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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 sediments are palaeoecologically interpreted as a prograding deltaic depositional system elongated from NW to SE in the Ardenno-Rhenish area. The Klerf Formation has, however, not been studied in full detail in terms of its microflora and microfauna. Our study of the sediments of the formation from two different quarries in the Waxweiler area yielded fairly diverse miospore assemblages dominated by abundant organic matter of varying degrees of coalification. The miospore assemblages are

mainly composed of classical 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 *Verrucosisporites 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 sediments 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 sediments and fossil biotas, a low relief deltaic complex with a variety of sub-environments was inferred (e.g., Fuchs 1982; Schweitzer 1983; Poschmann and Franke 2006; Kanzler 1985; Rebske et al. 1985; Stets and Schäfer 2002). 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 sediments 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. Riegel 1973, 1975, 1982; Schultz 1968; 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 the past years, special attention has been paid to the *in situ* spore fossil record, especially among Early Devonian plants (e.g. Wellman 2017; Bek 2017, 2021; Cascales-Miñana et al. 2022). This interest comes from the fact that *in situ* spores provide the sole evidence to link plant macrofossils to 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; Anderson et al. 1998; Basse and Franke 2006; Dunlop and Poschmann 1997; Poschmann et al. 2005; 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 metal-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 disparity and abundance of various fossils including early fish (jawless heterostracans, jawed placoderms, see Blicek 2018).

Here we document the palynological microfloral assemblages from Waxweiler in light of recent studies concerning the stratigraphic, palaeogeographic 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 sediments 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 Fig. 1). All of them provided palynomorphs WAX1-11. Two additional samples were collected from the Köppen quarry in Merlscheid (locality 2 in Fig. 1), of which one provided palynomorphs (Eifel II-1). The stratigraphical position between the two quarries is unclear, but all samples provide palynomorphs of a 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 standard 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 most 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 x40, x63 and x100 objectives. All rock samples, palynological slides and residues are stored in the palaeontological collections of the 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 have been 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 biostratigraphic correlation, we followed e.g. Breuer and Steemans (2013), Richardson and McGregor (1986), and Streel 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 within the 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 color, 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 *Verrucosisporites polygonalis*. The last is a well-known worldwide-distributed species appearing in the lowest part of the Pragian (Richardson and McGregor 1986; Steemans 1989; Streel et al. 1987). 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 Opper Biozone (Streel et al. 1987) above the AB Opper Biozone in the lower and middle Emsian. *Emphanisporites foveolatus* is the eponymous species of the Interval Zone Fov, the lowest biozone of the Opper 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 Streel 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 the taxon do not allow 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 charientos* 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 2017), 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 *Tricherophyton* (Gensel 1980; Wellman 2017; 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 (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 *Taenioocrada* (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 *Taeniocrada*, *Renalia* and *Psilophyton* with two species each: *Taeniocrada 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 phytogeographic 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 zosterophylloid-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 hot springs environment (Channing and Edwards 2009), would suggest a more complex palaeoenvironment than the coastal and shallow waters context previously proposed to the Rhineland flora by Schweitzer (1990, fig. 11).

Of particular interest for biostratigraphy, palaeogeography and palaeobotany is *Emphanisporites foveolatus*, a taxon that is only known in a small area of the Ardenno-Rhenish region and in the Emsian of Poland (i.e. Lanninger 1968; Rebske et al. 1985; Riegel 1973, 1975, 1982;

Stemans 1989; Strel et al. 1987; Turnau and Karczewska 1987; Turnau et al. 2005). This species could be the witness of a phytogeographic province, more or less equivalent to the S-Z province (Stemans and Lakova 2004).

3.4. Reworking observed in the samples

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; Stemans 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 (Stemans 1989). Furthermore, Stemans (1989) noted that reworked acritarchs in Belgium have been eroded from at least seven different horizons, ranging from the Cambrian to the Early 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 sediments 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 sediments.

Reworking of late Cambrian-Early Ordovician acritarchs and their subsequent deposition in the Waxweiler sediments are indicative for active erosional surfaces during the Early Devonian. These findings are in line with studies obtained from sedimentary petrography, provenance analysis of minerals and zircon ICP-MS laser ablation ages (Wierich 1999; Schäfer et al. 1997; 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 sediments 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 of the Rhynie Chert (e.g. *Rhynia gwyne-vaughanii* and *Horneophyton lignieri*). These plants have been described to be 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 phytogeographic province; more or less equivalent to the S-Z phytogeographic 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 sediments. This finding is in line with scenarios of active erosional surfaces, petrographic 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 provide interesting results.

