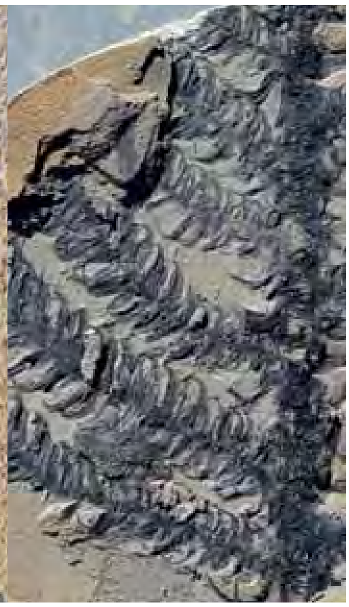
PERMIAN FOSSIL PLANTS FROM EUROPE AND THEIR EVOLUTION

The Niederhausen-Flora

by

THOMAS PERNER AND MICHAEL WACHTLER



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Summary

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THE CARBONIFEROUS-PERMIAN (KASIMOVIAN / GZHELIAN) FLORA FROM NIEDERHAUSEN (RHEINLAND-PFALZ, GERMANY)

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Abstract

A highly interesting Late Carboniferous-Early Permian paleo-ecosystem from Niederhausen (Saar-Nahe area, Rheinland-Pfalz, SW-Germany) will be described and shown. The Gzhelian-Asselian stage was established as a marker about 299 my years ago, until the blooming Carboniferous and arid Permian. However, on the Kasimovian/Gzhelian boundary (303.7 my years ± 1 my), in Europe, we have just a flourishing and all dominating conifer assemblage, and also other plant-families like ferns (*Todites* and *Scolecopteris*), seed ferns (*Peltaspermum*), and Cycadophyta can be regarded as typical Permian and not Carboniferous. Therefore, in this publication we elaborate arguments to bring the Carboniferous-Permian border to the Kasimovian-Gzhelian stage.

Here, the widely accepted ovuliferous dwarf-shoot-theory of conifer-evolution will be opposed by a totally new concept, based on these findings. At least three major components of Coniferophyta were recovered. *Perneria thomsonii* nov. gen. n. sp. is suggested to be close to the crown group of all conifers. It can be argued that we have to include this species with the last representative of an ancestral family like the Progymnosperms, but at the same time, due to its cone-structure, bracts, fertile scales, and needle-like leaves, it has to be inserted in the Coniferophyta. That the alar conifer-seeds were a solid dimension just over than 300 million years ago can be shown by *Wachtlerina bracteata* nov. gen. n. sp. Walchian-like conifers were present with *Seymourina niederhauseni* nov. gen. n. sp. This conifer is characterised by more or less fused three-fingered seed-scales surrounded by a collar of larger or smaller leaves, which can be regarded much more as protection-foliage than having reproduction-characteristics, as previously thought. That Ginkgophyta and Coniferophyta on this Kasimovian-Gzhelian boundary manifest a close relationship that is documented by *Baiera perneri* n. sp. Ginkgo-ovules and conifer-seed scales can therefore be deduced from a common ancestor.

The next big plant class comprises the Peltaspermales. They are present as highly evolved families like *Autunia* with its peltate ovuliferous organ in *Peltaspermum dammannii* n. sp., but in the same way as much more primitive genera like *Rachiphyllum hauptmannii* n. sp. and *Odontopteris lingulata,* that - because attached hat-like ovuliferous organs were found attached to the main rachis and in connection with the foliage - was removed from this morphogenus and inserted as *Hurumia lingulata* nov. gen. Relatively modern fern-families like the Marattiales, such as *Scolecopteris lothii* n. sp., or the Osmundaceae with *Todites muelleri* n. sp., were fully evolved. Surprisingly, the predominant Sphenophyta constitutes the dwarfish Calamitaceae, *Calamites wachtleri* n. sp., even though *Annularia spicata*-foliage is also reported although in lesser numbers. Nanoid *Selaginellites zollwegii* n. sp. is the only lycophyta encountered. Other rare plants are the putative cycadophyta *Taeniopteris* sp. and *Nilssonia* sp., as well as the gymnosperms *Cordaites* sp. and *Dicranophyllum* sp.

This strange plant association suggests that, apart from the dominating Carboniferous plant groups, giant lycophyta and sphenopyhta jungles coevally in the hinterland existed long before a much more aridity-adapted vegetation, which became dominant in the following million years and until the present day.

Online: December 2013.

Key words: Late Carboniferous, Early Permian floras, Coniferales, Peltaspermales, Rotliegend, Germany

Zusammenfassung

Ein höchst interessantes Paläo-Ökosystem aus dem Oberen Karbon-Unterstes Perm aus Niederhausen (Saar-Nahe-Gebiet, Rheinland-Pfalz, Deutschland) wird beschrieben. Obwohl es nach der herrschenden geologischen Lehrmeinung dem Karbon zugeordnet werden müsste, da noch immer Riesenbärlappbäume und Schachtelhalme ausgedehnte Teile der damaligen Kontinente beherrschten, stellt diese Vegetation eine typische Permflora dominiert von Koniferen, Peltaspermales und relativ modernen Farngewächsen dar. Deshalb werden in dieser Publikation Überlegungen angestellt, die Grenze Karbon-Perm auf den Übergang Kasimovium-Gzhelium zu verlegen.

Der weit verbreiteten Theorie, dass die ursprünglichsten Samenanlagen der Koniferen einen Blütenstand zusammengesetzt aus fertilen und sterilen Blättern darstellen wird aufgrund der Funde ein neues Konzept gegengestellt. Zumindest drei Koniferenfamilien kommen in Niederhausen häufig vor: Von *Perneria thomsonii* nov. gen. n. sp. kann angenommen werden, dass sie nahe am Ursprung aller Nadelbäume anzusiedeln ist. Wahrscheinlich haben wir es mit dem letzten Vertreter einer uralten Gruppe wie den Progymnospermen zu tun und trotzdem müssen wir diese Pflanze aufgrund seiner Zapfenstruktur, seiner Brakteen und fertilen Samenblätter, der nadelartigen Belaubung in die Gruppe der Koniferen aufnehmen. Dass Koniferen mit Flügelsamen – die häufigste heute vorkommende Form - eine große Rolle spielten wird durch *Wachtlerina bracteata* nov. gen. n. sp. unterstrichen, während in die Walchiaceaen zu klassifizierende Angehörige durch *Seymourina niederhauseni* nov. gen. n. sp. vorhanden sind. Diese Konifere zeichnete sich durch mehr oder weniger zusammengewachsene Samenblätter aus, welche von sterilen Blättern ummantelt werden. Dass die Ginkgogewächse und die Koniferen im Kasimovium-Gzhelium sehr nahe Verwandtschaftsverhältnisse aufwiesen wird durch *Baiera perneri* n. sp. aufgezeigt. Ginkgoales und Koniferen können demnach von einem gemeinsamen Stammbaum abgeleitet werden.

Eine weitere umfangreiche Pflanzengruppe beinhalten die Peltaspermales. Sie sind sowohl durch hoch entwickelte Familien wie durch ihre schirmförmigen Fruktifikationen auffallenden *Peltaspermum dammannii* n. sp. präsent, wie auch mit primitiveren Arten wie *Rachiphyllum hauptmannii* und *Odontopteris lingulata,* die, weil ihre Fortpflanzungsorgane im Zusammenhang mit ihrer Belaubung gefunden wurden, vom Morphogenus entfernt und als *Hurumia lingulata* nov. gen. neu klassifiziert wurde. Aber auch moderne Farnfamilien wie die Marattiales mit *Scolecopteris lothii* n. sp. oder die Osmundaceaen mit *Todites muelleri* n. sp. entwickelten sich in perfekter Symbiose mit alten Pteridophyta-Gruppen.

Überraschenderweise werden die Schachtelhalme vom Zwerg-Calamiten *Calamites wachtler*i n. sp. dominiert, wenn auch *Annularia spicata*-Blattwirtel in geringerer Anzahl vorkommen. Von den Bärlapps konnte nur der kleine *Selaginellites zollwegii* n. sp. angetroffen werden.

Zu andereren in geringer Zahl vorkommenden Pflanzenarten gehören die eventuellen Cycadophyten *Taeniopteris* sp. und *Nilssonia* sp. sowie die Gymnospermen *Cordaites* sp. und *Dicranophyllum sp*.

Diese eigenartige Pflanzensymbiose zeigt, dass es schon im Karbon, neben den zahlreichen Riesenbärlapp- und Schachtelhalmwäldern im Hinterland an periodische Trockenzeiten angepasste Vegetations-Biozönosen gab, welche in den folgenden Jahrmillionen die Oberherrschaft gewannen, um sie bis heute ausüben.

Introduction

Between the Late Carboniferous and Early Permian, the vegetation worldwide changed as never since. Whereas in wide areas, especially North-America, typical Carboniferous marshes and swamps with *Sigillaria, Lepidodendron* and *Calamites* predominated, in Western Europe, beginning from the Kasimovian, about 307 million years ago, the climatic conditions gradually changed. It became more arid; the yearly balanced rainfalls moved into long-lasting dry periods with only seasonal inundations and consequently, the plant kingdom also had to be adapted. One of the areas where this climate change was intensely studied, beginning from the nineteenth century, is the Saar-Nahe Basin in (SW-Germany). Extensive researches also incorporated nearby lying regions like Thüringen in Eastern Germany, with mainly the same paleo-ecological sedimentation conditions (GOTHAN & GIMM, 1930; KERP ET AL., 1990), as well as the Czech Republic and parts of Poland.

Although it is supposed that all of this intense research renders it impossible to ac-

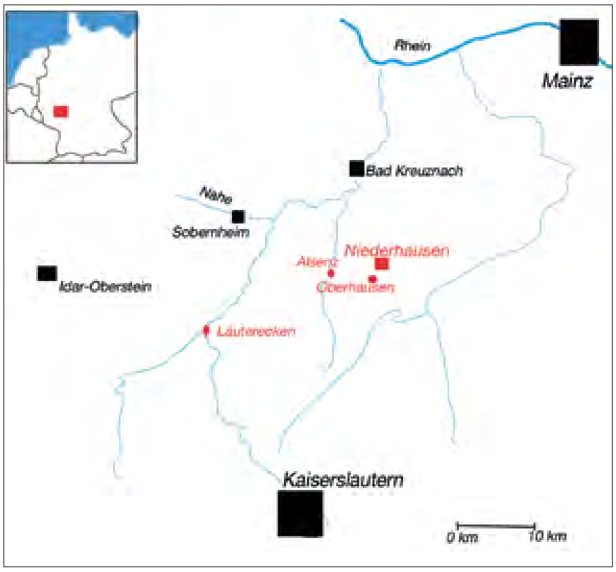

Fig. 1: Map showing the Niederhausen/Appel plant association locality.

System	System	Stage		Age	West. Europe
Permian	Lopingian	Changhsingian	4.8 Myr	252.2 +-0.1	Zechstein
		Wuchiapingian	4.8 Myr	254.1 +-0.1	
	Guadalupian	Capitanian	4.8 Myr	259.8 +-0.1	
		Wordian	3.3 Myr	265.1 +-0.4	
		Roadian	8.2 Myr	268.8 +-0.5	
	Cisuralian	Kungurian	8.0 Myr	272.3 +-0.5	Oberes Rotliegend
		Artinskian	7.7 Myr	283.5 +-0.6	
		Sakmarian	15.8 Myr	290.1 +-0.3	
		Asselian	8.0 Myr	295.0 +-0.2	Unteres Rotliegend
	Pennsylvanian	Gzhelian	4.8 Myr	298.9 +-0.2	
		Kasimovian	3.3 Myr	303.7 +-0.2	Stephanian BC
Carboniferous		Moscovian	8.2 Myr	307.0 +-0.2	Westphalian
		Bashkirian	8.0 Myr	315.2 +-0.2	Namurian
	Mississippian	Serpukhovian	7.7 Myr	323.2 +-0.4	
		Visèan	15.8 Myr	330.9 +-0.3	Visèan
		Tournaisian	8.0 Myr	346.7 +-0.4	Tournaisian
				358.9 +-0.4	

Fig. 2: Modified from Global Carboniferous Divisions ages from GTS 2012 and ICS chart developed for 34 IGC and International Commission of Stratigraphy. The Kasimovian-Gzhelian boundary would probably be better classified as the Carboniferous-Permian border.

cede uncharted scientific territories, surprises can never be excluded.
From 1971 until 1978, one of the authors, Thomas Perner, made intensive researches not far from Niederhausen/Appel, a small village, in the German Landkreis Bad Kreuznach. There, “Papierschiefer” (“paper-shales” in local terms) typically crop out, belonging to the Lower Meisenheim-Obere Lauterecken-Formation (Glan-Group). A well-justified stratigraphical correlation is not easily obtainable because of continental successions, but based on several analyses, the questionable radius could be restricted (BOY & FICHTER, 1982).

Geology

The Late Variscan, intermontane Saar–Nahe Basin in South-West Germany developed as a north-east–south-west-trend 120 km × 40 km half-graben, which is subdivided by sets of orthogonal transfer faults. During this late Variscan orogenic evolution, a crustal extension caused the formation of numerous intermontane basins. During a long lasting volcanic activity, which ended in Lower Permian time, the basin became filled purely by volcanic rocks and fluvio-lacustrine sediments revealing complex thickness and facies patterns as a result of contemporaneous tectonic faulting (LORENZ & HANEKE, 2004). This largest Late Palaeozoic basin in Europe, situated at the south-eastern margin of the Rhenish Slate Mountains, comprises about 4500 m of Late Carboniferous and about 3000 m Permian (Rotliegend) of sediments and volcaniclastics.
Radiometric measurements in the Saar-Nahe-Basin on lavas from the Grenzlager-vulcanism (Donnersberg-Formation), the closest unquestionable sediments and the beginning of Upper Rotliegend, classi-

fied them as being deposited about 298.7 ± 5.3 My and 297.8 ± 5.8 My years ago (LIPOLD & HESS, 1989). However, between the Donnersberg-Formation and the Lauterecken Formation, we have in succession from younger to older the Thallichtenbergen-, the Oberkirchen- the Disibodenberg-strata. That began an 800 m deposit of the Meisenheim-Formation and only after that do we arrive at the Upper Lauterecken-strata, where the plant-layers of Niederhausen can be encountered. The Meisenheim Formation, which is mostly grey in colour, is by far the thickest formation of the Glan Subgroup. Therefore, an age placement of this interesting plant-association in the Lower Meisenheim-Obere Lauterecken-Formation, or the lowest Gzhelian/Upper Kasimovian (303.7 my years ± 1 my) is suggested.

During Kasimovian–Gzhelian and Asselian time, extrabasinally-derived acidic volcanic ashes were deposited as distal pyroclastic fallout in lacustrine–deltaic dominated settings and subsequently altered to various clay mineral assemblages. Essentially, three depositional settings with contrasting preservation potential can be distinguished: tuffs inter-bedded with offshore-lacustrine (black) shales have the highest preservation potential, and are usually conserved as primary deposits showing sharp and planar contacts, planar lamination (multiple) graded bedding, and laterally constant thickness; ashes reworked by turbidity currents form erosionally-based, climbing-ripple and planar-bedded graded tuff horizons with load and flute casts at their bases; and tuffs inter-bedded with flood plain and crevasse splay sediments are often cross-bedded and display both current and tool marks. Reworking is common and associated with an abundant admixture of siliciclastic detritus or erosion of the entire tuff bed (LORENZ & HANEKE, 2004).

Palaeoecology and Palaeoclimatology

The sediments exposed in the Niederhausen-locality sandstone-quarry consist of alternations of grey-brown, sometimes slightly yellow sandstones and grey-brown finely laminated siltstones. Such fluvio-lacustrine environmental conditions are also known from other neighbouring areas like Alsenz or Oberhausen. All of these sediments form part of a continuous belt, several tens of kilometres wide and nearly 500 km long, ranging from Germany to the Czech Republic to its North-Eastern border and the adjacent part of Poland (OPLUŠTIL ET AL., 2013).

Plant fossils are usually common, but often strongly fragmented and randomly distributed in the sediment. Only some layers are relatively rich in larger specimens. Occasionally, in very shallow depressions, pocket-like concentrations are found. In the more sandy-to-silty layers, bedding planes can be covered with large amounts of highly fragmented plant parts, seeds or individual conifer leaves (KERP ET AL., 1990)

All of these sediments represent local swamps, lake shallows, floodplain deposits or seasonal inundation marshes caused by strong monsoon rainfalls and give good insight into how the new Pangaean climate development influenced the Permo-Carboniferous border by an extensive aridisation trend. These desertifications were not only caused by the drift of northern Pangaea to the arid climatic belt, but also by the successive closure of the Rheic Ocean, which caused the expansion of arid/semi-arid environments in the Lower/Middle Permian. The end of the Gondwana glaciation rearranged ocean circulation, leading to a cold, coast-parallel ocean current west of northern Pangaea, blocking moisture coming in with westerly winds (ROSCHER & SCHNEIDER, 2006).

Problematic Carboniferous-Permian boundary

The Gzhelian-Asselian stage was established as a marker about 299 my years ago, until the blooming Carboniferous and arid Permian, which could be valid mainly for the American Continent where in the Pennsylvanian region we still have giant lycopods and horsetails. However, it will doubtful for the ancient European landscape for several reasons. The earliest conifer remains are known from the Westphalian B of Yorkshire, England, about 307 million years ago, consisting of isolated leaves and twigs with cuticles (TAYLOR ET AL., 2009). However, on the Kasimovian/Gzhelian boundary, in the localities from Alsenz to Oberhausen and Niederhausen, we have a flourishing and all dominating conifer assemblage where most

Frequent insect and animal feeding

Herbivorised leaves often occur in the Niederhausen-sediments. Particularly, the Peltasperms and ferns (*Hurumia, Autunia* and *Scolecopteris*) preserve an exceptionally high foliation level. The major types of leaf damage are margin feeding, as seen in 1) PER 278, 2) PER 98 and 3) PER 84 on *Hurumia lingulata* branchlets. Others are hole feeding skeletonisation, as seen in 4) PER 109, and galling seen in 5) PER 308.

1) PER 278. *Hurumia lingulata.*
2) PER 98. *Hurumia lingulata.*
3) PER 84. *Hurumia lingulata.*
4) PER 109. *Hurumia lingulata.*
5) PER 308. *Scolecopteris lothii.*

of today's families have mainly developed. Other plant-families in these sediments like ferns (*Todites* and *Scolecopteris*), seed ferns (*Peltaspermum*), and Cycadophyta can be regarded as typical Permian and not Carboniferous. Therefore, it will be proposed to transfer the Carboniferous-Permian boundary to the Kasimovian-Gzhelian border, as even Carboniferous swamps and vegetation elements persisted in some parts of the world at the same time.

Insect and animal feeding

Ferns and in particular the seed ferns with the Peltaspermales (*Hurumia*) in this group are often infected by insect and animal feeding. Most of them consist of margin feeding with cuspate excisions of the foliar tissue along the pinnule margins (PER 278, PER 98, PER 84). Another form of damage is hole feeding, generating circular or polylobate surface patterns (PER 209). Skeletonisation occurs with only retention of the venation on completely mainly preserved leaves (PER 278). Galls are atypical spheroidal to ellipsoidal teratological structures with one or more internal chambers produced by mites or insects. They occur often on and parallel to the mid-vein (PER 308). However, whether this frequent insect and animal feeding is the beginning of the long lasting symbiosis between plants and animals must be established by further analysis.

Palaeoniscid fishes from the genus *Paramblypterus* sp. were found rarely in Niederhausen as well as Branchiosaurus amphibians (*Apateon* sp.) in larval stages between *Hurumia lingulata* leaves.

The Niederhausen living environment

All of the plant fossils were collected in a contained area of no more than 30 square metres and a deposit-thickness of 50 to 60 centimetres. The sediments consisted of rhythmic laminated clay- and algae-strata, silt and limebanks with different calcareous contents, often only in millimetre-thickness, the "Papier-Schiefer" ("paper-shales"). Plant-fossils can be sparsely found in all layers, from clay to limestone. *Branchiosaurus*-larvae or fishes are seldom, probably in an isolated manner, found in drying-out swamps and eutrophic micro-basins, rather than at meandering rivers. Through a more seasonal development of the climate during the Permo-Carboniferous period, just in the Stephanian (SCHÄFER ET AL., 1990; ZIEGLER, 1990), dry seasons changed to periodic inundation events with accompanying rhythmic silty sedimentation rates (KERP, 1996).

Comparisons with other Lower Rotliegend deposits

Clearly coeval plant deposits from the Lowest Rotliegend are not so frequent. Most are slightly or considerably younger, and often collected mixed fossils from diverse localities, meaning that an exact time-synchronisation is impossible, but almost two allochtonous floras from the Permo-Carboniferous can be regarded as almost stratigraphically synonymous: One is the locality Oberhausen/Appel and the other lies near Alsenz. Both are situated close to Niederhausen and can be regarded as belonging to the Jeckenbach-Lauterecken-Formation. The sediments of Oberhausen and Alsenz mainly consist of the same pelagic to hemipelagic deposits with locally precipitated carbonates, indicating an environment of slow deposition. Sedimentation took place in an open lake zone, distant from the densely vegetated, fluvially-influenced deltaic plain (LAUSBERG, 2002; KERP, 1990). Alsenz holds a lot of identical vegetation, but their conservation-status is not as good as in Niederhausen, so several plant-organs could be inserted only generally (*Peltaspermum sp., Odontopteris sp.*). Especially valid for the Coniferophyta, is the difficulties in imagining the real organisation of the plant, due to flattened or smashed conifer cones or isolated or detached seed scales. LAUSBERG, in her well written monumental inaugural-dissertation about the Rotliegend-flora from the Saar, figured (on plate 66) a characteristic bract of *Wachtlerina bracteata*, but probably due to the absence of well-connected cones and twigs, could only characterise them as "isolated conifer leaves".
The new genus *Wachtlerina* constitutes one of the most enigmatic plant species from Niederhausen. If not found in straight connection, one would classify them without doubt as *Ernestiodendron*, but only the winged seeds reveal the true character; they can be inserted much more appropriately in the group of Majonicaceae, a conifer family which has until now been recorded only from Upper Permian, and also generates winged seeds. Surprisingly, the conifers were much more diversified than previously thought; also, for true insertion, other samples must be just as well studied. Therefore, especially for Niederhausen, it helped that most of the specimens were recovered by one collector (Thomas Perner). It seems that in Alsenz, bracts from the *Gomphostrobus bifidus*-type are much more common than in Niederhausen, where only one uncertain specimen was found, whereas Ginkgoelean *Baiera* leaves are more widespread in Niederhausen (KLAUSBERG & KERP, 2000, Plate 66, Fig. 3). Also, the enigmatic morphogenus *Odontopteris* without any attached ovuliferous shields, could not be inserted in the group of Peltaspermaceae; fortunately, the Niederhausen-flora released fronds with connected fructifications which were splendidly conserved.

Components of the Niederhausen-flora:

Lycophyta
Selaginellites zollwegii n. sp

Sphenophyta
Calamites wachtleri n. sp.
Annularia spicata

Coniferophyta
Perneria thomsonii nov. gen. n. sp.
Wachtlerina bracteata nov. gen. n. sp.
Seymourina niederhauseni nov. gen. n. sp.
Cordaites sp.
Dicranophyllum sp.

Pteridospermatophyta
Peltaspermum dammannii n. sp.
Hurumia lingulata nov. gen.
Rachiphyllum hauptmannii n. sp.

Cycadophyta
Taeniopteris sp.
Nilssonia sp.

Pteridophyta
Scolecopteris lothii n. sp.
Todites muelleri n. sp.
Sphenopteris sp.

Ginkgophyta
Baiera perneri n. sp.

Material-preservation

All of the specimens are preserved as relatively small compressions and impressions which are characterised by sometimes excellent identification preservation conditions. Cuticles are only occasionally preserved.

Repository

In total, from the complete collection, 350 specimens were catalogued, because they were symptomatic for this locality. The investigated material, especially all holotypes and paratypes, are stored in the Senckenberg Forschungsinstitut und Naturmuseum at Frankfurt (Germany). Their numbers are prefixed by "PER" for Perner-Collection. The remainder of the collection is at the DoloMythos Museum at Innichen (Italy) or in Thomas Perner's private collection.

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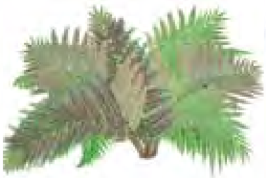
Reconstruction of the Earliest Permian (Kasimovian-Gzhelian) Niederhausen-Flora: (From the left to the right):

Scolecopteris lothii



Todites muelleri

Rachiphyllum hauptmannii

Hurumia lingulata

Peltaspermum dammannii

Selaginellites zollwegii

Perneria thomsonii female and male plant

Calamites wachtleri

Wachtlerina bracteata female and male tree

Seymourina niederhauseni

Baiera perneri

Lycophyta from the Carboniferous-Permian (Kasimovian/ Gzhelian) Niederhausen-Flora (Rheinland-Pfalz, Germany)

by Thomas Perner and Michael Wachtler

Division: Lycophyta
Order: Isoetopsida (PRANTL, 1874)
Family: Sellaginellaceae (PALISOT DE BEAUVOIS, 1805)
Genus: *Selaginellites* (ZEILLER, 1906)

***Selaginellites* zollwegii n. sp. (PERNER & WACHTLER, 2013)**

Holotype
PRE 173

Material
PRE 58, 336, 348, 235

Locality
Niederhausen, Rheinland-Pfalz, Germany

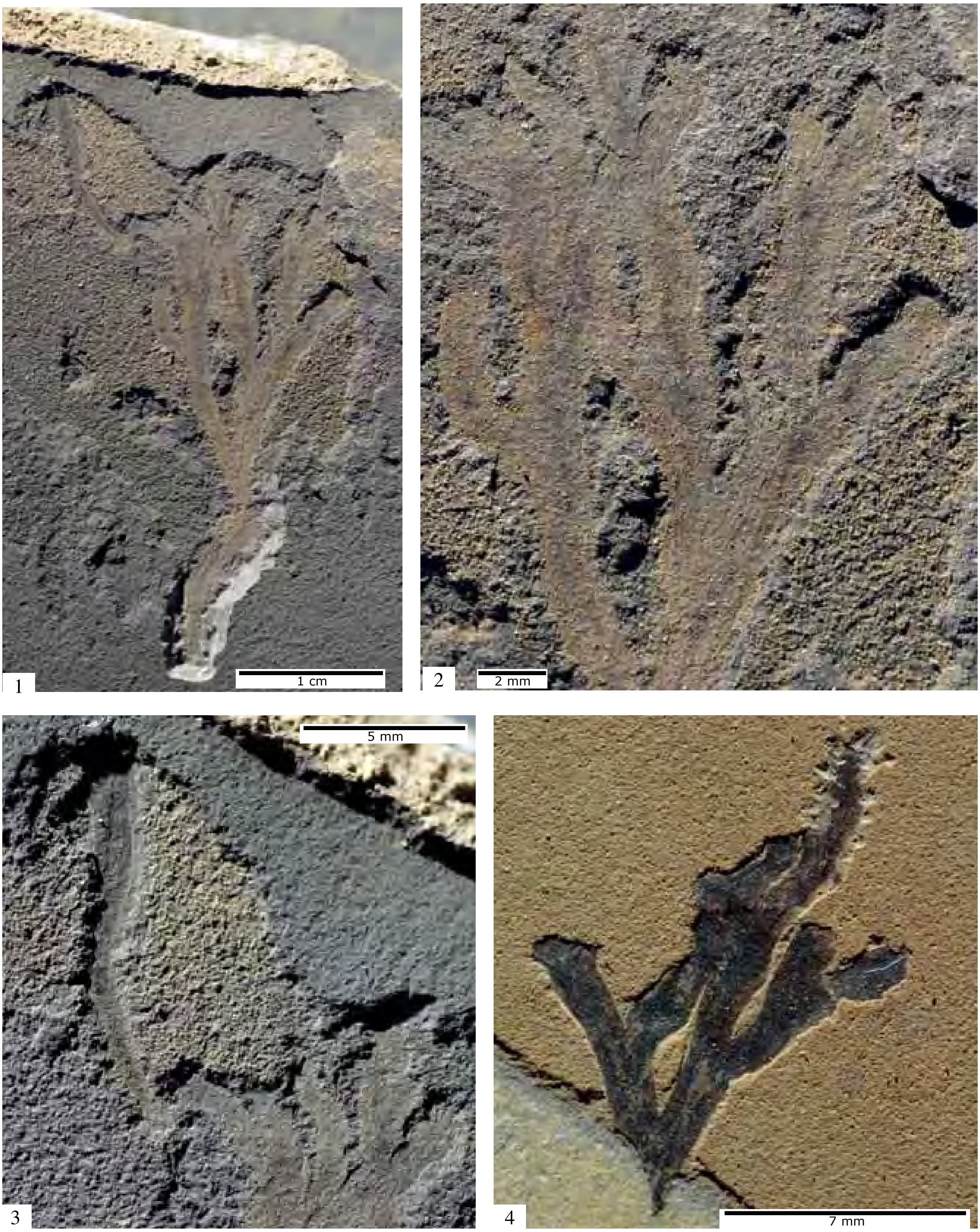
Type horizon and age
Upper Lauterecken-Lower Meisenheim-Formation, latest Kasimovian-Gzhelian, Regional stage Western Europe: Stephan B-C

Etymology
Named after Michael Zollweg, who performed extended research at the Messel fossil site.

