The origins of higher plants

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A fundamental task of paleobotany is to develop theories about the origin and evolution of the crown groups of different plant stems. In the Carboniferous period, we find fern families, lycopods and horsetails that are still found today, and beginning from the Carboniferous-Permian transition, we come across fully developed gymnosperms that are similarly recognisable even today. Astonishingly, these gymnosperms had reached such high level of development more than 300 million years ago, which makes it plausible that the splitting lines are to be found in the Devonian period. In fact, in the Middle Devonian, we encounter a conifer – *Eoconifera fuchsii* – with a symmetrical arrangement of branches, macrosporangia covered by microleaves and pollen cones showing clear tendencies resembling extant Araucarias. A subsequent lineage with a primitive coniferous character – that of *Calamophyton primaevum* – is found to have evolved only cone-like pollen organs with sparsely settled microsporangia on each scale, similar to presently existing two-seeded conifers like the Abietaceae or Pinoideae. Another group of protoconifers – *Schweitzeria enigmatica* – generates spreading branches and three- to multi-seeded scales, possibly an ancestor of the conifers *Cryptomeria, Sciadopitys* or *Sequoia*. Moreover Devonian *Flabellophyllum divisium*, can be regarded as ancestor of all ginkgos. Also the crown groups of both cycad-stems appeared in the Devonian: *Kraeuselia pohlii* with two-seeded scales corresponding to today's Zamiaceae, and the Cycas-cycad *Weylandia rhenana* with a large number of seeds lined up in parallel on both sides along an axis. In summary, all these Progymnosperms, difficult as they are to classify, outline the most important step in the development of the first microsporangia and macrosporangia. In the Middle Devonian just exist archaic ancestors of the ferns (*Protopteridium philippae*), the clubmosses (*Protolepidodendron leschii, Selaginellites devonianus)* and horsetails - one of them leading to today's Equisetum line (*Archaeoequisetites lindlarensis*) as well as to lycopod-horsetails (*Archaeocalamites antiquus*). Further back in the Lower Devonian, the evolutionary boundaries become blurred, such that the concomitant references to plant families existing today are hardly imaginable.

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A Middle Devonian gymnosperm community (Lindlar, 390 million years ago)

1. ***Flabellophyllum divisium:*** A ginkgo ancestor; 2. ***Eoconifera fuchsii:*** A precursor of the Araucarias; 3. ***Calamophyton primaevum,*** an ancestor of the two-seeded conifers; 4. ***Weylandia rhenana****:* The primitive cycad (Cycas-multi-seeded sporophylls); 5. ***Kraeuselia pohlii*** (Zamia, two-seeded) with a pollen cone. 6. ***Schweitzeria enigmatica,*** an ancestor of multi-seeded conifers in the background.

The evolution of the plant world in its early days has long fascinated researchers. It has been previously assumed that beginning from the Devonian period, the origins and lineages of plants can be discerned. However, while it is still difficult to derive convincing evidence of later plant families in the Lower Devonian, from the Middle Devonian onwards, the world's flora develops to such an extent that reasonably well-established classifications among presently existing tribes, such as ferns, clubmosses, horsetails and gymnosperms (conifers, ginkgos, cycads), are possible. In this regard, one site plays a special role in the recognition of the world's first plant tribes: the Lindlar quarries in North Rhine-Westphalia, Germany.

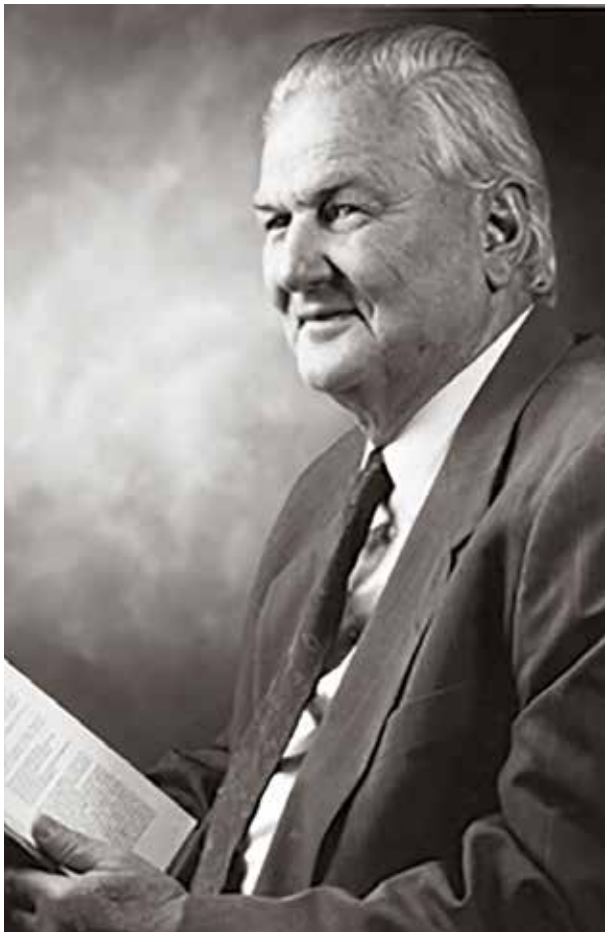
For decades, researchers have tried to study the Devonian flora of Lindlar. In addition to its small plants, the presence of previously unknown tree-like plants is particularly interesting. However, there are difficulties in classifying the plants in Lindlar based only on the branches or trunks found, especially when the well-preserved fertile plant parts are few, often unsightly and, therefore, hardly meaningful in terms of classification. Only after decades of collection by the local collector Manfred Fuchs – who worked especially on the rarely-coming-to-light thin lentils, which are characterised by extremely good preservation conditions, even of the small sporangia – could the appearance of Lindlar's flora be better woven into an overall picture. Fuchs later deposited his material primarily in the collections of Burkhard Pohl (Groß-Bieberau, Germany) and Michael Wachtler (Dolomythos Museum, Innichen, Italy).

It should be accepted that in the Middle Devonian, many plant tribes must have evolved within a very short time (Taylor et. al. 2009). In fact, although many of the microsporangia or macrosporangia of these tribes show similarities among themselves, the concomitant presence of many leaf-types of today's plant families, such as Gymnosperms, Pteridophyta, Equisetophyta or Lycophyta, can be accurately recognised. Hence, the evolution of the world's flora during this period must have occurred right from its beginning, faster than previously assumed and with surprising cross-connections hitherto not considered possible. Notably, although some of the researches presented in this publication can be completed and enlarged by further studies, they nevertheless form a solid basis for discussion on the above topic.

Historical overview

The first epochal works on the Middle Devonian flora of Germany appeared between 1923 and 1934, undertaken by German paleobotanists Richard Kräusel and Hermann Weyland (1923, 1925, 1926, 1929, 1932, 1933). These researchers were the first to describe important plants like *Calamophyton primaevum* (1925), *Rhacophyon gracilis* and *Thursophyton elberfeldense* (1926).

After a decline in related research around the Second World War, it was another German paleobotanist, the pharmacist Hans-Joachim Schweitzer, who made these floras popular worldwide not only through his publications (1966, 1972, 1973, 1974, 2009) but also with excellent supplementary diagrams. Schweitzer was the first to systematically study the Otto Schiffarth quarry in Lindlar. He recovered almost the entire pool of



The German pharmacist and paleobotanist Hans-Joachim Schweitzer (1928–2007). He studied the Devonian floras of Germany and also took part in paleobotanical expeditions to Svalbard, Jan Mayen, Bear Island, Iran and Afghanistan.

Czech geologist, mineralogist, cartographer and politician Jan (Johann) Krejčí. He published relatively unknown works on Middle Devonian plants from Bohemia. Photo taken around 1880.

material from the Mühlenberg Formation (Middle Eifelian, Lower Middle Devonian) within a stone lens that was only 3 m × 4 m in size and about 0.6 m thick. Owing to this quarry's collection, Schweitzer (1974) was able to describe *Weylandia rhenana*, an enigmatic plant, and *Lycopodites lindlarensis* (1974), which probably represented the cone of a primitive clubmoss.

A next milestone in this journey was achieved by Peter Giesen, who in 2008 recovered the completely preserved stems of *Calamophyton primaevum* from a nearby quarry (BGS Vitar quarry; GPS: N 051°01.740, E 007°22.420). In an outstanding publication Giesen & Berry, 2013, they were able to unite three plants that were previously classified as constituting different genera (*Calamophyton primaevum, Duisbergia mirabilis, Hyenia elegans*) by asserting that they belonged to a single small tree. For the first time, they achieved a reconstruction of this tree, which probably reached a height of around two metres.

