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The early land plants from the Armorican Massif: sedimentological and palynological considerations on age and environment

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Abstract – The Châteaupanne Unit belongs to the South Armorican domain of the Armorican Massif (France), which is part of the Variscan belt. This unit includes two Lower Devonian plant levels and one of them corresponds to the Basal Member of the Chalonnes Formation. A sedimentological and palaeontological analysis of these fossiliferous deposits from the Châteaupanne quarry (Montjean/Loire, Maine et Loire, France) is presented here for the first time. The age determination based on palynology indicates that the locality records the earliest occurrence of plant megafossils in the Armorican Massif. Their presence suggests an emergence event that has never been described before. Our study highlights the promising potential of the Basal Member of the Chalonnes Formation to aid in understanding these occurrences, and provides new insights into the history of the Variscan belt.

Keywords: early land plants, Lower Devonian, spores, acritarchs, emergence event, unconformity, storm.

1. Introduction

Evidence from cryptospores and cuticule-like fragments indicates that embryophytes had evolved by Darriwilian times (Middle Ordovician; Strother, Al-Hajri & Traverse, 1996). According to Steemans *et al.* (2009), the origin of vascular land plants, indicated by the occurrence of hilate/trilete spores, dates back to the Katian, more than 20 million years after the colonization of the land by bryophyte-like plants. However, vascular plant megafossils appear later in the fossil record: the earliest fertile axial land plant fossil is reported from the Homerian (Middle Silurian; Edwards & Feehan, 1980). The Lower Devonian plant-bearing deposits record some of the most striking changes occurring in the evolution of plants; by Emsian times, most major plant lineages were probably already established (Steemans *et al.* 2010). The occurrence of deposits of this age is therefore of great importance for our knowledge of early land plants.

A few plant-bearing deposits have been reported from Devonian sequences of the Armorican Massif, but they have not yet been studied in detail. The Armorican Massif is a small part of the Variscan belt that extends throughout western and central Europe (Ballèvre *et al.* 2009). It includes four domains, namely the Léon domain and the North, Central and South Armorican domains (Ballèvre *et al.* 2009). The South Armorican domain comprises the sedimentary series of the Chalonnes area. This series shows plant-bearing deposits within two distinct stratigraphic levels that are located below and above marine limestones (Le Maître, 1934). Plants occurring in these deposits are evidence of the proximity of land and, in addition to their palaeobotanical interest, they provide valuable information for palaeogeographic reconstruction. The upper plant level, the Sainte-Anne Formation, was first reported by Bureau *et al.* (1908). It has been recently reinvestigated and has been given an Emsian age (Ducassou *et al.* 2009; Ballèvre *et al.* 2010). The lower plant level was observed for the first time in 1969 by one of us (H.L.). It is mainly characterized by a rich and promising plant fragment content and by spherical quartz grains attributed to an aeolian sedimentation (Cavet *et al.* 1970; Cavet, Lardeux & Phillipot, 1971; M. Dubreuil, unpub. thesis, Univ. Nantes, 1986). The age of this plant-bearing level is still a matter of

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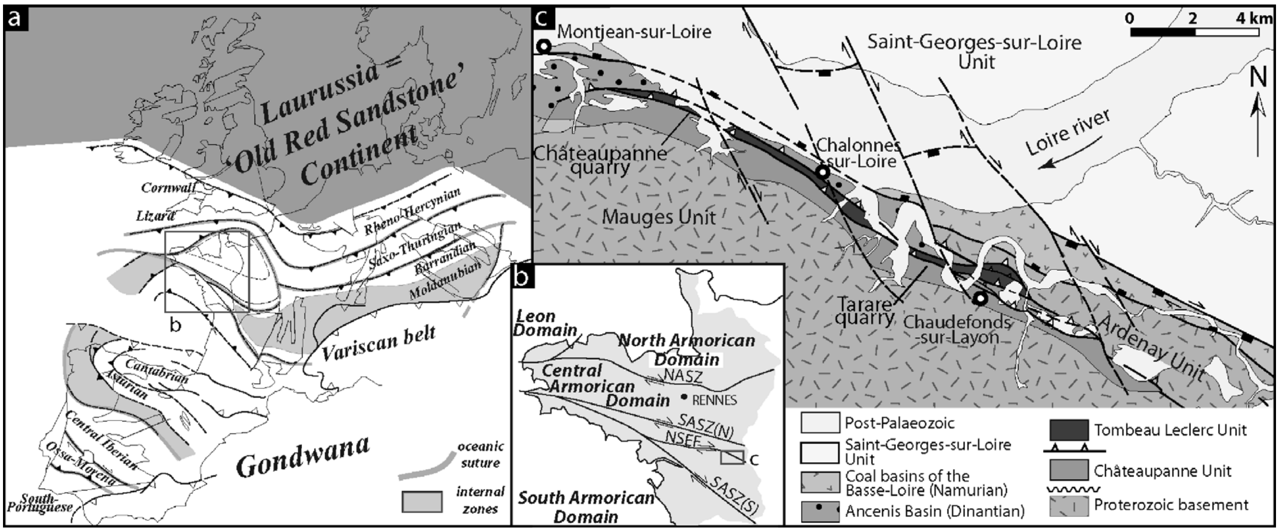

Figure 1. Location (rectangle) of the study area within the European Variscan belt (a) and the Armorican Massif (b). NASZ – North Armorican Shear Zone; SASZ(N) and SASZ(S) – South Armorican Shear Zone, northern branch and southern branch, respectively; NSEF – Nort-sur-Erdre Fault. (c) Structural map of the studied area. A colour version of this figure is available at http://journals.cambridge.org/geo.

debate. On the basis of the stratigraphic succession, Cavet *et al.* (1970) and Cavet, Lardeux & Phillipot (1971) suggested an age ranging from Silurian to Early Devonian. On miospore evidence, McGregor (unpub. report no. F1-15-1980-DCM, 1980) tentatively derived a late Pragian (Lower Devonian)–Eifelian (Middle Devonian) age.

Here we provide a sedimentological and palaeontological analysis of the lower plant-bearing level. The main aims of the study are: (1) to confirm the age of the deposits, (2) to characterize the depositional environment, and (3) to report and briefly describe the flora still under investigation. The plant megafossils from these deposits are placed in a chronological overview of the Devonian flora of the Armorican Massif.

2. Geological setting

The Armorican Massif is a small part of a Late Palaeozoic mountain belt, the Variscan belt, that resulted from the convergence of Laurussia and Gondwana (Fig. 1a). It is divided by late Carboniferous transcurrent shear zones into four domains: the Léon domain, and the North, Central and South Armorican domains (Fig. 1b). The South Armorican Domain is located south of the South Armorican Shear Zone. This major fault is divided in two branches (SASZ(N) and SASZ(S) in Fig. 1b). Between these two branches, the Nort-sur-Erdre Fault (NSEF in Fig. 1b) separates the northern Lanvaux Domain from the southern Mauges Domain (Ballèvre *et al.* 2009). In the latter, the Mauges Unit comprises deformed Proterozoic sediments unconformably covered by Cambrian sediments on its southern part (Cavet, Gruet & Pillet, 1966; Thiéblemont *et al.* 2001) and by Ordovician to Devonian sediments on its northern part. These northern Palaeozoic sediments are structured in two main units separated by a southward thrust (Figs 1b, 2) (Ducassou *et al.* 2009):

(1) The southern unit, the Châteaupanne Unit (Fig. 2) (Cavet, Lardeux & Phillipot, 1971), consists of Ordovician marine sediments (Moulin de Châteaupanne Sandstone and Fresne Siltstone) unconformably overlain by the Emsian Chalonnes Formation. This Formation, predominantly composed of massive limestone (Le Maître, 1934), shows at its base terrigeneous layers with occurrences of plant fragments (= Basal Member of the Chalonnes Formation). Conformably overlying the limestone is the Sainte-Anne Formation of Emsian age.

