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## A diverse Early Devonian palynoflora from the Waxweiler Lagerstätte (Klerf Formation, Rhenish Massif, Western Germany): palaeobotanical implications

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### ABSTRACT

The Lower Devonian Klerf Formation is an exceptional *Konservat-Lagerstätte*, exposed at multiple sites in the Waxweiler region in the Eifel area, western Germany. It has been studied for its various fossils, mainly arthropods, fishes, plants, molluscs, brachiopods and crinoids. At Waxweiler, the strata are palaeoecologically interpreted as a prograding deltaic depositional system elongate from NW to SE in the Ardenno-Rhenish area. The Klerf Formation has, however, not been studied in full in terms of its microflora and microfauna. Our study of the formation from two different quarries in the Waxweiler area yielded fairly diverse miospore assemblages dominated by abundant organic matter in varying degrees of coalification. The miospore assemblages are mainly composed of classic Lower Devonian taxa of the Old Red Continent (Laurussia). These belong, among others, to the genera *Ambitisporites*, *Apiculiretusispora* and *Retusotriletes*. Biostratigraphically more important species recovered include *Acinosporites lindlarensis*, *Apiculiretusispora brandtii*, *Cymbosporites asymmetricus*, *Diatomozonotriletes franklinii*, *Emphanisporites annulatus*, *Verruciretusispora dubia* and *Verrucosporites polygonalis*. In addition, *Emphanisporites foveolatus*, which is known only from a limited area in the Ardenno-Rhenish region, is also identified, indicating an earliest Pragian to middle Emsian age for the composite section. These assemblages are found to be accompanied by reworked phytoplankton to a much lesser extent. Our results reveal a much larger palaeobotanical diversity from the Rhineland outcrops than previously known, indicating a well-developed *Psilophyton*-type vegetation with related plants. The results further suggest a likely presence of plants such as *Leclercqia* and *Pertica*.

### KEYWORDS

Devonian; miospores; early land plants; *Psilophyton*; Rhenish Massif; Klerf Formation; Germany

### 1. Introduction

The west German Eifel Mountains are part of the Rhenish Massif and constitute the peneplain remains of a Variscan truncated upland formed by uplifting and erosion of the Variscan mountains. Most of its rocks comprise Devonian slates, sandstones and limestones, that were deposited along the southern margin of the Old Red Sandstone Continent (western part of Laurussia), a mountain chain that was formed by the Caledonian Orogeny during the Silurian. Situated at the interface between marine and terrestrial ecosystems, the Lower Devonian Eifel strata comprise transitional facies of erosional debris washed in from the northern Laurussian continent, and shallow marine Rhenish facies deposited in estuaries and lagoons. Based on the analyses of sedimentary rocks and fossil biotas, a low relief deltaic complex with a variety of sub-environments was inferred (e.g. Fuchs 1982; Schweitzer 1983; Kanzler 1985; Rebske et al. 1985; Stets and Schäfer 2002; Poschmann and Franke 2006). The sub-environments reported include deltaic floodplains, interdistributary bays, ephemeral lakes, lagoons, fluvial channels, crevasse splays and point bars, indicating a limited

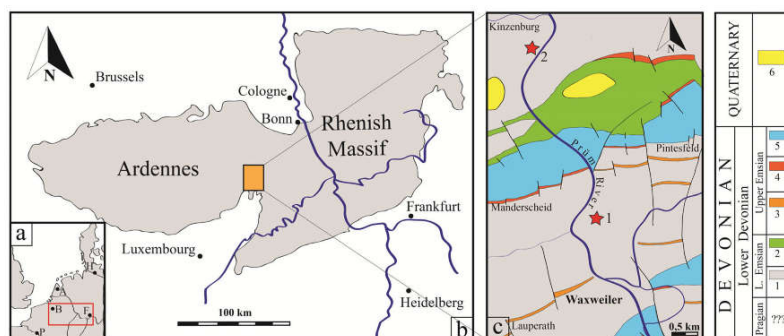
marine, brackish- to fresh-water, tidally influenced shallow-water setting. Despite being folded and overthrust in the Variscan Orogeny, the Lower Devonian strata preserve an exceptionally rich record of diverse biotas including e.g. fungi, algae, psilo- and filicophyta, bivalves, annelids, brachiopods, ostracods, eurypterids, arthropods, crinoids, cephalopods, trilobites, fishes and bryozoans (for an extensive list, see Franke 2006). Compared to reports on the biostratigraphy and palaeoecology of the Lower Devonian Eifel Mountains macrofossil assemblages, palynological studies on the microflora of the region are rare (e.g. Schultz 1968; Riegel 1973, 1975, 1982; Huwe et al. 2003). Furthermore, such studies mainly focus on the Ardenne, the western extension of the Eifel in Belgium and Luxembourg (Leclercq 1960; Strel 1986; Strel et al. 1987; Steemans and Brasseur 1999; Steemans et al. 2000) or the Hunsrück Mountains south of the Eifel region (Brocke et al. 2017).