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Declaration of Interest

No potential conflict of interest was reported by the authors.

References

- Anderson LI, Poschmann M, Brauckmann, C. 1998. On the Emsian (Lower Devonian) arthropods of the Rhenish Slate Mountains: 2. The synziphosurine *Willwerathia*. *Paläontologische Zeitschrift*. 72:325–336.
- Balme BE. 1988. Spores from Late Devonian (early Frasnian) strata, Carnarvon Basin, Western Australia. *Palaeontographica Abteilung B*. 209:109–166.
- Banks HP. 1968. The early history of land plants. In: Drake ET, editor. *Evolution and Environment. Symposium 100th Anniversary Foundation of Peabody Museum of Natural History*. Yale University Press, New Haven; p. 73-107.
- Basse M, Franke C. 2006. Marine Faunen aus dem frühen Unteremium (Unterdevon) des Givonne-Oesling-Antiklinorium (Luxemburg). In: Franke C, editor. *Beiträge zur Paläontologie des Unterdevons Luxemburgs (1)*. *Ferrantia*. 46:7–41.
- Bek J. 2017. Paleozoic *in situ* spores and pollen. Lycopsidea. *Palaeontographica Abteilung B*. 296:1–111.
- Bek J. 2021. Paleozoic *in situ* spores and pollen. Sphenopsida. *Palaeontographica Abteilung B*. 301:141–201.
- Blieck ARM. 2018. The Waxweiler project, Eodevonian heterostracan pteraspidomorphs and mythology of the big five. *Annales de la Société Géologique du Nord*. 25:69–74
- Braddy S, Poschmann M, Tetlie O. 2008. Giant claw reveals the largest ever arthropod. *Biology letters*. 4:106-109.
- Breuer P, Steemans P. 2013. Devonian spore assemblages from northwestern Gondwana: taxonomy and biostratigraphy. *Special Papers in Palaeontology* 89:1–163.
- Breuer P, Al-Ghazi A, Al-Ruwaili M, Higgs KT, Steemans P, Wellman CH. 2007. Early to Middle Devonian miospores from northern Saudi Arabia. In: Paris F., Owens B., Miller MA, editors. *Palaeozoic Palynology of the Arabian Plate and Adjacent Areas*. *Revue de Micropaléontologie*; 50:27–57.
- Brocke R, Kneidl V, Wilde V. 2017. Palynological data from sediments of the Hunsrückschiefer type, Lower Devonian of the SW Hunsrück, Germany. *Bulletin of Geosciences*. 92:59–74.
- Capel E, Cleal CJ, Gerrienne P, Servais T, Cascales-Miñana B. 2021. A factor analysis approach to modelling the early diversification of terrestrial vegetation. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 566:110170.
- Capel E, Cleal CJ, Xue J, Monnet C, Servais T, Cascales-Miñana B. 2022. The Silurian–Devonian terrestrial revolution: Diversity patterns and sampling bias of the vascular plant macrofossil record. *Earth-Sci Rev*. 231:104085.
- Cascales-Miñana B., Gerrienne P., Moreno-Dominguez, R., Xue J., Valenzuela-Rios, J. I., Diez, J. B., Rial, G., Steemans, P. 2016. A new highly diverse palynoflora from the Lower Devonian Noguerras Formation of the Iberian Peninsula. *Historical Biology*. 28:1118-1124.
- Cascales-Miñana B, Servais T, Capel E, Steemans P. 2022. Further observations on the spores of the Rhynie chert plant *Horneophyton lignieri* (Kidston & Lang) Barghoorn & Darrah, 1938: Implications for palaeodiversity studies. *Review of Palaeobotany and Palynology*. 296:104543.
- Channing A, Edwards D. 2009. Yellowstone hot spring environments and the palaeo-ecophysiology of Rhynie chert plants: towards a synthesis. *Plant Ecology and Diversity*. 2:111–143.
- Cramer FH. 1966. Palynology of Silurian and Devonian rocks in northwestern Spain. *Boletín del Instituto Geológico y Minero de España*. 77:223–286.

