Some considerations on Devonian miospore taxonomy

[Quelques considérations sur la taxonomie des miospores dévoniennes]

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Introduction

In order to be able to deal with objects human beings need to have name tags for them and to classify them in discrete boxes. It is primarily for this reason that miospore taxa are named using Linnaean-style Latinized binomial nomenclature, a system formally governed by the International Code of Botanical Nomenclature (ICBN). The purpose of formal nomenclature is to provide a precise, simple and stable system of unique names that can be used by scientists all over the world. This system must allow for expansion and refinement to accommodate increases in knowledge (see TRAVERSE, 1996). Currently however, Palaeozoic miospore taxonomy has become somewhat problematic. Indeed, the number of described species has become so enormous that it is difficult to cope with all of this information. In addition, each authors prefer to work with their own discriminatory criteria, so that each has a personnal conception of the miospore classification and so does not necessarily use the same discriminatory features when he erects a new taxon. Consequently comparisons between assemblages described by different authors are becoming more confusing. Also, many species have not been accurately described, either because the diagnosis is rather simplistic, or because it is based on but a few specimens resulting in an ignorance of their intraspecific morphological variability. Furthermore, diagnoses based on poorly preserved specimens are not always precise and so are often unusable by other authors. Finally, species defined in journals with a limited circulation are unknown to many miospore researchers and are often described in other languages than English. Consequently, most of these species have been used only by the local authors and have been either completely unusable and/or overlooked by most of the palynologists. All these reasons have caused increased taxonomic chaos resulting in the overlapping diagnoses of some taxa. The intention of this extended abstract is not to resolve the problems related to miospore taxonomy but rather to highlight some of them by using selected examples from Devonian assemblages from Libya and Saudi Arabia.

Discussion

The fact that miospores are generally retrieved from sediments after their dispersal from the parent plants often implies, at least for the Palaeozoic specimens, ignorance of their source and consequently for most, of the time their natural affinities. Therefore Palaeozoic miospore taxonomy is inevitably arbitrary and artificial. As the essential basis of palaeopalynology is dispersed spores, their morphology obviously provides the principal and unique basis for taxonomic discrimination.