In this vein, often overlooked were the contributions (1879, 1880, 1881) by the Prague paleontologist Jan (Johann) Krejčí (1825–1887), who, looking into the Bohemian localities Hostin, Hlubočep and Srbsko (currently Hostim, Hlubočepy and Srbsk; Beroun district), described supposedly Silurian plants such as *Protopterium hostinense, Sporochnus*, or *Protolepidodendon scharyanum*. Fortunately, today we know that they belonged to the Middle Devonian Givetian, thus being somewhat younger than the plants of Lindlar. To be precise, some of the vegetation described by Krejčí showed not only similarities due to age disparity but also differences with the flora of Lindlar.

However, a tussle began over the right nomenclature of these abovementioned plants because the Slovak paleontologist Dionýs Štúr (1827–1893) changed many of Krejčí's names just a year later in 1881, such as *Protolepidodendon scharyanum* to *Chauvinia scharyana* and *Protopterium hostinense* to *Hostinella hostinensis*. Over the coming decades, further attempts were made to discredit the older names, but a closer (Matten & Schweitzer, 1982) analysis showed that the classifications introduced by Krejčí should hold up. To sum up, although there are always efforts by later authors to gain fame with newly introduced terms or to use names of their paleontologist friends, one should exercise caution out of respect for the intellectual achievements of former scientists, which occurred under significantly more arduous circumstances.

Geology

Known as 'the oldest forest in the world' (Giesen & Berry, 2013), the Lindlar quarry has revealed for the first time the evolution of many modern-day plant tribes. The Mühlenberg Formation (Middle Devonian; Eifelium, approx. 390 million years ago) is characterised by the presence of a grey to brownish-yellow, slightly calcareous sandstone. Wave ripples and other indicators of periodically occurring storm events can be found everywhere in the Lindlar quarry (Giesen & Berry, 2013). Sporadically, entire trees in this area have been buried from crown to root, most likely not far from their original growth position, but the downside is that these sediments are relatively coarse-grained and the smallest details of fructifications can be rarely recognised to a sufficient extent. Moreover, this area's sandstones are rich in crinoid remains, while other invertebrates such as trilobites (*Asteropyge punc-*

The BGS Vitar quarry near Lindlar. It is characterised by different horizons consisting of yellow-brown, brownish grey, reddish or greenish Greywacke.

Manfred Fuchs searching for fossil plants. Thin, narrow lenses in greenish Greywacke, where the state of preservation is of the best quality, are particularly interesting.

tata) or brachiopods, as well as vertebrates such as Placoderma and Acanthodes, are sometimes found therein (Hartkopf-Fröder & Weber, 2016). The most detailed among fossil plants, especially with their fertile organs, are found in thin muddy lenses, usually only 1–2 cm thick.
Further, it is argued that some small tree-like plants from the group of protoconifers – especially *Calamophyton, Eoconifera* and *Schweitzeria* – may have reached heights of up to two meters in this region. In addition to these higher-growing gymnosperm ancestors, lower-growing plants, such as cycad precursors, as well as lycopods, horsetails and ferns, are found to have developed here.

A flora explosion in Middle Devonian

Contrary to conventional theories, the splitting-off of different gymnosperms (conifers, ginkgos and cycads), like those of different clubmosses (Lepidodendronales, Selaginellaceae) as well as those of ferns and horsetails, may have started in the Devonian. This assumption applies to another northern supercontinent, Angara – today's Ural region, including Siberia – even for the flowering plants, the angiosperms. In this respect, although different sub-lineages and refinements possibly occurred over the following 400 million years, the basic structures of these plants themselves developed over an extremely short time.

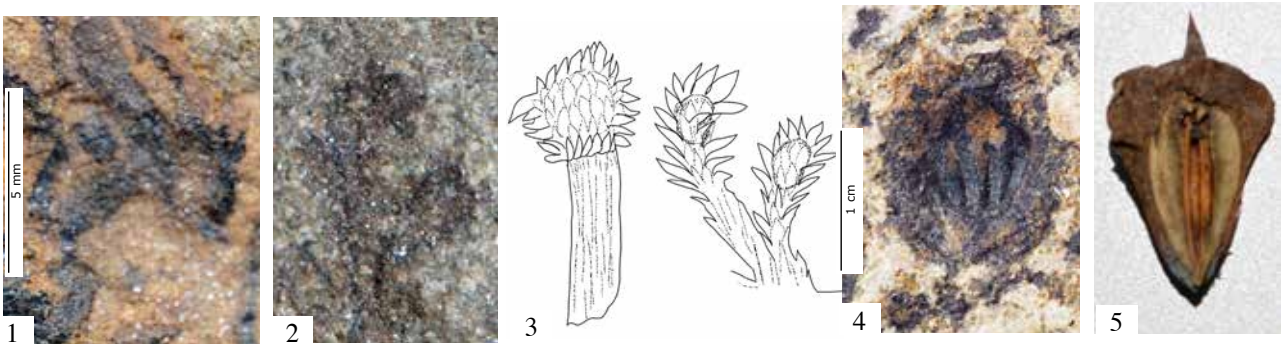
The diversity of progymnosperms in the Middle Devonian

What we know about the leaf and branch formation of progymnosperms in the Middle Devonian

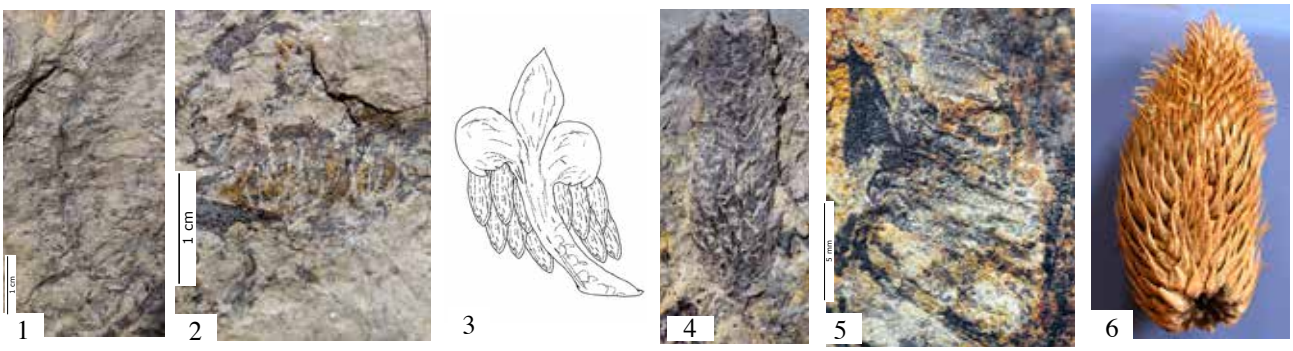
If we do not always have reliable knowledge of which macrosporangia or microsporangia are to be assigned to the individual branches of progymnosperms, the leaf shapes can still be distinguished from one another. 1. *Calamophyton primaevum* (LIND 123): It may be part of an ancestral lineage of the Abietaceae and Pinoidea; 2. *Eoconifera fuchsii* (LIND 238): Because of its strobili and the symmetrical evolved branchlets, it should be related to the Araucarias; 3. *Schweitzeria engimatica* (LIND 10): Spreading branches of this species may represent another conifer; 4. *Flabellophyllum divisium* (LIND 195): Fan-like forked leaves may represent an ancestor of Ginkgo; 5. *Weylandia rhenana* (LIND 154): Tongue-shaped fronds, in association with multi-seeded sporophylls emanating from both sides of a blade, may point towards Cycas progenitors. Others, with only two megasporangia per seed scale, may be considered as progenitors of Zamia cycads (*Kraeuselia pohlii,* LIND 242).

