploration wells of the Tabuk Formation in central and northwestern Saudi Arabia. In China, *V. rudii* was reported from the Arenig rocks of Yunnan Province by (Fang 1987; Gao 1991). The genus has so far not been found elsewhere in China (Yan Kui, pers. comm. 2021). Servais and

Molyneux (1997) recorded and illustrated this species from the subsurface material of Rügen, Baltic Sea, northeastern Germany within the late Tremadoc-early Arenig *messauoudensis-trifidum* acritarch assemblage. Vecoli (1999) reported *V. rudii* from the Tremadocian *Acanthodiacrodium angustum-Vulcanisphaera britannica* Zone of the Sn1 borehole located in southern Tunisia. Breuer and Vanguetaine (2004) also reported and figured *V. rudii* from the latest Tremadocian of the *messauoudensis-trifidum* acritarch assemblage in the upper part of the Lierneux Member, Salm Group, Stavelot Inlier, Belgium. The first occurrence of *V. rudii* from the late Cambrian was recorded by Albani et al. (2006) who retrieved this taxon from the La Matosa Member of the Barrios Formation in northern Spain within an acritarch assemblage correlated with the *Protopeltura praecursor* trilobite Zone which is corresponding to the earliest part of Cambrian Stage 10 age (Furongian). Paris et al. (2007) recorded *V. rudii* from the Middle Ordovician (late Darriwilian) of southeastern Turkey and illustrated one specimen. Al-Husseini (2010) reported *V. rudii* from the Arenig-Llanvirn Saq sandstone of Saudi Arabia but he did not illustrate this species. *Virgatasporites rudii* was also reported without illustrations from the middle-late Darriwilian of Oman by Rickards et al. (2010). The taxon was documented from the Arenig (Floian to early Darriwilian) of the Barrancos region of southern Portugal (Piçarra et al. 2011). The first occurrence of *V. rudii* and *V. sp.*

from *Laurentia* was recorded by Pedder (2012, unpublished Ph.D.) from the Nolichucky Shale in Thorn Hill, northeastern Tennessee, USA, where the Cambrian Miaolingian-Furongian (Marjuman-Steptoean) boundary is broadly identified. However, the attribution to *Virgatasporites* is highly questionable, and disregarded here, and the presence on the margin of *Laurentia* is not yet confirmed. White et al. (2012) recorded *V. rudii* from the late Tremadocian corresponding to the *murrayi* graptolite biozone in Elderkin Brook Formation, Nova Scotia, Canada. Le Hérissé et al. (2015) considered occurrences of *V. rudii* in the Late Ordovician Baq'a Shale Member of the Sarah Formation in Saudi Arabia as a result of reworking of Middle Ordovician acritarchs. Le Hérissé et al. (2017) similarly recorded *V. rudii* from the *Siphonochitina formosa* and *Linochitina pissotensis* biozones indicating a late-early to late Darriwilian age from the Saq and Hanadir formations in Saudi Arabia. Abuhmida and Wellman (2017) reported *V. rudii* as an *incertae sedis* taxon from the Middle Ordovician, most likely middle Darriwilian (Llanvirn), of the Hawaz Formation in the Murzuq Basin, southwestern Libya. Rubinstein et al. (2019) documented the species from the Lower Ordovician (upper Tremadocian?-Floian) in the Llanos Basin, Colombia. Ghavidel-Syooki (2019) recorded *V. rudii* from the late Cambrian (Furongian) of the Ilebeyk Formation in the High Zagros Mountains, southern Iran. The species has also been recorded by Vecoli and Cesari (2019) from the Dapingian part of the Sajir Member of the Saq Formation in Saudi Arabia.

Our own observations indicate the presence of *Virgatasporites rudii* in the Lower Ordovician Lashkarak Formation (Tremadocian-early Floian in age) in the eastern Alborz Mountains, and based on acritarch associations this species only occurred in the late Tremadocian part of the succession (Navidi-Izad, unpublished).

The biostratigraphic distribution of *Virgatasporites rudii* therefore ranges from the late Cambrian (Furongian Series) to the Middle Ordovician, late Darriwilian (Figure 1), with questionable occurrences in younger (Late Ordovician) and older (Miaolingian-Furongian boundary) sediments.