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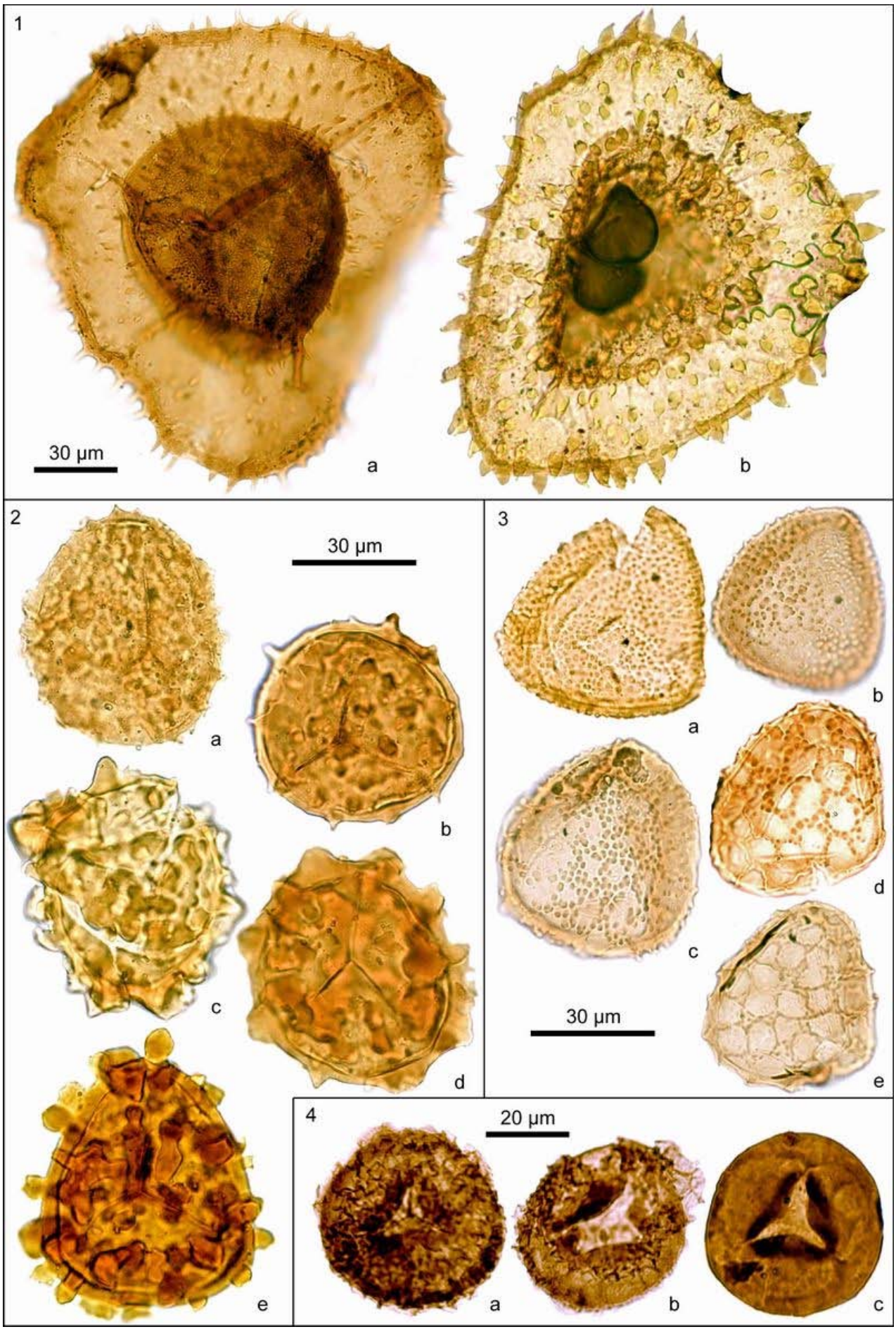
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◀ **Figure 1:** Microphotographs of Devonian miospores.
1.a. *Grandispora libyensis*. Well A1-69, sample 1416', slide 26993, EFC O43.
1.b. *Grandispora libyensis*. Well A1-69, sample 1296', slide 62645, EFC G47/2.
2.a. *Dibolisporites farraginis*. Well A1-69, sample 1334', slide 27127, EFC L44.
2.b. *Dibolisporites uncatus*. Well A1-69, sample 1277', slide 62637, EFC V-W42.
2.c. *Verrucosisporites scurrus*. Well A1-69, sample 1296', slide 62644, EFC P53/2.
2.d. *Verrucosisporites scurrus*. Well A1-69, sample 1277', slide 62637, EFC W48/3.
2.e. *Verrucosisporites premnus*. Well A1-69, sample 1277', slide 62636, EFC X41/4.
3.a. *Cymbosporites* sp. 1, Borehole BAQA-1, sample and slide 395.2', EFC G37/3.
3.b. *Cymbosporites* sp. 2. Borehole BAQA-1, sample and slide 395.2', slide, EFC X43/1.
3.c. *Cymbosporites*? sp. 3. Borehole BAQA-2, sample and slide 52.0', EFC N29/2.
3.d. *Dictyotriletes biornatus*. Borehole BAQA-1, sample 308.3', slide 62243, EFC U38.
3.e. *Dictyotriletes* sp. 1. Borehole BAQA-1, sample and slide 408.3', EFC G37/3.
4.a. sp. 1. Well UTMN-1830, sample 13689.7', slide 62317, EFC E33/4.
4.b. sp. 1.Well UTMN-1830, sample 13689.7', slide 62317, EFC Y42/1.
4.c. sp. 2. Well HWYH-956, sample 14195.2', slide 60550, EFC K35/1.

Therefore, miospores, as acritarchs, are classified into different groups by a simple morphological comparison. Indeed, miospore workers use form-genera and form-species ("parataxa"). At the suprageneric level, the completely informal subgroups of POTONIÉ (1956) are commonly used. His turmal system, which has been revised several times in his Synopsis volumes (POTONIÉ, 1956, 1970) is a scheme for classifying fossil miospores according to their morphological characters. However, one can choose any version of POTONIÉ's system or indeed make up one's own, and as the individual units in the system are not subject to rules of priority (see TRAVERSE, 1988), this kind of classification will inevitably cause much confusion. Miospore genera are normally defined according to the general structural features of miospores, such as equatorial outline, wall stratification, wall sculpturing, and any structural modifications of the spore wall (*e.g.* cingulum, zona or patina). Miospore species are generally described on the basis of ornaments, such as their size, shape, and distribution. At the infraspecific level, the rank of variety is rarely used. Other methods of classifying miospores have been proposed (see TRAVERSE, 1996). HUGHES's biorecord (1975, 1991) scheme is a parataxonomy; he recognized that conventional taxa tend to be expanded by inclusion in them of newly discovered but slightly variant forms until the taxa are "balloon taxa" of little stratigraphic use. This biorecord system treats every newly described form as completely unchangeable and independent of others, thus preventing "ballooning". In summary, palynological parataxonomy produce groupings with common morphological features whereas a true taxonomy describes the hierarchy of groupings of plants and is indicative of presumed natural relationships (see TRAVERSE, 1996).