The evolution of conifer cones from the Middle Devonian to the present

The evolution of the Araucarias



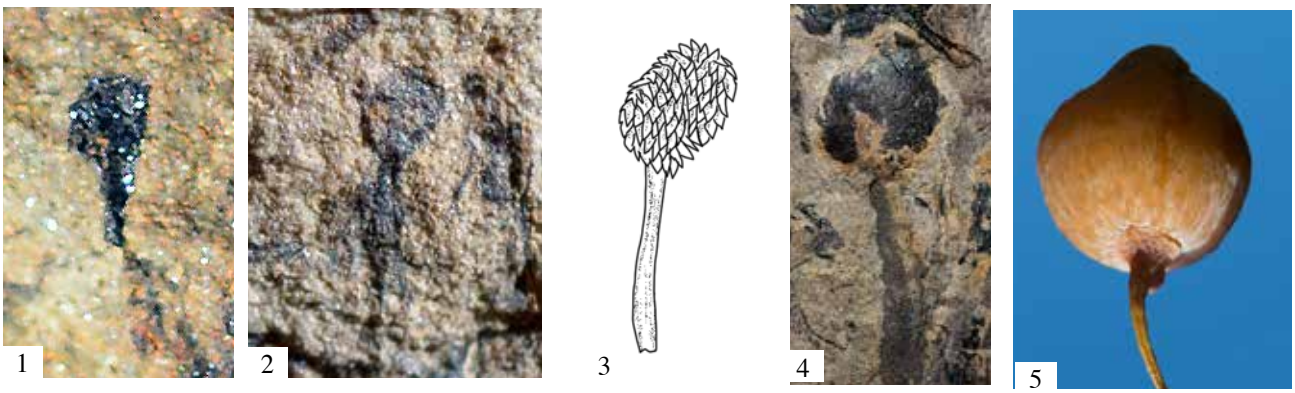
Seed cones: 1–3. Middle Devonian *Eoconifera fuchsii* (LIND 31, LIND 238) evolving dwarfish, sterile leaves that surround one sporangia/seed/ovule; 4. We find the first secured Araucaria *(Ortiseia*) beginning from the Early Permian (*Ortiseia leonardii,* CUEC 11, Upper Permian); 5. Araucaria seed in the present times (*Araucaria columnaris*).



Pollen cones: 1–3. Microsporophylls with a multitude of hanging pollen sacs (*Eoconifera fuchsii,* LIND 230, Middle Devonian); 4. The first confirmed Araucaria progenitor (*Ortiseia*) carried pollen cones and microsporophylls, similar to today's Araucaria (*Ortiseia zanettii,* CUEC 93, PAS 219, Late Permian); 5. Today's male cone (*Araucaria araucana*).

The evolution of gymnosperms from the Middle Devonian to the present

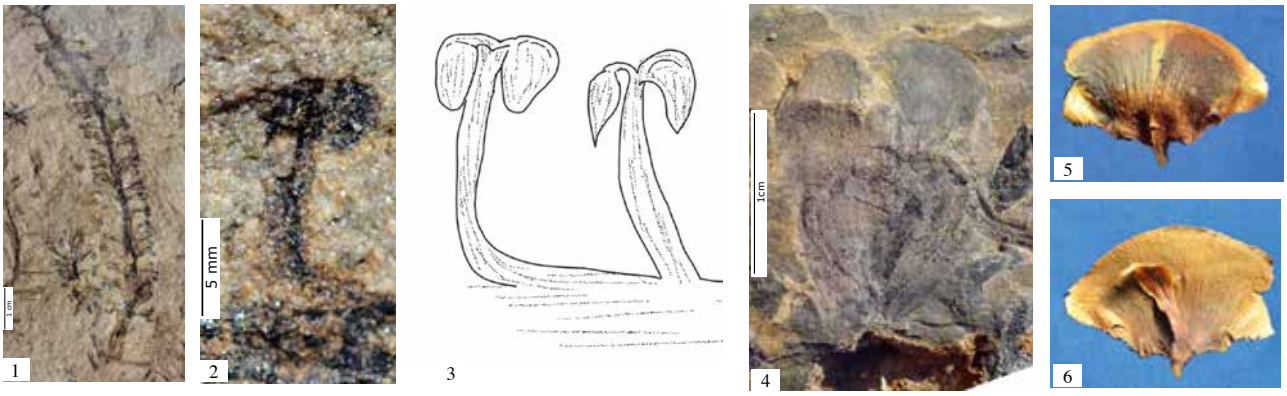
The evolution of the Ginkgo



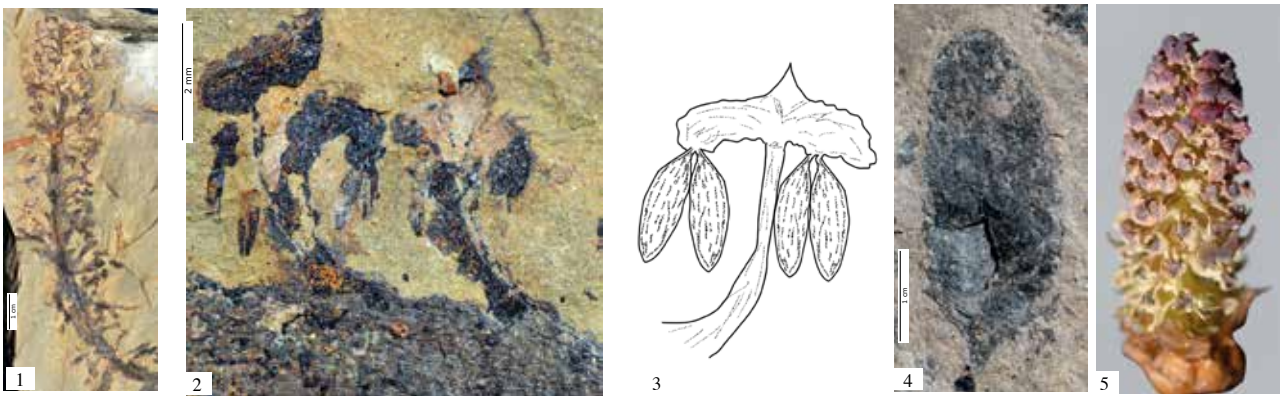
Ovules/Seeds: 1–3. Single-seeded megasporangia (*Flabellophyllum divisium*, LIND 03, LIND 225) already existed in the Middle Devonian: the seeds were covered with the finest dwarfish leaves; 4. The first ginkgos evolved in the Permian (*Ginkgoites gasseri,* MON 282, Middle Late Permian); 5. Today's Ginkgo seed.

The above information indicates that many gymnosperms went their own way from the Middle Devonian, and from then on, only miniscule evolutionary changes took place.

The evolution of conifer cones from the Middle Devonian to the present
The Evolution of the Abietaceae or Pinoidea

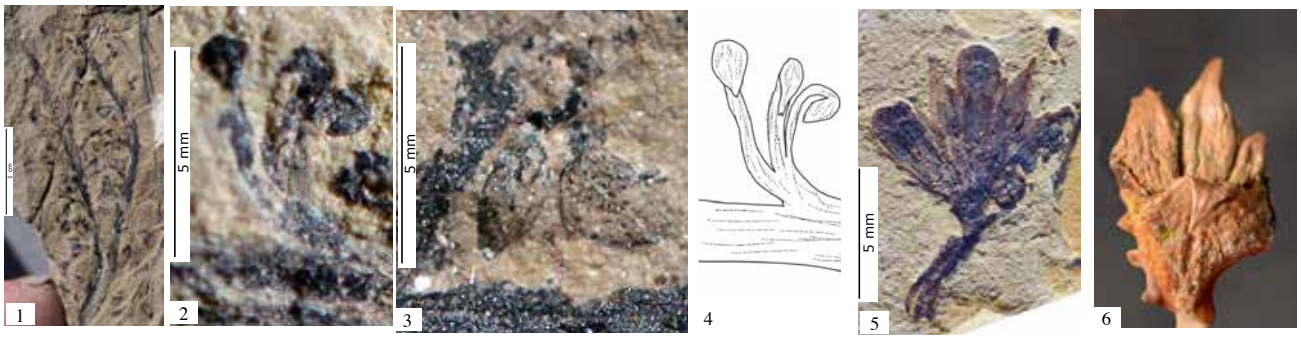


Seed cones: 1-3. In the Middle Devonian, Abietaceae formed seed scales with two megasporangia (*Calamophyton primaevum*, LIND 01). 4. The first verified Abietaceae evolved along the Carboniferous-Permian transition, with winged seeds (*Majonica suessi*, COL 143, Early Permian); 5. Seed scales of a fir (*Abies alba*) in the present times.

