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A reappraisal of Mississippian (Tournaisian and Visean) adpression floras from central and northwestern Europe

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Abstract

Mississippian plant fossils are generally rare, and in central and northwestern Europe especially Tournaisian to middle Visean fossil floras are restricted to isolated occurrences. While sphenophytes and lycophytes generally are represented by only a few widespread and long-ranging taxa such as *Archaeocalamites radiatus*, *Sphenophyllum tenerrimum* and several species of *Lepidodendropsis* and *Lepidodendron*, Visean floras in particular show a remarkably high diversity of fern-like foliage, including filiform types (*Rhodea*, *Diplotmema*), forms with bipartite fronds (*Sphenopteridium*, *Diplopteridium*, *Spathulopteris*, *Archaeopteridium*), others with monopodial, pinnate fronds (*Anisopteris*, *Fryopsis*) and still others characterized by several-times pinnate fronds (e.g., *Adiantites*, *Triphyllopteris*, *Sphenopteris*, *Neuropteris*). Most of these leaf types have been interpreted as belonging to early seed ferns, whereas true ferns seem to have been rare or lacking in impression/compression floras. In the upper Visean, two types of plant assemblages can be distinguished, i.e., the northern Kohlenkalk-type and the south-eastern Kulm-type assemblage. Although several compression/impression taxa have been revised in recent years to provide a more uniform classification, additional parameters such as different modes of preservation and imprecise information on stratigraphic age hamper detailed interregional comparisons of Mississippian floras.

Key words: Carboniferous, lycophytes, paleogeography, pteridophylls, sphenophytes

Zusammenfassung

Pflanzenfossilien aus dem Mississippium sind generell selten. Floren aus dem Tournaisium bis Mittel-Viseum hat man in Zentral- und Nordwesteuropa nur in wenigen isolierten Lokalitäten gefunden. Diese Floren sind von Sphenophyten und Lycophyten (z.B. *Archaeocalamites radiatus*, *Sphenophyllum tenerrimum* sowie Taxa aus den Gattungen *Lepidodendropsis* und *Lepidodendron*) dominiert, welche alle eine weite geographische Verbreitung und lange geologische Reichweite aufweisen. Demgegenüber weisen die Floren des jüngeren Viseum eine bemerkenswerte Diversität an Pteridophyllen auf. Neben filiformen Wedeln (*Rhodea*, *Diplotmema*) kennt man aus diesen Floren unterschiedliche Typen einfach gegabelter (*Sphenopteridium*, *Diplopteridium*, *Spathulopteris*, *Archaeopteridium*) sowie einfach (*Anisopteris*, *Fryopsis*) und mehrfach gefiederter Wedel (e.g., *Adiantites*, *Triphyllopteris*, *Sphenopteris*, *Neuropteris*). Der überwiegende Teil dieser Wedel wird den frühen Samenfarne zugeordnet; Nachweise von echten Farnen sind ausgesprochen selten. Im oberen Viseum können zwei unterschiedliche Pflanzenassoziationen unterschieden werden: eine nördliche Kohlenkalk-Assoziation und eine südöstliche Kulm-Assoziation. Obwohl mehrere Pflanzentaxa des Mississippiums in Europa in den vergangenen Jahren revidiert worden sind, bleiben doch überregionale Vergleiche sowie die Erstellung einer einheitlichen Klassifikation durch die z.T. großen Unterschiede in der Erhaltung der Fossilien aus den einzelnen Fundpunkten sowie durch Probleme bei der Bestimmung des exakten stratigraphischen Alters der jeweiligen Fundschichten schwierig.

Schlüsselwörter: Karbon, Lycophyten, Paläogeographie, Pteridophyllen, Sphenophyten

1. Introduction

The first systematic descriptions of fossil plants from the Mississippian of central and northwestern Europe have been published more than 200 years ago (e.g., Schlotheim 1804, 1820; Geinitz 1854; Un-

ger 1856). A comprehensive account on the Mississippian macrofloras of the Moravian-Silesian Zone has been given by Stur (1875, 1877). An overview of Mississippian pteridophylls from Great Britain was published by Kidston (1923–25); additional material, including sphenopsids and lycopsids, has been de-