Diagnosis
Stems densely cespitose, branching dichotomously, but irregularly forked. Leaves tightly appressed, strobili terminal on the branches, elongated and slender.

Description
Vegetative branches: Herbaceous lycopsid with ascending, on the upper part, often dichotomising axes, without an apparent decrease in the thickness of the lateral branches. PER 235 shows a clustered and mainly complete specimen, 4 x 4 cm in size. The thickness of the shoots is about 2 mm (PER 173); the ultimate branchlets are often only developed as short spurs.
Leaves: Minute, nearly invisible appressed to the branchlets. They are awl-shaped and highly overlap each other. Sometimes, they have a visual nature of naked stems (PER 58).
Fertile organs: Strobili are remarkably long in comparison to the shoots and the whole plant (PER 173 more than 10 mm), but in the same way are outmost filmy.

Discussion
Extant Selaginellaceae comprise 700 living species, which are encountered around the world, with genera adapted to grow in the arctic as frost-tolerant, in deserts as drought-adapted, and as long-lasting humid-resistant in the rainforests. Almost all are characterised by their delicate dichotomously branching stems that develop ranks of minute leaves. A cosmopolitan occurrence was only achieved in the Paleozoic, but due to their inconspicuous appearance, they are often overlooked or simply ignored; therefore, only a few specimens were described in the literature.
In the present and also in the fossil record, the *Selaginella*-species are subdivided into two distinct groups: The first group comprises isophyllous species with leaves of all one kind and arranged spirally on the shoots. The second group, known as anisophyllous, consists of species with leaves secondarily arranged in four rows along their shoots and with diverse leaflets.
Another question is whether some of the fossil species have so many affinities to the extant to insert them in some *Selaginella*-species, or if the range in time - in this case almost 300 million years - generate results in only misinterpretations. Based on this doubt, the name *Selaginellites* was chosen. The name *Selaginellites* has been instituted by René Zeiller for heterosporous species resembling *Selaginella* from Carboniferous sediments of Blanzy in France.



1) PER 173. *Selaginellites zollwegii. Designed* Holotype. Part of a branch.
2) PER 173. *Selaginellites zollwegii.* Holotype. Branches evidencing dichotomous forking.
3) PER 173. *Selaginellites zollwegii.* Holotype. Strobilus.
4) PER 58. *Selaginellites zollwegii.* Branch with part of a strobilus.

The earliest, undisputed record of anisophyllous shoots, with two different types of leaves on the same plant, came from the Bolsovian of the Saar-Lorraine Coalfield (Westphalian D), anisophyllous shoots are also known from much wider areas like the German-French Saar-Lorraine basin, Zwickau in Germany, Somerset, Britain, or Nova Scotia, Canada (THOMAS, 1997). Therefore, it can be suggested that the anisophyllous *Selaginella*-species originated before the isophyllous one.
Upper Carboniferous *Selaginellites gutbieri* (GÖPPERT) (KIDSTON, 1911), recorded in extraordinary complete and spectacular specimen holds from Westphalian D of Germany a well-developed planar branching. The arrangement of the leaves is anisophyllous, with two ranks of larger lateral leaves, ovate to lanceolote with acute apices, and two ranks of smaller median leaves. In that, the main difference to *Selaginellites zollwegii* n. sp. was isophyllous and bearing only dwarfish, tightly appressed and closely overlapping leaves.
A lot of other *Selaginellites*-species were recorded mostly from the Carboniferous, which are often only found in a few specimens. This is valid for *Selaginella primaeva, Selaginella macrophylla, Selaginellites elongatus* or *Selaginella zeilleri*. Also, *Selaginella suissei* from the Stephanian of France generate anisophyllous shoots.
The differences of *Selaginellites zollwegii* to the Carboniferous spikemosses are evident, but they differ from Early Triassic (Anisian) *Selaginellites leonardii* recovered in the Italian Dolomites (WACHTLER, 2011). This herbaceous plant was probably slightly bigger and its heterosporous strobilus was more massive, probably as a consequence of a more humid climatic. All indications are, that beginning from the Earliest Permian to the Early Triassic, this area and also other Euramerican parts suffered from extreme aridity for most of the year; this was true for almost 50 million years.
To summarise, it can be stated that at the end of the Carboniferous era, the time of the giant lycopods was over and only small-sized clubmosses eked out a marginal existence.

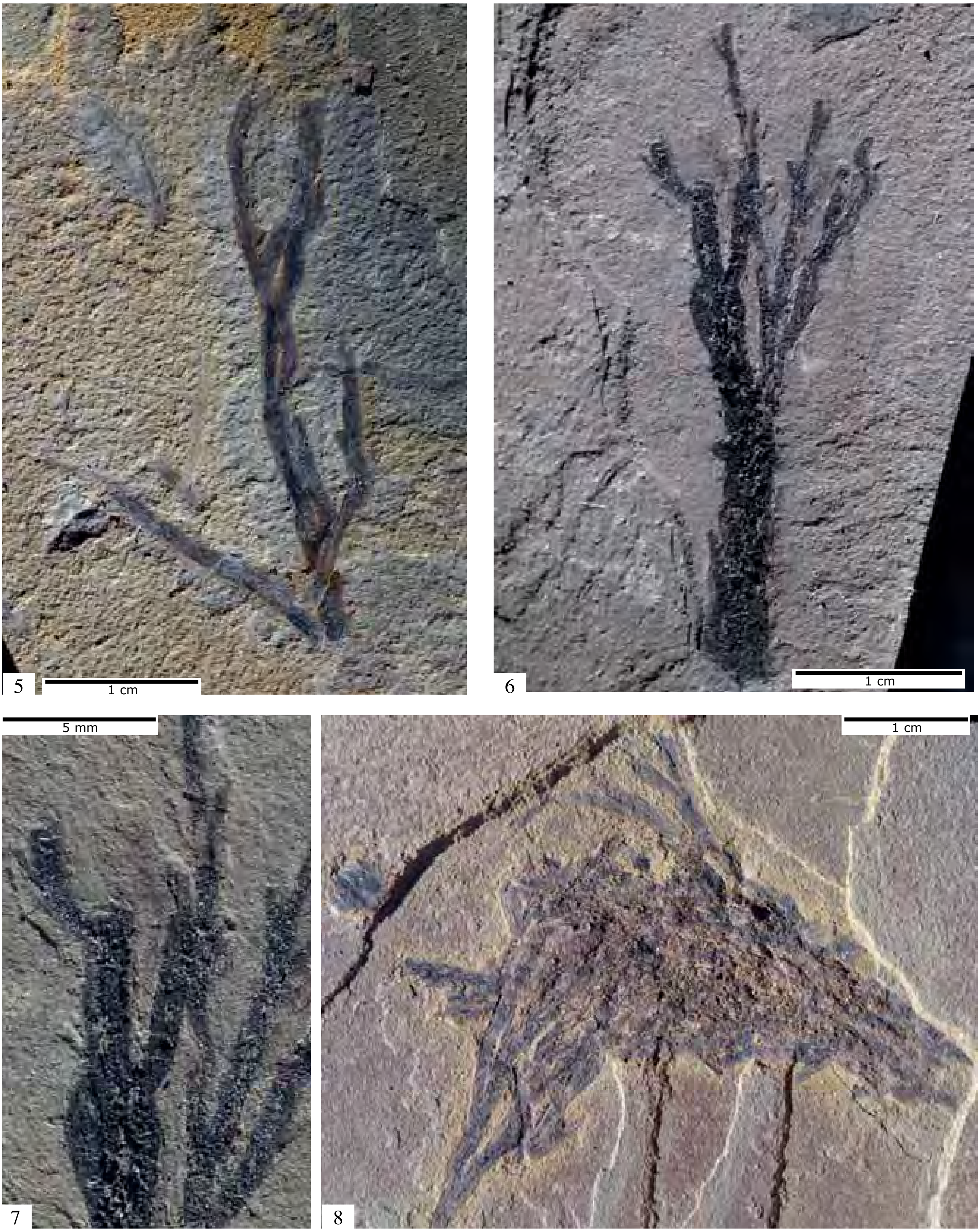
Selaginellites zollwegii. a) Strobilus (PER 173), b) Branch with a strobilus on the upper side (PER 173).

KIDSTON, R., (1901): Carboniferous Lycopods and Sphenophytes. Trans. Nat. Hist. Soc. Glasgow, 56: 25-140.

THOMAS B.A., (1997): Upper Carboniferous herbaceous lycopsids. Rev. Palaeobot Palynol 95: 129-153)

TOWNROW, J.A., (1968). A fossil *Selaginella* from the Permian of New South Wales. Bot. J. Linn. Soc. London, 61: 13-23.

WACHTLER, M., (12/2011): Lycophyta from the Early-Middle Triassic (Anisian) Piz da Peres (Dolomites - Northern Italy), Dolomythos, Innichen. p. 165 - 211



5) PER 336. *Selaginellites zollwegii.* Branch.
6) PER 348. *Selaginellites zollwegii.* Axes with slightly enlarged short spurs.
7) PER 348. *Selaginellites zollwegii.* Detail with a badly conserved strobilus.
8) PER 235. *Selaginellites zollwegii.* Mainly complete branch.

Sphenophyta from the Carboniferous-Permian (Kasimovian/ Gzhelian) Niederhausen Flora (Rheinland-Pfalz, Germany)

by Thomas Perner

Division: Sphenophyta
Order: Equisetales (DUMORTIER, 1829)
Family: Equisetaceae (MICHAUX, ex DC 1804)
Genus: *Calamites* (BRONGNIART 1828)

Calamites wachtleri sp. nov. (PERNER, 2013)

Holotype

PER 29

Paratype

PER 129 (cone) PER 206 (branching system)

Material

PER 60, 63, 142, 158, 160, 189, 254, 296

Locality

Niederhausen, Rheinland-Pfalz, Germany

Type horizon and age

Upper Lauterecken-Lower Meisenheim-Formation, latest Kasimovian-Gzhelian, Regional stage Western Europe: Stephan B-C

Etymology

This was named after Italian researcher Michael Wachtler, who discovered and described Alpine and German fossil plants.

Diagnosis

Horsetail with an erect axis and a fair amount of protruding secondary shoots. Diaphragms surrounded by a leaf sheath. Fertile organs were slender consisting of alternating whorls of sporangiophores and bracts.

Description

Whole plant: Designed holotype PER 29, shows a 11 cm long main stem, 1.5 cm wide, with almost eight 6 cm-long protruding whorls on the apex and some secondary shoots on the main axis. No bigger specimens have been recorded but many have the same size; therefore, it can be suggested that we have to compare them with the giant *Calamites* of Carboniferous due to the dwarfish horsetail. The distance between the sheaths on the main axis was 2 cm, but on the lateral whorls was only 2-4 mm. The plant can often end with a tuft of many secondary shoots, which is unusual for other horsetails of this period.

Whorls: Secondary whorls 5 mm wide, from 5 to 7 cm long characterised by closely spaced internodes surrounded by a leaf sheath. Leaves delicate, 2 mm long acuminate (PER 18, 206). Mainly, there are three leaves on one side forming a whorl. Therefore, it can be suggested that at all twelve leaves around the collar will be the predetermined character. Sheaths on the main axis were 15 mm long but often released.

Fertile parts: Complete cones 5-6 cm long and 2-3 mm wide. PER 129 represent a young immature cone consisting of alternating whorls (about 30-35) of sporangia and bracts. The pointed bracts claw densely the sporangiophores. The sporangiophores are rounded to elliptical and 1-2 mm in size. The cone is distinguished by a short basal stipe and is densely covered on the apical part by fine leaves. Individual cones are born at the distal end of a leafy branch.

Discussion

Calamites wachtleri has been recovered in a fair amount on Niederhausen (about 50 specimen and 10 cones), and is distinguished by its smallness. Also, adult specimens (like PER 29 or PER 296) never exceed the 1.5 cm thickness of the main stem.
Although being inserted in the group of Calamitaceae, *Calamites wachtleri* fits only due to the reproductive organs in this concept, whereas the organisation of the whorls sheaths is much more reminiscent of *Equisetites.* However the strobili are totally different. In *Equisetites* they consist of an arrangement of peltate shields with sever-

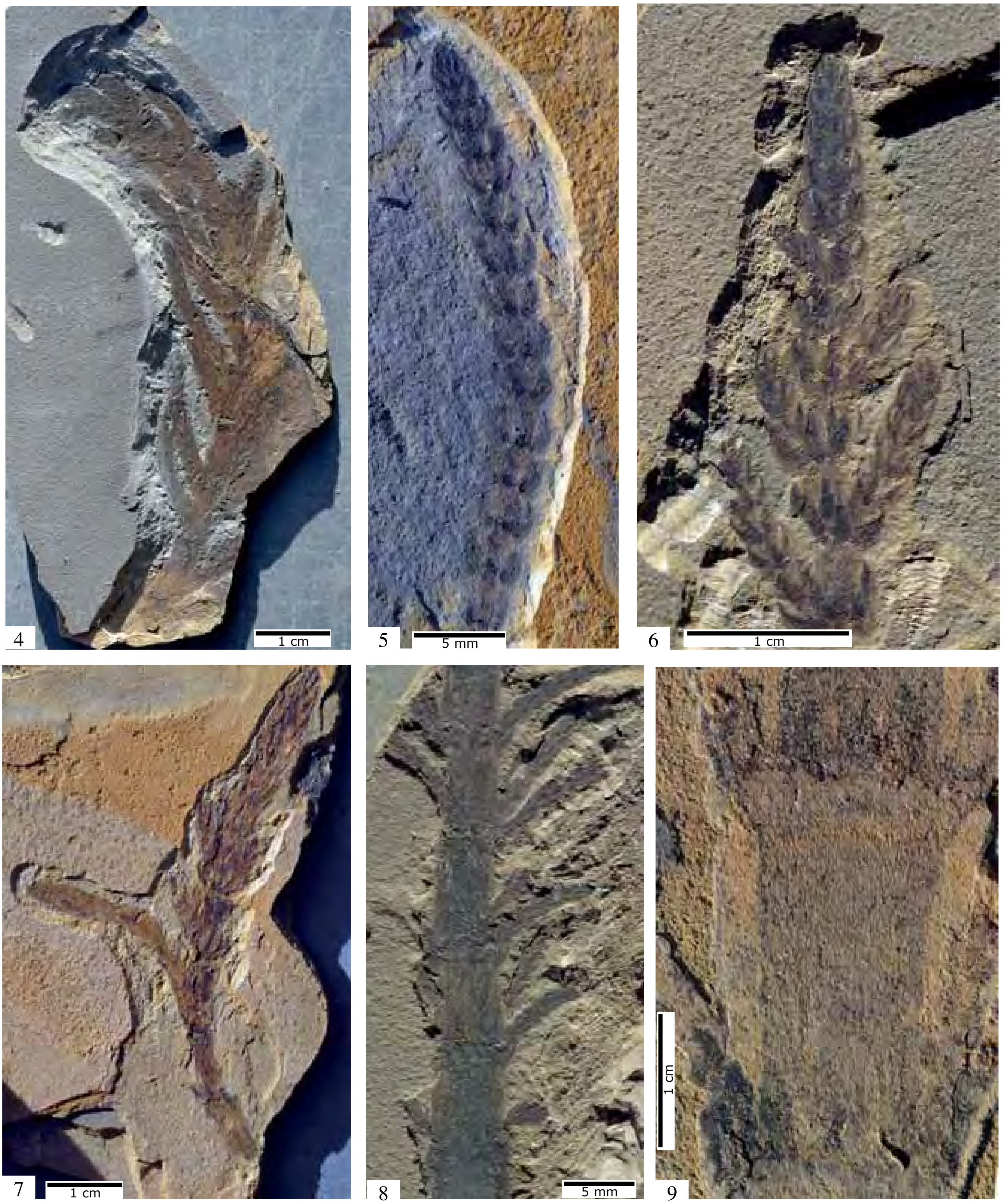
1) PER 29. *Calamites wachtleri.* Designed holotype. Apical part of a main stem with secondary whorls.
2) PER 158. *Calamites wachtleri.* Lateral branches sprouting from a stem.
3) PER 296. *Calamites wachtleri.* Leaf sheath.

al elongated fertile appendices on the lower surface directed towards the main axis. In contrast to the mainly coeval locality of Schallodenbach, where almost all of the sphenophyta (A*sterophyllites equisetiformis, Annularia carinata, Annularia stellata, Annularia spicata, Calamites gigas, Calamites multiramis*) fits with their pit casts still in the typical concept of Carboniferous parented horsetails, only isolated *Annularia spicata* leaves were found in Niederhausen.
Other Rotliegend places in the Thuringian-area differ with their richness in giant *Calamites (C. multiramis, C. gigas, suckowii)* from the Niederhausen-Sphenophyta (BARTHEL, 2009). The reasons for this gnomish growth in Niederhausen cannot be completely understood. It may be that the lakes and pools were so small that bigger sphenophyta could not survive and therefore it was only a local adaption to the paleo-environment.

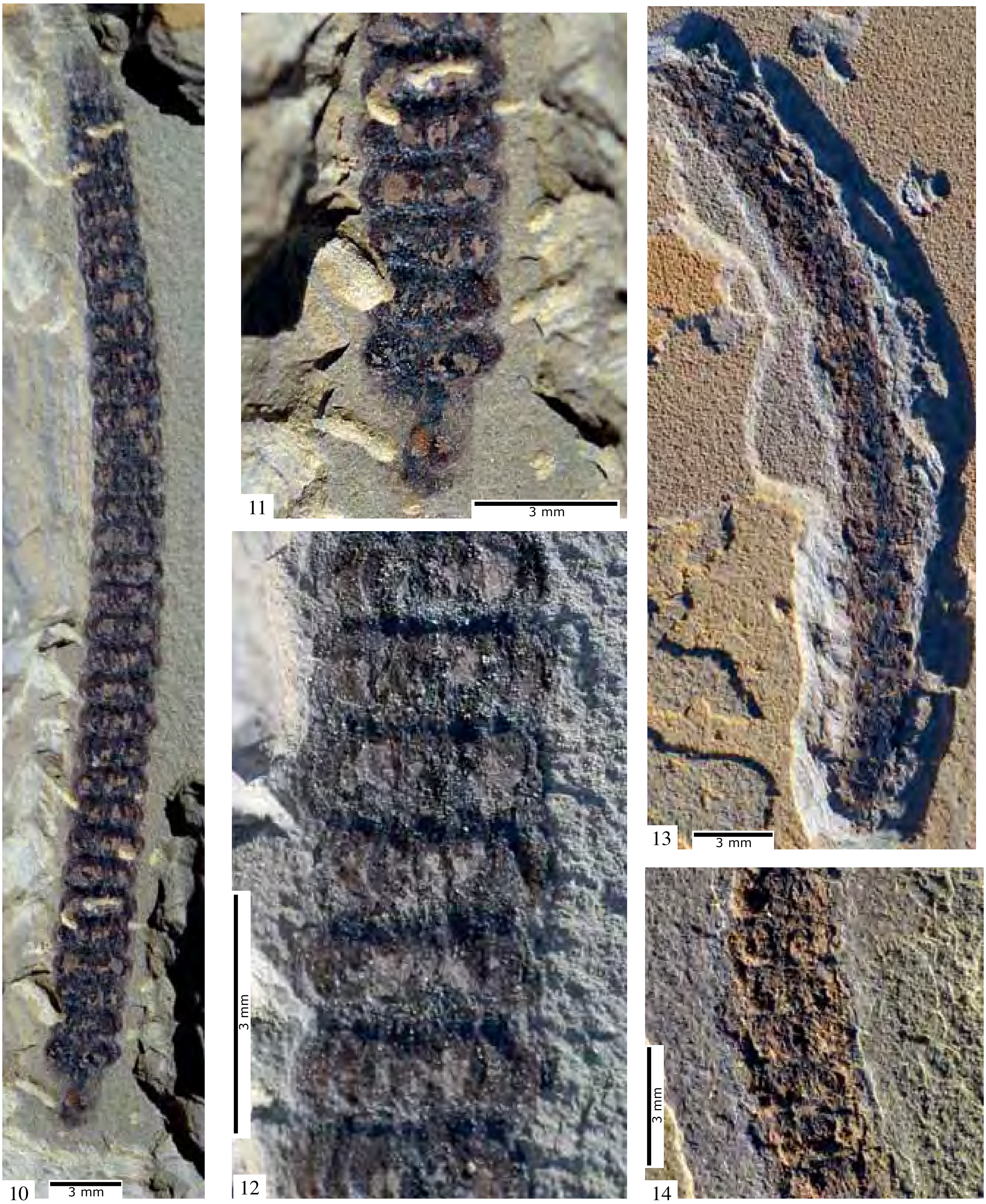
BARTHEL, M., (2009): Die Rotliegendflora des Thüringer Waldes. Veröff. Naturhist. Mus. Schleus., Schleusingen.

LAUSBERG S., (2002): Neue Kenntnisse zur Saarpfälzischen Rotliegendflora unter besonderer Berücksichtigung der Coniferentaxonomie und des Hinterlandes, Inaugural-Dissertation zur Erlangung des Doktorgrades der Naturwissenschaften im Fachbereich Geowissenschaften der Mathematisch-Naturwissenschaftlichen Fakultät der Westfälischen Wilhelms-Universität Münster

Calamites wachtleri. a) Whole plant (PER 29), b) Stem-fragment (PER 29B), c) Leaf sheath (PER 296), d) Secondary whorls (PER 206), e) young cone (PER 129) f) Mature cone with sporangiophora (PER 63).



4) PER 254. *Calamites wachtleri.* Apical part with secondary whorls.
5) PER 189. *Calamites wachtleri.* Part of the secondary whorls and the axis with leaves.
6) PER 206. *Calamites wachtleri.* Paratype. Secondary whorls with leaf sheath.
7) PER 160. *Calamites wachtleri.* Branching example of a stem.
8) PER 142. *Calamites wachtleri.* Ramifying secondary whorls from the main axis.
9) PER 29B. *Calamites wachtleri.* Main axis with leaf sheath.



10) PER 129. *Calamostachys wachtleri.* Paratype. Immature calamite cone with closely spaced nodes bearing whorls of bracts and sporangia.

11) PER 129. *Calamostachys wachtleri.* Basal part of the cone.

12) PER 129. *Calamostachys wachtleri.* Detail of the spaced nodes with the bracts and sporangia.

13) PER 50. *Calamostachys wachtleri.* Mature cone.

14) PER 63. *Calamostachys wachtleri.* Detail of the cone with the sporangia.

Division: Sphenophyta
Order: Equisetales (DUMORTIER, 1829)
Family: Calamitaceae

Annularia spicata GUTBIER, 1837

1837 Annularia spicata, GUTBIER S. 436

Material

PER 56, 156

Discussion

Ultimate whorls of the sphenophyta A*nnularia spicata* are rare in the Niederhausen-Flora. The recovered material consists only of some branchlets with clearly defined single whorls of 8 to 10 approximately equal-sized symmetrical leaves about 1 mm long. The leaves are spatulate to ellipsoidal, no midvein is visible, and the apical part of the leaves is rounded. The internodes distance between the whorls is approximately 5 mm. *Annularia* branchlets of last order, belonging to some Calamitaceae-species, are a common element of Upper Carboniferous ecosystems, but disappear gradually through the Permian, to be replaced by other sphenophyta like *Equisetites* or *Neocalamites* (BARTHEL, 2009; KERP ET AL., 1990; LAUSBERG, 2000). They are also recorded in mainly coeval formations like Alsenz or Oberhausen.

BARTHEL, M., (2009). Die Rotliegendflora des Thüringer Waldes. Veröff. Naturhist. Mus. Schleus., Schleusingen.

KERP, J.H.F., POORT, R.J., SWINKELS, H.A.J.M., VERWER, R., (1990). Aspects of Permian Palaeobotany and Palynology. IX. Conifer-dominated floras from the Saar-Nahe Basin (?Late Carboniferous-Early Permian; SW-Germany) with special reference to the reproductive biology of early conifers. Rev. Palaeobot. Palynol., 62: 205-248.

LAUSBERG S., (2002): Neue Kenntnisse zur Saarpfälzischen Rotliegendflora unter besonderer Berücksichtigung der Coniferentaxonomie und des Hinterlandes, Inaugural-Dissertation zur Erlangung des Doktorgrades der Naturwissenschaften im Fachbereich Geowissenschaften der Mathematisch-Naturwissenschaftlichen Fakultät der Westfälischen Wilhelms-Universität Münster

1) PER 156. *Annularia spicata.* Apical lateral shoot.

2) PER 56. *Annularia spicata. Lateral shoot.*

Pteridosperma from the Carboniferous-Permian (Kasimovian/Gzhelian) Niederhausen Flora (Rheinland-Pfalz, Germany)

by Michael Wachtler and Thomas Perner

Division: Pteridosperma
Order: Peltaspermales (TAYLOR, 1981)
Family: Peltaspermaceae (PILGER and MELCHIOR in MELCHIOR and WERDERMANN, 1954)

Hurumia gen. nov. (PERNER & WACHTLER, 2013)

Etymology

Named after Jørn Harald Hurum, a Norwegian paleontologist and populariser of science.

Diagnosis

Seedfern with oblong rounded and sometimes incised pinnules, but lacking a typical midvein. Umbrelliformous ovuliferous organs arranged around the main axis.

Hurumia lingulata (PERNER & WACHTLER, 2013), GOEPPERT 1846

1822 - *Odontopteris,* BRONGNIART, p. 34
1990 *Peltaspermum sp.* KKERP ET. AL., p. 68
2000 - *Odontopteris lingulata*, LAUSBERG & KERP, p. 68, fig. 7
2009 - O*dontopteris lingulata*, BARTHEL p. 55

Holotype

PER 69

Paratype

PER 32 (young fertile frond)

Material

PER 109, 110, 164, 104 (sterile fronds), PER 33, 46, 48, 313, 91 (leaves).

Locality

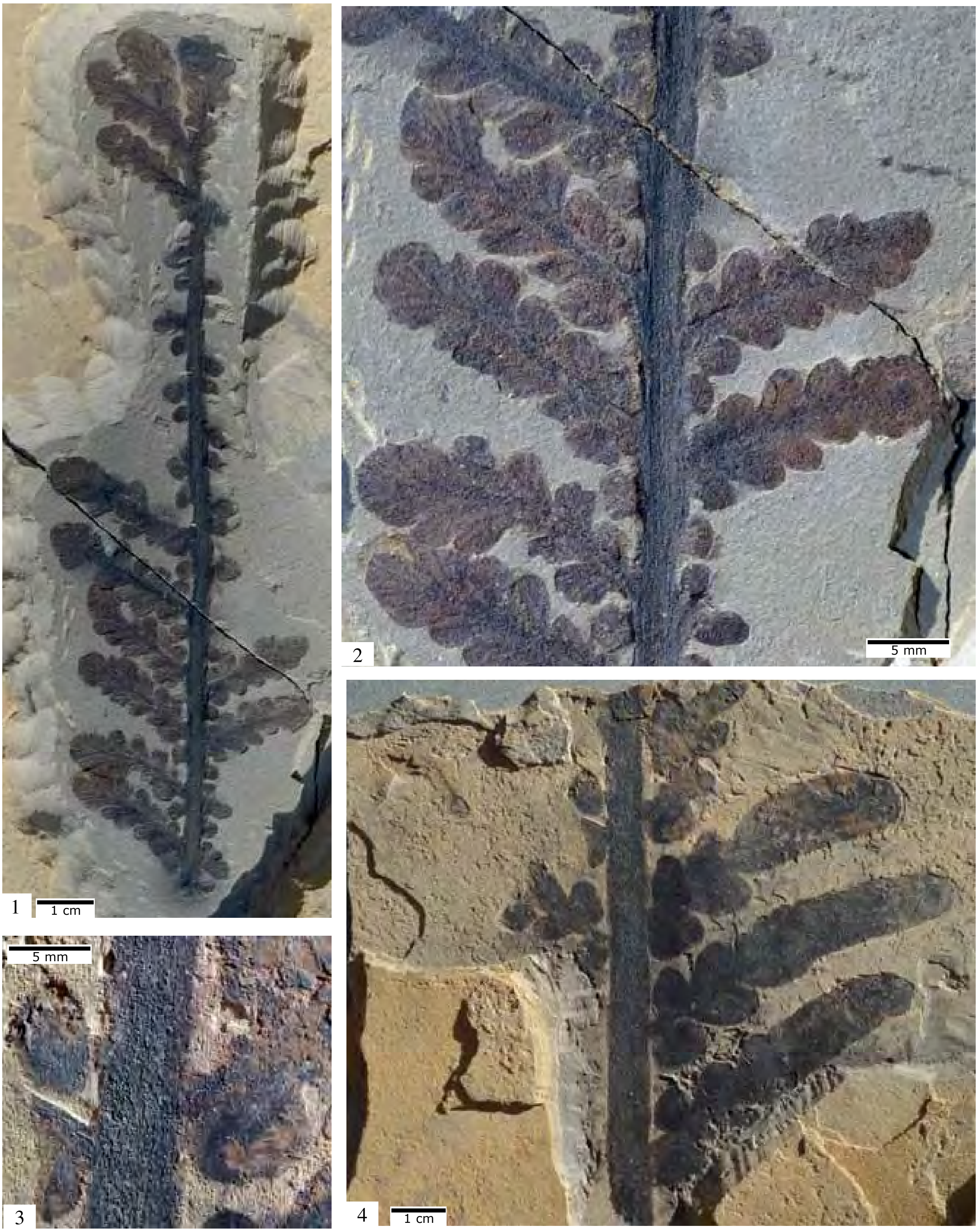
Niederhausen, Rheinland-Pfalz, Germany

Type horizon and age

Upper Lauterecken-Lower Meisenheim-Formation, latest Kasimovian-Gzhelian, Regional stage Western Europe: Stephan B-C

Description

Fronds: Bipinnate, pinnae arranged opposite to sub-alternate (PER 109, 110, 164).
Leaves: Pinnules of various forms, large, generally oblong, obtuse, joined to the rachis; incised one or two times on the lower part, remembering a former nature as an aggregation of different small leaflets. On the upper part becoming confluent towards the top till ending in one extensive not or only rudimentary constricted pinnula. Pinnules lacking a typical midvein but instead they are dotated with two to several veins that enter the pinnule and fork at irregular intervals till the margin (PER 33, 46, 48, 91, 313). Fully grown pinnules up to 10 cm long, and 2 cm wide. PER 104 is a good example, showing the characteristic abscission point of the leaflets. In most cases, this occurs after the first small pinnula, suggesting an aphlebia-attribute.
Fertile pinnules: Sprouting sparsely between the sterile leaflets on the lower part (PER 69), but forming a dense aggregation of peltate ovuliferous organs without sterile leaves in the upper part. PER 32 is a good example of a young fertile frond, which is 12 cm long, holding up to 20 ovuliferous organs that are mainly concentrated on the upper part. The fertile organs form flattened umbrelliferous shields, sometimes also being slightly incised in several segments on the apical part, as known for the Peltaspermales. The upper part of the fertile fronds ends with some sterile pinnules (PER 32). It becomes confluent towards the top of the pinnae and gradually effaced in passing to a terminal leaflet. Leaflets on fertile pinnulas are more



1) PER 32. *Hurumia lingulata nov. gen.* Fertile young frond. Peltate fertile hats attached on the main rachis.

