

Plants Associated with Tentaculites in a New Early Devonian Locality from Morocco

PHILIPPE GERRIENNE, MURIEL FAIRON-DEMARET, JEAN GALTIER, HUBERT LARDEUX,
BRIGITTE MEYER-BERTHAUD, SERGE RÉGNAULT & PHILIPPE STEEMANS*)

4 Text-Figures, 2 Tables and 2 Plates



*Morocco
Devonian
Plants
Miospores
Systematics
Tentaculites
Palaeogeography*

Contents

Zusammenfassung	323
Abstract	324
1. Introduction	324
2. Materials and Methods	324
3. Description of the Tentaculite Assemblage	325
4. Description of the Miospore Assemblage	325
5. Description of the Plant Assemblage	326
5. 1. <i>Pachytheca</i> sp.	326
5. 2. <i>Spongiophyton</i> sp.	326
5. 3. cf. <i>Sporogonites</i> sp.	326
5. 4. cf. <i>Uskiella</i> sp./ <i>Sartilmania</i> sp.	326
5. 5. Zosterophylloids-Like Stobilus	326
5. 6. <i>Dawsonites</i> sp.	327
5.6.1. <i>Dawsonites</i> -Type A	327
5.6.2. <i>Dawsonites</i> -Type B	327
5. 7. Lycopsid-Like Axis	327
5. 8. Gen. nov. 1	327
5. 9. Gen. nov. 2	327
5.10. Incertae Sedis 1	328
5.11. Incertae Sedis 2	328
6. Discussion	328
Acknowledgements	330
Plates 1-2	330
References	334

Eine Assoziation von Pflanzen und Tentakuliten aus einer neuen unterdevonischen Lokalität in Marokko

Zusammenfassung

Eine neue unterdevonische Florenvergesellschaftung wird von einer Lokalität in Zentralmarokko, etwa 20 km nordwestlich von Azrou, beschrieben. Sie stellt derzeit die am besten datierte Vergesellschaftung dieses Alters in Nord-Gondwana dar. Die Fossilien finden sich in einer marinen Fazies von alternierenden Schiefern und Sandsteinen. Assoziierte Miosporen sind schlecht erhalten und weisen auf ein Zeitintervall vom frühen Pragian bis zum frühen Eifelian hin. Fünf Tentakulitenarten werden angeführt, die ein Unter-Emsium-Alter angeben. Die Makropflanzenreste sind als „Adpression“ (sensu SHUTE & CLEAL, 1987) erhalten. Die Vergesellschaftung enthält klassische Florenkomponenten unterdevonischen Alters wie *Pachytheca* sp. (möglicherweise eine Alge), cf. *Sporogonites* sp. (ein angenommener frühes Moos),

*) Authors' addresses: PHILIPPE GERRIENNE (NFSR Research Associate), MURIEL FAIRON-DEMARET, PHILIPPE STEEMANS (NFSR Research Associate), Paléobotanique et Paléopalynologie, Université de Liège, B18, Sart Tilman, 4000 Liège 1, Belgium; JEAN GALTIER, BRIGITTE MEYER-BERTHAUD, Laboratoire de Paléobotanique, Institut des Sciences de l'Evolution (UMR 5554), Université Montpellier 2, Place Bataillon, 34095 Montpellier Cedex 5, France; HUBERT LARDEUX, Laboratoire de Géologie, IRFA-UCO, B.P. 808, F-49008 Angers Cedex 1, France; SERGE RÉGNAULT, Museum d'Histoire Naturelle, 12 rue Voltaire, F-44000 Nantes, France.

Dawsonites sp. (isolierte Paare von zugespitzten Sporangien, die in die Verwandtschaft der Trimerophytopsida gehören), cf. *Uskiella* sp./*Sartilmania* sp. (Sporangien-Enden von einer Basalgruppe der Eutracheophyten), ein zosterophyllopsidaartiger Strobilus und vegetative, unverzweigte Blattachsen angenommenerweise aus der Umgebung der Lycopside. Exemplare von *Spongiophyton* sp., angenommenermaßen Lichenes, wurden auch identifiziert. Vertreter zweier neuer Gattungen unsicherer verwandtschaftlicher Beziehung werden kurz beschrieben. Die Vergesellschaftung der neuen Lokalität weist größte Ähnlichkeit mit denen von Süd-Wales, Belgien und Deutschland auf. Aus paläogeographischer Sicht bestätigen die neuen Daten die Positionen von Wales, Belgien, Deutschland und Marokko, wie sie in den Rekonstruktionen von SCOTSE & MCKERROW (1990) für das Unterdevon hypothetisiert wurden. Hinsichtlich ihrer gattungs- und artmäßigen Zusammensetzung dürfte die marokkanische Vergesellschaftung eine eigene phytogeographische Untereinheit repräsentieren.

Abstract

A new Early Devonian plant assemblage is described from a locality of central Morocco, at about 20 km north-west of Azrou. It currently represents the best dated assemblage of this age from Northern Gondwana. The fossils occur in a marine facies of alternating shales and sandstones. Associated miospores are badly preserved; they indicate an early Pragian to early Eifelian age. Five species of Tentaculites are reported, that indicate a Lower Emsian age. The plant macro-remains are preserved as adpressions (sensu SHUTE & CLEAL, 1987). The assemblage includes classical floral components of Early Devonian age, such as *Pachytheca* sp. (a possible alga), cf. *Sporogonites* sp. (a putative early moss), *Dawsonites* sp. (detached pairs of fusiform sporangia related to the Trimerophytopsida), cf. *Uskiella* sp./*Sartilmania* sp. (terminal sporangium from a basal group of Eutracheophytes), a zosterophyllopsid-type of strobilus, and vegetative unbranched leafy axes of putative lycopside affinities. Specimens of *Spongiophyton* sp., a putative lichen, have also been identified. Representatives of two new genera of uncertain affinities are briefly described. The assemblage from the new locality shows the closest similarities with the more or less contemporaneous assemblages of Southern Wales, Belgium and Germany. From a palaeogeographical point of view, these new data favour the positions of Wales, Belgium, Germany, and Morocco hypothesised in the reconstructions of SCOTSE & MCKERROW (1990) for the Early Devonian. On the basis of its generic and specific composition, the Moroccan assemblage might represent a separate phytogeographic sub-unit.

1. Introduction

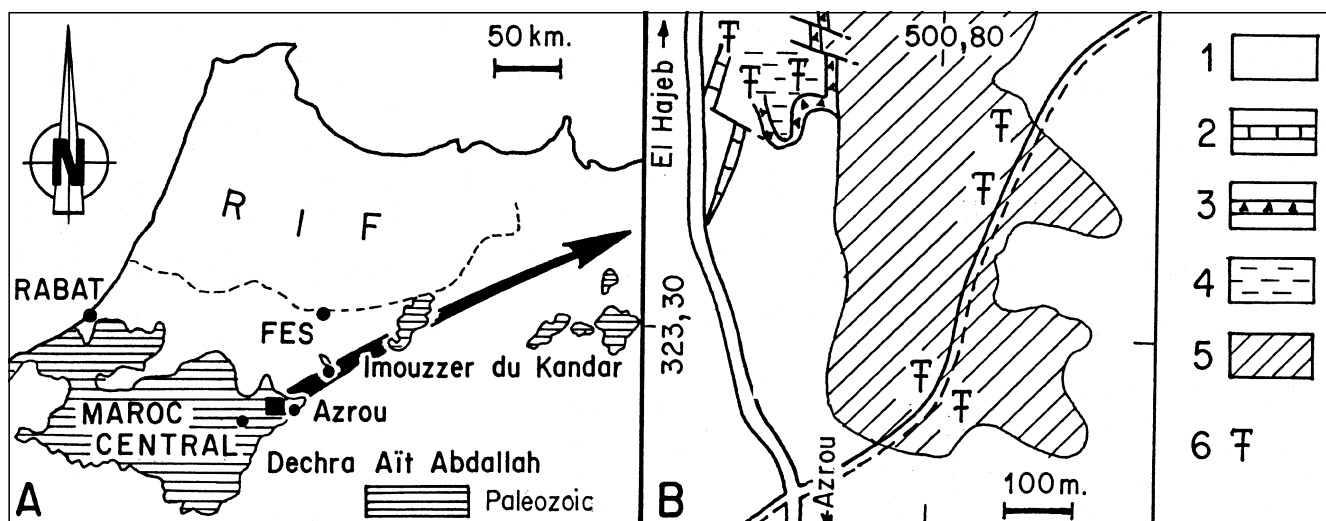
As emphasised by the latest phytogeographic reconstructions provided for the Early Devonian (RAYMOND et al., 1985; RAYMOND, 1987; EDWARDS, 1990), most of the fossiliferous localities reported for that time interval occur in the palaeocontinents Laurussia, Siberia and South China. Very few plant assemblages, except those from Australia, have been reported from Gondwana. In addition to their rarity, one of the critical problems encountered with those Gondwanan assemblages is related to the accuracy of their datings (RAYMOND, 1987; EDWARDS, 1990). This paper is a preliminary account of a new Early Devonian plant assemblage associated with a well-dated fauna of Tentaculites from a locality in central Morocco. This association provides a unique opportunity to accurately date Early Devonian plants from a north Gondwanan locality outside