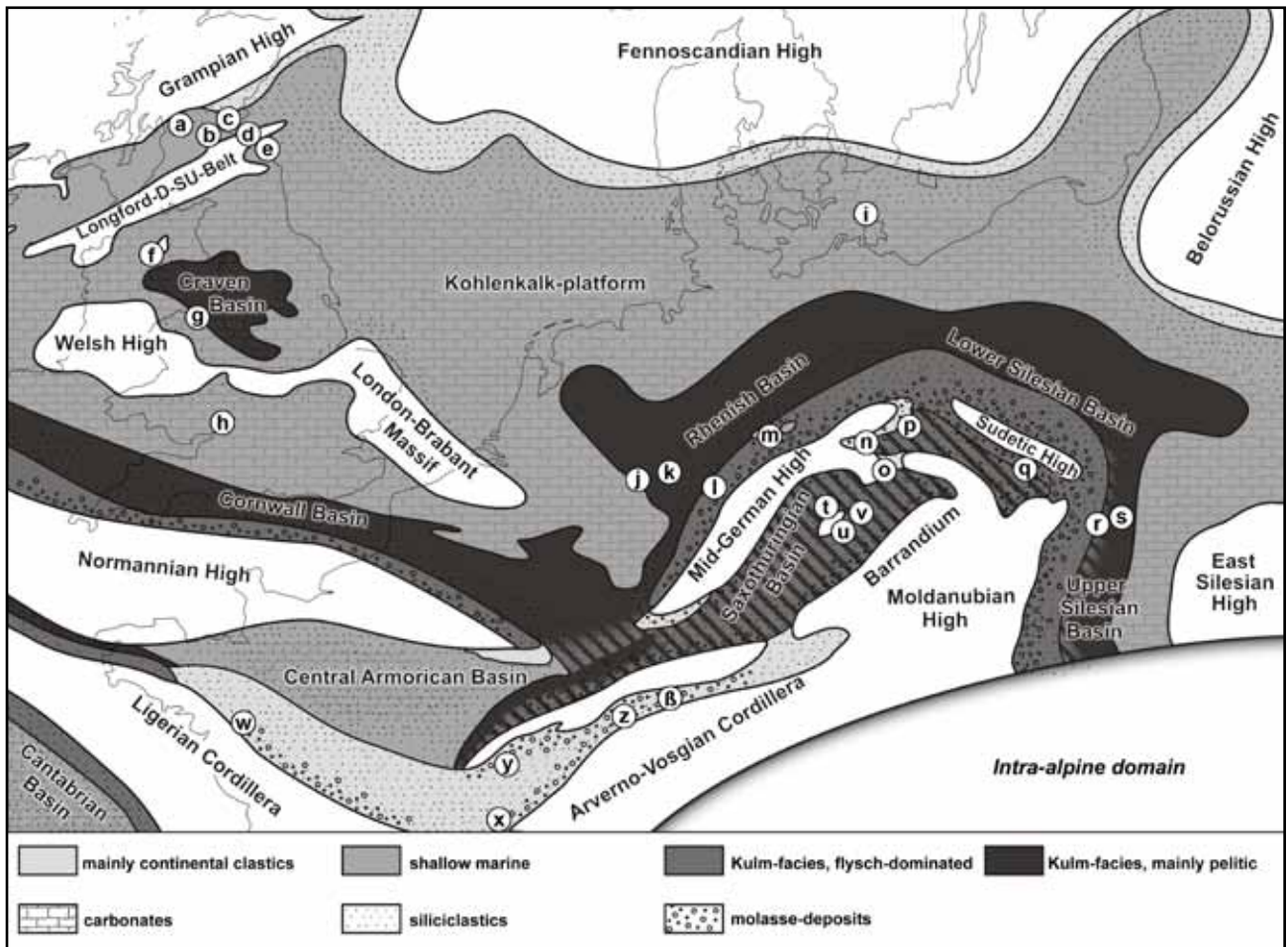


Figure 1: Paleogeographic reconstruction of central Europe during the Mississippian, showing facies distribution, prevailing lithologies and important plant fossil localities (map modified from Ziegler 1990). (a) Dumbartonshire; (b) West Lothian; (c) Pettycur; (d) East Lothian; (e) Berwickshire; (f) Isle of Man; (g) Gwaenysgor; (h) Forest of Dean; (i) Isle of Ruegen; (j) Aprath; (k) Becke-Oese and Neheim; (l) Lahn-Dill Syncline; (m) Harz Mountains; (n) Delitzsch; (o) Borna-Hainichen; (p) Doberlug-Kirchhain; (q) Walbrzych (former Waldenburg); (r) Stará Ves and Zalužne (former Altendorf and Mohradorf); (s) Ostrava (former Ostrau); (t) Saalfeld; (u) Hof; (v) Plauen; (w) Lower Loire Basin; (x) Esnot; (y) Roannais; (z) Giromagny; (β) Praeg. References: (a–e, x, y): Scott et al. (1984); (f): Walton (1931); (g): e.g., Walton (1926); (h): e.g., Lele & Walton (1962), Rowe (1988a,b,c); (i–p, t–v, β): Kerp et al. (2006); (q–s): Stur (1875, 1877); (w): Bureau (1913/1914); (z): Corsin et al. (1973).

scribed by Lele & Walton (1962), and Walton (1926, 1931), among other authors. In addition, numerous compression floras have been described from German Kulm deposits, mainly during the first half of the 20th century (e.g., Gothan 1927, 1949; Lutz 1933; Hartung 1938; Daber 1959), and from several localities in France (e.g., Bureau 1913/14; Corsin et al. 1973).

However, a detailed interregional comparison of the different Mississippian floras from Euramerica remains difficult. Several factors affecting the composition of a flora have to be taken into consideration (Scott & Galtier, 1996), including the mode of preservation and the precise stratigraphic age, the latter of which is often imprecisely known. An additional problem concerns the lack of a uniformly applied nomenclature for Mississippian plant adpressions. Several taxa have been revised in the last decades (e.g., Rowe 1988a,b,c, 1992a; Knaus 1994, Hübers 2012). However, the overall scarcity and poor preservation of the specimens hampers the revision of

additional taxa. Moreover, it is difficult to compare adpression floras that mostly have been collected many decades ago. Old museum collections are usually unsuitable for quantitative analyses, mainly due to a possible bias resulting from selective collecting. Moreover, the number of specimens is often limited and does not provide insight into intraspecific variability. Comparisons should therefore preferably be based on collections that were brought together by researchers with a similar collecting approach. However, hardly any Mississippian plant-fossil localities yielding rich and diverse floras are still accessible today. We are therefore able to provide only a relatively broad comparison of the Tournaisian and Viséan floras from central and northwestern Europe

2. Geological setting

A general sea-level rise during the Mississippian resulted in the flooding of most of the European de-

positional realms, and in many places fully marine conditions persisted throughout the entire Mississippian (Gursky 2006). The change in depositional setting had a profound impact on the plant fossil record and the modes of preservation. This is especially true of the Kulm basins (Fig. 1), in which residual basinal areas did hardly receive any terrigenous influx (Dvorak 1989), whereas, by contrast, sedimentary troughs flanking the advancing orogenic belts became filled via high-energy flysch- and molasse-type deposition (e.g., Gursky 2006). As a result, the majority of European Mississippian plant localities only yield poorly preserved impression and compression fossils. Anatomically preserved Mississippian plants have only been described from a few places, including Scotland and southern France. Silicification and phosphatization occurred in “starved” basinal areas of the Tournaisian, probably due to SiO₂-mobilisation from radiolarian ooze and distal volcanic ashes (Scott et al. 1984). In the Visean Kulm-sequences, a single occurrence of anatomically preserved plants has been reported from a road cut near Aprath, North-Rhine Westphalia (Rowe 1992b). By and large, the sedimentary settings in the Kulm basins did not favor preservation of plants. Moreover, the subsequent Variscan deformation caused more or less intense metamorphic overprinting of the Mississippian sedimentary record.

The occurrence of Kulm floras is restricted to parts of Germany, the Czech Republic and Poland, situated within the Rhenish, Saxothuringian, Intra-Sudetic and Silesian basins (Fig. 1). Coeval floras from Scotland (see Scott et al. 1984), England (Cleal & Thomas 1995), Wales (Walton 1931), the Loire Basin (Bureau 1913/1914), central France (see Scott et al. 1984), the Vosges Mountains (Corsin et al. 1973), the Black Forest (e.g., Sterzel 1907) and the Isle of Rügen (Kahlert 1993) occur in shallow marine or even continental settings. Well-known Serpukhovian floras, e.g., from Belgium (Stockmans & Willièrè 1953) or the Walbrzych and Ostrava formations (partly in Stur 1875, 1877), occur in paralic molasse deposits (see Walter 1995).