#### 4.2. Biostratigraphic distribution of *Virgatasporites baccatus*, *V. fenestratus* and *V. normalis*

Two additional species of *Virgatasporites* were described from the late Arenig of the Czech Republic by Vavrdová (1990): *Virgatasporites baccatus* and *V. fenestratus*. However, they have not been recorded subsequently, and they may well correspond to morphotypes that express a wider variability of the type-

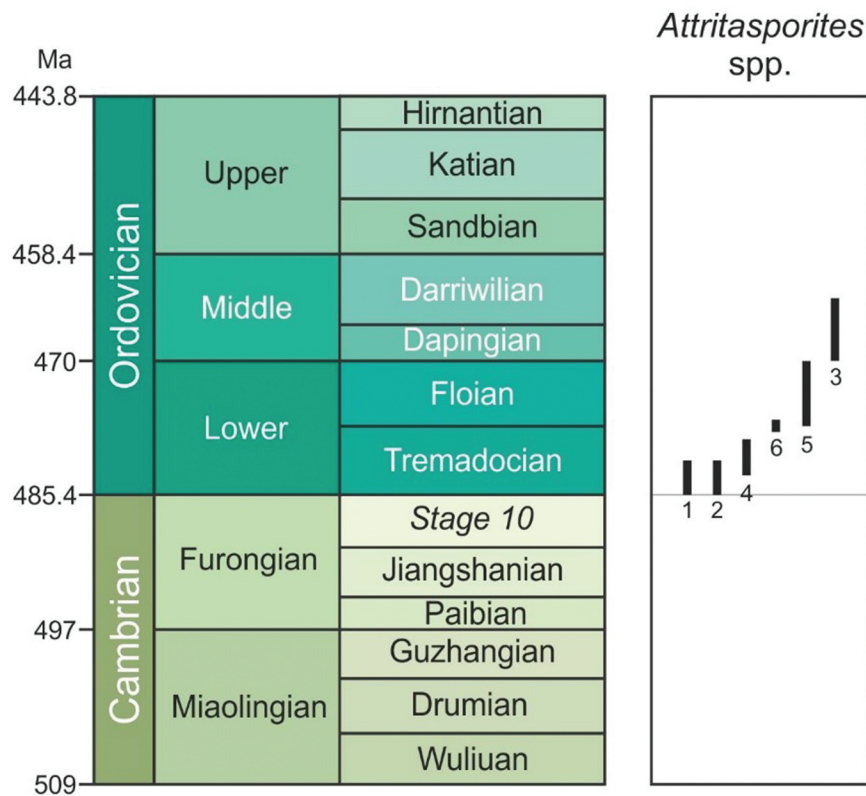
species, and thus, they are possibly junior synonyms of *V. rudii*.

Fombella (1978) described *Abacum normale* (now *Virgatasporites normalis*) from the Oville Formation in the Leon Province, Spain, in three zones ranging from the early middle Cambrian to the latest Cambrian or possibly earliest Tremadocian. As mentioned above, Fensome et al. (1990) transferred this species to *Virgatasporites*. The species has only been recorded in Spain (Fombella 1978, 1983).

#### 4.3. Biostratigraphy of *Attritasporites*

The biostratigraphic distribution of the species of *Attritasporites* is illustrated in Figure 2. *Attritasporites messaoudensis* was initially described with *Virgatasporites rudii* from the early Tremadocian sediments of the Hassi Messaoud region, Algerian Sahara (Combaz 1967). Subsequently Fombella (1983) and Fombella et al. (1993) recorded *A. messaoudensis* from the early Tremadocian rocks of northern Spain. Vavrdová (1990) also recognized this species from the late Arenigian of the Czech Republic. Vecoli (1999) documented poorly-preserved specimens resembling *A. messaoudensis* from Tremadocian sediments of southern Tunisia. Fatka and Brocke (1999) reported *Attritasporites* sp. from the middle part of the *Tetragraptus-Azygograptus* Biozone (Early Ordovician) in the Klabava Formation, Bohemia. Kalvacheva et al. (1986) recorded a specimen as ? *Attritasporites* sp. from a poorly preserved acritarch assemblage extracted from early Cambrian to Tremadocian phyllites in the Agordo area, south Alpine basement of the eastern Alps, Italy. Vecoli et al. (2008) noted that this specimen does not correspond to the diagnosis of *Attritasporites* and they considered the attribution by Kalvacheva et al. (1986) a misidentification. Wang et al. (2013) recorded *A. messaoudensis* within the latest Tremadocian-earliest Floian *Hunnegraptus copiosus-Tetragraptus approximatus* graptolite biozone of Ningkuo Formation of Yiyang, South China. The taxon only occurs in a single sample and is indicated to be rare (less than 10 specimens). If the identification could be verified and the presence of *Attritasporites* confirmed, it would be the first (and only) record of the genus from South China.