2) PER 32. *Hurumia lingulata nov. gen.* Detail of the lower part of the frond with the sparse fertile hats.

3) PER 69 *Hurumia lingulata nov. gen.* Designed Holotype. Detail of two fertile shields sustained by a massive peduncle.

4) PER 69. *Hurumia lingulata nov. gen.* Holotype. Fertile frond with the sterile parts on the lower and the fertile on the upper part arranged around the main rachis.

flattened with partially invisible to obscured veinlets.

Ovuliferous organs: Hat-like, attached to the main rachis by a relatively broad peduncle (PER 69: 3 mm). Hats are rounded and up to 10 mm wide, 8 mm high. Ovules on the lower part of the flattened shield are arranged around the stipe. PER 69 constitutes a juvenile megasporophyll due to the not fully grown sterile leaflets.

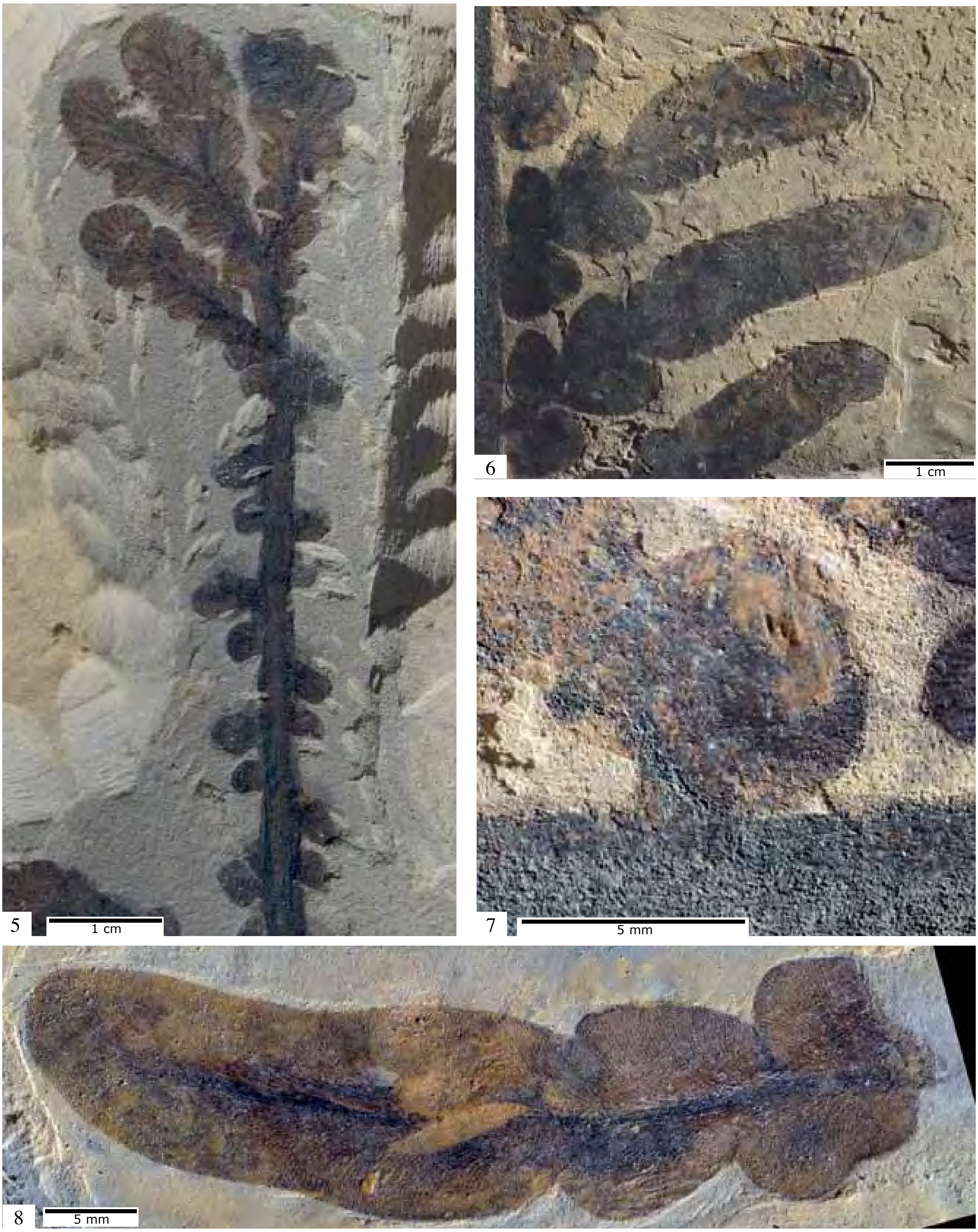
Discussion

The morphogenus *Odontopteris* constitutes one of the most well-known late Carboniferous-Early Permian fern foliage, predominantly described from Europe and North America and comprising about 200 species like *Odontopteris subcrenulata, O. schlotheimii, O. brardii, O. reichiana, O. wintersteinensis* and of course *Odontopteris lingulata* (KRINGS ET AL., 2006).

It is not the purpose of this publication to make an overview and correlation between the many different taxa of *Odontopteris*, often described because of microscopic differences in their leaf visual nature, and therefore making them harder to classify. Some probably belong to several different ferns and seedfern genera; therefore, we only concentrate our main attention on one Early Permian seed fern described in the literature as *Odontopteris lingulata.*

As lamented by other authors (BARTHEL, 2009; LAUSBERG & KERP, 2000), although *O. lingulata* foliage occurs relatively often in Early Permian European localities, to date, secure

Hurumia lingulata a) Sterile frond (PER 164), b) Single pinnula (PER 33), c) Part of a frond with peltate fructifications (PER 69, d) Megasporophylls (PER 69) e) Young fertile frond with attached fructifications (PER 32).



5) PER 32. *Hurumia lingulata.* Upper part of a frond with the ovuliferous organ attached on both sides of the rachis.
6) PER 69. *Hurumia lingulata nov. gen.* Detail of sterile fronds, with in the upper part a hat-like megasporophylls.
7) PER 69 *Hurumia lingulata nov. gen.* Detail of the megasporophyll.
8) PER 33. *Hurumia lingulata nov. gen.* Detail of a sterile leave originating from a fertile frond.

9) PER 290 Hurumia lingulata. Isolated juvenile megasporophyll.

references about fertile organs and therefore a certain insertion of this interesting plant in a broader context are still missing. On the locality of Niederhausen, this Pteriodospermae is one of the most commonly occurring foliage types, with mainly entire sterile and fertile fronds, as insolated pinnules, being found both in juvenile and adult stages. Therefore, we propose to remove *Odontopteris lingulata* from its morphogenus status and elevate it in the form of a natural genus with the name *Hurumia*, because attached fertile and sterile parts are now known.

A characteristic feature displayed by the foliage of *Hurumia* are pinnules that are wholly adherent to the axis and lacking a typical midvein, but instead they are vascularised by two to several veins that enter the pinnule and may fork at irregular intervals in their course to the margin (KRINGS ET AL., 2006). The fertile organs are characterised by their arrangement around the main axis, usually being dispersed on the lower part between the sterile foliage or the typically intercalary pinnnules and occurring freely hanging or attached on the rachis from the middle to the upper part of the fronds. PER 32, a juvenile and immature fertile frond, shows clearly and without doubt the nature and collocation of the hat-like megasporophylls. As seen on PER 69, the fertile organs are characterised by a mostly rounded hat, connected by a relatively thick but short stalk with the main rachis. The ovules are attached on the lower side of the peltate shield. Typically more or less flattened, radially symmetrical umbrella-shaped peltate discs are not rare in these strata, but not all can necessarily be classified as *Hurumia.* Due to the fact that *Autunia* foliage with more evolved *Peltaspermum*-organs will also occur, and *Rhachiphyllum* also show peltate shields around a main axis, we have to use at least three different genera of Peltaspermales.

The small-sized leathery leaflets of *Autunia dammannii* n. sp. cannot be seen with *Hurumia* foliage, and their segmented peltate shields are not confusing. Maybe, as evidenced in PER 32 or PER 290, unclear segments exist in *Hurumia*, but they are never as segmented as in *Peltaspermum dammannii.* Another distinct feature of *Hurumia lingulata* megasporophylls is the short solid stalk, which is different to the delicate elongated stipe of mostly all other Permian *Peltaspermum*-species. *Rachiphyllum* foliage with its massive venation holds just enough differentiation-possibilities, although both peltate shields have resemblances.

It is probable that *Hurumia* as well as *Rachiphyllum* hold more primitive features than *Peltaspermum dammannii* or other *Autunia* species. However, due to their umbrelliferous shields, they all have parental affinities to be inserted in the supergroup of Peltaspermales, which is characteristic for Permian-Triassic flora-elements.

KRINGS, M., KLAVINS, S.D., TAYLOR, T.N., TAYLOR, E.L., SERBET, R., KERP, H. (2006): Frond architecture of Odontopteris brardii (Pteridospermopsida, ?Medullosales): new evidence from the Upper Pennsylvanian of Missouri, U.S.A. – Journal of the Torrey Botanical Society 133, 33–45.

KERP, J.H.F., POORT, R.J., SWINKELS, H.A.J.M. & VERWER, R. (1990). Aspects of Permian palaeobotany and palynology. IX. Conifer-dominated Rotliegend floras from the Saar-Nahe Basin (?Late Carboniferous - Early Permian; SW-Germany) with special reference to the reproductive biology of the earliest conifers. Review of Palaeobotany and Palynology, 62: 205-248.

LAUSBERG, S., KERP, H. 2000. Eine Coniferen-dominierte Flora aus dem Unterrotliegend von Alsenz, Saar-Nahe-Becken. Feddes Repertorium, 111: 399-426.

BARTHEL, M., (2009). Die Rotliegendflora des Thüringer Waldes. Veröff. Naturhist. Mus. Schleus., Schleusingen.

10 -12) PER 109, 110, 164. *Hurumia lingulata nov. gen.* Several sterile fronds.

13) PER 104. *Hurumia lingulata.* Typical abscission points of the sterile leaves caused by transportation or weather-injuries.

14 - 16) PER 46, 48, 313 *Hurumia lingulata nov. gen.* Growing stages of several sterile leaves.

17) PER 91. *Hurumia lingulata nov. gen.* Venation of the sterile leaves. The veins arise all from the rachis, parallel at the base, forking from the middle.

Division: Pteridosperma
Order: Peltaspermales (TAYLOR, 1981)
Family: Peltaspermaceae (PILGER and MELCHIOR in MELCHIOR and WERDERMANN, 1954)
Genus: *Rhachiphyllum* (HEYER, 1884)

Rhachiphyllum hauptmannii* sp. nov. *(PERNER & WACHTLER, 2013)

Holotype

PER 211

Paratype

PER 105

Material

PER 35, 185, 208,

Locality

Niederhausen, Rheinland-Pfalz, Germany

Type horizon and age

Upper Lauterecken-Lower Meisenheim-Formation, latest Kasimovian-Gzhelian, Regional stage Western Europe: Stephan B-C

Etymology

After German Sepp Hauptmann (Bayreuth) an authority in Rhaeto-Liassic plant-fossils.

Diagnosis

Fronds dichotomously branched and pinnate. Pinnae alternately inserted, entirely margined with crenulate or lobed lateral margins, oval with thin midvein and sparse lateral veins bifurcating one or two times.

Description

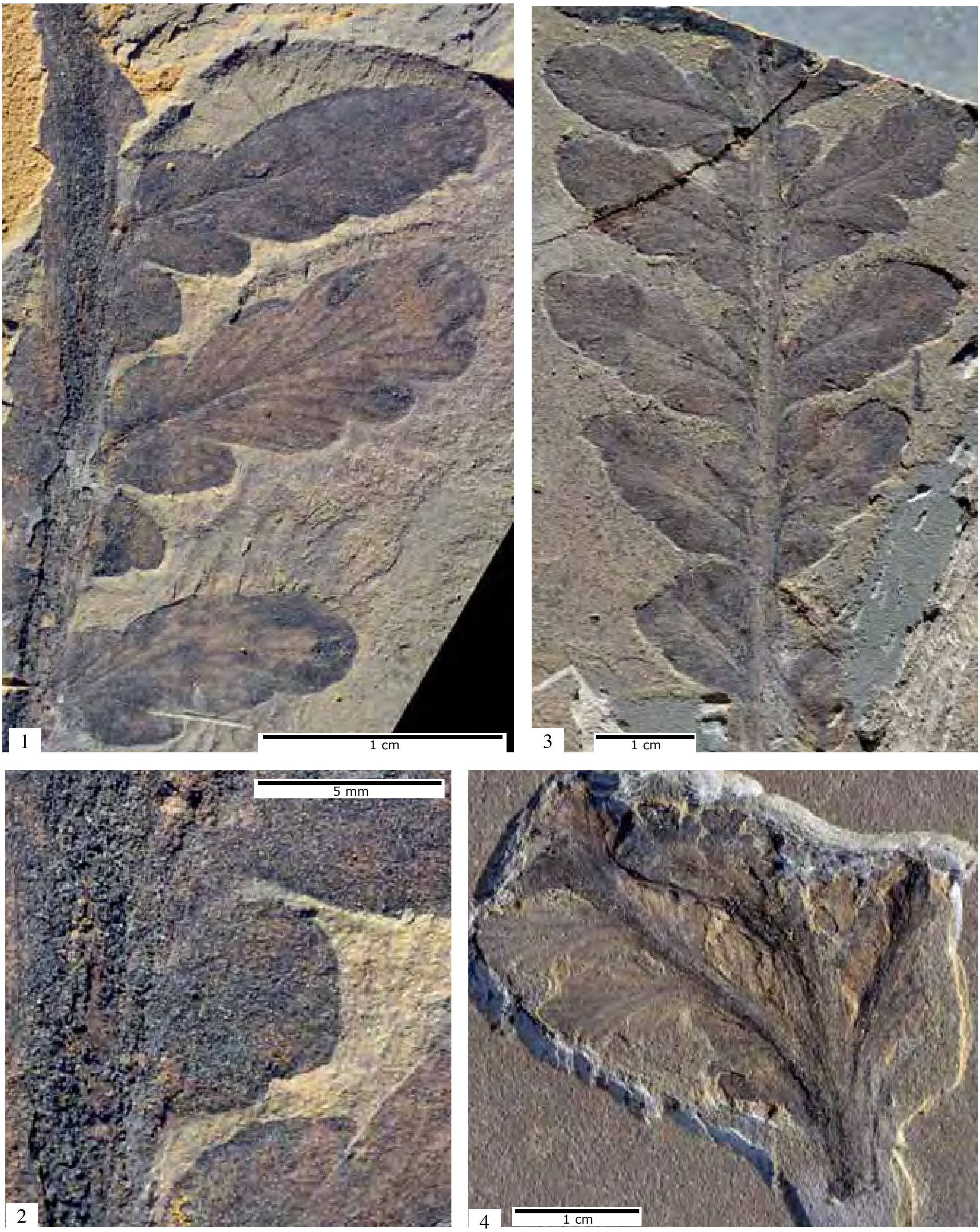
Fronds: Pinnate, bifurcating into equal rachises with alternating pinnae. Pinnae of the external side of the forked lamina are larger and more strongly developed than pinnae of the internal side, as evidenced in PER 185. On the basal part, some intercalary leaves are visible (PER 105).

Leaves: Pinnules are oval to oblong-oval, with wedge-shaped apex varying from entirely margined to lobed and incised. They are from 17-20 mm long and 5-7 mm wide (PER 211, 105). A thin midvein crosses about two-thirds of the leaves and then bifurcates (PER 211). The lateral veins are nearly invisible, sparse and bifurcating one or two times.

Ovuliferous organs: Attached direct to the main rachis, Peltaspermum-like, but with less segments, as in *Autunia* or *Lepidopteris*. Megasporophylls of *Rachiphyllum hauptmannii* (PER 290) are small, about 5 mm, circular, flattened on the upper side, and holding a minor amount of segments (about eight in PER 211 and suggested as an isolated ovuliferous organ in PER 290). The umbrelliferous shields are, like *Hurumia*, connected by a stipe with the main rachis. Sometimes, the fertile parts can be also confused with the intercalary pinnulas, especially in the basal part of the fronds; this suggests that they play a role in the development of the ovuliferous organs of the first Peltaspermales.

5) PER 195. *Peltaspermum sp.* Ovuliferous organ belonging to *Rhachiphyllum* or *Hurumia.* Abaxial side.

6) PER 327. *Peltaspermum sp.* Ovuliferous organ belonging to *Rhachiphyllum* or *Hurumia.* Adaxial side.



1) PER 211. *Rhachiphyllum hauptmannii.* Designed holotype. Single pinnules with attached ovuliferous organs on the main rachis.
2) PER 211. *Rhachiphyllum hauptmannii.* Detail of the ovuliferous organs attached on the main rachis.
3) PER 105. *Rhachiphyllum hauptmannii.* Part of a frond.
4) PER 185 *Rhachiphyllum hauptmannii.* Detail of a ramifying frond.

Discussion

In 1884, in his doctoral thesis about Carboniferous ferns, Fritz Heyer first described the genus *Rhachiphyllum (lyratifolius*) from Berschweiler in the Saar-Nahe-area; however, for about one hundred years, the publication fell into oblivion (BARTHEL, 2009). In this time, several attempts were made to insert sterile material in the callipterids, although fertile organs have never been recovered. As seen in *Hurumia (Odontopteris*), the ovuliferous organs are directly attached to the main lamina and can sometimes be confused with intercalary-pinnules.

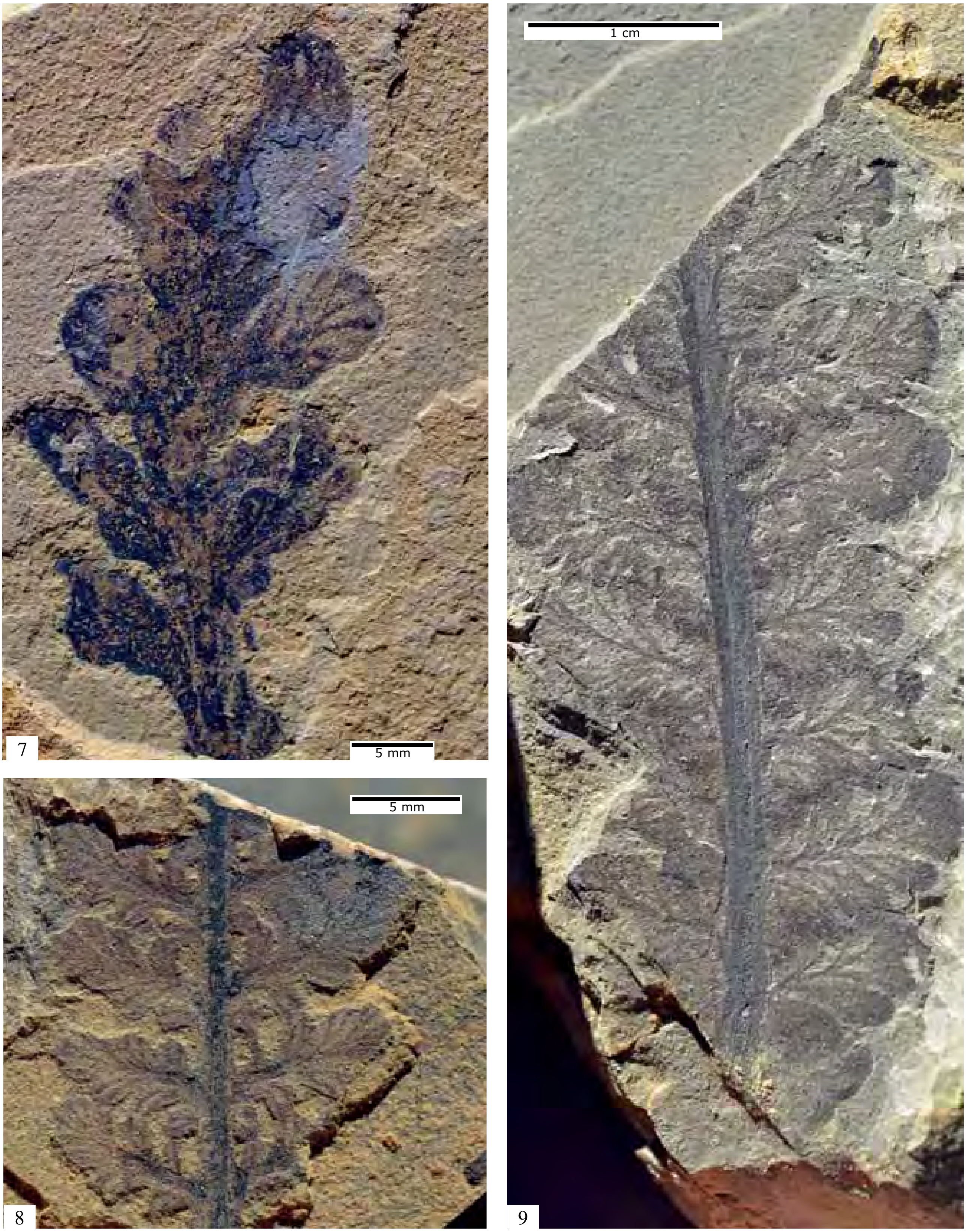
From other *Rachiphyllum*-species, like *Rachiphyllum curretiense* (ZEILLER) KERP, *R. diabolicus* (ZEILLER) KERP, *R. lodevense* (BRONGNIART) KERP, and *R. subauriculatus* (WEISS) KERP, only *Rachiphyllum schenkii* (HEYER) KERP reached a certain importance. Found especially in the slightly younger (Asselian-Sakmarian) Thuringian Manebach-, Goldlauter- or Oberhof-Formation, it holds more pronounced veins (BARTHEL, 2009). Other resembling genera are *Gondomaria* (ZEILLER) known from the Stephanian of France, or *Raminervia mariopteroides* and *Dichophyllum cuneata* from the Russian Early Permian (WAGNER, 2004), but their leaflet-structure differs just too much from *Rhachiphyllum hauptmannii* and the fertile organs are also not known.

BOYARINA N. (1994): Callipterid pteridosperms from the Early Permian of Ukraine, Acta Palaeontologica Polonica 39 (1), 117-133

HEYER, Fritz (1884): Beiträge zur Kenntniss der Farne des Carbon und des Rothliegenden im Saar-Rhein-Gebiete, Cassel : Fischer Thesis (doctoral, Universität Leipzig, 1884

KERP, J.H.F., HAUBOLD, H. (1988): Aspects of Permian Palaeobotany and Palynology. VIII. On the reclassification of the West- and Central european species of the form-genus Callipteris BRONGNIART 1849 - Rev. Palaeobot. Palynol., 54: S.135-150. 51. Taf.WAGNER, R.H. (2004): *Gondomaria grandeuryi (*Zeiller) Wagner & Castro 1998, in the context of an upper Stephanian flora from Surroca (prov. Girona,Catalonia,Spain) Treb. Mus.Geol. Barcelona 12 S.53-67 1 Taf.

Rhachiphyllum hauptmannii. a) Pinnulas with ovuliferous organs on the main axis (PER 211), b) Ramifying frond (PER 185), c) Part of a fertile frond with peltate ovuliferous shield (PER 105)



7) PER 176. *Rhachiphyllum hauptmannii.* Several leaflets.
8) PER 208. *Rhachiphlylum hauptmannii.* Apical part of a frond.
9) PER 35. *Rhachiphyllum hauptmannii.* Part of a frond.

Division: Pteridosperma
Order: Peltaspermales (TAYLOR, 1981)
Family: Peltaspermaceae (PILGER and MELCHIOR in MELCHIOR and WERDERMANN, 1954)
Genus: *Peltaspermum* (HARRIS, 1937)

Autunia dammannii **sp. nov. (STERNBERG, 1893) PERNER & WACHTLER, 2013**

Material
PER 201, 346, 347

Description
Fronds: Bipinnate to tripinnate fronds with alternating to supposite pinnae. Rachis massive, holding intercalary pinnules. PER 2O1 is a good example of a typical *Autunia*-frond with its leathery and deeply incised leaflets, sometimes overlaying each one.
Leaves: Pinnules entirely margined with a pronounced midrib and mainly invisible lateral veins. Leaves are coriaceous, superposing each other. Apex rounded to slightly tapered (PER 347).
Ovuliferous organs: Discs divided into radial segments holding inside the ovules.
Pollinferous organs: Stellate arranged leaves with the pollen sacs on their lower surface. A suggested pollen organ could be PER 165.

Peltaspermum dammannii **sp. nov. (PERNER & WACHTLER, 2013)**
1990 *Peltaspermum sp.* Kerp et. al., p. 68

Holotype
PER 165

Paratype
PER 197

Material
PER 12, 27, 233, 283 288

Locality
Niederhausen, Rheinland-Pfalz, Germany

Type horizon and age
Upper Lauterecken-Lower Meisenheim-Formation, latest Kasimovian-Gzhelian, Regional stage Western Europe: Stephan B-C.