Over recent years, special attention has been paid to the *in situ* spore fossil record, especially among Early Devonian plants (e.g. Bek 2017, 2021; Wellman 2018; Cascales-Miñana et al. 2022). This interest comes from the fact that *in situ* spores provide the sole evidence to link plant macrofossils to

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**Figure 1.** Location of the Waxweiler study area in the central area of the Ardennes-Rhenish Massif, Germany. (a and b) A: Amsterdam, B: Brussels, F: Frankfurt, H: Hamburg, P: Paris; (c) geological map of the Waxweiler area showing the position of the sampling sites (red stars); locations of the quarries at Waxweiler – WAX: 1 and Merscheid – EIFEL II: 2, respectively; modified after Streef et al. (1987) and Kanzler (1985). 1: Primary Quartzite; 2: Clayey Klerf beds; 3: Klerf beds; 4: Ems-Quartzite; 5: Wiltz beds; 6: Floodplain deposits; coordinates for the sampling sites.

dispersed spores, and consequently an unequivocal way for discerning parent plants. Isolated spore diversity further provides important information for vegetation reconstruction (e.g. Gibson and Wellman 2021). Hence, the detailed investigation of the palynoflora from the Eifel region provides new insights into the Rhineland vegetation during the late Early Devonian.

Among the key localities for Lower Devonian biotas of the Eifel mountains are outcrops at Waxweiler (Köppen Quarries, Rhineland-Palatinate), where the Emsian-aged Klerf Formation is found in a prograding deltaic depositional system (Fuchs 1982; Stets and Schäfer 2002). The Klerf Formation takes its name from the Luxembourg locality 'Clervaux' and was first described by the German palaeontologist Rudolf Richter (Richter 1919; see also Gosselet 1885). It is widely exposed in the Waxweiler area, where its outcrops are among the most diversified in the Rhenish Massif in terms of fossil content (e.g. Schweitzer 1982, 2000; Rebske et al. 1985; Dunlop and Poschmann 1997; Anderson et al. 1998; Poschmann et al. 2005; Basse and Franke 2006; Poschmann 2006; Poschmann and Franke 2006; Poschmann and Tetlie 2006; Braddy et al. 2008; Poschmann and Gossmann 2014; Poschmann et al. 2016; Poschmann 2021). They are composed of dark grey to black thinly laminated, organic- and mineral-rich shales and siltstones that have been slightly metamorphosed during the late and post-Caledonian tectonic phases. Waxweiler can be considered a 'Konservat Fossil-Lagerstätte', with a high diversity and abundance of various fossils including early fish (jawless heterostracans, jawed placoderms, see Blicek 2018).

Here we document the palynological assemblages from Waxweiler in light of recent studies concerning the stratigraphical, palaeogeographical and ecological distribution of early land plants with the objective to provide a better understanding of the palaeoenvironmental context of the region in the frame of early land plant evolution in a deltaic depositional system.