3. Composition of Tournaisian and Visean floras from central and northwestern Europe

3.1 Sphenopsids

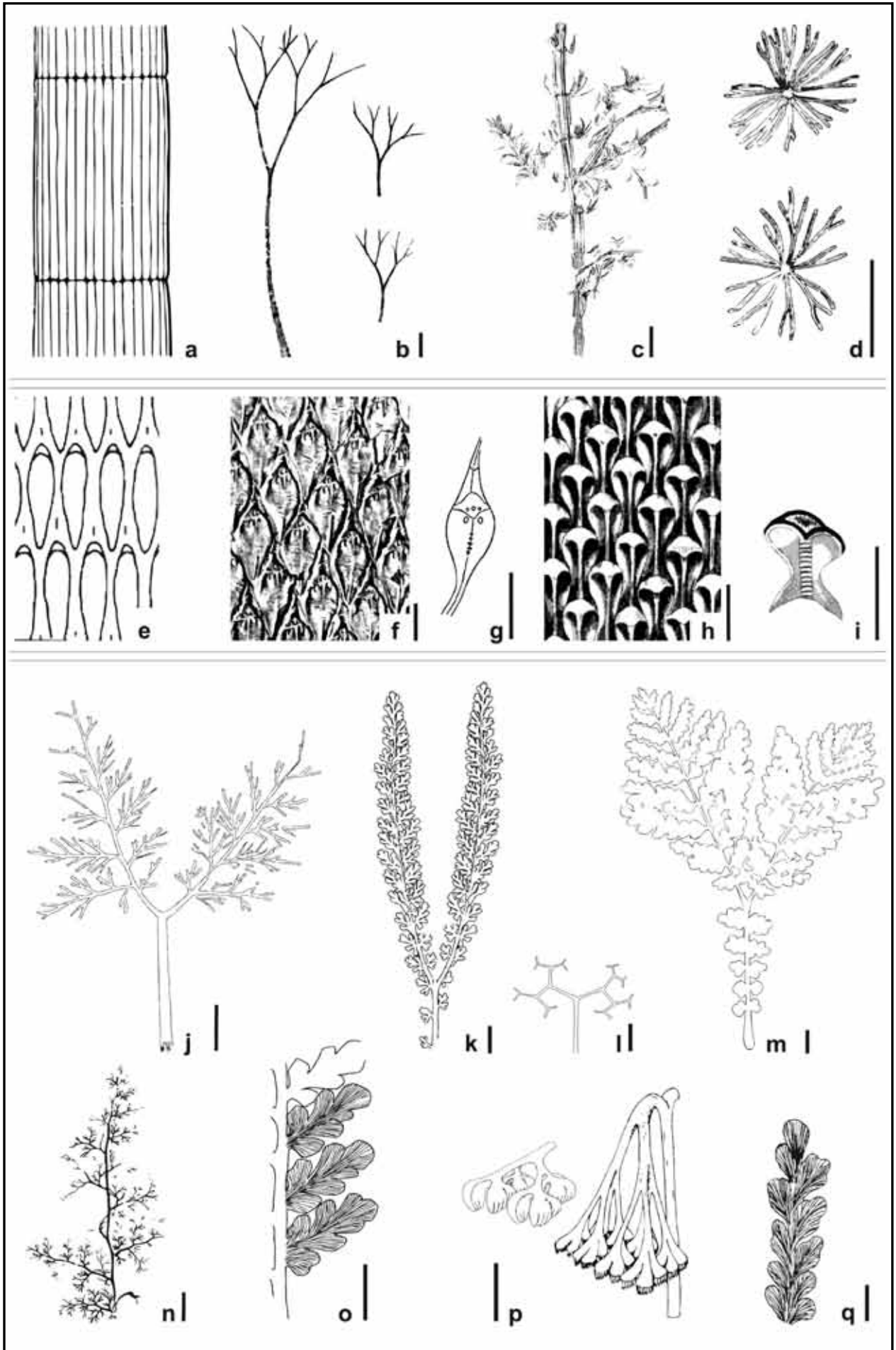
Archaeocalamites and sphenophylls range among the most common plant fossils from the European Mississippian. Most archaeocalamitean remains are stems. They can readily be distinguished from (eu-) calamitean stems, as the axial vascular bundles of two successive internodes are opposite at the nodes (Fig. 2a), whereas the bundles alternate at the nodes in calamites (Hirmer 1927). In compressions and

pith casts, the length/width-ratio of the internode segments may vary considerably from specimen to specimen; such vegetative characters are therefore considered of only limited diagnostic value (Lacey & Eggert 1964). Most sphenopsid remains from the Mississippian of Europe are assignable to *Archaeocalamites radiatus* (Brongniart) Stur (Fig. 4a, b). Although the validity of the genus *Archaeocalamites* has repeatedly been questioned (e.g., Remy & Remy 1978), the name is still widely being used today, and we refrain from detailing the taxonomic problems here. The slender single-veined leaves of *Archaeocalamites* Stur are up to 10 cm long (Jennings 1970) and dichotomize two to four times (Fig. 2b). *Archaeocalamites* in the Kulm facies are frequently found with preserved cortex and attached foliage. In this preservational mode, stems appear smooth and are slightly thickened at the nodes where the whorls of dense foliar segments emerge. Fructifications of *Archaeocalamites* are generally rare; they are assigned to *Pothocites* Paterson.

Stems of *Mesocalamites* Hirmer are believed to represent a morphological intermediate between archaeocalamitean and true calamitean stems because the internode bundles may be alternate or opposite at the nodes (Hirmer 1927). *Mesocalamites approximatifomis* (Stur) Hirmer has been recorded for the uppermost Visean sequences of the Moravian-Silesian zone (Boureau 1964) and from the Calciferous Sandstone Series of Linlithgowshire, Scotland. In addition, *Mesocalamites roemeri* Goepfert has been reported from Borna-Hainichen, Germany (Hartung 1938) and the Calciferous Sandstone Series of Scotland (see Crookall 1969). A second species from Borna-Hainichen has been described as *Mesocalamites* sp. (Hartung 1938).

“True” calamites first appear in the late Mississippian (Taylor et al. 2009). Several specimens from the Visean, which have previously been described as *Calamites* Schlotheim, were later transferred to *Archaeocalamites*, *Protocalamites* Goebel (anatomically preserved) and *Mesocalamites* (see Hartung 1938; Boureau 1964; Bateman 1991).

Among the sphenophylls, almost all specimens found in the Mississippian of central and northwestern Europe are assignable to a group of taxa that is characterized by dichotomizing, narrow to linear leaves. The most widespread form is *Sphenophyllum tenerimum* Ettingshausen ex Helmhacker (Havlina 1982) (Figs 2c, 4c). This species is characterized by up to 5 mm thick, ribbed axes with nodal whorls of relatively small leaves (4–11 mm), which are either simple or once to twice dichotomously divided into linear slips (Fig. 2d). Other Tournaisian and Visean sphenophylls such as *S. arcticum* Nathorst, *S. daberii* Kahlert, *S. kossbergense* Gothan and *S. pachycaule* Daber (including *S. subtenerimum* Friese et Gothan) are mostly based on isolated, fragmentary specimens that differ only slightly from *S. tenerimum*, or may simply reflect different modes of pre-



servation; for a detailed comparison of these taxa see Havlena (1982). *Sphenophyllum* Brongniart species possessing a more distinct, but still dissected, leaf lamina include *S. saxifragaefolioides* Leyh from Geigen near Hof (Lutz 1933) and *S. stimulosum* Hartung from Borna-Hainichen; the latter form apparently produced both entire-margined and dissected to linear leaves similar to *S. tenerrimum* (Hartung 1938). In addition, Havlena (1982) suggested that the oldest occurrence of *S. cuneifolium* (Sternberg) Zeiller may well date back into the Visean based on material figured by Zimmermann (1956). Fertile remains of *Sphenophyllum* are rare in Tournaisian and Visean deposits; they have been attributed to *Bowmanites* Binney (also described as *Sphenophyllostachys* Seward) and *Cheirostrobos* Scott (Boureau 1964).

