Late Silurian-Middle Devonian Miospores

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1. Introduction

Recent palynological researches on late Silurian to Middle Devonian terrestrial palynomorph have culminate on cryptospores and miospores zonation system (e.g., Richardson and McGregor 1986; Streel et al. 1987; Massa and Moreau-Benoît 1976; Melo and Loboziak 2003; Hassan Kermandji et al. 2008). Although stratigraphic, ecologic and geographic importance of these fossils grasp great effort, but much more work is required on their biostratigraphy and taxonomy before their complete potential can be understand. Nevertheless, palynological research is creating a major contribution to enable an overview of most important characteristics of cryptospores and miospores (Devonian miospore from Algeria, Tunisia and Libya, e.g., Magloire 1967; Moreau-Benoît et al. 1993; Loboziak et al. 1992; Spina and Vecoli 2009) also Silurian and Devonian miospore from Bolivia, Spain United Kingdom and Saudi Arabia (e.g., McGregor, 1984; Richardson et al. 2001; Wellman and Richardson 1993, 1996; Wellman et al. 1998; Steemans et al. 2007). Sporomorphs are more abundant and widely spread than cryptospores where decreasing in number and variety from older to the younger sediments (e.g., Rubinstein and Steemans 2002). Miospores by their structural complexity and augmentation they may provide more reliable evidence for formal zonal schemes to be proposed. However, uncertainty also exist the precise definition of the binomial species regarding their lateral distribution on local and regional scale, some may have restricted distribution pattern (e.g., Hassan Kermandji 2007), this is also may be due to the timing of their appearance and development and place of their parent plant evolutionary events (e.g., Edwards and Richardson 1996) and ecological niches.

Local or regional variations in plant distribution during late Silurian-Lower Devonian are due to: close contact of the Rheic Ocean during the early Lochkovian, or moderate distance separating Gondwana and Laurussia, or close proximity of the Avalonia Maguma and Aquitaine areas to the northern border of Gondwana during Přídolí times and or a possible land plant migration route between Laurussia and Gondwana (Rubinstein and Steemans 2002; Steemans and Lakova 2004; Hassan Kermandji 2007; Richardson et al. 2001; Spina and Vecoli 2009). Since the land invaded by plants, palaeoenvironment constrictions are possible. It is, however, significant in demonstrating the influence of Gondwanan parent flora on the miospore populations of the southern regions of Laurussia. This is may serve for providing a link between Laurussian and Gondwanan palynofloras.

Late Silurian-Lower Devonian stratigraphy is rather complicated where different miospore biozones are recognized. Correlations of North Africa Gondwanan miospore biozones
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remain hard to be compared precisely with Euramerica well established spore zonation but may be resolved by studies based on phytoplanckton, chitinozoa, conodonts and graptolites. Primary biostratigraphic subdivision within the late Silurian-Lower Devonian has been done by recognition of progressive change in terrestrial miospores. Subdivision is based on new incoming of well established miospores. Euramerican stages containing six Spore Zones and two Opple Zones where they provide bases for local and regional correlations. Although, some miospore assemblage similarities exist between Gondwana and Euramerica, there are significant differences as well. For instance species characteristics of Lochkovian (e.g., Streelispora newportensis s.s., Emphanisporites zavallatus, E. micrornatus s.s) are absent or rare in most parts of Gondwana (Melo and Loboziak 2003; Steemans et al. 2008), in Euramerica appear to be geographically well established which may suggests that they are apparently regionally confined. On the other hand, other biozonal species characteristics of late Silurian-Lower Devonian are found in Europe, North America and Gondwana (e.g., Chelinospora cassicula, C. hemiesferica, Leonispora argovejae, Perotrilites microbaculatus, Dictyotriletes ensiensis, Verrucosissporites polygonalis, D. subgranifer, E. annulatus, D. echinaceus, Calyptosporites velatus, Rhabdosporites langii). These palynological similarities might point out possible common constituents of their parent plants producing these miospores.

Late Silurian and Lower Devonian times are thus a key period for the developing of miospore zonation with confident suggestion in biostratigraphic, phytogeographic and palaeoenvironmental studies.

This chapter therefore will concentrate on late Silurian and early Devonian miospores biozones and systematic issues also will deal with early Middle Devonian miospores regarding their biozonation consequence and evolutionary significance.

2. Sporomorphs evolution

Richardson (1996) reviewed in brief development record of terrestrial sporomorphs. Stated that the problematic organic-walled microfossils occur in Vendian rocks and named by Volkova (1976) and ‘are associated with leiosphaerid acritarchs’ probably derived from brown alga. Also he believes that the first occurrence of cryptospores and miospores is approximate. The earliest terrestrial sporomorphs resembling miospores record is outside the scope of this chapter. However, it is extremely interesting to record the development of sporomorphs concerning the study.

The sporomorph events described below are based on data from type sequences. These will provide minimum age range for the events stated by, (Hassan Kermandji 2007; Hassan Kermandji et al. 2008) which agrees with (Richardson and McGregor 1986; Streel et al. 1987; Richardson et al. 2001) detection. Detailed review of the many palynological studies of Silurian and Devonian deposits of Euramerica and western Godwana, revels obvious coincidence of many of significant palynological events.

In both Euramerica and western Godwana, possibly Llanvirn-Caradoc cryptospore population are characterised by distinctive elements (permanent tetrads, pseudodyads and monads), they posses nearly identical structure and sculptural ornaments. Many studies (Gray 1992; Richardson 1988; Wellman et al. 1998; Steemans 1999a, b) reported possible cryptospores from Middle and late Ordovician. The recorded possible cryptospore assemblages from deposits older than Caradoc are either naked or enclosed within a thin, smooth or variously ornamented envelops. Consequently, Richardson (1988) considers that pseudotetrad,
pseudo dyads and monads envelop possibly developed prior to Caradoc. Cryptospore bearing plants were becoming more widespread and numerous during late Ordovician and early Silurian (Gray 1985, 1988; Burgess 1991; Burgess and Richardson 1991). They were reported from terrestrial and near shore environments. Many studies (e.g.; Vaverdova 1988) believe that high abundance of cryptospores may be facies controlled. Others (e.g.; Richardson 1992) relate high abundance to the upper Ashgill glacial period which played a major role in the extinction of faunas and floras and not affected the cryptospores of the high latitude. This is based on Burgess’s study (1991) on Llandovery deposits, south Wales that there is only minor differences between Ashgill and Llandovery cryptospore assemblages.