the Australian area. Plant transportation and deposition in a marine sediment certainly resulted in an under-representation of the original floral diversity that characterised land masses of this region. It also accounts for the fragmentary state of a number of specimens. Some plants, however, appear to have been less affected taphonomically and are represented by extensive portions of axes. The present contribution provides a brief description of all main types of plants collected in the new locality, including the new ones, but focuses on the taxa already described elsewhere for their significance in testing current early Devonian palaeogeographical reconstructions mainly based on palaeomagnetic data (SCOTSE & MCKERROW, 1990; VAN DER VOO, 1993; PLUSQUELLEC et al., 1997).

2. Materials and Methods

The fossils were collected in a locality at about 20 km north-west of Azrou and 1 km east of Jbel ben Aarab

(Text-Fig. 1). The fossiliferous beds consist of silty micaceous shales occurring within the so-called "flysch forma-



Text-Fig. 1.

Geographic location of the locality.

A = Occurrence in Central Morocco; B = East of Jbel Ben Aarab; 1 = Superficial formations; 2 = Limestone with Goniatites and Tentaculites (Frasnian); 3 = Limestone with cherts (Givetian); 4 = Siltites with corals and Hyolithes (Pragian?); 5 = So-called "flysch" with plants and Tentaculites; 6 = Fossiliferous outcrops.

Text-Fig. 2.

Stratigraphic extension of the Tentaculites (A) and spores (B) from the fossiliferous outcrops of the East of Jbel Ben Aarab.

tion" (Text-Fig. 1B; BOUABDELLI, 1982) and are reported as Siegenian–Emsian in age on the El Hajeb 1 : 100.000 geological map (MORIN et al., 1975). Except for the Tentaculites, the marine fauna is relatively poor and includes a few crinoids, brachiopods and trilobites. Other Moroccan localities with plant fragments associated with Tentaculites are cited in TERMIER & TERMIER (1950), BENSÂID (1979), and FAIRON-DEMARET & RÉGNAULT (1986). A field-trip, led by S. RÉGNAULT, R. CHALOT and J. GALTIER in 1987, yielded the Tentaculites reported in this paper and a large number of plant macro-remains. Palynological samples and a substantial complement of macro-remains were collected from nine layers of shales (AZ.A to AZ.I) from the southernmost outcrops (Text-Fig. 1B) during a second field-trip by Ph. GERRIENNE and B. MEYER-BERTHAUD.

Plant fossils were studied using standard palaeobotanical and palynological techniques. Plant macroremains which are preserved as adpressions (SHUTE & CLEAL, 1987) were degaged (sensu LECLERCQ, 1960) with steel needles. Parts and counterparts of the specimens were observed in light microscopy and photographed using a Tessovar Zeiss camera with a polarised light source. Contrast between plant and matrix was enhanced by wetting the specimens with water.

3. Description of the Tentaculite Assemblage

In this locality there are numerous Tentaculites (Dacryoconarides) associated with plants and mostly preserved as imprints or as internal moulds. In spite of their poor state of preservation, we were able to identify four species and to positively date the "flysch" formation with plants and Tentaculites to the Lower Emsian (Zlichovian) (Text-Fig. 2). Since these species have been described and illustrated elsewhere (BOUCEK, 1964; LARDEUX, 1969; ALBERTI, 1993), we shall provide a brief commentary here on their biostratigraphic interest.

Nowakia zlichovensis BOUCEK: This is a characteristic species of Bohemia from the Zlichov beds, with a wide geographic distribution. It is weakly represented here with one complete specimen and several fragments.

Stylianowakia aff. *ligeriensis* LARDEUX: This resembles *Nowakia zlichovensis* BOUCEK because the apical region of the shell lacks transversal rings, but the ringless part of *Stylianowakia* aff. *ligeriensis* is much longer relative to the ringed part. This species is of relatively limited distribution: the La Grange Limestone (Armorican Massif, France) and Solopysky (Bohemia), all of which are of Zlichovian age. The genus *Stylianowakia* is of very precisely limited vertical distribution. To date no examples have been identified outside the Lower Emsian (Zlichovian). The *Stylianowakia* aff. *ligeriensis* species is represented here by six specimens.

A		TENTACULITES	
		Biozones	
E M S I A N	D A L E	<i>Nowakia maureri</i>	
	J I A N	<i>Nowakia richteri</i>	
		<i>Nowakia cancellata</i>	
	Z L I C H O V I A N	<i>Nowakia elegans</i>	
		<i>Nowakia barrandei</i>	
		<i>Nowakia zlichovensis</i>	I
		<i>Guerichina strangulata</i>	
P R A G I A N		<i>Nowakia acuaria</i>	
L O C H K O V I A N		<i>Paranowakia intermedia</i>	
		<i>Homoctenowakia bohémica</i>	
		<i>Homoctenowakia senex</i>	

B		SPORES	
		Biozones	
E M S I A N		AP	
		FD	
		AB	
		Su	
		Pa	
	PoW	W	
		Po	
P R A G I A N		BZ	
L O C H K O V I A N		MN	

Costulatostyliolina cf. *roemeri armoricana* LARDEUX: the numerous fine longitudinal ribs make the examples from the East of Jbel Ben Aarab seem very close to the species described by LARDEUX (1969) from the La Grange Limestone. We found twelve specimens of this.

Viriatellina aff. *pseudogeinitziana* BOUCEK: This was the most common species. It is very close to the species present in Bohemia at the top of the Zlichov formation.

Styliolina sp.: This species is represented here by very small specimens.

4. Description of the Miospore Assemblage

The palynological samples ("a" to "i") were taken from nine fossiliferous layers (AZ.A to AZ.I) in the southernmost outcrops. A tenth sample ("bis") was collected from layers outcropping 200 metres north from these sites.

Organic matter within all the samples is very badly preserved, destroyed by pyrite, highly altered by the thermal gradient, and mechanically broken. In such taphonomic conditions, only very few specimens of miospores could be identified. Most of them come from the samples "E" and "bis". The most significant species are *Dibolisporites wetteldorfensis* LANNINGER 1968, *Dibolisporites* cf. *echinaceus* (RICHARDSON) MCGREGOR 1973, *Camaronotriletes* cf. *parvus* OWENS 1971, *Apiculiretusispora* sp., *Retusotriletes* sp. Some Cambro-Ordovician reworked acritarchs are also observed in these samples.

Recent analyses on Saudi Arabian assemblages by LOBOZIAK & STREEL (1995) and STEEMANS (1995) suggest that the Devonian palynological biozonation established in Europe can be used for northern Gondwana, as the same succession of first occurrences of the characteristic species is recognised in both areas. In Europe, the species *Dibolisporites wetteldorfensis* ranges from the W interval Biozone (in the PoW Oppel Biozone), to the lower part of the AP Oppel Biozone (STEEMANS, 1989; STREEL et al., 1987; RICHARDSON & MCGREGOR, 1986) (Text-Fig. 2). The base of the W Biozone is early Pragian in age, and the AP Biozone is late Emsian to early Eifelian in age. The Pragian-Emsian boundary is included in the Su interval Biozone, in the PoW Oppel Biozone (STREEL et al., in press).

5. Description of the Plant Assemblage

5.1. *Pachytheca* sp.

(Pl. 1, Fig. 4)

The two specimens of the assemblage are badly preserved. They consist of circular-elliptical thalli respectively 4.5×5.5 mm and 5.5×8.0 mm across. One specimen, illustrated in Pl. 1, Fig. 4, exhibits a 2.0–2.4 mm broad central zone (medulla) surrounded by a 2.5 mm wide rim (cortex), the radial organisation of which is observed in localised zones. This morphology is typical of *Pachytheca* HOOKER, a genus of possible algal affinities collected in a number of Early Devonian localities of Europe, North America and Australia (GERRIENNE, 1990). The lack of well preserved tubes in either the presumed central medulla or the peripheral cortex does not allow a specific identification of these specimens (KIDSTON & LANG, 1924; CORSIN, 1945).