(2) The northern unit, the Tombeau Leclerc Unit (Fig. 2), consists of an inverted Hirnantian (Upper Ordovician) to Emsian condensed sequence (Ducassou *et al.* 2009).

3. Materials and methods

The rock samples were collected from the plant-bearing deposits that crop out at seven places (to date) in the Châteaupanne quarry (Montjean/Loire, Maine et Loire, France); their locations are given in Figure 3. Plant macrofossils described here were collected from localities 11, 12 and 13; samples for palynological study were collected from localities 11, 13 and 14.

The plant specimens and the sections were observed using a Zeiss photomacroscope with a polarized light source. Approximately 1.5 mm thick sections were prepared through each pyritized axis embedded in resin. These sections were mounted on glass slides with epoxy resin and ground to a thickness sufficient for examination under the photomacroscope. The method described by Kenrick (1999) was used for etching the sections before examination.

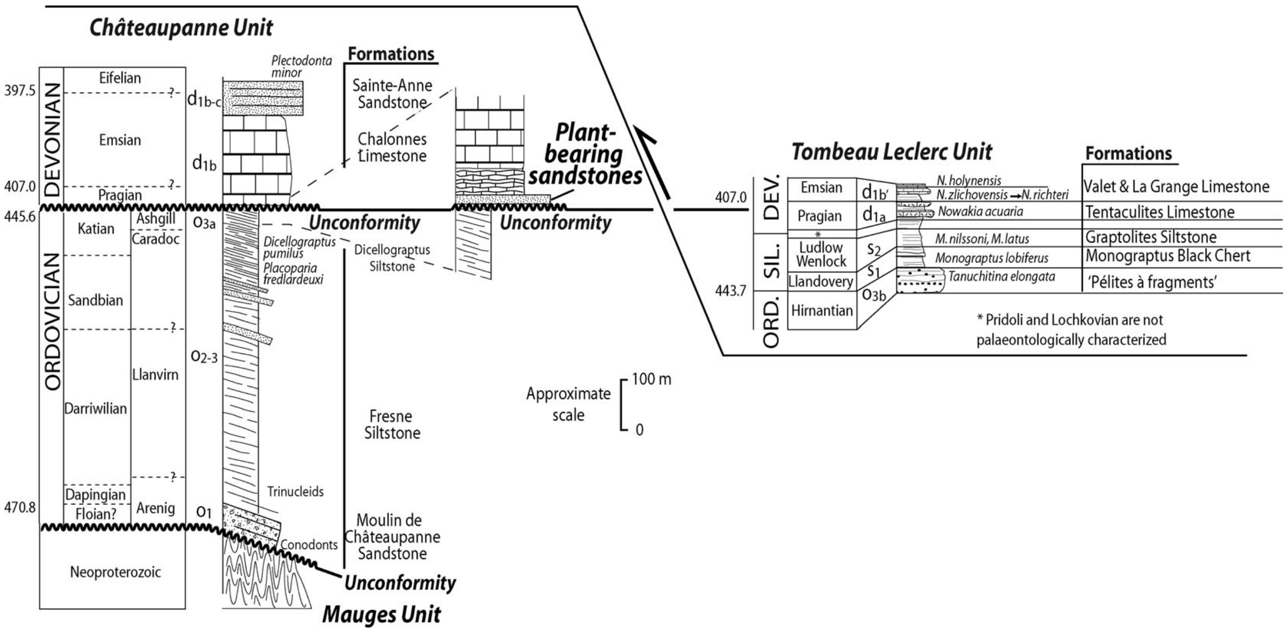

Figure 2. Lithostratigraphic columns of the Châteaupanne and Tombeau Leclerc units. A colour version of this figure is available at http://journals.cambridge.org/geo.

Five samples were processed for palynological study in the Paléobotanique, Palynologie et Micropaléontologie Unit at the University of Liège. They were prepared using standard palynological acid maceration techniques. The organic matter required oxidation in Schultz's solution during two hours. Slides of the samples were examined using standard light microscope analysis. England-Finder coordinates were used to locate the specimens on the palynological slides.

Specimens and palynological slides are housed respectively in the Laboratoire Mycorhizes of the University of Angers (France) and in the Paléobotanique, Palynologie et Micropaléontologie unit of the University of Liège (Belgium).

4. Results

4.a. Sedimentology and petrography of the sandstones

The basal unit of the Chalonnes Formation is rarely visible because of the poor outcrop, but it is well displayed along the southern working-face of the Châteaupanne quarry (Montjean-sur-Loire) (Fig. 1c). It is also present in the Tarare quarry (Blaise *et al.* 1986) (Fig. 1c) at the bottom of the Chalonnes Formation, but the contact with the underlying Fresne Formation has not been observed.

4.a.1. Facies description

The Basal Member of the Chalonnes Limestone is located just above the unconformity. This level is generally made up of a single sandy bed, 10 to 20 cm thick (Fig. 3), but it can be absent. Locally (e.g. 14 in Fig. 3), it reaches more than 1 m and is then composed of fine- to coarse-grained sandy layers interbedded with bluish shale. In the sandy beds hummocky cross-stratification (HCS) and swaley cross-stratification (SCS) are visible (Fig. 4a). These bedforms are characterized by gently curved and often erosional bases, and by laminae that are nearly parallel to the lower bounding surface; the latter thicken or get thinner laterally. The HCS shows a high rate of amalgamation (Fig. 4a) that records a low rate of preservation. Very coarse-grained sandy beds or lenses with pebbles and shaly clasts are present just above the unconformity and sometimes interbedded in the sandstone. The plant fragments are contained in the shale intercalations. The thickness of these micaceous shaly layers is generally less than 1 cm but can locally reach 20 cm. Bioturbation is rarely present.

4.a.2. Mineralogical analysis

Petrological and morphoscopic studies have been performed on samples from Châteaupanne quarry (samples C2, C8 and C9; Fig. 3). The sandstone consists of well-rounded detrital quartz (> 95 %), mainly monocrystallline, with some rare argillite fragments (Fig. 4b). Dark and light laminae are defined by the relative abundance of argillite fragments (Fig. 4b). The grain size ranges between 100 and 200 μm in fine-grained laminae, and between 300 and 500 μm in coarse-grained laminae. Some coarser grains (up to 2 mm) are found dispersed in the sandstone (Fig. 4b). Grains are predominantly well-rounded to sub-rounded with a matte surface (more than 75 %) (Fig. 4c). They are sometimes broken (less than 10 %), and angular or subangular grains occur (less than 25 %).