- Daners G, Le Hérisse A, Breuer P, Veroslavsky G. 2017. Pragian–Emsian palynomorphs from the Cordobés Formation, Norte Basin, Uruguay: stratigraphically restricted and regionally correlative palynological events in the cool-water Malvinokaffric Realm. *Palynology*. 41 suppl. 1:121-137.
- Dejonghe L, Colbach R, Goemaere E. 2017. The lithostratigraphy of the lower Devonian formations of the Eisleck region (northern Luxembourg). Comparison with their Belgian lateral equivalents. *Geologica Belgica*. 20:33–42.
- Dunlop J, Poschmann M. 1997. On the Emsian (Lower Devonian) arthropods of the Rhenish Schiefergebirge: 1. *Xenarachne*, an enigmatic arachnid from Willwerath, Germany. *Paläontologische Zeitschrift*. 71:231–236.
- Edwards D, Richardson JB. 1996. Review of *in situ* spores in early land plants. In: Jansonius J, McGregor DC, editors. *Palynology: Principles and Applications*. American Association of Stratigraphic Palynologists Foundation, Publishers Press; p. 391–407.
- Franke C. 2006. Die Klerf-Schichten (Unter-Devon) im Großherzogtum Luxemburg, in der Westeifel (Deutschland) und im Gebiet von Burg Reuland (Belgien): fazielle und biostratigraphische Deutungen. *Ferrantia*. 46:42–96.
- Franke W, Dulce JC. 2017. Back to sender: tectonic accretion and recycling of Baltica- derived Devonian clastic sediments in the Rheno- Hercynian Variscides. *International Journal of Earth Sciences (Geologische Rundschau)*. 106:377–386.
- Fuchs G. 1982. Upper Siegenian and lower Emsian in the Eifel hills. *Courier Forschungsinstitut Senckenberg*. 55:229–256.
- Gensel PG. 1980. Devonian *in situ* spores: a survey and discussion. *Review of Palaeobotany and Palynology*. 30:101–132.
- Gerrienne P. 1993. Inventaire des végétaux éodévoniens de Belgique. *Annales de la Société géologique de Belgique*. 116:105–117.
- Gerrienne P, Dilcher DL, Bergamaschi DL, Milagres I, Pereira E, Rodrigues MAC. 2006. An exceptional specimen of the early land plant *Cooksonia paranensis*, and a hypothesis on the life cycle of the earliest eutracheophytes. *Review of Palaeobotany and Palynology*. 142: 123–130.
- Gibson ME, Wellman CH. 2021. The use of spore-pollen assemblages to reconstruct vegetation changes in the Permian (Lopingian) Zechstein deposits of northeast England. *Review of Palaeobotany Palynology*. 288:104399
- Gosselet J. 1885. L'Ardenne. Note sur le Taunusien dans le bassin de Luxembourg et particulièrement dans le golfe de Charleville. *Annales de la Société Géologique du Nord*. p. 333–363.
- Granoff JA, Gensel PG, Andrews HN. 1976. A new species of *Pertica* from the Devonian of eastern Canada. *Palaeontographica Abteilung B*. 155:119–128.
- Hoffmeister WS. 1959. Lower Silurian plant spores from Libya. *Micropaleontology*. 5: 331–334.
- Hotton CL, Hueber FM, Griffing DH, Bridge JS. 2001. Early terrestrial plant environments: An example from the Emsian of Gaspé, Canada. In: Gensel PG, Edwards D., editors. *Plants Invade the Land: Evolutionary and Environmental Perspectives*. Columbia University Press, New York; p. 179–212.
- Huwe S, Brocke R, Wilde V. 2003. Unentdeckte Schätze im Sammlungs Archiv: Palynomorphen im Unterdevonder Eifeler Kalkmulden. *Natur und Museum*. 133:33–44.
- Kanzler HB. 1985. Die Geologie des Raumes Waxweiler – Lünebach (NE-Teil der Daleider Muldengruppe/SW-Eifel) unter besonderer Berücksichtigung der Sedimentologie und Palökologie der Klerfer Schichten [Dissertation]. Rheinische Friedrich-Wilhelms-Universität zu Bonn.
- Lanninger EP. 1968. Sporen-Gesellschaften aus dem Ems der SW-Eifel (Rheinisches Schiefergebirge). *Palaeontographica Abteilung B*. 122:95–170.
- Lele KM, Strel M. 1969. Middle Devonian (Givetian) plant microfossils from Goé (Belgium). *Annales de la Société géologique de Belgique*. 92: 89–121.
- Leclercq S. 1960. Sporomorphes du Dévonien de Belgique. *Bulletins de l'Académie royale des sciences*, 5(46):250–256.
- McGregor DC. 1961. Spores with proximal radial pattern from the Devonian of Canada. *Geological Survey of Canada Bulletin*. 76: 1–11.