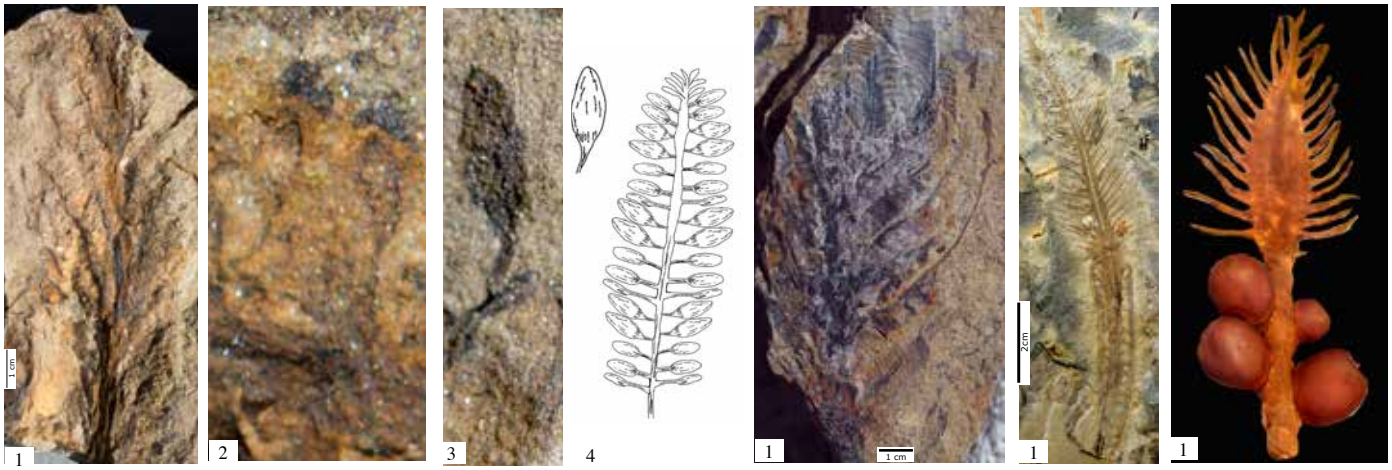


Pollen cones: 1–3. In the Middle Devonian, microsporophylls evolved with only two pollen sacs hanging on each side of a bract (*Calamophyton primaevum*, LIND 16); 4. From the Permian, their current form of pollen cones developed (*Majonica lyellae*, MON 301, Late Permian); 5. Pollen cones of a fir (*Abies alba)*.

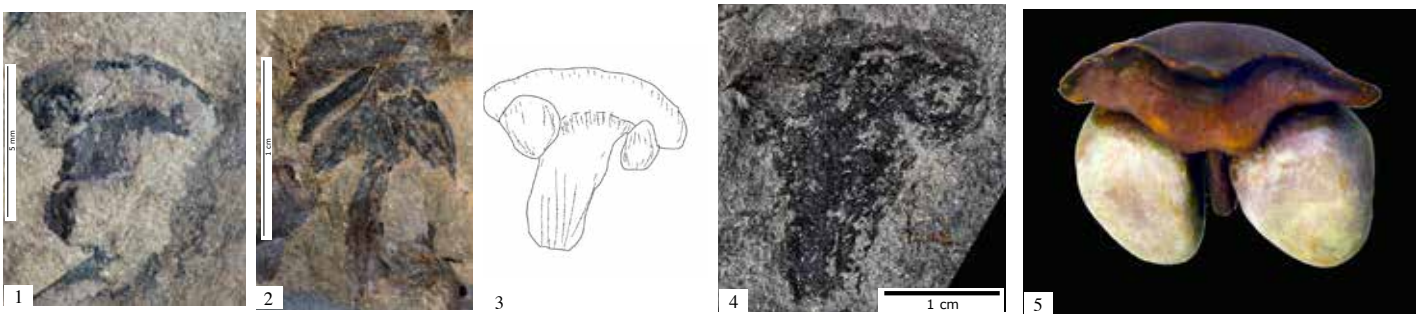
The evolution of multi-seeded conifers



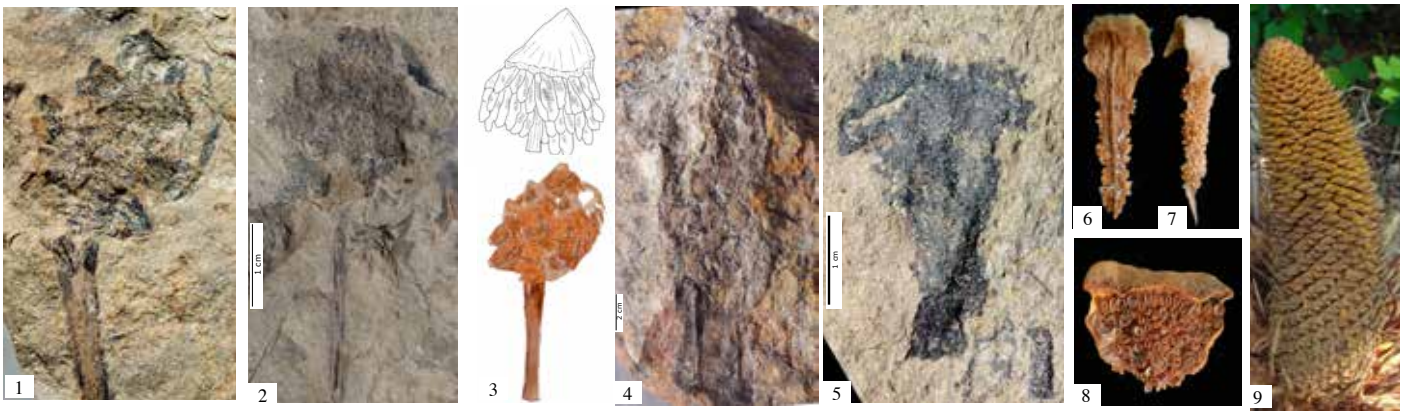
Ovules/Seeds: 1–4. In the Middle Devonian of Lindlar, multi-seeded megasporophylls were found on each scale (*Schweitzeria enigmatica*, LIND 185). 5. *Voltzia niederhauseni,* PER 163, Carboniferous-Permian: Although their form was not yet fully evolved, their basic features pointed to the group of conifers bearing three or more seeds per scale, such as are still found today in *Cryptomeria* (6), *Sciadopitys, Cunninghamia* or the Sequoias.



Cycas cycads. Ovules/Seeds: 1-4. From the Middle Devonian onwards, rows of ovules (*Weylandia rhenana,* LIND 125, LIND 203) could be found on both sides of a leaf-blade. From the Permian onwards and through the Triassic, similar megasporophylls, belonging to Cycas ancestors (*Taeniopteris, Macrotaeniopteris* KÜH 150, ILS 314) were found. These could be regarded as the forerunners of the multi-seeded Cycas cycads (*Cycas revoluta*).



Zamia cycads. Ovules/Seeds: 1–3. Two-seeded megasporophylls (*Kraeuselia pohlii*, LIND 76) could be found from the Middle Devonian onwards. They were widespread since the Permian and throughout the Triassic (4. *Nilssonia, Pseudoctenis* KÜH 1424) and represented Zamia precursors (5. *Macrozamia miquelii*).



Proto Cycads. Pollen cones: 1–3. From the Middle Devonian, primitive microsporophylls aggregated to cones (*Weylandia rhenana, Kraeuselia pohlii,* LIND 75, LIND 243) were found. They could be encountered throughout the whole Permian (4.) (PAS 536) and the Triassic (5. *Taeniopteris, Nilssonia, Pseudoctenis*, PIZF 79) and they resembled modern-day cycad microsporophylls (6–7. *Cycas revoluta*; 8. *Stangeria eriopus*; 9. *Cycas thouarsii* pollen cones).