5.2. *Spongiophyton* sp.

(Pl. 1, Figs. 1, 2)

The affinities of *Spongiophyton* KRÄUSEL, 1954 have long been unclear. STEIN et al. (1994) recently suggested that *Spongiophyton* is probably one of the oldest known lichens. Remains assignable to that genus are preserved as thallus fragments which exhibit a pseudo-cellular pattern and unevenly distributed dark zones interpreted as pores (GENSEL et al., 1991) (Pl. 1, Fig. 2). The cellular patterning has recently been demonstrated to be a reticulate network of hyphae comprising a medulla (STEIN et al., 1994). The most extensively preserved Moroccan specimen is 3.1 cm long and represents a twice-dichotomising distal portion of thallus (Pl. 1, Fig. 1). Individual segments are at least 1 cm long and range from 12 mm wide proximally to 7.5 mm wide distally. One entire terminal segment exhibits a rounded apex. Cell-like structures are isodiametric to elongate-angular, up to 150 μ m wide and 450 μ m long. Pores are oval-circular and about 0.5–1 mm across. Pore density varies from 20 to 40/cm².

The genus *Spongiophyton* currently includes four species. *S. articulatum* is poorly known but differs from the Moroccan specimens by the presence of conspicuous longitudinal striations on the thallus (KRÄUSEL, 1960). The three remaining species are all characterized by a higher density of pores. The closest species in terms of pore density and size of pseudo-cells is *S. lenticulare* from the Middle Devonian of Brazil and from the Middle (?) Devonian of Ghana (KRÄUSEL, 1954, 1960; CHALONER et al., 1974), but the specimens from Morocco should preferably be described as a new species, which will be done in a forthcoming paper.

5.3. cf. *Sporogonites* sp.

(Pl. 1, Fig. 9)

Sporogonites HALLE includes putative early mosses (KENRICK & CRANE, 1997). The single specimen of *Sporogonites*-type is preserved over a length of 3.6 cm. It comprises a long naked unbranched axis which gradually increases from 0.7 mm in diameter at its base to approximately 1.5 mm distally where it subtends a globose capsule-like structure. This structure is about 6 mm high and 4 mm broad. It is differentiated into two approximately equal parts: a solid sterile portion at base and a hemispherical empty cavity surrounded by a 0.5–0.8 mm wide unornamented wall. This organisation is typical of that of all *Sporogonites* sporophytes preserved in compression described so far.

The Moroccan specimen, however, lacks the series of longitudinal ridges that characterise the basal half of the sporangium of the species *S. exuberans* (HALLE, 1916, 1936; STOCKMANS, 1940) and *S. belgica* (LANG, 1937; BHARADWAJ, 1981), both from western Europe, and *S. chapmani* from Australia (LANG & COOKSON, 1930). This feature is part of the original generico-specific diagnosis (HALLE, 1916) and of the emendation of the genus (BHARADWAJ, 1981). Its absence, together with a lack of preserved spores in the cavity precludes a definitive assignation of this specimen to the genus *Sporogonites*.

5.4. cf. *Uskiella* sp./*Sartilmania* sp.

(Pl. 1, Figs. 6, 7)

The single specimen definitely included in this category is a 6 mm long and 4 mm wide sporangium-like structure borne terminally on a narrow axis preserved over a length of 3 mm only. It is club-shaped (Pl. 1, Fig. 6) and shows parallel lateral sides and a slightly convex apex bordered by a thickened rim of coalified material (Pl. 1, Fig. 7). A part of the wall that was naturally detached from the specimen, was macerated but did not yield any spores.

Elongate isovalvate sporangia that resemble this specimen are borne on dichotomously branched systems of the genera *Sartilmania* (FAIRON-DEMARET, 1986) and *Uskiella* (SHUTE & EDWARDS, 1989), both from the Lower Devonian of western Europe. According to KENRICK & CRANE (1997), these two genera are closely related and possibly included in one basal group of Eutracheophytes. *Sartilmania* sporangia differ by their spatulate outline and the possession of prominent striations radiating from the base. The sporangia in both species *Uskiella spargens* (SHUTE & EDWARDS, 1989) and *U. reticulata* (FANNING et al., 1992) are smaller than the Moroccan sporangium and their apical outline is more convex. Sporangia of *Uskiella* exhibit a thin layer of extra-sporogenous material between the wall and the spore mass, often replaced by limonite. Such a pattern may have accounted for the easy detachment from the matrix of the sporangial wall of the Moroccan specimen, but additional specimens are needed to properly identify the generic affinities of this sporangium.

5.5. *Zosterophylloids*-Like Strobilus

(Pl. 1, Fig. 5)

The single specimen of this type consists of the distal part of an axis, ending in a strobilus. The sporangia are inserted laterally, on short stalks, and look helically arranged on the axis. They are all seen in profile and their 3-D shape is difficult to assess accurately. A thick distal

dehiscence line is visible on some sporangia. This badly preserved specimen conforms to the concept of *Zosterophyllopsida* (sensu BANKS, 1992, not KENRICK & CRANE, 1997); its sporangial characters (size, arrangement, dehiscence) are close to those of some specimens of *Zosterophyllum australianum* (LANG & COOKSON, 1930).

5.6. *Dawsonites* sp.

All specimens herein referred to *Dawsonites* consist of clusters of fusiform sporangia arranged in pairs and borne at the end of dichotomously branched axes. The genus *Dawsonites* HALLE, 1916 is an artificial taxon erected for isolated sporangia of the *Psilophyton*-type. Today, such sporangia are known to belong to several Trimerophytosida genera: *Psilophyton* DAWSON, *Trimerophyton* HOPPING, *Pertica* KASPER & ANDREWS, *Tursuidea* SCHWEITZER, etc.

5.6.1. *Dawsonites*-Type A

(Pl. 1, Figs. 10–12)

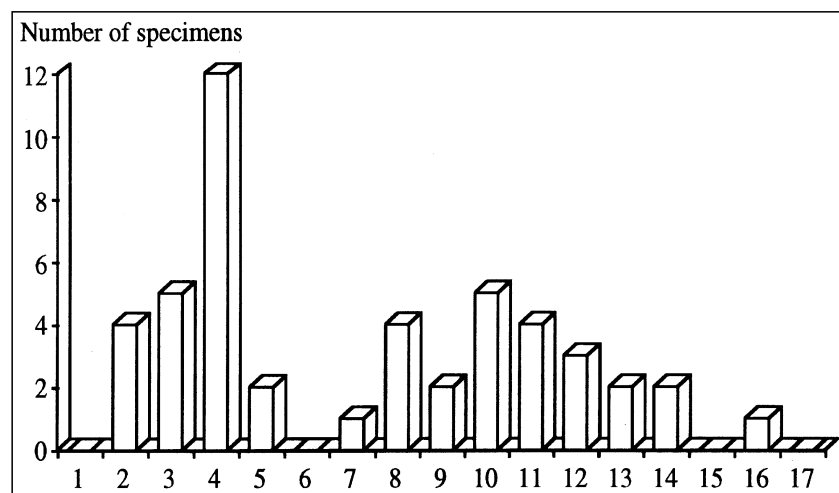
One of the most extensive specimens assigned to this type consists of a cluster of pairs of fusiform sporangia produced terminally on an isotomously branched system (Pl. 1, Fig. 10). Sporangia (Pl. 1, Fig. 11) are 4–5 mm long and 1–1.5 mm broad. The branched system is three-dimensional and shows three levels of dichotomies. Branching angle is about 55° at all levels. Axis width ranges from 2.5 mm wide proximally to 1.5 mm distally. Scar-like structures occur on both sporangial and axis surfaces. Those on the axes are more elongate than those scattered on the sporangial wall. Their significance remains problematic as neither the margins of the axes nor those of the sporangia show any epidermal outgrowth.

Another specimen consists of two pairs of sporangia (Pl. 1, Fig. 12). In each pair, the sporangia are clearly twisted around each other in an anti-clockwise arrangement. They are 5–6 mm long and 1.5–2 mm wide. Oval to elongate longitudinal scar-like structures are scattered all over their surface.