## 2. Materials and methods

Samples for this study were collected from two quarries in the Waxweiler region (Figure 1). These strata consist of the above-described deltaic complex deposits manifested in the alternation of sub- to supratidal facies. The Klerf Formation has been assigned to the lower Emsian (Lower Devonian; e.g. Solle 1956; Braddy et al. 2008; Poschmann and Gossmann 2014; Dejonghe et al. 2017). In ascending order, eleven samples were collected from the Köppen quarry in Waxweiler (locality 1 in Figure 1); all of them provided palynomorphs (WAX1-11). Two additional samples were collected from the Köppen quarry in Merscheid (locality 2 in Figure 1), of which one provided palynomorphs (Eifel II-1). The stratigraphical correlation between the two quarries is unclear, but all samples provide palynomorphs of the same assemblage that is described below. The samples were processed in the palynological laboratory of the Palaeontology research team of the UMR 8198 CNRS unit Evo-Eco-Paleo at the University of Lille (France). Following standard procedures, palynomorphs were extracted from fine-grained samples such as shale and siltstone, using traditional palynological techniques. This involved cold hydrochloric (HCl), cold hydrofluoric (HF) and hot hydrochloric (HCl) acid maceration to remove carbonates, silicates, and fluorosilicates, respectively. The organic residues were sieved through 15 µm nylon meshes. Nine of the processed samples contain palynomorphs, with abundant land-plant derived spores, but also few acritarchs and scolecodonts, in varying abundances and states of preservation, but generally moderately to poorly preserved. Each palynological slide was observed using a ZEISS Axioskop optical microscope equipped with ×40, ×63 and ×100 objectives. All rock samples, palynological slides and residues are stored in the palaeontological collections of the UMR 8198 CNRS of the University of Lille (France). Additional palynological slides are also stored in the collections of the University of Liège (Eddy Laboratory). Palynological constituents were recorded and identified to species level wherever possible. The relative abundances have

been recorded as 'rare, common or abundant' to shed more light on the environmental setting (Table 1). For the identification and biostratigraphical correlation, we followed e.g. Breuer and Steemans (2013), Richardson and McGregor (1986) and Strel et al. (1987).

### 3. Results and discussion

#### 3.1. Assemblage composition, biostratigraphy and sedimentology

A total of 28 species and 14 genera of miospores were identified from the samples analyzed (Table 1; Plate 1). In addition to the miospores, numerous phyto- and zooclasts have been observed. The description of these elements is not the main aim of the present study. Among the identifiable palynomorphs are also very few acritarchs (Plate 1).

The preservation of the palynomorphs, including the miospores, varies from sample to sample and ranges from moderate to poor. In terms of palynofacies, the samples show numerous types of organic matter of differing degrees of coalification, dominating the other main components in the assemblages. However, there are still sufficient numbers of miospores in most of the samples (Table 1). These miospores are usually brown to dark brown in colour, and many of them are fragmented.

Most of the miospore taxa identified belong to the genera *Ambitisporites*, *Apiculiretusispora* and *Retusotriletes*. The majority of these are typical forms dominating the Early Devonian assemblages of the Old Red Sandstone Continent. However, biostratigraphically more important species have also been identified (Figure 2). They include: *Acinosporites lindlarensis*, *Apiculiretusispora brandtii*, *Cymbosporites asymmetricus*, *Diatomozonotriletes franklinii*, *Emphanisporites annulatus*, *Emphanisporites foveolatus*, *Verruciretusispora dubia* and *Verrucosporites polygonalis*. The last is a well-known worldwide distributed species appearing in the lowest part of the Pragian (Richardson and McGregor 1986; Strel et al. 1987; Steemans 1989). The remaining taxa are typical of lower/middle Emsian strata, except for *A. brandtii*, which appears close to the Pragian/Emsian boundary, either just above or just below. According to the authors, *E. annulatus* appears at the Pragian/Emsian boundary (Richardson and McGregor 1986) or just above (Breuer and Steemans 2013). *Emphanisporites foveolatus* and *Verruciretusispora dubia* both characterise the FD Opperl Biozone (Strel et al. 1987) above the AB Opperl Biozone in the lower and middle Emsian. *Emphanisporites foveolatus* is the eponymous species of the Interval Zone Fov, the lowest biozone of the Opperl Biozone FD. *Verruciretusispora dubia* has been very rarely recorded from Gondwana, but it is known from Saudi Arabia (Breuer and Steemans 2013) from the *lindlarensis*-*sextantii* up to the *svalbardiae-eximius* zones, which are respectively correlated with the upper part of the FD Biozone up to the upper part of the AP Biozone of Strel et al. (1987). Therefore, the Waxweiler samples correspond to the early/middle Emsian. However, both species, in particular *B. foveolatus*, are not well known outside the Ardenno-Rhenish area.