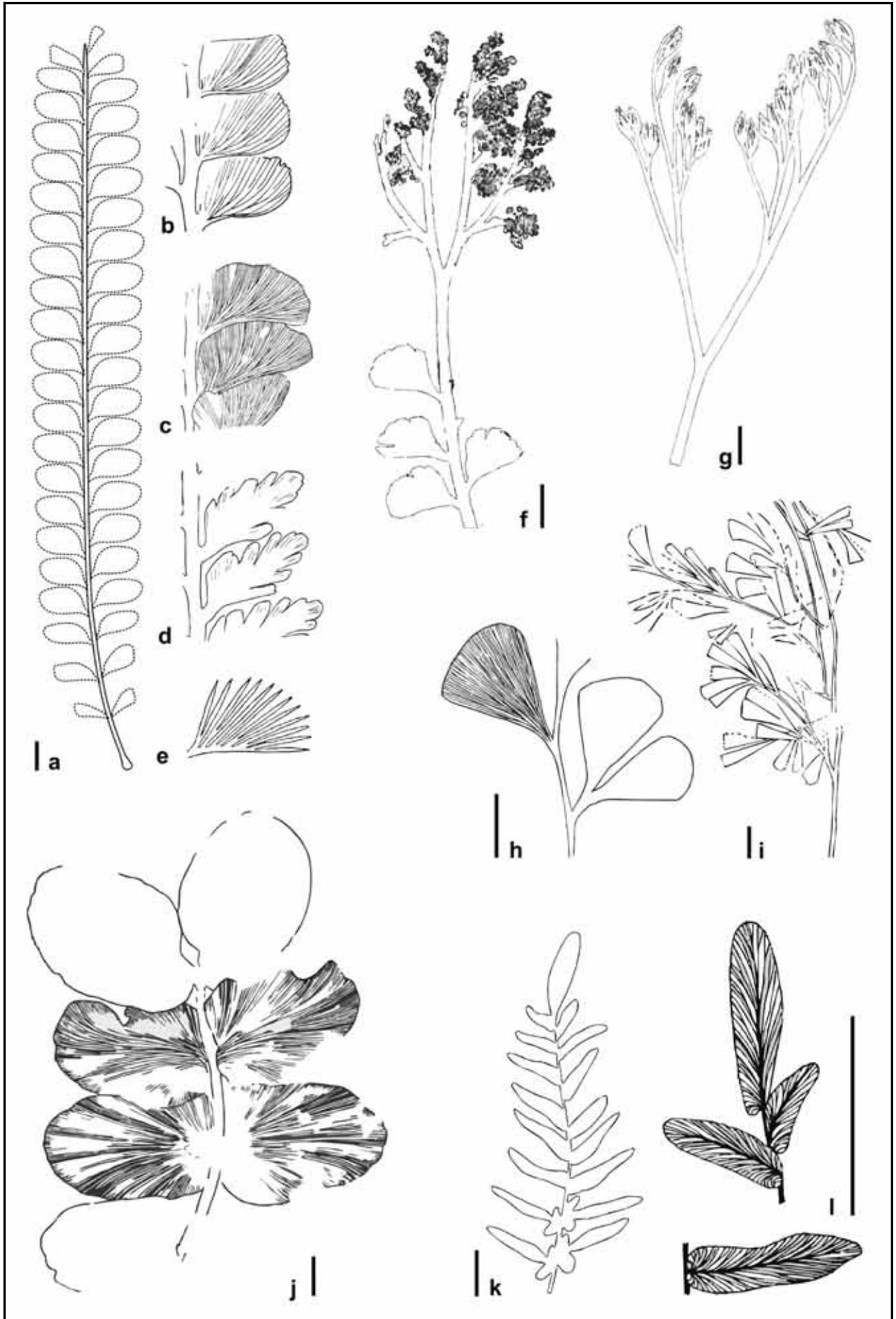
3.2 Lycopoids

Mississippian lycopoids include both herbaceous forms (e.g., *Selaginellites* Zeiller, *Oxroadia* Alvin) and arborescent taxa (e.g., *Lepidodendron* Sternberg, *Lepidophloios* Sternberg, *Eskdalia* Kidston, *Sublepidodendron* Nathorst ex Hirmer, *Lepidodendropsis* Lutz). Some of these forms are regarded as Devonian relict taxa (i.e. Protolopodendrales), while others appear to be early representatives of the Lepidodendrales. The protolopodendralean genus *Lepidodendropsis* Lutz has been established based on Tournaisian/early Visean fossils from Hof, Bavaria (Lutz 1933). The genus also occurs in the upper Tournaisian of Wales (Cleal & Thomas 1995), and possibly the Vosges Mountains, France (Corsin et al. 1973). The slender leaf cushions are arranged in very steep spirals, which sometimes may appear like vertical and horizontal rows, and the leaf scars are situated in the uppermost portion of the cushion (Thomas & Meyen 1984) (Fig. 2e). The Protolopodendrales are believed to represent the first lycophyte group to develop a shrubby to small arborescent habit (Thomas 1978).

Apart from decorticated specimens (*Knorria*-type preservation), the compressions of true lepidodendrids can be classified into two groups: (1) forms with broadly rhomboidal leaf cushions and (2) forms with narrowly rhomboidal leaf cushions. The most commonly encountered types in the former group are *Lepidodendron veltheimii* Sternberg and *L. volkmannianum* Sternberg, two taxa that are characterized by prominent more or less asymme-

trical leaf cushions, each with a distinct keel and transverse wrinkles (Crookall 1964). *Lepidodendron veltheimii* is characterized by spirally arranged leaf-cushions (Figs 2f, 4d), whereas they are organized in vertical rows in *L. volkmannianum* (Fig. 2h). The form of the leaf cushions in *L. veltheimii* varies considerably, and the cushions can be separated from one another by massive strings of bark depending on the degree of maturation of the stem (Crookall 1964). The leaf cushions of both species usually show characteristic scars and cicatricules (Fig. 2g, i). Common representatives of small lepidodendrids with slender leaf cushions are *Lepidodendron spetsbergense* Nathorst and *L. lossenii* Weiss. Both forms have straight, elongated fusiform leaf cushions that normally display only few diagnostic features (Crookall 1964). Isolated parts of lepidodendrid underground organs (*Stigmara* Brongniart) and leaves (*Lepidophyllum* Cassini / *Lepidostrobophyllum* Hirmer) are abundant. Apart from these widespread taxa, compressions of lycopoids are generally rare in the Mississippian of central and northwestern Europe, although several taxa have been described. *Lepidophloios* is known only from a few isolated occurrences of *L. laricinus* Sternberg (Patteisky 1929; Kerp et al. 2006), and *L. cf. kilpatrickensis* Smith, which has been described from the middle Visean of Loch Humphrey Burn, Scotland (Cleal & Thomas 1995). *Bothrodendron kidstonii* (Weiss) Nathorst has been reported from Delitzsch, Saxony (Kahlert 1975), and Becke-Oese, North-Rhine Westphalia (person. observation). Additional species have been described from Wardie Shore, Edinburgh, Scotland (*Bothrodendron wardiense* Crookall; Cleal & Thomas 1995) and the Lower Loire Basin, France (*Bothrodendron depereti* Vaffier; Bureau 1913/1914). *Lepidobothrodendron dobrilugkianum* (Gothan) Daber is based exclusively on material from Doberlug-Kirchhain, Brandenburg (Daber 1959). *Ulodendron* Lindley et Hutton occurs in the Mississippian of Midlothian and Linlithgowshire, Great Britain (Crookall 1964) and the Vosges Mountains, France (Corsin et al. 1973). Other lycopoids that have been reported from the Tournaisian and Visean of Great Britain include *Archaeosigillaria* Kidston, *Lycopodites* Lindley et Hutton, *Clwydia* Lacey, *Eskdalia* Kidston and *Selaginellites* Zeiller (Crookall 1964; Cleal & Thomas 1995). These lycopoids are generally rare; *Eskdalia* and *Selaginellites*, however, are abundant in the upper Visean of

Figure 2: Common plant fossils of the Kulm facies. (a): archaeocalamitean stem (redrawn from Crookall 1969); (b): archaeocalamitean foliage segments (based on Stur 1875: pl. IV, figs 5, 8); (c): *Sphenophyllum tenerrimum* (based on Stur 1877: pl. VII, fig. 2); (d): isolated leaf whorls of *S. tenerrimum* (after Stur 1877: pl. VII, figs 9, 10); (e): Phyllotaxy of *Lepidodendropsis* (redrawn from Thomas & Meyen 1984); (f, g): *Lepidodendron veltheimii*; (f) stem (based on Stur 1877: pl. XIX, fig. 6), (g) leaf scar (after Crookall 1964); (h, i): *Lepidodendron volkmannianum*; (h) stem, (i) leaf scar (after Crookall 1964); (j): *Diplotmema subgeniculatum* (after Stur 1883); (k): *Diplopteridium*-/ *Sphenopteridium*-type frond morphology; (l): fertile median rachis associated with *Archaeopteridium* and *Diplopteridium*; (m): frond morphology of *Archaeopteridium tschermakii* (after Rowe 1992a); (n): *Rhodea goepperti* (based on Stur 1875: pl. XI, fig. 7b); (o): *Sphenopteridium dissectum*; (p): cupulate (left) and microsporangiate (right) organs of *Diplopteridium* (both after Rowe 1992a); (q): isolated pinna of *Archaeopteridium tschermakii* (after Rowe 1992a). – Scale bars = 1 cm.