Although, there is no specific record for the earliest cryptospore creator, it is very hard to analyse that the cryptospores reflects true diversity. Because, different cryptospore morphotypes have similar envelope (taking in consideration that many envelopes may be lost or changed during preparation). Furthermore, many of these forms, morphologically and structurally, are simple. Such simple forms could have been produced by a number of plant types or by the same parent plant (Richardson 1988, 1992; Gray 1991; Strother 1991). Similarly, Fanning et al. (1988) refer to morphologically identical plant may produce different spore forms; they reflect it to the rapid evolution of the spore morphology. Wellman et al. (1998) came to the comparable conclusion that superficially morphologically similar miospores were produced by different plant types. This is all because the unavailability of studies denotes the in situ relationship between the parent plants and dispersal cryptospores and miospores.

Studies of (Gray et al. 1982; Gray 1985; Vaverdova 1984; Burgess and Edwards 1991; Gensel et al. 1991; Wellman 1995; Edwards and Wellman 1996; Hassan 1982; Hassan Kermandji and Khelifi Touhami 2008) show that the enigmatic dispersal phytodebris and land plants of the late Lower and Middle Palaeozoic sediments probably, are the core stone of the plants produced dispersal cryptospores and miospores. They show that the dispersal fragments consist of ornamented and laeavigate types of cuticles, tubular structures, tissues and filamentous, occurs isolated or commonly in complex form mainly in continental deposits. The oldest known record of permanent tetrad and dyads is from the early Llanvirn of Bohemia by Vaverdova (1984) and Vaverdova’s (1990) record for Prague basin. Although, cryptospore spreading declined upward, it exists in its diversity until to the early Devonian. Early cryptospores, permanent tetrads, dyads and monads, though it is not well documented, believed that they are of terrestrial origin (non marine sediments) and near shore environment (Strother and Traverse 1979; Wellman and Richardson 1993; Richardson 1996) and that ‘cryptospores are more abundant than miospores in inshore sediments’ Richardson and Rasul (1990). Many of these cryptospores (dyads and tetrads) were derived from plants with bifurcating axes and sporangia Wellman et al. (1998). It appears that monads, dyads and tetrads frequently have similar envelopes, this tend to suggest that they closely related, probably derived from the same species (Richardson 1988, 1992; Johnson 1984). Whereas trilete miospores dissociated from immature tetrads which are match forms among existing embryophytes.

The cryptospore assemblages decline in its taxonomic diversity in Homeric and younger sediments perhaps is environmental effect (probably facies controlled) Richardson (1988) and or an evolutionary indication (Hassan Kermandji et al. in preparation).

The earliest recorded embryophyte miospores was by Vaverdova (1984) from early Llanvirn of Bohemia; also identical miospore assemblages were reported from mid Ordovician to early Silurian by: Richardson (1988) Gray (1985, 1991), Burgess (1991) Strother (1991),
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Strother et al. (1996), Wellman (1996), Steemans (1999a). However, (Wellman and Richardson 1993; Strother and Traverse 1979; Richardson 1992; Gray et al. 1992; Wellman and Gray 2000; Steemans 1999b) believe that the structure and morphology of these early miospores are atypical comparing with existing miospores of younger ages, therefore some times, embryophyte miospores been used as cryptospores. This is due to that the widely spread vegetation was of restricted diversity and diminutive evolutionary change.

Most studies reveal that major changes occur to the miospore nature during late Lower Silurian. The mature miospores of existing embryophytes become dominant and more abundant than cryptospores by Ludlow Wellman and Gray (2000, fig. 1). Their diversity and abundance increased throughout the late Silurian. Steemans et al. (1996), Wellman, Higgs and Steemans (2000) studies show that trilete miospores and hilate monads of northeast Gondwana appear during late Ordovician and early Silurian. Sculptured forms of both trilete miospore and hilate monads flourished throughout late Silurian and early Devonian Burgess and Richardson (1995); Steemans (1999b). The hilate monads number decline in latest Silurian and earliest Devonian, and cryptospores exist as a minor constituents in miospore assemblages through Lower Devonian and extinct at the end of Emsian Hassan Kermandji et al. (In the press).

Considerable variations in dispersed miospore record exist through late Silurian and early Devonian, (mainly Přídolí and Lochkovian). This creates problems when trying to recognize phytogeographic variations (Rubinstein and Steemans 2002; Richardson et al. 2001; Hassan Kermandji 2007). Sequences of spore assemblages from Western Europe are similar in composition except some minor differences, this is indicate that it contain a flora representing a single paleo-phytogeographic province. Although miospore assemblages sequences of northern Gondwana sharing some elements but display striking differences, signifying that they belong to a different paleo-phytogeographic province. Comparison between Lochkovian miospore assemblages of the two provinces is difficult; probably they belong to different parent plants. The differences become less obvious during late Emsian and Eifelian.

Although, the in situ miospore records for early land plant megafossils are rare, it is more common in higher sediments. This is due to nature of land plant preservation, where they preserved as coalified compressions. Though, suitable preservations (uncompressed coalifications with splendid cellular detail) have been recorded in Lochkovian localities of south Wales (Edwards and Richardson 1996; Edwards 1996). The record of early land plants show that many miospores (Ambitisporites, Synorisporites, and Streelispora) have been recovered from the sporangia of rhyniophyte Cooksonia (Funning et al. 1988; Richardson 1996) which is a factual tracheophyte Edwards et al. (1992) and most trilete miospores appear to have consisted of plants with bifurcating axes/sporangia and more frequently stomata (Edwards 1995; Wellman et al. 1998). On the other hand, some dispersed miospore assemblages such as patinate species and Emphanisporites are abundant, but there in situ forms are extremely rare. This is probably facies and/or preservational effect.

The main evolutionary performance divided into events based on dispersed palynomorphs (text fig. 1), nearly all events described below are based on information from type sequences.

2.1 Crassitate, distally laevigate miospore event

The Aeronian and early Telychian miospores are distally laevigate and equatorially crassitate and belong to the genus Ambitisporites avitus, Amitisporits dilutes. Also appear some tetrads and
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Fig. 1. Summery of principle Silurian-Devonian sporomorphs evolution.
some dyads and cryptospores are present (Hassan Kermandji et al. in preparation). The age is based on acritarchs and chitinozoans in the type Llndover area Burgess and Richardson (1991).