4.b. Palynological analyses

The palynomorph assemblages contain much phytodebris (e.g. well-preserved tracheids), abundant

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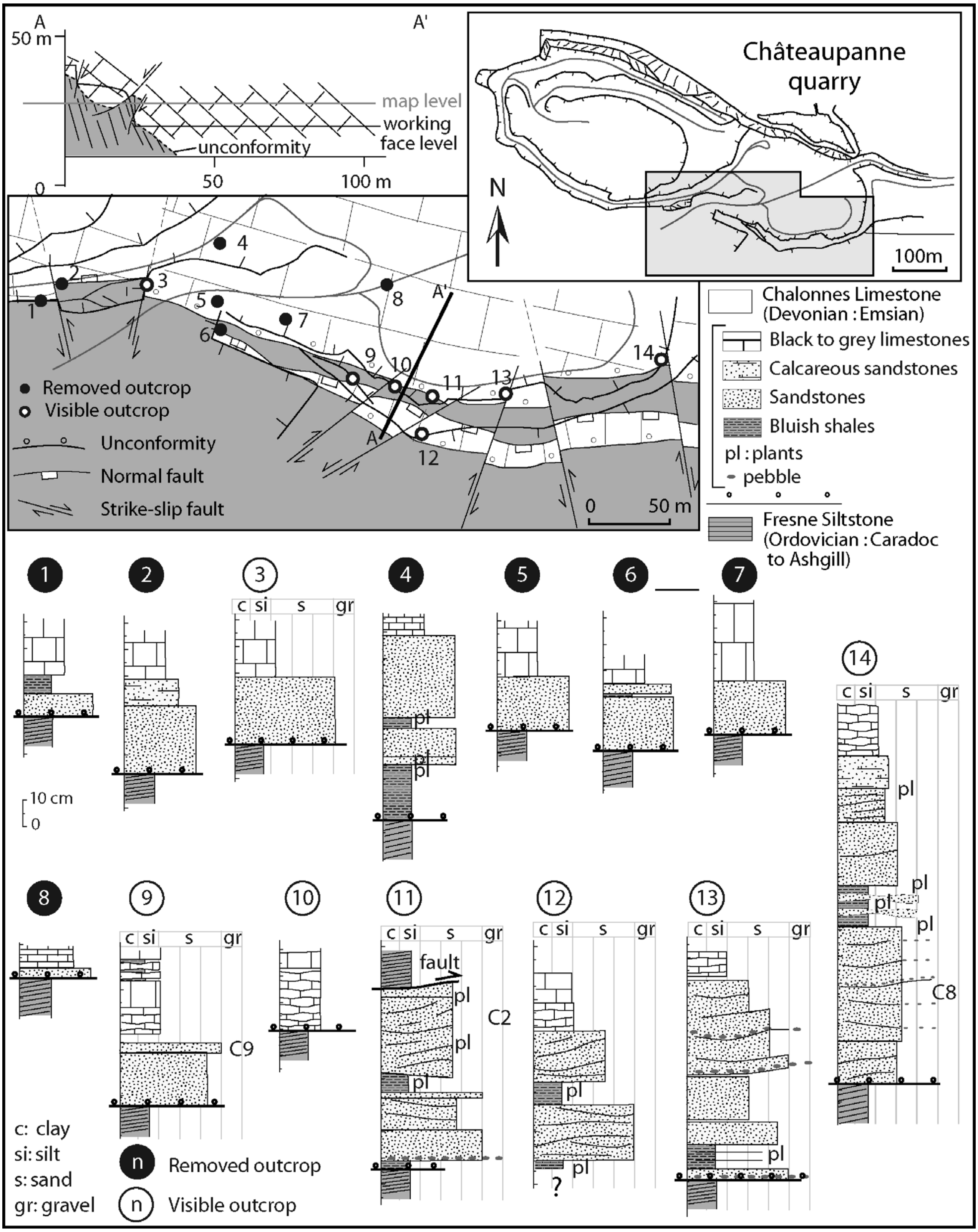

Figure 3. Schematic map of the southern working face of the Châteaupanne quarry (location shown on Fig. 1b), established at a nearly 30 m level as schematized on the cross-section A–A′. The position of the logs detailed below is reported on the map. Positions of samples C2, C8, C9 are shown on the logs. For the removed outcrops, the granulometry reported on the logs is only schematic. A colour version of this figure is available at http://journals.cambridge.org/geo.

terrestrial plant spores and relatively few marine elements. The latter include acritarchs and prasinophycean phycomata, but no chitinozoans or scolecodonts. In all samples, palynomorphs are poorly preserved, with colour ranging from brown to black. Many specimens are not suitable for detailed description. Nevertheless, the information provided by identifiable spores and marine palynomorphs is essential to document the age and

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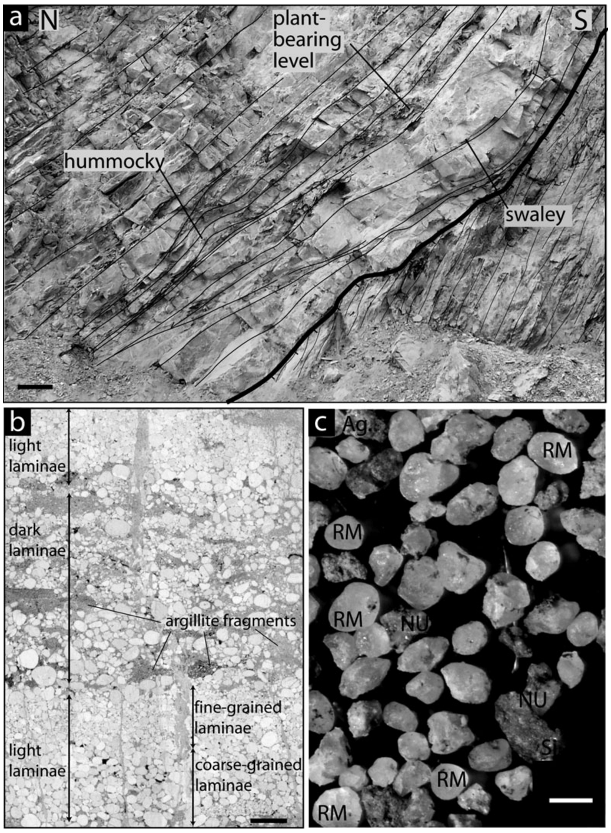

Figure 4. (a) Outcrop of the Basal Member of the Chalonnes Formation that unconformably overlies the Fresne Siltstone showing hummocky cross-stratifcations (log 14 on Fig. 3), scale bar = 20 cm. (b) General view of the sandstone petrography showing well-rounded quartz grains and laminae, PPL (sample C2, Fig. 3); scale bar = 2 mm. (c) Photography of the sand grains under stereomicroscope (fraction > 160 µm, < 500 µm on sample C9, Fig. 3) showing mainly round and matte grains (RM). Some angular grains (NU), aggregates (Ag.) of quartz grains with matrix and argillite or siltite fragments (Si) are also present. Scale bar = 500 µm. A colour version of this figure is available at http://journals.cambridge.org/geo.

the stratigraphic relationships of the local geological units.