The two additional species, *Attritasporites scabra* and *A. velata*, were originally introduced by Combaz (1967) from the early Tremadocian of Algeria together with the type-species *A. messaoudensis*. *Attritasporites scabra* has never been recorded subsequently, whereas *A. velata* was recorded only once after the original description: Vavrdová (1990) reported *A. scabra* from the late Arenigian of the Czech Republic.



**Figure 2.** Stratigraphic distribution of *Attritasporites* species. 1. Combaz (1967), Algeria. 2. Fombella (1983, 1993), Spain. 3. Vavrdová (1990), Czech Republic. 4. Vecoli (1999), southern Tunisia. 5. Fatka and Brocke (1999), Bohemia, Czech Republic. 6. Wang et al. (2013), South China.

### 5. Palaeobiogeographical distribution of *Attritasporites* and *Virgatasporites*

In order to understand the palaeobiogeographic distribution of *Virgatasporites* and *Attritasporites*, occurrence data from the literature were plotted on palaeogeographic reconstructions based on the PALEOMAP project (Scotese 2016), using the software GPlates (Boyden et al. 2011). Only occurrences with validated identification and relatively precise and robust information in terms of stratigraphic assignment and geography were considered. In accordance with the stratigraphic distribution (Figures 1–2) the occurrences during a few time intervals, the late Cambrian (Furongian), the Early Ordovician and the Middle Ordovician, are displayed and illustrated in Mollweide projection maps (Figure 3).