Drybrook, Forest of Dean, England. *Lepidocladus fuisseensis* Vaffier and *Sublepidodendron robertii* (Nathorst) Chaloner et Bureau occur in Mississippian deposits of France (Bureau 1913/1914; Corsin et al. 1973).

3.3 Pteridophylls

Pteridophylls are the most abundant and diverse group of plant fossils in the Mississippian of central and northwestern Europe. However, only in rare cases is there clear evidence of the systematic affinities of a particular foliage type (i.e., ferns or pteridosperms). As a result, fern-like foliage is listed here together and grouped based exclusively on macro-morphological features.

3.3.1 Filiform foliage

Probably the broadest-defined foliage type from Mississippian deposits is *Rhodea* Presl (Figs 2n, 4e, f). The genus initially served as a repository for all kinds of fronds with filiform or very slender, single-veined pinnules (see Jennings 1976). However, characteristically forked fronds have subsequently been included in *Diplotmema* Stur (Fig. 2j) (Stur 1877). Other species originally included in *Rhodea* have later been transferred to other genera such as *Ootheca* Nathorst, *Telangium* Benson, *Urnatopteris* Kidston, and *Zeillera* Kidston after details on the reproductive structures had become available. Many *Rhodea*-type foliage fossils are fragmentary and do not show features of sufficient clarity to allow a safe generic assignment. In several recent publications on Mississippian compression floras, the authors have avoided tackling this taxonomic problem by using informal terms such as “cf. *Rhodea* sp. foliage type” (e.g., Meyer-Berthaud & Rowe 1997).

3.3.2 Bipartite fronds

This common complex of pteridophylls is comprised of small- to medium-sized, once to three times pinnate fronds characterized by a proximal dichotomy of the rachis. The genera included in this group are discriminated based on their frond architecture, structural elements of the main axis (e.g., longitudinal striations, transverse bars), venation pattern, and fertile structures (if known). *Sphenopteridium* Schimper is a genus characterized by a comparatively acute-angled bifurcation and dense, fine, and dichotomizing venation of equal strength (Kidston 1923). Two common species are *S. dissectum* (Goeppert

(Figs 2o, 4i) and *S. pachyrrhachis* (Goeppert) Schimper (Kerp et al. 2006). *Diplopteridium* Walton (Figs 2k, 4g, h) comprises fertile *Sphenopteridium*-type fronds in which a third, leafless fertile spike extends from the lower side of the frond slightly below the bifurcation of the rachis; this repeatedly dichotomizing spike (Fig. 2l) bears either cupulate female or synangiate male reproductive structures (Fig. 2p) (Lele & Walton 1962; Rowe 1988a). *Diplopteridium* was long known only from British floras; the first records of this genus from the upper Visean of the Rhenish Kulm basin have been published by Rowe (1992b) and Kerp et al. (2006).

Another genus similar to *Sphenopteridium* is *Spathulopteris* Kidston, which differs from the former in having a smooth rachis lacking longitudinal striations or transverse ridges (Kidston 1923). *Spathulopteris* fronds were believed to be dichotomously divided and leafless below the bifurcation. However, the morphologies *Spathulopteris* may be more heterogeneous and a clear distinction from *Sphenopteridium* more difficult than currently recognized (see Hübers 2012). *Spathulopteris* is mainly known from Mississippian strata of Great Britain, but is also common at Becke-Oese, western Germany (unpublished data; see Hübers 2012). A few specimens have also been described from eastern Germany and the Moravian-Silesian Zone (Hartung 1938; Stur 1875).

Archaeopteridium tschermakii (Stur) Kidston emend. Rowe (Fig. 2m, q) is another well-known and widely distributed bipartite pteridophyll from the Mississippian. Rowe (1992a) has given a detailed emendation of the genus and its type species based on material from the Visean Drybrook Sandstone, Forest of Dean, UK. The form differs from *Sphenopteridium* primarily in that fronds are more complex and the frond portions above the bifurcation are more broad-lanceolate in outline. Reproductive structures of *Archaeopteridium* Kidston are borne on dichotomously branched leafless spikes comparable to those seen in *Diplopteridium* (Fig. 2l). Based on the morphology of the fertile structures referred to these bipartite foliage forms, most taxa are today interpreted as belonging to the seed-fern order Lyginopteridales.

3.3.3 Monopodial once-pinnate fronds

Anisopteris (Oberste-Brink) Hirmer (also known as *Rhacopteris* W.P. Schimper) consists of characteristically once-pinnate, linear fronds with circular to rhomboidal, asymmetrical pinnules (Fig. 3a) with an open dichotomous venation (see Lacey 1962: pl. II,

Figure 3: Common plant fossils of the Kulm facies. (a): Frond morphology of *Anisopteris*; (b): *A. lindseaeformis* (after Galtier et al. 1998: p. 200, fig. 2B); (c): *A. inaequilatera* (after Kidston 1923: pl. LI, fig. 3); (d): “*Rhacopteris transitionis*” (after Kidston 1923: pl. LI, fig. 4); (e): *A. petiolata* (after Lacey 1962); (f): “*Rhacopteris paniculifera*” (after Stur 1883); (g): isolated cupulate organ (*Stannostoma huttonense*, after Long 1962); (h): *Adiantites tenuifolius* (drawing based on specimen 1875-03-99, Stur collection in the GBA Vienna); (i): *Adiantites machanekii* (after Walton 1931); (j): *Fryopsis polymorpha* (after Stur 1875: pl. XIII, fig. 1, originally named *Cardiopteris frondosa*); (k, l): *Neuropteris antedecens* (both after Havlena 1969). – Scale bars = 1 cm.