5.6.2. *Dawsonites*-Type B

(Pl. 1, Fig. 8)

The *Dawsonites*-type B clusters of sporangia are borne terminally on isotomously branched systems whose axes are 2–4 mm broad (Pl. 1, Fig. 8). Type-B sporangia are larger (5–7 mm long; 2–3 mm wide) and less clearly twisted around each other in a given pair. Their walls lack scars.



5.7. Lycopsid-Like Axis

(Pl. 1, Fig. 3)

Several specimens consist of an undivided axis 2–4 mm wide, bearing numerous small triangular emergences, 0.2–0.3 mm wide at their base and up to 1 mm long. Those emergences are inserted in irregular helices. They leave rounded scars on the axis surface. Even though the presence of a vascular bundle has to be demonstrated, the disposition of those emergences suggests that they were microphylls. The shape, size and density of those putative microphylls are different from those of primitive Lycopsids, such as *Asteroxylon* KIDSTON & LANG or *Drepanophycus* GOEPPERT. The Moroccan specimens possibly represent a new genus of primitive Lycopsids, but more specimens have to be discovered to allow a precise formal description.

5.8. Gen. nov. 1

(Pl. 2, Figs. 1–7)

Representatives of this new genus are typically very abundant in the locality, and more than a hundred specimens have been collected. This morphological type consists of 2.2–4.8 mm wide main axes that divide either isotomously or anisotomously (Pl. 2, Figs. 1, 4–7). The axes are devoid of epidermal outgrowths. Branching pattern is unusual: most anisotomous divisions are short and end in a 2–6 mm wide dichotomous globose structure. This structure is always adaxially and abaxially recurved (Pl. 2, Figs. 2–3). Some of those lateral structures bear elongate organs, presumably sporangia, 2–4 mm long and 1–2 mm wide (not illustrated). The morphology of these specimens is unique amongst the early land plants, and will justify the creation, in another paper, of a new genus for them.

5.9. Gen. nov. 2

(Pl. 2, Figs. 8–10)

This other new morphological type is also very abundant in the locality. This small plant has 1–2 mm wide axes; branching is profuse and isotomous or anisotomous (Pl. 2, Fig. 10); the plant also shows frequent K- and H-branching. The small lateral axes resulting from anisotomous divisions are generally circinate and abaxially and/or adaxially recurved. Small circular scars on the surface of the axes (Pl. 2, Figs. 8, 9) are indicative of the presence of small spines. Axes of gen. nov. 1 and 2 might appear as having more or less similar branching pattern, but the size range of main axis diameter (Text-Fig. 3) demonstrates that we are dealing with two different populations, and most probably with two different taxa. There are no reproductive structures preserved for gen. nov. 2 and the affinities of this new plant are presently impossible to assess.

Text-Fig. 3.

Main axis width frequency of gen. nov. 1 and gen. nov. 2 from the East of Jbel Ben Aarab locality.

Size classes:

1 = 0.00–0.99 mm; 2 = 1.00–1.24 mm;
3 = 1.25–1.49 mm; 4 = 1.50–1.74 mm;
5 = 1.75–1.99 mm; 6 = 2.00–2.24 mm;
7 = 2.25–2.49 mm; 8 = 2.50–2.74 mm;
9 = 2.75–2.99 mm; 10 = 3.00–3.24 mm;
11 = 3.25–3.49 mm; 12 = 3.50–3.74 mm;
13 = 3.75–3.99 mm; 14 = 4.00–4.24 mm;
15 = 4.25–4.49 mm; 16 = 4.50–4.74 mm;
17 = > 4.74 mm.

5.10. Incertae Sedis 1

(Pl. 2, Fig. 11)

Two specimens consist of narrow isotomously branched axes ending in small, dense clusters of sporangia (Pl. 2, Fig. 11). The shape of the latter is unclear, either fusiform or ovoid. Sporangia are terminal on the axes and possibly borne in pairs. These specimens resemble fertile structures of the Trimerophytopsida (sensu BANKS, 1992). However, the shape and arrangement of the sporangia are too unclear to assign them to *Dawsonites* and they are better left as incertae sedis.

5.11. Incertae Sedis 2

(Pl. 2, Fig. 12)

This morphological type is represented by one badly preserved axis with two rows of lateral opposite organs (Pl. 2, Fig. 12). The axis is 35 mm long and 5 mm wide. Its surface seems to be covered with rounded swellings (some scars are visible in the lower part of Fig. 12 on Pl. 2). If the lateral organs are sporangia, the overall organisation of the specimen would be that of a *Zosterophyllopsida* (sensu KENRICK & CRANE, 1997).

6. Discussion

Early Devonian localities yielding plants are relatively rare in Gondwana and dating is problematic for most. The assemblages from Sahara (LEMOIGNE, 1967) and Spain (ALVAREZ RAMIS, 1981) were dated from the plants themselves. The Early Devonian age assignment of the Lybian lycophytes from the Tadrart and Ouan-Kasa Formations (LEJAL-NICOL & MASSA, 1980) on the basis of long distance lithological correlations was later proved to be inaccurate (STREEL et al., 1990). In South African plant localities (ANDERSON & ANDERSON, 1985), the associated fish remains do not allow an accurate estimation of their age. Also controversial are the putative Late Silurian assemblages yielding *Baragwanathia* in Australia (GARRATT et al., 1984) and lycophytes of evolved types at Dor El Goussa in Lybia (KLITZSCH et al., 1973), which may well be Early Devonian (HUEBER, 1983; STREEL et al., 1990). The new plant assemblage from Central Morocco occurs in marine beds and its

association with well-preserved *Tentaculites* provides independent evidence for its biostratigraphical determination as Emsian. This age is corroborated by the analysis of the miospore assemblage.

The accurate and independent dating of this new North Gondwanan plant assemblage offers a good opportunity to compare its evolutionary level with other assemblages of equivalent age from Laurussia. The evolutionary level of a given locality can be estimated by the method of GERRIENNE & STREEL (1994). This method is taxon-free and has been calibrated using well-dated European and North American plant assemblages of Early Devonian age. It consists of calculating, for any given locality, a biostratigraphic coefficient from the evolutionary coefficients assessed for eleven significant individual plant characters (GERRIENNE & STREEL, 1994; GERRIENNE, 1996). The resulting coefficient reflects the mean evolutionary level of the plant assemblage. Ten different morphological types from Morocco, including vegetative axes, have been quantified (Table 1). The coefficient of the new Moroccan assemblage is 38.5, which demonstrates an evolutionary level intermediate between the mid-Pragian Brecon Beacons assemblage (Wales) and the early Emsian Marchin locality (Belgium) (GERRIENNE & STREEL, 1994). This means that the North Gondwanan locality from the East of Jbel Ben Aarab had approximately reached the same evolution level as the coeval European assemblages.

This result contradicts previous suggestions that the early land plants would have first evolved on Gondwana and would have afterwards colonized the other continents (LEJAL-NICOL & MASSA, 1980).

The plant assemblage from the East of Jbel Ben Aarab is allochthonous. It includes about 400 specimens from which about 1/3 is identifiable. The majority is assignable to the two new taxa with still unknown affinities; this includes long specimens, some preserved in organic connection with tiny lateral organs. The remaining specimens consist of a large number of disarticulated fragments (isolated sporangia and tips of branched axes, whether indeterminable or identified as cf. *Uskiellal Sartilmania*, *Zosterophyllum* or *Dawsonites*, and representatives of several major groups of plants recorded during Early Devonian times). The coexistence of well preserved and disarticulated specimens suggests that these remains

Table 1.

Quantification table of the plants collected from the East of Jbel Ben Aarab locality. I = cf. *Uskiellal Sartilmania*; II = *Zosterophyll*; III = *Dawsonites* type A; IV = *Dawsonites* type B; V = *Lycopsid*; VI = Gen. nov. 1; VII = Gen. nov. 2; VIII = Incertae sedis 1; IX = Incertae sedis 2; X = wide vegetative axes with elongated scars.