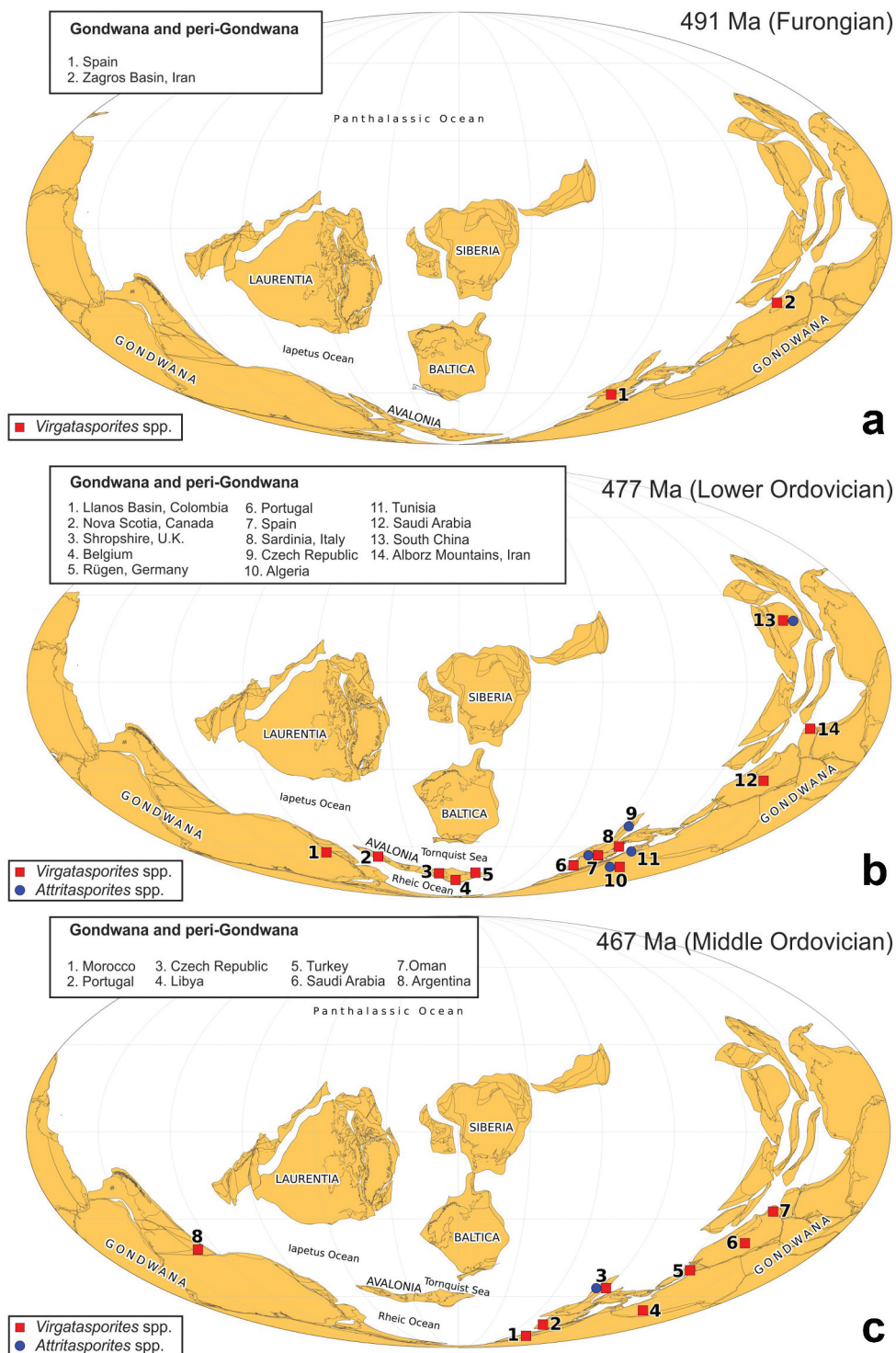
During the Furongian, occurrences of *Virgatasporites* are very limited, with *V. rudii* being only known from Spain (Albani et al. 2006) and the Zagros Basin in southern Iran (Ghavidel-Syooki 2019), both located on the western margin of Gondwana at that time. The genus becomes more widely distributed, and has been reported from the Avalonian locations of Nova Scotia, Canada (White et al. 2012), England (Rasul and Downie 1974), Belgium (Herbosch et al. 1991; Breuer and Vanguetaine 2004), and Rügen, Germany (Servais and Molyneux 1997), and in the periphery of the Gondwanan supercontinent from the

Llanos Basin in Colombia (Rubinstein et al. 2019), Portugal (Piçarra et al. 2011), Spain (Fombella 1983), Sardinia, Italy (Albani 1989), Algeria (Combaz 1967), Tunisia (Vecoli 1999), Saudi Arabia (Jachowicz 1995; Al-Husseini 2010), and the Alborz Mountains, Iran (this study). In the Middle Ordovician, the distribution of *Virgatasporites* becomes more limited, with findings in Morocco (Cramer and Díez 1977), the Czech Republic (Vavrdová 1990, 1993), Libya (Abuhmida and Wellman 2017), Turkey (Paris et al. 2007), Saudi Arabia (Le Hérisse et al. 2017; Vecoli and Cesari 2019), Oman (Rickards et al. 2010) and Argentina (Volkheimer et al. 1980). No records of *Virgatasporites* are known from the Middle Ordovician of Avalonia, which had already moved substantially northwards.

*Attritasporites* did apparently not appear before the Tremadocian. Records are known from southwestern Gondwanan localities in the Lower Ordovician: Algeria (Combaz 1967), Spain (Fombella 1983; Fombella et al. 1993), the Czech Republic (Fatka and Brocke 1999), Tunisia (Vecoli 1999) and South China (Wang et al. 2013). Only one occurrence of *Attritasporites* is recorded in the Middle Ordovician, where it appears in assemblages from the Czech Republic (Vavrdová 1990).

