

FOSSIL FLORA FROM THE UPPER TRIASSIC GRABOWA FORMATION (UPPER SILESIA, SOUTHERN POLAND)

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Abstract: Upper Triassic fossil plants are well documented from the Keuper of Europe. Carnian and Rhaetian floras are rich in a variety of plant taxa, whereas in comparison, the Norian is limited to a few localities with poorly preserved fossil plant communities showing low diversification. The Norian Grabowa Formation in Zawiercie-Marciszów, Upper Silesia, southern Poland, contains fossils of arborescent gymnosperms, including petrified conifer trunks. In this study, we present a fossil plant assemblage, containing fragmented plant parts in multiple forms of preservation, i.e., permineralised trunks and rooting structures, stems compressions, dispersed cuticles, and megaspores. Analysis of the macromorphological characters proved the presence of gymnosperms, including the arborescent conifer *Agathoxylon* cf. *keuperianum*, known already from this locality from fragments of charcoallified wood. Sphenophytes are represented by disarticulated stems of *Equisetites* sp., and *Neocalamites* sp. The variation in plant fossils indicates the possibility of higher plant diversity. Analysis of cuticles, macerated from different plant-bearing lithologies, revealed a variety of conifer foliage, expressed as five *cuticulae dispersae* morphotypes (needle-leaf *Elatocladus*-type and scale-leaf *Pagio-Brachyphyllum*-like). Plant fossils at Zawiercie-Marciszów are preserved in calcareous mudstones and micritic limestone concretions, developed in a fluvial environment. The presence of sphenophyte stems (*Equisetites* and *Neocalamites*) indicates that local conditions were more humid and suitable for spore-producing plants, appearing in the mid-Norian tectonic-pluvial episode, recorded in the Grabowa Fm.

Key words: Macroflora, fossil plants, cuticle, megaspore, German Basin, Norian, Upper Silesia.

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INTRODUCTION

Upper Triassic fossil plants are well documented from the Keuper of Europe. Carnian and Rhaetian floras are rich in a variety of plant taxa. However, the most flourishing floras during Norian are known from eastern and central Asia and North America (Ash, 1989, 2005; Ash and Basinger, 1991; Dobruskina, 1994; Fraser *et al.*, 1996; Axsmith *et al.*, 1997, 2013; Volynets and Shorokhova, 2007; Sun *et al.*, 2010; Yukawa *et al.*, 2012, 2020; Sadler *et al.*, 2015; Wan *et al.*, 2017; Kustatscher *et al.*, 2018). In Europe, Norian floras are surprisingly rare (see Kustatscher *et al.*, 2017, 2018). A few localities in the Apennines, Carnian Alps and Dolomites, Italy, Seefeld in Austria and Norian/Rhaetian Seinstedt in Germany, have fossil assemblages low in plant diversity and with a high prevalence of gymnosperms, especially conifers (Dalla Vecchia, 2000, 2012; Barth and Kozur, 2011; Barth *et al.*, 2014; Kustatscher *et al.*, 2017, 2018). Recently documented outcrops of Norian strata in Upper Silesia, southern Poland, provide new palaeobotanical insights into the composition of the flora.

Dominated by fluvial, siliciclastic deposits, intercalated with evaporites and freshwater carbonates, terrigenous Keuper deposits of the German Basin are exposed in Upper Silesia in few outcrops: Krasiejów, Woźniki, Patoka, Poręba, Zawiercie-Marciszów, Lipie Śląskie-Lisowice and Kocury (Fig. 1A; e.g., Dzik *et al.*, 2008a, b; Niedźwiedzki and Sulej, 2008; Niedźwiedzki *et al.*, 2012, 2014; Sulej *et al.*, 2012; Pieńkowski *et al.*, 2014; Bodzioch, 2015; Zatoń *et al.*, 2015; Racki and Lucas, 2018; Bajdek *et al.*, 2019; Sulej and Niedźwiedzki, 2019; Szczygielski and Sulej, 2019). Famous for yielding the remains of vertebrate biotas, these localities also contain plant fossils, although preservation is often insufficient for a detailed taxonomic identification, e.g., the plant fossil assemblage from the well-known Krasiejów locality (Pacyna, 2019). There exist also exceptions, such as in Patoka (*Patokaea silesiaca* Pacyna *et al.*, 2017).

Fossils from Zawiercie-Marciszów record a relatively diverse, terrestrial ecosystem with preserved microbial structures, plant remains (miospores, Fijałkowska-Mader

et al., 2015; gymnosperm wood, Kubik *et al.*, 2015; Philippe *et al.*, 2015; plant detritus, Szulc *et al.*, 2015b), bivalves (Skawina and Dzik, 2011), ostracods and conchostracans (Niedźwiedzki and Budziszewska-Karwowska, 2018), as well as vertebrate remains, including a predatory archosaur (*Smok* sp.) and a giant herbivorous dicynodont (Budziszewska-Karwowska *et al.*, 2010; Niedźwiedzki and Budziszewska-Karwowska, 2018), sharks, actinopterygians, dipnoan fish and tetrapod trace fossils (Sadlok and Wawrzyniak, 2013; Sadlok, 2020, 2022; see Tabs 1, 2).

This is the first time that plant macrofossils other than charcoalfied wood, (Philippe *et al.*, 2015) are described from this site. In this study, we present different types of plant remains (petrified wood, *cuticulae dispersae*, megaspores), preserved in Norian sediments at the Zawiercie-Marciszów site providing clues about the prevailing environmental conditions during sedimentation.

GEOLOGICAL SETTING

General outline

An outcrop yielding Upper Triassic plant remains is situated in the western district of the town Zawiercie-Marciszów, located in Upper Silesia (Fig. 1B). Upper Silesia during the Late Triassic was the most southeasterly region of the

German Basin, also known as the Central European Basin (Fig. 1A). This subtropical, low-relief, continental basin extended from western France to eastern Poland (e.g., Beutler and Nitsch, 2005; Feist-Burkhardt *et al.*, 2008; Bachmann *et al.*, 2010). The successions of variegated mudstone and claystone, intercalated with sandstone and conglomerate and locally developed carbonates, are known as the Keuper Group. In Upper Silesia, these deposits are about 400 m thick, but increase in thickness toward the northern parts of the basin, up to 2,000 m (Deczkowski *et al.*, 1997; Jewuła *et al.*, 2019). The Upper Triassic succession in Upper Silesia is typical for the German Basin, with characteristic lithofacies changes matching the climatic conditions of the Western Tethys domain throughout the Carnian–Rhaetian (Feist-Burkhardt *et al.*, 2008). During the middle Norian, climate oscillations between humid and dry conditions (Jewuła *et al.*, 2019) are reflected in vertical facies variation. The Grabowa Fm is an equivalent for the Arnstadt Fm (Steinmergelkeuper) of the German lithological scheme (Szulc *et al.*, 2015a, b). The mudstone- evaporite succession is replaced by the marly mudstones and sandstones of the Patoka Mbr, which contains two bone-bearing levels, Krasiejów and Lisowice. In the upper part of the Grabowa Fm, dark grey mudstones and sandstones are accompanied by the micritic limestone and travertine with gypsum-rich and cherty horizons of the Woźniki Member (Szulc *et al.*, 2015a, b).

Table 1

List of animal taxa described or mentioned from the Zawiercie-Marciszów site and adjacent areas.

Taxa	Group	Fossil type	References
Vertebrates			
?Archosauromorpha indet.	Sauropsida	toothmarks/bitemarks	Budziszewska <i>et al.</i> , 2010; Sadlok, 2022
?Archosauromorpha indet.	Sauropsida	footprints	Sadlok and Wawrzyniak, 2013
Archosauria indet.	Sauropsida	footprints	Sadlok and Wawrzyniak, 2013
Archosauria indet.	Sauropsida	bones	Malinowska, 2015, after Piechowski
Coelacanthiformes indet.	Osteichthyes	bones	Malinowska, 2015, after Piechowski
Dicynodontia indet.	Synapsida	bones	Budziszewska <i>et al.</i> , 2010
?Dicynodontia indet.	Synapsida	footprints	Sadlok and Wawrzyniak, 2013
Dipnoi indet.	Osteichthyes	teeth	Malinowska, 2015, after Piechowski
<i>Smok</i> sp.	Sauropsida	bones, teeth	Niedźwiedzki and Budziszewska-Karwowska, 2018
Tetrapoda indet.	Tetrapoda	footprints	Sadlok and Wawrzyniak, 2013
Invertebrates			
Conchostraca indet.	Crustacea	imprints and casts of shell surface	Niedźwiedzki and Budziszewska-Karwowska, 2018
Ostracoda indet.	Crustacea	imprints and casts of shell surface	Niedźwiedzki and Budziszewska-Karwowska, 2018
<i>Tihkia silesiaca</i>	Bivalvia	imprints and casts of shell surface	Szulc <i>et al.</i> , 2015a; Niedźwiedzki and Budziszewska-Karwowska, 2018
<i>Unionites posterus</i>	Bivalvia	imprints and casts of shell surface	Dadlez and Kopik, 1968; Grodzicka-Szymanko, 1971
Crustaceae indet.	Crustacea	burrows	Sadlok, 2021

Table 2

List of micro- and macrofloral taxa described or mentioned from the Zawiercie-Marciszów site.

Taxa	Group	References
Microflora		
<i>Alisporites</i> sp., <i>Brachysaccus neomundanus</i> , <i>Brachysaccus</i> sp., <i>Cedripites</i> sp., <i>Classopollis meyeriana</i> , <i>Classopollis simplex</i> , <i>Classopollis torosa</i> , <i>Duplicisporites granulatus</i> , <i>Enzonalasporites</i> sp., <i>Falcisporites</i> sp., <i>Geopollis zwolinskae</i> , <i>Granuloperculatipollis rudis</i> , <i>Labiisporites</i> sp., <i>Lunatisporites</i> sp., <i>Minutosaccus</i> sp., <i>Ovalipollis</i> sp., <i>Parillinites</i> sp., aff. <i>Pinuspollenites</i> sp., <i>Platysaccus</i> sp., <i>Protodiploxypinus</i> sp., <i>Pseudoenzonalasporites summus</i> , <i>Vallasporites ignacii</i>	Coniferales	Fijałkowska-Mader <i>et al.</i> , 2015
<i>Cycadopites</i> sp., <i>Monosulcites</i> sp.	Cycadales, Bennettitales, Pteridosperm	Fijałkowska-Mader <i>et al.</i> , 2015
<i>Baculatisporites</i> sp., <i>Carnisporites</i> sp., aff. <i>Conosmundasporites</i> sp., <i>Cyclotriletes</i> sp., <i>Corrugatisporites</i> sp., <i>Deltoidospora</i> sp., <i>Polycingulatisporites</i> sp., <i>Todisporites</i> sp., <i>Verrucosisporites</i> sp.	Pteridopsida	Fijałkowska-Mader <i>et al.</i> , 2015
<i>Anapiculatisporites</i> sp., <i>Microreticulatisporites</i> sp., <i>Neoraistrickia</i> sp., <i>Nevesisporites</i> sp., <i>Reticulatisporites</i> sp.	Lycopodiales	Fijałkowska-Mader <i>et al.</i> , 2015
<i>Densoisporites</i> sp. reworked, <i>Uvaesporites</i> sp.	Lycopodiales: Pleuromeiaceae	Fijałkowska-Mader <i>et al.</i> , 2015
<i>Densosporites</i> sp.	Lycopodiales: Selaginellaceae	Fijałkowska-Mader <i>et al.</i> , 2015
<i>Calamospora</i> sp.	Equisetales	Fijałkowska-Mader <i>et al.</i> , 2015
<i>Porcellispora</i> sp., <i>Taurocusporites</i> sp.	Bryophyta	Fijałkowska-Mader <i>et al.</i> , 2015
<i>Schizosporis</i> sp.	Algae	Fijałkowska-Mader <i>et al.</i> , 2015
<i>Foveolatitriletes</i> sp.	incerte sedis	Fijałkowska-Mader <i>et al.</i> , 2015
fungal spores	Fungi	Fijałkowska-Mader <i>et al.</i> , 2015
Macroremains		
<i>Agathoxylon keuperianum</i> , charcoal and fossil wood	Coniferales	Philippe <i>et al.</i> , 2015
charcoal	Gymnosperm	Kubik <i>et al.</i> , 2014

Lithology and biostratigraphy of Zawiercie-Marciszów

The plant remains were found in a pile of sediment left after the creation of a niche for a new city dump. This makes all the findings presented here *ex situ*. Before the hole was filled with waste, the exposed natural section was investigated by Joachim Szulc in 2000 (Szulc *et al.*, 2006; Fig. 2A). In 2012, a drillhole, completed on Kobylarz Hill near the city dump, allowed extension of the previous profile (Fig. 2B). The core from the Kobylarz 1 borehole is 55 m long. It consists of red and grey mudstone, representing middle Keuper strata, with different levels of debris flows, pedogenic levels, and intercalations of carbonate nodules, bivalve-oncoidal calcareous conglomerates and plant debris. It is essential for the correlation of these middle Keuper sediments that the base of the Woźniki limestone is above the top of the core and was poorly exposed in the nearby road cut (Szulc *et al.*, 2015a; Fig. 2B).

Sediments exposed at Zawiercie-Marciszów represent fluvial facies, developed as grey fine-grained clastics, red mudstone, and siltstone with sporadic pedogenic nodules.

At the site, conglomerates contain the remains of microbial structures (oncoids and stromatolites), plant fragments including charcoalfied wood, freshwater bivalves, and vertebrate remains, such as bones, teeth, and tetrapod traces (Tab. 1). The fossilised remains are often associated with pyrite concentrations. Some carbonate concretions contain plant remains (Fig. 3). Preliminary research by Sadlok and Wawrzyniak (2013) revealed a miospore assemblage with well-known palynomorphotypes from the Polish Upper Triassic (Orłowska-Zwolińska, 1985; Fijałkowska-Mader *et al.*, 2015), e.g., *Brachysaccus neomundanus*, *Classopollis meyeriana*, *Enzonalasporites* sp., *Ovalipollis ovalis*. This confirms the findings of Szulc *et al.* (2006) that the clastic and carbonate deposits in the Zawiercie-Marciszów area are of middle Norian age, on the basis of the assignment of them to the *Classopollis meyeriana* IVb Subzone (Fijałkowska-Mader *et al.*, 2015; Tab. 1).