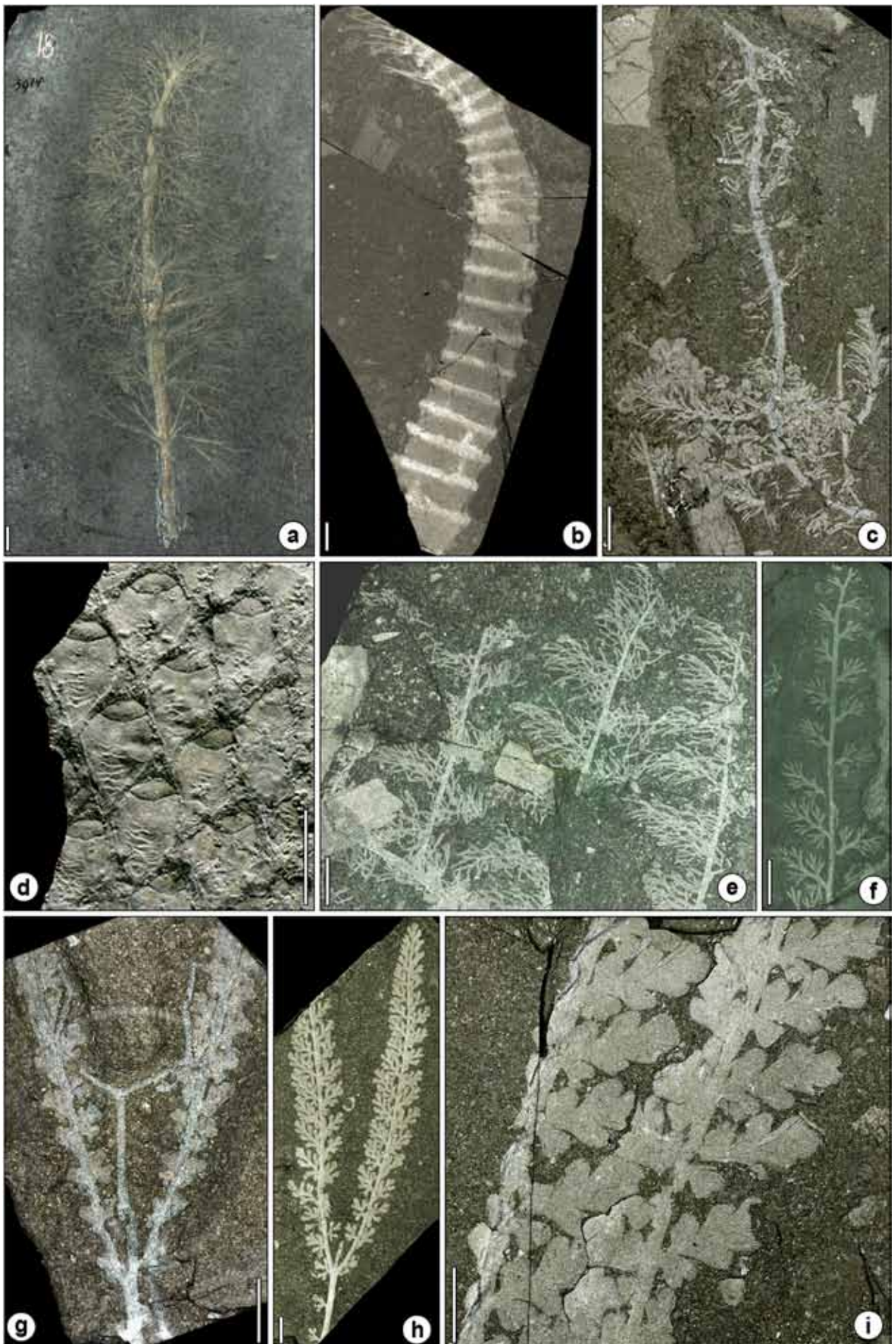


fig. 1). Common and relatively well-known *Anisopteris* species include *A. circularis* (Walton) Hirmer (Fig. 5g), *A. lindseaeformis* (Bunbury) Kidston (Fig. 3b), *A. inaequilatera* (Goeppert) Stur (Fig. 3c) – all with entire-margined pinnules – and *A. petiolata* (Goeppert) Schimper (Fig. 3e) with dissected pinnules. The taxonomic status of other species continues to be problematic; several of the species described from Great Britain, Germany, and the Moravian-Silesian Zone may be conspecific with one of the species listed above [*A. robusta* (Kidston) Hirmer = *A. petiolata*; *A. machanekii* (Stur) Hirmer = *A. lindseaeformis*] or belong to different genera [e.g., *A. subcuneata* (Kidston) Hirmer]. *Anisopteris semicircularis* (Lutz) Hirmer is based on an unidentifiable specimen (Hübers 2012), and *Rhacopteris transitionis* Stur (Figs 3d, 5c) may represent an immature pteridosperm frond. Two fertile *Anisopteris* fronds have been described to date, one as “*Rhacopteris paniculifera* Stur” (belonging to *Anisopteris lindseaeformis*; see Hübers 2012) (Fig. 3f) from the Moravian-Silesian zone and a second as “*Anisopteris fertilis* (Walton) Hirmer” from the Calciferous Sandstone Series of Scotland. Both specimens show a main axis that bifurcates near the apex, with the two emerging secondary branches bearing pinnately arranged, densely spaced clusters of sporangiate organs. *Anisopteris fertilis*, however, lacks sterile pinnules below the bifurcation, and a relationship to the genus remains speculative. The biological affinities of *Anisopteris* with either ferns, pteridosperms, or even progymnosperms have long remained unclear. Characteristic stem anatomy, however, indicates affinities with lycopodioid seed ferns (Galtier et al. 1998).

Another foliage type with once pinnate, linear fronds is the pteridosperm genus *Fryopsis* (Goeppert) Wolfe (Figs 3j, 5b) (Hübers & Kerp 2011). Apart from being considerably larger, *Fryopsis* fronds differ from *Anisopteris* in that their heart-shaped pinnules are attached to the rachis at nearly right angles and have a more symmetrical, radiating venation. *Fryopsis* occurs in Mississippian deposits of central Europe, but is absent in coeval strata of Great Britain (Hübers & Kerp 2011).

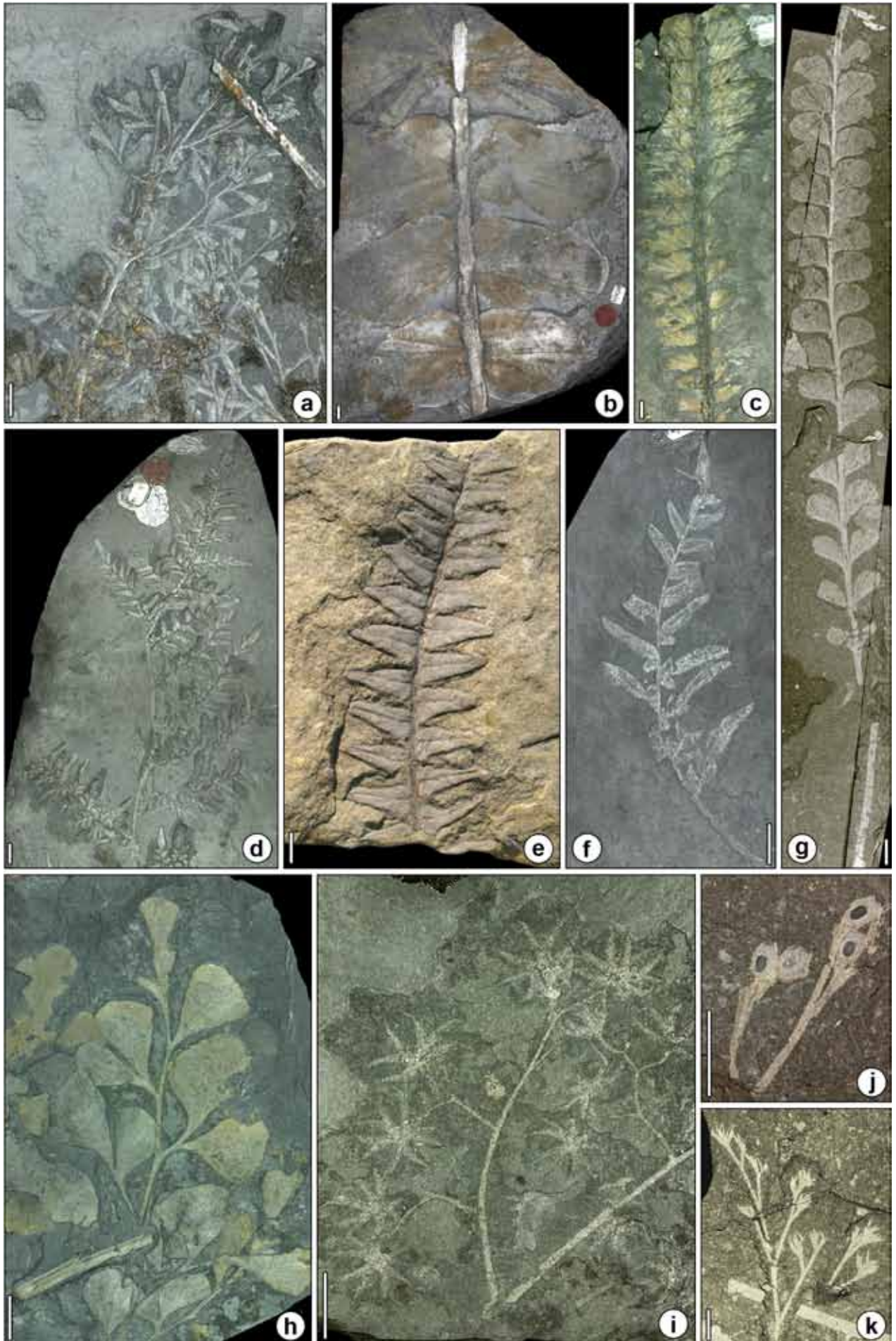
3.3.4 Several-times pinnate monopodial fronds