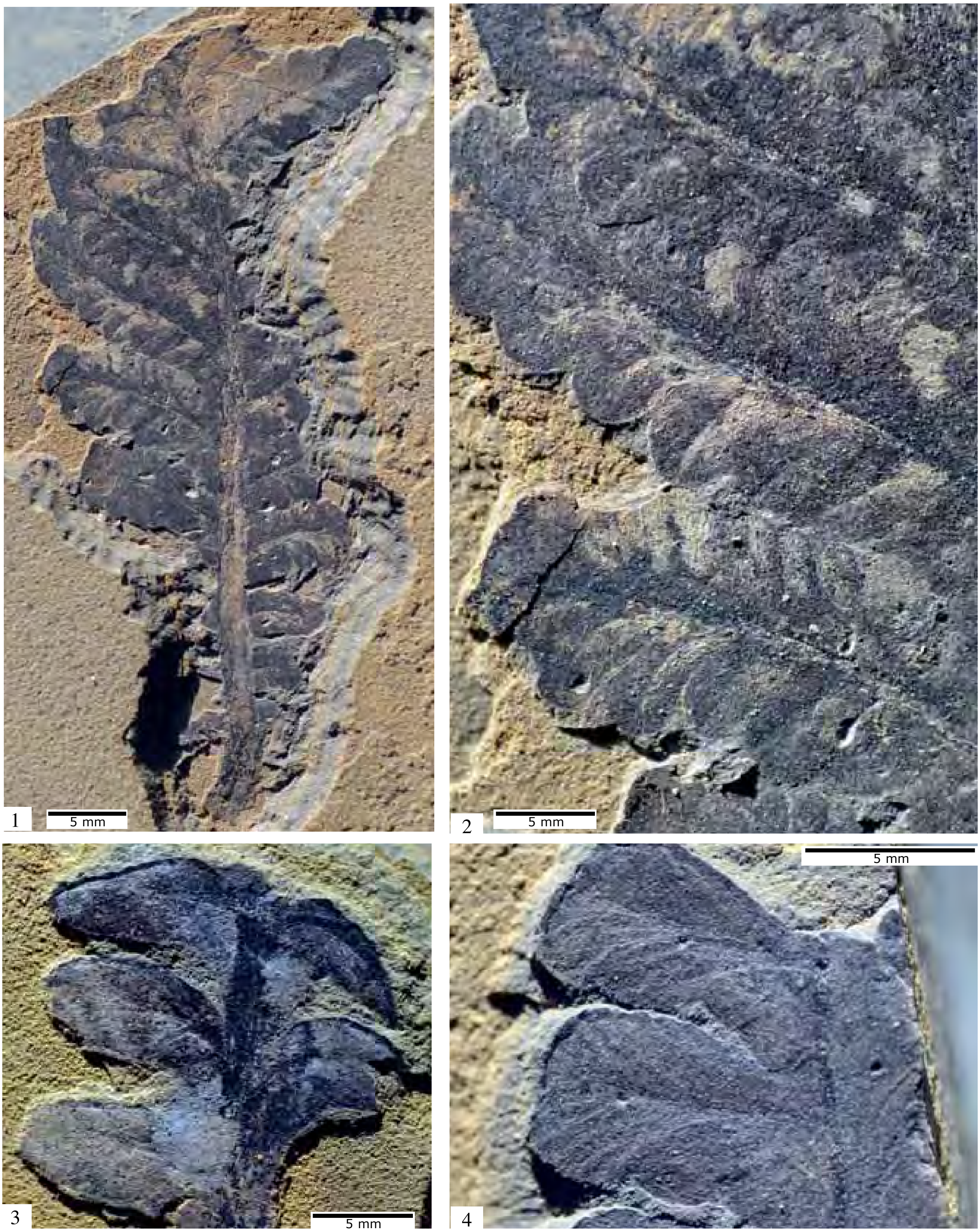
Etymology
Named after Martin Dammann, genius artist, profound researcher and collector of Carboniferous-Permian floras.

Diagnosis
Seed fern with ovuliferous organs resembling peltate shields divided into a fair amount of segments holding inside the ovules.

Description
Ovuliferous organs, with a size of 5 to 10 mm in diameter, appear umbrella-like and are divided into 10 to 16 distinct segments (PER 165 holotype = 14 sections); this constitutes one of the common Niederhausen Kasimovian-Gzhelian-Flora-elements. As for other *Peltaspermum*-species from Permian to Triassic, they hold the ovules on the adaxial side, turned to the slender stipe.

Discussion
Until Peltaspermaceae-fronds with attached fertile organs were discovered with certainty, a holotype (PER 165) was chosen only for the ovuliferous organs, whilst accompanying *Autunia*-foliage for more clarity was only named *Autunia dammannii* n. sp. without choosing a particular specimen as a holo-

PER 165. Suggested pollen organ of Autunia dammannii.

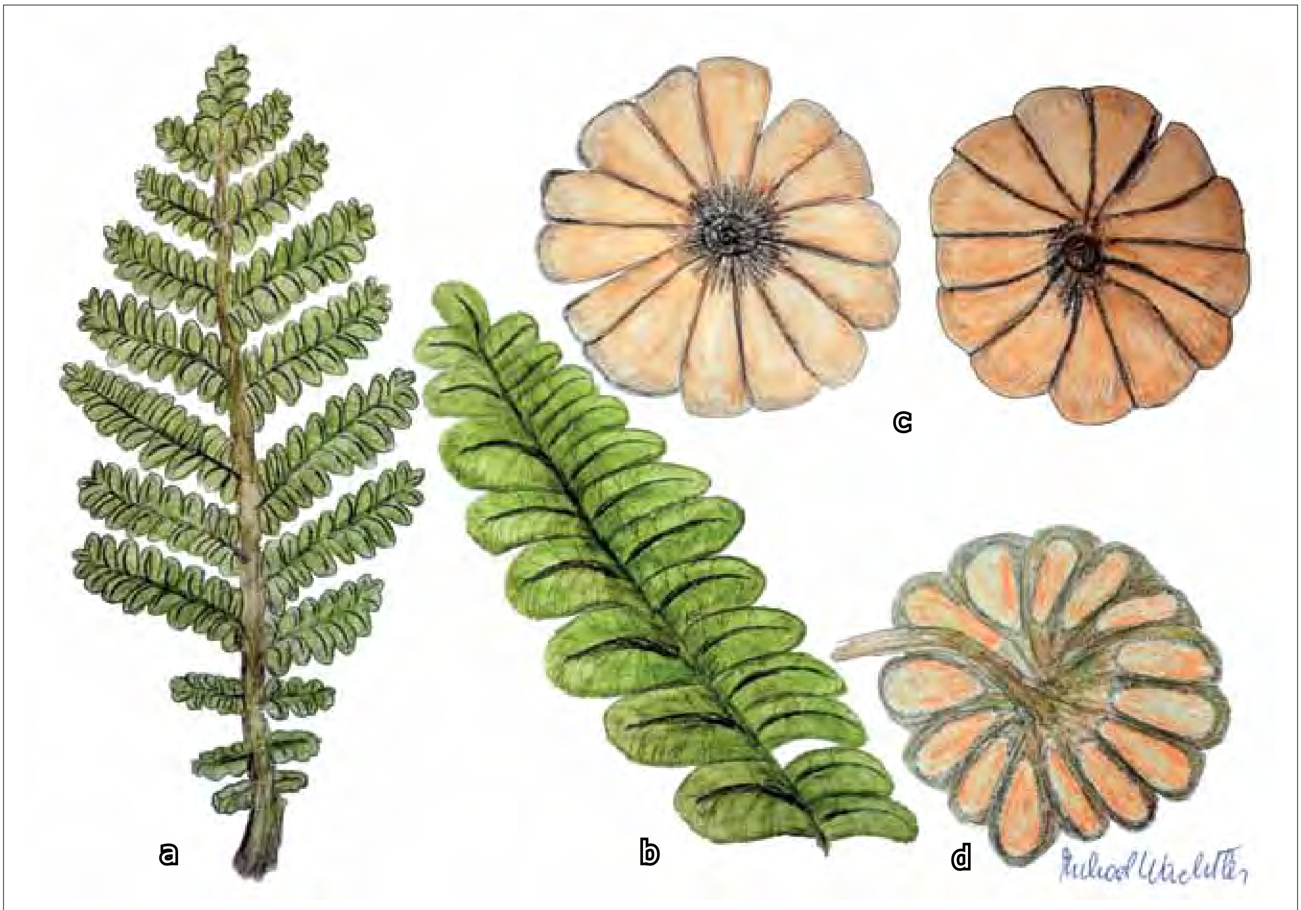


1) PER 201. *Autunia dammannii.* Characteristic callipteridic pinnula.
2) PER 201. *Autunia dammannii.* Pinnula-detail evidencing the sunken mid-veins.
3) PER 347. *Autunia dammannii.* Detail of a leaflet.
4) PER 346. *Autunia dammannii.* Detail evidencing the indistinct venation.

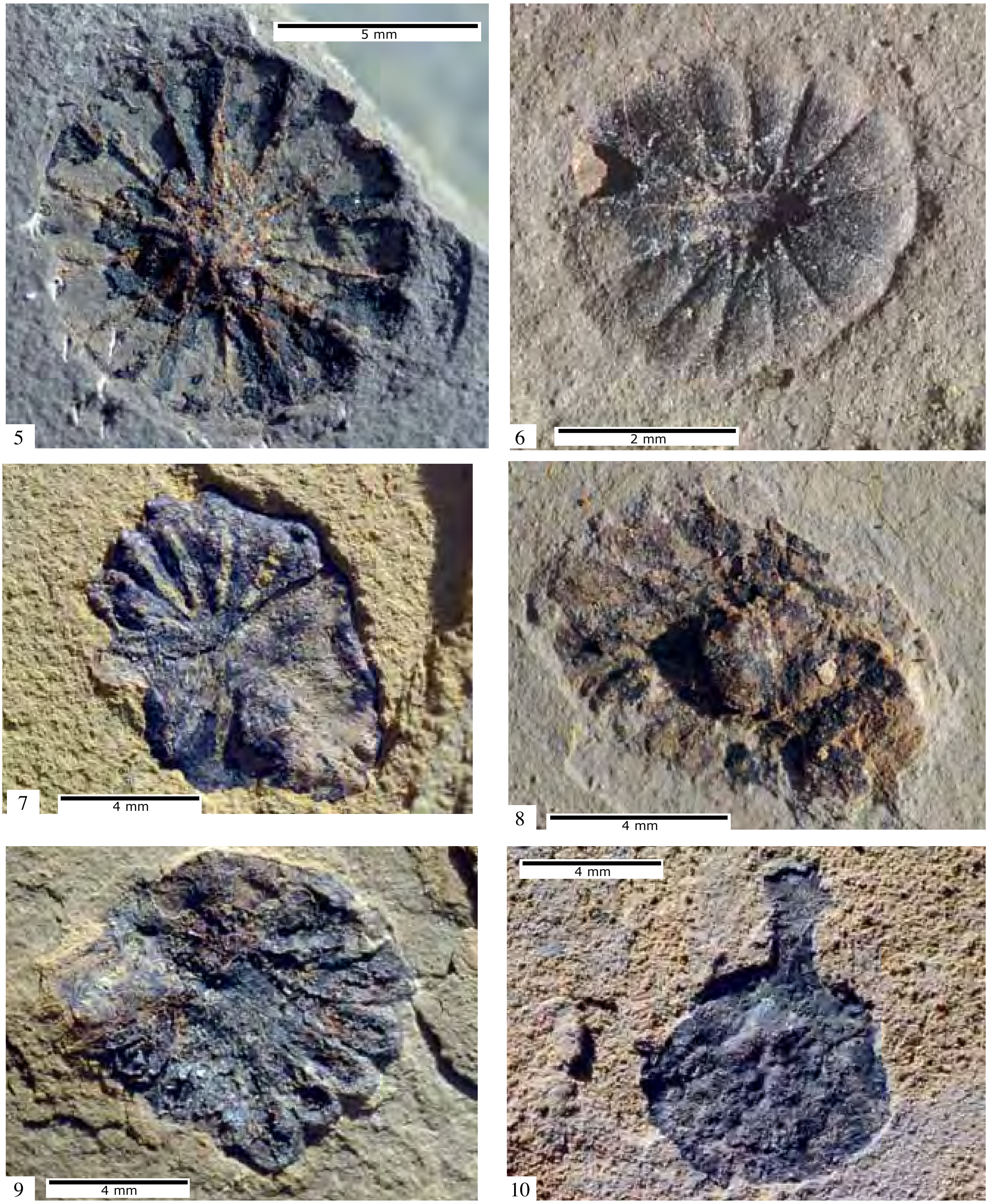
type. Isolated recovered *Peltaspermum*-ovuliferous organs belong to the characteristic Permo-Triassic flora elements because of their robustness. Until now, it was supposed that they have their origin in Early-Middle Permian, but with the unquestionable finding of Later-Carboniferous-Earliest Permian Peltaspermum discs, the oldest recovered to date, we have to date back the origin of this representative Pteridosperma. Now, we have the opportunity to follow a mainly uninterrupted transition-line from Upper-Carboniferous-Earliest Permian *Peltaspermum dammannii* (Kasimovian-Gzhelian) over Early Permian *Peltaspermum meyeri* (Artinskian-Kungurian) to Later Permian *Peltaspermum martinsii* (Wuchiapingian). In Permian, the peltate shields usually have only a diameter of 5-10 mm, and after the Early Triassic they increase in size arriving at 15-25 mm in diameter (*Peltaspermum bornemannii* (Anisian) (VAN KONIJNENBURGH-VAN CITTER ET AL., 2007; WACHTLER, 2010, 2011). More complex will be the question of the porter of these organs. In Niederhausen, the small-sized *Lepidopteris* leaf type, representative for Middle-Upper Permian Peltaspermum species, have never been recorded, but *Autunia* fronds are common. *Autunia conferta* guide fossils for later Asselian-Sakmarian vegetation have close parental affinities with *Autunia dammannii* fronds and therefore it is suggested that the group of Peltaspermaceae seed ferns clearly exhibit the change to a much more arid and dry climate.

WACHTLER, M. (2012). The latest Artinskian-Kungurian (Early Permian) Flora from Tregiovo - Le Fraine in the Val di Non (Trentino - Northern Italy) - Preliminary researches, Dolomythos, 3-56 Innichen. ISBN 978-88-904127

VAN KONIJNENBURGH – VAN CITTERT J.H.A, WACHTLER M. & KUSTATSCHER E. (2007) Horsetails and seedferns from the middle triassic (Anisian) locality Kühwiesenkopf (Monte Prà della Vacca) in the Dolomites (Northern Italy) Palaeontology, Vol. 50, Part 5, Elsevier Publishing House, Oxford, p. 1277-1298.



Autunnia dammannii a) Frond (PER 201), b) Pinnula fragment (PER 347), c) Female fructifications - front side (PER 165, PER 283), d) Megasporophyll back side with arrangement of the seeds (PER 197).



5) PER 165. *Peltaspermum dammannii.* Designed holotype. Female fructification. Abaxial side.
6) PER 283. *Peltaspermum dammannii.* Ovuliferous organ in form of peltate umbrella-like discs. Abaxial side.
7) PER 27. *Peltaspermum dammannii.* Single megasporophyll.
8) PER 288. *Peltaspermum dammannii.* Adaxial side, evidencing the ovules.
9) PER 197. *Peltaspermum dammannii.* Adaxial side, evidencing the seed apparate.
10) PER 12. *Peltaspermum dammannii.* Adaxial side with the peduncle were they are attached to the main rachis.

Pteridophyta and Cycadophyta from the Carboniferous-Permian (Kasimovian/Gzhelian) Niederhausen Flora (Rheinland-Pfalz, Germany)

by Thomas Perner and Michael Wachtler

Division: Pteridophyta
Family: Marattiaceae (BERCHTOLD & PRESL, 1820)
Genus: *Scolecopteris* (ZENKER, 1837)

Scolecopteris lothii sp. nov. *(PERNER & WACHTLER, 2013)*

Holotype

PER 272

Paratype

PER 85

Material

PER 210, 219, 108, 123

Locality

Niederhausen, Rheinland-Pfalz, Germany

Type horizon and age

Upper Lauterecken-Lower Meisenheim-Formation, latest Kasimovian-Gzhelian, Regional stage Western Europe: Stephan B-C

Etymology

Honouring the German collector of fossil plants, Günther Loth (Reyershausen).

Diagnosis

Fern with protruding fronds holding closely spaced obliquely inserted pinnules on the entire base. Venation markedly asymmetrical, and generally twice forked. Sporangia on the margins of the pinnules.

Description

Fronds: Medium-sized fronds, at least bipinnate, with intercalated pinnules in the upper part of primary pinnae. Ultimate pinnae gradually tapering.
Leaves: Pinnules strongly asymmetrical, with the basiscopic side fused with the rachis entirely or partially. Single leaflets about 10 mm long, 5 mm width, and rachis 1 mm (PER 272, PER 219). Pinnule sides straight to slightly convex, tapering in the upper half into a rounded apex. Midrib exocentrically placed, and dissolving into numerous lateral veins in the apical part of pinnules. Lateral veins ascending and oblique, forking generally twice.
Fertile leaves: Resembling the sterile pinnules, elongated and rounded on the apex. The lamina of the pinnules laterally extends to completely envelop the abaxially positioned synangia. Venation only sometimes recognisable (Holotype PER 85).

Discussion

Marattialian ferns appeared in the Namurian the latest Early Carboniferous on the Euramerican area, and literally exploded to a global radiation in the Stephanian (DIMICHELE & PHILIPS, 2002). The fern *Scolecopteris* within the Lower Permian Marattiaceae has a wide stratigraphical distribution that ranges from the early Pennsylvanian to the Early Permian in Euramerica, and rarely also to the Middle Triassic. Over 30 species of *Scolecopteris* have been recorded from the Euramerican Flora (XIAO-YUAN ET AL. 2006). It is suggested that we have to include it with the straight-growing, arboreous plants, several to perhaps 10 m or more in height, as its primary stem is mantled by adventitious roots, topped by a crown of large, graceful, compound fronds.
Paleozoic bipinnate fronds with elongated rounded pinnules, holding a midrib with forking lateral veins, are generally known as *Pecopteris* or *Scolecopteris* (MILLAY, 1979). Most of them are recorded without any knowledge of the fertile parts and a classification will be difficult; however, some foliage with isolated radially symmetrical synangia on the lower side is known. Due to the poor preservation conditions, comparisons are difficult. *Scolecopteris cyathea* from Manebach (BARTHEL, 2009) could have some similarities with *S. lothii*, as fertile pinnules were also found, but apart from its younger geological age, the

1) PER 272. *Scolecopteris lothii.* Paratype. Sterile frond.
2) PER 272. *Scolecopteris lothii.* Detail of the arrangement of the single pinnulas.
3) PER 210. *Scolecopteris lothii.* Apical part of a frond.

synangia are more delicate. Also, its sterile foliation seems to be more leathery. Whether *Scolecopteris lothii* holds *Psaronius*-type arborescent stems has not been proven, but it could be possible. *Scolecopteris oreopteridia* evidences fewer ramifying veins on their pinnules. A characteristic of mainly all Lower-Middle Permian *Pecopteris-Scolecopteris* fern-species is their much more coriaceous aspect. Examples are *Scolecopteris arborescens, S. candolleana, S. pseudobucklandii S. unita,* and also *Pecopteris potoniei*.

Only *Scolecopteris densifolia* (found in the Manebach-Formation = Asselian) bears some affinities with S. lothii, but apart from a leathery visual nature, their much more geometric pinnules contradict an identical species classification.

It seems that the *Scolecopteris* species survived the coming aridity by developing a thicker foliage habitus and therefore they can be taken as an excellent climatic indicator.

BARTHEL, M., (2009). Die Rotliegendflora des Thüringer Waldes. Veröff. Naturhist. Mus. Schleus., Schleusingen.

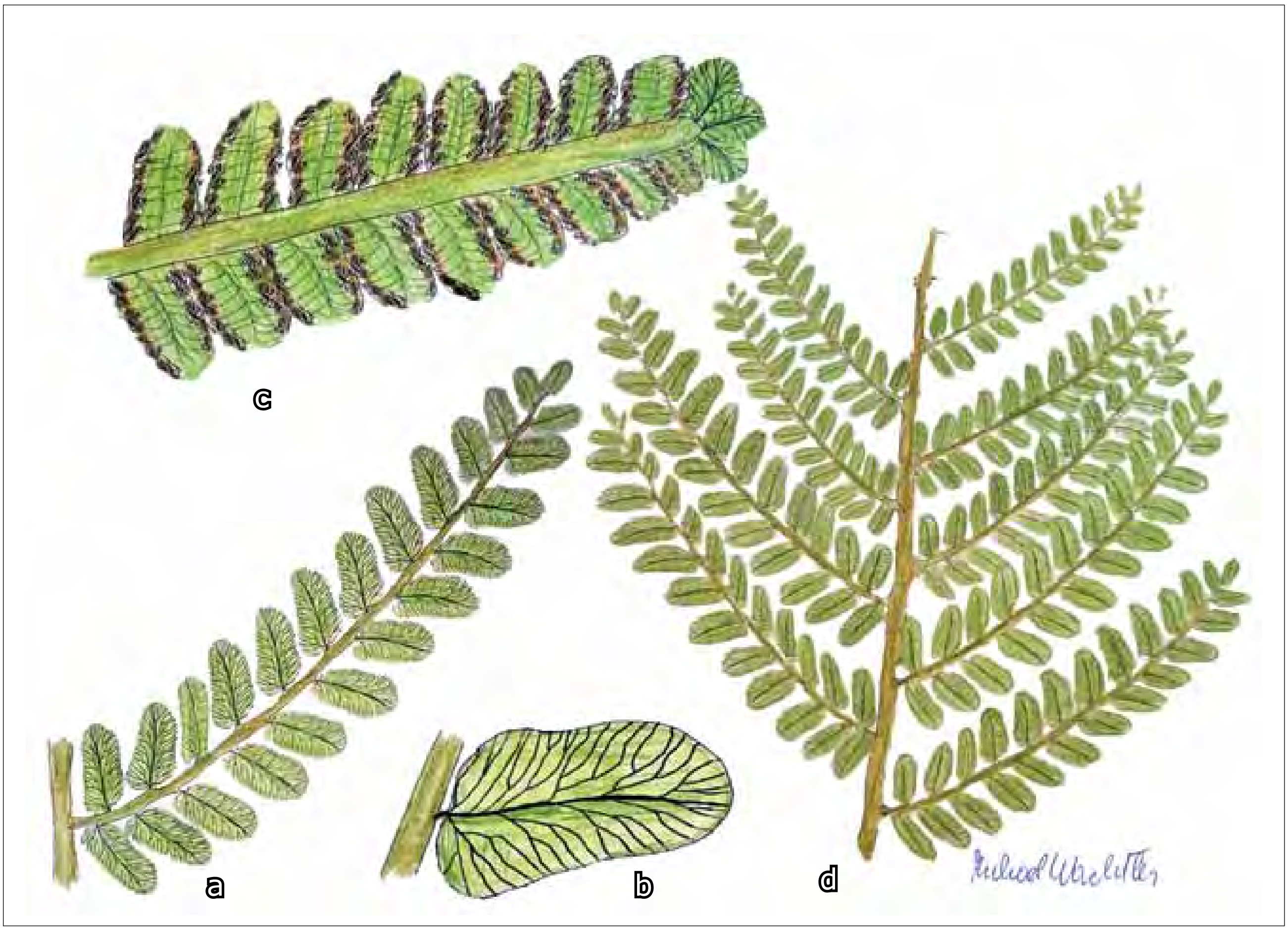
DIMICHELE, WILLIAM A., PHILIPS, T. L. (2002): The ecology of Paleozoic ferns, Review of Palaeobotany and Palynology, 119:143-159

HE, XIAO-YUAN; WANG, SHI-JUN; HILTON, JASON; ZHOU, YI-LONG, (2006): A new species of the marattialean fern Scolecopteris (Zenker) Millay from the uppermost Permian of Guizhou Province, south-western China. Botanical Journal of the Linnean Society, Volume 151 Issue 2 279-288

MILLAY MA. (1979). Studies of Paleozoic marattialeans: a monograph of the American species of Scolecopteris. Palaeontographica Abt B 169:1–69.

WACHTLER, M., (01/2011) Ferns and seed ferns from the Early-Middle Triassic (Anisian) Piz da Peres (Dolomites - Northern Italy), Dolomythos, Innichen, pp. 57-79.

ZENKER E., (1837): Scolecopteris elegans, ein neues fossiles Farrngewächs mit Fructification. Linnaea 11, 509-12.



Scolecopteris lothii a) Pinnula fragment (PER 210), b) single leaflet, c) Fertile pinnula (PER 85), d) part of a sterile frond.

4) PER 272. *Scolecopteris lothii.* Detail of the single pinnulas.

5) PER 310. *Scolecopteris lothii.* Apical part of a frond.

6) PER 85. *Scolecopteris lothii.* Designed holotype. Fertile pinnulas.

7) PER 85. *Scolecopteris lothii.* Holotype. Fertile pinnulas with the sporangia attached on the boarder of the single leaflets.

Division: Pteridophyta
Family: Osmundaceae (BERCHTOLD & PRESL, 1820)
Genus: Todites (SEWARD, 1900)

Todites muelleri sp. nov. *(PERNER & WACHTLER, 2013)*

Holotype

PER 107

Paratype

PER 200 (sterile frond)

Material

PER 135, 120, 152, 218, 275 (Fertile)

Locality

Niederhausen, Rheinland-Pfalz, Germany

Type horizon and age

Upper Lauterecken-Lower Meisenheim-Formation, latest Kasimovian-Gzhelian, Regional stage Western Europe: Stephan B-C

Etymology

Named after the German Wolfgang Müller (Wehrheim), a collector of Permian fossil plants.

Diagnosis

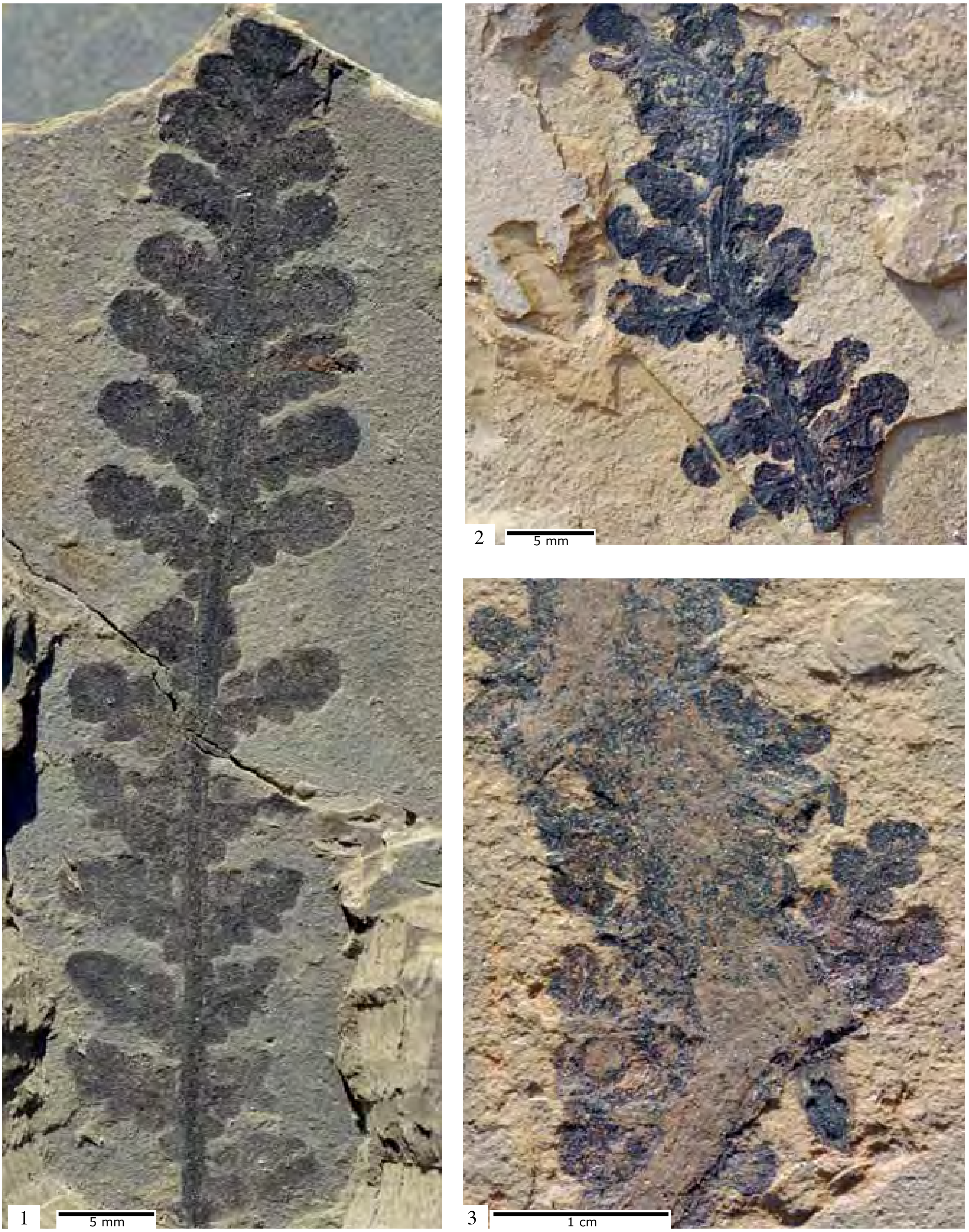
Tripinnate fern with relatively small pinnules rounded in an outline with a short midrib forking in secondary veins, attached by their whole base to the rachis. Sporangia on the lower side. Fertile pinnules dotated with a completely rounded lamina.

Description

Fronds: Tripinnate and protruding, arising alternately to sub-oppositely from a relatively broad first rachis. PER 218 represents a fragment of a tripinnate frond with some preserved pinnae of the second order. Aphlebia are absent. Pinnae of the second order short, 7 cm long and 1.5 cm wide (PER 200, Paratype) with small pinnules of the last order. The pinnules are attached to the pinna rachis in regularly alternate order.
Leaves: Pinnules of the last order small, sometimes only 1 x 1 mm (PER 200), never overlapping, attached with the whole base to the rachis, with apex-rounded pinnula. The pinnate venation is typically neuropterid. One well-developed but short vein enters each pinnule from which the secondary veins ramify, usually forking one or two times. Pinnules usually end in an agglomerate of several coalescing leaves.
Fertile leaves: Fertile pinnules evidence a more reduced, completely rounded lamina (2 x 2 mm; PER 275, PER 107). The abaxial surface of the leaf lamina is covered by closely-spaced sporangia that they appear to form a mass. Fertile leaves finish in one never fertile more or less deeply dissected pinnula-appendix.