In the section presented by Szulc *et al.* (2006, 2015a, b; Fig. 2), two conglomerate horizons are marked that could have been the primary source of the fossil material found on the pile. In the lower part of the section, playa deposits with

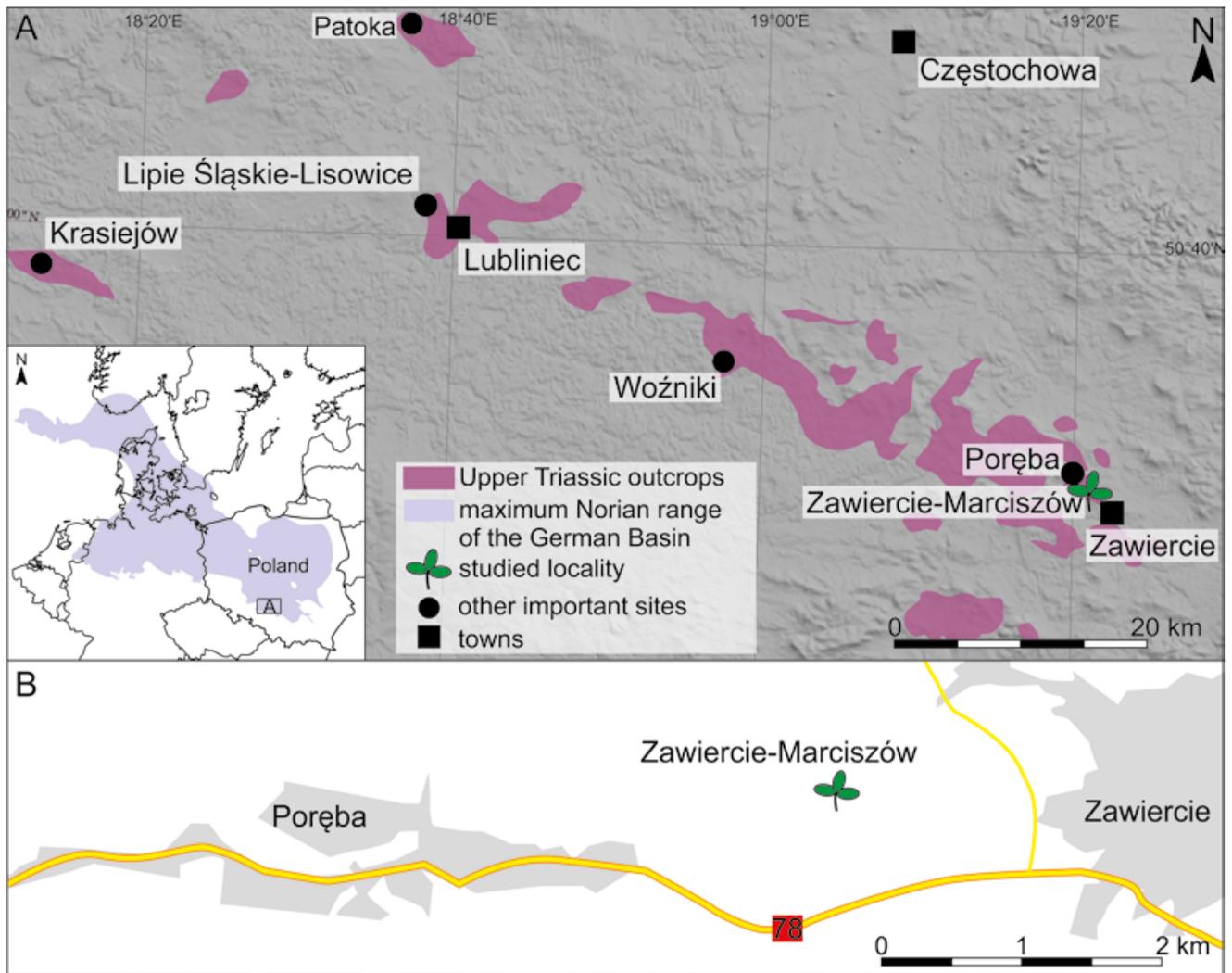


Fig. 1. Locality of the study area. **A.** Maximum extent of the German Basin during the Norian with the Upper Silesia Upper Triassic fossil sites (rectangular; after Feist-Burkhardt *et al.*, 2008; Fijałkowska-Mader, 2015; Szulc *et al.*, 2015a; shaded relief from SRTM). **B.** Zawiercie-Marciszów fossil site.

evaporites are visible. The upper part of the section comprises mudstones and siltstones with stromatolites and conglomerates. The bone-bearing bed is considered to be equivalent in age to the fossil-bearing horizons, exposed at the Lipie Śląskie-Lisowice clay-pit (“Lisowice bone-bearing level”; Szulc and Racki, 2015; Szulc *et al.*, 2015a, b; Racki, 2017).

PLANT-BEARING LITHOLOGIES

The plant fossils were found in five different types of sediment left after the preparation of the city waste dump:

Nodular concretions of micritic limestone (lithological type I; Fig. 3A–C) contain scarce plant remains, i.e., roots (Fig. 11A–E). Bioturbation (Fig. 3B), fragments of ostracod shells (Fig. 3C) and rare plant cuticle fragments are visible in thin sections.

Calcareous concretions, covered with microbial structures (lithological type II; Fig. 3D–G), relatively common on site, contain compressed plant macro remains in a wide range of sizes (stems up to 10 cm long and 5 cm wide).

arranged horizontally (Fig. 3E, F). Plant tissue is coalified, less often charcoalfied, and sometimes the epidermal pattern is recognisable (Fig. 4B). Dispersed cuticles are abundant, as well as palynoflora. The micritic limestone matrix in thin sections show bioturbation (Fig. 3J). Present also are crumbled, smooth-shelled ostracods (Fig. 3J) and fragments of phosphorous fossils, probably fish elements.

Graded conglomerate with a calcareous mudstone matrix, containing irregularly arranged plant remains (lithological type III; Fig. 3H, I). Thin sections show microfacies of the conglomerate matrix (Fig. 3I). Macrofossils are diversified in size (stems, isolated twigs and leaves, dispersed cuticles, miospores). Apart from the plants, bone fragments, fish elements, cuticles of arthropods, fragmented ostracods and bivalve shells were found in mudstone (Fig. 3I).

Calcareous, light-grey coloured mudstone, densely packed with accumulated plant detritus (lithological type IV; Fig. 3J–L), is another type of plant preservation. A major component of the accumulation is plant cuticles (Fig. 3L), coalified to different degrees, with smaller amounts of charcoalfied woody particles, and rare megaspores.

The least common form of plant fossils, found in Zawiercie-Marciszów, are isolated, three-dimensionally preserved stems with a hollow central pith (lithological type V; Fig. 3M–O), filled with neomorphized micritic limestone, containing detrital quartz grains, pyrite and fragments of smooth-shelled ostracods (Fig. 3N, P). The remaining tissues are partially petrified and partially charcoaled (Fig. 3F).

MATERIALS AND METHODS

The most informative specimens are presented in Figures 3–15. The specimens were collected by the first author during the excavations, organised by the Faculty of Natural Sciences University of Silesia in Katowice (UŚ) and the Museum of Earth Sciences UŚ from 2009–2019.

Thin sections were prepared at the Institute of Earth Sciences UŚ. Fragments of petrified woody stems were embedded in EpoFix epoxy resin and sectioned, using a Logitech GTS 1 Thin Section Cut-Off, and Trim Saw with a diamond blade. Sections of thickness ca. 2 mm were ground and polished with the Logitech PM5 precision lapping and polishing systems, using abrasive diamond powder of 3, 1, 0.25 μm and 0.04 μm silicon powder.

Bulk maceration was conducted, following techniques described in Reymanówna (1960), Batten (1999), Pearson and Scott (1999), Wellman and Axe (1999), Worobiec (2003) and Florjan and Worobiec (2016). Samples, ca. 1 x 1 cm in size, were washed and left to dry naturally, later inserted in a glass beaker and stored under the fume hood. The sample was covered with 10% HCl. After the reaction stopped and the residuum sank, the acid was gently decanted, and the step was repeated. Next, 38% HCl acid was added, and after the response stopped and the remaining residuum sank, the acid was gently decanted. Leftovers were neutralised by adding distilled water and decanting after the residuum sank. This step was repeated five to six times, until a neutral pH was achieved. The neutralised residuum was transferred to polypropylene containers. 20 ml of 40% HF acid was added. After 24 hours, samples were neutralised with distilled water and decanted. This step was repeated until the residuum was neutral. Selected and investigated cuticles were mounted on glass slides in distilled water, and afterwards placed in a glass container, filled with pure glycerine with a few drops of thymol to prevent fungal growth. Cuticles retrieved in bulk maceration were grouped into morphotypes, on the basis of a combination of characters, considered to have taxonomical importance among the gymnosperms (e.g., Harris, 1935; Oldham, 1976; Kerp, 1990; Karasev, 2013), namely differentiation of adaxial and abaxial leaf side, presence, orientation, arrangement and density of stomata, shape and structure of stomata complex, shape and arrangement of other epidermal cells, ornamentation of epidermal cells and the presence of trichomes. The types are assigned the Latin alphabet letters A to E. The term cuticle relates here to the extracellular layer, which overlies the plant epidermis and other cutinised plant parts (i.e., cutinised megaspore membrane). Cuticles were grouped into morphotypes and identified at the lowest taxonomical level. The exact number of cuticles in each morphotype retrieved with bulk-maceration

is only estimated when the amount of cuticle fragments, often minute, is of high volume. Therefore, unless indicated otherwise, categorized cuticles are kept collectively in 20 ml glass containers.

Hand specimens were photographed, using digital Canon cameras with objectives: Canon EFS 18-55 and Canon Macro Lens EF 100 mm 1: 2.8 USM for macrophotography. Fine details of hand specimens (ca. < 5 mm), thin sections, and megaspores were photographed using a Leica Wild M10 compound microscope, equipped with a NikCam Pro

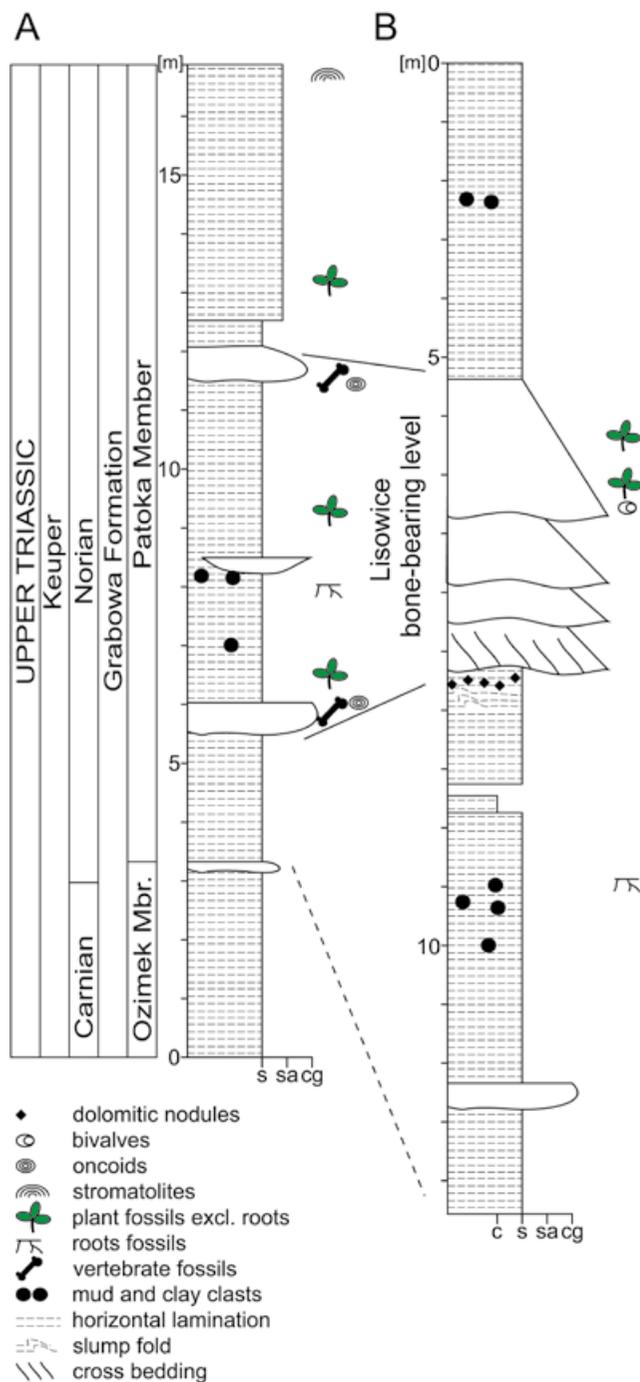


Fig. 2. Lithology of the Zawiercie-Marciszów site. **A.** Lithological column of the strata exposed in the niche of the new city dump (after Szulc *et al.*, 2006; 2015a). **B.** Kobylarz 1 borehole log (after Szulc *et al.*, 2015a). Abbreviations: c – claystone, s – siltstone, sa – sandstone, cg – conglomerate.

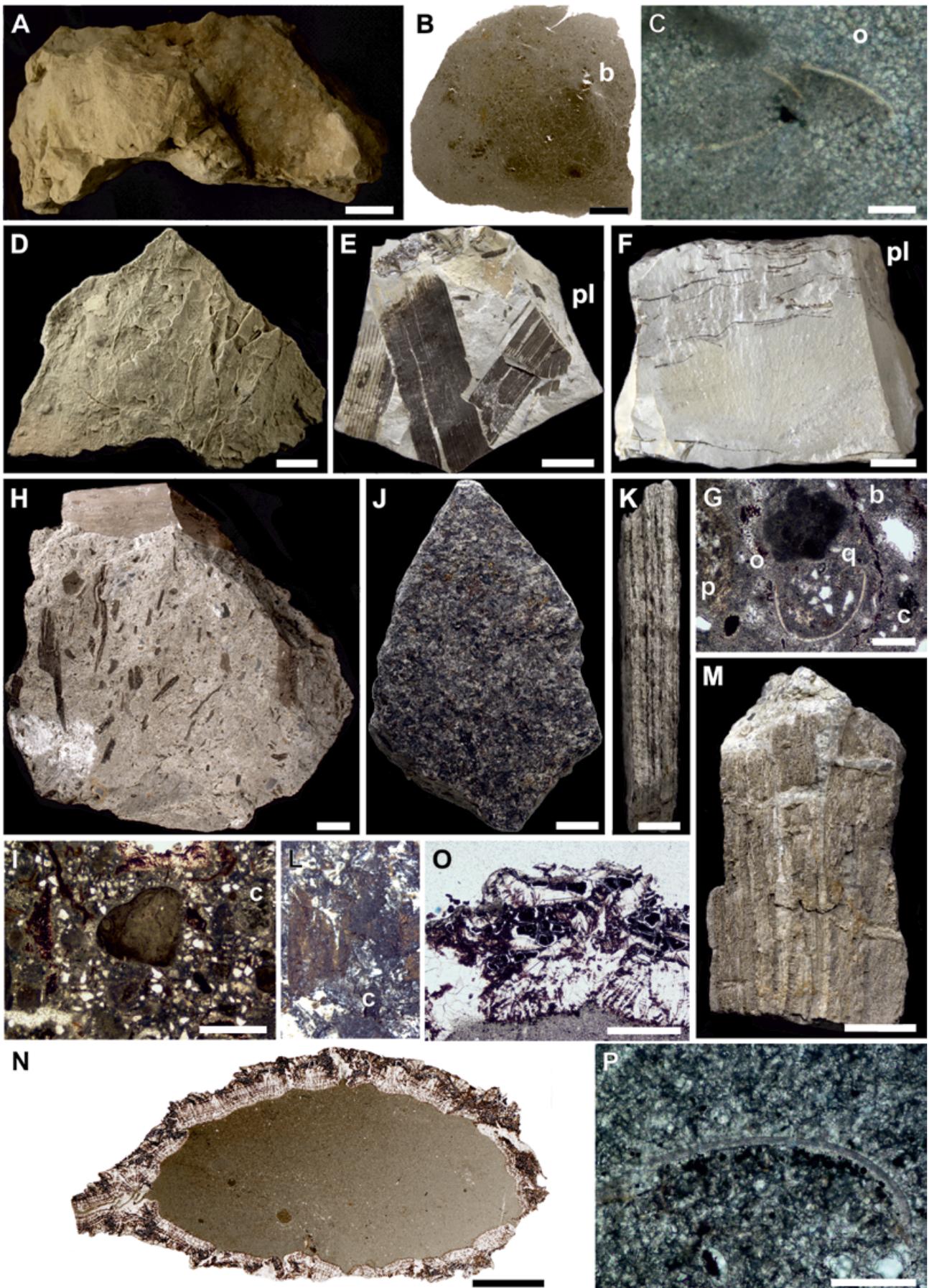


Fig. 3. Different lithology of fossil bearing sediments from the Upper Triassic of Zawiercie-Marciszów, southern Poland. **A–C.** Micritic limestone concretion with rare macrofossils, specimen ZK1; **A** – outer surface of the concretions lacking microbial structures; **B** – thin section of the concretion from **A**, showing bioturbations; **C** – fragments of ostracods (Crustaceae) shells. **D–G.** Micritic limestone

1 camera and NIS D Elements software. Objects were illuminated from different angles with a gooseneck dual illuminator. Cuticles were photographed, using a Nikon Eclipse 50i transmitted light microscope with an integrated DS-Fi2 digital camera and NIS D Elements software. Photographs were edited in Adobe Photoshop software.

Specimens were analysed and photographed under an environmental scanning electron microscope (ESEM) Philips XL 30 electron microscope with Element Energy Dispersive Spectroscopy (EDS) Sapphire EDAX at the Institute of Earth Sciences, Faculty of Natural Sciences (UŚ) in Sosnowiec. Low vacuum settings of the SEMs were used. Before being inserted into the microscope chamber, the specimens were coated with gold. Analysis was done in secondary electron (SE) and backscattered electron (BSE) modes with a large field detector (LFD) on a CENTaurus Detector on a Philips XL 30 SEM.

Specimens are stored at the Museum of Earth Sciences (UŚ) in Sosnowiec, collection acronym WNoZ_S_7. For the research purpose, working numbers were added starting with the prefix "Z"; Z01–Z25, ZK1–ZK2, ZST1–ZST4 (macrofossils), ZCD_A–ZCD_E (*cuticulae dispersae*), ZM01 (megaspore).