2.2 Patinate, proximaly hilate laevigate miospore event

The exact stratigraphic range where equatorially crassitate, patinate miospores, tetrads and dyads occur is uncertain, possibly they appear in rocks older than Homerian probably Upper Aeronian (Richardson 1988, 1996), they include Archaeozonotriletes chulus/nanus complex where associated with graptolite zone (turriculatus or cripus) (Richardson 1996). The A. chulus/nanus compound occurs in Libyan sediments of Middle and Upper Telychian (Al-Ameri 1980 in Richardson 1996). The assemblages are probably of Middle and Upper Telychian, they may extend to late Homrian.

2.3 Hilate monad miospore event

These palynomorphs include Laevolancis divellomedia, recorded in marine sediments as Tasmanites avelinoi by Al-Ameri (1980), ranging from Landovery to Lower Devonian. This is also including pseudodyads, dyads, tetrads and halite cryptospore monad. They occur possibly in Telychian to become predominant in much younger sediments.

2.4 Murornate, verrucate miospore event

Appearance of sporomorphs with varied distal sculpture including verrucate, murornate Synorisporites and emphanoid forms. Both cryptosporos and miospores were appeared with distal verrucae and proximal radial muri. Cryptospores were first appeared with verrucate-murinate distal sculpture and proximal radial muri in south Wales by Burgess and Richardson (1991). This event is also, include patinate miospore with distal radial muri. Telychian to Sheinwoodian.

2.5 Murinate, verrucate crassitate miospore event

Appearance of murinate, verrucate, crassitate, confined proximal radial muri radiating from curvaturae perfectae trilete Upper Homarian miospores including Emphanisporites protophanus. In addition, it is including, distally verrucate, murinate hilate alete monads and some cryptospores with radial proximal muri (Richardson and McGregor 1986; Richardson et al. 2001; Hassan Kermandji 2007).

2.6 Granulate, apiculate, crassitate miospore event

It is characterized by miospores with equatorial radial thickening “curvatural crassitude” becoming indistinct towards the proximal pole, proximally with radial anastomosing muri and/or regularae, distally apiculate granulat and minutely verrucate of Scylaspora and Synorisporites species. In addition it is including cryptospores Burgess and Richardson (1995). Early and late Homarian.

2.7 Apiculate, patinate with faint radial muri miospore event

Appearance of granulate, micro rugulate curvatural proximal sculpture, distally with low narrow murornate, verrucate patinae and narrow hilum Chelinospora, Scylaspora species.
This is also including cryptospores (Burgess and Richardson 1995; Richardson et al. 2001; Hassan Kermandji et al. in preparation). Grostian to Lower Ludfordian.

2.8 Patinate, proximally hilate with distal faint muri miospore event

Characterised by the diversification of verrucate, apiculate patinate, domination of crassitate and cingulated and proximally radially ribbed forms of *Chelinospora*, *Cymbosporites*, *Concentricosisporites* and *Emphanisporites* miospores (Richardson and Ioannides 1973; Richardson et al. 2001; Hassan Kermandji 2007) and cryptospores. Early and late Ludfordian

2.9 Murornate, apiculate patinate miospore event


2.10 Diversification of crassitae, disto-equatorially multi sculptured miospore event

Characterized by diversification of equatorially crassitate and proximally triapillate, distally murornate, apiculate patinate miospores of *Scylaspora*, *Synorisporites*, *Cymbosporites* and *Chelinospora* (Richardson and Lister 1969; Burgess and Richardson 1995). Proliferation of verrucate, retusoid, apiculate and radially ribbed, foveolate and murornate miospores of *Apiculiretusispora* and *Dictyotriletes*. Permanent tetrads and cryptospores also occur, Hassan Kermandji (2007).

2.11 Proximally slightly ribbed, distally apiculate, crassitate, perinate miospore event

Proliferation of apiculate and proximally radially ribbed miospores (*Apiculiretusispora* and *Emphanisporites*). Persistence of apiculate, proximo-equatorial microgranulate crassitate, patinate and perinate miospores of (*Scylaspora*, *Perotilites* and *Cymbosporites*) Hassan Kermandji et al. (2008). Early (but not earliest) to early late Lochkovian.

2.12 Diversification of distally cingulate, patinate miospore event

Appearance of cingulated, annulate and patinate miospores of *Amocosporites* and *Cybosporites*. Persistent of perinate and crassitate species of the older strata. Late early and early late Lochkovian.

2.13 Distally murornate, proximally radially ribbed miospore event

Proliferation and diversification of proximally retusoid, distally apiculate, reticulate *Dictyotriletes*. Increasing of the variety of distally granulate-apiculate-spinose, proximally radially ribbed *Emphanisporites* and incoming of bizonate, proximally with highly irregular’scalloped’ folds and distally with distinct annular thickening *Breconsporites* Richardson et al. (1982). Latest Lochkovian and earliest Pragian.
2.14 Coarse biform apiculae with cingulicavati and foveolae miospore event

In coming of *Dibolisorites* species with prominent spines, tubercles and biform elements. Diversification of *Camptozonotriletes* and *Clivosispora* and *Apiculiretispora* species. Late early to early late Pragian.

2.15 Diversification of proximal prominent stout radial muri miospore event

Appearance of retusoid reticulate, non reticulate and foveolate species of *Dictyotriletes* and *Brochotriletes*. Proliferation of regularly verrucate taxa of *Verrucosisporites*. Persistent of tuberculornati and cingulicavati species from the previous zone. Latest Pragian and earliest Emsian.

2.16 Bizonate, proximally cristate and distally annulate miospore event

First appearance and diversification of proximally radially ribbed and distinct delimited distally annulate species of *Emphanisporites* and distally convoluted murornate species of *Acinosporites*. Abundance of biform sculptured forms of *Dibolisorites*. First appearance of stout, prominent-spined species of *Acanthotriletes*. Proliferation of distally patinate species of *Tholisorites* and *Chelinospora*. Diversification of zonate and pseudosaccates forms of *Camarozonotriletes* and *Geminispora* species. Disappearance of most reticulate and tripapillate miospores (Richardson and McGregor 1986; Streele et al. 1987; Hassan Kermandji et al. 2008). Early and early late Emsian.