The widespread genus *Adiantites* Goeppert consists of lax, tri- to quadripinnate fronds with a slender rachis. Pinnules are obovate to wedge-shaped and constricted at the base to form a more or less distinct pedicel. The veins radiate from the pinnule base and dichotomize repeatedly in their course to the margin, thus forming an equal and dense venation pattern (Kidston 1923). The most common species are *A. tenuifolius* (Goeppert) Schimper (including *A. antiquus* (Ettingshausen) Stur; see Hübers 2012) (Figs 3h, 5h) and *A. machanekii* Stur (Figs 3i, 5a), both based on material from the Mississippian of the Czech Republic (Stur 1875/1877). *Adiantites tenuifolius* has broader pinnules with a convex, rounded apex, while those of *A. machanekii* are very slender, wedge-shaped, and have an almost flat truncate apex. The systematic affinities of *Adiantites* remain unknown.

Triphyllopteris Schimper emend. Knaus is used for fronds with a complex architecture. Knaus (1994) has given a detailed emendation of the genus based on Gothan's (1927) specimens from the Kossberg near Plauen. The pinna length gradually decreases towards the frond apex, giving the frond a characteristic triangular outline. Pinnule shape is highly variable, whereas the degree of complexity (size, degree of lobation) of the pinnules decreases from the proximal part of the main rachis towards the apex, as well as from the proximal to distal portion of individual pinnae (Knaus 1994). All North American fossils previously included in *Triphyllopteris* have been transferred to the genus *Genselia* Knaus (Knaus 1994).

Early representatives of *Sphenopteris* (Brongniart) Sternberg and *Neuropteris* (Brongniart) Sternberg also occur in the Mississippian of central and northwestern Europe. Both genera are heterogeneous morphotaxa that reached peak diversity during the Pennsylvanian. *Sphenopteris* is characterised by tri- to quadripinnate fronds and pinnules with a constricted base. One common species is *Eusphenopteris foliolata* (Stur) Van Amerom. *Neuropteris* is characterised by ovoid to elongate, usually entire-

Figure 4: Common plant fossils of the Kulm facies. (a): *Archaeocalamites radiatus* (Brongniart) Stur, Altendorf (Stará Ves; Czech Republic), ?upper Visean. Collection of the Geological Survey of Austria, Vienna, 1875-03-33, figured in Stur (1875: pl. V, fig. 2); (b): *Archaeocalamites radiatus* (Brongniart) Stur, Becke-Oese quarry (northern Rhenish Slate Mountains), upper Visean. Collection Sommer/Paleobotany Research Group Münster, OES-328; (c): *Sphenophyllum tenerrimum* Ettingshausen ex Helmhacker, Becke-Oese quarry (northern Rhenish Slate Mountains), upper Visean. Collection Sommer/Paleobotany Research Group Münster, OES-150; (d): *Lepidodendron veltheimii* Sternberg, Becke-Oese quarry (northern Rhenish Slate Mountains), upper Visean. Collection Sommer/Paleobotany Research Group Münster, OES-10; (e): *Rhodea machanekii* (Ettingshausen) Stur, Becke-Oese quarry (northern Rhenish Slate Mountains), upper Visean. Collection Sommer/Paleobotany Research Group Münster, OES-134; (f): *Rhodea* sp., Mohradorf (Zalužne; Czech Republic), ?upper Visean. Collection of the Geological Survey of Austria, Vienna, 1875-03-68, figured in Stur (1875: pl. X, fig. 4) as *Rhodea moravica* (Ettingshausen) Stur; (g): *Diplopteridium teilianum* (Kidston) Walton with fertile third rachis, Becke-Oese quarry (northern Rhenish Slate Mountains), upper Visean. Collection Sommer/Paleobotany Research Group Münster, OES-311; (h): *Diplopteridium teilianum* (Kidston) Walton, Becke-Oese quarry (northern Rhenish Slate Mountains), upper Visean. Collection Sommer/Paleobotany Research Group Münster, OES-20, figured in Kerp et al. (2006: pl. IV, fig. 1); (i): *Sphenopteridium dissectum* (Goeppert) Schimper, Becke-Oese quarry (northern Rhenish Slate Mountains), upper Visean. Collection Sommer/Paleobotany Research Group Münster, OES-135, figured in Kerp et al. (2006: pl. III, fig. 4). – Scale bars = 1 cm.



margined pinnules that are attached to the axis by a short pedicel. The typical neuropterid pinnule has a cordate base (Clea & Shute 1995). *Neuropteris antiqua* (Stur) Sterzel (Fig. 5e), *N. Ioshii* Brongniart, *N. broillii* (Lutz) Hartung and *N. antecessens* Stur emend. Havlena (Figs 3k, l, 5d, f) have been described from the Kulm sequences in the Silesian and Saxothuringian basins (Hartung 1938; Havlena 1969). The latter species has also been reported from the upper Visean of Wales (Walton 1931). *Neuropteris*-foliage is generally considered to belong to medullosan seed-ferns. The occurrence of *Neuropteris*-foliage in Visean deposits, however, predates the earliest unequivocal anatomically preserved medullosan stem, which has been reported from the lower Namurian A (Chesterian) of the Fayetteville Shale, Arkansas (Dunn et al. 2003).

3.4 Axes

Leafless stem fragments frequently occur in Mississippian deposits of central and northwestern Europe. Many of these fossils are unidentifiable; others, however, display characteristic surface and structural features such as distinct patterns formed by cortical sclerenchyma (e.g., transverse sclerotic bars, nests, longitudinal striae, *Dictyoxylo-* or *Sparganium*-type cortex) that allow an assignment to a particular plant group. For instance, axes referred to *Caulopsis punctata* Goeppert from the Visean of Doberlug-Kirchhain have later been documented in organic connection with foliage assigned to *Sphenopteris simplex* Gothan et Hartung (Daber 1959). Most of these identifiable axes are today known to have been produced by lyginopteridalean seed ferns.

3.5 Isolated fructifications

Mississippian deposits have yielded a variety of fertile structures, most of which assignable to seed ferns. These structures have received considerable scientific attention based on their significance as transitional between the earliest seed plant reproductive structures from the Upper Devonian and the well-known fructifications of the Pennsylvanian. The

most common fertile remains in Mississippian deposits are branch systems bearing terminal cupules (e.g., *Calymmatotheca* Stur [Fig. 5i], *Stamnostoma* Long [Fig. 3g, 5k]) which are interpreted as belonging to the Lyginopteridales. In rare instances, cupulate organs have been discovered with the seeds/ovules still in place (Fig. 5j).