SYSTEMATIC PALAEOLOGY

Macrofossils

Class Equisetopsida Agardh, 1825

Order Equisetales de Candolle ex von Berchtold
& Presl, 1820

Family Equisetaceae Michaux ex de Candolle, 1804

Remarks: Specimens show the typical morphology for sphenophyte stems, that is, a characteristically grooved surface and straight, linear shape and central cavity (cf. Grauvogel-Stamm, 1978; Kelber and Hansch, 1995; Pott *et al.*, 2008; Jarzynka and Pacyna, 2015). However, specimens lack features that would allow more precise taxonomic determination. From the Early Mesozoic, the most common sphenophyta morphogenera are *Equisetites*, *Neocalamites*, *Schizoneura* and *Phyllotea*. The most reliable feature that distinguishes forms is the shape of the leaves. *Equisetites* have leaves fused for most of their length and pressed to the stem (i.e., Schweitzer *et al.*, 1997; Pott *et al.*, 2008). *Neocalamites* leaves are longer than the internodes and free for their entire length or fused only close to the base

(Bomfleur *et al.*, 2013), *Schizoneura* leaves are also longer than the internodes, but they are usually fused into two to four groups (Bomfleur *et al.*, 2013), and *Phyllotea* possess leaves shorter than the internode, fused closer to the base and diverging from the stem in the upper parts (Harris, 1931; Anderson and Anderson, 2018;). Specimens from Zawiercie-Marciszów are mostly preserved as decorticated stems, without scars or leaf traces. Described axes are, however, too wide for most *Schizoneura* (i.e., Harris, 1931; Grauvogel-Stamm, 1978; Kelber, 1983); the exception is *Schizoneura africana* Feistmantel, 1889 emend Bomfleur (Bomfleur *et al.*, 2013). Identification of articulated sphenophyte stem is confined to speculation.

Genus *Equisetites* Sternberg, 1833

Type species: *Equisetites muensterii* Sternberg, 1833; Abtswind, Bavaria, Germany, Carnian.

Equisetites sp.

Fig. 4

Material: Z01–14, 16–20, 22, 23, 67; compressed stems with coalified tissues.

Description: Leafless stems, representing incomplete internodes (Fig. 4A). Nodes are not preserved as well as nodal diaphragms. Stems are straight, no tapering is visible that would indicate swelling at the nodes. Stems are 3.0–52.9 mm wide in compression and 5.1–130.0 mm long. Surface is covered with longitudinal grooves spaced every 0.9–1.5 mm. Cell patterns on the surface of specimen number stem are isometric to elongated longitudinally, oblique and arranged in rows (Fig. 4B). Exterior cortex surface is smooth, the underlying cortex layer ridged; ridges every 2.1 mm (Fig. 4G). Delicate striae are discernible on ridges, alternating grooves surface. At the nodes, vascular strands of the following internodes are mostly alternating (Fig. 4C–E), less often opposite (Fig. 4F).

Remarks: No leaves or leaf-sheaths were found that could be associated with the specimens, which would provide a particular distinction between the main Triassic sphenophyta morphogenera. Most specimens represent a decorticated internal cylinder, covered with longitudinal grooves corresponding to vascular strands (Fig. 4C, G, H). Fragment of the surface shows a cellular pattern visible on the widest stem, probably representing an endodermis (Fig. 4B).

concretion with plant remains; D – outer surface of the concretion covered with microbial structures, specimen ZC2; E – inside of the concretion with compressed sphenophyta stems, specimen Z22; F – side view of the specimen from E, with compressed sphenophyta stems oriented horizontally; G – thin section showing bioturbations, fragments of ostracods (Crustacea) shells, dispersed cuticle fragments and quartz grains, specimen ZC2. **H, I.** Calcareous mudstone containing disoriented plant remains; H – fragments of light-grey mudstone yielding plant remains of different sizes, including fragments of gymnosperms stems, specimen ZST5; I – thin section showing fragmented cuticles, animal remains (probable fish element), detrital quartz grains, specimen ZC2. **J–L.** Piece of mudstone densely packed with plant detritus; J – surface of a lamina covered with plant remains of similar size; K – side view of mudstone with dark lamina of accumulated plant remains; L – light brown leaf cuticle fragment. **M–O.** Three-dimensionally preserved stems with inner-cavities filled with sediment, specimen ZS1; M – outer surface of a stem; N – cross thin section of a stem showing stem pith filled with neomorphized micritic limestone; O – details of calcified plant tissue with fragments of charcoal; P – fragment of smooth-shell ostracoda (Crustacea). Abbreviations: b – bioturbations, ch – charcoal, c – cuticle, f – fish scale, o – ostracoda, pl – plant, q – quartz, r – ribs. Scale bars: A, D–F, H, J, K, M – 10 mm; B, N – 5 mm; O – 500 µm; G – 200 µm; C, I, L, P – 100 µm.

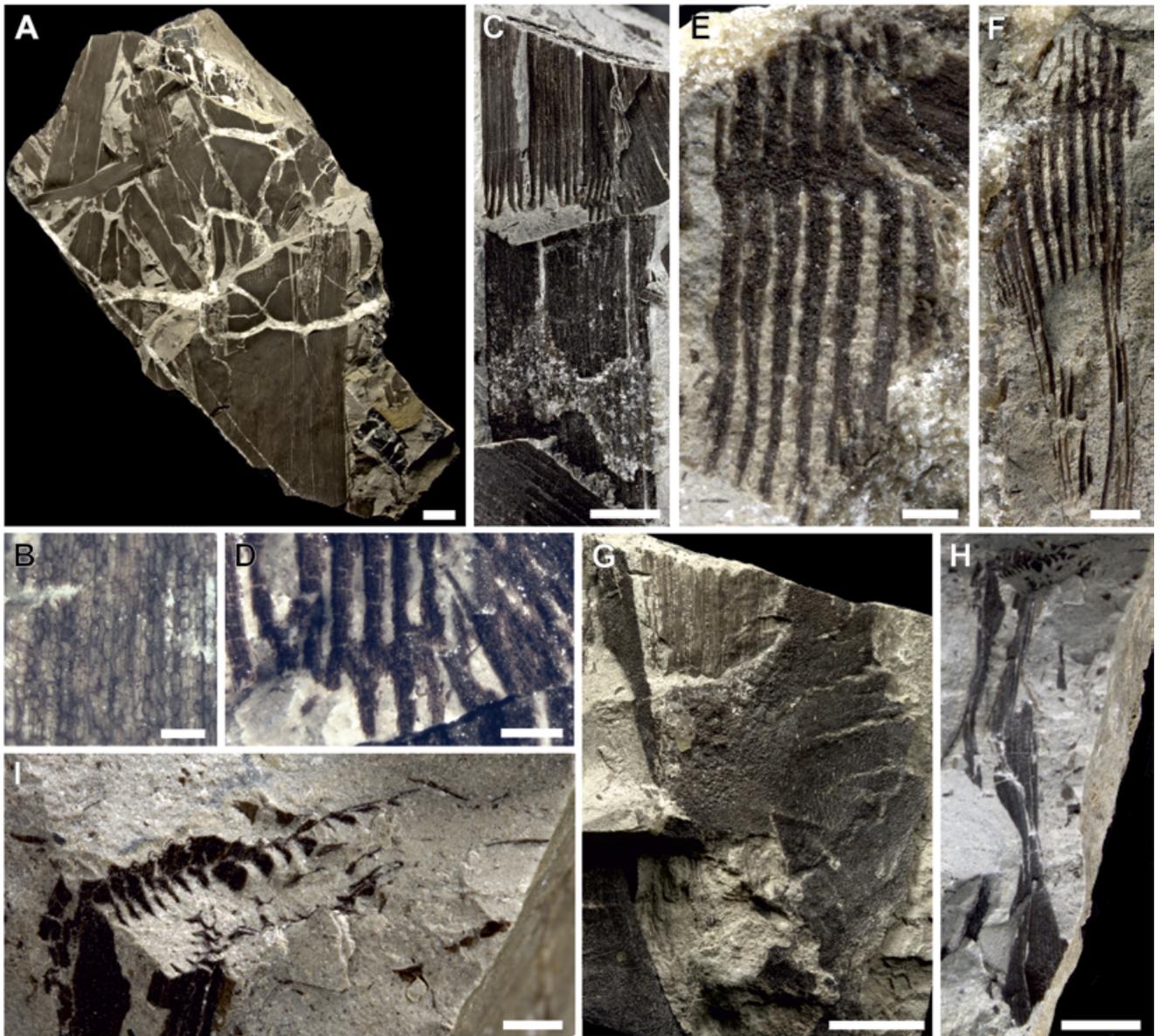


Fig. 4. Sphenophyta from the Upper Triassic of Zawiercie-Marciszów, southern Poland. **A–F.** *Equisetites* sp.; **A** – compressed stems of sphenophytes, specimen Z01A; **B** – epidermal cell pattern of the outer layer of stem from **A**; **C** – compressed stem of *Equisetites* sp., with preserved internodal regions and an internode between them, specimen Z22; **D** – details of the node from **C**; **E** – internodal region separated with the node, specimen Z07; **F** – stem with preserved internodal and nodal regions, specimen Z02. **G.** Stem with preserved outer smooth layer and exposed underlying ridged surface, specimen Z02. **H.** Internodal region of compressed stem, specimen Z05. **I.** Transversal view of the specimen from **H**, showing stem filled with sediment. Abbreviations: ec – external cortex, n – node, rg – ridge, v – vascular strand. Scale bars: **A**, **G**, **H** – 10 mm; **B**, **C** – 5 mm; **D–F**, **I** – 2 mm.

No morphological differences between narrower and broader stems are distinguishable. Stems lack any branch scars or signs of lateral branching.

Genus *Neocalamites* Halle,
1908 emend. Bomfleur *et al.*, 2013

Type species: *Neocalamites lehmannianus* (Goepfert, 1846) Weber, 1968; Wilmsdorf, Landsberg, Silesia (today Gorzów Śląski, Poland), Rhaetian.

Neocalamites sp.
Fig. 5A–D

Material: Z24, Z25; stems fragments.

Description: Leafless stems, 35.6 and 36.3 mm wide, 107.8 and 108.6 mm long, respectively. Stems representing straight internodal region, without tapering (Fig. 5A, C). Ridges covering outer surface spaced every 3.1–3.4 mm are alternated with flat grooves. Groove surface is marked with longitudinal striae 50.0 μm wide (Fig. 5B). Charcoalified cortical tissue with occasionally preserved longitudinally oriented tubular structures 10.0–12.0 μm wide (Fig. 5D).

Owing to the absence of leaves and leaf-sheaths associated with the stems, assigning specimens to either *Equisetites* or *Neocalamites* is difficult. Prominent ridges (“costae”; Fig. 5A, C), have been previously shown, i.e., *Neocalamites*

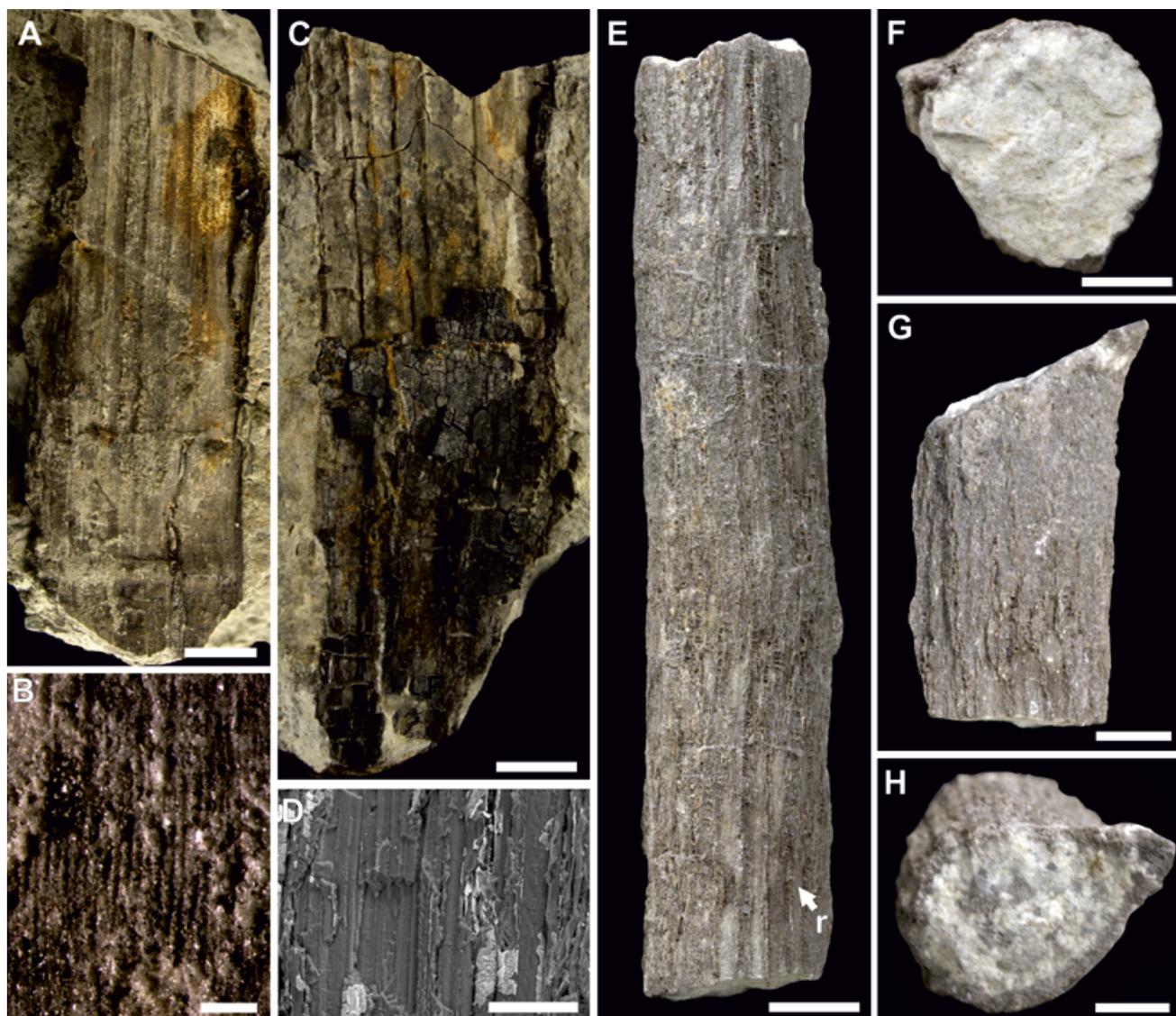


Fig. 5. Sphenophyta from the Upper Triassic of the Zawiercie-Marciszów, southern Poland. **A–D.** *Equisetites* sp. **B.** **E–H.** cf. *Neocalamites* sp.; **A** – impression of the sphenophyte stem with ridges and grooves well marked; specimen Z24; **B** – thin longitudinal striae on the ridged surface from **A**; **C** – impression of the sphenophyte stem with ridges and partially preserved charcoalified tissue; specimen Z25; **D** – SEM photo of charcoalified tissue from **C**; **E** – outer surface of the stem showing damaged tissue and ribs; specimens ZST2; **F** – cross view of the stem with pith, filled with micritic limestone; specimen ZST2; **G** – outer surface of a stem with less discernible ribs; specimen ZST3; **H** – cross view on the stem showing a pith filled with micritic limestone. Abbreviations: r – ribs. Scale bars: **A, C** – 10 mm; **E–H** – 5 mm; **B** – 200 μ m; **D** – 50 μ m.

merianii (Brongniart, 1828) Halle, 1908 and *N. suberosus* (Artabe and Zamuner, 1991) Bomfleur *et al.*, 2013. Characteristic longitudinal pattern on the outer surface is a result of stem desiccation and/or compaction (Bomfleur *et al.*, 2013; Kelber and Hansch, 1995; Kustatscher and Van Konijnenburg-van Cittert, 2008; Mazaheri-Johari *et al.*, 2021).

cf. *Neocalamites* sp.
Figs 3M–O, 5E–H

Material: ZST1–ZST3; three-dimensionally preserved stems with central piths, filled with sediment and charcoalified tissues.

Description: Stems are leafless, straight, no tapering or slight narrowing on one end. Incomplete internodes (Figs 3M, 5E, G); no nodes preserved. Stems range from round in transverse section (Fig. 7F, H) to fusiform, compressed (Fig. 3N). Round stems measure 12.5 mm in diameter and between 26.5 and 63.4 mm long, fusiform specimen is 36.0 x 15.4 mm wide and 73.5 mm long. Preserved internal cylinder shows degraded tissues (Fig. 3N, O). Layer of tissue remnants in round specimen is 0.5–1.0 mm wide (Fig. 5F, H), in fusiform specimen 0.53–3.5 mm (Fig. 3N, O). Ribs are discernible. Distance between ribs 1.5 mm in round specimen (Fig. 5E, G), 2.0 mm in fusiform specimen (Fig. 3M).