4.b.1. Spores

The spore assemblage is of low diversity and exclusively represented by trilete spores (Fig. 5). Spore size varies from 18 to 45 µm. The assemblage is dominated by *Dibolisporites wetteldorfensis* Lanninger, 1968 and *Apiculiretusispora plicata* (Allen) Streel, 1967. The second component of the assemblage comprises *Amicosporites jonkeri* (Riegel) Steemans, 1989, which is relatively abundant, cf. *Amicosporites discus* Wellman & Richardson, 1996 and *Ambitisporites avitus* Hoffmeister, 1959. Other species such as *Emphanisporites rotatus* McGregor, 1961; *E. multicostatus* Rodriguez, 1978; *Synorisporites sp*. and *Archaeozonotriletes chulus* (Cramer) Richardson & Lister, 1969 are represented in the assemblage, together with rare specimens of *Acinosporites sp*. and *Raistrickia* sp. A few specimens are referred with doubt to the genus *Camarozonotriletes* Naumova ex Ishchenko, 1952. One specimen resembles *C. filatoffii* described by Breuer *et al.* (2007), but is too poorly preserved to confirm the determination. Rare specimens of *Apiculiretusispora brandtii* Streel, 1964 and *Dictyotriletes* cf. *kerpii* Wellman, 2006 are also present.

4.b.2. Marine palynomorphs

Marine palynomorphs are dispersed in the material. They are mainly represented by acritarchs and prasinophytes (Fig. 6). Taking account of their known distribution, the assemblage of acritarchs and prasinophycean phycomata appears to be mixed, containing Devonian species and reworked ones. The Devonian assemblage of acritarchs includes the following species: *Winwaloeusia distracta* (Deunff, 1966) Deunff, 1977; *Multiplicisphaeridium raspa* (Cramer) Eisenack, Cramer & Diez, 1973; *Multiplicisphaeridium* cf. *paraguaferum* (Cramer, 1964) Lister, 1970; *Micrhystridium* sp.; ?*Induoglobus* sp.; *Ammonidium* sp.; *Veryhachium* cf. *rosendae* Cramer, 1964; *Evittia* sp. prasinophycean phycomata consist of simple leiospheres and *Cymatiosphaera* spp. Acritarch species such as *Eupoikilofusa platynetrella* Loeblich & Tappan, 1978; *Eupoikilofusa stiatifera* (Cramer, 1964) Cramer, 1970; *Veryhachium subglobosum* Jardiné *et al.* 1974 and *Villosacapsula setosapellicula* (Loeblich, 1970) Loeblich & Tappan, 1976 are reworked from Upper Ordovician sediments, although some species are known to range into the Silurian.

4.c. Plant megafossils

The plant megafossils occurring in these deposits are represented by compression/impression and permineralized specimens (Fig. 7). The compressions have been found at locality 11 (see log 11, Fig. 3). Axes are up to 15 cm long. They divide anisotomously and produce helically arranged lateral branches that divide again up to three times. They bear longitudinal ribbing and punctiform scars. Only vegetative lateral branches have been found in attachment. Some of those plants are close in vegetative morphology to the trimerophyte genera *Pertica, Trimerophyton* and *Psilophyton.* Their gross morphology also resembles the plant described by Gensel (1984) from the Battery Point Formation (Gaspé Bay, Canada).

Short length axes are permineralized by pyrite and occur isolated in the sediment, at locality 13 (see log 13, Fig. 3). Their anatomical structure is relatively well preserved. Two main types of structures have been observed. Fertile organs of two types also occur.

First plant type. Numerous axes that are 1 to 3 mm in diameter have been found. Pairs of fusiform sporangia twisted around each other, characteristic of *Psilophyton* (Gerrienne, 1997), also occur dispersed in the sediment. In transverse section, axes show a massive circular to elliptical xylem strand with an elongate centrarch to mesarch protoxylem area. The

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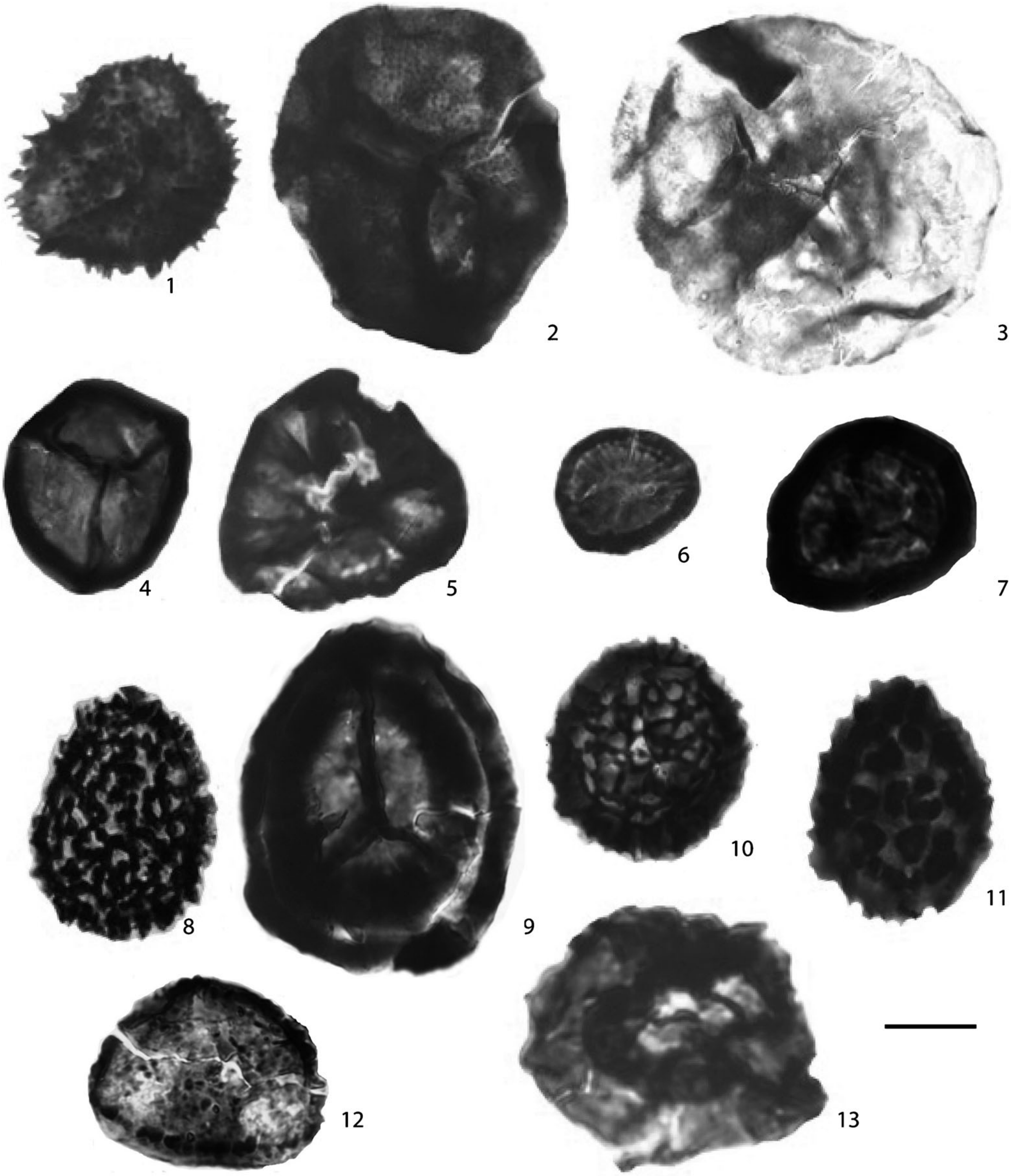