4. Interpretation

Mississippian plant fossils are generally rare in central and northwestern Europe, and especially Tournaisian to middle Visean floras are restricted to a few isolated occurrences. Their biostratigraphic significance is overall limited, since many of the widespread compression plant taxa, e.g., *Archaeocalamites*, *Adiantites*, *Sphenopteridium*, *Rhacopteris*, and *Rhodea*-type foliage, represent long-ranging elements occurring in middle Tournaisian to late Visean floras. Devonian “relict taxa”, such as protopityalean/aneurophytalean progymnosperms and members of the Cladoxylales, are restricted to permineralized floras in Tournaisian deposits. The overall differences between Tournaisian and Visean floras may also be based on differences in the taphonomic settings in which they occur. Moreover, the lack of a uniform taxonomy aggravates a closer comparison between the anatomically preserved plant assemblages and impression/compression floras. Major changes in the compression assemblages concur with the transition to paralic conditions during the Namurian A. Patteisky (1957) has established a biostratigraphic zonation of the Visean to Westphalian record of the genus *Lyginopteris* that also includes *Sphenopteris*- and *Diploptema*-type foliage from the Kulm basins.

Mississippian floras reflect a distinct palaeophytogeographic pattern. While compression and petrification Kulm floras from the lower and middle Tournaisian (Bitterfeld/Saalfeld area, Oberrödinghausen) are generally similar in appearance to coeval floras from the UK, southern France, and the USA (see Scott et al. 1984; Meyer-Berthaud & Rowe 1997), the late Visean Kulm floras show pronounced regional differences. Two major association types are distin-

Figure 5: Common plant fossils of the Kulm facies. (a): *Adiantites machanekii* Stur, Tschirm (Cermná ve Slezsku; Czech Republic), ?upper Visean. Collection of the Geological Survey of Austria, Vienna, 1875-03-105, figured in Stur (1875: pl. XVII, fig. 6) as *Adiantites Machaneki*; (b): *Fryopsis polymorpha*, (Goeppert) Wolfe Altendorf (Stará Ves; Czech Republic), ?upper Visean. Collection of the Geological Survey of Austria, Vienna, 1875-03-79, figured by Stur (1875: pl. XIV, fig. 1) as *Cardiopteris frondosa* (Goeppert) Stur; (c): “*Rhacopteris transitionis*” Stur, Altendorf (Stará Ves; Czech Republic), ?upper Visean. Collection of the Geological Survey of Austria, Vienna, 1875-03-113, figured in Stur (1875: pl. VIII, fig. 5); (d): *Neuropteris antecessens* Stur emend. Havlena, Mohradorf (Zalužne; Czech Republic), ?upper Visean. Collection of the Geological Survey of Austria, Vienna, 1875-03-86, figured in Stur (1875: pl. XV, fig. 5); (e): *Neuropteris antiqua* (Stur) Sterzel, Borna (Saxony), upper Visean. Collection of the Museum of Natural History Chemnitz, figured in Sterzel (1918: pl. II, fig. 40); (f): *Neuropteris antecessens* Stur emend. Havlena, Mohradorf (Zalužne; Czech Republic), ?upper Visean. Collection in the Geological Survey of Austria, Vienna, 1875-03-83; (g): *Anisopteris circularis* (Walton) Hirmer, Becke-Oese quarry (northern Rhenish Slate Mountains), upper Visean. Collection Sommer/Paleobotany Research Group Münster, OES-169; (h): *Adiantites tenuifolius* (Goeppert) Schimper, Altendorf (Stará Ves; Czech Republic), ?upper Visean. Collection of the Geological Survey of Austria, Vienna, 1875-03-99, figured in Stur (1875: pl. XVI, fig. 4) as *Adiantites antiquus* Stur; (i–k): Isolated cupulate organs, (i) Mohradorf (Zalužne; Czech Republic), ?upper Visean. Collection of the Geological Survey of Austria, Vienna, 1875-03-02, figured in Stur (1875: pl. I, fig. 2) as a fern fructification, later assigned to *Calymmatotheca haueri* (Stur, 1877), (j, k) Becke-Oese quarry (northern Rhenish Slate Mountains), upper Visean. Collection Sommer/Paleobotany Research Group Münster, OES-154 and OES 373. – Scale bars = 1 cm.

guished. Floras from the siliciclastic flysch- and molasse-deposits in the eastern part of Germany (e.g., Borna-Hainichen, Doberlug-Kirchhain, Kossberg near Plauen) and the Moravian-Silesian zone (e.g., Stará Ves [Altendorf], Zalužne [Mohradorf]) are characterised by the abundance of *Fryopsis*, *Cardiopteridium* Nathorst, *Triphyllopteris* and early representatives of *Neuropteris* and *Sphenopteris*. These genera are rare or absent from floras west of the Mid-German Crystalline Rise (e.g., Becke-Oese, Aprath, Neheim), which are characterised by abundant remains of *Diplopteridium* and associated fructifications that are otherwise absent in central Europe, but common in coeval floras from Great Britain. Similar regional differences have also been documented for the microfloras, although these differences have been suggested to reflect a taphonomical bias rather than regional vegetation patterns (Jäger & Wierich 2006). However, the distribution patterns correspond well with the palaeogeographic reconstruction (Fig. 1) in that the northern Kohlenkalk facies and its clastic derivatives (in Great Britain, western and northern Germany) and the south-eastern siliciclastic facies (in eastern Germany, Czech Republic, southern Poland) each have yielded characteristic plant assemblages, principally separated from one another by the northern edge of the Mid-German Crystalline Rise and its accompanying clastic wedge. On a greater scale, all localities belong to the South Euramerican *Vallatisporites* Region, which is supposed to represent the Early Carboniferous (sub)tropical dry climatic belt (Van der Zwan 1981). The phytogeographic pattern seen in the Mississippian macrofloras is thus probably not a result of large-scale climatic differences, but may possibly be linked to the presumably much more stressed and unstable environmental conditions in the tectonically active advancing orogenic belt compared to the uniform and stable conditions along the southern margin of the Laurasian landmass. Local differences in the compositions of the southern Kulm floras have also been interpreted as representing differing associations of hydro- to mesophile biotopes (Remy & Remy 1977).

5. Summary

Mississippian compression floras from central and northwestern Europe are overall dominated by sphenophytes (*Archaeocalamites*, slender-leaved sphenophylls), lycophytes (*Lepidodendropsis*, *Lepidodendron*), and pteridophylls. Based on frond morphology and venation, the latter fossils can be grouped into (a) filiform foliage types, e.g., *Rhodea*, *Diploptema* pro parte; (b) monopodial, simple pinnate fronds, e.g., *Anisopteris* and *Fryopsis*; (c) bifurcate fronds, e.g., *Sphenopteridium*, *Diplopteridium*, *Spathulopteris*, and *Archaeopteridium*; and (d) simple, up to four times pinnate frond types, e.g., *Adiantites*, *Triphyllopteris*, *Sphenopteris*, and *Neuropteris*.

A pteridospermous affinity has been established or postulated for most of these taxa, with the Lyginopteridales being the most common group of pteridosperms. True ferns are rare elements in compression floras. Major floristic changes from the Tournaisian to the late Visean include the disappearance of the Devonian relict taxa and increasing appearance and diversification of seed-fern taxa. Another change concurs with the transition from the deeper-basinal Kulm-type deposition to paralic conditions, when early representatives of the typical Pennsylvanian coal-forming assemblages make their first appearance (e.g., *Neuropteris*, *Eusphenopteris* Gothan et Simson-Scharold). Late Visean floras display a differentiation into an eastern palaeophytogeographic region characterised by abundant *Fryopsis*, *Cardiopteridium*, *Triphyllopteris*, and early neuropterids, and western assemblages with common occurrences of *Diplopteridium*.

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