Discussion

The Osmundales have often been considered a primitive group intermediate between eusporangiate and leptosporangiate ferns because they possess a mixture of sporangial features from both types. Today, the family is represented by the three genera *Osmunda, Todea* and *Letopteris*. Sporangia are not grouped into sori and no indusium is present (TAYLOR ET AL., 2009).
Representatives of *Todites* are the more typical elements of Mesozoic flora, rather than Palaeozoic ones. Therefore, the presence of this fern-genus, characterised both by sterile and fertile pinnae attributed to *Todites,* lets us more precisely reconstruct the history of the early development of this interesting fern-family.
Until now only a few Osmundaceae ferns were described from the Paleozoic, especially the Permian. *Todites lobulatus* from the lowermost Upper Permian (Ufimian) of the Russian Pechora basin belongs to the protoleptosporangiate ferns of the Osmundaceae, and is characterised by tripinnate fertile fronds with deeply dissected lobate pinnules and round apexes (NAUGOLNYKH, 2002).
Another putative fern belonging to the Osmundaceae is *Thamnopteris kazanensis*, from the Upper Permian of Orenburg, Russia. It includes arborescent stems that consist of a mantle of adventitious roots. *Palaeosmunda* from the Upper Permian Coal Measures of Queensland is also recorded from well-preserved stem remains.
Beginning from the Early Mesozoic (Olenekia-Anisian), we have more representatives of the Osmundaleans. Anisian *Gordonopteris lorigae* from the Italian Dolomites also holds tripinnate fronds with small pinnules, attached by the whole base to the rachis. Some affinities with *Todites muelleri* are



1) PER 200. *Todites muelleri.* Paratype. Detail of a frond.
2) PER 135. *Todites muelleri.* Part of an old frond.
3) PER 218. *Todites muelleri.* Tripinnate branching of a frond.

obvious, but the difference of more than 50 million years in geological time makes it only a putative descendant. However, the fertile parts with their reduced, completely rounded lamina and sporangia on the lower side resemble *Todites muelleri* from the Carboniferous-Permian border. Another fern-genus that is supposed to belong to the Osmundaceae is *Anomopteris (mougeotii)*, which is widespread in the European Early Triassic. However, their characteristic aphlebia on the main rachis, their bipinnate frond-system and their microsopic pinnules differs considerably from *Todites muelleri*. The same is valid for the type−species *Todites williamsonii* (BRONGNIART, 1828) SEWARD (1900) in having deeply dissected pinnules and round pinnule apices. Other foliage impressions, like *Osmundopsis, Hausmannia, Coniopteris* and *Cladophlebis*, ranging mainly from the Triassic to the Jurassic lie just directly on the evolving line of the Osmundaceae, whereas *Osmundastrum cinnamomea* from the Upper Cretaceous is just closely comparable to extant forms.

BARTHEL, M., (2009). Die Rotliegendflora des Thüringer Waldes. Veröff. Naturhist. Mus. Schleus., Schleusingen.

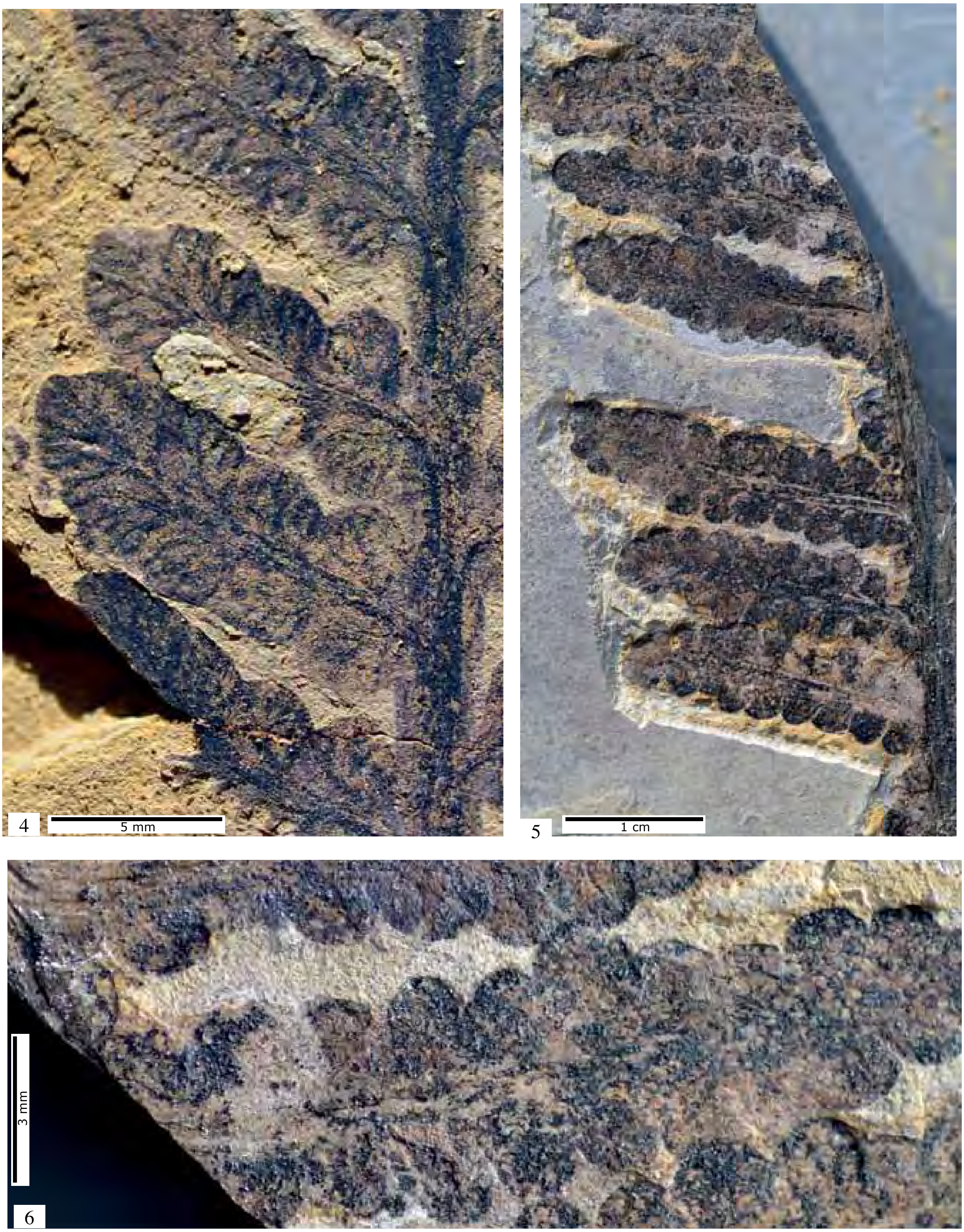
NAUGOLNYKH, S. V. (2002). A new species of Todites (Pteridophyta) with in situ spores from the Upper Permian of Pechora Cis-Urals (Russia). Acta Palaeontologica Polonica 47: 469-478 (http://www.paleo.pan.pl/acta/app_info.htm).

WACHTLER, M., (01/2011) Ferns and seed ferns from the Early-Middle Triassic (Anisian) Piz da Peres (Do- lomites - Northern Italy), Dolomythos, Innichen, pp. 57-79.

VAN KONIJNENBURG-VAN CITTERT, J. H. A., KUSTATSCHER, E. & WACHTLER, M., (2006). Middle Triassic (Anisian) ferns from the locality Kühwiesenkopf (Monte Prà della Vacca) in the Dolomites (Northern Italy). Palaeontology, 49 (5), pp. 943-968.

TAYLOR, T.N., TAYLOR, E.L., KRINGS M. (2009). Paleobotany. The Biology and Evolution of Fossil Plants. Burlington MA, London, San Diego CA, New York NY, Elsevier/Academic Press Inc., xxi + 1230 pp.

Todites muelleri. a) Detail of a sterile pinnula (PER 200). b) Fertile pinnula fragment (PER 107), c) Whole tripinnate frond.



4) PER 275. *Todites muelleri.* Detail of some fertile and sterile pinnules.
5) PER 107. *Todites muelleri.* Designed Holotype. Fertile frond.
6) PER 107. *Todites muelleri.* Holotype. Detail of the fertile leaflets.

Division: Protoconiferophyta
Order Cordaitanthales, MEYEN, 1984
Family Cordaitanthaceae
Genus *Cordaites,* UNGER, 1850

Cordaites sp. UNGER, 1850

Material

PER 229

Discussion

Only a few leaf-fragments of *Cordaites* were found in the Niederhausen-Flora. Fossilised remains of this plant are recorded from Namurian (Bashkirian) to Early Permian of Euramerica, representing a range of about 25 million years. The leaves reached an extraordinary, sometimes up to 1 metre, length; they were ribbon-shaped or lanceolate and parallel-veined. Parameters for taxonomy are usually the size and shape of the leaves and the number and distance of their veins crossing the whole leaf.
Further considerations about their role in this flora, such as if they represent brackish water settings, lived in drier sites or form upland communities (TAYLOR ET AL., 2009; BARTHEL, 2009), cannot be made, but it is believed that they played a bigger role in the Earliest Permian of Europe, as could be presumed by the isolated remains recovered (KERP ET AL., 2007) in this location.
Whether and what part they also played in the evolution of conifers could not be discussed in this publication.

BARTHEL, M., (2009): Die Rotliegendflora des Thüringer Waldes. Veröff. Naturhist. Mus. Schleus., Schleusingen.

FLORIN, R., 1931. Untersuchungen zur Stammesgeschichte der Coniferales und Cordaitales. Sv. Vet.-akad. Handl. 111. 10: 1-588. pls. 1-58. [Classic treatment of vegetative anatomy of the conifers; Pinaceae, 93-111, 306-347, pls. 34-39; generic relationships and classification of the Pinaceae, 476-483.]

KERP, H., NOLL, R., UHL, D. (2007): Übersicht über Pflanzengruppen und Vegetationsentwicklung im Permokarbon des Saar-Nahe-Becken, Pollichia Sonderv. Nr.10 S.42 - 74 37 Abb.

KERP, H., NOLL, R., UHL, D. (2007): Vegetationsbilder aus dem saarpfälzischen Permokarbon, Pollicha Sonderv. Nr.10 S.76 - 109 30 Abb.

TAYLOR, T.N., TAYLOR, E.L., KRINGS M. (2009). Paleobotany. The Biology and Evolution of Fossil Plants. Burlington MA, London, San Diego CA, New York NY, Elsevier/Academic Press Inc., xxi + 1230 pp.

1) *Cordaites sp*. Part of a leave with a conifer twig (*Perneria*).

2) *Cordaites sp*. Detail of the leave evidencing the parallel veined foliage.

Division: Protoconiferophyta
Order Dicranophyllales, NĚMEJC 1959 emend. ARCHANGELSKY & CÚNEO, 1990
Family Dicranophyllaceae NĚMEJC 1959 emend. ARCHANGELSKY & CÚNEO, 1990
Genus *Dicranophyllum* GRAND'EURY, 1877

Dicranophyllum sp. GRAND'EURY, 1877

Material

PER 314

Discussion

A genus of still problematical affinities is *Dicranophyllum*, with approximately 30 species and an occurrence from Asia through Europe and North America. The order Dicranophyllales is split between *Trichopitys* and *Dicranophyllum*, and is sometimes suggested as an ancestor to the Ginkgopsida.
The plant is characterised by shoots with repeatedly bifurcating leaves (WAGNER, 2005). Suggested seed and pollen bearing organs occur interspersed with and in substitution of leaves; both female and male strobili are found on the same axes (BARTHEL, 2009). However, due to the fact that other ginkgophyta-material is recorded from mainly coeval layers, it seems unlikely that *Dicranophyllum* could be adducted as a closer ancestor of the Gingkophyta.
The only mainly complete terminal but not well-conserved shot from Niederhausen (PER 314) is 30 cm long, and the tuft of leaves reach a width of 15 cm. The main stipe is 1 cm thick. Another estimation is that the figured specimen constitutes only a root system of some unknown plant.

BARTHEL, M., (2009). Die Rotliegendflora des Thüringer Waldes. Veröff. Naturhist. Mus. Schleus., Schleusingen.

WAGNER, R.H. (2005): Dicranophyllum glabrum (DAWSON) Stopes, an unusual Element of lower Westphalian Floras in Atlantic Canada Rev. Esp. de Paleont. 20 S.7-13

PER 314. *Dicranophyllum.* Putative terminal shot.

Division: Cycadophyta
Order: Taeniopteridaceae (WACHTLER, 2012)
Genus *Taeniopteris* sp. (KURTZE, 1839)

Taeniopteris sp. (KURTZE, 1839)

Material

PER 230

Discussion

Some incompletely preserved leaves (PER 230), with their oblong and unsegmented structure, resemble the morphogenus *Taeniopteris*, which is thought to belong to the Cycadophyta-ancestors. It is a common but still enigmatic element of many Paleozoic to Mesozoic flora, but only a few compounds found with leaves and fertile parts in association are recorded (WACHTLER, 2010; WACHTLER, 2013). PER 230 is characterised by a relatively broad and hairy stipe (5 mm), whereas the venation on the fronds is not recognisable with regard to the poorly preserved material.

BRANDT, S., (1997). Die Fossilien des Mansfelder und Sangerhäuser Kupferschiefers. - Schriftenreihe des Mansfeld-Museums (Neue Folge) Heft 2, S. 1- 68, Hettstedt.

BRAUN, C.F.W., (1843) Beiträge zur Urgeschichte der Pflanzen", Münster, G.G. (Eds.), Beiträge zur Petrefactenkunde, vol. 6, 1843, p.5-25, Bayreuth; 7.

WACHTLER, M., (05/2010) About the origin of Cycads and some enigmatic Angiosperm-like fructifications from the Early-Middle Triassic (Anisian) Braies Dolomites (Northern Italy). Dolomythos, Innichen, n. 1, pp. 3-55.

WACHTLER, M., (2013a): Ursprünge und Entwicklung der Cycadeen. Dolomythos, 3-62 Innichen. ISBN 978-88-904127

1) PER 230. *Taeniopteris* sp. Basal part with stipe of this presumed Cycadophyta.

Division: Cycadophyta
Order: Cycadales (DUMORTIER, 1829)
Genus: *Nilssonia* (BRONGNIART, 1828)

Nilssonia sp. (BROGNIART, 1828)

Material

PER 73

Discussion

Apart from some isolated taeniopteroid leaves, also enigmatic fronds are recorded from the Niederhausen-Flora, which were inserted with caution as *Nilssonia* sp.
PER 73 is 16 cm long, 2 cm wide and holds closely spaced slightly incurved leaflets. Also, it evidences some Cycadalean aspects. Based on findings from China to the United States (DI MICHELE ET AL., 2001; POTT ET AL., 2010; WACHTLER, 2013), it could be presumed that on the Permian-Carboniferous border, we have well evolved Cycadophyta and their ancestors have to be looked for earlier. However, until female or male organs are obtainable, further theories about the first evolutionary lines remain problematic. All *Nilssoni*a species bear clearly and geometrically-segmented pinnas; therefore, this frond was inserted in this group of Cycadophyta.

DIMICHELE, W. A., MAMAY, S. H., CHANEY, Dan S., HOOK, R. W. and NELSON, J. W., (2001). An Early Permian Flora with Late Permian and Mesozoic Affinities from North-Central Texas, Journal of Paleontology, n. 75, pp. 449-460.

FLORIN, R. 1933. Studien über die Cycadales des Mesozoikums (Bennettitales, pp. 12-30). – Kungliga Svenska Vetenskapsakademiens Handlingar 12: 4-134

POTT, C., McLOUGHLIN, S. & LINDSTROEM, A., (2010). Late Palaeozoic foliage from China displays affinities to Cycadales rather than to Bennettitales necessitating a re-evaluation of the Palaeozoic Pterophyllum species. Acta Palaeontologica Polonica, n. 55, pp.157-168.

Wachtler M., (2012): The latest Artinskian/Kungurian (Early Permian) Flora from Tregiovo-Le Fraine in the Val di Non (Trentino, Northern Italy) – DoloMythos, Innichen

Wachtler, M., (2013a): Ursprünge und Entwicklung der Cycadeen. Dolomythos, 3-62 Innichen. ISBN 978-88-904127

1) PER 73. *Nilssonia sp.* Complete frond.

2) PER 73. *Nilssonia sp.* Detail of the leaves on the lower part of the frond.

3) PER 73. *Nilssonia sp.* Detail of the leaves on the upper part of the frond.

Protoconiferophyta from the Carboniferous-Permian (Kasimovian/Gzhelian) Niederhausen Flora (Rheinland-Pfalz, Germany)

by Michael Wachtler

Division: Protoconiferophyta
Family: Perneriaceae (WACHTLER, 2013)

Perneria gen. nov. (WACHTLER, 2013)

Etymology

Honouring German Thomas Perner, expert and authority in paleontology and paleobotany, who discovered the Niederhausen-plant association.

Diagnosis

Plant with gymnospermous anatomy and ultimately four-lobed branching. Fertile parts, distinct on male and female organs, irregularly emerge on the apical part of modified leaves.

Perneria thomsonii sp. nov. (WACHTLER, 2013)

Holotype

PER 249

Paratype

PER 237 (branch), PER 161 (female cone), PER 17, (male cone)

Material

PER 77, 194, 170, 42, 112, 174, 338, 294, 341, 186, 344, 169, 236

Etymology

Named after David Thomson, Toronto (Canada), one of the leading fossil plant collectors worldwide and supporter of developing paleobotany.

Locality

Niederhausen, Rheinland-Pfalz, Germany

Type horizon and age

Upper Lauterecken-Lower Meisenheim-Formation, latest Kasimovian-Gzhelian, Regional stage Western Europe: Stephan B-C

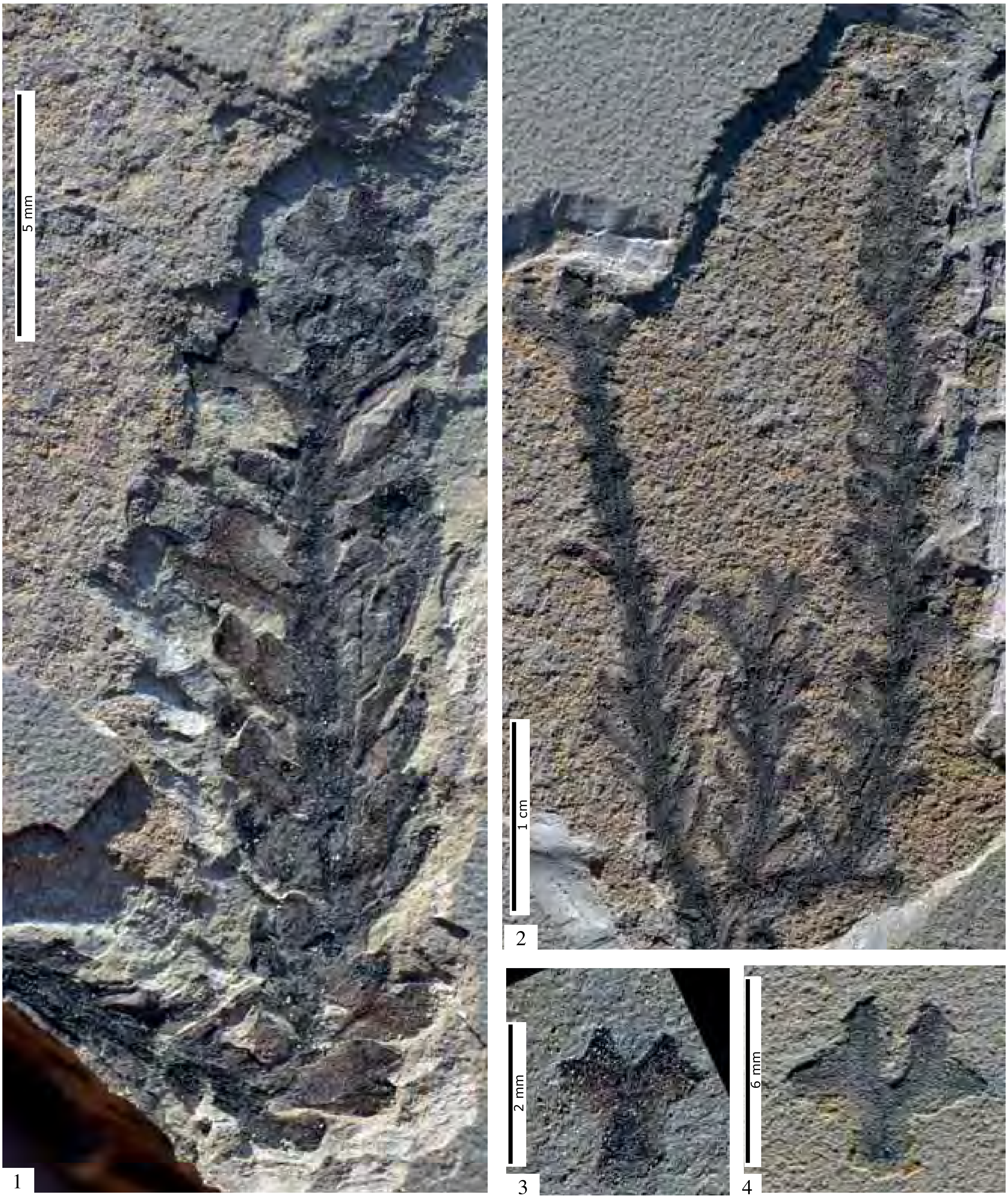
Diagnosis

Putatitive proto-conifer with two foliage types: Four-fingered laminate and needle-like elongated. Polliniferous and ovuliferous zones are on different plants. These are irregularly settled on the upper part of branches, with ovules and microsporophylls apical on modified leave-scales and sustained by a sterile bract. Cone structure is cognisable, but very primitive.

Description

Whole plant: Arborescent to shrubby plant with ramifying branches. PER 237, part of a 5 cm long shoot, exhibits in the upper part characteristic laminate four-lobed leaves, whereas in the lower part these are fluently changed to needle-like, apically rounded foliage. PER 112, 170, 174 and 37 sustain this feature.

Leaves: The plant manifests two types of foliage-structures: the first (Isolated leave-scales PER 77, 194, 338, 294, 341, 186), generated from an axis fan-shape, evolved leaves which divide approximately in the middle into two identical dichotomously branching segments. In this manner, one leaf can be defined as quadrilobed or four-fingered. The apex is rounded, and a conducting strand or vein follows the foliage in every part. The complete scale-leaf can reach a length of 4-8 mm, and a width of 5-8 mm. PER 77, 194, 338, 294, 341, 186 are good examples of abscised leaves; on PER 237, 170, 112, they are in straight connection with the twig. They can be sterile or evolve to fertile ones; in this case, they hold the ovules on one or two of the four segments. Another type of leaf, which usually grows on the lower part of the branches or also in the upper part between irregularly distributed pollen organs (PER 236, 17, 42), is needle-like elongated, which reaches in proportion a considerable length (up to 10 mm), but only has a width of 1 mm; these leaves are rounded on the apex. Sometimes they can also be slightly curved, in which case they are defined as conifer-like.



1) PER 249. *Perneria thomsonii nov. gen. sp. n.* Designed holotype. Semi-mature cone evidencing modified fertile seed-leaves with bracts and the different needle-like leaves on the basal part.

2) PER 237. *Perneria thomsonii.* Paratype. Branch with changing sterile leaves. Double bifurcated in the upper part and rounded undivided needles in the lower part.

3) PER 77. *Perneria thomsonii.* Isolated young leave.

4) PER 194. *Perneria thomsonii.* Single leave showing well the connecting mid-vein.

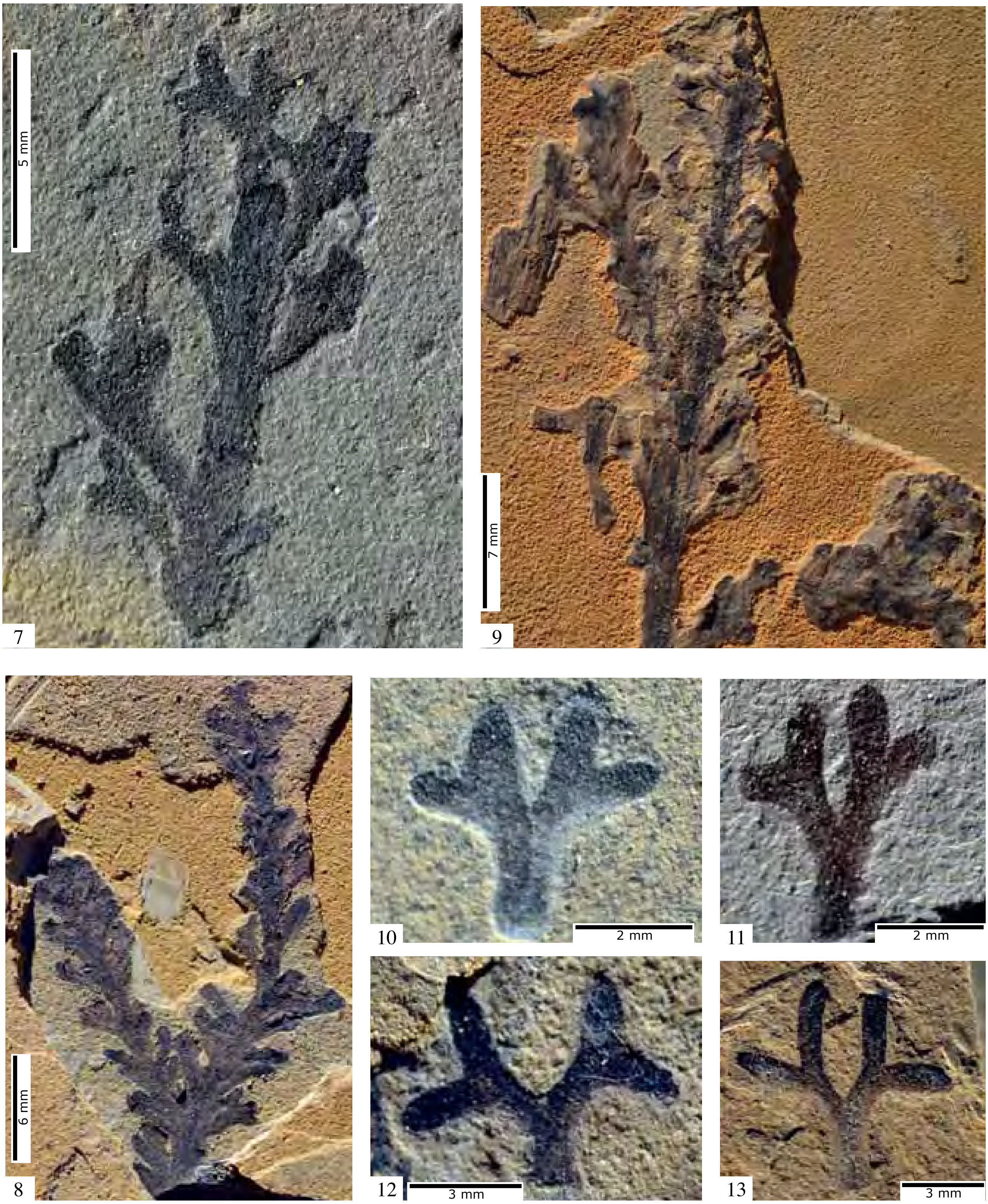
Ovuliferous organs: Cone-like body structure, not totally closed, largely fan-shaped building on the same quadri-lobed leaves, normally two rounded to ellipsoid seeds with rudimentary wings on the basal to middle part of the lobes (PER 54). A sterile acuminate ending bract, slightly overlapping the seed scale, gives them a coniferous character. Isolated four-fingered seed-scales are from 10 to 12 mm wide and approximately 10 mm long (PER 54, 64, 88). On the basal part, they are surrounded by sterile leaves or spines, which could be considered protection-foliage. Young complete cones are 30-40 mm long and 5-7 mm wide (PER 161, 344, 215, and 169). Not all of the scales generate ovules; some remain sterile. On the basal part (PER 249) of the branchlets, the fan-shaped and lobed fertile or sterile leaves cross over to curved needles.
Polliniferous organs: Needle-like area changes abruptly to a fertile zone, which must not necessarily incise with the outermost top (PER 17), but can also be settled beneath. Spore-sacs on the apical part are only exceeded by a small pointed bract. Pollen-scales are much filmier than the surrounding sterile leaves, and are slightly curved (PER 17). Pollen repositories are divided into two segments for each fertile leaf, forming a shield-like appendix (PER 236).

Discussion

Perneria, a main component of the Niederhausen-Flora, can be regarded as one of the most enigmatic plants of the Lowest Rotliegend-Floras. It holds several properties of older plant groups like the Progymnosperms, but at the same time, due to their cone character, bracts and fertile scales, as well as needle-like leaves, it has to be inserted in the coniferophyta. It will be found in Niederhausen approximately in the same quantity as other conifer families, like the wing-seeded *Wachtlerina* or the Walchiacean *Seymourina*.
It can therefore be argued that we have to include it as the last representative of an ancestral family and we can be grateful that this plant survived long enough, probably in the hinterland, giving a deep insight into the evolutionary scenery of all conifers.
First of all, we have to establish whether some of the known plant classes have af-

5) PER 170. *Perneria thomsonii.* Part of a twig with bilobed leaves. Usually female plants hold this kind of leaves.

6) PER 42. *Perneria thomsonii.* Part of a twig with apically rounded leaves. Male plants bear this kind of foliage also in the upper part, female plants only in the basal part.