Figure 5. Spores. 1 – *Dibolisporites wetteldorfensis* Lanninger, 1968 (slide no. 64343); 2 – *Apiculiretusispora plicata* (Allen) Streel, 1967 (slide no. 64349); 3 – *A. brandtii* Streel, 1964 (slide no. 64064); 4 – *Ambitisporites avitus* Hoffmeister, 1959 (slide no. 64343); 5 – *Emphanisporites rotatus* Mc Gregor, 1961 (slide no. 64349); 6 – *E. multicostatus* Rodriguez, 1978 (slide no. 64064); 7 – *Archaeozonotriletes chulus* (Cramer) Richardson & Lister, 1969 (slide no. 64065); 8 – *Acinosporites* sp. (slide no. 64065); 9 – *Amicosporites jonkeri* (Riegel) Steemans, 1989 (slide no. 64064); 10 – *Dictyotriletes* cf. *kerpii* Wellman, 2006 (slide no. 64065); 11 – *Raistrickia* sp. (slide no. 64064); 12 – *Synorisporites* sp. (slide no. 64064); 13 – cf. *Amicosporites discus* Wellman & Richardson, 1996 (slide no. 64064). Scale bar = 12 μm. A colour version of this figure is available at http://journals.cambridge.org/geo.

central part of the strand with randomly arranged tracheids is surrounded by a zone of tracheids placed in radial rows. Xylem comprises P-type tracheids with well-preserved scalariform pitting. Those anatomical features are characteristic of the genus *Psilophyton*. To date, it is unknown if these pyritized axes and the axes preserved in compression (see above) belong to the same plant. On the basis of their anatomy and the presence of dispersed paired fusiform sporangia, our permineralized specimens are attributed to *Psilophyton* sp. *Psilophyton* is known from a number of Lower Devonian localities distributed worldwide. The stratigraphic range of the genus is Pragian–lowermost Middle Devonian (Gerrienne, 1997). The genus is of great importance in the evolution of vascular plants, as it is considered the earliest Euphyllophyte, a clade

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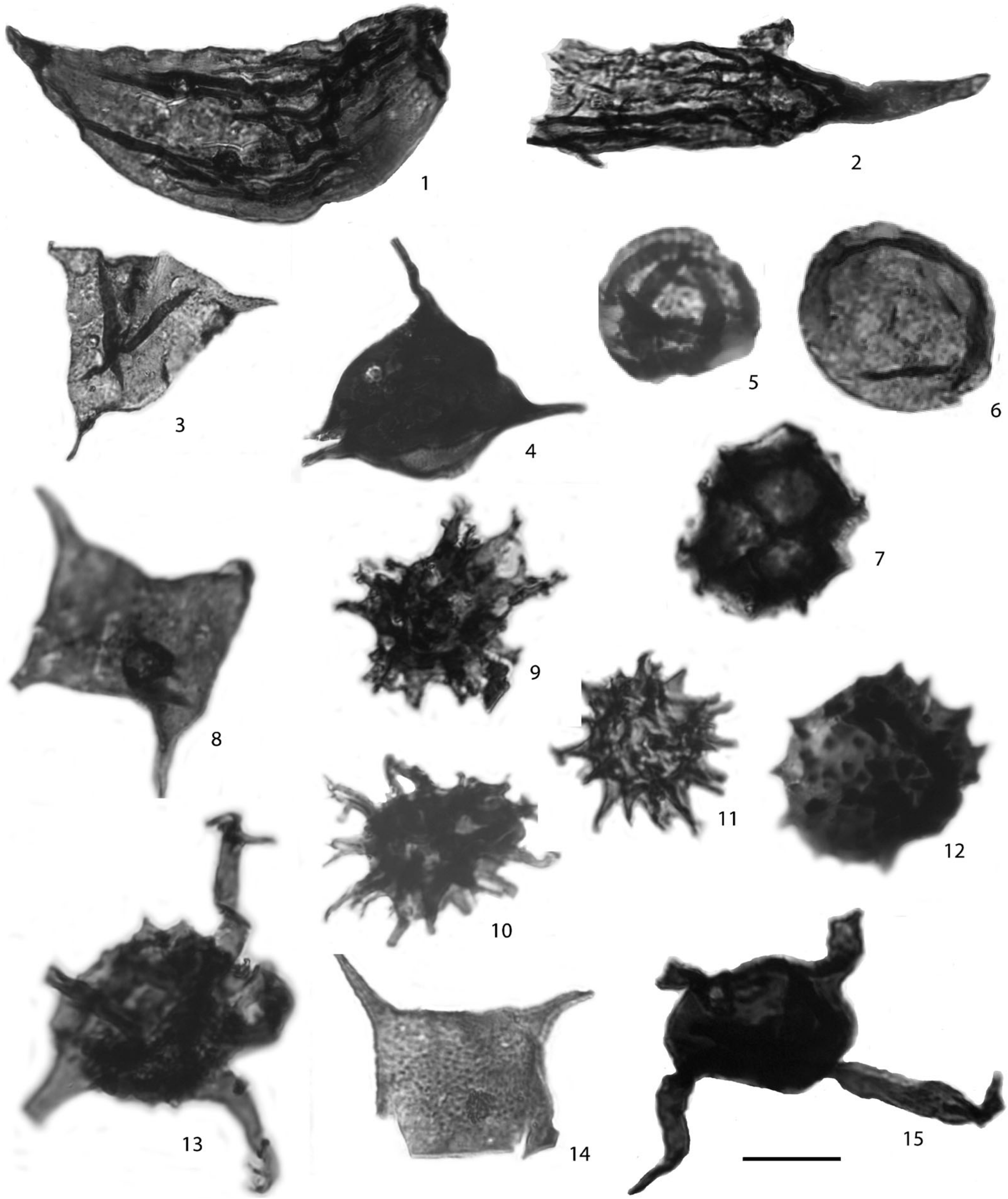