Remarks: Specimen ZST1 differ from ZST2 and ZST3 in terms of dimensions and shape, but all three specimens represent the same type of preservation. Stems are isolated, with hollow pith, filled with calcareous mudstone. They do

not show features that would allow assigning them with certainty to a particular genus. The central canal must have been filled with sediment shortly after the death of the plant, so that the remains could have retained their cylindrical shape. The surface of the specimens bear traces of charcoalification. Longitudinal ribbing visible on specimen ZST2 (Fig. 5E) resembles the structure of *Neocalamites* sp. outer layer that is considered to be characteristic of *Neocalamites* (Kustatscher and Van Konijnenburg-van Cittert, 2008).

Class Pinopsida

Order Pinales

Family ?Araucariaceae Henkel & Hochstetter, 1865

Genus *Agathoxylon* Hartig, 1848

Type species: *Agathoxylon cordaianum* Hartig, 1848; Coburg, Germany, Triassic.

Agathoxylon cf. *keuperianum* (Unger) Philippe, 2015

Figs 6–9

Material: ZS4; permineralised stem with preserved internal anatomy; thin sections ZS4_L, ZS4_T.

Description: Stem, 24.5 mm in diameter and 66.8 mm in length. Secondary xylem is preserved, cortex, periderm and bark are not preserved. Outer surface is smooth (Fig. 6A, B). Wood is of homoxylous type, pycnoxylic. Pith is circular, slightly elongated, 289 µm in diameter (Fig. 6C, E). Secondary xylem with discernible growth rings (Figs 6C, 8). Early wood tracheids are square to rounded, late wood tracheids are rounded in cross section (Fig. 7C, D). Tracheids in transverse section are irregularly arranged or in loose rows. The transition from early to late wood is rapid (Fig. 7E–H). Intracellular spaces are irregular (Fig. 7D). Rays separated by 2–15 rows of tracheids (mean of 7 rows; Fig. 7E–G). Radial tracheid pitting uniseriate, representing araucarian type (Fig. 8A, C–E, I). Radial pits are mostly contiguous, sometimes separated (Fig. 8C). Bordered pits are circular, adjacent or separated by small distances (Fig. 8E). Pore pits are round to elongate, with aperture diameter 3.0–5.0 mm. Sanio rims are absent. Cross-fields with one to six circular pits (Fig. 8B, F–I), araucaroid, cupressoid oculipores (Fig. 8G, H). Pit pore ellipsoidal; ca. 4.0–5.0 µm in diameter; longer axis of the pit pore oriented uniformly (Fig. 8F, I). Axial parenchyma is undetermined. Resin canals are absent.

Remarks: Terminology used in the description follows the IAWA Committee (Richter *et al.*, 2004) and the key for identifying coniferous morphogenera by Philippe and Bamford (2008).

Agathoxylon keuperianum was previously recorded from Zawiercie-Marciszów (Philippe *et al.*, 2015). Although the specimen is preserved relatively well and anatomical details of the wood can be observed, taphonomical processes altered natural shapes and dimensions. Rays and rows of tracheids in transverse section show undulating (Fig. 7E, F), cell walls of tracheids are broken, and tracheid outline observed in transverse section is irregular (Fig. 7H). It is important to note that measurements of anatomical elements,

i.e., tracheid radial and cross-fields pitting, could be biased by taphonomical processes; crystallisation influences the size and shape of pit pores, making them sometimes rhomboidal in outline (Fig. 8D).

In the observed sample, tracheids represent the araucarian type; only uniseriate chains of round pits were observed (Fig. 8A, B–E). This might be a result of an insufficient number of samples. Other authors observations suggest that some diversity could be expected (e.g., Gnaedinger and Zavattieri, 2020).

In transverse section, irregularities in wood development are visible. Growth rings became eccentric, and reaction (compression) wood has formed (Figs 6C, 7A), probably in response to mechanical stress.

The helical thickening, observed sporadically only in transmitted light (Fig. 6L–N), might be an artefact caused by wood degradation or mineralisation processes (Philippe *et al.*, 2019; Boura *et al.*, 2021). It was observed only in regions, where tracheids are damaged and disturbed (Fig. 6L). No such characters were observed under the SEM.

Pith cavity cells contain rounded structures (Fig. 6E–I), 25.0–50.0 µm in diameter. They may represent secretory cells, but some possess a round operculum (Fig. 6G–I), which might indicate their fungal affinity (fungal spores).

Agathoxylon is a cosmopolitan fossil wood genus, recognised in the strata throughout the Palaeozoic to Cenozoic (Gou *et al.*, 2021). *A. keuperianum* is characterised by stratigraphical and geographical limitations. It has been so far identified from the Upper Triassic Keuper (Carnian, Norian, Rhaetian) in the Central European Basin sediments (Philippe *et al.*, 2015).

Gymnospermae *Incerte sedis*

Stem A

Fig. 9

Material: WNoZ_S_7_159, WNoZ_S_7_193, ZST5; permineralised stems.

Description: Permineralised stems; 81.1–100.0 mm long and, 21.8–82.5 mm wide. Stems unbranching, without cortex. Bark is not preserved.

Remarks: Three-dimensionally preserved stems were found as separate, isolated fragments or entombed in calcareous mudstone (Fig. 3H). Unfortunately, the specimen with the widest diameter (82.5 mm; WNoZ_S_7_159; Fig. 9A) has a very short length (ca. 30 mm). Another specimen has a diameter ca. half width of WNoZ_S_7_158 (21.8–44.0 mm). The outer surface is either smooth (Fig. 9B) or bulging with branch scars and wrinkles (Fig. 9D, E). Specimen WNoZ_S_7_159 shows a thin (2.5 mm), darker layer resembling bark, partially surrounding the stem (Fig. 9A). All specimens have an inner structure that forms a concentrating tissue arrangement from the central pith through the stem radius (Fig. 9A, C, F). Although specimens show the same preservation mode, they could be three different genera or even different classes of gymnosperm. General appearance makes the specimen resemble *Agathoxylon*, but further identification is doubtful without thin section preparation and analysis of anatomical structure.

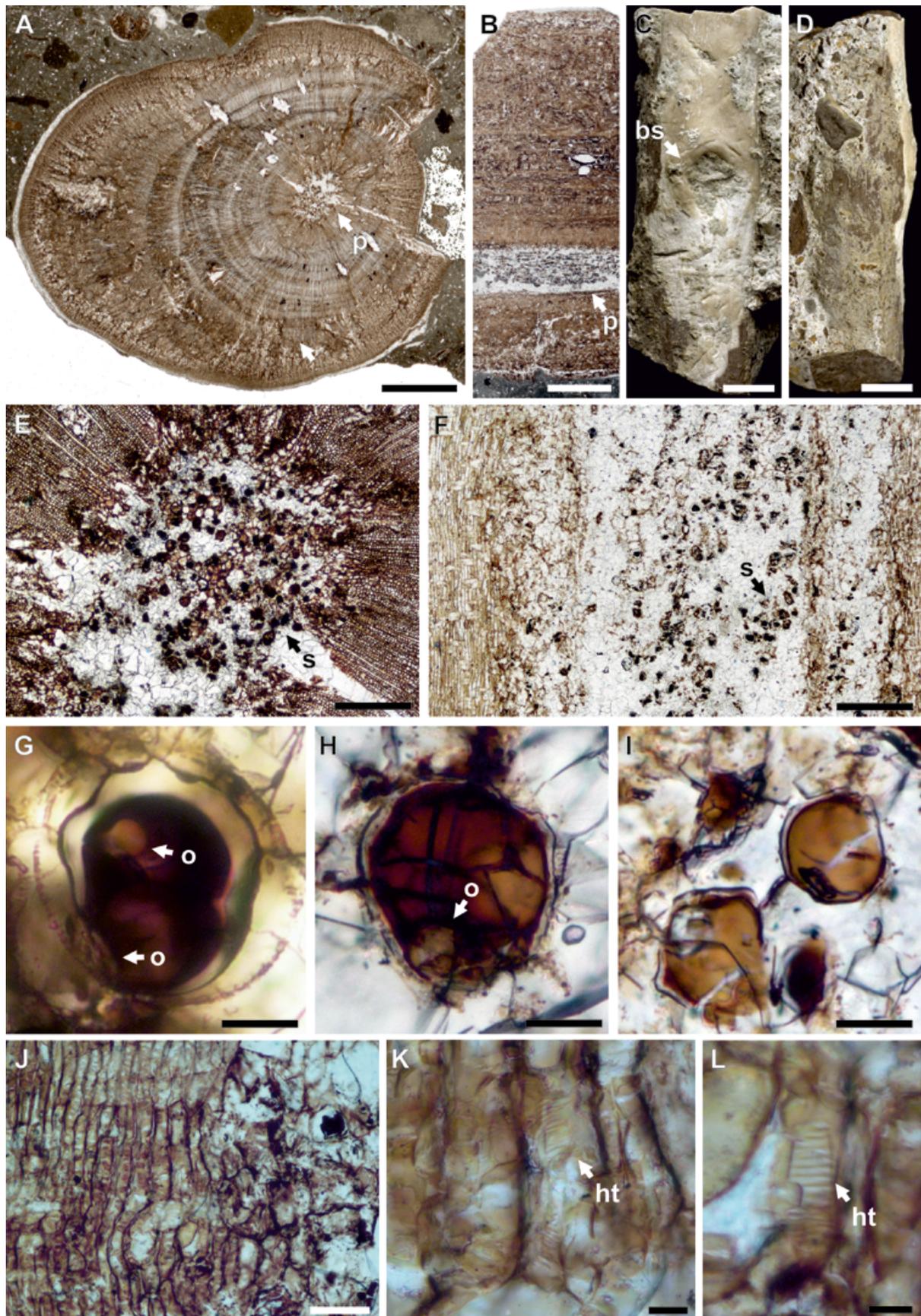


Fig. 6. *Agathoxylon cf. keuperianum* (Unger) Philippe stem from the Upper Triassic of Zawiercie-Marciszów, southern Poland. **A, B.** Outer surface of the stem. **C.** Cross thin section of the permineralised stem. **D.** Radial thin section of the stem. **E.** Details of the pith in cross section. **F.** Details of the pith in radial section. **G–I.** Spherical structures in pith tissues. **J–L.** Tracheid deformations (radial section). **K, L.** Helical thickenings on the tracheids walls. Abbreviations: bs – branch scar, ht – helical thickenings, p – pith, o – operculum, s – spherical structures. Scale bars: A, B – 10 mm; E, F – 500 µm; G–I – 25 µm, L – 100 µm; M, N – 20 µm.

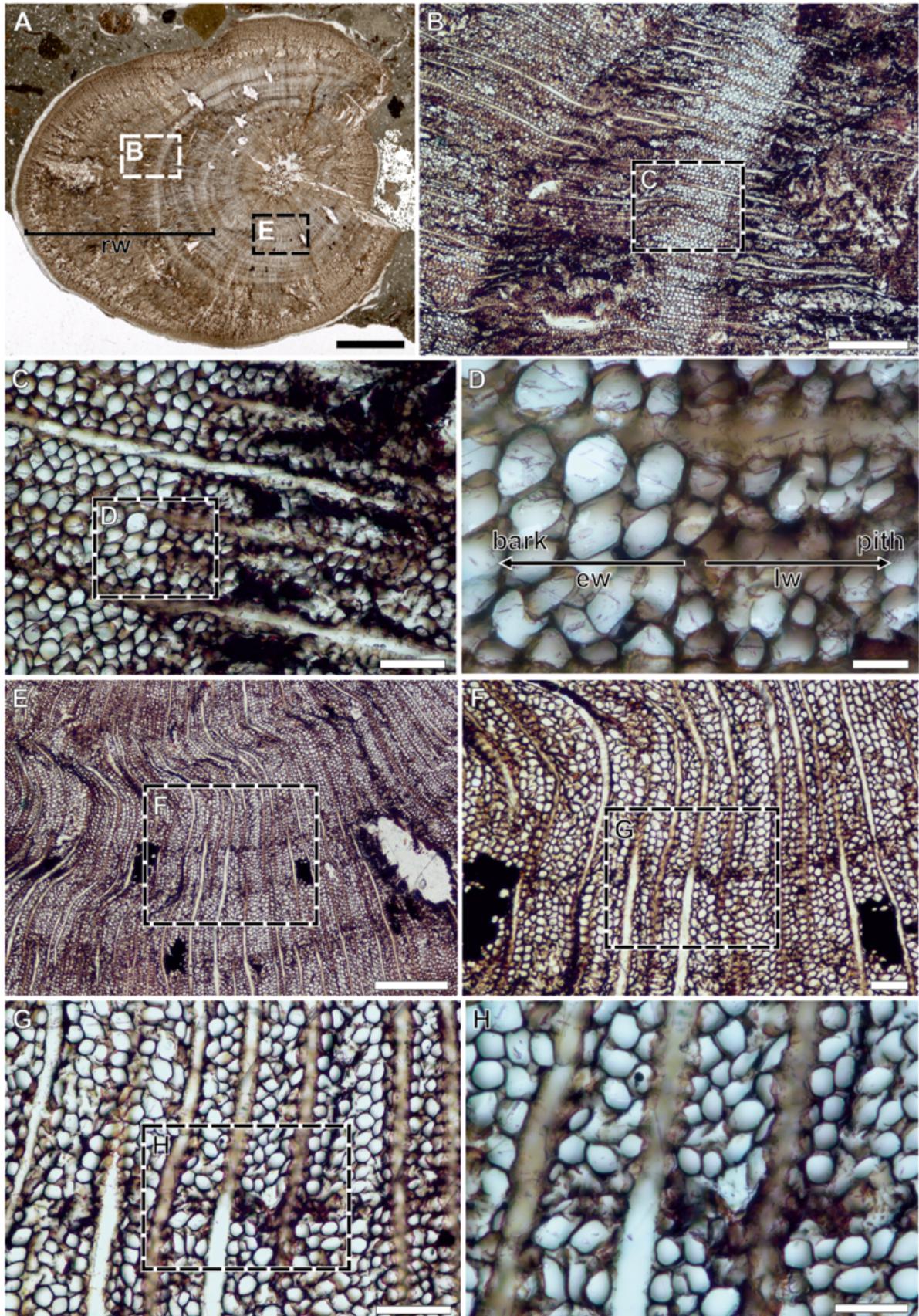


Fig. 7. *Agathoxylon* cf. *keuperianum* (Unger) Philippe stem from the Upper Triassic of Zawiercie-Marciszów, southern Poland. **A.** Cross thin section of the stem with permineralised tissue. **B.** transition between regular wood and reaction wood. **C.** Transition between probable late and early wood. **D.** Magnification of fragment from C, showing irregular spaces between tracheids. **E.** Rays and tracheid rows showing straight and waiving arrangement. **F, G.** Rays separated with tracheids. **H.** Tracheids with damaged cell walls and irregular shape. Abbreviations: ew – early wood, lw – late wood, rw – reaction wood. Scale bars: A – 10 mm; B, E – 500 μ m; C, F, G – 100 μ m; D – 25 μ m; H – 50 μ m.