Besides locally known taxa, a species outside of NW Gondwana observed for the first time, *Cymbosporites asymmetricus*, appears higher in the Emsian of Saudi Arabia (Breuer and Steemans 2013), but also in the late Pragian of Brazil (Mendlowicz Mauller et al. 2007). The poor quality of the available material and incomplete data on the stratigraphical distribution of this taxon do not allow us to provide more precision. *Cymbosporites asymmetricus*, *Apiculiretusispora brandtii* and *Rhabdosporites minutus* (the eponymous species of the ORSC Min Interval Zone) seem to be related and have been included in the same morphon (Breuer and Steemans 2013), making long distance correlations difficult.

The miospore assemblages are representatives of typical shallow-water habitats (e.g. Cascales-Miñana et al. 2016; Daners et al. 2017) with autochthonous open marine phytoplankton (acritarchs) being absent in the slides. The assignment to this environment is supported by abundant sedimentological and palaeontological evidence showing e.g. fine-grained, parallel bedded slabs and well preserved imprints of *Undichna* trails. Evidence for endogenic bioturbators is lacking but the association with *Diplichnites* trackways influenced by currents also points to a very shallow depositional environment, possibly influenced by tides and situated on a deltaic floodplain (Poschmann and Franke 2006).

#### 3.2. Palaeobotanical associations

The miospore assemblages also give insights into the palaeovegetation. *Acinosporites lindlarensis* is a miospore that can be related, at least, to two *Leclercqia* macroplant species: *Leclercqia complexa* and *Leclercqia uncinata* (Xu et al. 2011; Bek 2017). Likewise, the miospore *Apiculiretusispora brandtii* has been related to the plant species *Psilophyton charientis* and *P. forbesii* (Gensel 1980), but also to *Pertica dalhousii* (Edwards and Richardson 1996). Evidence of the presence of *Pertica* is indirectly provided by *Apiculiretusispora plicata* (Granoff et al. 1976; Edwards and Richardson 1996). However, arguably, the most interesting fact is that *A. plicata* is also documented from *Rhynia gwynne-vaughanii* (Wellman 2018), a plant that has never been found outside of the Rhynie chert assemblage, despite the fact that *A. plicata* is widely distributed around the world. The same context is observed for the miospore *Emphanisporites rotatus*, also globally known, that has recently been related to *Horneophyton lignieri* (Cascales-Miñana et al. 2022). Other spore taxa with implications for vegetation reconstruction are *Retusotriletes rotundus*, documented from the plant genera *Crenaticualis* and *Sawdonia* (Gensel 1980; Hotton et al. 2001), and *Retusotriletes* cf. *triangulatus*, documented from *Asteroxylon*, *Psilophyton* and *Tricherothyton* (Gensel 1980; Wellman 2018; Neregato and Hilton 2019).

#### 3.3. Reconstruction of vegetation and palaeoenvironmental interpretation

The current knowledge of the Lower Devonian (early Emsian) deposits of the Eifel region shows a fairly diverse flora formed by at least 17 plant species belonging to 11 genera

**Table 1.** Distribution of species within the samples, geographical coordinates of individual sampling sites and information on the relative abundance of individual taxa (based on individual counts).