Figure 6. Marine palynomorphs. Reworked acritarchs: 1 – *Eupoikilofusa platynetrella* Loeblich & Tappan, 1978 (slide no. 64064); 2 – *Eupoikilofusa striatifera* (Cramer, 1964) Cramer, 1970 (slide no. 64343); 3 – *Villosacapsula setosapellicula* (Loeblich, 1970) Loeblich & Tappan, 1976 (slide no. 64064); 4 – *Veryhachium subglobosum* Jardiné *et al*. 1974 (slide no. 64064). prasinophycean phycomata: 5, 6 – Leiospheres (slide nos 64348 and 64064); 7 – *Cymatiosphaera* sp. (slide no. 64065). *In situ* (Devonian) acritarchs: 8 – *Winwaloeusia distracta* (Deunff, 1966) Deunff, 1977 (slide no. 64064); 9 – *Multiplicisphaeridium raspa* (Cramer) Eisenack *et al.* 1973 (slide no. 64065); 10 – *Multiplicisphaeridium* cf. *paraguaferum* (Cramer, 1964) Lister, 1970 (slide no. 64348); 11 – *Micrhystridium* sp. (slide no. 64349); 12 – ?*Induoglobus* sp. (slide no. 64348); 13 – *Ammonidium* sp. (slide no. 64343); 14 – *Veryhachium* cf. *rosendae* Cramer, 1964 (slide no. 64065); 15 – *Evittia* sp. (slide no. 64065). For specimens 6, 7, 8, 9, 10, 11, 12, 13, 14, the scale bar = 10 µm: for specimen 3, the scale bar = 15 µm: for specimens 1, 2, 4, 5, 6, 15, the scale bar = 20 µm. A colour version of this figure is available at http://journals.cambridge.org/geo.

that comprises both the Monilophytes (ferns *sensu lato*) and the Lignophytes (seed plants and their free-sporing ancestors).

Second plant type. Rather badly preserved tiny axes display a dissected stele of primary xylem comparable in transverse section either to a *Gothanophyton*-type or

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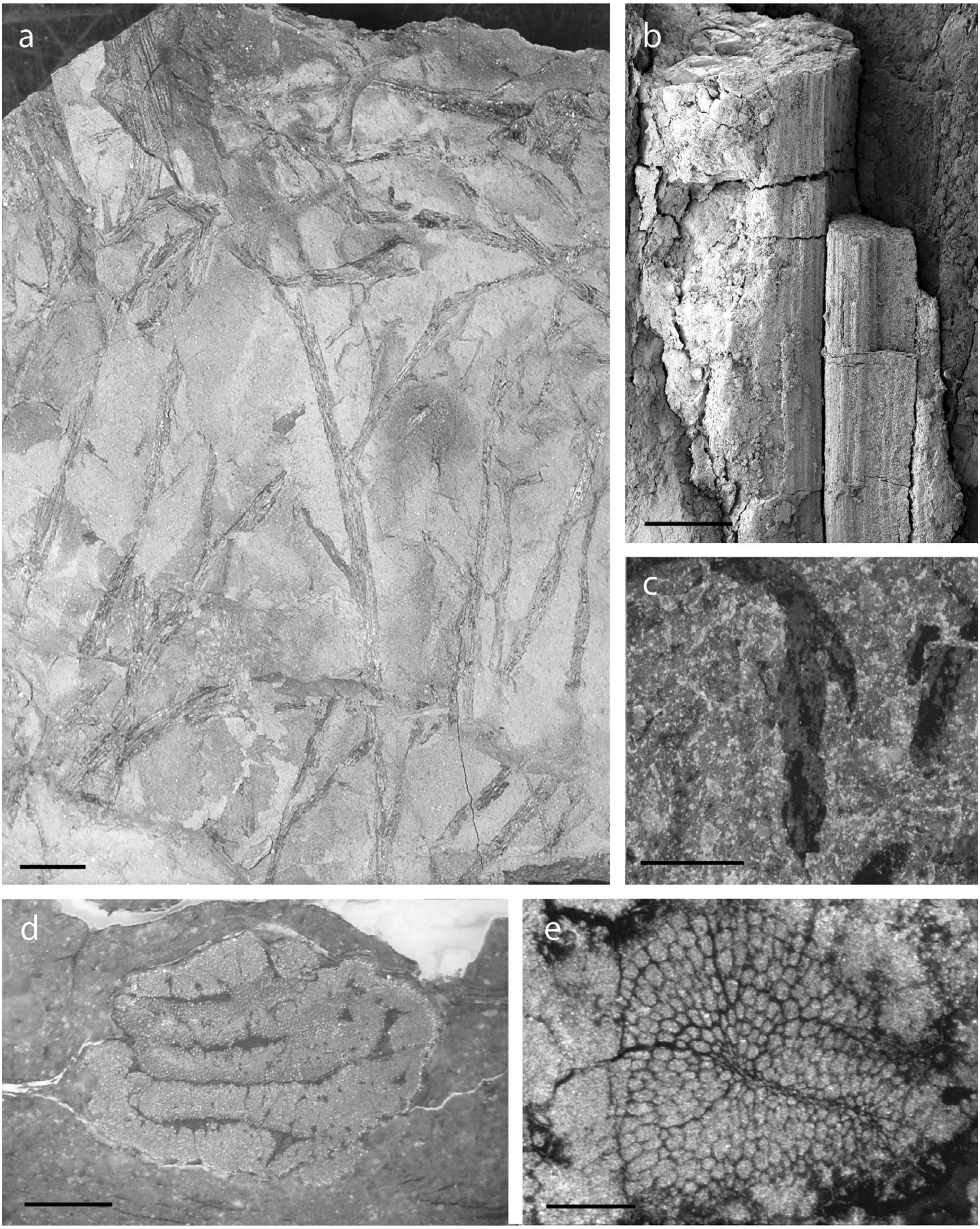

Figure 7. Plant megafossils occurring in the Basal Member of the Chalonnes Formation. (a) Compressions found at locality 11 (see log 11, Fig. 3); scale bar = 5 mm (sample no. CSD-07M-01). (b) Short length axes, permineralized by pyrite, occurring isolated in the sediment at locality 13 (see log 13, Fig. 3); scale bar = 0.5 mm (sample no. CSD-06C-501A). (c) Pair of fusiform sporangia twisted around each other, characteristic of *Psilophyton*; scale bar = 0.5 mm (sample no. CSD-06M-02B). (d) Transverse section of an axis of the first plant type; scale bar = 2 mm (sample no. CSD-06C-C08). (e) Transverse section of an axis of the second plant type; scale bar = 0.4 mm (sample no. CSD-06C-004). A colour version of this figure is available at http://journals.cambridge.org/geo.

to a small compressed cladoxylopsid axis. Reticulate elements with slightly bordered pits similar to those of *Foozia* decribed by Gerrienne (1992) from the Early Devonian of Belgium have been observed in the palynological slides. Additionally, pairs of sporangia similar in size and morphology to those of *Foozia* have been found dispersed in the sediment. *Dibolisporites echinaceus* has been identified in the sporangia of *Foozia* while *Dibolisporites wetteldorfensis* occurs, dispersed in the sediment from the Basal Member of the Chalonnes Formation. This suggests that the plant from Châteaupanne, as *Foozia*, possibly represents an early cladoxylopsid.