2.17 Bifurcate-tipped appendages and monopseudosacciti miospore event


2.18 Zonate-pseudosaccate and coarse bifurcate spinose miospore event

Characterized by incoming of finely-sculptured zonate-pseudoccate miospores of *Calyptosporites* and *Rhabdosporites* species. Proliferation of *Samarisporites*, *Corystisporites* and *Ancyrospora* species. Gradually waning of *Acinosporites* and patinate taxa (Richardson and McGregor 1986; Streele et al. 1987; Hassan Kermandji et al. 2008). Early Eifelian.

The correlation between the Algerian miospore assemblage biozones and the standard Euramerican North Gondwanan miospore biozones is shown in Figure 2. All these data originated from the Tidikelt Plateau, Triassic Province, Oued Saoura and Illizi regions, west and east Sahara Algerian Desert synclines, North Africa, Old Red Sandstone continent and adjacent regions, but other regions may contribute for improvement of the results. For instance, I have used in the legend of the figure additional correlation data from south Wales.

3. Stratigraphic miospore distribution

Significant progress has been made in areas regarding morphologic events of the sporomorphs stratigraphic distribution Richardson (1996) and Zonal concepts were used by many workers;
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some described it as local events (Loboziak et al. 1992; Rubinstein and Steemans 2002; Richardson and Edwards 1989; Wellman and Richardson 1996; Jardiné and Yapaudjian 1968; Melo and Loboziak 2003; Moreau-Benoît et al. 1993; Hassan Kermandji et al. 2008; Richardson and Ioannides 1973, Massa and Moreau-Benoit, 1976), others are used the concept in more wider sense “on global scale” (e.g. Richardson and McGregor 1986; Streel et al. 1987). Richardson and McGregor (1986) concept for Devonian miospore zonation, based on spore assemblage biozones to describe miospore distributions of the Old Red Sandstone Continent and adjacent regions, whereas Streel et al. (1987) employed the scheme based on spore Oppel zones and Interval zones recognized in the progressive changes from shallow to more deeper marine sediments of the Ardenne-Rhenish region. Both schemes have been utilized beyond their regions where they established (e.g. McGregor and Playford 1992, Loboziak and Streel 1995). Fundamentally both schemes based on the appearance of well recognized, laterally extensively distributed spore taxa. Although the Richardson and McGregor’s magnificent zonation concept is loose (Streel and Loboziak, 1996), it is practical, based on assemblages of characteristic taxa allow correlations on great scale. The branded Interval zone concept of Streel et al. (1987) is build up within a single great phytogeographic province and on distinctive miospore taxa, to some extent, many of their typical taxa hard to occur in another region (Wellman 2006; Breuer et al. 2007; Steemans et al. 2008; Hassan Kermandji et al. 2008). Nevertheless, Streel and Loboziak (1996) are employed Western Gondwana and southern Euramerica as a single major phytogeographic province.

There are significant difficulties concerned correlations between Upper Silurian-early Lower Devonian miospore assemblage sequences of north Africa (Sahara Algeria, Libya and Tunisia) and those of Old Red Sandstone and adjacent regions by Richardson and McGregor (1986) and the Ardenne-Rhenish regions by Streel et al. (1987). The major differences between miospores sequences of Moreau-Benoit et al. (1993), Melo and Loboziak (2003), Steelmans et al. (2008), Rubinstein and Steemans (2002), Steemans et al. (2007), Hassan Kermandji (2007), Hassan Kermandji et al. (2008), Spina and Vecoli (2009) and many others are that: they contain groups of palynomorphs of different stratigraphic significance. They are different particularly, in terms of the characteristic taxa and the absence of common index species from the zones. The degree of similarities in terms of the general characteristics and composition between Euramerican and Gondwana miospores were overestimated by many workers: Loboziak and Streel 1989; Loboziak et al. 1992, and many others. However, some similarities exist between Euramerica and Western Gondwana but many regions of northern Gondwana contain limited numbers of Euramerican characteristics zonal miospores within assemblages of different composition Wellman (2006). Therefore, Upper Silurian-early Lower Devonian Euramerican miospore biozones are hard to be in use in the Western Gondwana province.

Comparable zonation schemes for the Upper Silurian and Lower Devonian of North Africa are unexpectedly few despite a long history of investigations that have concentrated on phytoplankton and land plant miospore assemblages of deep drillings. No Proposal exists for a formal zonation. Nevertheless, the Silurian and Devonian biostratigraphic studies neither for the Western Libyan deep drilling deposits by: Massa and Moreau Benoit 1976; Richardson et al. 1981; Rubinstein and Steemans 2002; Le Hérissé 2002; Spina and Vecoli 2009; nor those of Mid Palaeozoic Algerian Sahara petroleum sediments by Magloire 1967; Jardiné and Yapaudjian 1968; Moreau-Benoit et al. 1993; Abdesselam-Rouighi, 1986, 1996,
2003. They are preliminary and do not permit exact correlation with standard zonations of Euramerican palynozones by Richardson and McGregor (1986), Strel et al. (1987) and Richardson et al. (2001). However, detail proposal do exist for the Tidikelt and Oued Myia deposits in the central and south western Algerian Sahara synclines (Hassan Kermandji 2007, Hassan Kermandji et al. 2008) which are equivalent to the Přídolí, Lochkovian, Pragian, Emsian and Eifelian deposits of Euramerica. They establish well-defined ten miospore assemblage biozones and one interval zone extending from the Homerian to early Eifelian. Zonal index taxa were recognized and the general pattern of changes in miospore distribution through Homerian and early (but not earliest) Emsian to Lower Eifelian, more or less, comparable to those changes reported in Euramerica region. While the pattern of changes in miospore distribution through Ludfordian, Přídolían, Lochkovian, Pragian and Lower Emsian does not reflects changes comparable to those stated in Euramerican province. They are differing in the selection of zonal index taxa, zonal miospore composition and vertical stratigraphic occurrence.

The most diverse and distinctive, moderately well preserved Silurian and Devonian sporomorphs assemblages occur in shallow marine and terrestrial strata of the Triassic Province and Tidikelt plateau were studied biostratigraphically. This is well coincide with Richardson (1984) finding that ‘sporomorph assemblages occur in rocks deposited either on land or in marine environments’.