The Evolution of Cycads

1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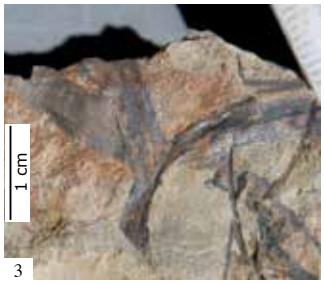
6



3

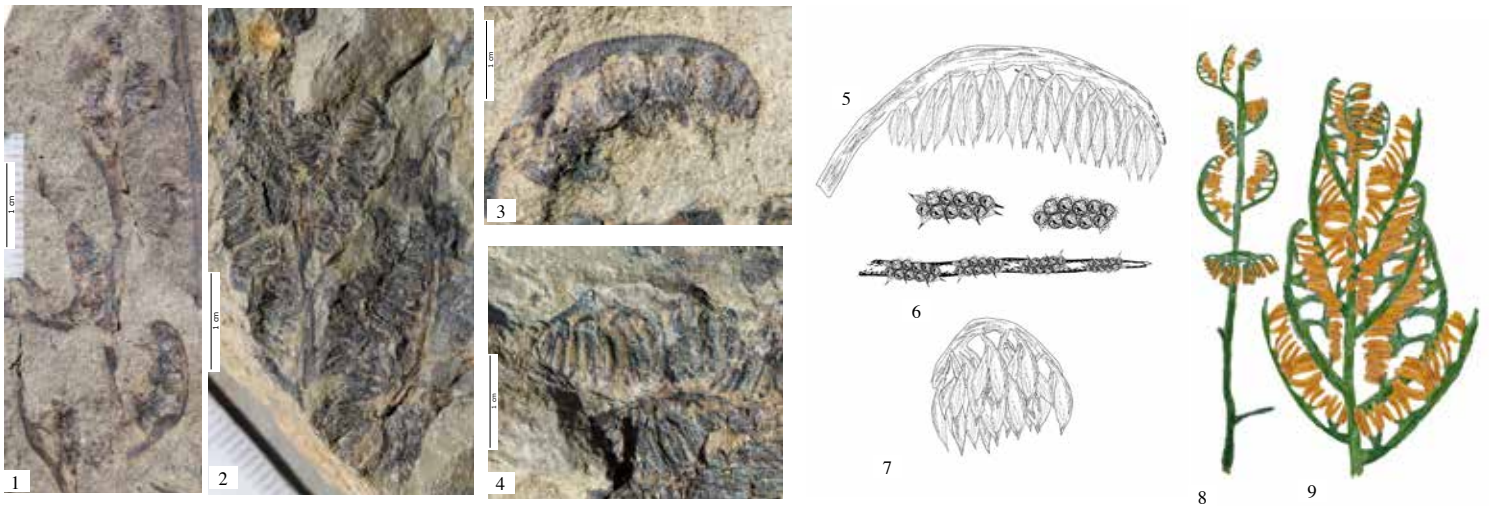
From the Middle Devonian, two different lineages of protocycads could be found. 1–2. The first protocycad (*Weylandia rhenana*, LIND 182) developed tuft-like multi-seeded fructifications, whereas the second (3. *Kraeuselia pohlii,* LIND 242) developed two seeds on each megasporophyll. Both were represented since the Middle Devonian as separate families. In contrast to today's cycads, they were taller-growing plants with tongue-shaped, forked leaves. They retained this character at least until the Permian (4–5. *Wachtleropteris valentinii,* Early Permian). Today, however, they are characterised by fronds developing at the same level.

Beginning in the Middle Devonian, there was probably an unprecedented flora explosion that remains unmatched in the subsequent history of the world: within a very short time, even plant subgroups, such as the conifers (not only Araucarias and Abietaceae but also the multi-seeded conifers) and the cycads had greatly diversified. This phenomenon also occurred in various fern families, such as Osmundaceae, Cyatheaceae and those belonging to other genera. Some, like the gymnosperms, became seed carriers, while others like the ferns, horsetails, and some lycopods found their way with just one kind of spores. The development of a megasporangium/seed may have occurred several times independently, specifically in some clubmosses (*Sigillaria, Selaginella*), gymnosperms and flowering plants.

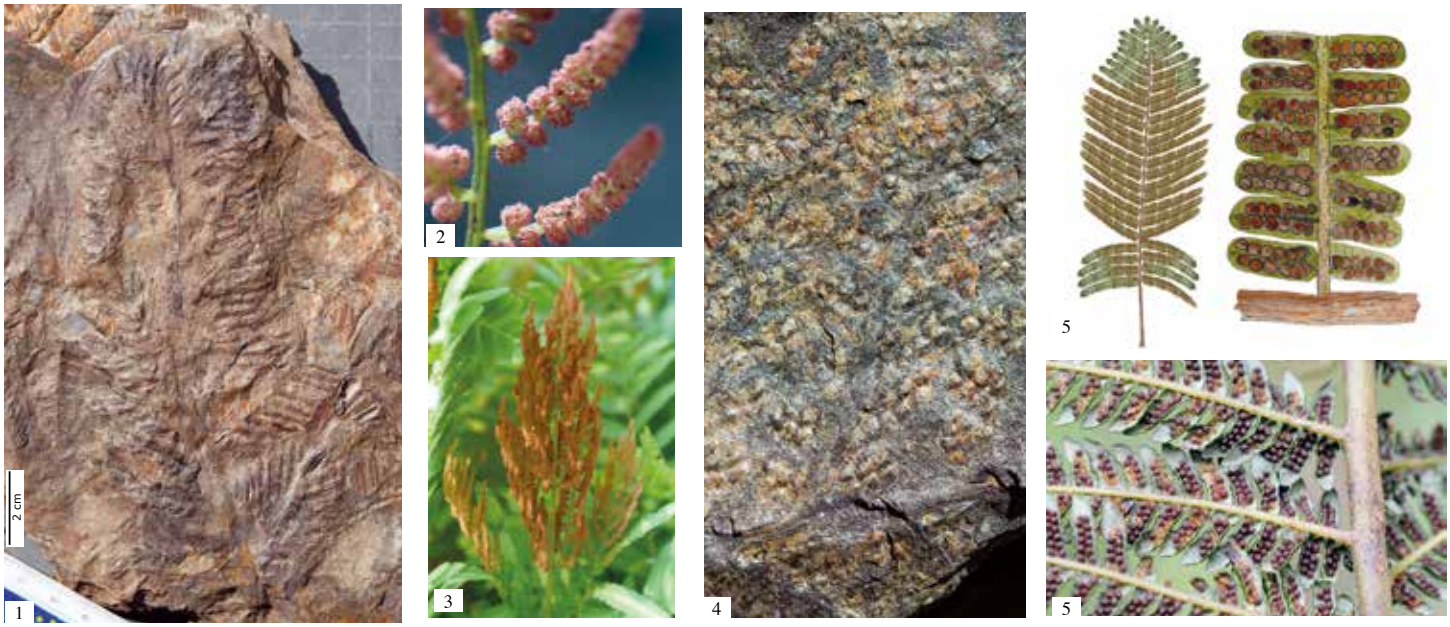
Different male and female cones in the conifer precursors: As per the different blueprints of branches, male and female cones, and different microsporangia and macrosporangia, at least two to three different protoconifers must have developed in the Middle Devonian.

Rudimentary cones with one-seeded scales *(Eoconifera fuchsii*) and cones with multiple hanging microsporangia, indicating relationships with the Permian conifer *Ortiseia*, in terms of common ancestry with the Araucaria family, were found in Lindlar. Additionally, there were two-seeded seed scales (*Calamophyton primaevum*), resembling the Pinoidea or the Abietaceae. The pollen cones were characterised by a few sporophylls, including only two microsporangia. These may have had a progenitor status with regard to the Permian genera *Gomphostrobus, Wachtlerina* and *Majonica,* as the more evolved progenitors of firs. Also, there must have been a third genus with a different arrangement of branches – *Schweitzeria enigmatica* – whose classification has not yet been satisfactorily resolved. These may have been precursors of the Votziales, which were widespread in the Permian and the Triassic and which presumably led in the direction of multi-seeded conifers such as *Cryptomeria, Sciadopitys* or certain cypresses. Further, according to the variable cone structures of the Protoconifers, the development into one, two or more seed-bearing scales was not yet complete.

First cycads: Although the argument is doubtful, the basic features of both cycad families that are dominant today must have developed at an early evolutionary stage.



Fern sporangia distinction in the Middle Devonian: During this period, the first plants correctly recognisable as fern precursors appeared (*Protopteridium philippae*, LIND 240, LIND 111). Although they seemed similar to each other, there were certain differences. Some may have evolved in the direction of tree ferns, the Marattiales (1, 5, 6, 8), while others were possible precursors of the Osmundaceae (2, 4, 7, 9).