5. Discussion

5.a. Age of the deposits

The *in situ* (Devonian) acritarch assemblage is of low diversity, represented by simple long-ranging forms, and is devoid of stratigraphically significant taxa. There are relatively few publications on Early Devonian acritarchs (Le Hérissé, Servais & Wicander, 2000). However, low-diversity phytoplankton assemblages associated with nearshore environment conditions are common in the Pragian–Emsian interval in other localities of northern Gondwana (e.g. North Africa, Spain) and peri-Gondwanan domain (e.g. Armorican Massif, Normandy) (Cramer, 1964; Rauscher, Doubinger & Manche-Bain, 1965; Magloire, 1967; Jardiné, 1972; Moreau-Benoit, 1974; Deunff, 1976; Le Hérissé, 1983).

Reliable age determinations for the samples studied are provided by spore assemblages. *Dibolisporites wetteldorfensis* represents a major component. Based on the presence of this species, the general characteristics of the assemblage (general form and size of the spores) and the absence of spores characteristic of younger intervals, it is considered that the assemblage belongs to the PoW Oppel Zone of Streel *et al.* (1987). This zone ranges from early Pragian to earliest Emsian. Few assemblages belonging to the PoW Oppel Zone are described in the literature (e.g. Steemans, 1989; Wellman *et al.* 1998; Turnau, Milaczewski & Wood, 2005; Wellman, 2006; Hassan Kermandji, Kowalski & Touhami, 2008). A comparison of most of the assemblages reported belonging to this zone has been made by Wellman (2006). The majority of them are from Euramerica and northern Gondwana. Correlations with the Armorican Massif are provided by the work of Le Hérissé (1983), who described spore assemblages from two marine sections, Sablé-sur-Sarthe (Upper part of the Saint-Cénéré Formation) and Saint-Pierre-sur-Erve (Montguyon Formation) in the Central Armorican domain. Three spore assemblages have been recognized and dated from Pragian to Lower Emsian. It appears that the spore assemblage described herein from the Basal Member of the Chalonnes Formation has much in common with the assemblages from Saint Pierre-sur-Erve. *Apiculiretusispora plicata, A. brandtii, Retusotriletes sp., Dibolisporites wetteldorfensis Raistrickia sp., Emphanisporites rotatus* and *Archaeozonotriletes chulus* are common in the two assemblages. The Montguyon Formation has also been studied for palaeontological content and is considered to be Upper Pragian/Lower Emsian (Botquelen, 2003).

5.b. Depositional environment

The basal sandy beds are mainly made up of rounded and smoothed quartz grains, shaped by the wind (Cailleux, 1962). These quartz grains could come from sub-contemporaneous deposits such as beach sands, or from older eroded sedimentary series. Our study partly supports this latter hypothesis. Indeed, the ‘Pélites à fragments’ Formation, of Hirnantian age (Upper Ordovician) (Robardet & Doré, 1988) and belonging to the Armorican Massif, contains rounded-quartz sandstones. This glacio-marine formation is unknown in the Châteaupanne Unit, but is present in the northern Tombeau Leclerc Unit (A. Bourarhouh, unpub. Ph.D. thesis, Univ. Rennes, 2002; Piçarra *et al.* 2002, 2009) (Fig. 2). It is possible that this series has been deposited on the top of the Fresne Formation and then eroded. This erosion occurred before the sedimentation of the Basal Member of the Chalonnes Formation and consequenty enriched this level in aeolian quartz grains. The reworked acritarchs found in our assemblage include some classic Upper Ordovician species, such as *E. platynetrella, V. subglosum* or *V. setosapellicula,* that are recorded in pre-glacial series of the upper Ordovician or are restricted to the Hirnantian deglaciation time (Vecoli & Le Hérissé, 2004). The discovery of these acritarchs in the studied sandstones supports the reworking of the rounded quartz grains from the ‘Pélites à fragments’ Formation.

On the other hand, two points may be added: (1) *E. stiatifera* has been previously found in the Katian (Upper Ordovician) ‘*Dicellograptus* Siltstone’ (upper part of the Fresne Siltstone), located just below the Chalonnes Limestone (Moreau-Benoit, 1974). (2) A large amount of dark shale fragments is present in these sandstones and could come either from sub-contemporaneous mud layers or from the underlying Fresne Formation (Fig. 2). The basal surface of the Basal Member of the Chalonnes Formation represents an unconformity within a stratigraphic gap including uppermost Ordovician, Silurian and Lochkovian (early Lower Devonian) deposits. As a result, this unconformity could be related to a major aerial erosional surface overlain by terrigeneous inputs. These inputs could come both from reworked underlying sediments (from the Fresne and the ‘Pelite à fragments’ Formations) and from contemporaneous aeolian sand and clay chips.

The sediments forming the Basal Member of the Chalonnes Formation are characterized by *in situ* (Devonian) acritarchs and an important input of continental palynomorphs. This palynofacies suggests a nearshore marine environment. The low diversity of the *in situ* (Devonian) acritarch assemblage recovered from these deposits can be related to the local nearshore situation of the deposits, which is in general an unfavourable environmental condition to produce abundant and complex phytoplankton assemblages (see e.g. Strother, 1996). The absence of chitinozoans and scolecodonts could be due to possible mechanical phenomena during sedimentation of organic material,

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Table 1. Survey of the plant-bearing deposits reported from the Devonian formations of the Armorican Massif

Location	Formations	Originally described floristic list	Authors	Reinvestigated floristic list	Authors
Central Armorican Domain					
(1) Rade de Brest	**Shales of Porsguen** Famennian	*Lepidodendron africanum*	Babin & Lejal, 1968		
		Leptophloeum rhombicum, Protolepidodendropsis frickei, P. pulchra, Protolepidodendron sp, *Archaeocalamites* sp., *Pothocites sp., Platyphyllum browniannum, P.* sp, *Tancrea porsguenense, Carpolithes armoricense*	Babin *et al*. 1976; Lejal-Nicol, 1977		
(2) Ménez Bélair Synclinorium	**Bosquen Formation** Emsian	Protolepidodendrales, Psilophytales, sporangia traces (*Sporogonites*) (Y. Lemoigne, pers. comm. to Régnault)	Régnault, 1981	Synaeresis cracks?	Strullu-Derrien, (pers. observation)
	La Rabine Formation Upper Devonian	Nodules with plant fragments	Babin & Paris, 1973		
(3) Laval basin	**First level of the Huisserie Formation** Carboniferous	Reworked *'Psilophyton'* (impression)	Lejal-Nicol *et al.* 1982		
(4) Angers – Saint-Julien-de-Vouvantes	**Sandstones from La Vallée** Famennian	Unidentifed plant remains	Cavet & Lardeux, 1968		
	Arkoses of La Chapelle-Glain Famennian	Fragments that looked like Famennian '*Psilophyton*' from the Ardennes	Barrois, 1889	Indeterminable	Péneau, 1928
South Armorican Domain					
(5) Châteaupanne Unit	**Basal Member of the Chalonnes Formation** Pragian–Early Emsian	Tiny plant remains	Cavet *et al*. 1970	*Psilophyton* sp., Cladoxylale?	Strullu-Derrien *et al.* (this paper)
	Ste-Anne Formation Emsian	*Hostimella* sp., *Asteroxylon elberfeldense, Lepidodendron gaspianum, Psilophyton princeps, P. robustius, P. elegans, P. spinosum, Bornia transitionis.*	Bureau *et al.* 1908, 1910; Bureau 1911, 1913; Carpentier, 1920, 1927	*Hostimella* sp., Lycopsid (genus and species undetermined) Zosterophyllopsid? Cf *Psilophyton*	Ducassou *et al.* 2009
(6) Ancenis Basin	**Ancenis Shales** Upper Devonian (from Bureau)	*Bornia transitionis, Calamodendron tenuistriatum, Pinnularia mollis, Sphenophyllum involutum, Lepidodendron acuminatum, Lepidostrobus* sp., *Cephalotheca mirabilis, Psilophyton princeps, Barrandenia dusliana, Pteridorachis sp., Psilophyton ?glabrum*	Bureau, 1911, 1913, 1914	*Archaeocalamites transitionis, Archaeocalamites, Pinularia mollis, Sphenophyllum involutum, Sublepidodendron robertii, Dawsonites arcuatus*? *Pteridorachis sp.*	Beaupère, 1973 (only the species names are updated)
(7) Vendée (Villedé d'Ardin)	**Fontaine de la Marbrière Formation** Givetian	*Protolepidodendron scharianum/pulchra* (E. Boureau, pers. comm. to Camuzard)	Camuzard *et al.* 1969		