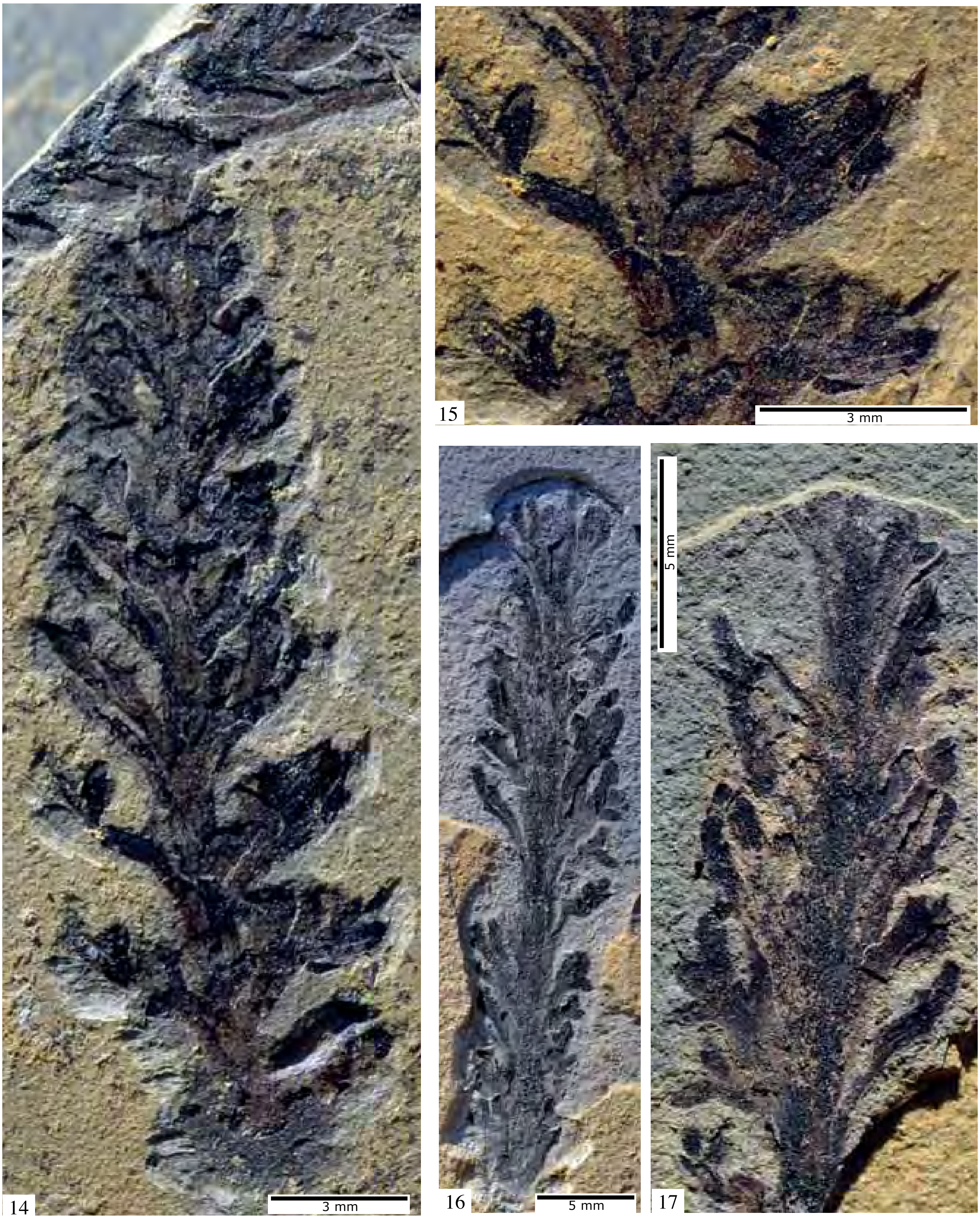


7) PER 112. *Perneria thomsonii.* Shoot with quadrilobed foliage-structure. The leave with the acuminate bract on the lower left side indicate the building of fertile zones.

8) PER 174. *Perneria thomsonii.* Part of a twig with bifurcating leaves on the upper part and unlobed on the lower.

9) PER 37. *Perneria thomsonii.* Shoot.

10-13) PER 338, 294, 341, 186. *Perneria thomsonii.* Isolated abscised adult leaves.

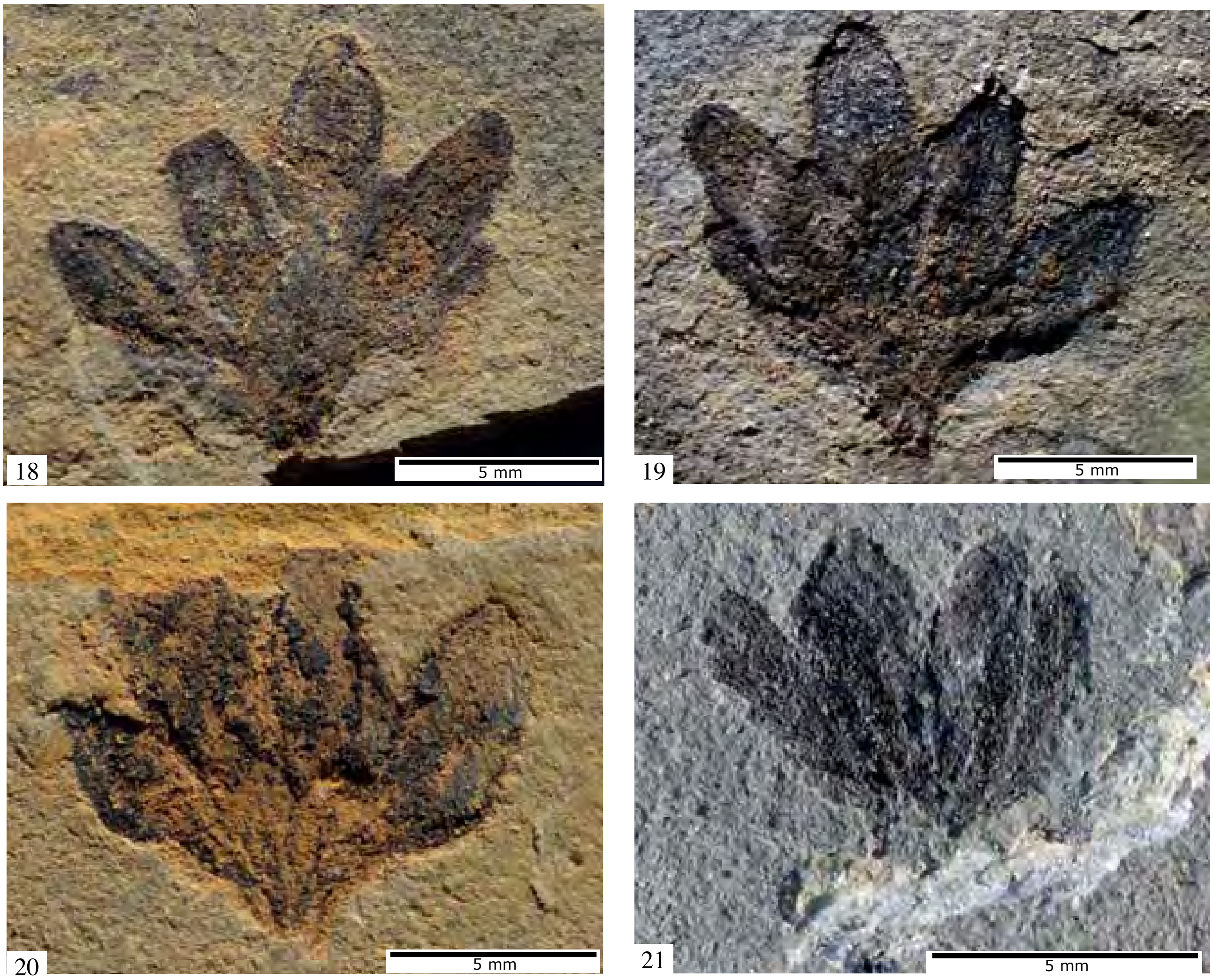


14) PER 161 *Perneria thomsonii.* Paratype. Mainly mature female cone with four-lobed seed-scales and sustaining bracts.15) PER 161 *Perneria thomsonii.* Detail of single seed-scales and bracts.

16) PER 344 *Perneria thomsonii.* Another mainly complete cone.

17) PER 169. *Perneria thomsonii.* Fertile parts with ovules.

finities with *Perneria*. The Sphenophyta have to be eliminated first; the lycophyta bear bifurcating terminal branches, but the cone concept, mega- and microsporophylls on the upper basal part of fertile leaves, are too different and can also be excluded. Also, in the ferns, a relative is lurking, so apart from the conifers, only some of the obscure and superficially known Progymnosperms could be taken into consideration.
The Progymnosperms are actually classified in three orders, the Archaeopteridales, Aneurophytales and Protopityales, ranging from Middle Devonian to Early Mississippian (approximately 390-350 mya) and representing the earliest trees with quite modern growth habit (TAYLOR ET AL., 2009). In the foliage structure we approach: They generate either dichotomously- or trichotomously-branched laminate leaves with dichotomous venation. *Svalbardia* from Middle Devonian, which are found in several localities in the Northern hemisphere, have bifurcating leaves with sporangia produced terminally, as seen in *Psilophyton* from Euramerica. Also, the German Rhineland originates important discoveries of Devonian floras with trichotomously-branched primitive plants like Sawdonia or *Psilophyton arcuatum* (SCHWEITZER, 1994). However, we have to cover a vacuum of almost 50 million years where seed ferns, horsetails and giant



18) PER 54. *Perneria thomsonii.* Fertile scale with ovule and wing grooves on the right lobe.
19) PER 202. *Perneria thomsonii.* (Counterpart of PER 54). Seed scale.
20) PER 64. *Perneria thomsonii.* Fertile scale with protection leaves on the lower side.
21) PER 88. *Perneria thomsonii.* Mainly fused four fingered seed scale, abaxial side.

22) PER 17. *Perneria thomsonii.* Paratype. Microsporophyll with sterile leaves and in the middle a cone-like evolved fertile polliniferous zone.

23) PER 17. *Perneria thomsonii.* The microsporophylls evidence archaic coniferous character.

24) PER 17. *Perneria thomsonii.* Detail of some polliniferous scales.

25) PER 236. *Perneria thomsonii.* Polliniferous organs on a twig.

26) PER 236. *Perneria thomsonii. Detail of two polliniferous organs. Only some leaves hold pollen sacs. These are sustained by a bract.*

Perneria thomsonii a) Sterile twig (PER 237), b) Sterile young and adult leaves (PER 194, PER 294), c) male cone with basal sterile leaves and cone-forming process in the middle (PER 17), d) Detail of the microsporophylls (PER 17, 236), e) Seed-scales adaxial and abaxial side, f) Young female cone (PER 67).

clubmosses began to appear in the plant kingdom, covering swamps and marshes. Therefore, it is supposed that *Perneria* or their closest relatives were restricted to dry and arid zones and only became visible after the climatic change.

The general look of the branches (PER 237) can be regarded as coniferoid, as can the basal needles. Although appearing terminally-rounded, but being falcate, they fit in the concept of needle-trees. Much more complex and at the same time important will be the arrangement and composition of female and male cones.

Almost all extant conifers hold their microsporophylls on a central axis. The pollen scales consist of a slender stalk and end in a blade of varying shape, in that way, making the surface with two (for example Pinaceae and Cupressaceae) or more (Auracariaceae) microsporangia attached to the lower edge at the bottom. They can be free hanging, as in Auracarians with their numerous sacs, or attached to the stalk, as in the Pinaceae. Archaic *Perneria* also hold the pollen sacs terminally on a slender stalk, which ends in a pointed protection leaf and they are arranged on the abaxial side. However, different to all other Permian, Triassic and extant conifer cones, the cone is only rudimentarily evolved (PER 17, PER 236), and mixed with sterile leaves, rather than developed as a distinct cone structure. Nevertheless, the terminally hanging pollen sacs classify them as conifer-like.

If pollen cones are relatively uniform in all conifer-families, we have within the seed-bearing structures genera with only one seed, like the Auracariaceae and Podocarpaceae, or two in the Pinaceae. The Auracarias have their seeds sunken in a groove in the seed scale and the whole scale acts as a dispersal unit. Pinaceae on the other side are wind-dispersed with an attached wing or have scales that enfold a seed, in order to be animal dispersed (ECKENWALDER, 2009).

In *Perneria,* we have primitive cone-structures arranged around a main axis, consisting of four-fingered fertile scales with two seeds, which are sustained by a sterile bract and sometimes coated by minute sterile spines or leaves on the basal part. This feature is unique in the contemporary plant kingdom.

The most accepted interpretation to date about the evolutionary trends of conifers, the work of the Swedish palaeobotanist Rudolf Florin (FLORIN, 1938-1945), theorises the seed scale as a fertile dwarf-shoot with seed-bearing and sterile leaves in the axils of bracts. He hypothesised that all extant conifers derived from a common ancestor, and have to be grouped into the Paleozoic Cordaitales. An evolving line with multi-leaved dwarf-shoots fusing more and more through time across the Walchiaceae and Voltziaceae is suggested. No specification is given about the origin of the winged seeds (in extant conifers the most conspicuous group) or families like the Taxaceae with its berries. It is not clear why in the Earliest Permian we have mainly naked scales with no apparent composition of sterile leaves forming a dwarf-shoot.

Therefore, all of the conifer-derivation theories must be revised and the "dwarf-shoot" theory - that all extant conifers were generated gradually from one ancestor by fusing their ovuliferous scales more from *Walchia* through *Pseudovoltzia* and *Voltzia* to arrive to all extant Pinaceae, Araucariacea, Cupressaceae and other conifer-families - should probably be abandoned. However, this theory cannot give a satisfying answer of the question why in the Earliest Permian, *Voltzia*-like coalesced ovuliferous scales coexisted with aliform scales from *Majonica*-typus, (like extant Norway spruce) as well as conifer nut generating plants.

Much easier designations supported by the flora elements of this time can be established: all conifer seed scales probably derived from a quadrilobed scale. The Walchian-Voltzian, Araucarian-type by coalescence, and the *Majonica*, Pinaceae-type by the development of a filmy to winged scale with attached seed.

FLORIN, F. (1938-1945): Die Koniferen des Oberkarbons und des Unteren Perms. - Palaeontographica, 65, Abt. B, 1-729, 65 Fig, 186 Taf, Stuttgart.

SCHWEITZER, H.J., (1994): Die ältesten Pflanzengesellschaften Deutschlands in Koenigswald & MEYER W. Erdgeschichte mitteleuropäischer Regionen, Band 1: Erdgeschichte im Rheinland - Fossilien und Gesteine aus 400 Millionen Jahren, Pfeil-Verlag, München

TAYLOR, T.N., TAYLOR, E.L., KRINGS M. (2009). Paleobotany. The Biology and Evolution of Fossil Plants. Burlington MA, London, San Diego CA, New York NY, Elsevier/Academic Press Inc., xxi + 1230 pp.

ECKENWALDER, J.E. (2009). Conifers of the World: the complete reference. Portland (OR): Timber Press. 720 pp.

Division: Ginkgophyta
Order: Ginkgoales (ENGLER, 1897)
Family: Ginkgoceae (ENGLER, 1897)
Genus: *Baiera* (BRAUN, 1843)

***Baiera perneri* n. sp. (WACHTLER, 2013)**

Holotype

PER 154

Paratype

PER 62

Material

PER 116, 240

Locality

Niederhausen, Rheinland-Pfalz, Germany

Type horizon and age

Upper Lauterecken-Lower Meisenheim-Formation, latest Kasimovian-Gzhelian, Regional stage Western Europe: Stephan B-C.

Etymology

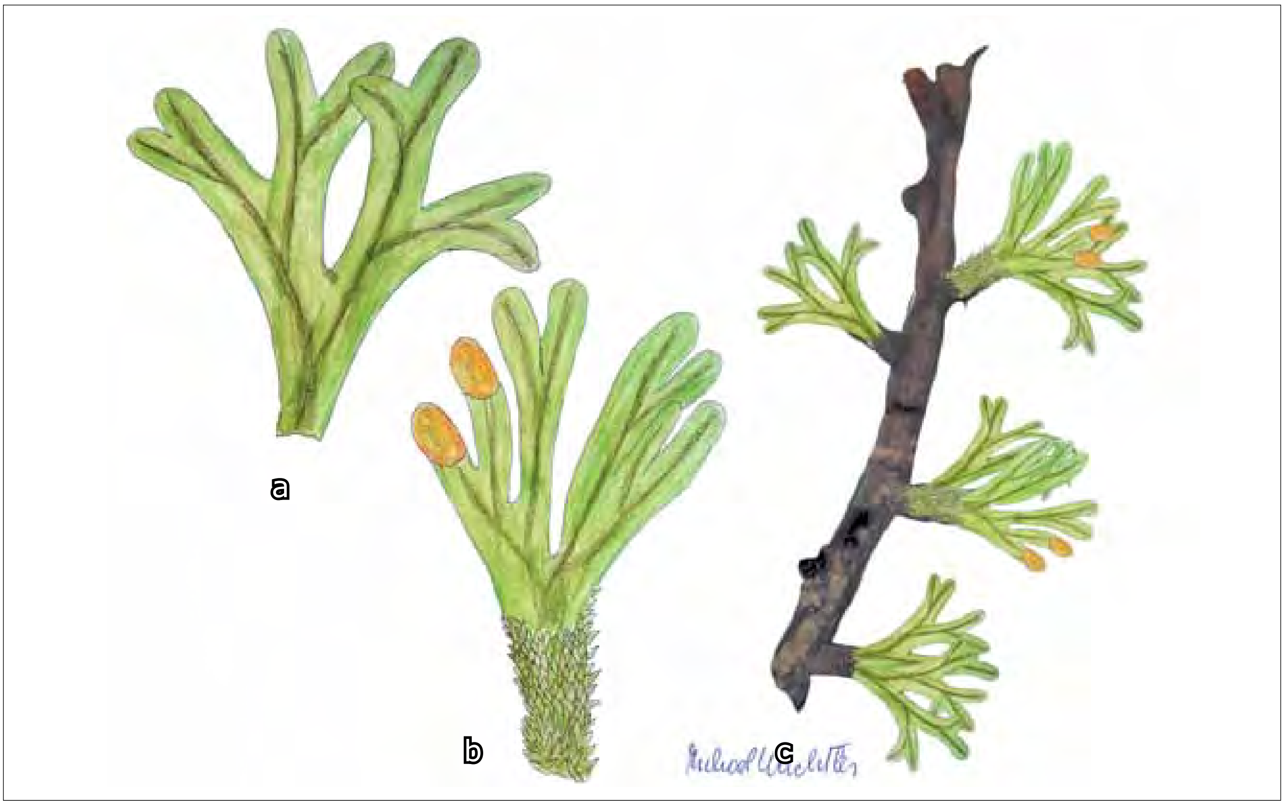
Named after Thomas Perner, who spent many years in Niederhausen recovering fossils and conserving them.

Diagnosis

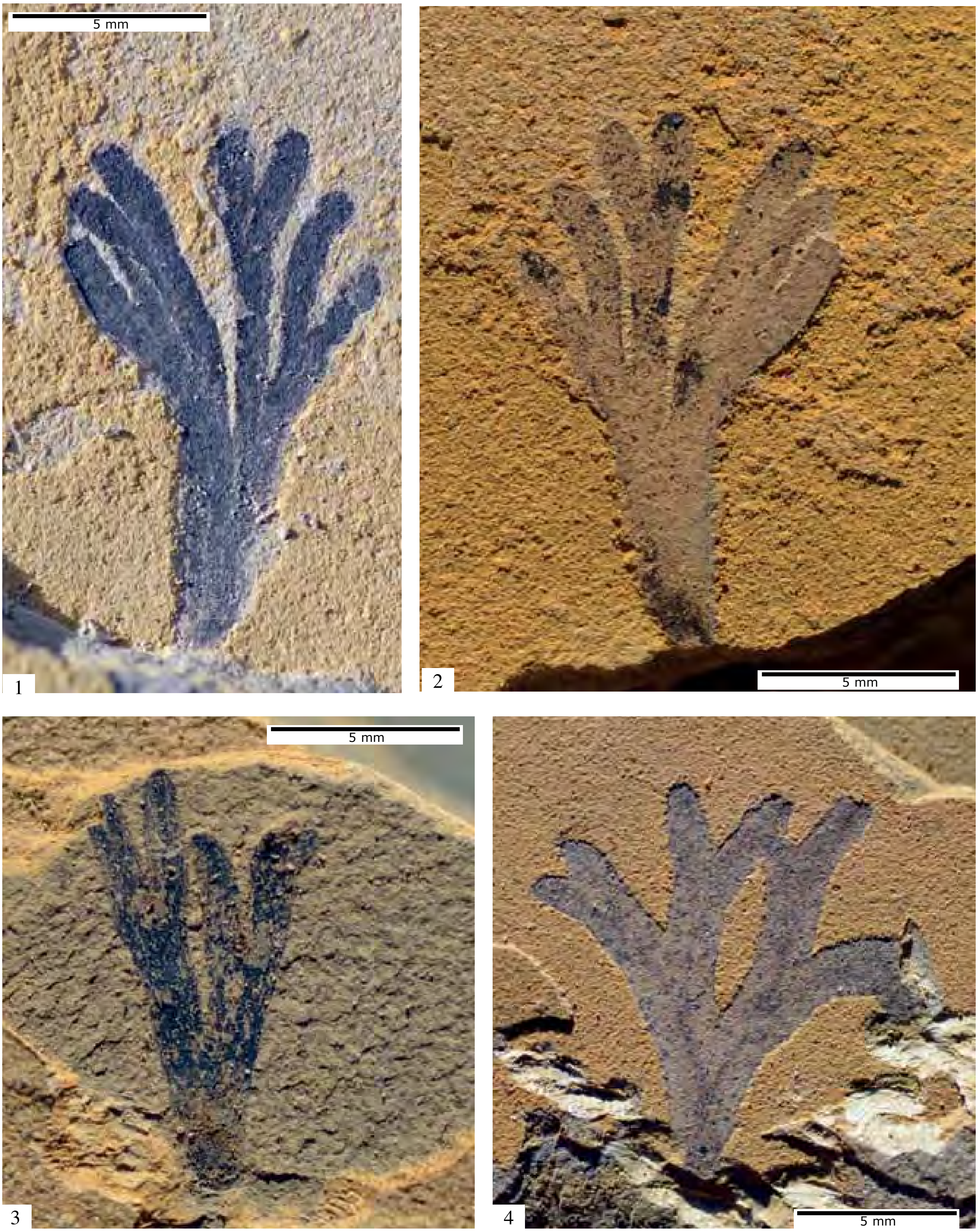
Foliage arranged into two symmetrical groups with regular bifurcation pattern. Single leaves with rounded apex.

Description

Leaves: About 15 mm long, from 10 to 15 mm broad, (PER 154, 240, 116), sprouting from one leaf-base (2 mm broad). They divide approximately in the middle, forking into two mainly identical segments in which each one forms a four-fingered, sometimes-overlapping foliage-structure. The incision is distinctive in the middle and less prominent between the lateral lobes. All leaves end in a geometrically-rounded apex. PER 240 evidences one distinctive middle vein, which follows and connects all leaves; others are less prominent. Single leaves are about 1 mm wide. Dwarfish micro-leaves resembling a collar intensely cover the combined base.



Baiera perneri, reconstruction a) leave PER 240. b)leave holotype PER 154. c) Suggested reconstruction



1) PER 154. *Baiera perneri.*Designed holotype. Isolated leave.
2) PER 62. *Baiera perneri .* Counterplate holotype.
3) PER 116. *Baiera perneri.* Leaf.
4) PER 240. *Baiera perneri.* Leaf.

Fertile organs: Some accentuations on the apex of two lateral leaves (PER 154) could be interpreted as ovules.

Discussion

Friedrich Wilhelm Braun instituted the genus *Baiera* in 1843 for lacerated leaves thought to be precursors of the extant *Ginkgo*-tree. If foliage units of such lacerated typus were found in Upper Permian to Triassic, they would be accepted as belonging to the ginkgophyta genus *Baiera*. But for these enigmatic leaves from the Late Carboniferous-Earliest Permian Flora of Niederhausen, a classification will be much more complicated. Without doubt, they have all items to be inserted as ginkgophyta-ancestors but in the same way, parental affinities with much older groups like the progymnosperms with terminally-arranged fertile zones could not be disregarded. To deal with the problematic insertion of this plant, similar leaves in the outer aspect, from *Perneria*-type, but smaller would be found in the same locality, in connection with mainly unquestionable properties of the coniferophyta. In contrast, they are never divided into two reflecting quadrilobed parts, but are only in one part.

An answer, it could be that the often suggested common origin of the Coniferophyta and Ginkgophyta took place effectively in this time or previously, from one common ancestor, in order to be settled in the group of Progymnosperms. The subdivision then occurred in the manner where the elongated double four-fingered leaves tended towards the Ginkgoales, whereas the single quadrilobed was in the direction of the Coniferales, as frequently seen in this strata, in fertile conifer-scales.

This putative ginkgophyta from the Earliest Permian Niederhausen-Flora are densely covered with minute basal leaves, which concur with the assumption that the typical collar of all extant ginkgo-trees is nothing other than a dwarfish foliage-coating.

The fact that this hypothesis cannot be ruled out is manifested by the visual nature of recently discovered younger (Artinskian-Kungurian) *Baiera*-plants in the Tregiovo Flora in the Dolomites (WACHTLER, 2012). The basal collar exists in that time just like in extant ginkgo; the leaves consist of two per two times bifurcating leave-elements and the ovules are developed on the apex of normal sterile leaves.

This evolutionary trend can be followed to the Jurassic. *Baiera digitata* (Kupferschiefer, Wuchiapingian, upper Permian) (BAUER ET AL., 2013) holds the same character as raetho-liassic *Karkenia hauptmannii* or *Baiera taeniata*.

Other Kasimovian-Gzhelian putative ginkgophyta (*Ginkgophyllum grasseti*, DOUBINGER, 1956; pl. 16 fig. 1-4) from Lodéve in France show more developed ginkgo-leaves than *Baiera perneri*. This is in contrast with the fact that, as seen also in other plant-groups (*Walchia-Perneria/ Calamites-Sphenophyllum*), some archaic plants lived for a certain time together with others; most of them had a xerophytic character, which in the following million years become dominant. Different altitudes as well as local climatic environments are probably the background of this often discussed problem.

BAUER K., KUSTATSCHER E., KRINGS M. (2013): The ginkgophytes from the German Kupferschiefer (Permian), with considerations on the taxonomic history and use of Baiera and Sphenobaiera. In: Bulletin of Geosciences. 88, 2013, p. 539 - 556 [Esterella, Ginkgophyta, late Permian, radiation, foliage fossil, macromorphometry, Central European Basin, Germany.].

DOUBINGER, J.: Contribution ä l'etude des flores Autuno-Stephaniennes. - Mem. S. G. F , 35, 1-2, 180 S., 20 Fig., 17 Taf., Paris 1956.

FLORIN, R., (1936): Die fossilen Ginkgophyten von Franz-Joseph-Land nebst Erörterungen über vermeintliche Cordaitales mesozoischen Alters. II. Allgemeiner Teil. Palaeontographica 1936, 82(B):1-72.

WACHTLER, M., (2012A): The latest Artinskian/Kungurian (Early Permian) Flora from Tregiovo-Le Fraine in the Val di Non (Trentino, Northern Italy) - Preliminary researches. Dolomythos, 3-56 Innichen. ISBN 978-88-904127

Wachtlerina bracteata a new conifer from the Carboniferous-Permian (Kasimovian/Gzhelian) Niederhausen Flora (Rheinland-Pfalz, Germany)

by Thomas Perner

Division: Coniferophyta
Order: Coniferales (TAYLOR, 1981)
Family: Majonicaceae (CLEMENT-WESTERHOF, 1986)

Wachtlerina gen. nov. (PERNER, 2013)

Etymology

Named after the researcher Michael Wachtler, who described European fossil floras.

Diagnosis

Plant with protruding branches and flexuous deeply incised leaves. Female cones are characterised by a long and distinctive bract, protecting two winged seeds.

Wachtlerina bracteata sp. nov. (PERNER, 2013)

Holotype

PER 15

Paratype

PER 67 (young cone), PER 100 (Bract) PER 6 (Seed) PER 34 (Male cone) PER 38 (leaves),

Material

PER 207, 114, 335, 203, 223, 182, 234, 78, 180, 167, 60, 220, 77, 114, 285, 205, 282, 247, 303, 246, 119, 258.

Etymology

Focused on the dominant and long bracts on the female cones.