The maps clearly show that the two genera had a rather limited distribution, and seem to have





**Figure 3.** Palaeobiogeographical distribution of *Attritaspores* spp. and *Virgataspores* spp. for the Furongian (a), the Early Ordovician (b) and the Middle Ordovician (c). a) 1. Spain, Albani et al. (2006). 2. Zagros Basin, Iran, Ghavidel-Syooki (2019). b) 1. Colombia, Rubinstein et al. (2019). 2. Nova Scotia, Canada, White et al. (2012). 3. Shropshire, England, Rasul and Downie (1974). 4. Belgium, (Herbosch et al. 1991; Breuer and Vanguetaine 2004). 5. Rügen, Germany, Servais and Molyneux (1997). 6. Portugal, Piçarra et al. (2011). 7. Spain, Fombella (1983). 8. Sardinia, Italy, (Albani 1989; Albani et al. 2006). 9. Czech Republic Vavrdová (1990, 1993). 10. Algeria, Combaz (1967). 11. Tunisia, Vecoli (1999). 12. Saudi Arabia (Jachowicz 1995; Al-Husseini 2010). 13. South China (Fang 1986; Gao 1991; Wang et al. 2013). 14. Alborz Mountains, Iran (This study). c) 1. Morocco, Cramer and Diez (1977). 2. Portugal, Piçarra et al. (2011). 3. Czech Republic Vavrdová (1990, 1993). 4. Libya, Abuhmida and Wellman (2017). 5. Turkey, Paris et al. (2007). 6. Saudi Arabia, (Le Hérisse et al. 2017; Vecoli and Cesari 2019). 7. Oman, (Rickards et al. 2010). 8. Argentina, (Volkheimer et al. 1980). Palaeogeographical reconstruction based on Scotese (2016), palaeoclimate zones based on Boucot et al. (2013).

exclusively occurred along the Gondwana margin, or peri-Gondwana (including Avalonia). No validated occurrences are known from any other palaeocontinent.

The record of *Virgataspores* in Furongian material from Laurentia (Tennessee, U.S.A., Pedder 2012, unpublished Ph.D.) is doubtful, with only one specimen

attributed to *V. rudii* and seven specimens to *V. sp.1*. The illustrated microfossils do not correspond to the genus and are thus not considered herein. The occurrences in the Ordovician of South China, recorded by Fang (1987) and Gao (1991) indicate an extension of the palaeobiogeographical distribution towards the North-East. It appears that the two genera occurred widely along the western and southern margins of Gondwana, but a few occurrences from the eastern side of the continent, with occurrences from Argentina (Volkheimer 1980) and Colombia (Rubinstein et al. 2019), have also been mentioned. The known distribution area of *Attritasporites* is even more limited than that of *Virgatasporites*, and confined to the southern European and North African part of Gondwana, with a possible extension of the palaeogeographical distribution towards South China (Wang et al. 2013).

In addition to the palaeogeographically relatively confined distribution, the maps show that the taxa appeared in rather high latitudes, with most records reported from regions that were located south of the 30° S palaeolatitude. The northernmost occurrence of *Attritasporites* is even further south, at around 50° S. This distribution pattern allows for some presumptions about the palaeoecology of these taxa: by comparing the distribution of *Virgatasporites* and *Attritasporites* with the climate zone models by Boucot et al. (2013), we can infer that these taxa were preferring cool-temperate climates along the Gondwanan margin. This is supported by the absence of *Virgatasporites* on Avalonia during the Middle Ordovician, possibly as a result of the northward drift of this microcontinent, bringing these localities into lower latitude regions and warmer climate.

The palaeobiogeography of acritarchs during the Early to Middle Ordovician interval was characterized by a high degree of provincialism, with two major distinct microfloras, the peri-Gondwanan and the Baltic provinces (Molyneux et al. 2013). This provincialism was probably controlled by several palaeoenvironmental factors, such as water temperature and ocean currents (Playford et al. 1995; Tongiorgi et al. 1995; Molyneux et al. 2013; Servais et al. 2014). Several acritarch taxa have been proposed as indicators for the peri-Gondwanan province: *Arbusculidium*, *Coryphidium* and *Striatotheca* are restricted to the peri-Gondwana margin (Li 1989). *Barakella* and *Vavrdovella* are also considered to be characteristic for this palaeoprovince (Tongiorgi and Di Milia 1999; Li and Servais 2002; Yan et al. 2017). With all occurrences of *Virgatasporites* and *Attritasporites* coming from the margins of Gondwana, it may be worth considering to include these taxa also as indicators for the peri-Gondwanan acritarch province.