	I	II	III	IV	V	VI	VII	VIII	IX	X	TOTAL
Axis diameter (/5)	0	2	2	3	3	3	1	0	3	3	20 (/50)
Axis branching (/4)	?	?	1	1	?	2	2	1	?	2	9 (/24)
Axial emergences (/5)	0	0	1?	0	4?	0	1	0	0	1	7 (/50)
Photosynthetic surfaces (/3)	?	?	?	?	3	0	1	?	?	?	4 (/9)
Stelar type (/2)	?	?	?	?	?	?	?	?	?	?	0 (/0)
Xylem maturation (/2)	?	?	?	?	?	?	?	?	?	?	0 (/0)
Tracheid ornamentation (/3)	?	?	?	?	?	?	?	?	?	?	0 (/0)
Sporangial shape (/1)	1	1	1	1	?	1	?	1	?	?	6 (/6)
Sporangial aggregation (/2)	0	2	1	1	?	2	?	2	2	?	10 (/14)
Sporangial dehiscence (/2)	2	2	1	1	?	?	?	?	?	?	6 (/8)
Spore production (/2)	?	?	?	?	?	?	?	?	?	?	0 (/0)
TOTAL: 62 (/161)											
BIOSTRATIGRAPHIC COEFFICIENT = 38.5											

Table 2.

Comparison chart between the Moroccan plant assemblage and Early Devonian assemblages from other areas. a = GERRIENNE, 1993; b = SCHWEITZER & HEUMANN, 1993; c = SHUTE & EDWARDS, 1989; d = CROFT & LANG, 1942; e = GENSEL & ANDREWS, 1984; f = GENSEL et al., 1991; g = LANG & COOKSON, 1930; h = COOKSON, 1949; i = TIMS & CHAMBERS, 1984; j = DORF & RANKIN, 1962; k = ANDREWS et al., 1977; l = LI & CAI, 1977; m = LI & CAI, 1978.

	East of Jbel ben Aarab	Belgium (a)	Rhineland (b)	Wales (c,d)	Canada (e,f)	Australia (c,g, h, i)	USA (j,k)	S. China (*) (l,m)
Total number of genera	11	23	28	15	17	8	11	9?
<i>Spongiophyton</i>	1	0	0	0	1	0	0	0
<i>Pachytheca</i>	1	1	1	1	1	1	0	0
cf. <i>Sporogonites</i> (**)	1	1	1	1	0	1	1	0
cf. <i>Uskiella/Sartilmania</i> (***)	1	1	1	1	0	1	0	0
<i>Zosterophyll</i>	1	1	1	1	1	1	1	1
<i>Dawsonites</i> (twisted type)	1	1	1	1	1	0	1	1
Short leaved Lycopsid-like	1	1	1	1	1	0	1	1
Total of genera common with the East of Jbel ben Aarab locality	11	6	6	6	5	4	4	3
Percentage of genera common with the East of Jbel ben Aarab locality	100	26	21	40	29	50	36	33?

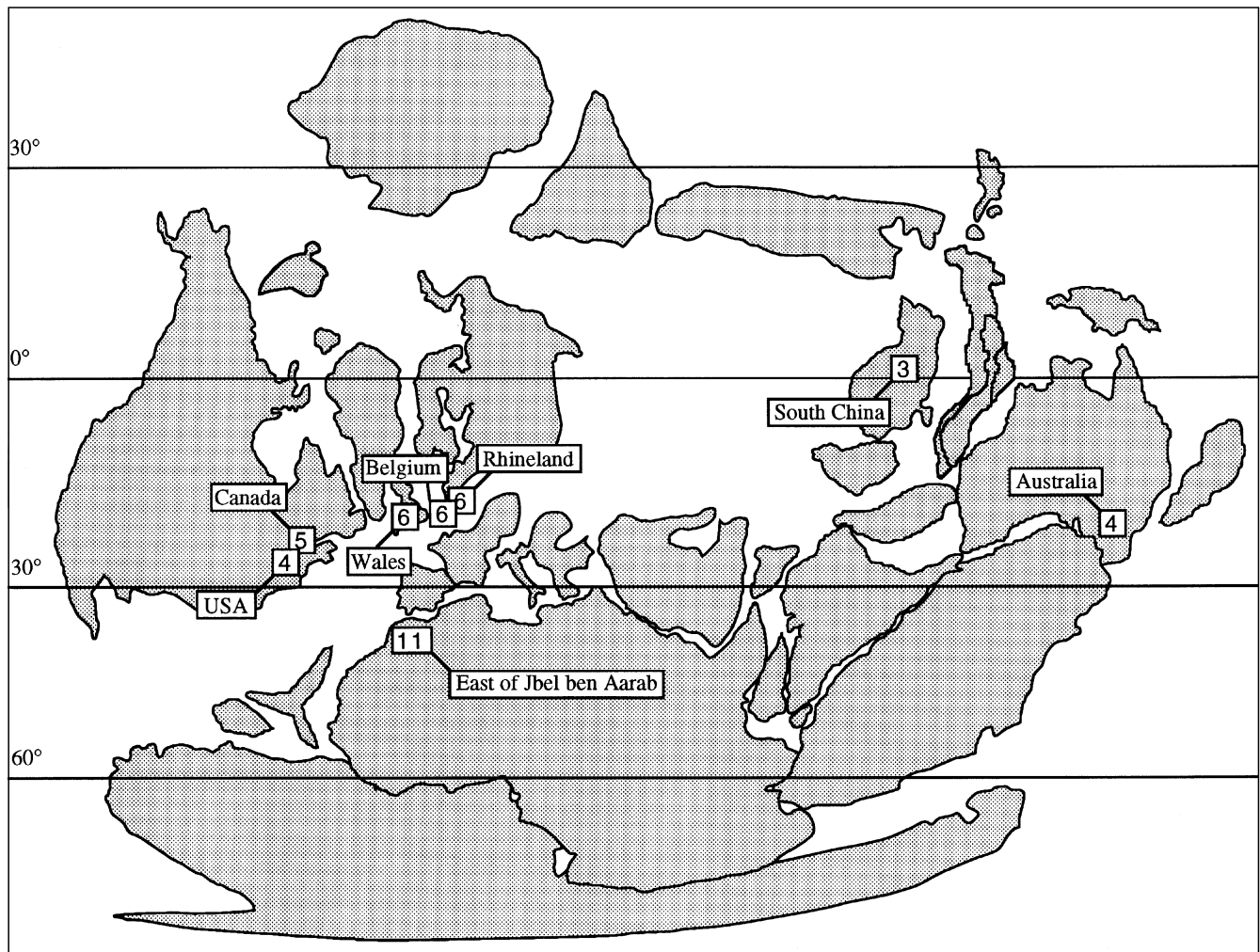
*) We consider CAI & WANG's (1995) identification of *Sporogonites* in S. China as problematical, and have excluded this reference from our analysis.

**) This category includes specimens assigned to the genus *Sporogonites* and specimens which share a similar morphology but lack striations on part of the unbranched sporophyte.

***) cf. *Uskiella/Sartilmania* represents a category of basal eutracheophytes which includes specimens with rounded to spatulate, isovalvate sporangia, borne terminally on axes.

were parts of two different communities, the latter originally growing closer to the site of fossilisation and having withstood shorter transportation.

Early Devonian plants from the new locality were all herbaceous. Unlike the ligneous taxa that evolved in the Middle Devonian, they could not withstand extensive flu-



Text-Fig. 4.

Number of genera common between the East of Jbel Ben Aarab locality and some other Early Devonian plant assemblages. Redrawn from SCOTSE & MCKERROW (1990).

vial and marine transport, and long stays in water before being fossilised. Therefore, we think that the plant communities represented at the new Moroccan locality inhabited emergent lands nearby their site of deposition and that their use in palaeobiogeographic analyses is relevant. This assemblage has been analysed in terms of its generic composition and major morphological traits.

It has been compared with the approximately coeval plant assemblages from Australia, Belgium, Canada, Germany, South China, and Wales (Table 2); only limited comparison is possible since each of the latter is represented by a large number of localities. Although geographically close to Morocco, the Early Devonian localities of Sahara (LEMOIGNE, 1967) and Spain (ALVAREZ-RAMIS, 1981) have been omitted because of the doubtful identification of their remains, due to both their poor state of preservation and insufficient illustration.

When percentages of common taxa are used, the Moroccan assemblage looks more similar to those of Australia, Wales and the USA than to any other ones (Table 2). This treatment, however, is biased towards assemblages with fewer taxa. Therefore, we prefer using raw numbers of common genera. In this case, the total number of taxa shared by the Moroccan assemblage and those from Wales, Belgium and Germany indicates that floral exchanges might preferentially have occurred be-

tween Gondwana and Laurussia (Table 2 and Text-Fig. 4). From a palaeogeographic point of view, these similarities favour the positions of those areas hypothesised by the reconstructions of SCOTSE & MCKERROW (1990) for the Early Devonian.