4. Sporomorphs distribution development

Detailed studies of many local and regional palynological zonations of the middle to late Silurian and early to early Middle Devonian deposits in the Euramerica and Western Gondwana reveal many difficulties, probably due to the time of closure (Lochkovian or Pragian-Emsian) of the Rheic Ocean which may cause climate and palaeophytogeographic isolation. On the other hand, this may lead to widespread dispersal ability and climatic tolerance of late Silutian and early Devonian land plants Raymond et al. (2006). This palaeophytogeographic differentiation of macroflora does not imitate spore distributional pattern. On the basis of dispersal miospores distribution patterns Wellman and Gray (2000) and Edwards and Wellman (2001) distinguished a Euramerican miospore biogeographic unit from a Gondwanan unit for late Silurian times. Though palaeophytogeographic differentiation does not well reflects miospores distribution patterns for this period Richardson et al. (2001).

On the basis of sporomorphs classification which is based on morphology, appears that earliest cryptospores with apparent thick curvatural crassitude may have close relation with initial Ambitisporites. This is may indicate that plants producing cryptospores may be predecessors of those producing Ambitisporites miospores Richardson (1996). Morphological features show that there are close relation between some cryptospore tetrads with retusoid miospores bearing distinct contact areas, curvatureae perfectae not confined to the equator and distally patinate with thin proximal wall (Ambitisporites and Archaeozonotriletes which occur a little latter). The progressive advantages in complexity of morphological structure occur in sequence of parallel changes in both closely related cryptospores and miospores. The appearance of some types of ornaments was not always synchronous in both groups, for instance proximal papillae first occur on miospores in early Přídoli, whereas it appears on cryptospores in early Lochkovian. This is probably related to the environmental responses with two closely related groups of plants responding to the same motivation.
With reference to the main spromorphs evolution events, their distribution patterns are discussed. However, the appearance or the disappearance of structural group or a single genus and/or whole complex of forms provides helpful indicators in establishing local or regional miospore zonations.

4.1 Cryptospores

Cryptospores are usually more abundant and diversified than miospores in early sediments, mainly occur in inshore environments, and decline in abundance offshore more than miospores. They decrease in abundance number in younger sediments and taxonomically become more varied. This is may indicate that their parent plants possibly were living on sediments of ephemeral environment. The high abundance and diversity of cryptospores suggesting that their parent plant flourishing and occurred together with miospores producing plants, probably of vascular type Wellman and Richardson (1996). The earliest geological record of cryptospores was in Caradoc, late Ordovician, but probably they appear much earlier.

The cryptospore diversifications are varied from place to place. The variations are due to the nature of depositional environment. Laevigate taxa are more diverse than sculptured forms. Some granulate; apiculate cryptospore types are found in situ (Funning et al. 1991).

Cryptospores ‘generally’ are represented by long ranging taxa such as, Tetrahedraletes mediensis (Pl.1, Fig.2, Pl.2, Fig.6), Laevolancis divellomedia (Pl.1, Figs. 8, 13), Cheirotetras caledonica (Pl.1, Fig.1), Cymbohilates horidus, (Pl.1 Figs. 3, 5, 6, 11) and Cymbohilates allenii var. allenii (Pl.1, Fig.14), Cymbohilates allenii var. magnus (Pl.1, Fig.4), Hispanaediscus verrucatus (Pl.1, Figs.7, 12), Artemopyra scalariformis (Pl. 1, Fig. 9) and Acontotetras inconspicuis (Pl.1, Fig.10). All these taxa have been recorded in many late early Silurian to Lochkovian sedimentary sequence, from many Euramerican and Gondwanan areas.

On the basis of proliferation and diversification of cryptospores from the Type Wenlock and Towy Anticline, Burgess and Richardson (1991, 1995) confirmed the first occurrence of seven zonally significant species in Sheinwoodian to Ludfordian and graptolite bearing strata of Euramerican province. Most of these sub-zones are regionally confined and have not been observed in North Africa. Out of two spore assemblage biozones, two spore biozones, two sub-biozones and one spore interval biozone of Ludfordian-Lochkovian from the Cantabrian Mountains, NW Spain by Richardson et al. (2001), only Scylaspora vetusta-Scylaspora kozlica (Dufka) Spore Assemblage Biozone and the spore interval biozone correspond to just two Přídoli spore interval biozone (hemiesferica) and the Scylaspora radiate-Apicalretusispora synoria Miospore Assemblage Biozone of western and central Algeria by Hassan Kermandji (2007, Fig.3). The endemism of some miospore species caused many terrestrial plants to appear earlier in Gondwana, also infrequency of plants producing these palynomorphs, palynologically unfavorable types of sediments, incomplete study of available rocks and inappropriate environments may originate these variations.

4.2 Miospores

The earliest recorded laevigate retusoid, equatorially thickened miospores is specimens resemble Ambitisporites appear little earlier than true Ambitisporites Hoffmeister (1959) Pl. 2,
Figs. 2, 4, of latest Aeronian. Whereas laevigate, distally patinate, proximally generally hilate, *Archaeozonotriletes* (Naumova) Allen (1965), appear in Telychian. Both taxa persist into Lower Devonian. This is indicating that land flora producing these taxa are uniformly distributed over wide regions. Some retusoid forms are found *in situ*, for instance *Retusotriletes coronatus* found in the lower Downton Group, also some sporangia have yielded verrucate crassitate *Synorisporites verrucatus* and some others has yielded, crassitate papillate *Synorisporites tripapillatus*. Whereas, no laevigate patinate *Archaeozonotriletes* has been found *in situ*, this is may indicate that their parent plants lived in ephemeral environment Richardson (1996). Nevertheless, equally crassitate and patinate taxa are remarkably abundant in offshore environment. Richardson and McGregor (1986) in their zonal concept used *A. avitus-A. dilutus* for Aeronian and *A. chulus-A. nanus* for Sheinwoodian as cosmopolitan assemblage zones. The two assemblage zones are considered by McGregor and Playford (1992) and Strel and Loboziak (1996) as loose biozones.

There are some familiarities in miospore assemblage composition throughout Homerian-Přídolían sediment reported from Euramerican and Gondwanan phytogeographic provencies. The common zonal species are represented by: *S. kozlica* Pl.2, Fig.3; *S. vetusta* Pl.2, Fig. 11; *C. hemiesferica* Pl.2, Fig. 5; *C. sanpetrensis* Pl.4, Fig.12, Pl.5, Fig. 13; *C. (Lophozonotriletes?) poecilomorpha* Pl.2, Figs. 7, 8). The first two species form nominal taxa of the Middle Homerian sediments, whereas, the rest are nominal taxa for Ludfordian and Přídolían strata (Burgess and Richardson 1995, Richardson et al. 2001, Hassan Kermandji 2007).