Locality

Niederhausen, Rheinland-Pfalz, Germany

Type horizon and age

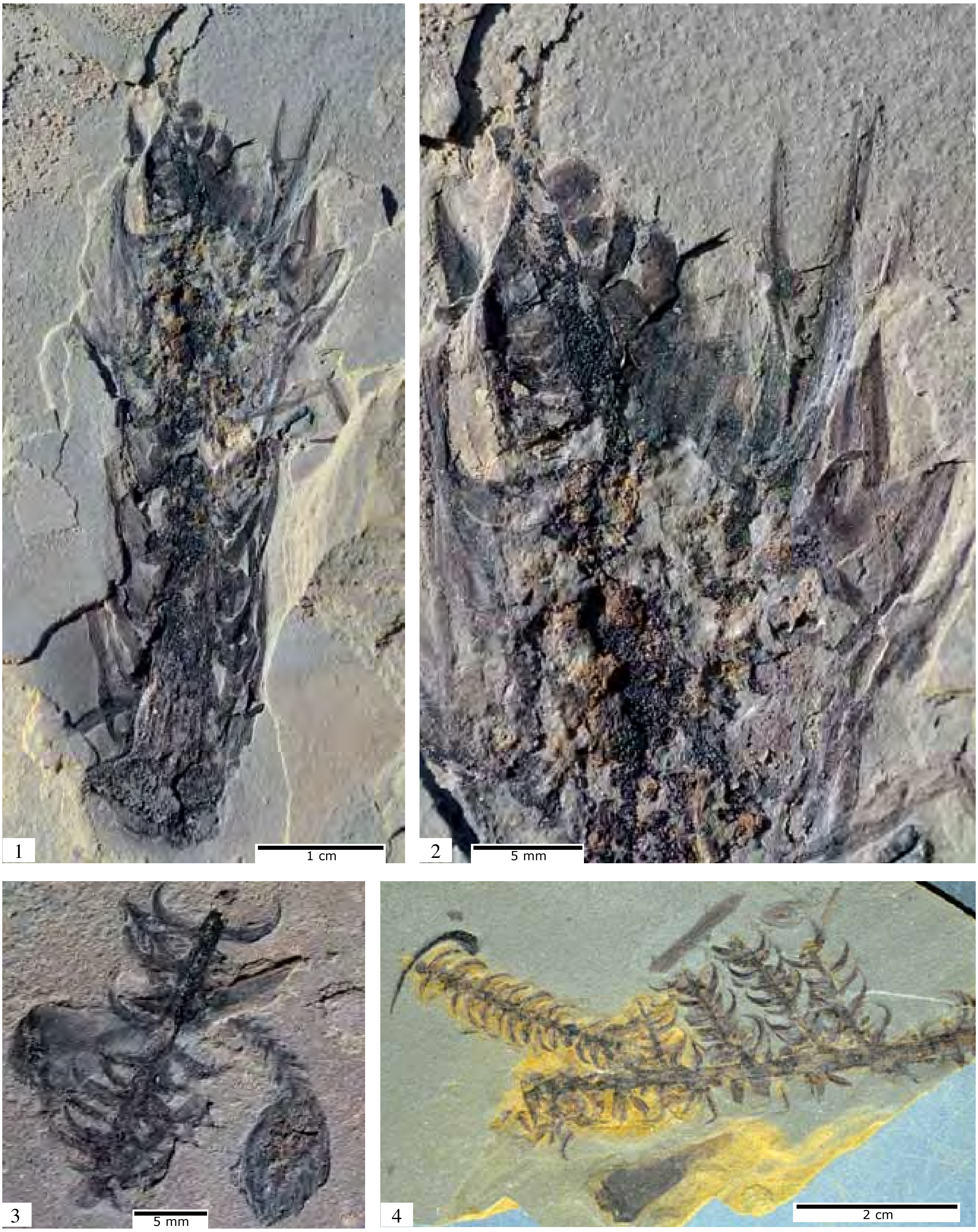
Upper Lauterecken-Lower Meisenheim-Formation, latest Kasimovian-Gzhelian, Regional stage Western Europe: Stephan B-C

Diagnosis

Conifer with awl-shaped, cuspid leaves crossed by a distinct midvein. Female cones have a long apically acuminate bract, holding two winged ovules. Bracts shed after maturity to leave naked cones. Polliniferous cones with microsporophylls arranged on a main axis and the sporangia on the lower apical side.

Description

Branchlets: Arborescent conifer with extensions, bearing two evenly spaced combs of branchlets, for much of their length.
Leaves: Needles are massive and falcate, especially when fully developed (PER 247), and never overlapping. They stick straight out and are bent inward on the apical part, being attached by the whole width to the main rachis. A prominent mid-vein crosses over the whole leaf. They can reach a length of 10 mm and a width of 2 mm (PER 100, 282, 303).
Ovuliferous cones: In an adult stage, cones are 10 cm long, 1.5 cm wide, without counting the length of the prominent long bracts (PER 223). Sterile bracts were 50 mm long and 5-8 mm wide (PER 78, PER 270), crossed by a central rib for the entire length. Bracts gradually narrow to the end in a pointed apex. They could sometimes be falcate to concave and are released after maturity. Isolated bracts can therefore often be found in these layers, as can totally shed cones (PER 234, PER 182). Seed-scales are not attached directly to the axil of the bracts but slightly above and directly to the cone rachis, in order to be released after maturity. Ovules are in pairs, leaving pronounced grooves on the upper side of the bracts. Juvenile ovules are winged with a proportion of two-thirds for the wing and one-third for the ovule (PER 77). In an adult stage, the seed increases considerably until it reaches a length of 15 x 10 mm. Seed as well as ovules are distinguished by a median rib, which is split in an adult stage. It is possible

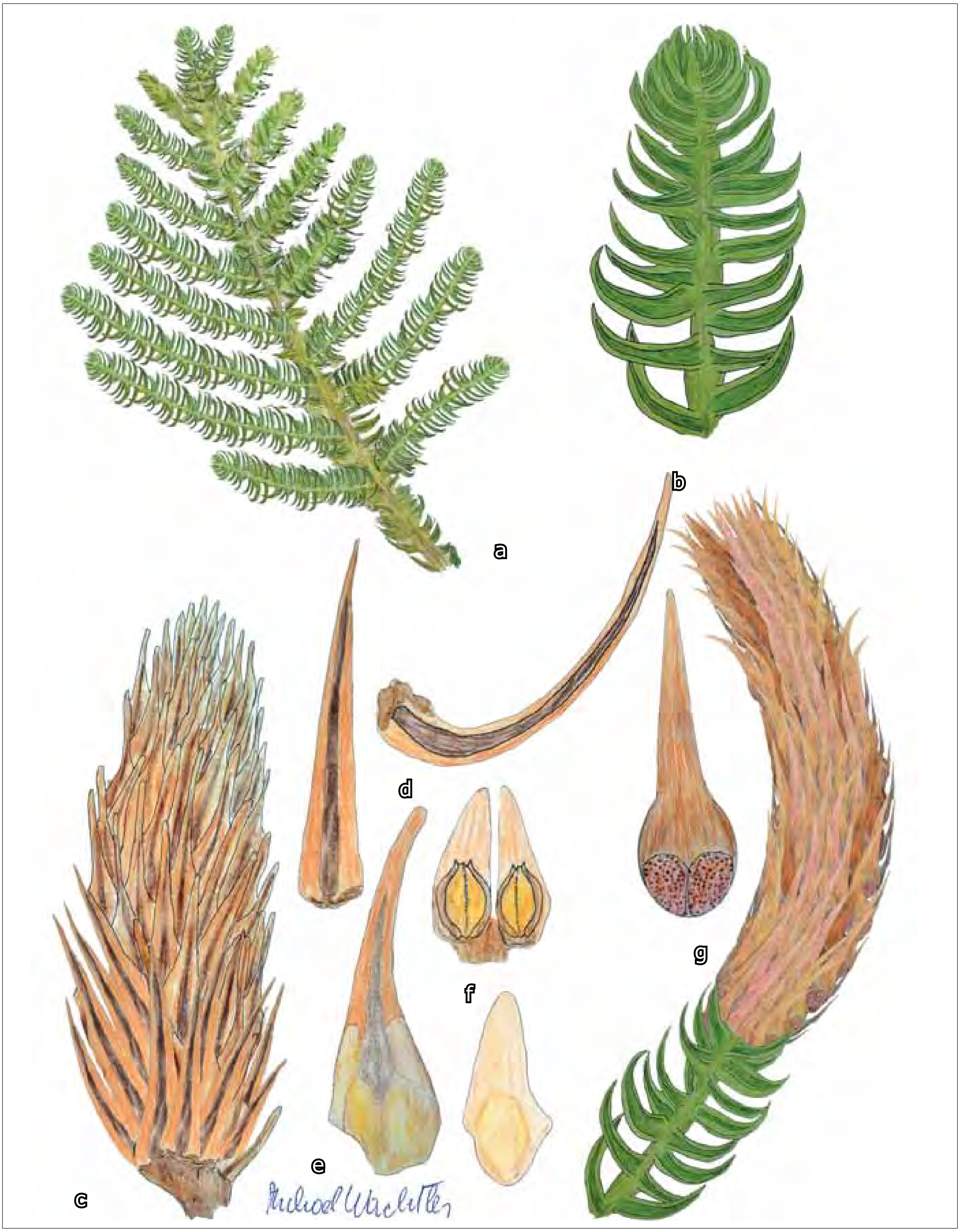


1) PER 15. *Wachtlerina bracteata n. gen. sp. n.* Holotype. Mainly complete ovuliferous cone.

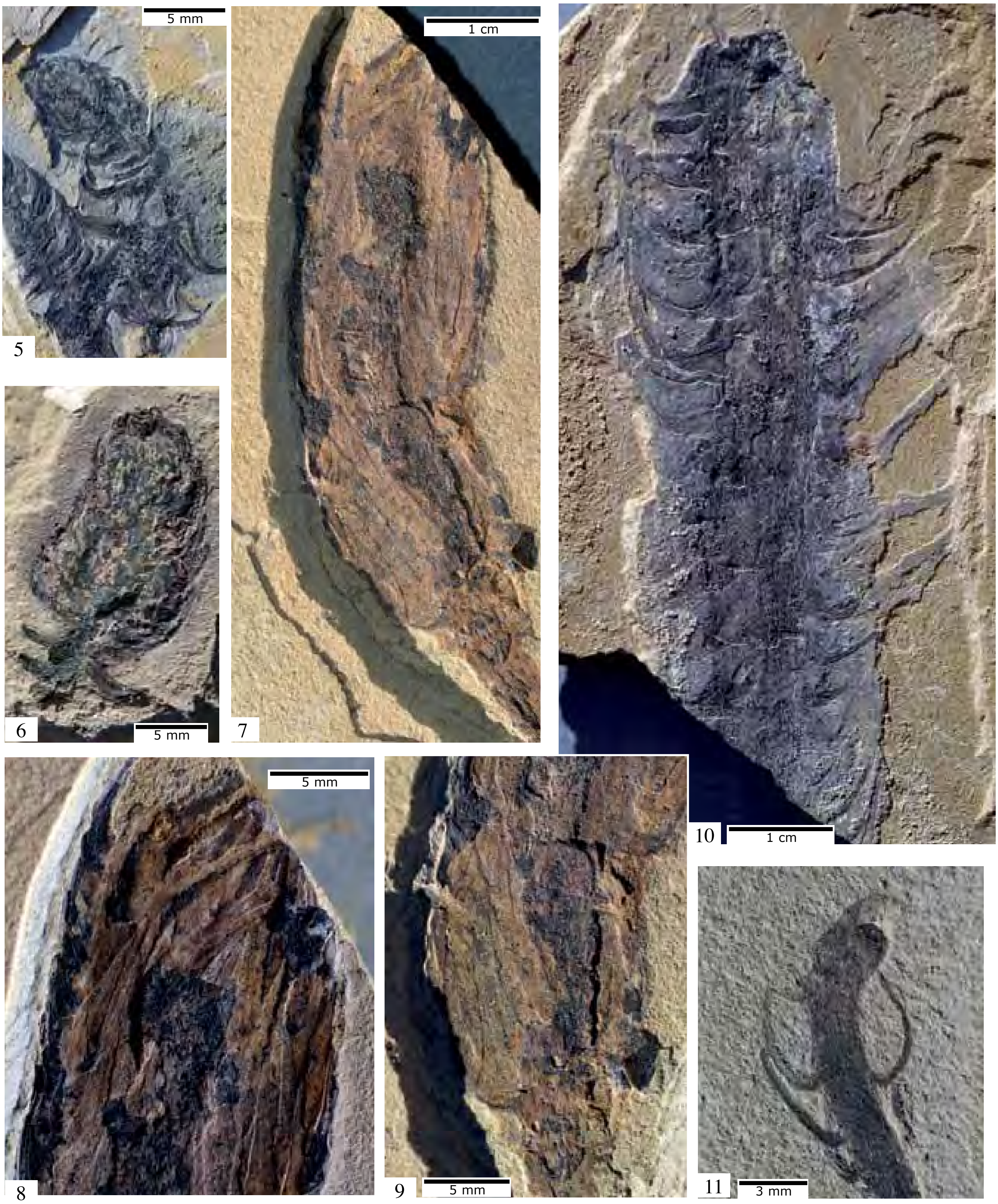
2) PER 15. *Wachtlerina bracteata n. gen. sp. n.* Holotype. Detail of the cone with the long pointed bracts.

3) PER 207. *Wachtlerina bracteata n. gen. sp. n.* Lovely arrangement of a twig with a young cone and a dispersed bract.

4) PER 114. *Wachtlerina bracteata n. gen. sp. n.* Twig with two bracts (one lateral, one abaxial) and a winged seed on the upper part.



Wachtlerina bracteata a) Twig (PER 38), b) Leaves (PER 100, 119), c) Young female cone (PER 67, d) Bracts from the female cone lateral and abaxial (PER 220, PER 66), e) Bract with ovule and wing-grooves, adaxial side (PER 100), e and f) Winged seeds in various growing stages (PER 77, 114), g) male cone and bract (PER 34).



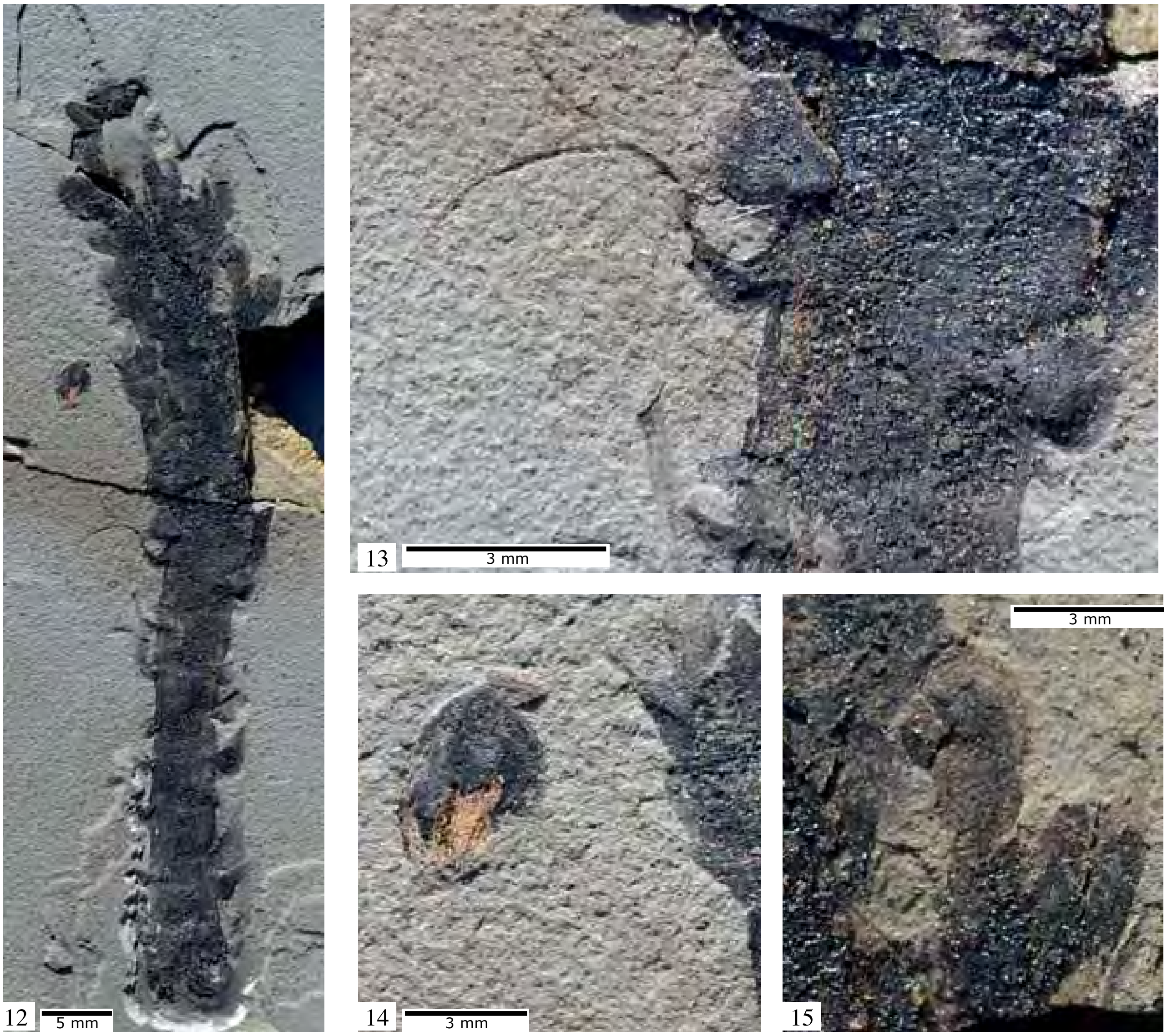
5) PER 335. *Wachtlerina bracteata n. gen. sp. n.* Juvenile cone.

6) PER 203. *Wachtlerina bracteata n. gen. sp. n.* Juvenile cone attached to the twig.

7-9) PER 67. *Wachtlerina bracteata n. gen. sp. n.* Paratype. Semi-mature cone evidencing well the long sterile apical pointed, basally bulgly bracts.

10) PER 223. *Wachtlerina bracteata n. gen. sp. n.* Adult cone.

11) PER 182. *Wachtlerina bracteata n. gen. sp. n.* Naked female cone with all bracts shed.



12) PER 234. *Wachtlerina bracteata n. gen. sp. n.* Naked ovuliferous cone with mainly all bracts shed. Winged seed scales partially still attached to the cone. A mature seed lies on the left side.

13-15) PER 234. *Wachtlerina bracteata n. gen. sp. n.* Detail of the winged and the fully developed seeds.

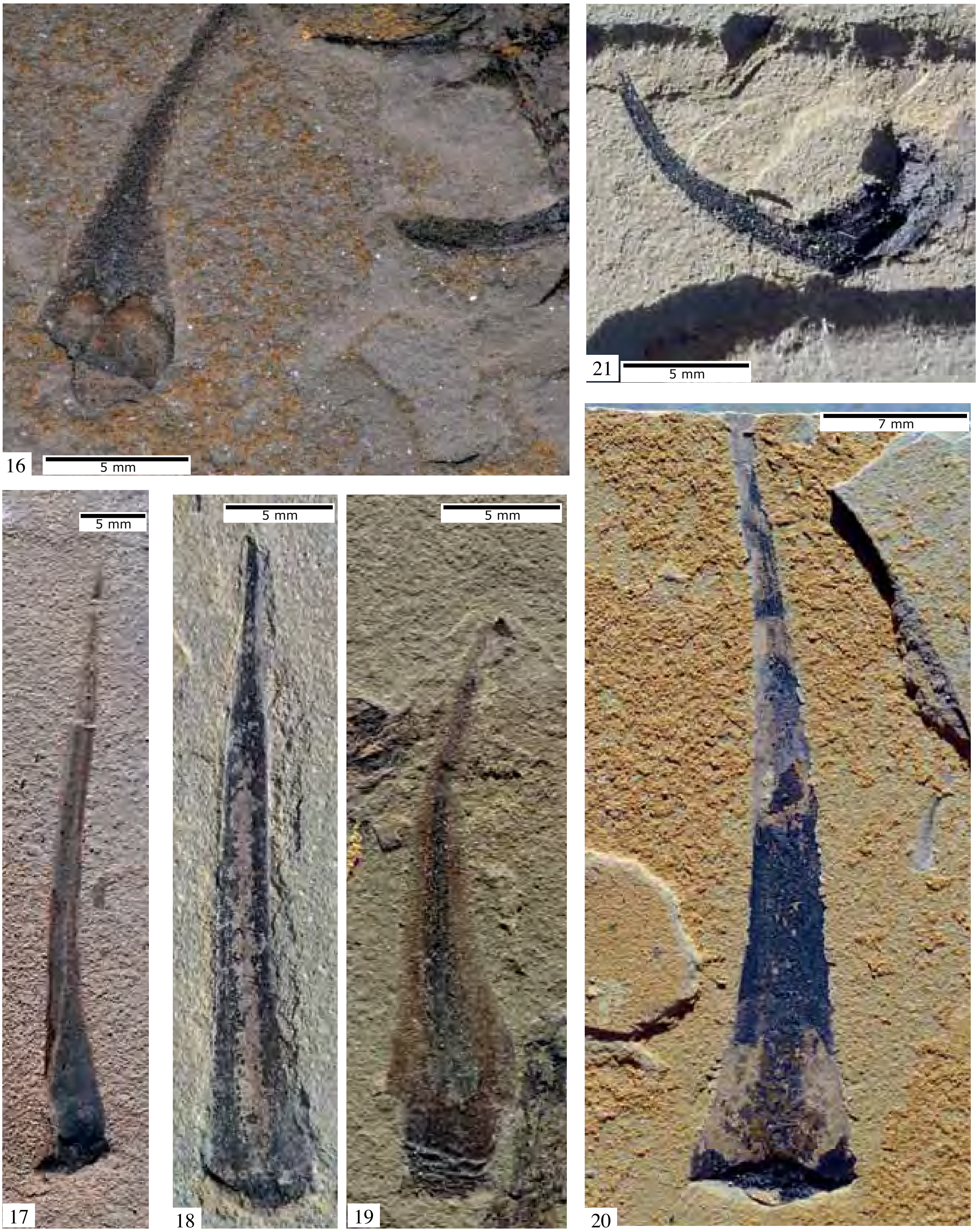
that the seeds were shed from the cones before maturity, and grew out in the soil until they fractured to release the embryos.

Polliniferous cones: 80 mm long and 15 mm wide (PER 34), holding a fair quantity of stalked microsporophylls on a main axis, each ending in a relatively long and pointed bract (up to 5 mm). Microsporangia are on the lower part of the microsporophylls.

Discussion

In the last decades, by studying fossil plants, especially conifers, primary attention was given to the visual nature of leaves: if they were more or less falcate, fan-shaped, acuminate or rounded. Less attention was given to their stratigraphical placement, and therefore many collectors brought from various localities similar looking mostly sterile material which increased the collections, but complicated the classification. Lower Rotliegend or Early Permian material is not the same everywhere, especially the deepest Carboniferous species with *Sigillaria, Lepidodendron* or *Calamites* dominated floras. Even Oberhausen, only a distance of a few kilometres produces slightly different flora-elements (KERP ET AL., 1990).

By superficially examining the long and multiple conifer bracts of the new genera *Wachtlerina*, one could insert them without

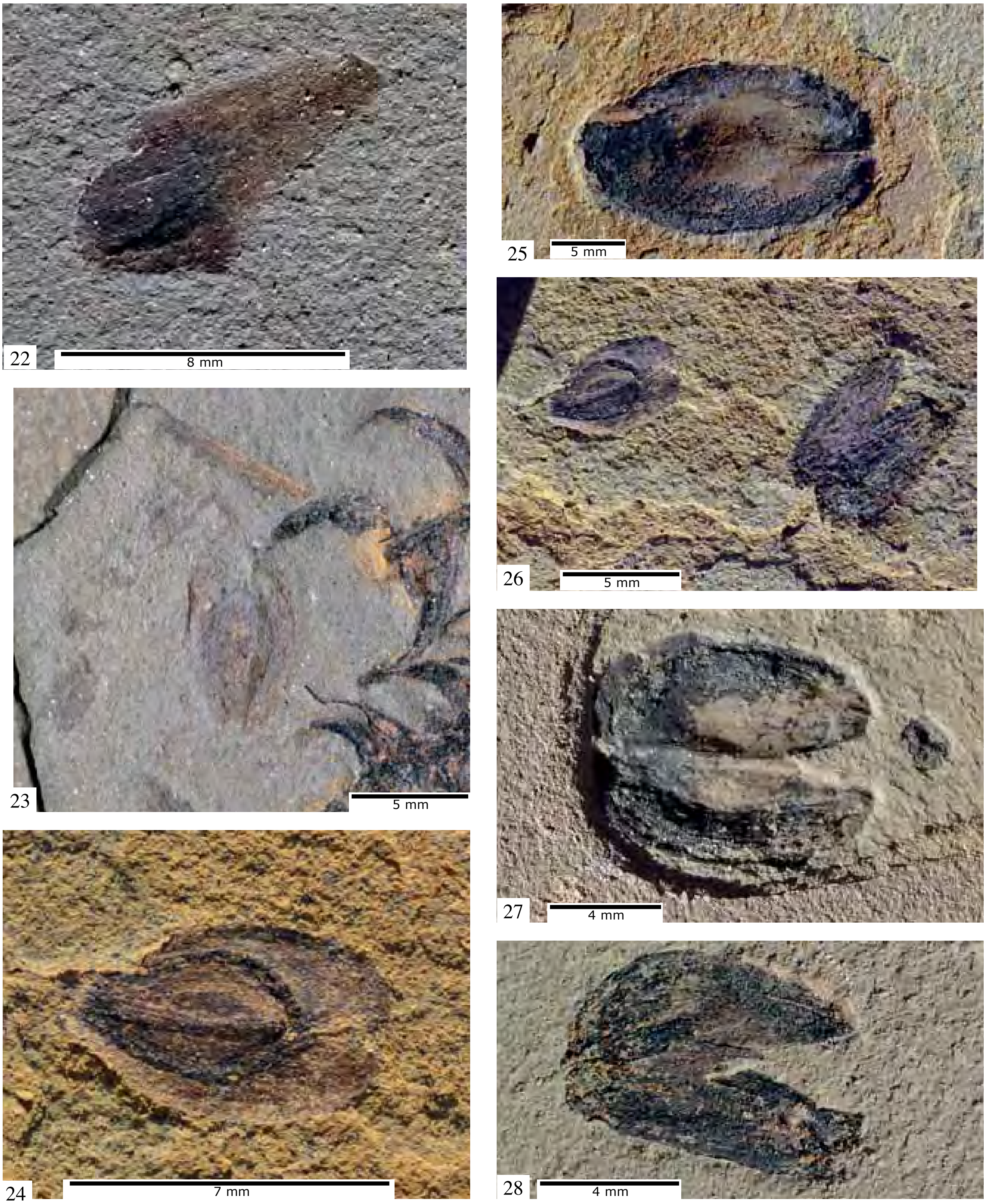


16) PER 100. *Wachtlerina bracteata n. gen. sp. n. Paratype. Bract evidencing well the appressed two seed grooves.*

17) PER 78. *Wachtlerina bracteata n. gen. sp. n.* Bract seen from the lower side.

18 - 20) PER 180, 167, 60. *Wachtlerina bracteata n. gen. sp. n.* Bract outer side. Note the spinose aspect of PER

21) PER 220. *Wachtlerina bracteata n. gen. sp. n.* Bract seen from the lateral side.



22) PER 77. *Wachtlerina bracteata n. gen. sp. n.* Ovule with attached mainly complete wing.
23) PER 114. *Wachtlerina bracteata n. gen. sp. n.* Ovule with attached lacerated wing.
24) PER 6. *Wachtlerina bracteata n. gen. sp. n.* Semi-mature Ovule.
25) PER 205. *Wachtlerina bracteata n. gen. sp. n.* Semi-mature seed. Note the typical lateral furrow.
26) PER 6. Paratype. *Wachtlerina bracteata n. gen. sp. n.* Juvenile ovule with abscised wing and adult bursted seed.
27 - 28) PER 286, 74. *Wachtlerina bracteata n. gen. sp. n.* Split mature seeds.

29) PER 34. *Wachtlerina bracteata n. gen. sp. n. Paratype.* Complete male cone.

30) PER 34. *Wachtlerina bracteata n. gen. sp. n.* Male cone with single bract and sporangia on the lower side.

31) PER 34. *Wachtlerina bracteata n. gen. sp. n.* Lateral view of the microsporophylls.