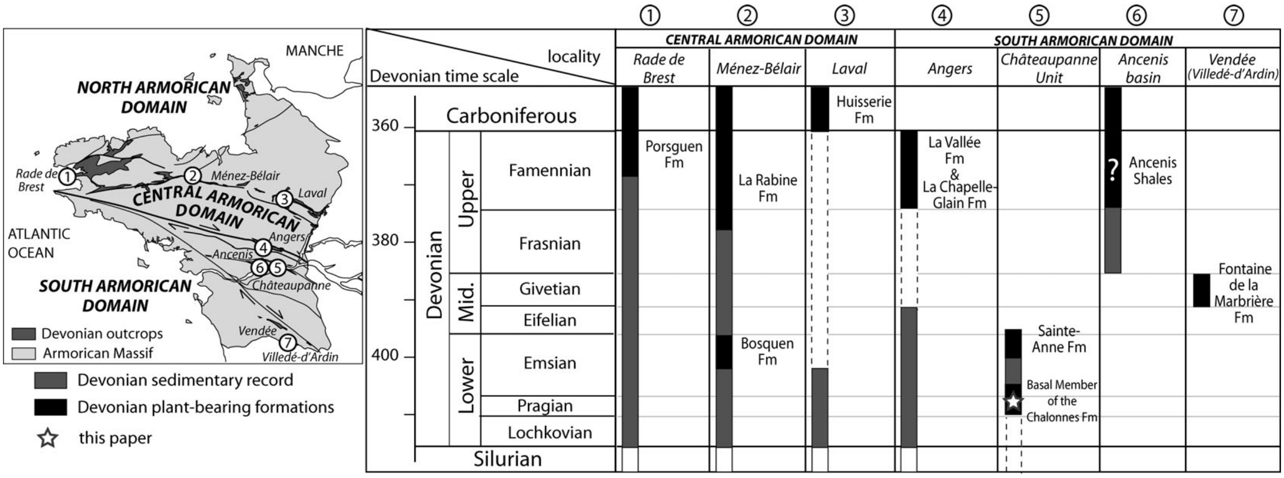

Figure 8. Stratigraphic position and location of the Devonian plant-bearing deposits from the Armorican Massif. Only megafossil plant remains are taken into account. A colour version of this figure is available at http://journals.cambridge.org/geo.

separating forms with good buoyancy, like spores and phytodebris, from the heaviest forms. Despite the important continental supply, the diversity in spore species is very low for such sedimentary facies. This could reflect that sediments contain only local dispersed spores without remote input from rivers. However, these conclusions need to be tempered because of the poor palynomorph preservation which could modify the assemblage content.

Hummocky cross-stratification (HCS) and swaley cross-stratification (SCS) occur in the sandy beds of the Basal Member of the Chalonnes Formation; these structures are related to storm wave action (Leckie & Walker, 1982; Aigner, 1985; Einsele, 1992). According to the depositional models proposed for storm wave-dominated shelves (Dott & Bourgeois, 1982; Aigner, 1985; Guillocheau & Hoffert, 1988), they may be located from the shoreface (SCS–HCS) to the proximal and median parts of the inner shelf (HCS). The scarce bioturbation would imply that storm events were close in time. For the coarse-grained levels, they could be considered as lag deposits related to by-pass episodes or, for the lowermost one, as basal lag. The plant-rich shaly layers could have been deposited during quiet phases, perhaps in a relatively protected area. This suggestion supports the palynological conclusion expressed above.

The palynological and sedimentological data are in agreement with a nearshore depositional environment for the Basal Member of the Chalonnes Formation. This level is interpreted as a transgressive sandbody whose material has been continuously reworked by storm waves during landward migration of the shoreface.

6. The Devonian flora from the Armorican Massif

A survey of the plant-bearing deposits reported from the Devonian formations of the Armorican Massif is presented in Table 1; their stratigraphic position and location are given in Figure 8. Almost all of these remains need to be reinvestigated; some might not even be plants. In the Ancenis Basin, a flora from the Culm (Frasno-Dinantian period s*ensu* Bureau) has been described (Bureau, 1911, 1913; Carpentier, 1920; C. Beaupère, unpub. Thèse Doctorat, Univ. Paris, 1973; Ballèvre & Lardeux, 2005). The strictly Upper Devonian (Famennian) plant-bearing deposits are not well known in this area. To date, most of the plants reported in these articles are known as Carboniferous plants. A reinvestigation of the sedimentology and palaeontology of these deposits is necessary.

The Emsian Sainte-Anne Formation is to date the only unequivocal Devonian flora described from the Armorican Massif (for the description of this flora, see Ducassou *et al.* 2009). On the other hand, palynological studies have shown spores and phytodebris in the Lower Devonian (Lochkovian to Emsian) and the oldest (Silurian) deposits from the Armorican Massif (e.g. Moreau Benoît, 1974; Le Hérissé, 1983; V. Baudu, unpub. Ph.D. thesis, Univ. Rennes, 1994; Baudu & Paris, 1995), but these scarce plant elements have not been reported associated with macroflora. The palynomorph assemblages studied here provide a reliable Pragian–earliest Emsian age for the Basal Member of the Chalonnes Formation. The flora from these deposits is thus older than that described from the Sainte-Anne Formation (Ducassou *et al.* 2009) and represents the earliest Devonian macroflora recorded in the Armorican Massif.

7. Conclusions

The Armorican Massif is known to provide an excellent record of the Palaeozoic history of the Variscan belt. The study presented here adds new information to this history. The Basal Member of the Chalonnes Formation consists of transgressive nearshore sediments deposited over the previously emergent land surface. The emergence preceding the transgression has never been observed before, and has still to be investigated in terms of the geodynamic evolution of the Variscan belt. The deposits described here are attributed to

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the Pragian–earliest Emsian interval, and record the earliest indication of terrestrial colonization in the Armorican Massif. The report of plant megafossils also shows the promising potential of the Basal Member of the Chalonnes Formation for further palaeobotanical studies.

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