Sample number	WAX1	WAX2	WAX3	WAX4	WAX5	WAX6	WAX7	WAX8	WAX9	WAX10	WAX11	Eifel II-1
Location of site	6°21'31.67"E	6°21'32.04"E	6°21'32.32"E	6°21'32.51"E	6°21'32.17"E	6°21'32.41"E	6°21'32.71"E	6°21'33.43"E	6°21'33.97"E	6°21'23.86"E	6°21'23.14"E	6°20'41.38"E
Species	50° 5'59.45"N	50° 5'59.34"N	50° 5'59.16"N	50° 5'59.03"N	50° 5'59.00"N	50° 5'58.87"N	50° 5'58.58"N	50° 5'58.22"N	50° 5'57.84"N	50° 5'56.22"N	50° 5'56.27"N	50° 6'56.18"N
<i>Actinosporites cf. apiculatus</i>	C											R
Streef, 1967												
<i>Actinosporites lindlarsensis</i>												R
Riegle, 1968												
<i>Ambisporites avitus</i>									R			R
Hoffmeister, 1959												
<i>Aneurospora</i> sp.	R											
<i>Apiculitessipora brandtii</i>	A						R			A		C
Streef, 1964												
<i>Apiculitessipora plicata</i>	A											R
Streef, 1967												
<i>Apiculitessipora</i> sp.	C	A										R
<i>Archaeozantriletes chuluis</i>	R	R		R		R						C
Richardson and Lister, 1969												
<i>Cymbosporites asymmetricus</i>	C											R
Breuer et al., 2007												
<i>Cymbosporites</i> sp.	R											R
Richardson and Camfield, 1982												
<i>Diatomozantriletes franklinii</i>	R											R
Richardson, 1965												
<i>Dibolisporites echnaceus</i>	R											R
Richardson, 1965												
<i>Dibolisporites eifelensis</i>												R
McGregor 1973												
<i>Dibolisporites wetterdarfensis</i>												R
Lanninger, 1968												
<i>Dictyotriletes</i> sp.												R
McGregor, 1961												
<i>Emphanisporites annulatus</i>	R											R
McGregor, 1961												
<i>Emphanisporites biradialatus</i>												C
Steeemans, 1989												
<i>Emphanisporites foveolatus</i>												R
Schultz, 1968												
<i>Emphanisporites mcgregorii</i>							R					R
Cramer, 1906												
<i>Emphanisporites rotatus</i>	A								R			C
McGregor emend. McGregor 1973												
<i>Emphanisporites schultzi</i>	C											R
McGregor 1973												
<i>Emphanisporites</i> sp.												R
McGregor 1973												
<i>Gneudhaspora divellomedia</i>										C		R
Baime 1988												
<i>Grandispora</i> sp.												R
Richardson and Basul, 1978												
<i>Retusotriletes rotundus</i>	R											R
Lele and Streef, 1969												
<i>Retusotriletes</i> sp.	A											A
Streef, 1967												
<i>Retusotriletes triangulatus</i>	A			A	R							A
Streef, 1967												
<i>Verrucitessipora dubia</i>	R											C
Richardson and Basul, 1978												
<i>Verrucosporites polygonalis</i>												R
Lanninger, 1968												

R: Rare (1–2 individuals); C: Common (4–10 individuals); A: Abundant (≥ 20 individuals).



**Plate 1.** Spores and acritarchs found in this study. Identification followed by sample number and England Finder Graticule Coordinates.

1. *Cymbosporites asymmetricus* WAX1, SF-92; 2. *Apiculiretusispora brandtii* WAX1, SF-96; 3. *Emphanisporites annulatus* WAX11-1, Q-72; 4. *Verruciretusispora dubia* WAX1, SF-135; 5. *Acinosporites* cf. *apiculatus* EIFEL II-1-1, H-46-2; 6. *Verrucosporites polygonalis* WAX11-1, D-58-3; 7. *Diatomozonotriletes franklinii* EIFEL II-1-1, M-53; 8. *Emphanisporites foveolatus* WAX11-1, R-69-3-1; 9. *Acinosporites lindlarensis* WAX11-1, V-70-2; 10. *Apiculiretusispora brandtii* WAX11-1, J-74-3; 11. *Apiculiretusispora plicata* WAX11-1, F-70-3-3; 12. *Acinosporites* cf. *apiculatus* WAX11, SF-159; 13. diacrodian acritarch (late Cambrian to Early Ordovician) WAX11, SF-445; 14. cf. *Vavrdovella areniga* (Vavrdova 1973) Loeblich and Tappan 1976 (Early Ordovician) WAX11, SF-102; 15. *Cymatogalea* sp. (late Cambrian to Early Ordovician) WAX11-1, E-50-2-1; 16. *Acanthodiacrodium-Coryphidium* transient (Early Ordovician) WAX3, SF-78.

Chronostratigraphy	Spore Biostratigraphy		Important Spore Species (ranges based on Breuer and Steemans, 2013)	
	Pragian	Emsian		
	<i>brecomensis</i>	<i>apiculatus</i>	ARDEENNO-RHENISH Strel et al. (1987)	<i>Actinosporites lindlarensis</i>
	<i>zavallatus</i>	<i>foveolatus</i>	OLD RED SANDSTONE Richardson and McGregor (1986)	<i>Apiculiretusispora brandtii</i>
	<i>wetteldorfensis</i>	<i>dubia</i>		<i>Cymbosporites asymmetricus</i>
	<i>polygonalis - emsiensis</i>	<i>annulatus</i>		<i>Diatomozonotriletes franklinii</i>
		<i>sextantii</i>		<i>Emphanisporites annulatus</i>
				<i>Emphanisporites foveolatus</i>
				<i>Verruciretusispora dubia</i>
				<i>Verrucosporites polygonalis</i>

Figure 2. Biostratigraphical comparison chart (a and b: *annulatus-bellatulus*).