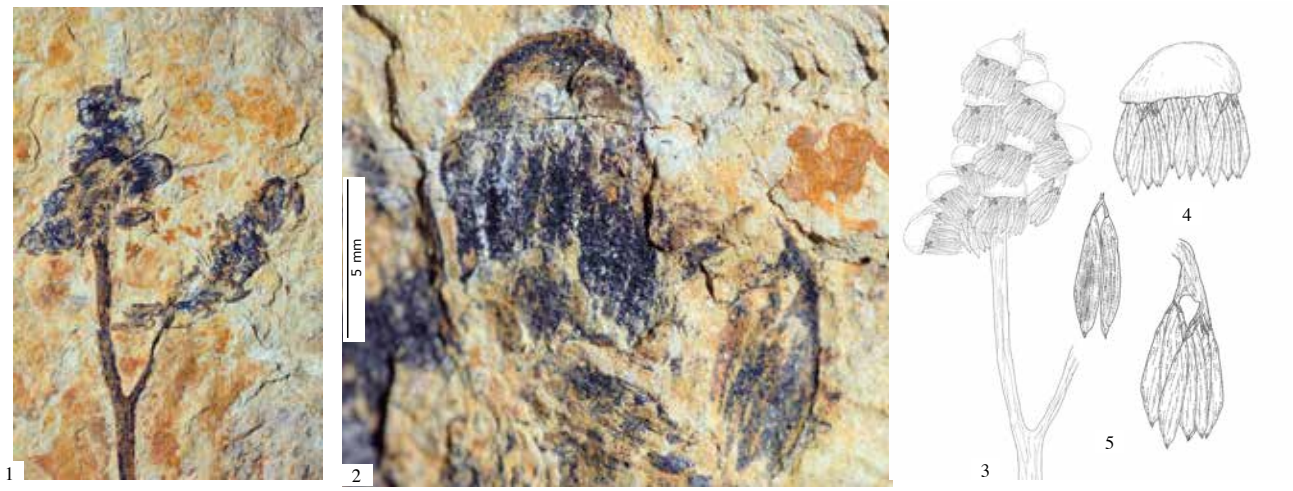


Fern sporophylls in the Upper Carboniferous: In this period, individual fern families became clearly distinct: *Osmundites polymorphus* (1, KRON 198). Similarities to today's fern families (*Osmunda regalis,* 2–3; or *Cyatheites alpinus,* 4–5, KOEN 273) and today's *Cyathea melleri* could be observed. In fact, certain archaic Devonian structures are still recognisable to this day.

In fact, the seed scales and leaf parts of *Kraeuselia pohlii* pointed in the direction of the two-seeded Zamiaceae (*Stangeria, Bowenia, Encephalartos, Zamia*) and showed similarities with the Early Permian *Wachtleropteris*, which can be clearly characterised as a very primordial cycad. The enigmatic *Weylandia rhenana* evolved, in parallel in the Middle Devonian and generate on both sides of an axis a multitude of seeds. The apical tuft of megasporophylls reportedly resembled the Permo-Triassic *Taeniopteris* or *Macrotaeniopteris* cycads, or the modern-day genus Cycas.

Ginkgo ancestors: Ginkgos must also have developed in the Middle Devonian. Divided, elongated leaves (*Flabellophyllum divisium*) reinforce this assumption. Single-seeded

The evolution of Equisetum horsetails



Horsetail sporophyll-cones in the Middle Devonian: Aggregated strobili as well as stem parts from Lindlar may represent an early development of the Equisetum horsetail lineage (1, 2, 3, 4, 5; *Archaeoequisetites lindlarensis*, LIND 17).

Horsetail sporophylls in the Triassic: The sporangiophores of *Archaeoequisetites lindlarensis* showed similarities with Triassic *Equisetites (arenaceus)* (1, 2, 3). Even today's *Equisetum* horsetails still show the basic features developed during the Devonian (*Equisetum arvense,* 4, 5, 6)

berries on a short stalk, not uncommon in Lindlar, could indicate their development.

Forerunners of ferns: Especially in the case of the Filicales family, the findings from Lindlar show how extant pinnae developed from dichotomous appendixes (*Protopteridium philippae*) till the veins were covered by an epidermis in the course of the Upper Devonian (*Rhacophyton*). The sporangia were more highly developed from the beginning of this period (based on different kinds of fertile organs being available in the Lindlar quarry itself). Some *Protopteridium* plants evolved different sporophylls and tropophylls, in the direction of the Osmundaceae, but looser arrangements in the direction of tree ferns or other fern families were also present. A clear splitting into more species or genera of Lindlar's *Protopteridium philippae* remains unestablished till date, owing to similarities among all the components of this group.

Forerunners of the horsetails: Since it was not possible to bring the two different (so-called) horsetail genera *Equisetes* and *Calamites* into relationships or branch lines over the entire Carboniferous-Permian, arguably they must have gone their separate ways from the Middle Devonian onwards. Hence, the telescopic stem, consisting of individual branches growing together, was 'invented' just before the Middle Devonian. Indeed, there were indications of completely separate lineages of these genera, owing to the strobili of *Archaeoequisetites lindlarensis* – with its spore receptacles sitting in groups on the underside of a sporophyll – as well as to the *Archaeocalamites antiquus,* whose spore-cones showed the basic features of the Calamitaceae that were so dominant later in the Carboniferous. *Archaeocalamites* appeared to be more closely related to lycopods such as *Protolepidodendron,* while *Archaeoequisetites* was to be placed in close proximity to the fern precursors (*Protopteridium)* or the progymnosperms.

Forerunner of the club moss family: The development of the lycopods must have occurred differently; their spore receptacles are located in the axils of terminal cones, which can be clearly seen in *Protolepidodendron leschii* and *Selaginellites devonianus* that were found in Lindlar. In the Middle Devonian, they were still small, creeping plants, which developed into giant trees in the course of the Carboniferous, at least in the case of the Lepidodendronales. The question of why certain clubmoss plants such as *Selaginellites* formed heterosporous sporophylls from the beginning, while *Protolepidodendron* was homosporous (i.e. with only one type of spores), must be explored further. Also unresolved are the role and the development of the other giant clubmoss *Sigillaria* in the Middle Devonian of Lindlar – so widespread in the Carboniferous, with an evolutionary level almost reaching the ovules of the gymnosperms – as well as the relationships between the lycopods and other plant families in this period.

Possible relationships between the different plant tribes: Assumptions have often been made (Taylor et al. 2009) that the recent two-seeded genera (*Zamia, Encephalartos* etc.) split off from an older ancestor of the multi-seeded Cycas-cycads by reduction, or that the Araucariaceae represented the most archaic conifers and the Marattiales the most primitive genus of ferns. However, on the Carboniferous-Permian boundary, we encountered fully developed Araucariaceae (*Ortiseia*), Abietaceae (*Gomphostrobus, Wachtlerina, Majonica*), Pinoidea (*Férovalentinia*) and multi-seeded conifers (*Voltzia)*; and on the Angara paleocontinent (presently the Urals and Siberia), in addition to the most archaic angiosperms, other primordial conifer lines were found to be present (such as *Kungurodendron,* probably an ancestor of the spruce family, or of the *Taxodiella* cypress). Moreover, fully developed ginkgoes and cycads existed on this boundary, but only on the Euramerican landmass. Therefore, other explanations for the evolution and splitting-off of the major abovementioned plant lineages must be found. This assertion also applies to the horsetail genera *Calamites* and *Equisetites,* with their different sporophyll cones.

There is no other explanation that refutes the argument that all plant families existing today, including those of flowering plants, developed between the Devonian and the Carboniferous. More obviously, the crown groups of the entire world's flora had already developed in the Devonian. With this observation, attempts to find later splitting lines become obsolete: only the question of possible side lines in the plant kingdom remains.