On the other hand, it is also interesting to note that the oldest cryptospore assemblages, that can

uncontroversially be related to land plants, have been found in sediments of early Middle Ordovician age that are also from Gondwana, *i.e.* from the Dapingian of Argentina (Rubinstein et al. 2010) and from Saudi Arabia (Strother et al. 2015). Similar assemblages have subsequently been distributed over all other continents (Servais et al. 2019).

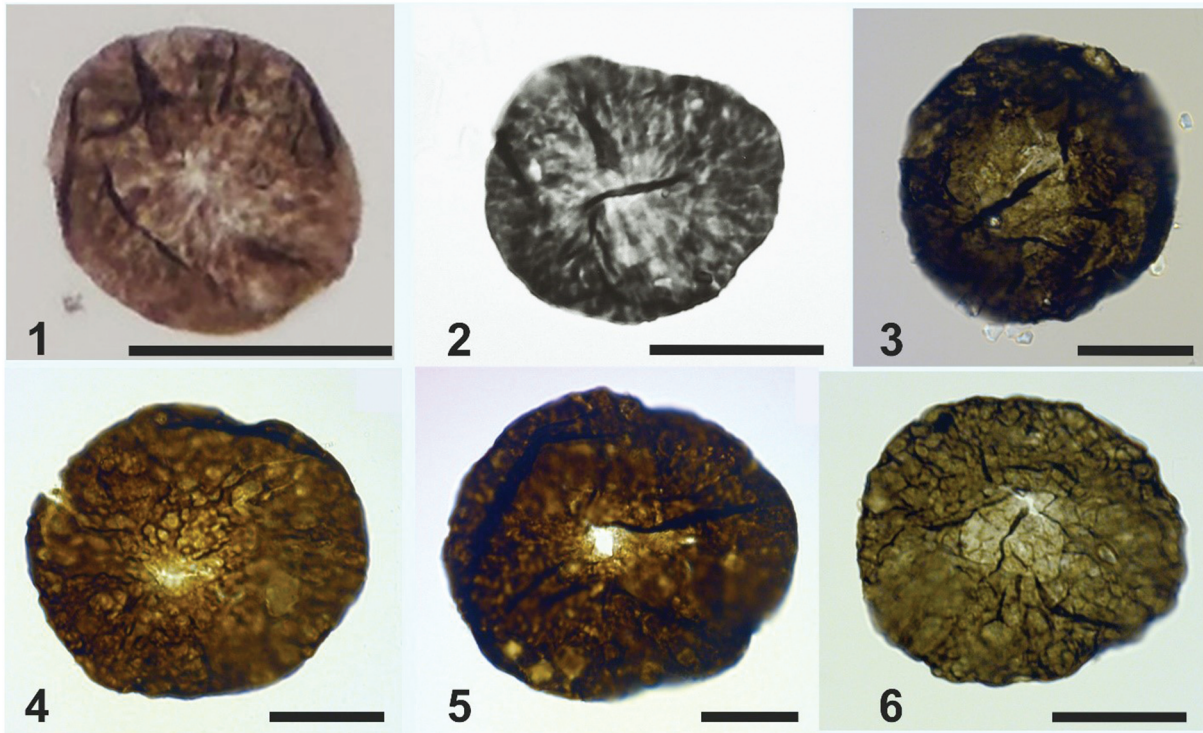
## 6. Land plant derived spores, cryptospores or acritarchs?

### 6.1. Affinities with cryptospores

Figure 4 illustrates some specimens of *Virgatasporites* and related forms. If these specimens were found in the Silurian or Devonian, they would most probably be related to the cryptospores. However, the taxonomic position and the biological affinity of both *Attritasporites* and *Virgatasporites* remain questionable. Combaz (1967) supposed these taxa to be of land plant origin, and related them to the “tetraspores.” But are they really land plant derived, terrestrial spores?