The present analysis indicates that two new genera characterized by unusual branching patterns occur together with specimens which may represent several new species of genera known elsewhere. We suggest that the two new genera could be interpreted as illustrating the Gondwanan affinities of the locality. The new species may result from speciation processes of the Laurussian components of the plant assemblage, as a possible result of the latitudinal position of Morocco outside the tropical area. Thus, despite its gross resemblance with Wales, Belgium and Germany, the Moroccan plant assemblage might be representative of a separate phytogeographic unit.

Acknowledgements

We would like to thank Drs. Raimund FEIST and John TALENT for their invitation to join the IGCP Project 421. We are indebted to M. BENSaid and M. DAHMANI (Ministère de l'Energie et des Mines, Rabat, Morocco) for the issue of a working permit and the export of samples. Bernard ORTH (UMR 5554, Montpellier) is gratefully acknowledged for his assistance in the field. Publication n° 98–108 of the Institut des Sciences de l'Evolution de Montpellier (UMR 5554).

Plate 1

- Fig. 1: *Spongiophyton* sp.
Gross view of the dichotomising thallus.
AZC 275, $\times 2.4$.
- Fig. 2: *Spongiophyton* sp.
Detail of Pl. 1:1, showing the pseudo-cellular pattern and the unevenly distributed pores.
AZC 275, $\times 12$.
- Fig. 3: Lycopsid-like axis, with emergences inserted in irregular helices.
Note the rounded scars.
AZR 123, $\times 3.2$.
- Fig. 4: Badly preserved specimen of *Pachytheca* sp.
AZR 299, $\times 5$.
- Fig. 5: Zosterophylloids-like strobilus. The sporangia are helically inserted and show a thick dehiscence line.
AZR 134, $\times 3$.
- Fig. 6: cf. *Uskiella* sp./*Sartilmania* sp.
Isolated rounded-spatulate sporangium, photographed under water immersion.
AZE 230, $\times 5$.
- Fig. 7: cf. *Uskiella* sp./*Sartilmania* sp.
The thick distal dehiscence line (?) is visible. Photographed dry.
AZE 230, $\times 5$.
- Fig. 8: *Dawsonites*-type B.
Big oval-elongate sporangia borne by pairs at the end of an isotomous branching system.
AZR 60, $\times 2$.
- Fig. 9: cf. *Sporogonites* sp.
Isolated sporangium borne terminally on an unbranched axis. The sporangium is differentiated into two approximately equal parts.
AZA 281a, $\times 3$.
- Fig. 10: *Dawsonites*-type A.
Pairs of fusiform sporangia borne terminally on isotomous axes. Scar-like structures occur on both sporangial and axial surface.
AZD 201b, $\times 2$.
- Fig. 11: *Dawsonites*-type A.
Pairs of fusiform sporangia of Pl. 1, Fig. 10, enlarged.
AZD 201b, $\times 5$.
- Fig. 12: *Dawsonites*-type A.
Detached pairs of fusiform sporangia. They are twisted around each other in each pair; their surface bears scar-like structures.
AZE 255a, $\times 6$.

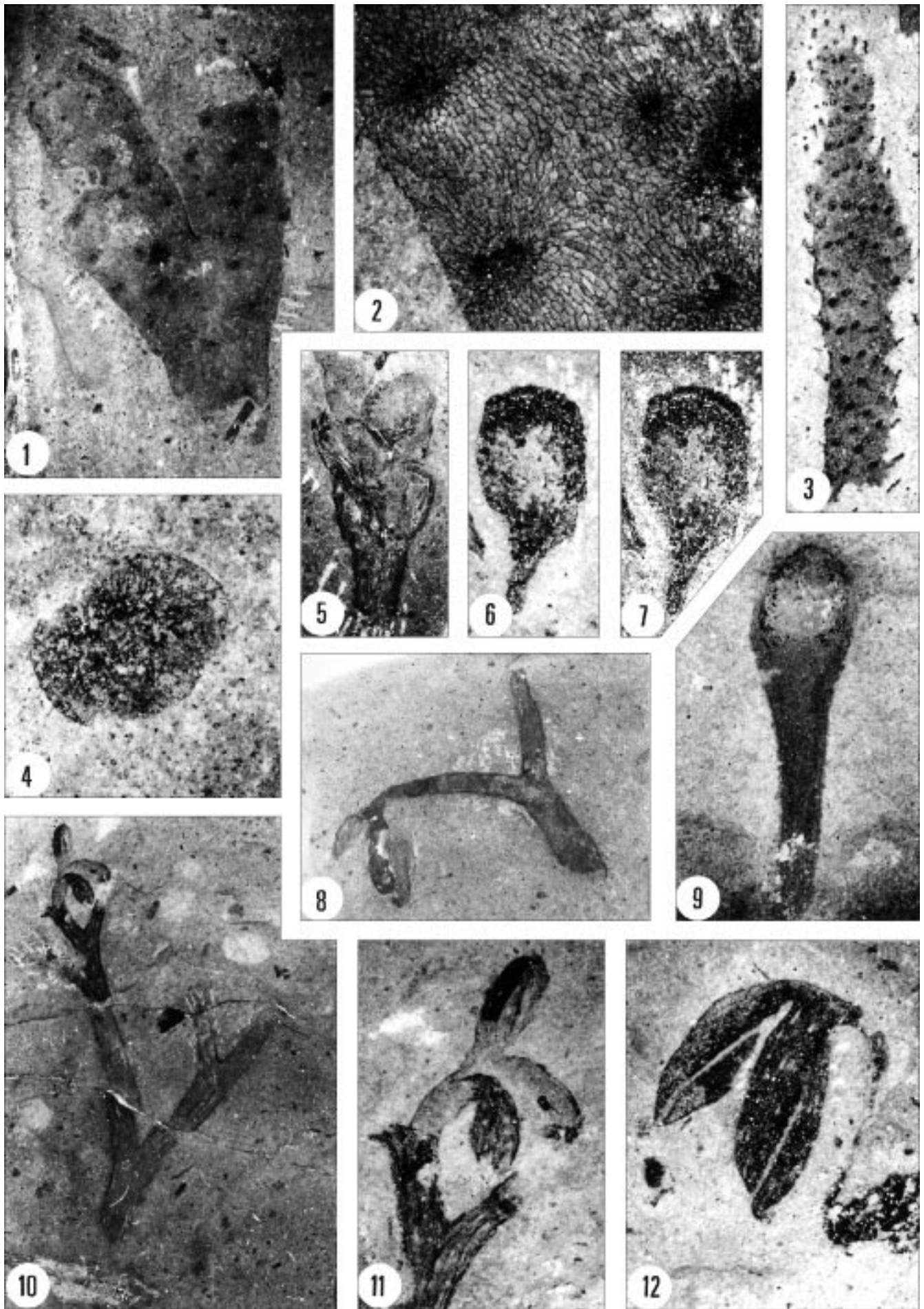
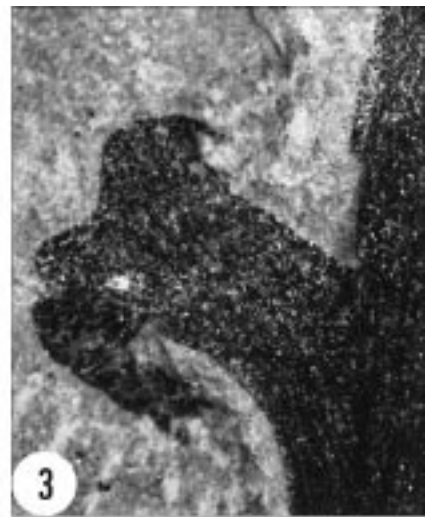
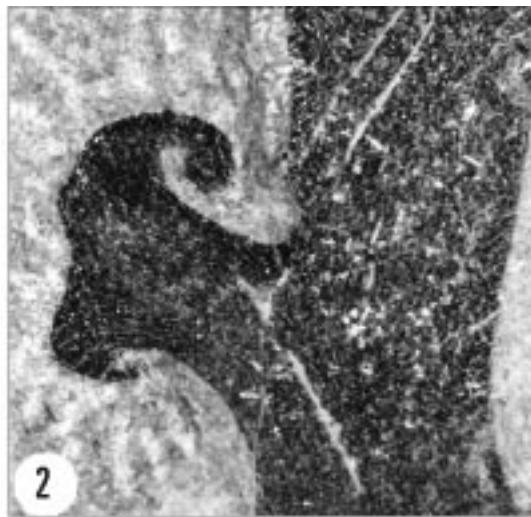