- McGregor DC. 1973. Lower and Middle Devonian spores of Eastern Gaspé Canada. I. Systematics. *Palaeontographica Abteilung B*. 142: 1–77.
- McGregor DC, Camfield M. 1982. Middle Devonian miospores from Cap de Bray, Weatherall and Hecla Bay Formations of the Northeast Melville Island, Canadian Arctic. *Geological Survey of Canada Bulletin*. 348:1-105.
- Mendlowicz Mauller P, Machado Cardoso T, Pereira E, Steemans P. 2007. Resultados palinoestratigráficos do Devoniano da Sub-Bacia de Alto Garças (Bacia do Paraná - Brasil). In: Carvalho IS, Cassab RCT, Schwanke C, Carvalho MA, Fernandes ACS, Rodrigues MAC, Carvalho MSS, Arai M, Oliveira MEQ, editors. *Paleontologia: cenários de Vida*, Interciência, Rio de Janeiro. P. 607-619.
- Neregato R, Hilton J. 2019. Reinvestigation of the enigmatic Carboniferous sphenophyte strobilus *Cheirostrobos* Scott and implications of *in situ* *Retusotriletes* spores. *International Journal of Plant Sciences*. 180:811–833.
- Poschmann M. 2006. The eurypterid *Adelophthalmus sievertsi* (Chelicerata: Eurypterida) from the Lower Devonian (Emsian) Klerf Formation of Willwerath, Germany. *Palaeontology*. 49:67–82.
- Poschmann M. 2021. A new sea scorpion (Arthropoda, Eurypterida) from the Early Devonian of Willwerath (Rhineland-Palatinate, SW Germany). *Paläontologische Zeitschrift*. 95:17–26.
- Poschmann M, Franke C. 2006. Arthropods and trace fossils from the Lower Devonian (Emsian). *Ferrantia*. 46:97–115.
- Poschmann M, Tetlie O. 2006. On the Emsian (Lower Devonian) arthropods of the Rhenish Slate Mountains: 5. Rare and poorly known eurypterids from Willwerath, Germany. *Paläontologische Zeitschrift*. 80:325–343.
- Poschmann M, Gossmann R. 2014. Wurzelstrukturen früher Gefäßpflanzen aus der Klerf-Formation (Unterdevon, höchstes Unter-Emsium) von Waxweiler (SW-Eifel, Rheinland-Pfalz, SW-Deutschland). *Mainzer Naturwissenschaftliches Archiv*. 51:33–44.
- Poschmann M, Anderson L, Dunlop J. 2005. Chelicerate arthropods, including the oldest Phalangiotarbid arachnid, from the early Devonian (Siegenian) of the Rhenish Massif, Germany. *Journal of Paleontology*. 79:110–124.
- Poschmann M, Schoenemann B, McCoy VE. 2016. Telltale eyes: the lateral visual systems of Rhenish Lower Devonian eurypterids (Arthropoda, Chelicerata) and their palaeobiological implications. *Palaeontology*. 59:295–304.
- Rebske W, Rebske C, Bless MJM, Paproth E, Steemans P. 1985. Over enkele fossielen uit de Klerf-Schichten (Onder-Emsien) bij Waxweiler (Eifel, BRD) en hun leefmilieu. *Grondboor en Hamer*. 5:142–155.
- Richardson JB, 1965. Middle Old Red Sandstone spore assemblages from the Orcadian Basin north-east Scotland. *Palaeontology*. 7:559–605.
- Richardson JB, McGregor DC. 1986. Silurian and Devonian spore zones of the Old Red Sandstone Continent and adjacent regions. *Bulletin Geological Survey of Canada*. 364:1–179.
- Richardson, JB, Lister TR. 1969. Upper Silurian and Lower Devonian spore assemblages from the Welsh Borderland and South Wales. *Palaeontology*. 12:201–252.
- Richardson JB, Rasul SM. 1978. Palynological evidence for the age and provenance of the Lower Old Red Sandstone from the Apley Barn Borehole, Winey, Oxfordshire. *Proceedings of the Geologists' Association* Vol. 90(1):27–42.
- Richter R. 1919. Zur Stratigraphie und Tektonik der Oesling-Eifel-Mulde. I. Über den Muldenabschnitt südlich der Schneifel. *Centralblatt Mineralogie*. p. 44–62.
- Riegel W. 1973. Sporenformen aus den Heisdorf-, Lauch-, und Nohn-Schichten (Emsium und Eifelium) der Eifel, Rheinland. *Palaeontographica Abteilung B*. 142:78–104.
- Riegel W. 1975. Palynological sequence from Lower Emsian to Givetian of the Eifel Region. *Commission Internationale de Microflore du Paléozoïque, Newsletter*. 10:6.
- Riegel W. 1982. Palynological aspects of the Lower/Middle Devonian transition in the Eifel Region. *Courier Forschungsinstitut Senckenberg*. 55:279–292.