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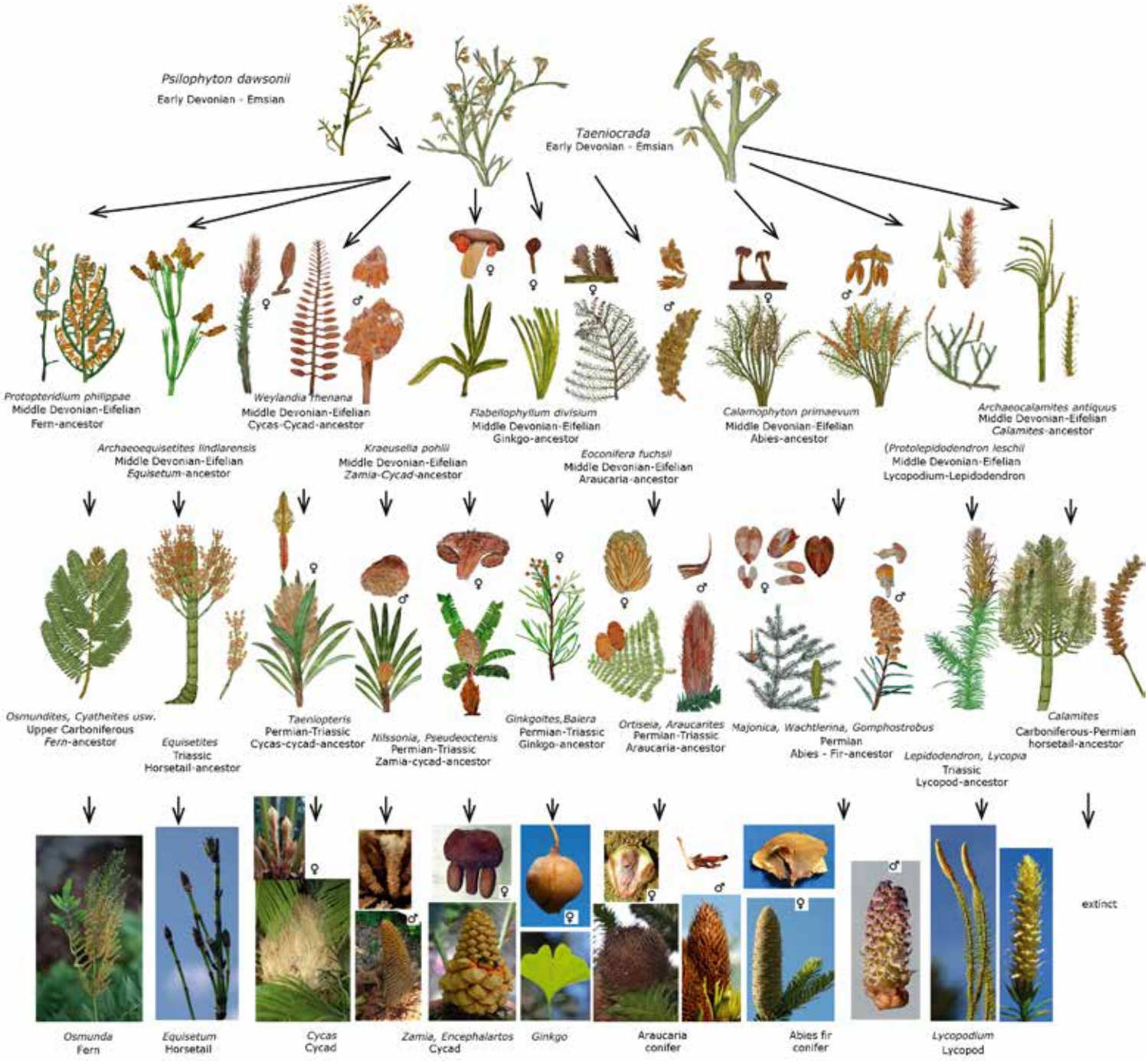
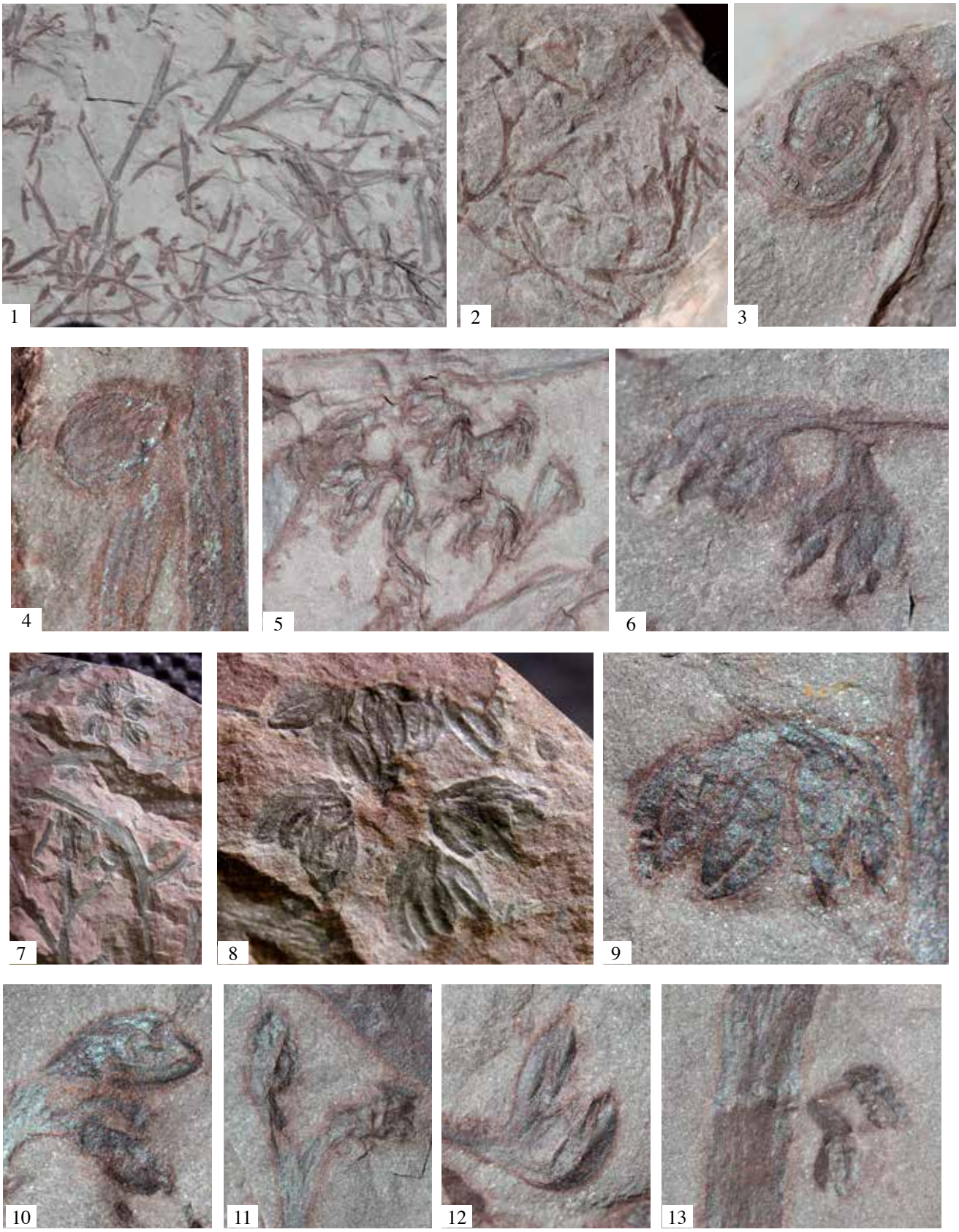
The Middle Devonian Flora Explosion

In the Middle Devonian, there was a sudden development of all extant gymnosperm lines (conifers, cycads and ginkgoes) – with their diverse ovules/seeds – as well as of the fern families, horsetails, and clubmoss. In the following 390 million years, however, there were only minor evolutionary changes.



The evolution of plants from the Devonian

While in the Lower Devonian (Emsian, about 400 million years ago), plants such as *Psilophyton* or *Taeniocrada* rarely give indications of which present-day families could be derived from them, since the Middle Devonian (Eifelian, about 390 million years ago), clearly recognisable contemporary plant families –



Plant development in the Lower Devonian. In the Klerf Formation (Lower Devonian, highest Lower Emsian, more than 400 million years ago) of the Olkenbacher Mulde (SE-Eifel, Rhineland-Palatinate, SW-Germany), there are plants which are usually classified as *Taeniocrada longisporangiata* and which show primitive branching (1). However, the lycopod family must have gone its own way (2); there are already curled leaves (3) and various sporophyll forms (4–13), so that they would have to be classified under several species or genera (Dolomythos Collection, Pohl Collection, collected by Manfred Fuchs).