Plate 2

- Fig. 1: Gen. nov. 1.
Axis with lateral branches ending in a globose dichotomous structure.
AZG 240a, $\times 2$.
- Figs. 2,3: Gen. nov. 1.
Enlargement of two lateral dichotomous structures of the axis in Pl. 2, Fig. 1.
AZG 240a, $\times 12$.
- Fig. 4: Gen. nov. 1.
Specimens showing isotomous and anisotomous branching.
AZD 233B, $\times 1.2$.
- Fig. 5: Gen. nov. 1.
Axis with lateral branches ending in a globose dichotomous structure.
AZD 202a, $\times 2$.
- Fig. 6: Gen. nov. 1.
Specimens showing isotomous and anisotomous branching.
AZC 287b, $\times 2$.
- Fig. 7: Gen. nov. 1.
Specimens showing isotomous and anisotomous branching.
AZR 3 (transfer), $\times 2$.
- Figs. 8,9: Gen. nov. 2.
Enlargement of Pl. 2, Fig. 10, showing circinate, abaxially recurved lateral branches, and H-branching.
Small circular scars are visible on the axis.
AZR 10, $\times 5$.
- Fig. 10: Gen. nov. 2.
Profusely branched specimen. The axes bear little scars.
AZR 10, $\times 2$.
- Fig. 11: Incertae sedis 1.
Narrow isotomously branched axis ending in cluster of sporangia.
AZD 204 $\times 3.75$.
- Fig. 12: Incertae sedis 2.
Badly preserved axis with two rows of lateral opposite organs (sporangia?).
AZH 258, $\times 2$.



References

- ALBERTI, G.: Dacryonocaride und homoctenide Tentaculiten des Unter- und Mittel-Devons. – Int. Cour. Forsch. Senck., **158**, 1–228, Frankfurt a.M. 1993.
- ALVAREZ-RAMIS, C.: Devonian plants from Hornachos (Badajoz), Spain. – *Palaeobotanist*, **28–29**, 15–19, Lucknow 1981.
- ANDERSON, J.M. & ANDERSON, H.M.: Palaeoflora of Southern Africa, Prodromous of South African Megafloras, Devonian to Cretaceous. – 277 p., Rotterdam (Balkema) 1985.
- ANDREWS, H.N., KASPER, A.E., FORBES, W.H., GENSEL, P.G. & CHALONER, W.G.: Early Devonian flora of the Trout Valley formation of northern Maine. – *Rev. Palaeobot. Palynol.*, **23**, 255–285, Utrecht 1977.
- BANKS, H.P.: The classification of early land plants – revisited. – *Palaeobotanist*, **41**, 36–50, Lucknow 1992.
- BENSAÏD, M.: L'Ordovicien supérieur, le Silurien et le Dévonien dans l'Est du Maroc Central. – Mines, Géol. & Énergie, **46**, 83–86, Rabat 1979.
- BHARADWAJ, D.C.: On *Sporogonites* Halle: a morphologic, taxonomic and phylogenetic appraisal. – *Palaeobotanist*, **28–29**, 26–35, Lucknow 1981.
- BOUADELLI, M.: Stratigraphie et évolution structurale du Paléozoïque d'Azrou (NE du Maroc central). – Unpublished thesis, 164 p., Strasbourg 1982.
- BOUCEK, B.: The Tentaculites of Bohemia. – Publishing House of the Czechoslovak Academy of Sciences, 215 p., Prague, 1964.
- CHALONER, W.G., MENSAH, M.K. & CRANE, M.D.: Non-vascular land plants from the Devonian of Ghana. – *Palaeontology*, **17**, 925–947, London 1974.
- COOKSON, I.C.: Yeringian (Lower Devonian) plant remains from Llydalyde, Victoria, with notes on a collection from a new locality in the Siluro-Devonian sequences. – *Mem. Nat. Museum*, **16**, 117–130, Melbourne 1949.
- CORSIN, P.: Les algues de l'Eodévonien de Vimy (P. de C.). – *Soc. Sci. Agr. Arts Lille*, **9**, 1–86, Lille 1945.
- CROFT, W.N. & LANG, W.H.: The Lower Devonian Flora of the Senni Beds of Monmouthshire and Breconshire. – *Phil. Trans. Roy. Soc. Lond. (B)*, **231**, 131–163, London 1942.
- DORF, E. & RANKIN, D.W.: Early Devonian plants from the Traveler Mountain area, Maine. – *J. Paleontology*, **36** (5), 999–1004, London 1962.
- EDWARDS, D.: Constraints on Silurian and Early Devonian phyto-geographic analysis based on megafossils. – In: MCKERROW, W.S. & SCOTSE, C.R. (Ed.): *Palaeozoic, palaeogeography and biogeography*, *Geol. Soc. Mem.*, **12**, 233–242, London 1990.
- FAIRON-DEMARET, M.: Les plantes emsiennes du Sart-Tilman (Belgique). II. *Sartilmania jabachensis* (KRÄUSEL & WEYLAND) comb. nov. – *Rev. Palaeobot. Palynol.*, **47**, 225–239, Utrecht 1986.
- FAIRON-DEMARET, M. & REGNAULT, S.: Macroflores dévoniennes dans le Nord du Maroc (Boutonnière d'Imouzzur-du-Kandar, Sud de Fès). Etude paléobotanique – Implications stratigraphiques et paléogéographiques. – *Ann. Soc. Géol. Belg.*, **109**, 499–513, Bruxelles 1986.
- FANNING, U., EDWARDS, D. & RICHARDSON, J.B.: A diverse assemblage of early land plants from the Lower Devonian of the Welsh Borderland. – *Bot. J. Linn. Soc.*, **109**, 161–188, London 1992.
- GARRATT, M.J., TIMS, J.D., RICKARDS, R.B., CHAMBERS, T.C. & DOUGLAS, J.G.: The appearance of *Baragwanathia* (Lycophytina) in the Silurian. – *Bot. J. Linn. Soc.*, **89**, 355–358, London 1984.
- GENSEL, P.G. & ANDREWS, H.N.: Plant life in the Devonian. – 380 p., New-York (Praeger) 1984.
- GENSEL, P.G., CHALONER, W.G. & FORBES, W.H.: *Spongiophyton* from the Late Lower Devonian of New Brunswick and Quebec, Canada. – *Palaeontology*, **34** (1), 149–168, London 1991.
- GERRIENNE, P.: Les *Pachytheca* de La Gileppe et de Nonceveux (Dévonien inférieur de la Belgique). – *Ann. Soc. géol. Belg.*, **113** (2), 267–285, Bruxelles 1990.
- GERRIENNE, P.: Inventaire des végétaux éodévonien de Belgique. – *Ann. Soc. géol. Belg.*, **116** (1), 105–117, Bruxelles 1993.
- GERRIENNE, P.: A biostratigraphic method based on a quantification of fossil tracheophyte characters – its application to the Lower Devonian Posongchong flora (Yunnan Province, China). – *Palaeobotanist*, **45**, 194–200, Lucknow 1996.
- GERRIENNE, P. & STREEL, M.: A biostratigraphic method based on a quantification of the characters of Devonian tracheophytes. – *Paleobiology*, **20**, 208–214, Washington 1994.
- HALLE, T.G.: Lower Devonian Plants from Rörågen, in Norway. – *Kungl. Sv. Vetensk. Handl.*, **57** (1), 1–46, Stockholm 1916.
- HALLE, T.G.: Note on the Devonian genus *Sporogonites*. – *Sv. Bot. Tidst.*, **30**, 613–623, Stockholm 1936.
- HUEBER, F.M.: A new species of *Baragwanathia* from the Sextant Formation (Emsian), northern Ontario, Canada. – *Bot. J. Linn. Soc.*, **86**, 57–79, London 1983.
- KENRICK, P. & CRANE, P.R.: The Origin and Early Diversification of Land Plants. A Cladistic Study. – 441 p., Washington and London (Smithsonian Institution Press) 1997.
- KIDSTON, R. & LANG, W.H.: Notes on fossil plants from the old red Sandstone of Scotland. II. *Nematophyton fortarensense* KIDSTON sp. III. On two species of *Pachytheca* (*P. media* and *P. fasciculata*) based on the characters of the algal filaments. – *Trans. Roy. Soc. Edinburgh*, **53**, 603–614, 1924.
- KLITSCH, E., LEJAL-NICOL, A. & MASSA, D.: Le Siluro-Dévonien à Psilophytes et Lycophytes du Bassin de Mourzouk (Libye). – *Comptes Rendus de l'Académie des Sciences, D*, **277**, 2465–2467, Paris 1973.
- KRÄUSEL, R.: *Spongiophyton* nov. gen. (Thallophyta) und *Haplostigma* SEWARD (Pteridophyta) im Unter-Devon von Paraná. – In: *Paleontologia do Paraná. Vol. Comemorativo do 1 Centenario de Estado do Paraná, Curitiba, Publicado pela Comissao de Comemoracoes do Centenario do Paraná, 195–210, Brasilia 1954.*
- KRÄUSEL, R.: *Spongiophyton* nov. gen. (Thallophyta) e *Haplostigma* SEWARD (Pteridophyta) no Devoniano Inferior do Paraná. – *Serviço Grafico do Instituto Brasileiro Geografia e Estatística, Monografia XV*, 1–41, Brasilia 1960.
- LANG, W.H.: A specimen of *Sporogonites* from the “Grès de Wépion” (Lower Devonian, Belgium). – *Bull. Mus. roy. Hist. Nat. Belg.*, **13** (29), 1–7, Bruxelles 1937.
- LANG, W.H. & COOKSON, I.C.: On a flora, including vascular land plants, associated with *Monograptus*, in rocks of Silurian age, from Victoria, Australia. – *Phil. Trans. Roy. Soc. Lond.*, **224**, 421–449, London 1930.
- LANNINGER, E.P.: Sporen-Gesellschaften aus dem Ems der SW-Eifel (Rheinisches Schiefergebirge). – *Palaeontographica B*, **122**, 95–170, Stuttgart 1968.
- LARDEUX, H.: Les Tentaculites d'Europe occidentale et d'Afrique du Nord. – *Cah. Paléont. CNRS*, 238 p., Paris 1969.
- LECLERCQ, S.: Refendage d'une roche fossilifère et dégagement de ses fossiles sous binoculaire. – *Senckenbergiana Letheae*, **41**, 483–487, Frankfurt a.M. 1960.
- LEJAL-NICOL, A. & MASSA, D.: Sur des végétaux du Dévonien inférieur de Libye. – *Rev. Palaeobot. Palynol.*, **29**, 221–239, Utrecht 1980.
- LEMOIGNE, Y.: Reconnaissance paléobotanique dans le Sahara occidental (Région de Tindouf et Gara-Djebilet). – *Ann. Soc. Géol. Nord*, **87** (1), 31–38, Lille 1967.
- LI, X. & CAI, C.Y.: Early Devonian *Zosterophyllum* remains from southwest China. – *Acta Palaeont. Sin.*, **16**, 12–36, Beijing 1977.
- LI, X. & CAI, C.Y.: A type section of Lower Devonian strata in southwest China with brief notes on the succession and correlation of its plant assemblages. – *Acta Geologica Sinica*, **1**, 12–34 (In Chinese), Beijing 1978.
- LOBOZIAK, S. & STREEL, M.: Late Lower and Middle Devonian miospores from Saudi Arabia. – *Rev. Palaeobot. Palynol.*, **89**, 105–113, Utrecht 1995.