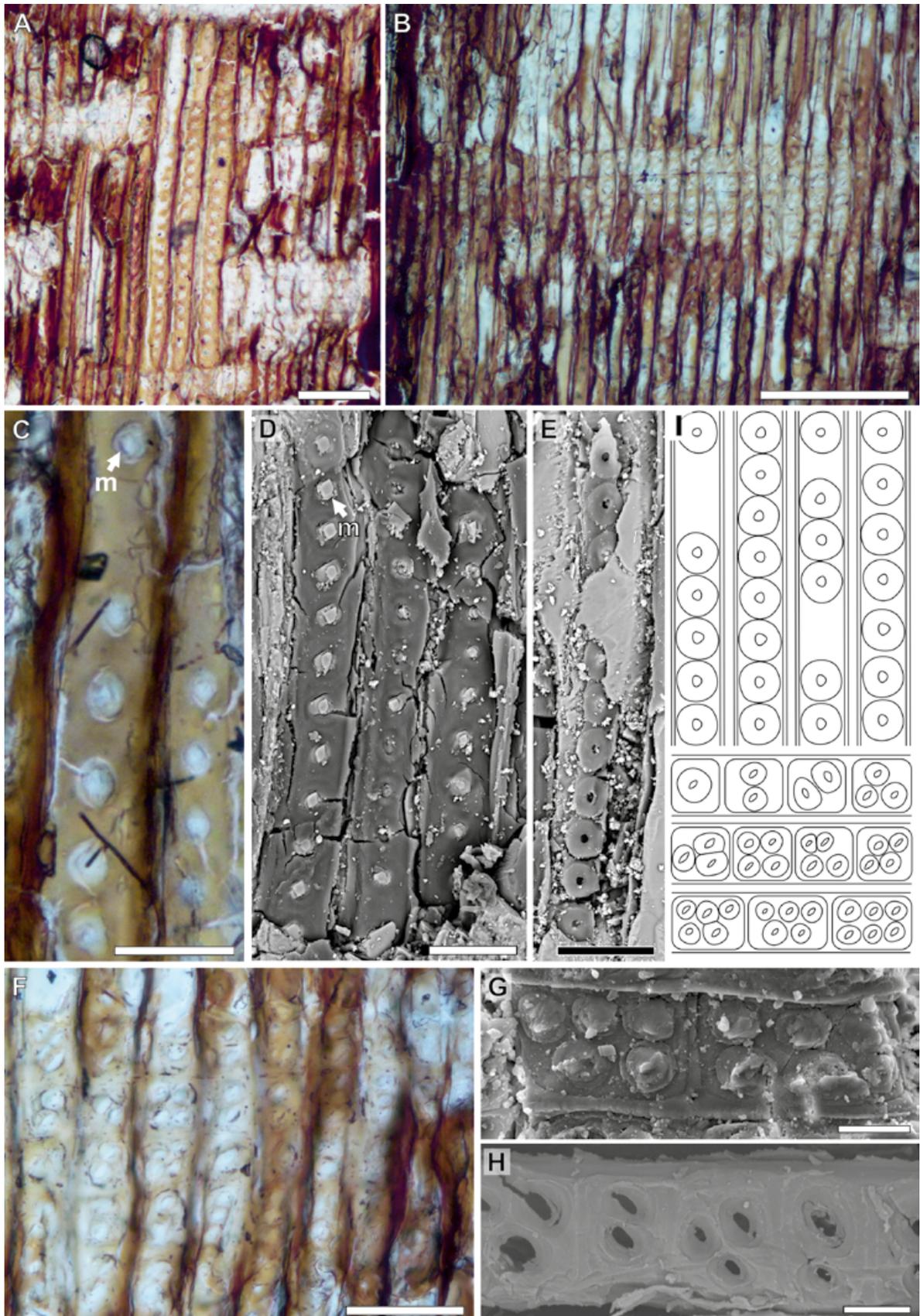


Fig. 8. *Agathoxylon* cf. *keuperianum* (Unger) Philippe stem from the Upper Triassic of Zawiercie-Marciszów, southern Poland. **A.** Tracheid in radial section, showing uniseriate pitting. **B.** Cross-fields in radial view. **C–E.** Tracheid radial pitting, uniseriate, araucarian, pits adjacent or separated by small distances; **D.** Tracheids with pit pores deformed by crystallising minerals. **F.** Cross-fields in radial view. **G, H.** SEM of araucaroid cross-fields with one to six circular pits, cupressoid oculipores. **I.** Schematic drawing of radial pitting and cross fields variety in the ZST4 specimen. Abbreviations: m – mineralisation. Scale bars: A, B – 100 μ m; F – 50 μ m; C–E – 25 μ m; G, H – 10 μ m.

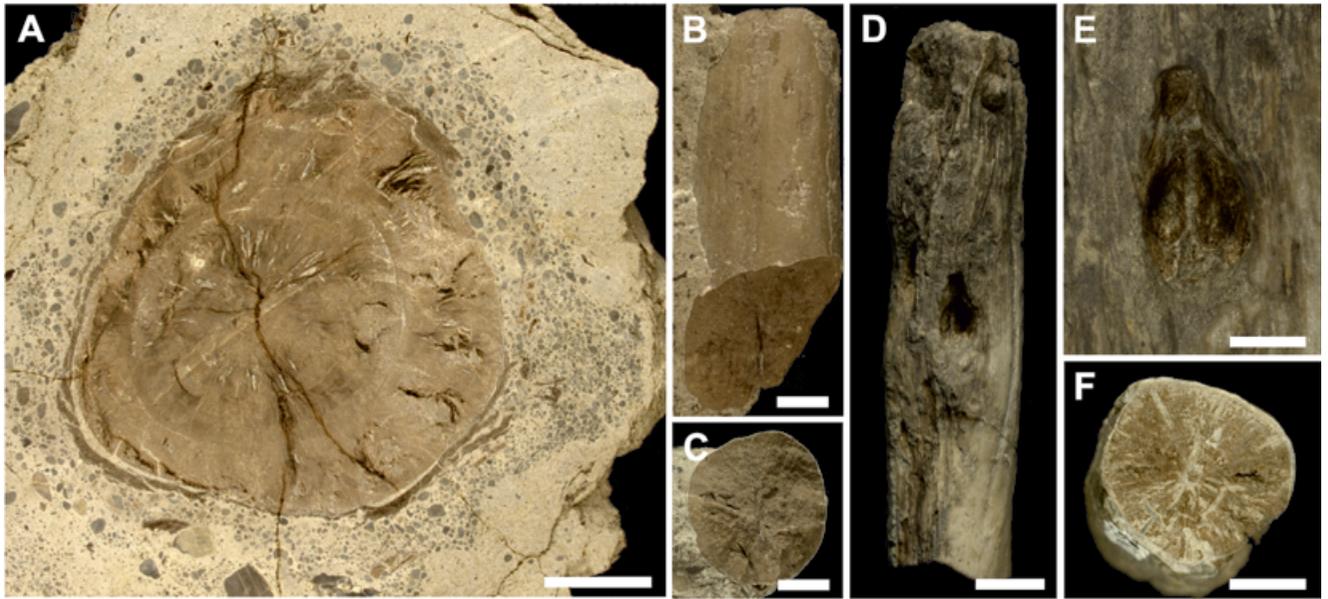


Fig. 9 *Incerte sedis* Gymnospermae, Stem A from the Upper Triassic of Zawiercie-Marciszów, southern Poland. **A.** Cross section of the permineralised stem preserved in calcareous mudstone, showing concentric arrangement of inner tissue; polished surface; specimen WNoZ/S/7/159. **B.** Permineralised stem with smooth surface, specimen ZST5. **C.** Transversal view of the specimen from B; inner structure is massive, concentric tissue arrangement is barely visible. **D.** Permineralised stem with irregular surface; specimen WNoZ/S/7/193. **E.** Details of branch scar from D. **F.** Transversal view of the specimen from D; discernible concentric arrangement of inner tissue. Abbreviations: bs – branch scar. Scale bars: A–C – 20 mm; D, F – 10 mm; E – 5 mm.

Stem B
Fig. 10

Material: Z21; impression of two stems on one rock slab.
Description: Stems 107.2 mm long and 44.5 mm wide, 83.9 mm long and 18.8 mm wide. Larger fragment is straight (Fig. 10B), smaller widening on one end (Fig. 10A). Preserved branch scars are round (Fig. 10D) to rhomboidal (Fig. 10C), 6.0 mm wide. On stem present are patches of thick cuticle. Cell pattern or stomata are not discernible, only longitudinal parallel striae are clearly marked (10 per 100 μ width; Fig. 10E, F, H).
Remarks: Cuticle obtained from the specimen is very brittle and prone to mechanical damage. Observed holes and breaks in the cuticle surface in places resemble stomata (Fig. 10F, G), but no confirming features can be observed. Branch scars (bundle scar) found on both specimens are round to rhomboidal (Fig. 10C, D); they show a resemblance to a scar found on permineralised specimens with gymnosperm anatomy (Figs 6A, 9F, G). Fragment of charcoalfied tissue shows longitudinal striae on the surface but has a completely homogenised internal structure. Although the fossil is preserved in diverse modes, to classify it with certainty as any particular group was not possible. On the basis of size, the stem could also represent a sphenophyte. A retrieved cuticle also shows some resemblance to a sphenophyte cuticle, similar to *Equisetum filum* (Harris, 1979; personal observation), but stomata are not discernible. Rounded scars visible on the investigated stem have dimensions that could agree with sphenophyta branch scars, but no nodal region is visible. Therefore, the stem was classified as *Gymnospermae incertae sedis*, because so far, no other plant group is confirmed to have grown in the area at that time.

Root A
Fig. 11A–E

Material: ZR1; compression of isolated root fragment, preserved in a calcareous concretion.
Description: Isolated root fragment with secondary branching (Fig. 11A). The main root axis is 79.6 mm long and 3.3–3.6 mm wide. Three secondary roots emerge from one side of the main axis (Fig. 11A) and are irregularly spaced. Secondary roots are 9.9–31.0 mm long and 0.9–1.9 mm wide, slightly narrowing towards the tip, delicate bulging is visible close to the main axis (Fig. 11D). Secondary root tips are rounded (Fig. 11B, C).
Remarks: One outgrowth is (Fig. 11A, D) much broader than the others, 2.8–3.3 mm wide. This might be a branching of the main axis. Along the main root axis, a 1.8–2 mm wide darker, coalified layer is marked, probably representing a vascular cylinder surrounded by cortical tissue (Fig. 11D). The vascular cylinder enters into the secondary roots (Fig. 11E) but is less clearly visible in thinner branches.

Root B
Fig. 11F–K

Material: ZR2.1–ZR2.9; nine fragments of isolated root compression and petrification preserved in a calcareous concretion.
Description: Isolated root fragments with secondary and tertiary branching. The main root axis is 2.1–3.3 mm wide. Secondary roots are 1.1–1.7 mm wide and emerge from the main axis at 70–80° (Fig. 11F, G, H). Tertiary order roots are 0.3–0.56 mm wide and 1–1.3 mm long, emerge at an 80–90° angle (Fig. 11H). Root tip is rounded. Surface is smooth (Fig. 11K).

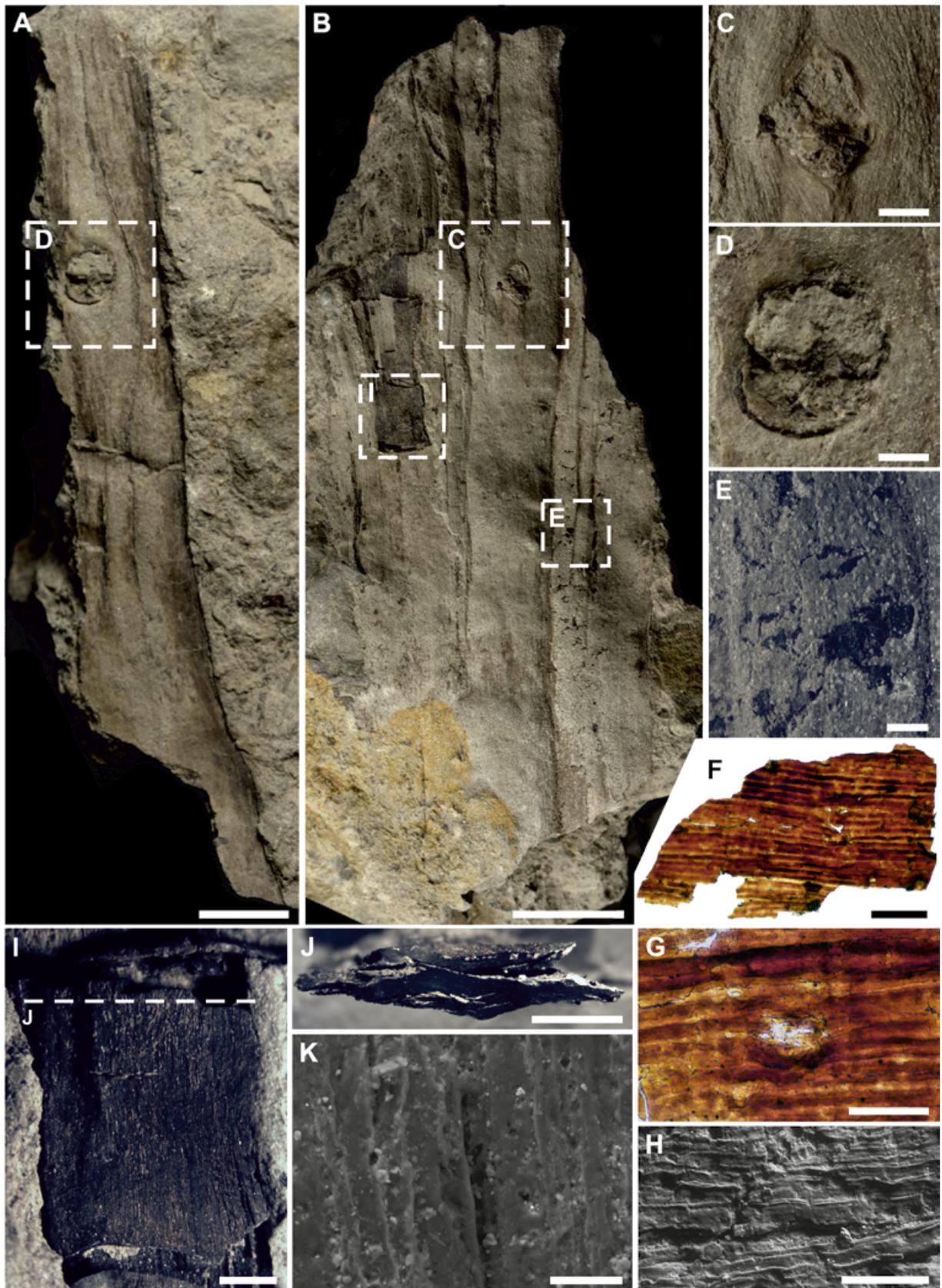


Fig. 10. *Incerte sedis* Gymnospermae, Stem B from the Upper Triassic of Zawiercie-Marciszów, southern Poland. **A.** Negative impression of a stem with probable nodal region and branch scar. **B.** Positive impression of a stem with preserved charcoaled tissue fragments and patches of cuticle, with branch scar. **C–D.** Magnified branch scars from specimen in A and C. **E.** Patches of cuticle preserved on stem from B. **F.** Macerated cuticle from stem in B, in transmitted light. **G.** Magnification of cuticle fragment in F, in transmitted light. **H.** SEM photo of cuticle from stem in B. **I.** Fragment of charcoaled tissue from stem in B. **J.** Transverse section of charcoaled fragment on I, showing completely homogenised structure. **K.** SEM photo of a charcoaled fragment from stem in B. Scale bars: A, B – 1 cm; C, D – 2 mm; E, H–J – 1 mm; F – 100 μm ; G – 50 μm ; K – 50 μm .

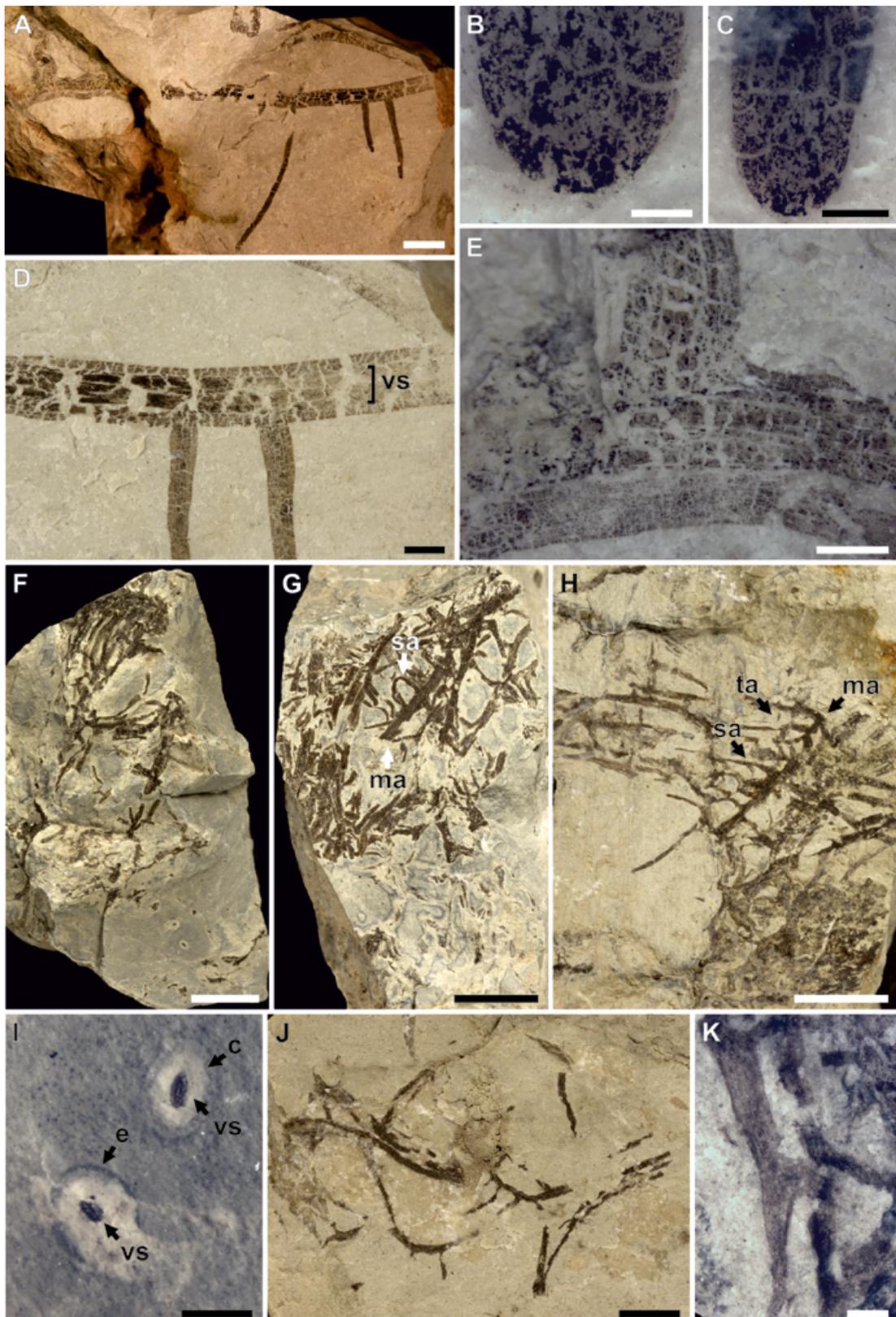


Fig. 11. Isolated rooting system from the Upper Triassic of Zawiercie-Marciszów, southern Poland. **A–E.** An isolated fragment of Root A, specimen ZK1; **A** – laterally branching root with secondary order roots; **B, C** – magnification of secondary branching root tips; **D** – details of Root A fragment showing a vascular cylinder in the middle part of the main root axis; **E** – magnification of probable branching of the main axis, with discernible vascular cylinder. **F–K.** An isolated fragments of Root B, specimen ZK2; **F–H, J** – tangled lateral roots with secondary and tertiary branching; **I** – Details of transverse section of the three-dimensionally preserved root axis from **F** showing differentiation to vascular cylinder, cortical region and epidermis; **K** – magnification of the secondary and tertiary branches. Abbreviations: **c** – cortical region; **e** – epidermis; **ma** – main axis; **sa** – secondary axis; **ta** – tertiary axis; **vc** – vascular cylinder. Scale bars: **A, F, G, H, J** – 10 mm; **B, C** – 0.5 mm; **D** – 3 mm; **E, I, K** – 1 mm.