- Schäfer J, Neuroth H, Ahrendt H, Dörr W, Franke W. 1997. accretion and exhumation at a Variscan active margin, recorded in the Saxothuringian flysch. *Geologische Rundschau* 86:599–611.
- Schultz G. 1968 Eine unterdevonische Mikroflora aus den Klerfer Schichten der Eifel (Rheinisches Schiefergebirge). *Palaeontographica Abteilung B*, 123:5-42.
- Schweitzer HJ. 1982. Zwei neue Pflanzen aus dem Unterdevon der Eifel. *Bonner Palaeobotanische Mitteilungen*. Universität Bonn. 9:1–15.
- Schweitzer HJ. 1983. Die Unterdevonflora des Rheinlandes, 1. Teil. *Palaeontographica Abteilung B*, 189:1–138.
- Schweitzer HJ. 1990. Pflanzen erobern das Land: Kleine Senckenberg-Reihe. 18:1–75.
- Schweitzer HJ. 2000. Neue Pflanzenfunde im Unterdevon der Eifel (Deutschland). *Senckenbergiana Lethaea*. 80:371–395.
- Solle G. 1956. Gliederung und Aufbau der Klerfer Schichten am Nordrand der Olkenbacher Mulde (Unterdevon, Sudost-Eifel). *Notizblatt des Hessischen Landesamtes für Bodenforschung*. 84:85–92.
- Stemans P. 1989. Etude palynostratigraphique du Dévonien inférieur dans l'Ouest de l'Europe. *Memoirs of the Geological Survey of Belgium*. 27:1–453.
- Stemans P, Brasseur O. 1999. Rapport d'analyse de 60 échantillons de l'Emsien du nord du Grand-Duché de Luxembourg. Unpublished report. Laboratoire de Paléontologie Végétale, Palynology et Micropaléontologie. Université de Liège; p. 1-279.
- Stemans P, Debbaut V, Faber A. 2000. Preliminary survey of the palynological content of the Lower Devonian of the Oesling, Luxembourg. *Bulletin de la Societe des Naturalistes Luxembourgeois*. 100:171–186.
- Stemans P, Lakova I. 2004. The Moesian Terrane during the Lochkovian - A new palaeogeographic and phytogeographic hypothesis based on miospore assemblages. *Palaeogeography, Palaeoclimatology, Palaeoecology*. 208:225–233.
- Stets J, Schäfer A. 2002. Depositional environments in the Lower Devonian siliciclastics of the Rhenohercynian Basin (Rheinisches Schiefergebirge, W-Germany) – case studies and a model. *Contributions to Sedimentary Geology*. 22:78.
- Strel M. 1964. Une association de spores du Givétien Inférieur de la Vesdre, à Goé (Belgique). *Annales de la Société Géologique de Belgique*. 87:2–30.
- Strel M. 1967. Associations de spores du Dévonien inférieur beige et leur signification stratigraphique. *Annales de la Société Géologique de Belgique*. 90:11–54.
- Strel M. 1986. Miospore contribution to the upper Famennian-Strunian event stratigraphy. *Annales de la Société Géologique de Belgique*. 109:75–92.
- Strel M, Higgs K, Loboziak S, Riegel W, Stemans P. 1987. Spore stratigraphy and correlation with faunas and floras in the type marine Devonian of the Ardenne-Rhenish regions. *Review of Palaeobotany and Palynology*. 50:211–229.
- Turnau E, Karczewska J. 1987. Size distribution in some Middle Devonian dispersed spores and its bearing on the problem of evolution of heterospory. *Review of Palaeobotany and Palynology*. 52:403–416.
- Turnau EL, Miłaczewski, Wood G. 2005. Spore stratigraphy of Lower Devonian and Eifelian (?), alluvial and marginal marine deposits of the Radom-Lublin area (Central Poland). *Annales Societatis Geologorum Poloniae*. 75 :121-137.
- Vanguetaine M. 1979. Remaniements d'acritarches dans le Siegenien et l'Emsien (Dévonien Inférieur) du Synclinorium de Dinant (Belgique). *Annales de la Société géologique de Belgique*. 101:243–267.
- Wellman CH. 2017. Palaeoecology and palaeophytogeography of the Rhynie chert plants: further evidence from integrated analysis of *in situ* and dispersed spores. *Philosophical Transactions of the Royal Society of London B*. 373(1739):20160491.
- Wierich F. 1999. Orogene Prozesse im Spiegel synorogener Sedimente, korngefügekundliche Liefergebietsanalyse siliziklastischer Sedimente im Devon des Rheinischen Schiefergebirges. *Marburger Geowissenschaftliche Vereinigung*. 1:264.