Lower Devonian sediments of the Gondwanan province includes many miospore species known elsewhere, though striking assemblages of the same stratigraphic range are difficult to be found in other studied regions. For instance *S. tidikeltense* Pl.2, Fig. 10 of early Lochkovian and *C. triangulates* Pl.2, Fig. 9 of Ludfordian are recorded only in Gondwanan province. Whereas, *S. newportensis* ss, *E. micrornatus* ss, *E. zavallatus* ss are recorded in Lochkovian sediments of Euramerican phytogeographic province. Some other characteristic species such as *C. cassicula, L. argovejae* have different stratigraphic occurrence in the two provinces. This is probably are due to insufficient favorable sediment, nature or rarity of plants producing these miospores, unsuitable environments, the absence of an effective physiographic barrier ( Steemans 1999b; Steemans et al.2007, 2008; Edwards and Richardson 2004; Richardson 2007).

To illustrate these differences between the two phytogeographic provinces, the miospore zonal scheme of text figure (2) demonstrate these differences. A comparison with the Old Red Sandstone Continent zonation shows that only two Western Sahara Algeria syncline (*annulatus-sextantii* and *velatus-langii*) is correspond to just two Emsian to early Middle Eifelian assemblage zones of Richardson and McGregor (1986). Nearly 6 Interval zones (Po-AB) of the Ardenne-Rhine regions zonation of Strel et al. (1987) correspond to just two Middle and Upper Pragian miospore assemblage biozones (*arenorugosa-caperatus* and *polygonalis-subgranifer*) of Western Sahara Algeria syncline of Hassan Kermandji et al. (2008, Fig.4). Despite this limited matching, they contain many more identical characteristic species of Lochkovian to early Eifelian but of different occurrence and stratigraphic range. The Innovation contrast with miospore assemblages is by their cosmopolitanism culminating in the Emsian *Emmanisporites annulatus*. This species began in early but not earliest Emsian and well expanded during Emsian and early Eifelian and collapsed at latest Devonian, allowing accurate correlations throughout the world.
Late Silurian-Middle Devonian Miospores

Fig. 2. Correlation between miospore zonation in the Lower and Middle Silurian and Devonian of Euramerica and Western Gondwana.
PLATE 1

All figures x 1000 where stated otherwise.

Figure 1. *Cheilotetras caledonica* Wellman and Richardson, 1993. (NL: samp. 1/21, sl. 3/1) Sheinwoodian, ECF-1 borehole, Illizi Basin, Sahara Algeria.

Figure 2. *Tetrahedraletes medinensis* (Strother and Traverse, 1979) Wellman and Richardson, 1996. (NL: samp. 1/14, sl. 2/1), Upper Homerian, NGS-1 borehole, Triassic Province, Sahara Algeria.

Figures 3, 5, 6 & 11. *Cymbohilates horridus* Richardson, 1996. Figs. 3 & 6 (NL: samp. 21082.5m, sl. 224), figs. 5 & 11 (NL: dep. 2082.5m, sl. 223), Lower Lochkovian, GMD-3 & ISS-1 boreholes respectively, Tedikelt Plateau, Sahara Algeria. Figs. 5, 6 x500.

Figure 4. *Cymbohilates allenii* var. *magnus* Richardson, 1996. (NL: dep. 2082.5m, sl. 223), Lower Lochkovian, ISS-1 boreholes, Tedikelt Plateau, Sahara Algeria.

Figure 7 & 12. *Hispanaediscus verrucatus* (Cramer) Burgess and Richardson, 1991. (NL: samp. 7/20, sl. 15/2), Homerian, ECF -1 borehole, Illizi Basin, Sahara Algeria.


Figure 9. *Artemopyra? scalariformis* Richardson, 1996. (NL: dep. 2082.5m, sl. 223) Lower Lochkovian, ISS-1 borehole, Tedikelt Plateau, Sahara Algeria.

Figure 10. *Acontotetras inconspicuis* Richardson, 1996. (NL: dep. 2082.5m, sl. 223) Lower Lochkovian, ISS1-borehole, Tedikelt Plateau, Sahara Algeria.

Figure 14. *Cymbohilates allenii* var. *allenii* Richardson, 1996. (NL: samp. 1/14, sl. 2/1), Homerian, NGS-1 borehole, Triassic Province, Sahara Algeria.
PLATE 2

All figures x 1000 where stated otherwise.

Figure 1. *Apiculiretusispora spicula* Richardson and Lister, 1969. (NL: dep. 2082.5m, sl.222), Prídoli, GMD-3 borehole, Tidikelt Plateau, Sahara Algeria.

Figure 2. *Ambitisporites dilutus* Hoffmeister, 1959. (NL: samp.2/11, sl. 9/2), Homerian, GMD-2 borehole, Tidikelt Plateau, Sahara Algeria.

Figs.3. *Scylaspora kozlica* (Dufka) Richardson, Rodriguez and Sutherland, 2001. (NL: samp. 1/14, sl. 2/1), Homerian, NGS-1 borehole, Triassic Province, Sahara Algeria.

Figure 4. *Ambitisporites avitus* Hoffmeister, 1959. (NL: samp.4/11, sl. 16/4), Sheinwoodian, GMD-2 borehole, Tidikelt Plateau, Sahara Algeria.

Figure 5. *Chelinospora hemiesferica* (Cramer and Diez) Richardson, Rodriguez and Sutherland, 2001. (NL: samp.5/13, sl. 7/5), Lower Prídoli, NGS-1 borehole, Triassic Province, Sahara Algeria.

Figure 6. *Tetrahedraletes mediensis* Strother and Traveres, 1979. (NL: samp.2/21, sl. 5/2) ECF-1 borehole, Sheinwoodian, Illizi Basin, Sahara Algeria.


Figure 9. *Cymbosporites triangulatus* Hassaan Kermandji, 2007. (NL: 3/13, 5/3), Ludfordian, NGS-1 borehole, Triassic Province, Sahara Algeria.

Figure 10. *Scylaspora tidikeltense* Hassaan Kermandji 2008. (NL: dep. 2082.5m, sl. 223), Lower (but not lowermost) Lochkovian, GMD-3 borehole, Tidikelt Plateau, Sahara Algeria.