Richardson (1996a), based on the distribution pattern and the robust nature of the wall of *Virgatasporites*, pointed out that a derivation from terrestrial vegetation with a probable algal affinity could be possible. Richardson (1996a) considered those genera of a Tremadoc-Arenig “pre-cryptospore phase” because there is no strong evidence for derivation from land plants. Most surprisingly, Richardson was involved in the creation of a genus from the Wenlock (Silurian) of Shropshire, England, that is very similar to (and difficult to distinguish from) *Virgatasporites*: *Artemopyra* Burgess and Richardson (1991). Burgess and Richardson (1991) created the genus *Artemopyra* to encompass cryptospores of the following description: “Alete proximally hilate cryptospores; originally elliptical to hemispherical in equatorial view. Proximal hilum sculptured with predominantly radial muri. Distal exine laevigate or sculptured with grana, coni, biform elements or spinnae.” Subsequently, Richardson (1996b) emended the diagnosis to: “Proximally hilate cryptospore monads; originally elliptical to hemispherical in equatorial view. Hilum sculptured with predominantly radial muri. Distal exine laevigate.” With this emended diagnosis Richardson (1996b) eliminated the evident link, proposed in the original description by Combaz (1967), with the trilete spore genus *Emphanisporites* McGregor 1961, that may be distally ornamented.

Clearly, the diagnoses of *Virgatasporites* and *Artemopyra* are very close, if not identical. The differentiation of both genera is difficult when based on morphological criteria, and was possibly only based on their different stratigraphic distributions. The type species, *Artemopyra brevicosta* Burgess and



**Figure 4.** Microphotographs of *Virgatasporites rudii* and *Virgatasporites*-like materials. The scale bar indicates 20  $\mu\text{m}$ . 1. *Virgatasporites rudii* Combaz 1967, slide and sample number LG.22, Early Ordovician (late Tremadocian) Lashkarak Formation, northeastern Iran. 2. *Virgatasporites rudii* Combaz 1967, Early Ordovician (latest Tremadocian) Lierneux Member, Jalhay Formation, Salm Group, Stavelot Inlier, Belgium (Breuer and Vanguetaine 2004). 3–6. *Virgatasporites*-like species from the Late Ordovician (Katian-Hirnantian) Ghelli Formation, northeastern Iran. 3. slide and sample number GH.33.1, and 5. slide and sample number GH. 128.2. 3, 5. Specimens show a relatively thick periphery with thin central area or a circular aperture in figure 5, the surface of the specimens does not show significant ornamentations. 4. slide and sample number GH. 128.2 and 6. slide and sample number 120. 4, 6. Specimens with thick periphery, a circular aperture in the center of the body and alveolate structure.

Richardson 1991, shows short radial proximal muri like the trilete spore *Emphanisporites protophanus* Richardson and Ioannides 1973. *Artemopyra laevigata* Wellman and Richardson 1996 differs from *V. rudii* by its much more numerous variable proximal muri and *A. robusta* Wellman and Richardson 1996 by its larger size and its much more numerous proximal muri. Due to its small size and the relatively few radial muri, *V. rudii* is close to *Emphanisporites neglectus* Vigran 1964 which is well known from many different successions. Up to now, *Artemopyra* has never been found below the Wenlock (Dufka 1995). Future studies are needed to compare all these taxa in detail, because the two genera *Virgatasporites* and *Artemopyra* are morphologically very similar, and it appears possible that *Artemopyra* is a junior synonym of *Virgatasporites*. However, currently *Artemopyra* is clearly considered a cryptospore, whereas *Virgatasporites* is not, because it is found in sediments that are much older. *Virgatasporites* was described with terminologies usually applied to younger miospores, and before the definition of the cryptospores, adding to the confusion.

Another fact is intriguing. The diagnoses of *Attritasporites* and *Virgatasporites* clearly include the

description and the recognition of a proximal and a distal face. However, as the type material studied by Combaz (1967) is currently not available, it is not possible to confirm the presence of proximal and distal faces in the type material. Such morphological characteristics are so far only found on spores produced by land plants.

