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Late Triassic Flora of Southern Poland
Późnotriasowa flora południowej Polski

Ph.D. Thesis
rozprawa doktorska

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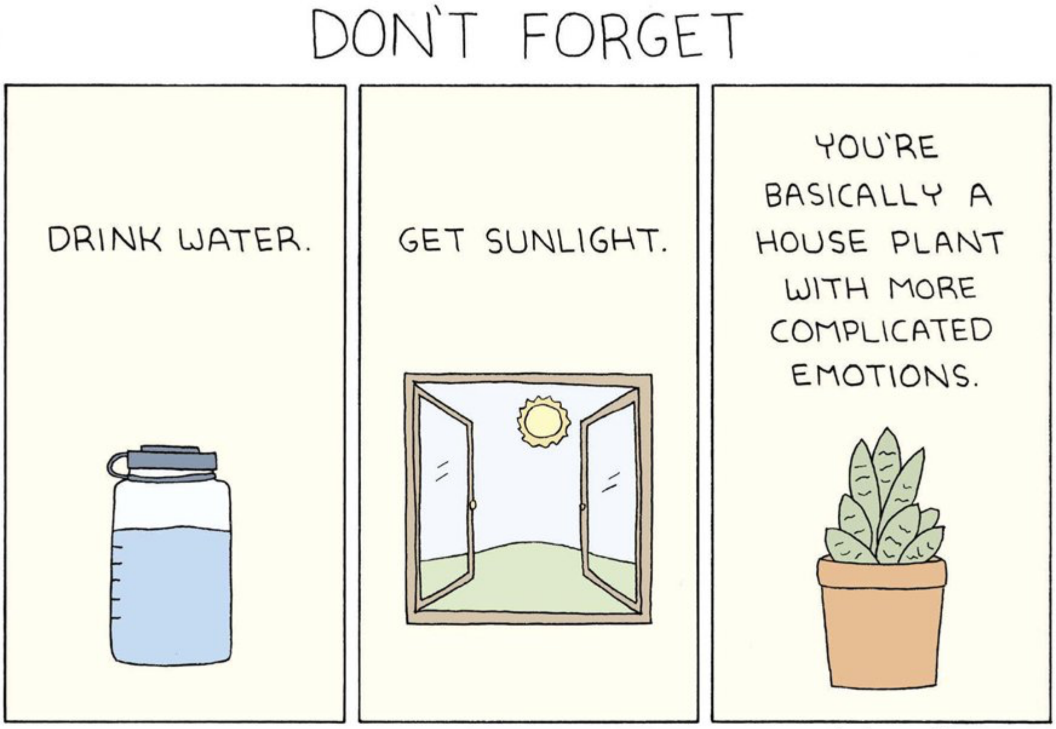

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1. Introduction

Results presented here are an effect of research conducted on plant fossils from the three Upper Triassic localities – two are new (Zawiercie-Marciszów) and one classic (Czerwone Żlebki; Fig. 1).

The Triassic is an important period in the evolution of terrestrial ecosystems. Plant fossils from this period show that plants are able to recover and thrive after catastrophic environmental events. The Triassic period starts with trauma for almost every living creature on Earth – the Permian-Triassic great extinction (Benton, 1995). However, despite this catastrophic event, the fossil record indicates that plants evolved to become prime environmental engineers. It should be recognised that plant fossilisation potential leaves a fossil record with a somewhat limited data entry. Rarely are plants preserved in situ (autochthonous) or close to the place where they grew and more often than not their isolated parts are transported and deposited away from where they grew. The biggest challenge is in the nature of fossil plant assemblages, which usually are a mixture of isolated fragments of different parts of plant bodies. Therefore, collected specimens do not always represent a natural habitat, and reconstruction of the whole plant can be troublesome. Yet still, researching fossil plants is not only valuable in terms of understanding plants themselves and their evolution, but it provides an opportunity to collect data on past climates and environments.

Plant macrofossils from the Upper Triassic, and Triassic in general, from Poland, are very scarce. Apart from sporadic findings from the 19th and 20th centuries by for example, Göppert (1836), Roemer (1870), Gothan (1909) and a small collection by Raciborski (1890), research of Triassic flora was limited to a palynological analysis (e.g., Orłowska-Zwolińska, 1983; Marcinkiewicz, 1969). Recently discovered sites with terrestrially derived sediment successions brought new discoveries, yet only the Krasiejów and Patoka has been studied so far (Pacyna *et al.*, 2017; Pacyna, 2019). Zawiercie-Marciszów and Lipie Śląskie-Lisowice are situated along the Upper Silesia Upper Triassic belt and represent sediments of the German Basin (Fig. 2). Excavations organised by the Institute of Paleobiology of the Polish Academy of Sciences, Institute of Earth Sciences (formerly Faculty of Earth Sciences), and Museum of Earth Sciences of the University of Silesia in Katowice, from 2008 to 2014, were an opportunity to collect a representative amount of fossil plant specimens, which later were analysed at the Institute of Earth Sciences in Sosnowiec (formerly at the Department of Palaeontology and Stratigraphy). In addition to the research of freshly collected material, is the revision of the over hundred years old collection described by Maryjan Raciborski from the Upper Triassic of the Czerwone Żlebki in the Tatra Mountains (Fig. 3). The collection is spread between the Geological Museum of the Institute of Geological Sciences, the Polish Academy of Sciences in Kraków, the Tatra Museum in Zakopane, and the Swedish Museum of Natural History in Stockholm. Fieldwork carried out from 2010 to 2016 at the Czerwone Żlebki site failed to bring any new specimens.