Figure 11. *Scylaspora vetusta* (Rodriguez) Richardson, Rodriguez and Sutherland, 2001. (NL: samp.2/11, sl.5/2), Homerian, NGS-1 borehole, Triassic Province, Sahara Algeria.
PLATE 2

Figure 2. *Emphanisporites neglectus* Vig ran, 1964. (NL: samp.2/11, sl.8/2), Ludfordian, NGS-1 borehole, Triassic Province, Sahara Algeria.

Figure 3. *Cymbosporites cyathus* Allen, 1965. (NL: samp. MD42, sl. 42/3), late Pragian-earliest Emsian, Djabel el Kahla, Oued Saoura, Western syncline, Sahara Algeria. x700.

Figures 4, 7&10. *Perotrilites microbaculatus* Richardson and Lister, 1969. (NL: dep.2082.5m, sl. 224), Lower (but not lowermost) Lochkovian, GMD-3 borehole, Tidikelt Plateau, Sahara Algeria.

Figures 5&11. *Amocosporites miserabilis* Cramer, 1966. (NL: dep. 1183.0m, sl. 102), Lower Lochkovian, MSR-1 borehole, Tedikelt Plateau, Sahara Algeria.

Figure 6. *Brochotiletes libyensis* Moreau-Benoît, 1979. (NL: dep.1012.7m, sl. 419), Pragian, MSR-1 borehole, Tidikelt Plateau, Sahara Algeria.

Figure 9. *Emphanisporites spinaeformis* Schultz, 1968. (NL: samp. MD21, sl. 21/5), late Lochkovian, Moungar Debad Km 30, Oued Souara, Western syncline, Sahara Algeria.

Figure 12. *Dibolisporites echinaceus* (Eisenack) Richardson, 1965. (NL: dep. 1911.0m, sl. 511), late Pragian-earliest Emsian, ISS-1 borehole, Tidikelt Plateau, Sahara Algeria.

PLATE 3
PLATE 4

All figures x 1000 where stated otherwise.

Figures 1 & 4. *Clivosispora verrucata* var. *convoluta* McGregor and Camfield, 1976. (NL: dep. 1012.7m, sl. 419), Middle Pragian, MSR-1 borehole, Tidikelt Plateau, Sahara Algeria.

Figure 2. *Corystisporites* cf. *multispinosus* Richardson, 1965. (NL: samp. MD56, sl. 56/5) latest Emsian, Moungar Debad Km 30, Oued Saoura, Western syncline, Sahara Algeria.


Figure 7. *Samarisporites mediconus* (Richardson) Richardson, 1965. (NL: samp. MD62, sl. 62/3), Eifelian, Moungar Debad Km 30, Oued Saoura, Western syncline, Sahara Algeria.

Figure 8. *Geminospora* cf. *treverica* Riegel, 1973. (NL: dep. 955.0 m, sl. 405), Eifelian, MSR-1 borehole, Tidikelt Plateau, Sahara Algeria.


Figure 13. *Dictyotriletes subgranifer* McGregor 1973. (NL: dep. 1027.5m, sl. 405), latest Pragian, MSR-1 borehole, Tidikelt Plateau, Sahara Algeria.
PLATE 5

All figures x 1000 where stated otherwise.

<table>
<thead>
<tr>
<th>Figure</th>
<th>Description</th>
</tr>
</thead>
<tbody>
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<td>2</td>
<td><em>Grandispora inculta</em> Allen, 1965. (NL: dep. 955.0m, sl. 405), Eifelian, MSR-1 borehole, Tidikelt Plateau, Sahara Algeria.</td>
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<td>3</td>
<td><em>Rhabdosporites langii</em> (Eisenack) Richardson 1960. (NL: dep. 955.0m, sl. 312), Eifelian, MSR-1 borehole, Tidikelt Plateau, Sahara Algeria.</td>
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<td>4</td>
<td><em>Apiculiretusispora arenorugosa</em> McGregor, 1973. (NL: dep. 1055.7m, sl. 400), Middle Pragian, MSR-1 borehole, Tidikelt Plateau, Sahara Algeria.</td>
</tr>
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<td>5</td>
<td><em>Grandispora protea</em> (Naumova) Allen, 1965. (NL: samp. MD56, sl. 56/9), latest Emsian, Mounarg Debad Km 30, Oued Saoura, Western syncline, Sahara Algeria.</td>
</tr>
<tr>
<td>6 &amp; 7</td>
<td><em>Calyptosporites velatus</em> (Eisenack) Richardson 1962. (NL: dep. 955.0m, sl. 310), Eifelian MSR-1 borehole, Tidikelt Plateau, Sahara Algeria.</td>
</tr>
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<td>8</td>
<td><em>Emphanisporites annulatus</em> McGregor, 1961. (NL: dep. 955.0m, sl. 425), Emsian, MSR-1 borehole, Tidikelt Plateau, Sahara Algeria.</td>
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<td>9 &amp; 12</td>
<td><em>Camarozonotriletes filatoffi</em> Breur, Al-Ghazi, Al-Ruwaili, Higgs, Steemans and Wellman, 2007. (NL: dep. 955.0m, sl. 427), Emsian, MSR-1 borehole, Tidikelt Plateau, Algeria.</td>
</tr>
<tr>
<td>10 &amp; 14</td>
<td><em>Rhabdosporites parvulus</em> Richardson, 1965. (NL: dep. 955.0, sl. 312), Eifelian, MSR-1 borehole, Tidikelt Plateau, Sahara Algeria.</td>
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<td>11</td>
<td><em>Ancyrospora ancyrea</em> var. <em>brevispinosa</em> Richardson 1962. (NL: dep. 955.0m, sl. 311), Eifelian, MSR-1 borehole, Tidikelt Plateau, Sahara Algeria.</td>
</tr>
<tr>
<td>13</td>
<td><em>Chelinospora sanpetrensisi</em> (Rodriguez) Richardson, Rodriguez, Sutherland, 2001. (NL: samp. OA, sl. 7/2), Ludfordian, NGS-1 borehole, Triassic Province, Sahara Algeria.</td>
</tr>
</tbody>
</table>
5. Appendix 1 List of species