(see Schweitzer 1990, table 3, for details). This flora includes six cosmopolitan genera and one endemic genus. Concerning widely distributed genera, the flora is composed of *Taeniochrada* (Göppert) Kräusel & Weyland, *Zosterophyllum* Penhallow, *Distichophytum* Mägdefrau, *Sawdonia* Hueber, *Drepanophycus* Göppert and *Psilophyton* Dawson. Endemicity is represented by *Tursuidea* Schweitzer. Interestingly, numerous taxa of the Emsian flora constituents are monospecific, including *Stockmansella langii* (Stockmans) Fairon-Demaret, *Sartilmania jabachensis* (Kräusel & Weyland) Fairon-Demaret, *Sawdonia spinosissima* Schweitzer, *Distichophytum mucronatum* Mägdefrau, *Drapnophycus spinaeformis* Göppert and *Tursuidea paniculata* Schweitzer. The species diversity is completed by *Taeniochrada*, *Renalia* and *Psilophyton* with two species each: *Taeniochrada decheniana* (Göppert) Kräusel & Weyland and *T. dubia* Kräusel & Weyland, *Renalia graberti* Schweitzer and *R. major* Schweitzer, as well as *Psilophyton arcuatum* (Halle) Schweitzer and *P. burnotense* (Gilkinet) Kräusel & Weyland (= *Psilophyton goldschmidtii* Halle).

*Zosterophyllum* is present with three species: *Zosterophyllum rhenanum* Kräusel & Weyland, *Z. spectabile* Schweitzer and *Z. fertile* Leclercq. To this list some tentative taxonomic assignments can be added, such as ?*Protobarinophyton* sp. and ?*Drepanophycus gaspianus*.

According to current plant classification, the early Emsian flora of the Eifel contains many different basal forms of tracheophytes (Capel et al. 2021, 2022). Such forms include rhyniopsids (e.g. *Renalia*), paratracheophytes (former Rhyniaceae, Gerrienne et al. 2006, i.e. *Stockmansella*) and zosterophylloids (e.g. *Sawdonia*), barinophytoid-like plants, as well as basal euphyllophytes (former trimerophytes *sensu* Banks 1968, i.e. *Psilophyton*) and lycopsids (i.e. *Drepanophycus*). Hence, the floristic composition of this Rhineland flora is characterized by an important richness of zosterophylloids and the absence of well-defined rhyniopsids such as typical rhyniopsids, i.e. *Cooksonia*-like plants.

Rhyniopsids experienced a great diversification through the earliest Early Devonian although many taxa do not

extend into the Pragian (middle Lower Devonian; Capel et al. 2021). Interestingly, the closely coeval Emsian flora of Wépion (Belgium) is more dominated by rhyniopsids and *Psilophyton*-like plants than by zosterophylls (see Gerrienne 1993, for summary), which likely reflects the phytogeographical importance of the Rhineland flora. Moreover, in a larger framework, the Emsian floras of the Rhineland represent the early steps of the Eophytic turnover from which extant floras turn from a zosterophyllopid-dominated to a lycopsid-dominated vegetation. This scenario suggests an early Eophytic character to the described Rhineland assemblage. However, the findings of our study suggest the presence of a well-developed *Psilophyton*-type vegetation and related plants. It further reveals a hidden diversity from the Rhineland outcrops, with a likely presence of *Leclercqia* and *Pertica*. Moreover, the presence of *in situ* spores from the Rhynie chert, a plant diversity interpreted as belonging to a hot springs environment (Channing and Edwards 2009), would suggest a more complex palaeoenvironment than the coastal and shallow waters context previously proposed for the Rhineland flora by Schweitzer (1990, fig. 11).