The possible presence in the Ordovician of hilate monads of cryptospores is unusual, because up to now only rare specimens of the very simple *Gneudnasporea divellomedica* (Chibrikova) Balme 1988 var. *minor* Breuer et al. 2007 (or *Laevolancis divellomedium* according to other authors) are recorded in Ordovician sediments, as they are already present in the Middle Ordovician Zanjón Formation, Argentina (Rubinstein et al. 2010). This type of cryptospore is usually considered as biologically evolved, suggesting that more primitive cryptospores could have existed before the Middle Ordovician. There are thus a series of arguments suggesting that the taxa of Combaz (1967), and at least *V. rudii*, could be considered as cryptospores deriving from a land plant.

With the objective to understand the relationships between different wall types in spores and cryptospores, Taylor (2003) analyzed the wall ultrastructure of *Virgatasporites* and noted that the genus “possesses

a robust wall and equatorial crassitude, but its relationship to the embryophyte lineage remains equivocal.” The spore wall of *Virgatasporites* was compared with those of Silurian trilete spores, but it would be interesting to compare the spore wall ultrastructure of *Virgatasporites* with that of Silurian and Devonian cryptospores, such as *Artemopyra*.

## 6.2. Affinities with acritarchs and palynomorphs deriving from algae

Fensome et al. (1990) considered *Attritasporites* and *Virgatasporites* as belonging to the acritarch group, because the biological affinity remains uncertain. Rasul and Downie (1974), Servais and Molyneux (1997) and Vecoli (1999) followed this concept and retained *Virgatasporites* as an acritarch.

If these microfossils cannot be related to land plant derived spores, are they possible related to a specific algal group? To what group could they be compared?

It is clear that both genera show absolutely no morphological characters of the dinoflagellates, although several acritarch genera show great similarities to this group (e.g. Servais et al. 2004; Penaud et al. 2018). Similarly, *Attritasporites* and *Virgatasporites* show no similarities with prasinophytes or chlorophytes. They also do not resemble zygmatophytean zygospores or other freshwater algae reported in the fossil record.

Possible similarities could be drawn with some charophyceae algae, and the presence of tetrads, already described in the type material by Combaz (1967), might indicate a relationship with streptophytic algae, but also points to a relationship with embryophytes. The genera *Attritasporites* and *Virgatasporites* could thus possibly, like some of the Cambrian spore-like palynomorphs, represent transitional forms between streptophytic algae and true land plants.

To sum up, the taxa *Virgatasporites* and *Attritasporites* remain to date of unknown biological affinity. Therefore, they should be temporarily classified as *incertae sedis*, i.e. as acritarchs. Only at the moment when their true biological affinity becomes clearer will they no longer be consigned to the wastebasket group of the acritarchs.

## 6. Conclusions

The two genera *Virgatasporites* and *Attritasporites*, described in the 1960's from the Early Ordovician (Tremadocian) of Algeria, are morphologically very close to spores, and they have been compared to Devonian and Carboniferous miospores, such as *Emphanisporites*, *Crassispora* and *Densosporites*. The genus *Virgatasporites* shows greatest similarities with the Silurian cryptospore *Artemopyra*, and detailed

taxonomical comparisons are needed to clarify if the latter genus is a junior synonym of *Virgatasporites*.

The biostratigraphic and palaeobiogeographical distributions of *Virgatasporites* and *Attritasporites* are revised, indicating that both genera are widely recorded on the Gondwanan margin from sediments of Early and Middle Ordovician age, with first occurrences in the late Cambrian of the genus *Virgatasporites*. This stratigraphical distribution clearly poses a dilemma, because these spore-like microfossils are recorded before the first appearance of the oldest land plant derived spores in the Middle Ordovician.

The biological affinity of these taxa remains uncertain. They are clearly spore-like microfossils, and in younger sediments they would have been identified and classified as cryptospores. However, there is so far no evidence for a biological affinity and a relationship to the embryophyte lineage. Therefore, both taxa must be classified as *incertae sedis*, i.e. as acritarchs, that are defined as organic-walled microfossils of unknown biological affinity.

Additional studies, including a reinvestigation of assemblages from the type locality, and comparisons with younger cryptospores, such as *Artemopyra*, are necessary to understand the biological affinities of the enigmatic spore-like palynomorphs *Virgatasporites* and *Attritasporites*.

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PS and TS designed the research program and the paper concept. HB, NNI, DMK, PS and TS carried out palynological studies and provided data. HB, NNI and DMK designed the figures, all authors participated in writing the manuscript.

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