Some authors urge the stratigraphic utility of subdividing miospore groupings as much as possible; however, others note that gradations between taxa may be so subtle that intermediates can often be found between species, or even genera, commonly regarded as discrete. Many cases of such intergrading taxa are common in the fossil record (*e.g.* PLAYFORD, 1983; STEEMANS & GERRIENNE, 1984; RICHARDSON *et alii*, 1993; BREUER *et alii*, 2005). Such palynomorphs often transgress the taxonomical boundaries between genera and higher categories as they were originally defined and thus formed the bases of their taxonomy. That is why the concepts of palynodeme (VISSCHER, 1971) and morphon (VAN DER ZWAN, 1979) were introduced. A palynodeme defines a group of palynomorph species that intergrade and probably represent the palynological reflection of a known or hypothetical plant species (VISSCHER, 1971). As originally defined, this concept was also phylogenetic and referred to characters changing with time. In contrast, a morphon delimits a group of palynological species (form-species) simply united by a continuous variation of morphological characteristics (VAN DER ZWAN, 1979). However in practice the two concepts are considered by many as synonymous (TRAVERSE, 1988). We can reiterate the main idea of these concepts as follows: the apparent morphological continua may represent spore variation in a particular known or hypothetical natural plant species or group of related species. However, evolutionary convergence may cause morphological similarities between miospores that do not necessarily reflect links between their parent plants. During Palaeozoic times, different plant groups often produced miospores of very similar morphology (GENSEL, 1980; FANNING *et alii*, 1992). In contrast, a single sporangium can produce two different genera of trilete spore (HABGOOD *et alii*, 2002). In palynology, the palynodeme and morphon concepts are complementary to the typological approach of traditional taxonomy. They emphasize the continuity of the morphological characters more than the discontinuity. They integrate morphological trends which are space- or time-dependent but also sensitive to various environmental conditions. They may also facilitate the interpretation of the morphological variations in terms of natural variation. Unfortunately, studies treating of the environmental influences on miospore variability are rare or nonexistent. For Devonian miospores, MCGREGOR and PLAYFORD (1992) have defined several morphons based on the

significant variation that has been observed in certain morphological characters. Those morphons are useful for comparison of assemblages on a second level (McGregor & Playford, 1992).

A few authors have mentioned phylogenetic miospore evolution in Palaeozoic sediments (*e.g.* Breuer *et alii*, 2005; Marshall, 1996; Maziane *et alii*, 2002; van der Zwan, 1979). Some of these authors have demonstrated continuous morphological intergradation among some dispersed spores that have previously been attributed to different form-species and even genera. However, the morphological signal presented by miospores may not reflect biological evolution alone. Indeed, it may be influenced locally by other parameters such as the state of preservation, sedimentary sorting (Jäger, 2004) and/or reworking of simpler and older morphotypes into assemblages that contain more complex and younger forms (Breuer *et alii*, 2005).

Selected examples

In this section, three examples of continuous morphological intergradation are presented and one about a possible taphonomic problem. These specimens were isolated from Devonian core samples in Libya and Saudi Arabia. All material presented herein is housed in the collections of the Unit of "Paléobotanique, Palynologie et Micropaléontologie", University of Liège.

Continuous morphological intergradation within a unique form-species

Grandispora libyensis Moreau-Benoit, 1980 is a characteristic form found in the Middle Devonian sediments of Libya (see *e.g.* Massa & Moreau-Benoit, 1976; Loboziak & Streel, 1989). This species of *Grandispora* is defined mainly by its equatorially thickened exoexine (3-7 µm thick) and its distal surface sculpture of spines or biform elements with 3-7 µm wide bulbous bases, commonly 3-10 µm high (rarely up to 13 µm); the rounded apices supporting a small spine. The ornament is usually densely spaced. After a study of some Libyan material, it appears that the specimens show a continuous morphological variation in ornamentation, intergrading from a morphotype with rather slender spines (Fig. 1.1.a) to one characterized by bulbous biform elements (Fig. 1.1.b). Although two end-members exist, all the intermediate forms are present. The morphotype characterized by the most massive sculptural elements seems to appear later than the morphotype with more slender ornaments, but in the youngest samples, the two-end members co-occur.