Acanthotriletes raptus Allen 1965
Acinosporites verrucatus Streel 1967
Acinosporites conatus Hassann Kermandji 2008
Acontotetras inconspicuis Richardson 1996
Ambitisporites avitus Hoffmeister 1959
Ambitisporites dilutus (Hoffmeister) Richardson & List 1969
Ambitisporites tripapillatus Moreau-Benoît, 1976
Amocosporites miserabilis Cramer and Diez 1975
Anacyurospera ancyrea var. brevispinosa Richardson 1962
Apiculiretusispora arenorugosa McGregor 1973
Apiculiretusispora plicata (Allen) Streel 1967
Apiculiretusispora spicula Richardson and Lister, 1969
Apiculiretusispora sytonia Richardson & Lister 1969
Archaeozonotriletes chulus var. chulus Richardson and Lister 1969
Archaeozonotriletes chulus var. nanus Richardson and Lister 1969
Artemopyra scalariformis Richardson 1965
Brochotriletes foveolatus ? Naumova 1953
Brochotriletes libyensis Moreau-Benoît 1979
Calyptosporites velatus (Eisenack) Richardson 1965
Camarozonotriletes filatoffi Breur, Al-Ghazi, Al-Ruwaili, Higgs, Steemans and Wellman 2007
Camarozonotriletes sextantii McGregor and Camfield 1976
Camptozonotriletes caperatus McGregor 1973
Camptozonotriletes aliquantus Allen 1965
Cheilotetras caledonica Wellman and Richardson 1993
Chelinospora cassicula Richardson & List 1969
Chelinospora hemiesferica (Cramer & Diez) Richardson, Rodriguez and Sutherland 2001
Chelinospora perforata Allen 1965
Chelinospora (Lophasporesagittarius ?) poecilomorpha (Richardson & Ioannides) Richardson, Rodriguez and Sutherland 2001
Chelinospora sanpetrensis (Rodriguez) Richardson, Rodriguez and Sutherland 2001
Clivosispora verrucata var. Convoluta McGregor and Camfield 1976
Concentricosporites sagittarius (Rodriguez) Rodriguez 1983
Corystisporites cf. multispinosus Richardson 1965
Cymbohilates horridus Richardson 1996
Cymbohilates allenii var. allenii, Richardson 1996
Cymbosporites cf. dittonensis Richardson and Lister 1969
Cymbosporites proteus McGregor and Camfield 1976
Cymbosporites cf. proteus McGregor and Camfield 1976
Cymbosporites catillus Allen 1965
Cymbosporites cyathus Allen 1965
Cymbosporites triangulatus Hassan Kermandji 2007
Dibolisporites saharansis Hassan Kermandji 2008
Dibolisporites echinaceus (Eisenack) Richardson 1965
Dibolisporites cf. gibberosus (Naumova) var. major (Kedo) Richardson 1965
Dictyotriletes emsiensis (Allen) McGregor 1973
Dictyotriletes subgranifer McGregor 1973
Emphanisporites annulatus McGregor 1973
Emphanisporites decoratus Allen 1965
Emphanisporites epicautus Richardson and Lister 1969
Emphanisporites cf. micrornatus Richardson and Lister 1969
Emphanisporites neglectus Vigran 1964
Emphanisporites protophanus Richardson and Ioannides 1973
Emphanisporites spinaeformis Schultz 1968
Emphanisporites splendens (Richardson and Ioannides) Richardson and Ioannides 1979
Geminospora cf. spinosa Allen 1965
Geminospora svalbardiae (Vigran) Allen 1965
Geminospora cf. treverica Reigel 1973
Grandispora diamphida Allen 1965
Grandispora inculta Allen 1965
Grandispora libyensis Moreau-Benoit, 1980
Grandispora protea (Naumova) Allen 1965
Hispanaediscus lamontii Wellman 1993
?Hystricosporites cf. corystus Richardson 1962
Hystricosporites microancyreus Reigel 1973
Laevolancis divellomedia (Chibrikova) Burgess and Richardson 1991
Leonispora argovejea Cramer and Diez 1975
Lophozonotriletes curvatus Naumova 1953
Perotrilites microbaculatus Richardson and Lister 1969
Retusotriletes abundo Rodriguez 1978
Retusotriletes actinomorphus Chibrikova 1962
Retusotriletes cf. frivolus Chibrikova 1959
Retusotriletes triangulatus (Streel) Streel 1967
Rhabdosporites langii (Eisenack) Richardson 1960
Rhabdosporites parvulus, Richardson 1965
Samarisporites mediconis (Richardson) Richardson 1965
Samarisporites orcadiensis Richardson 1965
Scylaspora cymba Hassan Kermandji 2007
Scylaspora distincta Hassan Kermandji 2007
Scylaspora kozlica (Dufka) Richardson, Rodriguez and Sutherland 2001
Scylaspora radiata Hassan Kermandji 2007
Scylaspora undulata Hassan Kermandji 2007
Scylaspora vetusta (Rodriguez) Richardson, Rodriguez and Sutherland 2001
Scylaspora tidikeltense Hassan Kermandji 2008
Synorisporites tipapillatus Richardson and Lister 1969
Synorisporites verrucatus Richardson and Lister 1969
Stenozonotriletes furcitus Allen 1965
Tetrahedralets medinensis (Strother and Traverse) Wellman and Richardson 1993
Tholisporites anculus Allen 1965
Verrucosisporites polygonalis (Lanninger) McGregor 1973
6. References


Vaverdová, M. 1988. Further acritarchs and terrestrial plant remains from the Late Ordovician at Hiásná Třebaň (Czechoslovakia). Časopis pro Mineralogii a Geologii 33, 1-10.
Vaverdová, M. 1990a. Early Ordovician acritarchs from the locality Myto near Rokycany (late Arenig, Czechoslovakia) Časopis pro Mineralogii a Geologii 35, 239-250.
Stratigraphy, a branch of geology, is the science of describing the vertical and lateral relationships of different rock formations formed through time to understand the earth history. These relationships may be based on lithologic properties (named lithostratigraphy), fossil content (labeled biostratigraphy), magnetic properties (called magnetostratigraphy), chemical features (named chemostratigraphy), reflection seismology (named seismic stratigraphy), age relations (called chronostratigraphy). Also, it refers to archaeological deposits called archaeological stratigraphy. Stratigraphy is built on the concept "the present is the key to the past" which was first outlined by James Hutton in the late 1700s and developed by Charles Lyell in the early 1800s. This book focuses particularly on application of geophysical methods in stratigraphic investigations and stratigraphic analysis of layered basin deposits from different geologic settings and present continental areas extending from Mexico region (north America) through Alpine belt including Italy, Greece, Iraq to Russia (northern Asia).

How to reference
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