Xu HH, Berry CM, Wang Y, Marshall JE. 2011. A new species of *Leclercqia* Banks, Bonamo et Grierson (Lycopsida) from the Middle Devonian of North Xinjiang, China, with a possible climbing habit. *International Journal of Plant Sciences*. 172:836–846.

Figure, Plate, and Table Captions :

Figure 1. Location of the Waxweiler study area in the central area of the Ardenno-Rhenish massif, Germany. (a-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 Merlscheid - EIFEL II: 2, respectively); modified after Streel et al. (1987) and Kanzler (1985). 1: Primary Quartzite; 2: Clayey Klerf beds; 3: Klerf beds; 4: Ems-Quartzite; 5: Wiltzer beds; 6: Floodplain deposits; coordinates for the sampling sites).

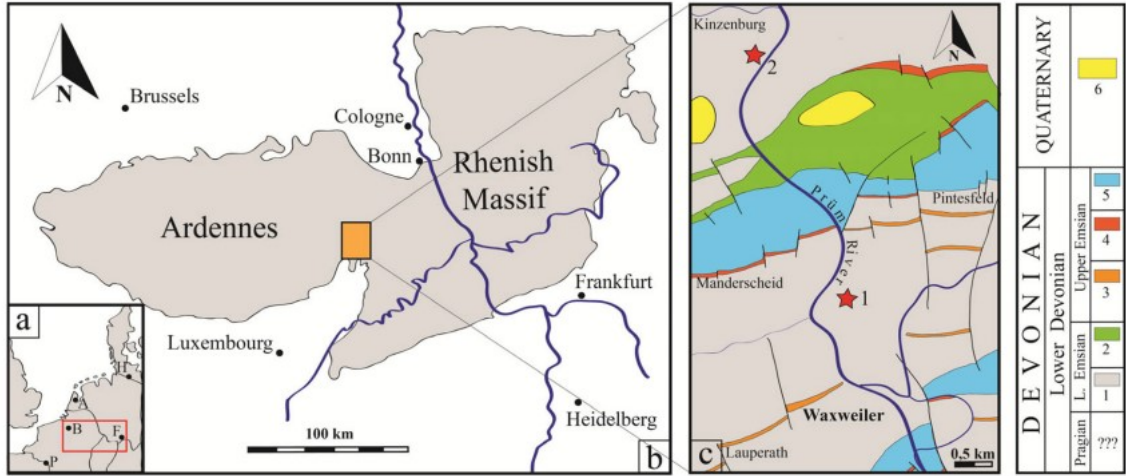
Figure 2. Biostratigraphic comparison chart (a-b: *annulatus-bellatulus*).