A Rapid Diversification of Ferns in the Middle Devonian

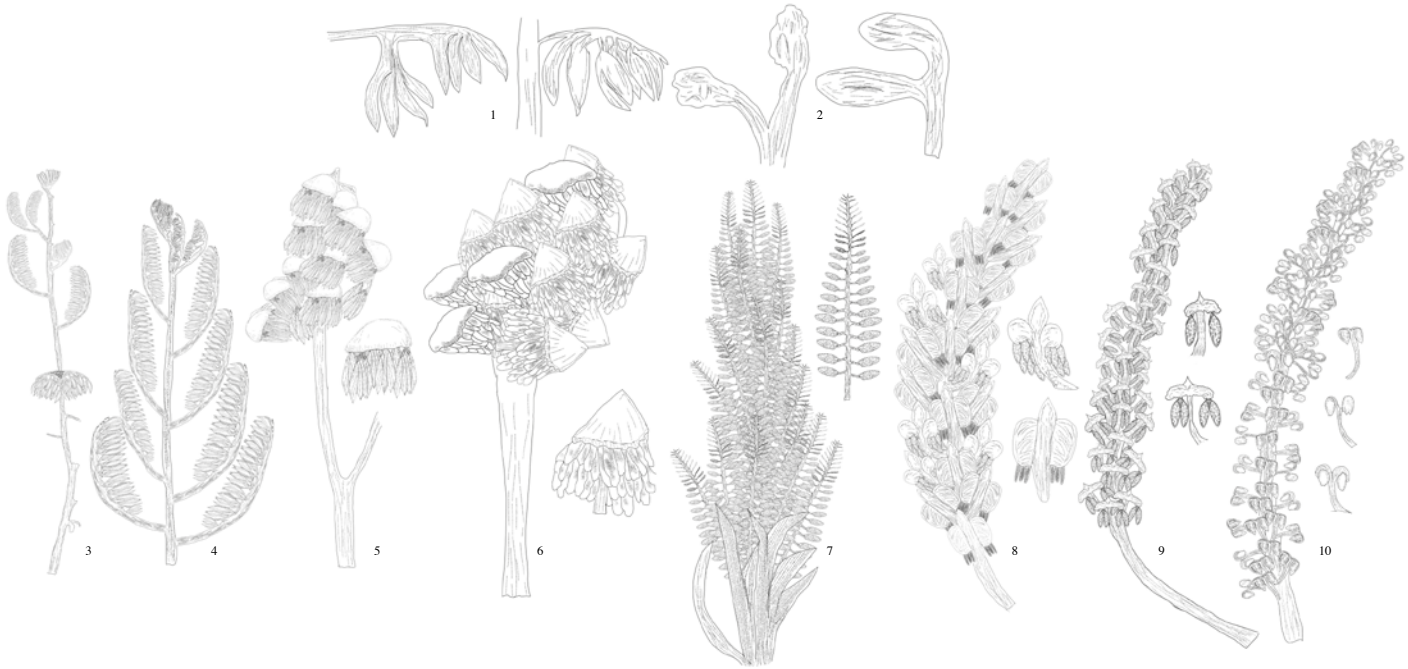
All protoferns were classified as *Protopteridium philippae.* But they showed variations. One already developed flat fronds (LIND 249, LIND 106), another developed slender fronds (LIND 240), while a third approached the Osmundaceae (LIND 111). However, the differences were not yet sufficient to classify them as three genera or species. Still, they should be considered as a crown group of a later variety.

A Middle Devonian Lycopod variety

A Middle Devonian clubmoss community (Lindlar 390 million years ago)

On the left, a lycopod-horsetail ***Archaeocalamites antiquus;*** in the middle, ***Selaginellites devonianus;*** on the right, the club moss *Protolepidodendron leschii.*

A strange plant development from the Lower Devonian to the Middle Devonian



In the Lower Devonian, more than 400 million years ago, we encountered only rudimentary microsporangia (1) and attempts at forming macrosporangia (2). Both of these were grouped together under the genus name ***Taeniocrada***. Within a short period of ten million years, there was a complete change in vegetation towards the Middle Devonian. In many variations, fern precursors emerged with uniform sporangia, such as ***Protopteridium philippae (***3–4), horsetails (5. ***Archaeoequisetites lindlarensis)***, and also seed plants such as cycad ancestors (***Weylandia rhenana;*** 6. male, 7. female), including the first conifers. 8. Pollen cone from ***Eoconifera fuchsii*** (Araucaria ancestor), ***Calamophyton primaevum*** (Abietaceae or Pinoidea ancestor); 9. Pollen cone; 10. Seed cone. The development of microsporangia and megasporangia on the same fructification may also have arisen independently in the club moss family and the flowering plants.

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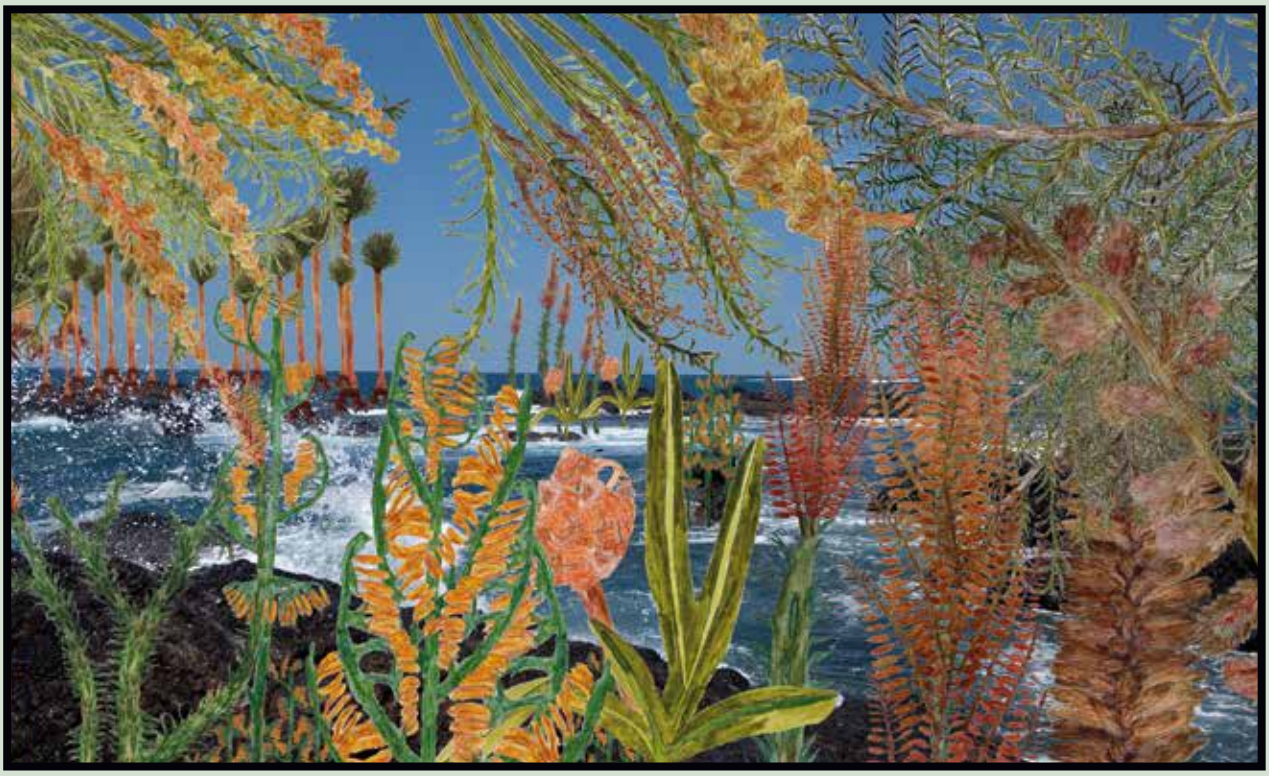

The Middle Devonian Flora Explosion

The Origins of Higher Plants

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A fundamental task of paleobotany is to find theories about the origin and evolution of the crown groups of different plant stems. In the Carboniferous, we find fern families, lycopods and horsetails that still exist today; fully developed and recognisable gymnosperms can be seen from the Carboniferous-Permian transition onwards. Astonishingly, these gymnosperms reached an incredible level of development more than 300 million years ago, which makes it plausible that the splitting lines are to be found in the Devonian period. In fact, in the Middle Devonian, we encounter barely recognisable ancestors of these gymnosperms, such as conifers, gingkos or cycads, as well as archaic progenitors of the ferns, clubmosses and horsetails. Further back in the Lower Devonian, the boundaries become blurry, such that references to plant families existing today are hardly imaginable.

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