Remarks: Tree dimensionally preserved roots in transversal section show a vascular strand ca. 2.5 mm in diameter, surrounded by light-colour mineralisation of the cortical region and a darker circle, probably representing the root epidermis (Fig. 11I). Roots are tangled together, and determination of root length is difficult to measure (Fig. 11F, G, H, J); the longest distinguishable main axis is 46 mm.

Botanical determination of the roots of type A and type B remains uncertain, as there is no organic connection between them and above-ground plant parts, nor are there any other plants in the concretions they are preserved in. The lack of anatomical details precludes recognition of any reliable affinity with a particular plant group; therefore, both types are discussed below. Both types of roots are preserved in a calcareous concretion lacking any other plant remains. Root A is generally more robust than root B. Root A is preserved as compression with a thin layer of coalified tissue. Similarly preserved type B is also found as three-dimensionally mineralised axes. Specimens of type B are more ramified and sometimes form a tangled, dense net. Both types seem to represent a lateral type of root branching. Considering differences in morphology between Root A and Root B, it could be assumed that they originate from plants belonging to different groups. Root A perhaps represents a gymnosperm or herbaceous lycophyte.

Isolated rooting systems are sometimes assigned to a morphogenus *Radicitis*, known from late Palaeozoic and Mesozoic localities, i.e., the early Permian of Brazil (Boardman *et al.*, 2016), Middle Permian of Russia (Naugolykh, 2015), Middle Triassic of Germany (Kustatscher and Van Konijnenburg-van Cittert, 2008; Kustatscher *et al.*, 2019b), Late Triassic (Mazaheri-Johari *et al.*, 2021) and Early Jurassic of Iran (Schweitzer *et al.*, 1997). Botanical affiliation of *Radicitis* is associated with Equisetales (Schweitzer *et al.*, 1997; Kustatscher *et al.*, 2012; Boardman *et al.*, 2016). The dominance of sphenophyta macro-remains in the fossil assemblage from Zawiercie-Marciszów might indicate that the described root specimens originate from that plant group. Also, documented by Kustatscher and Van Konijnenburg-van Cittert (2008), fragments of a rooting system with secondary roots branching laterally from the main axis in the Ladinian deposits of Thale, Germany, and associated with equisetalean remains, show similar gross morphology and dimensions to specimens of type B from Zawiercie-Marciszów.

Cuticulae dispersae

Morphotype A

Fig. 12A–F

Material: Cuticle fragments bulk-macerated from mudstone with cuticle accumulation (plant-bearing lithology IV) and mudstone with macrofloral remains (plant-bearing lithology II, III); ZCD_A.

Description: Thick cuticles. The largest retrieved fragment is 25 mm long and 5 mm wide, straight. Apex acute (Fig. 12A), base unknown. Leaf margins are smooth (Fig. 12B). Epidermal cells are arranged loosely in longitudinal rows. Cells are polygonal, sometimes rectangular to isodiametric. Anticlinal walls are thick and straight, evenly cutinised.

Periclinal walls are smooth or bear a faint, hollow papilla (Fig. 12C). Cuticle is amphistomatic. Stomata are evenly distributed on both cuticles in rows, more or less regularly (Fig. 12A, C, D). Stomatal complexes are round, 40–65 µm in diameter. Guard cells are deeply sunken, orientated irregularly, rarely visible. Usually, six subsidiary cells bearing a solid papilla are directed towards the stomata pit, overarched the aperture (Fig. 12E). Anticlinal walls of subsidiary cells are strongly cutinised but not thicker than normal epidermal cells (Fig. 12E). Encircling cells unspecialised, but sometimes forming a discernible circle of secondary cells (Fig. 12F).

Remarks: Cuticles from morphotype A show a resemblance to conifer cuticles. The size and shape of the largest fragments indicates that the cuticles belong to a needle-leaf type of conifer. The epidermal pattern is unified; no midrib or vein region can be distinguished. Therefore, probably did not come from single-veined conifer foliage, i.e., *Elatocladus*-like (Harris, 1935). Cuticles from type A show some similarities to *Pagiophyllum*-like foliage, such as stomata distribution in more or less regular longitudinal rows. *Pagiophyllum* is a conifer foliage morphogenera for conifer vegetative organs covered by leaves that are at least twice as long as wide, known from Late Triassic to Upper Cretaceous (i.e., Kendall, 1948; Harris, 1979; Cantrill *et al.*, 1995). Elongated leaves with stomata in rows on the adaxial and abaxial sides are documented, i.e., from *Pagiophyllum kurri* from Jurassic of Yorkshire (Harris, 1979).

Morphotype B

Fig. 12G–L

Material: Cuticle fragments and cuticles of isolated leaves, bulk-macerated from mudstone with cuticle accumulation (plant-bearing lithology IV) and mudstone with macrofloral remains (plant-bearing lithology II, III); ZCD_B.

Description: Moderately thick cuticles. Elongated, flattened leaves are straight (Fig. 12G–I), leaf base is not preserved. Leaf tip is rounded (Fig. 12G–I). Margins are smooth. The most complete leaves cuticles are 9–10 mm long and 3–4 mm wide, usually 4–5 times longer than wide. Epidermal cells are arranged in loose longitudinal rows. Epidermal cells are rectangular to polygonal, isodiametric to slightly elongated in rows between stomata rows (Fig. 12J). Anticlinal walls are thick and well-marked. Periclinal walls are equipped with round shallow papillae in the middle or slightly in the upper part of the epidermal cell (Fig. 12K–L). Cuticle is amphistomatic. Stomata are evenly distributed on whole surface of the cuticle. Sunken stomata are arranged in longitudinal rows, single stomata wide. Stomata complex is round, 40–55 µm in diameter. In rows stomata are distributed more or less regularly. Adjacent stomata are not sharing subsidiary cells. Stomatal complex is round, comprising of thinly cutinised guard cells surrounded by 5 or 6 subsidiary cells with prominent papillae overarched the stomata aperture (Fig. 12K–L). Papillae are straight, sometimes slightly swollen at the tips. A faint groove in the middle of the papilla is visible along its longer axis (Fig. 12L). Outer anticlinal walls of stomata are thicker than other epidermal cells anticlinal walls. No additional encircling cells are present.

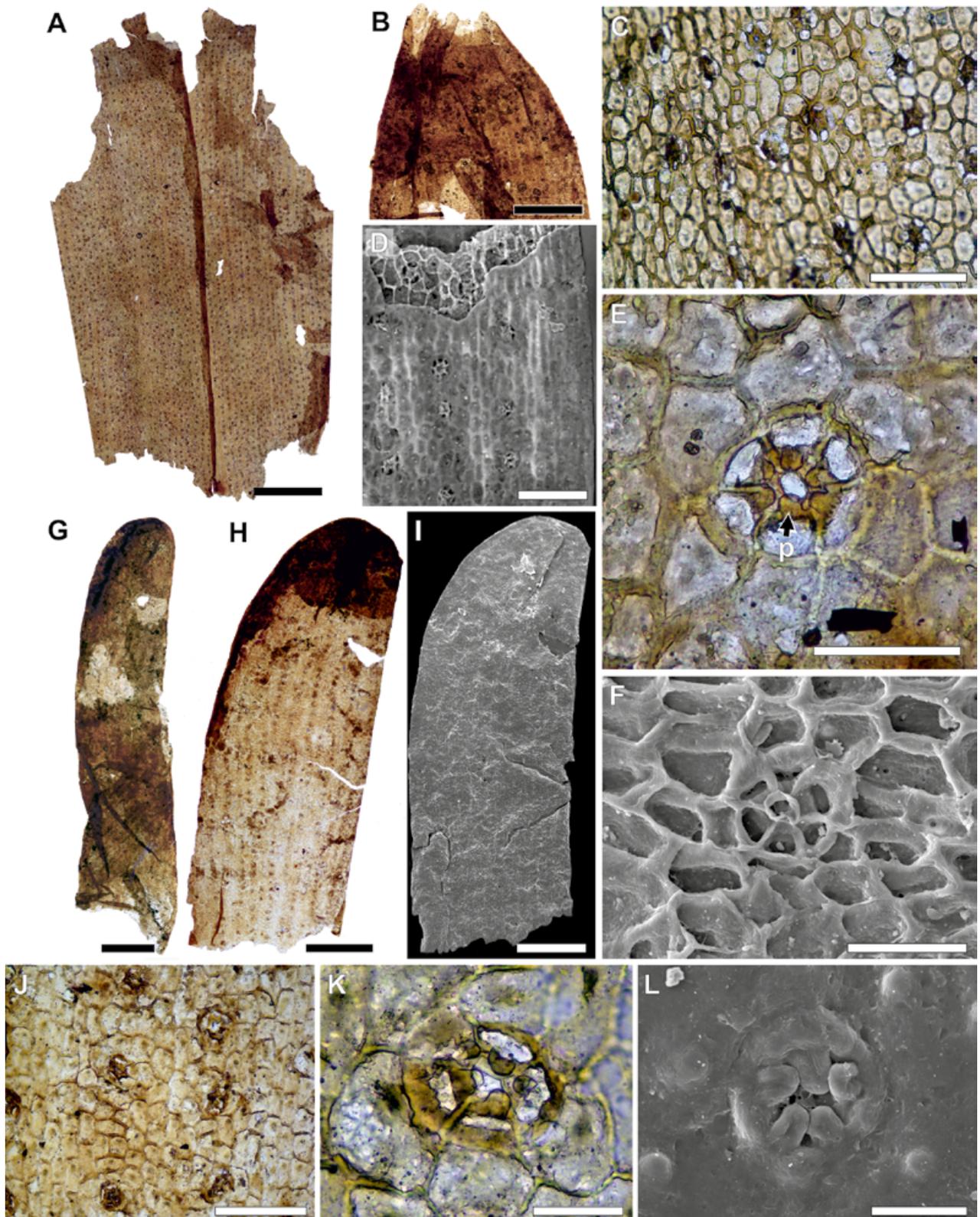


Fig. 12. *Cuticulae dispersae* from the Upper Triassic of Zawiercie-Marciszów, southern Poland. **A–F.** *Cuticulae dispersae* Type A; **A** – cuticle fragment showing upper and lower cuticle and smooth margin; visible are rows of stomata evenly distributed; **B** – incomplete leaf tip; **C** – details of cuticle in **A**; epidermal cells differ in size and shape, from isodiametric to polygonal and elongated; **D** – SEM of outer cuticle surface; **E, F** – details of stomata complex; stomata pore surrounded with subsidiary cells equipped with papillae; **F** – SEM image of inner cuticle surface and stomata. **G–L.** *Cuticulae dispersae* Type B; **G–I** – cuticles of elongated linear leaves with rounded tips, transmitted light; **I** – leaf from **H** in SEM showing entire margin and surface covered with papillae, including the tip; stomata are present through the whole length of a leaf; **J** – magnification of stomata rows; **K** – details of stomata complex, outer anticlinal walls showing thickening, transmitted light; **L** – SEM photo of stomata complex showing prominent papillae overarching the stomata aperture. Abbreviation: p – papillae. Scale bars: **A, B** – 10 mm; **C, D, J** – 100 μ m; **E, F** – 50 μ m; **I** – 1 mm; **K, L** – 20 μ m.

Remarks: The overall shape of the leaf indicates that it might come from *Elatocladus*-type foliage. Leaf attachment cannot be determined, because leaf base is not preserved, and distal part of the leaf blade shows no constriction or widening. However, the type of cuticle and arrangement of the cells make this diagnosis unlikely as the *Elatocladus*-type foliage and other needle-leaf Mesozoic conifers had stomata, usually gathered in bands (Harris, 1935, 1979; McIver, 2001). Cuticles of type A and B show a close resemblance, especially in detailed comparison. Type A cuticles have more robust appearance, the cuticle is thicker, anticlinal walls of epidermal cells are wider (thicker). The leaf tip of type A is acute, whereas that of type B is rounded and blunt (Fig. 12A, G, H). Stomatal complexes of type A are slightly wider in diameter than in type B (40–65 vs. 40–55). There are six subsidiary cells surrounding stomata surround stomata guard cells in type A. The number of subsidiary cells in type B range from five and six. Differences between cuticles type A and type B could be considered superficial and reflect intraspecific variation, rather than defining different taxa. However, separate morphogroups are presented here due to the fragmentary preservation of cuticles.

Morphotype C
Fig. 13A–D

Material: ZCD_C; cuticle fragments and cuticle of fragmentary leafy twig from mudstone with cuticle accumulation (plant-bearing lithology IV) and mudstone with macrofloral remains (plant-bearing lithology II, III).

Description: Moderately thick cuticles. The largest and most complete cuticle of the leafy twig is 43 mm long with elongated lanceolate leaves attached to the whole leaf base (Fig. 13A). Leaves are linear, slightly lanceolate, attached alternatively, 9 to 12 mm long and 3 to 4 mm wide. Leaf base is wide, leaf cushion is decurrent. Leaves are acuminate, but leaf tip is not preserved. Margins are smooth. Epidermal cells are arranged in longitudinal, loose rows (Fig. 13B, C). Epidermal cells are shaped from rectangular, isodiametric to strongly elongated. Anticlinal walls of epidermal cells are evenly cutinised, sometimes gently undulating. Periclinal walls are thin and smooth, or with prominent hollow papilla in the middle of the longer axis of the periclinal wall or on the apex side. Papillae are triangular to rounded. Leaves are amphistomatic. Stomata are spaced in rows single stomata wide, and mainly evenly distributed. Stomatal complex is round, between 50 and 60 μm in diameter. Guard cells are indiscernible. Stomata pore is encircled by 5–6 subsidiary cells (Fig. 13D). Subsidiary cells possess a short hollow papilla directed toward the pore. Outer anticlinal walls of subsidiary cells are not thicker than ordinary epidermal cells (Fig. 13D). No specialised encircling cells can be distinguished.

Remarks: Preserved fragment of a leafy twig proves a diversification of cuticular characters within a single taxon or even specimen. Cuticle fragments from higher leaves are slightly thinner, stomata are more scattered along the rows; epidermal cells are more elongated and rounded in outline (Fig. 13B, C). Lower leaves cuticle consists of cells arranged similarly, but cells are shorter with sharper

corners and equipped with triangular papillae (Fig. 13D). Heteromorphy in cuticle development within a single plant is connected more to pre-adaptations to biotic and abiotic environmental conditions and plant ontogeny than to taxonomical affinity (Kerp, 1990; Bomfleur *et al.*, 2011; Webster *et al.*, 2022). A similar specimen was described previously by Ash (1970) from the Upper Triassic Chinle Formation, Arizona, USA. It was classified as *Pagiophyllum simpsonii*. Cuticles described here show general morphological similarity, but *P. simpsonii* leaves are much smaller: 1.7–2 mm long and 0.8–1.2 mm wide (Ash, 1970).