Continuous morphological intergradation within a unique form-genus

The genus *Verrucosiporites* is also a significant form in Middle Devonian samples. In Libyan samples, this very confused group probably includes the following described species (Fig. 1.2): *V. premnus* Richardson, 1965, *V. scurrus* (Naumova) McGregor et Camfield, 1982, *Dibolisporites farraginis* McGregor et Camfield, 1982 and *D. uncatus* (Naumova) McGregor et Camfield, 1982. Although the two latter species are included in the genus *Dibolisporites*, many authors consider them to belong to *Verrucosisporites*. All of these described species co-occur and in most of the levels of Libya where they are common they can be discriminated only with difficulty. Indeed, this group of form-species have very similar diagnoses. Specimens herein assigned these species seems to form a more or less intergrading series from those with predominantly conate and small verrucose sculpture (*D. farraginis* and *D. uncatus*) to those with large verrucate sculptural elements, and thus conform rather closely to the diagnosis of *V. scurrus* and *V. premnus*. In addition, McGregor and Playford (1992) designated *D. farraginis* and *V. scurrus* as morphons when they noted morphological intermediates between them.

Continuous morphological intergradation between two form-genera

A continuous morphological intergradation between two genera has been highlighted in Early Devonian miospore assemblages from Saudi Arabia. The ornament and its organization on the spore distal surface varies between the two end-members which correspond to two distinct genera: *Cymbosporites* and *Dictyotriletes* (Fig. 1.3). All the intermediary forms between them co-occur in the assemblages. This "lineage" includes morphotypes undescribed in the literature except for *Dictyotriletes biornatus* Breuer *et alii*, in press. In the simplest form of the spore ornament, small cones are evenly distributed on the distal surface (*Cymbosporites* sp. 1). In the intermediary forms cones organize progressively and combine until they form a pseudo-reticulum, the walls of which are constituted by lines of discrete ornaments (*Dictyotriletes biornatus*). In the most complex spore form ornaments merge to form an elongated ornament which constitutes a perfectly closed reticulum (*Dictyotriletes* sp. 1). Thus a progressive organization of the ornamentation appears from the simplest spores to the most evolved ones. This example illustrates that the miospore taxonomy is artificial because the two end-members of this lineage belong to two distinct genera.

Taxonomical confusion as a result of preservation?

Finally, palynologists must be careful because morphological differences may depend on the state of preservation or the transport

undergone by the miospores, and hence not necessarily on the original features. In Saudi Arabia, two as yet unpublished Emsian form-species have been recognized. They can either co-occur in the same layers or they are found separately. The first species (sp. 1) is two-layered and rounded; the intexine has a dark triangular thickening of the proximal pole and the exoexine is very thin and strongly folded (Fig. 1.4.a). The second species (sp. 2) does not have an exoexine but has the same intexine as sp. 1 (Fig. 1.4.c). Although they can be clearly discrete morphologically, they may either represent two varieties of a single species of parent plant, or that one form (sp. 2) may result from the corrosion of the other (sp. 1). Indeed, a slight detachment of the exoexine can be seen locally on some specimens of sp. 1 (Fig. 1.4.b), thus the very delicate exoexine may have been torn off by sedimentary or taphonomic processes. This situation can be confusing when comparing different assemblages.

Conclusion

The examples of continuous intergrading morphological variation outlined above illustrate one of the major problems in miospore taxonomy: the morphological variability of each taxon, combined with the description of individual forms, that are rarely studied within large populations. In older papers the rather basic description of many new taxa does not meet the modern standards for palynology. Furthermore, new taxa are often illustrated by too few specimens. Most authors have preferred to place their new taxa into well-defined boxes rahter than to introduce a palynodeme or morphon, which are concepts introduced for those species of miospore linked by a continuous variation of morphological characters. Ideally, in order to understand better the nature of a miospore taxon, larger populations and the relationships between the taxa should be studied. But in reality, the available material for study rarely allows the attainment of this level. The material can be badly preserved or is rare in most Devonian sediments. But these hindrances should not prevent improvement of our knowledge of palynological assemblages.

Another important factor in miospore taxonomy is the search for characters useful for the separation of taxa. We have to question the level at which such discriminatory criteria should be used: generic, specific or intraspecific. And their usage should be common to all authors in order to rein in the ongoing current taxonomical chaos.

The purpose of this short paper is neither to solve problems related to the somewhat chaotic miospore taxonomy nor to call into question the numerous stratigraphic correlations based on it, but rather to highlight some of these issues and to encourage a common approach to systematics.

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