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. *Verrucosisporites 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. *Cymatiogalea* sp. (late Cambrian to Early Ordovician) WAX11-1, E-50-2-1;
16. *Acanthodiacrodium-Coryphidium* transient (Early Ordovician) WAX3, SF-78.

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). R: Rare (1-2 individuals); C: Common (4-10 individuals); A: Abundant (≥ 20 individuals); abundance information in italics represent unusual occurrences).





1 _____



2 _____



3 _____



4 _____



5 _____



6 _____



7 _____



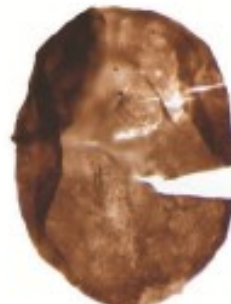
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16 _____

Pragian	Emsian			Chronostratigraphy
	<i>breconensis</i> - <i>zavallatus</i> <i>polygonalis</i> - <i>wetteldorfensis</i> <i>polygonalis - emsiensis</i>	<i>foveolatus</i> - <i>dubia</i> <i>annulatus</i> - <i>sextantii</i>	<i>apiculatus</i> - <i>proteus</i> <i>douglastownensis</i> - <i>eurypterota</i>	
				Spore Biostratigraphy ARDENNO-RHENISH Streef et al. (1987) OLD RED SANDSTONE Richardson and McGregor (1986)
				<i>Acinosporites</i>
				<i>lindlarensis</i>
				<i>Apiculiretusispora</i> <i>bramhii</i>
				<i>Cymbosporites</i> <i>asymmetricus</i>
				<i>Diatomozonotriletes</i> <i>franklinii</i>
				<i>Emphanisporites</i> <i>annulatus</i>
				<i>Emphanisporites</i> <i>foveolatus</i>
				<i>Ferraciretusispora</i> <i>dubia</i>
				<i>Ferrucosporites</i> <i>polygonalis</i>

Sample number	WAX1	WAX2	WAX3	WAX4	WAX5	WAX6	WAX7	WAX8	WAX9	WAX10	WAX11	Eifel II-1
Location of site	6°21'31.67"E 50° 5'59.45"N	6°21'32.04"E 50° 5'59.34"N	6°21'32.32"E 50° 5'59.16"N	6°21'32.51"E 50° 5'59.03"N	6°21'32.17"E 50° 5'59.00"N	6°21'32.41"E 50° 5'58.87"N	6°21'32.71"E 50° 5'58.58"N	6°21'33.43"E 50° 5'58.22"N	6°21'33.97"E 50° 5'57.84"N	6°21'23.86"E 50° 5'56.22"N	6°21'23.14"E 50° 5'56.27"N	6°20'41.38"E 50° 6'56.18"N
Species												
<i>Acinosporites cf. apiculatus</i> Streel, 1967	C										R	
<i>Ambitisporites avitus</i> Hoffmeister, 1959									R		R	C
<i>Aneurospora sp.</i>	R											
<i>Apiculiretusispora brandtii</i> Streel, 1964	A						R			A	C	
<i>Apiculiretusispora plicata</i> Streel, 1967	A									A	C	R
<i>Apiculiretusispora sp.</i>	C		A						R	A	R	C
<i>Archaeozonotriletes chulus</i> Richardson and Lister, 1969	R		R	R		R				R	R	R
<i>Cymbosporites asymetricus</i> Breuer et al., 2007	C											
<i>Cymbosporites sp.</i>	R											
<i>Diatomozonotriletes franklinii</i> McGregor and Camfield, 1982	R		R							R	R	
<i>Dibolisporites echinaceus</i> Richardson, 1965	R		R							R	R	
<i>Dibolisporites eifeliensis</i> McGregor, 1973										R		R
<i>Dibolisporites wetterdorfensis</i> Lanninger, 1968			C							R	R	R
<i>Dictyotriletes sp.</i>											R	
<i>Emphanisporites annulatus</i> McGregor, 1961	R										R	R
<i>Emphanisporites biradiatus</i> Stemans, 1989			R								C	
<i>Emphanisporites foveolatus</i> Schultz, 1968											R	
<i>Emphanisporites mcgregorii</i>							R				R	