- MCGREGOR, D.C.: Lower and Middle Devonian spores of Eastern Gaspé, Canada. – *Palaeontographica Abt. B.*, **142**, 1–77, Stuttgart 1973.
- MORIN P. et al.: Carte géologique du Maroc au 1/100 000: El Hajej. – Notes & M. Serv. Géol. Maroc, **160**, Rabat 1975.
- OWENS, B.: Miospores from the Middle and Early Upper Devonian rocks of the western Queen Elisabeth Island, Arctic Archipelago. – *Geol. Survey Can.*, **70** (38), 1–157, Montreal 1971.
- PLUSQUELLEC, Y., BOUMENDJEL, K., MORZADEC, P. & PARIS, F.: Les faunes dévoniennes d'Ougarta dans la paléogéographie des régions maghrébo-européennes. – *Ann. Soc. Géol. Nord*, **5** (2ème sér.), 123–128, Paris 1997.
- RAYMOND, A.: Paleogeographic Distribution of Early Devonian Plant Traits. – *Palaios*, **2**, 113–132, 1987.
- RAYMOND, A., PARKER, W.C. & BARETT, S.F.: Early Devonian phyto-geography. – In: TIFFNEY, B.H. (Ed.), *Geological factors and the evolution of plants*, 129–167, New Haven (Yale University Press) 1985.
- RICHARDSON, J.B. & MCGREGOR, D.C.: Silurian and Devonian spore zones of the Old Red Sandstone continent and adjacent regions. – *Geol. Survey Can., Bull.*, **364**, 1–79, Montreal 1986.
- SCHWEITZER, H.-J. & HEUMANN, G.: Die Unterdevon-Flora von Røragen in Norwegen. – *Palaeontographica B*, **229** (1–3), 1–52, Stuttgart 1993.
- SCOTese, C.R. & MCKERROW, W.S.: Revised World maps and introduction. – In: SCOTese, C.R. & MCKERROW, W.S. (Ed.), *Palaeozoic Palaeogeography and Biogeography*, *Geol. Soc. Mem.*, **12**, 1–21, London 1990.
- SHUTE, C.H. & CLEAL, C.J.: Palaeobotany in museums. – *Geol. Curator*, **4**, 553–559, London 1987.
- SHUTE, C.H. & EDWARDS, D.: A new rhyniopsid with novel sporangium organization from the lower Devonian of south Wales. – *Bot. J. Linn. Soc.*, **100**, 111–137, London 1989.
- STEEMANS, P.: Palynostratigraphie de l'Eodévonien dans l'ouest de l'Europe. – *Mém. pour servir à l'Explication Cartes Géol. & Minières Belg.*, **27**, 1–453, Bruxelles 1989.
- STEEMANS, P.: Silurian and Lower Emsian spores in Saudi Arabia. – *Rev. Palaeobot. Palynol.*, **89**, 91–104, Utrecht 1995.
- STEIN, W.E., HARMON, G.D. & HUEBER, F.M.: *Spongiophyton* from the Lower Devonian of North America reinterpreted as a lichen. – *Int. Workshop Biol. Evol. Implic. Early Devonian Plants*, Münster September 14–17, 1994, Abstract Volume, **19**, Münster 1994.
- STOCKMANS, F.: Végétaux éodévonien de la Belgique. – *Mém. Mus. roy. Hist. Nat. Belg.*, **93**, 1–90, Bruxelles 1940.
- STREEL, M., FAIRON-DEMARET, M., GERRIENNE, P., LOBOZIAK, S. & STEEMANS, P.: Lower and Middle Devonian miospore-based stratigraphy in Lybia and its relation to the megaflores and faunas. – *Rev. Palaeobot. Palynol.*, **66**, 229–242, Utrecht 1990.
- STREEL, M., HIGGS, K., LOBOZIAK, S., RIEGEL, W. & STEEMANS, P.: Spore stratigraphy and correlation with faunas and floras in the type marine Devonian of the Ardenno-Rhenish regions. – *Rev. Palaeobot. Palynol.*, **50**, 211–229, Utrecht 1987.
- STREEL, M., LOBOZIAK, L., STEEMANS, P. & BULTYNCK, P.: Devonian miospore stratigraphy and correlation with the global stratotype sections and points. – *Cour. Forsch. Senck.*, Frankfurt (in press).
- TERMIER, H. & TERMIER, G.: La flore eifélienne de Dechra Ait Abdallah (Maroc Central). – *Bull. Soc. Géol. France*, **20**, 197–224, Paris 1950.
- TIMS, J.D. & CHAMBERS, T.C.: Rhyniophytina and Trimerophytina from the early land floras of Victoria, Australia. – *Palaeontology*, **27**, 265–279, London 1984.
- VAN DER VOO, R.: *Paleomagnetism of the Atlantic, Tethys and Iapetus Oceans*. – 411 p., Cambridge (Cambridge University Press) 1993.

Manuskript bei der Schriftleitung eingelangt am 2. Oktober 1998

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Abhandlungen der Geologischen Bundesanstalt in Wien](#)

Jahr/Year: 1999

Band/Volume: [54](#)

Autor(en)/Author(s): Gerrienne Philippe, Fairon-Demaret Muriel, Galtier Jean, Lardeux Hubert, Meyer-Berthaud Brigitte, Regnault Serge, Steemans Philippe

Artikel/Article: [Plants Associated with Tentaculites in a New Early Devonian Locality from Morocco 323-335](#)