32) PER 34. *Wachtlerina bracteata n. gen. sp. n.* Lower part of the male cone.

hesitation in the walchiaceous ovuliferous cones of *Gomphostrobus bifidus* (from the Latin name bifidus). In comparison, bifid ending bracts are unknown in Niederhausen, whereas *Wachtlerina bracteata* generates only undivided bracts. The same is valid for the leaf-type (KERP ET AL., 1990). Foliage characterised by fairly small falcate leaves was often inserted as *Ernestiodendron filiciforme* and thought to belong to the group of Walchiaceae. When observing only branches from *Wachtlerina* they would undoubtedly be classified as *Ernestiodendron*. In connection with the whole plant, however, this could not be maintained, especially for the female cones. *Wachtlerina*-cones generate aliform seeds without accompanying collar leaves. Therefore, the family of Walchiaceae must be excluded as the mother family of *Wachtlerina*. In 1987, the Dutch paleobotanist Johanna CLEMENT-WESTERHOF described wing-seeded conifers from Upper Permian localities in the Italian Dolomites, naming them *Majonica (alpina*). She inserted these conifers into the Majonicaceae, including the genera *Majonica, Dolomitia* and *Pseudovoltzia*. However, the winged seeds differ too much from the coplanar-surfaced Voltzialean-like *Dolomitia* and *Pseudovoltzia.* Therefore, it will be proposed to utilise the family Majonicaceae for aliform conifer-seeds, and Voltziaceae for the group of *Pseudovoltzia, Dolomitia* and *Voltzia*. It is suggested that the second group was created due to their microsporophylls dorsiventrally on the lower edge hanging numerous pollen sacs to the present-day Araucarians, whereas the winged seeds guided towards other important conifer families like the Pinaceae and Cupressaceae.
That the alar conifer-seeds were a solid dimension just over than 300 million years ago can be shown as in these Niederhausen sediments, apart from *Wachtlerina bracteata*, seeds with much more pronounced wings were recovered, and classified as *Majonica* sp. The difficulty is to find sufficient material of winged seeds, being easily destroyed by climatic circumstances or by not enough silty sediments.
Wachtlerina bracteata will be inserted in the most archaic genus of Majonicaceae to date. Their wings in connection with the ovules,

33) PER 282. *Wachtlerina bracteata n. gen. sp. n.* Twig.

34) PER 100. *Wachtlerina bracteata n. gen. sp. n.* Detail of twig evidencing the strong mid-vein.

35) PER 247. *Wachtlerina bracteata n. gen. sp. n.* Awl-shaped leaves.

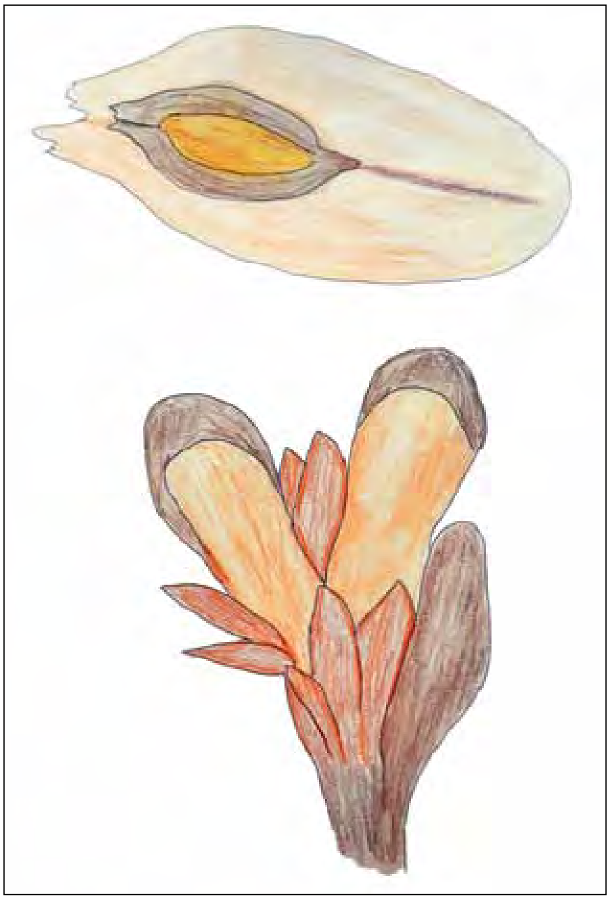
36) PER 303. *Wachtlerina bracteata n. gen. sp. n.* Detail of the leaves.

37) PER 38. *Wachtlerina bracteata n. gen. sp. n.* Paratype. Branch.

38) PER 246. Wachtlerina bracteata n. gen. sp. n. Apical and basal shoot.

39) PER 119. *Wachtlerina bracteata n. gen. sp. n.* Apical part of a shoot.

40) PER 258. *Wachtlerina bracteata n. gen. sp. n.* Overview of the leaves.



Majonica sp. Reconstruction of the defined seed scales with compressions of winged seeds (PER 264, PER 333).

1) PER 264. *Majonica sp.* Undefined seed scales with compressions of winged seeds.

2) PER 333. *Majonica sp.* Winged seed with the ovule in the middle.

look unskilful and cannot be distinct from *Perneria* seed-wings.
The question has to be asked what natural reason led to the formation of aliform seed-scales? If the climate all over the Permian become more arid, desert-like and dry, maybe interrupted only by seasonal inundations, plants could expand their natural range to all others. This successful group of Coniferophyta was manifested in two ways: One group increased their seed size, making them comestible for a lot of animals, as happened for *Walchia-, Voltzia*-and *Ortiseia*-conifers, and the other group choose a way to make its seeds more and more volant. Both groups were successful until the present day, and strangely for plant evolution, both groups started at the same and in a relatively short time probably from their common ancestor *Perneria*.

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Seymourina niederhauseni, a new conifer from the Carboniferous-Permian (Kasimovian/Gzhelian) Niederhausen Flora (Rheinland-Pfalz, Germany)

by Thomas Perner and Michael Wachtler

Division: Coniferophyta
Order: Coniferales (TAYLOR, 1981)
Family: Walchiaceae (BRONGNIART, 1828)

Seymourina gen. nov. (PERNER & WACHTLER, 2013)

Diagnosis

Conifer with symmetrical branching-system bearing slightly incurved needles. Extraordinary long female cones with seeds fixed on the upper part of the scale. Protection leaves on the seed scales occurring.

Etymology

Honouring Kevin Seymour, zoologist at the Royal Ontario Museum, Toronto.

Seymourina niederhauseni sp. nov. (PERNER & WACHTLER, 2013)

Holotype

PER 163

Paratype

PER 138 (branchlet), PER 168 (ovuliferous cone), PER 24 (Seed scale) PER 49 (Ovule)

Material

PER 14, 21, 28, 36, 65, 70, 86, 94, 127, 144, 150, 155, 163, 271, 279.

Etymology

After the locality of Niederhausen (Landkreis Bad Kreuznach) in the German Rheinland-Pfalz, where this fossil conifer was recognised for the first time.

Locality

Niederhausen, Rheinland-Pfalz, Germany

Type horizon and age

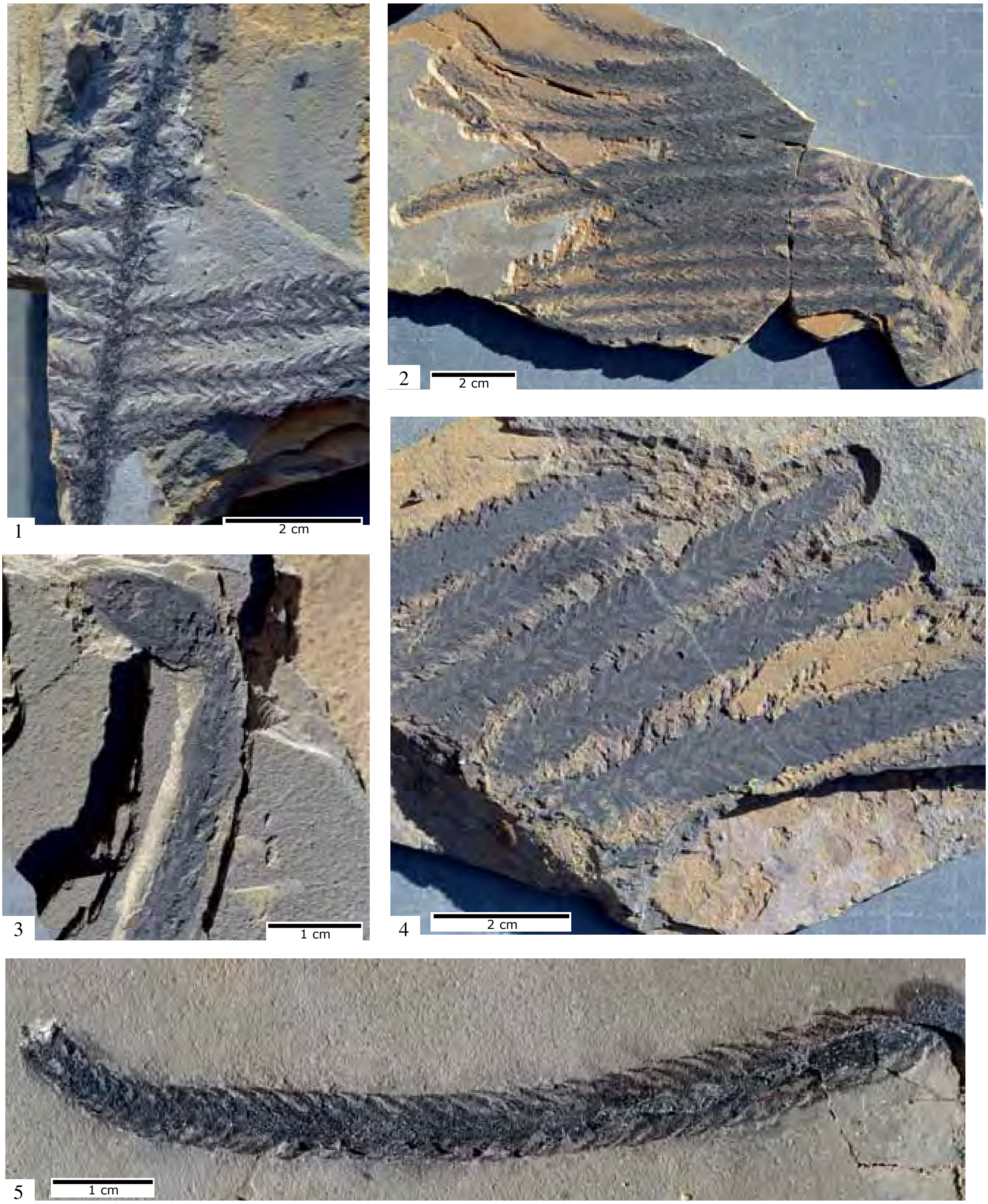
Upper Lauterecken-Lower Meisenheim-Formation, latest Kasimovian-Gzhelian, Regional stage Western Europe: Stephan B-C.

Diagnosis

Branches slender, in a flat horizontal plane, and emerging in a regular and precise pattern from the axis. Leaves narrowly and only slightly incurved. Female cones extraordinary long holding in the axils of the bracts trilobed seed-scales. Seeds on the two outer scales fixed on the upper part. Fertile scales covered with tapered protection leaves that can also overlap the seed scale.

Description

Branchlets: Slender and spreading in a flat plane. Symmetrical in appearance (PER 138).
Leaves: Juvenile needles sticking straight out or bent inward, not overlapping, around 2 mm long (PER 86). Adult leaves were transitional between scale-like and claw-like, tightly overlapping, and 5 mm long (PER 150).
Ovuliferous cones: Extraordinarily long (up to 25 cm, with a 3 cm width specimen BSGP), collocated terminally on the branchlets and equipped with a large amount of loosely arranged bract-seed-scales. Fertile scales in the axils of the bracts. Bracts were up to 2 cm long, apically rounded (PER 14), not entirely covering the fertile scale. Seed-scales were three-partite lobed, in one plane (PER 163, 24, 155), circularly rounded on the apex and more or less covered by lanceolote to narrow subtriangular sterile leaves with an acute apex. This interpreted protection foliage started from the base, sometimes as dwarfish foliage, others, but not many (probably 4 to 6) extend to the apex, sometimes also overlapping the sterile scales (PER 163). They have some papery characters and it cannot be excluded that they are relicts of winged scales. Stipes of the bract-seed scale are conspicuous, 2-3 mm wide, and also more than 10 mm long. Ovule/seeds on the upper side, inverted hanging, covering mainly the two outer lobes. Median lobe is mostly sterile.



1) PER 86. *Seymourina niederhauseni n. gen. sp. n.* Part of a twig.
2) PER 138. *Seymourina niederhauseni n. gen. sp. n.* Paratype. Juvenile branch.
3) PER 36. *Seymourina niederhauseni n. gen. sp. n.* Shoot with probably young male cone.
4) PER 150. *Seymourina niederhauseni n. gen. sp. n.* Adult twig.
5) PER 127. *Seymourina niederhauseni n. gen. sp. n.* Single branchlet.

6) PER 65. *Seymourina niederhauseni n. gen. sp. n.* Juvenile female cone.
7) PER 65. *Seymourina niederhauseni n. gen. sp. n.* Detail of the young cone.
8) PER 70. *Seymourina niederhauseni n. gen. sp. n.* Detail of a not fully grown female cone.
9) PER 70. *Seymourina niederhauseni n. gen. sp. n.* Female cone.

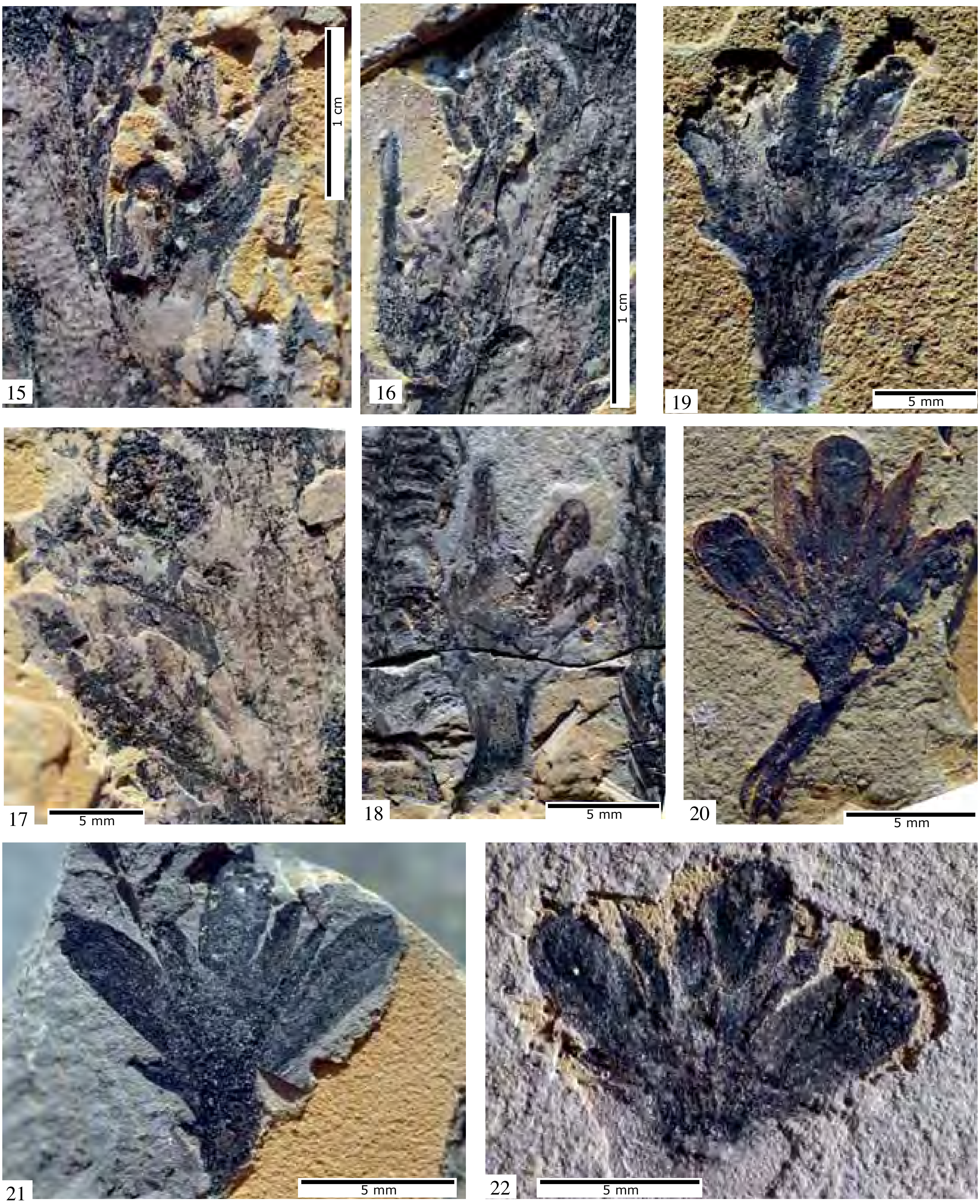
10) *Seymourina niederhauseni n. gen. sp. n.* Complete female cone. Note the long slender size of the cone. Courtesy Bayrische Staatssammlung für Paläontologie und Geologie.

11) *Seymourina niederhauseni n. gen. sp. n.* Detail of a bract. Courtesy BSPG.

12) PER 168. *Seymourina niederhauseni n. gen. sp. n.* Paratype. Fully grown female cone.

13) PER 168. *Seymourina niederhauseni n. gen. sp. n.* Detail of a seed scale and bract.

14) PER 144. *Seymourina niederhauseni n. gen. sp. n.* Old dissolved female cone.



15-17) PER 168. *Seymourina niederhauseni n. gen. sp. n.* Paratype. Detail of bracts, seeds and scales from the female cone.
18) PER 14. *Seymourina niederhauseni n. gen. sp. n.* Well-evidenced bract and scale.
19) PER 94. *Seymourina niederhauseni n. gen. sp. n.* Seed scale exterior side.
20) PER 163. *Seymourina niederhauseni n. gen. sp. n.* Designed Holotype. Single mainly complete seed scale.
21) PER 24B. *Seymourina niederhauseni n. gen. sp. n.* Paratype. Complete seed scale with sterile encasing leaves.
22) PER 155. *Seymourina niederhauseni n. gen. sp. n.* Seed scale, exterior side.

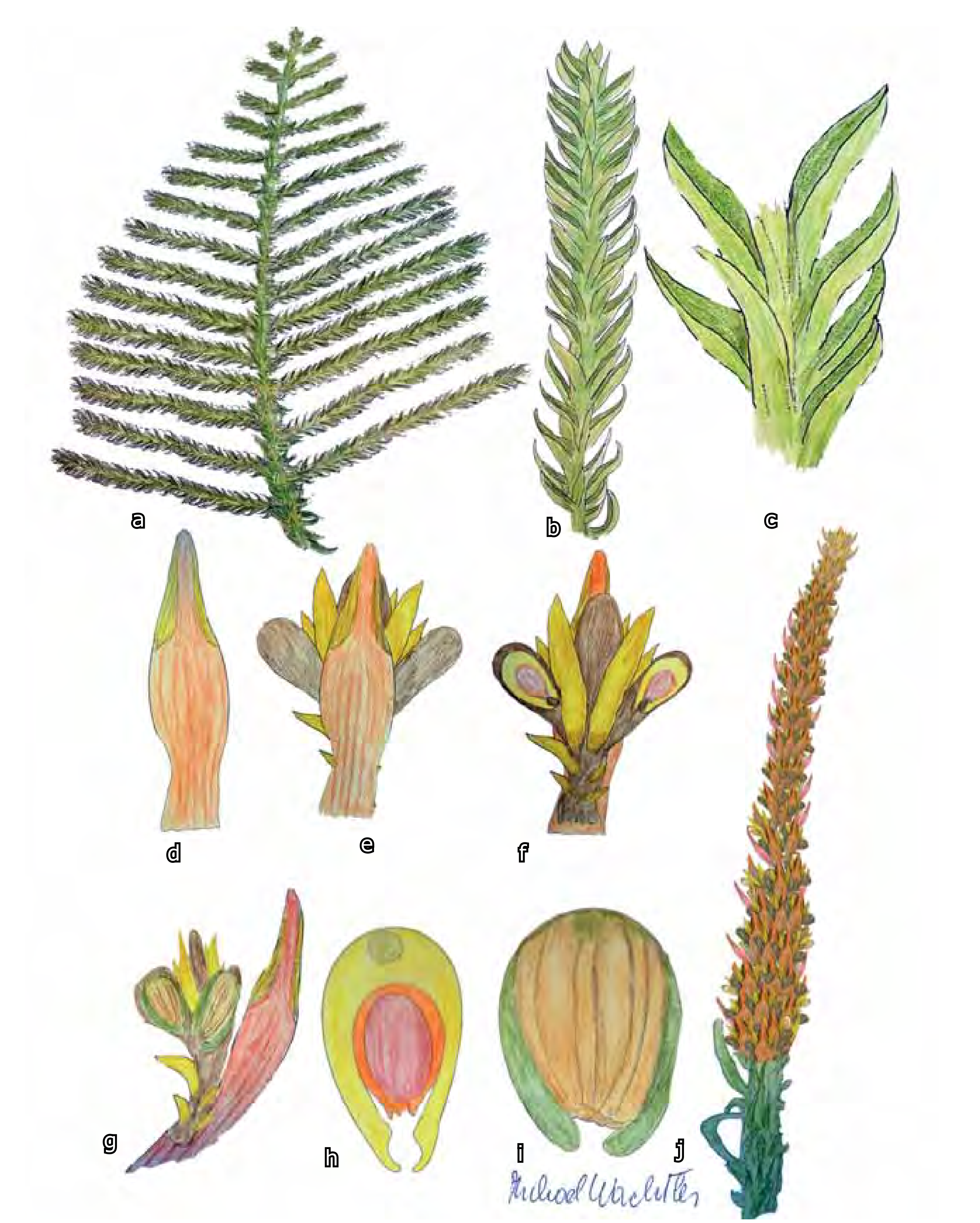
23) PER 49. *Seymourina niederhauseni n. gen. sp. n.* Paratype. Branchlet with ovule on the right side.

Juvenile ovules are 8 mm long, and 4-5 mm wide (PER 198, 183) with a characteristic acuminate-curved micropyle opening on the lower side. Mature seeds can reach a considerable size, sometimes up to 15 mm long and 8 mm wide (PER 205, 204, 188). Seeds or nuts are egg-shaped.

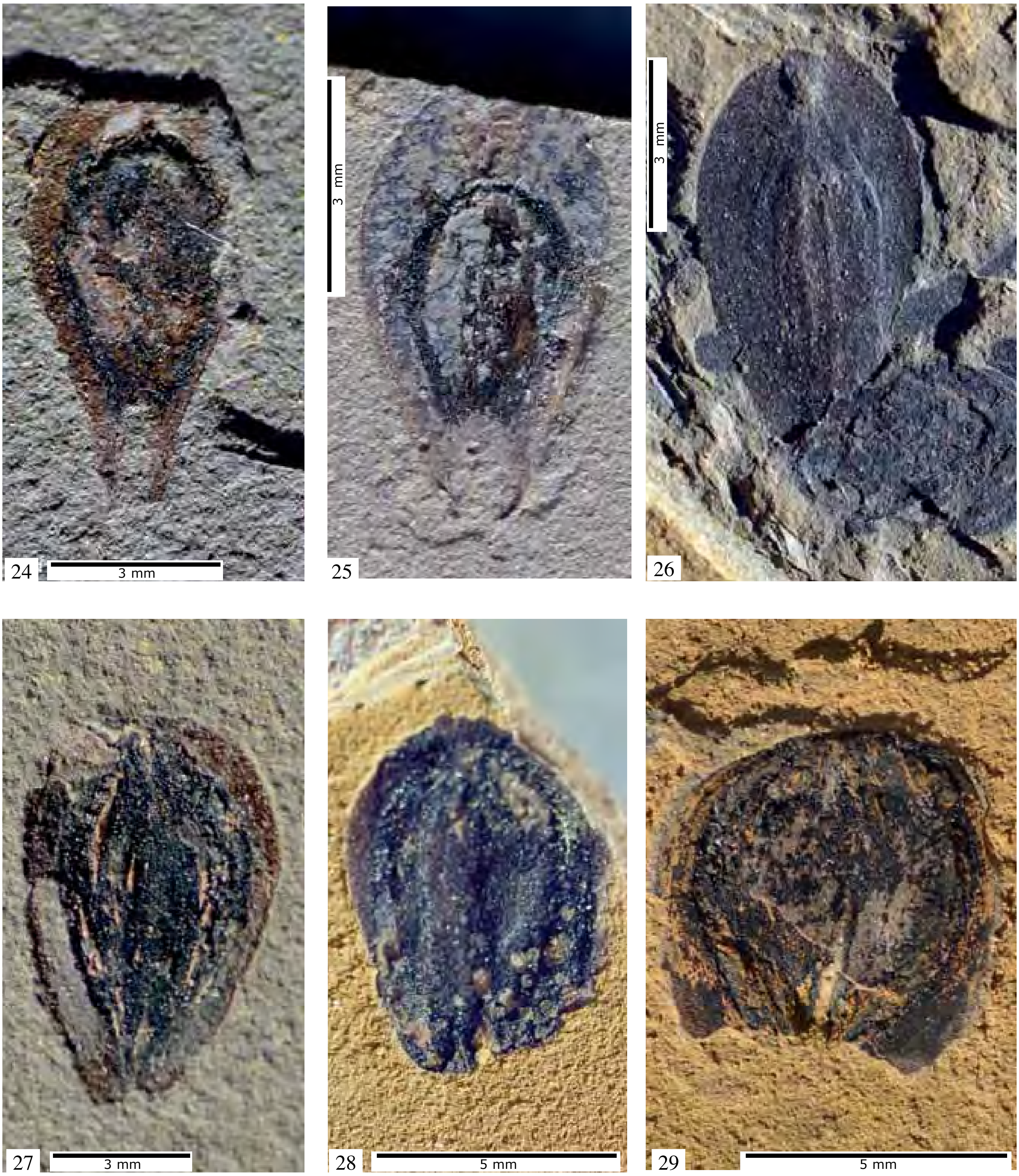
Discussion

From the three main conifer-families recognised in the Kasimovian-Gzhelian sediments of Niederhausen, *Seymourina* holds the closest affinities with the Walchiaceae. *Seymourina* holds fewer sterile protection leaves as the Lower Permian character conifer *Walchia piniformis*, which is in net contrast to the established dwarf-shoot theories (FLORIN, 1939-45). There is only one seed in *Walchia*, and a distinguishing feature is that it is collocated on a bilobed central fertile scale; in contrast, in *Seymourina*, the two seeds are fixed on the upper side of the lateral lobes. This is a net contradiction to the most accredited theory, which is that all conifers originate from an accumulation of sterile and fertile scales. This newly described conifer exhibits much more affinity with the Triassic Voltziaceae. Flattened megasporophylls with the seed-scales arranged on one level as a crown group of all conifers makes all dwarf-shoot considerations superfluous. Taken further into account must be a derivation from the still archaic four lobed seed scale *(Perneria*), by fusing or repressing the scale. In that way, *Seymourina* constitutes a possible evolutionary stage to modern Araucarias.

Seymourina niederhauseni differs from the conifer *Otovicia (hypnoides)*, which is found in the Lower Rotliegend Lauterecken-Oderheim-Formation (KERP ET AL., 1990), in that their sustaining bifid tapered bracts do not correspond to the rounded nature of Seymourina. This has many sterile leaves (12-18), and the crowded seed scale differs also, although the ovules and seeds are mainly equal. It can therefore be suggested with caution that between the two exist parental or evolutionary affinities.



Seymourina niederhauseni n. gen. sp. n. a) Part of a twig (PER 150), b) Isolated leaves, c) Detail of the needles. d - j) Detail of a female cone. d) Isolated bract (PER 14), e) Bract-seed-scale outer side, f) seed-scale with two lateral ovules. (PER 163) g) Bract seed-scale lateral side. h) Ovule with attachment groove to the scale (PER 49), i) Mature seed (PER 21, PER 28), j) Complete female cone (PER 168)



24) PER 279. *Seymourina niederhauseni n. gen. sp. n.* Ovule.
25) PER 196. *Seymourina niederhauseni n. gen. sp. n.* Ovule.
26) PER 49. *Seymourina niederhauseni n. gen. sp. n.* Ovule. Note the attachment grooves on the upper side.
27) PER 271. *Seymourina niederhauseni n. gen. sp. n.* Semi-mature ovule/seed.
28) PER 21. *Seymourina niederhauseni n. gen. sp. n.* Paratype. Dispersed seed.
29) PER 28. *Seymourina niederhauseni n. gen. sp. n.* Seed.

Other Permian ovuliferous cones or isolated bracts could have some parental relations, but they usually hold many more sterile leaves or supposed seeds (*Thuringiostrobus meyenii* (6 ovules, *Thuringiostrobus florinii,* 3 ovules) (KERP & CLEMENT-WESTERHOF, 1991).

The ovuliferous cone genera *Walchiostrobus* was established for Walchiaceaen-conifers. If all Walchias generate only one median ovule on a bilobated apex, no *Walchiostrobus*-cone could be accepted for *Seymourina.* The same is valid for the one seed-bearing *Ortiseia* from the Italian Dolomites, having in this case more parental affinities with Walchia.

Later conifers, especially the Voltziaceae (*Dolomitia, Voltzia*), also generate three-lobed seed scales (CLEMENT-WESTERHOF, J., 1987) and descending relationships are highly probable. Lower Permian *Dolomitia nonensis*, as well as Upper Perman *Dolomitia cittertae*, both from the Italian Dolomites, have mainly equal seed scales, but bear many more protection leaves.

Therefore, it will be reasonable to look at the necessity and reason for the sterile scale leaves. If on the Carboniferous-Permian border the most archaic conifers manifest only a few to none sterile leaves, then the dwarf-shoot-theory, as the base of all conifers, has to be cancelled. It could be that in the changing climate, the increase of accompanying foliage was much more of a protection against the aridity or due to their prickly spines to ward off animals or insects.

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