Of particular interest for biostratigraphy, palaeogeography and palaeobotany is *Emphanisporites foveolatus*, a spore that is only known in a small area of the Ardenno-Rhenish region and in the Emsian of Poland (i.e. Lanninger 1968; Riegel 1973, 1975, 1982; Rebske et al. 1985; Streel et al. 1987; Turnau and Karczewska 1987; Steemans 1989; Turnau and Miłaczewski 2005). This species could be evidence for a phytogeographical province, more or less equivalent to the S-Z province (Steenmans and Lakova 2004).

### 3.4. Reworking

All acritarchs identified in this study are of late Cambrian to Early Ordovician age and therefore, reworked. Reworked acritarchs are common in the Ardenne (Belgium) and the Siegerland (Germany) (Vanguetaine 1979; Steemans 1989). Schematically, in the Ardenne, it has been observed on the northern side of the Dinant Synclinorium that reworked Silurian acritarchs are abundant and Cambro-Ordovician specimens are rare. On the contrary, on the southern side of the Dinant Synclinorium, the Cambro-Ordovician acritarchs dominate the assemblages (Steenmans 1989). Furthermore, Steemans (1989) noted that reworked acritarchs in Belgium have been eroded from at least seven different horizons, ranging from the Cambrian to the Lower Devonian. The studies in Belgium suggest at least two different sources of sediments to the basin. A northern source, the Brabant Massif, would have delivered Silurian sediments, and a southern source, the 'Mittel Deutsche Schwelle', would have provided reworked palynomorphs from Cambro-Ordovician strata into the basin (see also Vanguetaine 1979). The results obtained in the Waxweiler locality only include patchy observations, with very few acritarchs recorded, that are clearly reworked from Cambro-Ordovician rocks.

Reworking of late Cambrian-Early Ordovician acritarchs and their subsequent deposition in the Waxweiler strata are indicative for active erosional surfaces during the Early

Devonian. These findings are consistent with studies on sedimentary petrography, provenance analysis of minerals and zircon ICP-MS laser ablation ages (Schäfer et al. 1997; Wierich 1999; Stets and Schäfer 2002; Franke and Dulce 2017), showing (1) that the exhumation of the basement of the Rhenish Massif lead to substantial erosion and reworking, and (2) that synorogenic clastic strata in the prograding Ardenno-Rhenish delta are derived from the northern continent Baltica to be ultimately deposited in the Rheno-Hercynian Belt of Germany in the Rhenish Massif (Franke and Dulce 2017).

## 4. Conclusions

The new palynological analysis from the Devonian Klerf Formation deposits at Waxweiler revealed assemblages from deltaic and nearshore coastal settings comprising abundant phyto- and zooclasts, together with palynomorphs, mostly miospores and rare acritarchs. The poorly to moderately well-preserved taxa provide the following results:

1. The assemblages from the Waxweiler outcrops reveal a much more diverse palynoflora than those formerly known from the Lower Devonian of the German part of the Rhenish Massif, comprising 28 miospore species from 14 genera, indicating a well-developed *Psilophyton*-type vegetation and related plants, with a likely presence of *Leclercqia* and *Pertica*.
2. Some of the spores found in this study (e.g. *Apiculiretusispora plicata* and *Emphanisporites rotatus*) have been found *in situ* in the sporangia of plants previously regarded to be exclusive to the Rhynie chert (e.g. *Rhynia gwyne-vaughanii* and *Horneophyton lignieri*). These plants have been described as being associated with hot spring systems, and would be indicative of a more complex palaeoenvironment than what was previously considered to represent the Rhineland flora, or, on the other hand, indicate that some of the typical plants of the Rhynie chert had a much wider geographical distribution.
3. *Emphanisporites foveolatus* could correspond to a phytogeographical province; more or less equivalent to the S-Z phytogeographical province of Steemans and Lakova (2004).
4. Very few acritarchs recovered from the samples are all of Cambro-Ordovician age, and thus clearly not *in situ*, and represent reworked material derived from older strata. This finding is in line with scenarios of active erosional surfaces, petrographical provenance studies and laser ablation ages of zircon minerals.
5. Future examination of the abundant phyto- and zooclasts, in terms of detailed palynofacies analysis, could provided interesting results.

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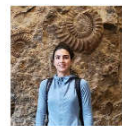
## Disclosure statement

No potential conflict of interest was reported by the authors.

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