Morphotype D
Fig. 13E–J

Material: Cuticle fragments and isolated leaf cuticles bulk-macerated from mudstone with cuticle accumulation (plant-bearing lithology IV) and mudstone with macrofloral remains (plant-bearing lithology II, III); ZCD_D.

Description: Relatively thick cuticles. Leaves are elongated, lentiform to falcate laterally flattened (Fig. 13E, F), 5–7 mm long and 2–3 mm wide. Leaf tip is acute and incurved from the lateral view (Fig. 13E, F), leaf base unknown. Adaxial and abaxial sides are evenly cutinised. Epidermal cells are arranged irregularly. Cells are rectangular to elongated in outline. Anticlinal walls between epidermal cells are slightly thickened. Periclinal walls bear an elongate triangular hollow papilla, 5.0–55.0 μm high (Fig. 13G). Papillae on marginal cells are longer, up to 70 μm and spiky. Stomata are evenly scattered on adaxial and abaxial sides. Stomatal complex consists of sunken guard cells (Fig. 13H–J) and 5 or 6 subsidiary cells (Fig. 13H), and measure between 30–50 μm in diameter. Proximal walls thickened, sometimes with faint papillae pointing towards the stomatal aperture (Fig. 13H, I). Encircling cells form an indistinctive ring of cells equipped with long papillae with blunt tip directing toward the centre of stomata (Fig. 13H–J).

Remarks: Shape of isolated leaves possessing type D cuticle indicate that they probably belong to a conifer. Small, elongated leaves without discernible venation could originate from *Pagiophyllum*-type species. Cuticle, however, is thinner than typical in *Pagiophyllum*-type (Harris, 1979). Also, thickenings of stomata complex anticlinal walls are not as prominent. The leaf base was not preserved in any of the collected specimens. Therefore reconstructing accurate leaf shape is challenging. The biggest cuticle of type D is 3.1 mm long and 12.3 mm wide. It is irregular in shape and has no natural margins.

Morphotype E
Fig. 14

Material: ZCD_E; cuticle fragments, isolated leaves cuticles and fragmentary leafy twigs cuticle bulk-macerated from mudstone with cuticle accumulation (plant-bearing lithology IV) and mudstone with macrofloral remains (plant-bearing lithology II, III).

Description: very thick cuticles. Twigs are comprised of helically arranged scale-like leaves (Fig. 14A–E, G). Twigs are up to 4 cm long and 3–8 mm wide, unbranching. Leaves are

tightly appressed to the axis, except for free leaf tip. Leaves are scale-like, wider than long, sometimes isodiametric and widest in approximately middle of their length. Leaves measure from 2.0 mm wide and 1.8 long, up to 10.0 mm wide and 10.0 mm long. Leaves in distal view are rhomboidal (Fig. 14A–E, G) tapering towards the apex. Leaf tip is acute to obtuse. In lateral view, leaf tip is incurved. Leaf base is broad, usually round. Leaf margins possess wavy fringe (Fig. 14F), ending with spines elongated towards the leaf tip. Fibrous tissue is on the upper cuticle's inner side, between stomata rows (Fig. 14E, H). The surface of the adaxial cuticle is smaller than abaxial. Epidermal cells

are isodiametric, slightly elongating in rows between stomata rows (Fig. 14H, I). Epidermal cells with strongly cutinised anticlinal walls, periclinal walls are smooth. Papilla is present on periclinal walls near the leaf tip. Leaves are amphistomatic. Stomata are arranged in rows (Fig. 14F, H–J) spreading from leaf tip towards the base (Fig. 14G). Stomata are sunken, scattered in rows unevenly, oriented irregularly (Fig. 14H, I). Stomatal complexes consist of guard cells and 5–7 subsidiary cells. Guard cell cuticle is very thin. Prominent papilla is present on subsidiary cell directing toward the stomata aperture. Subsidiary cells papillae possess a shallow groove, parallel to the papillae longer axis

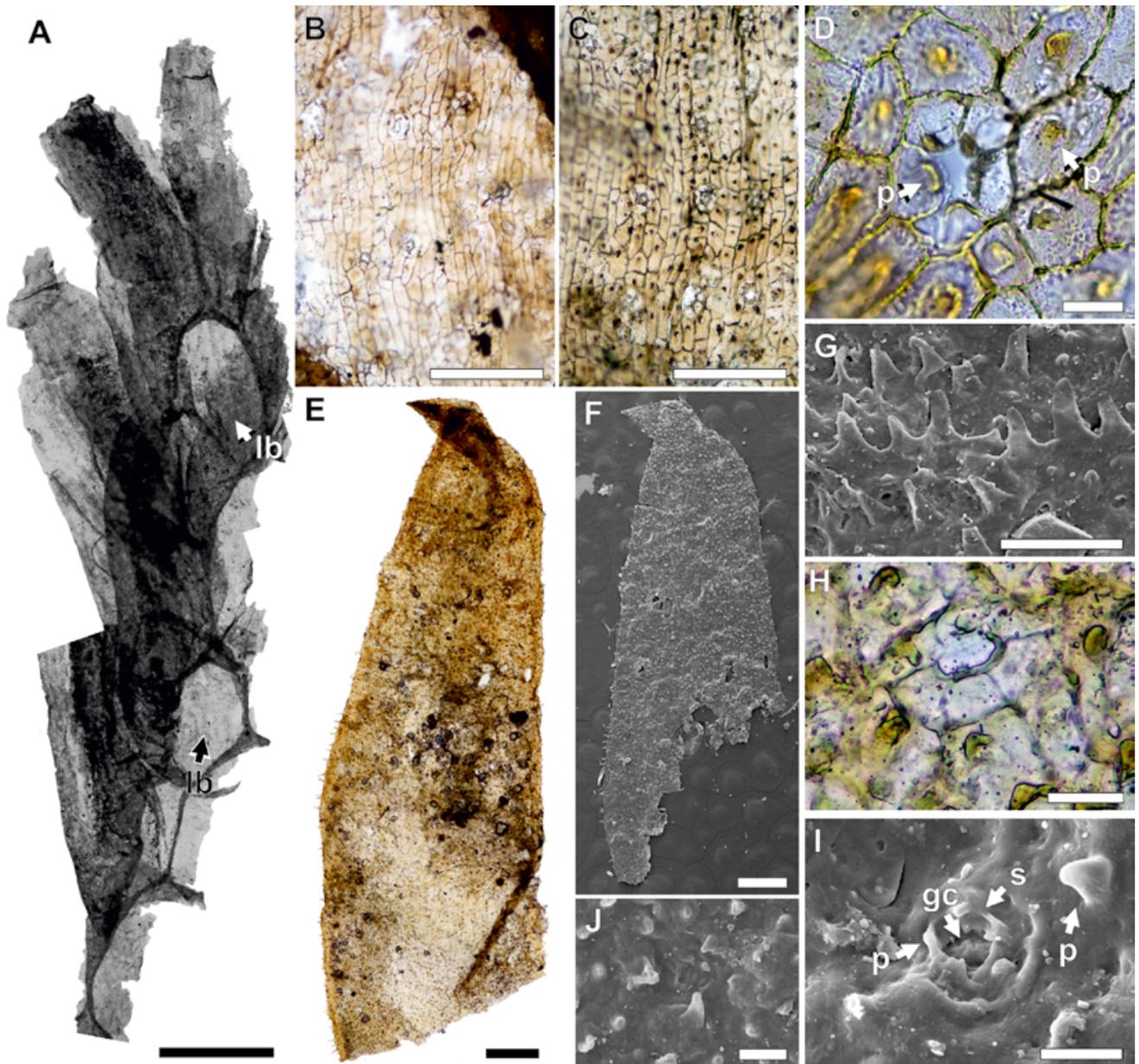


Fig. 13. *Cuticulae dispersae* from the Upper Triassic of Zawiercie-Marciszów, southern Poland. **A–D.** *Cuticulae dispersae* Type C; **A** – cuticle of a partially preserved leafy twig with elongated leaves; **B** – cuticle fragment from upper part of the twig showing more elongated cells without papillae; **C** – fragment of cuticle from lower leaves with epidermal cells and stomata subsidiary cells equipped with papillae; **D** – details of stomata from lower part of the twig. **E–J.** *Cuticulae dispersae* Type D; **E, F** – elongated leaf with adaxial and abaxial cuticle evenly developed; **G** – epidermal cells equipped with papillae; **H–J** – details of stomata complex; **I, J** – SEM photos of stomata complex. Abbreviations: gc – guard cell, lb – leaf base, p – papilla, s – subsidiary cell. Scale bars: **A** – 1 mm; **E, F** – 500 µm; **B, C** – 200 µm; **G** – 100 µm; **D, H–J** – 20 µm.

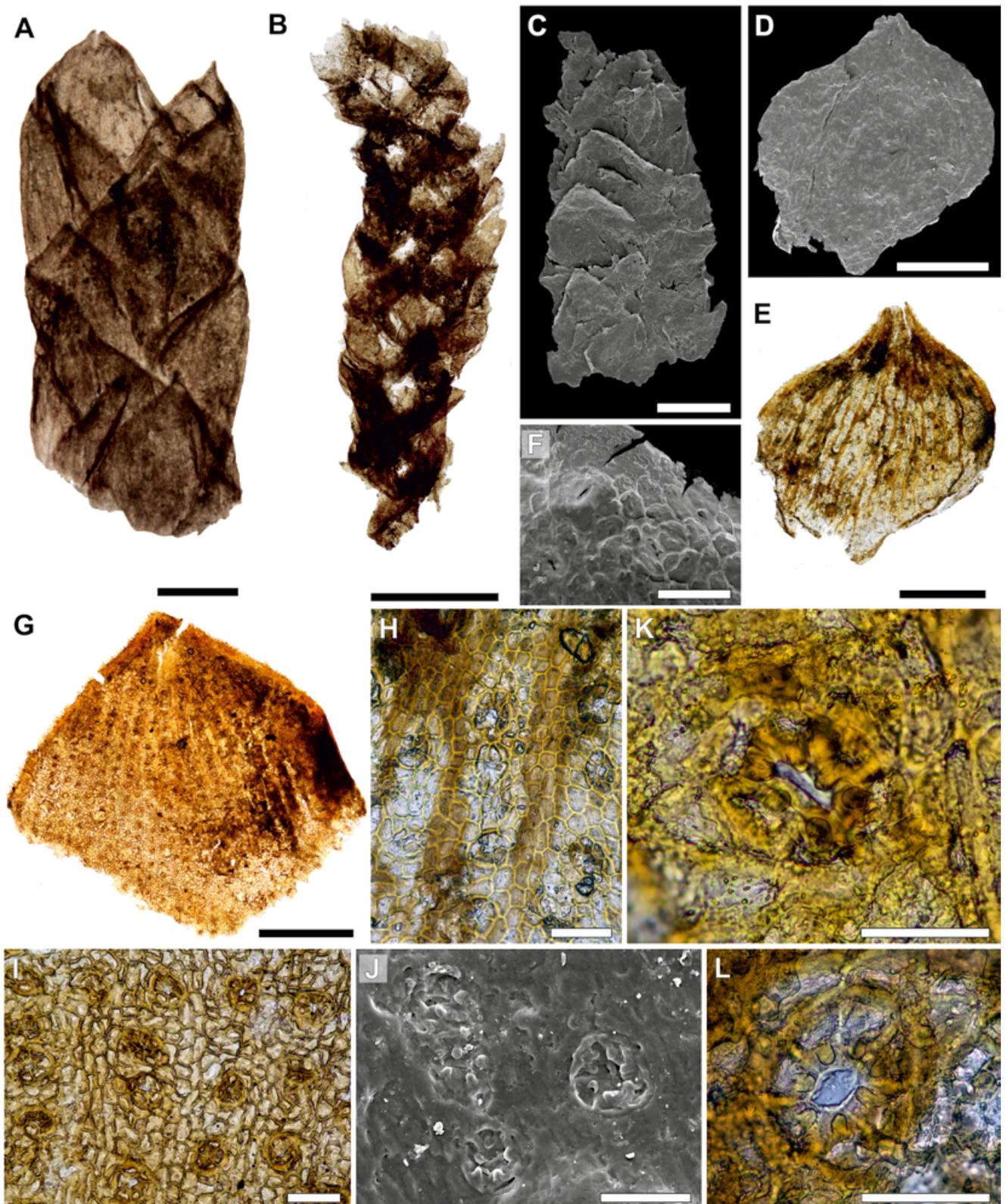


Fig. 14. *Cuticulae dispersae* from the Upper Triassic of Zawiercie-Marciszów, southern Poland. A–L. *Cuticulae dispersae* Type E; A – fragment of a twig with helically arranged leaves; B – fragment of a twig with helically arranged twigs, leaves smaller than in specimen in A; C – SEM photo of a twig from B; D, E, G – isolated, scale-like leaves of rhomboidal shape; F – SEM photograph of fringed leaf margin; H–J – stomata arrangement on abaxial cuticle; H – abaxial cuticle showing an underlying fibrous tissue between stomata rows; J – SEM photo of stomata complexes on abaxial cuticle, stomata with prominent papillae on subsidiary cells; K, L – details of stomata complex with prominent papillae on subsidiary cells, directed towards the stomata pit. Scale bar: A–E, G – 10 mm, F, H–L – 50 μ m.

(Fig. 14K, L). Tip of the papilla is slightly swollen. Anticlinal walls of subsidiary cells are heavily thickened (Fig. 14J–L). Adjacent stomata do not share subsidiary cells.

Remarks: All cuticles from Type E represent *Brachyphyllum*-like foliage. *Brachyphyllum*-foliage is a leaf morphogenus recognised from Triassic to Cretaceous and associated with different conifer groups: Cupressaceae, Podocarpaceae, Araucariaceae, Cheirolepidiaceae (Meyen, 1987; Stockey, 1994) and Patokaeeae (Pacyna *et al.*, 2017). Type E cuticles show gross characteristics of Cheirolepidiaceae family (i.e., random orientation of stomata, 4 to 6 subsidiary cells and distinctive papillae on them; Watson, 1988; Ash, 1999; Bomfleur *et al.*, 2011). Separated leaves, as well as short twigs, were found during a bulk maceration. Some cuticles show diverse characters but still remain within the *Brachyphyllum*-like genera as *Brachyphyllum*-like foliage is often accompanied by another foliage type, i.e., *Pagiophyllum*-like (Pacyna *et al.*, 2017) within one

fossil plant. Investigated cuticles are not classified as *Brachyphyllum* sp., but as a separate *cuticulae dispersae* morphotype.

Megaspores

Striatriletes ramosus Marcinkiewicz, 1985

Fig. 15

1960 *Erlansonisporites sparassis* (Murray) Potonie; Marcinkiewicz, tab. 5, figs 4, 5.

1969 *Erlansonisporites ramosus* Marcinkiewicz, p. 108.

1985 *Striatriletes ramosus* Marcinkiewicz, p. 699–698, tab. III, figs 1–4.

Material: ZM01; 7 megaspore specimens.

Description: Outline subcircular, 400–500 µm in diameter. Trilete mark with ridges 60–70 µm high. Ridges are ca. 80% of the megaspore radius (Fig. 15A, D, G). Trilete mark ridges

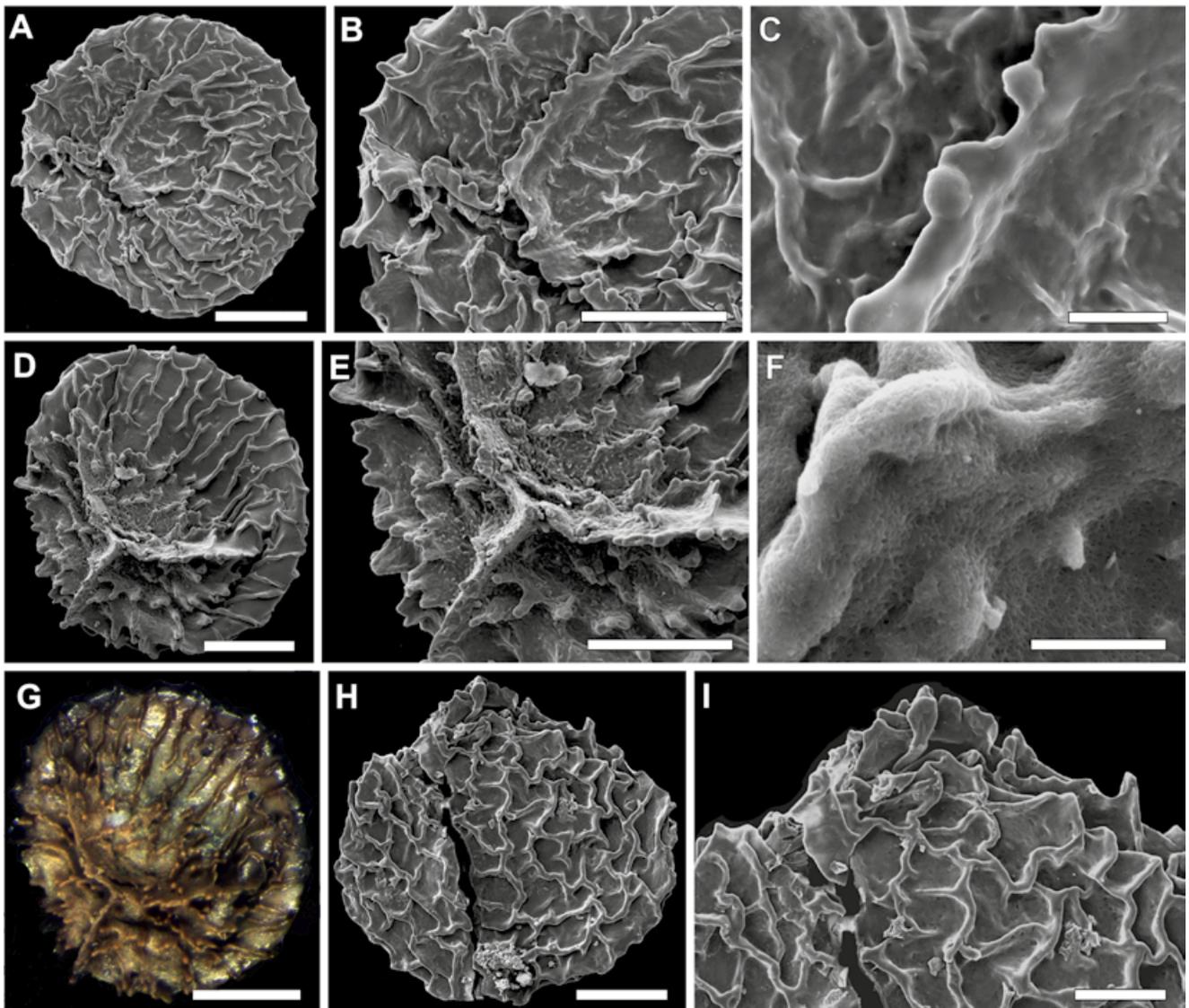


Fig. 15. Megaspore *Striatriletes ramosus* Marcinkiewicz, 1985 from Upper Triassic of Zawiercie-Marciszów, southern Poland. A–F. SEM photographs of proximal side; B – magnification of trilete mark of megaspore in A; C – higher magnification of trilete mark of megaspore from A, showing a wavy margin on top of the mark arm; E – magnification of trilete mark of megaspore in D; F – higher magnification of megaspore surface in E showing a fine mesh structure. G. Proximal side in reflected light. H–I. SEM photographs of distal side; I – magnification of megaspore in H. Scale bars: A, D, G, H – 200 µm; B, E, I – 100 µm; C – 20 µm; F – 10 µm.

are crested with a wavy margin, occasionally topped with granular to spiky ornamentation (Fig. 15B, C, E). Proximal and distal surfaces are covered with ornamentation in the form of ridges radiating from the mark area. Ridges branch towards the edge of the megaspore and form a mesh on the distal surface (Fig. 15H, I). Ridges are 20–30 μm tall and 6–10 μm thick at the base. On some specimens the area between trilete mark arms is covered with shorter ridges (Fig. 15B, E). Megaspore wall is composed of fine mesh (Fig. 15F).

Remarks: Megaspores from Zawiercie-Marciszów were obtained during bulk maceration of mudstone samples with dense accumulation of dispersed plant cuticles. Representatives of only one taxon was found so far. The macrospores fit description of *Striatriletes ramosus* Marcinkiewicz (Marcinkiewicz and Orłowska-Zwolińska, 1985). *S. ramosus* Marcinkiewicz was first described from boreholes found in the Upper Triassic Zbąszynek Beds; (*Erlansonisporites sparassis* Marcinkiewicz 1960, later changed to *Erlansonisporites ramosus nomen nudum* Marcinkiewicz 1969 and finally reclassified as genus *Striatriletes* (van der Hammen, 1954) Potonie, 1956; Marcinkiewicz and Orłowska-Zwolińska, 1985; Marcinkiewicz *et al.*, 2014). Subzone *Striatriletes ramosus* is a lower part of the *Trileites pinguis* zone and is correlated with subzones b and probably c of the miospore *Classopollis meyeriana* zone, dated as late Norian (Marcinkiewicz *et al.*, 2014).

DISCUSSION

The multiple sources of plant fossils available at the Zawiercie-Marciszów locality (calcareous concretions, mudstone, detritus accumulations) and the variety of plant fossil types (petrified stems, dispersed cuticles, compressions) could potentially deliver complementary data about the floral assemblage. However, the *ex situ* character of the sediments presents an obstacle to a comprehensive

palaeoecological reconstruction. Nevertheless, the studied fossils give a general picture of the Norian plant assemblage, consistent with other observations on Norian floras from Northern Hemisphere (Dobruskina, 1994; Pacyna *et al.*, 2017; Kustatscher *et al.*, 2018; Pacyna, 2019). Generally, the dry Norian, favoured xerophytic plants, but dry-humid climate fluctuations (Szulc *et al.*, 2006) facilitated the growth of other plant ecogroups.

The Seefeld Formation flora of the Northern Calcareous Alps (Tyrol, Austria; Fig. 16) is dominated by conifer remains (*Brachyphyllum*, *Pagiophyllum*, *Elatocladus*, *Voltzia*, Cheirolepidiaceae), which include vegetative plant parts and reproductive structures. Cycads (*Taeniopteris*) and lycophytes (*Lepacyclotes*) are marginal components of the fossil assemblage (Dobruskina, 1993; Kustatscher *et al.*, 2017). Scarce fossil floral records from the Norian of Dolomia di Forni Formation (Italy), Giffoni, Filetino (Apennines, Italy) Rio Serai, Carnia (Pre-Alps, Italy; Fig. 16) also is indicative of conifer dominance (*Brachyphyllum*, *Pagiophyllum*, *Pelourdea*, *Voltzia*, *Podozamites*; Dalla Vecchia, 2000, 2012; Kustatscher *et al.*, 2019a). So far, research demonstrates conifer dominance in the Norian localities of Grabowa Fm (this study; Pacyna *et al.*, 2017; Pacyna, 2019). Another locality yielding fossil plants from the Central European Basin is in the Lower Saxony, near the village of Seinstedt, Germany. Delta plain deposits, shaped by fluvial processes are younger than the Grabowa Fm at Zawiercie-Marciszów (Barth *et al.*, 2014). Palynostratigraphy and conchostracan stratigraphy determined age of the succession as the upper Norian–lower Rhaetian (Barth and Kozur, 2011). Disarticulated, preserved in coarse sandstone plant remains are mostly impressions, nevertheless taxonomic diversity is much higher than that observed in older Norian fossil floras of Europe. Conifers of Seinstedt are limited to scale-leaf *Hirmeriella muensteri* (Schenk) Jung 1968, (Cheirolepidiaceae), preserved as shoots and male cones. Common element with Norian Zawiercie-Marciszów is presence of *Neocalamites* (Sphenophyta; Barth *et al.*, 2014). Completely absent from Zawiercie-Marciszów,

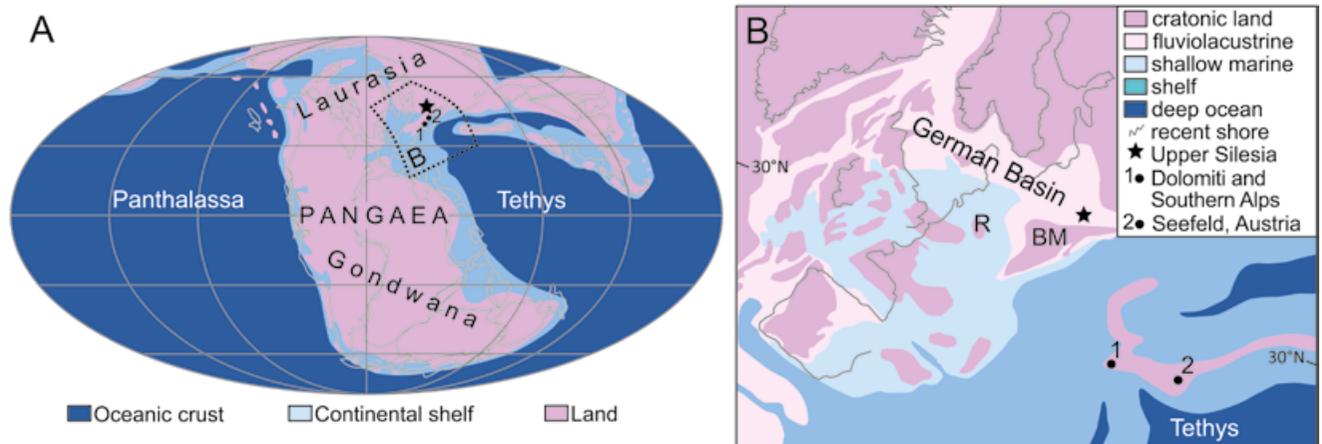


Fig. 16. Late Triassic palaeogeographic reconstructions. **A.** Global palaeogeographical setting during Late Triassic, showing the position of the research area (after Scotese, 2014). **B.** Palaeogeography of the German Basin and Northern Tethys during Late Triassic (after Feist-Burkhardt *et al.*, 2008 and Schobben *et al.*, 2019). Abbreviations: BM – Bohemian Massif; S – Upper Silesia region; R – Rhenish Massif; 1 – Seefeld, Austria; 2 – Dolomiti and Southern Alps.

are abundant in Seinstedt Cycadophyta (*Nilssonia*, *Pterophyllum*) Pteridophyta (*Clathropteris*, *Dictyophyllum*, *Phlebopteris*), and Pteridospermophyta (*Ctenozamites*, *Lepidopteris*, *Ptilozamites*; Brauns, 1862, 1866; Schenk, 1867; Schimper, 1869, 1870–72, 1874; Barth *et al.*, 2014). Fragmented nature and poor preservation of plant remains at Seinstedt are effect of transportation of the material from upstream terrain (Barth *et al.*, 2014)

Conifers are considered well adapted to environments and climates with occasional problems with water deficiency (Farjon, 2010). Especially abundant in Zawiercie-Marciszów are the scale-leaves conifers, *Pagiophyllum* and *Brachyphyllum*. Tightly addressed small leaves, thick cuticle, presence of papillae and sunken stomata help conifers to reduce water loss through transpiration (Thevenard *et al.*, 2005). This could explain their high abundance during the generally drier Norian period (Berra *et al.*, 2010; Preto *et al.*, 2010; Fijałkowska-Mader, 2015; Kustatscher *et al.*, 2018; Bahr *et al.*, 2020). However, local conditions could create conditions suitable for hygrophilous plants, i.e., ferns (Pacyna, 2019), but the fossil record could be biased by the taphonomical persistence of conifer remains.

The presence of sphenophyta macrofossils (genus *Equisetites*, Figs 4–5) at the studied locality, indicates humidification of the environment, which is consistent with palynological and lithological findings of other authors (Szulc, *et al.*, 2006, 2015a, b; Fijałkowska-Mader, 2015; Fijałkowska-Mader *et al.*, 2015; Jewuła *et al.*, 2019). Sporomorph ecogroup (SEG) model and palyno-palaeoclimatic (PPC) model created by Fijałkowska-Mader (2015) indicate the development of conditions preferred by

spore-producing horsetails, at the Zawiercie-Marciszów, such as riparian habitats. The relatively low diversity of sphenophyta is not unusual, e.g., in Carnian flora from Lunz (Austria) there are “only” *Equisetites arenaceous*, *E. conicus* and *Neocalamites myerianii* (Pott *et al.*, 2008, 2018). Sphenophyta can form monotypic communities, which are partially connected with vegetative reproduction common in this plant group (Taylor *et al.*, 2009).

Macro-remains of other plant groups (lycophytes, ferns, seed ferns, ginkgophytes, cycads) are not discernible at the Zawiercie-Marciszów site and the presence of greater plant diversity can only be considered on the basis of miospores (Tab. 3).

Fragmentation of the material indicates that plants were transported for some distance. Multiple types of plant-bearing lithologies give a picture of a different taphonomical history. Particularly interesting are the accumulations of plant detritus. A very dense accumulation of small (less than 3–5 cm) plant particles (leaves, megaspores, twigs, etc.) is a mixture of plants, growing along the river but also collected by water during flood episodes from floodplain areas.

Selectiveness of transport could be a reason behind the reduced diversity of plant remains. Fragile fern fronds during transportation by water currents would be shredded into very small fragments, sphenophyta stems would undergo disarticulation, and secondary axes and leaves would be detached from the main axis. In contrast, the thicker main axis of sphenophyta, woody gymnosperm shoots and strongly cutinised organs have high taphonomical potential (Sweetman and Insole, 2010; Kustatscher *et al.*, 2017).

Table 3

Comparison of fossil plant record from Zawiercie-Marciszów.
Recovered miospores show higher diversification of flora than macrofossils.

Plant group	Microflora (Fijałkowska-Mader <i>et al.</i> , 2015)	Macroflora
Coniferales	<i>Alisporites</i> , <i>Brachysaccus</i> , <i>Cedripites</i> , <i>Classopollis</i> , <i>Duplicisporites</i> , <i>Enzonalasporites</i> , <i>Falcisporites</i> , <i>Geopollis</i> , <i>Granuloperculatipollis</i> , <i>Labiisporites</i> , <i>Lunatisporites</i> , <i>Minutosaccus</i> , <i>Ovalipollis</i> , <i>Parillinites</i> , <i>Pinuspollenites</i> , <i>Platysaccus</i> , <i>Protodiploxypinus</i> , <i>Pseudoenzonalasporites</i> , <i>Rhaetipollis</i> , <i>Vallasporites</i>	<i>Agathoxylon keuperianum</i> (Philippe <i>et al.</i> , 2015; this study) Stem A (this study) Cuticle A–E (this study)
Cycadales, Bennettitales, Pteridosperm	<i>Cycadopites</i> , <i>Monosulcites</i>	–
Pteridopsida	<i>Baculatisporites</i> , <i>Carnisporites</i> , <i>Conosmundasporites</i> , <i>Corrugatisporites</i> , <i>Cyclotriletes</i> , <i>Deltoidospora</i> , <i>Polycingulatisporites</i> , <i>Todisporites</i> , <i>Verrucosisporites</i>	–
Equisetales	<i>Calamospora</i>	<i>Equisetites</i> sp. (this study), <i>Neocalamites</i> sp. (this study)
Lycopodiales	<i>Anapiculatisporites</i> , <i>Densoisporites</i> , <i>Densosporites</i> , <i>Microreticulatisporites</i> <i>Neoraistrickia</i> , <i>Nevesisporites</i> , <i>Reticulatisporites</i> , <i>Uvaesporites</i>	–
Bryophyta	<i>Porcellispora</i> , <i>Taurocusporites</i>	–
Algae	<i>Schizosporis</i>	–
<i>incerte sedis</i>	<i>Foveolatitriletes</i>	–
Fungi	fungal spores	–

CONCLUSIONS

The Norian plant assemblage from Zawiercie-Marciszów, described for the first time, is dominated by conifers, as in other Norian localities in Europe (i.e., Seefeld in Austria; Filettino in Italy).

The presence of sphenophyta (genus *Equisetites* and *Neocalamites*) indicates that local conditions were more humid and suitable for spore-producing plants, as in the mid-Norian tectonic-pluvial episode, recorded in the Lisowice bone-bearing level.

The composition of the fossil plant assemblage studied is dominated by conifer remains, which can be an effect of: (1) selective preservation (i.e., taphonomy), due to relatively long transport distances that resulted in damaged and/or shredded delicate leaves of ferns, and long leaf blades of cycads/Bennettitales and ginkgophytes; and (2) relatively low plant diversity (i.e., palaeoecology), because conifers dominated the environment with minimal or no participation of other plant groups. The second case is considered to be far more probable. The microfloristic record is more diversified (Tab. 3). Miospores of Bryophyta, Lycopodiales, Pteridopsida, Cycadales, Bennettitales and Pteridosperm were recorded from the Zawiercie-Marciszów sediments.

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