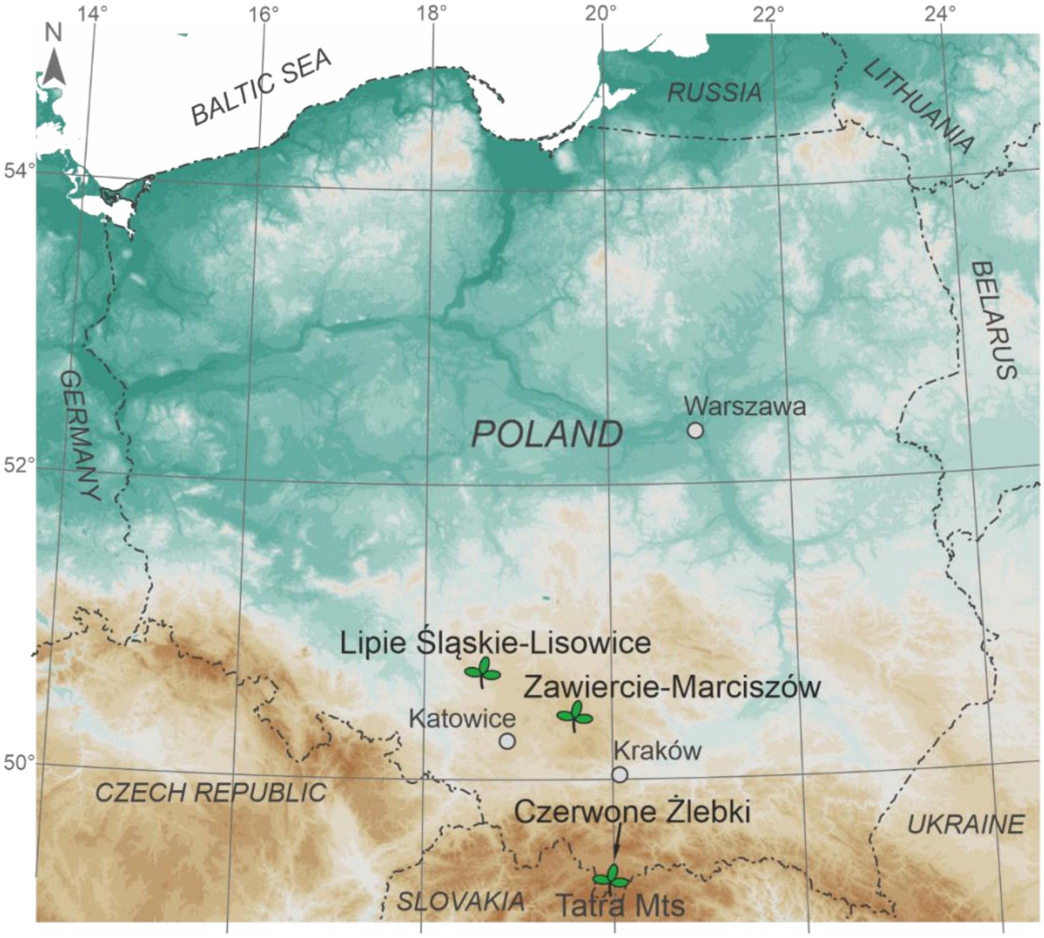

Figure 1. Localisation of selected Upper Triassic sites with plant fossils.

Specimens from all sites vary in preservation quality; those found in the Silesia Upper Triassic localities share some similarities but vary considerably when compared to specimens from the Tatra Mts. Fossils from Silesia (Zawiercie-Marcisżów, Lipie Śląskie-Lisowice) are all embedded in a generally similar grey calcareous mudstone and siltstone. They share some features, such as the presence of cuticles, charcoaled stems, seeds, and reproductive organs. In contrast, the fossil assemblage from Czerwone Żlebki in the Tatra Mountains is preserved in a dark claystone and contains strongly carbonised adpressions, casts, and imprints of leaves, twigs, and stems. When possible, the study of macrofossils should be complemented by observations of cuticles. Cuticles are common in specimens from Silesia, but the Tatra specimens lack them completely. Bulk maceration can also be employed to obtain cuticles from the sediments encapsulating plant fossils. Samples from all sites underwent a chemical maceration adjusted to the type of sediment. A positive result was yielded from sediments from Silesia. Results from Tatra Mountains are satisfactory, although specimen are in poor shape. Current analysis of fossil macro-flora from Upper Silesia and Tatra Mountains uses classic optical methods, such as light microscopy in transmitted and reflected modes. Where it was possible, scanning electron microscopy was in use in addition to a confocal laser scanning microscope.

The main aims of the research conducted for this thesis are:

1) Completing a record of fossil plants from the Upper Silesia Upper Triassic belt, from the outcrops at three new sites: Zawiercie-Marciszów, and Lipie Śląskie-Lisowice, and establishing a taxonomical position of identified remains to reconstruct a relatively comprehensive picture of floral assemblages.
2) A modern revision of the historical collection of Upper Triassic plant fossils from Czerwone Żlebki in the Tatra Mountains, first described by Maryjan Raciborski in 1890, including a re-examination of the specimens and updating the taxonomical description.
3) Reconstruction of plant-animal interactions through plant remains preserved in coprolites.

Interpreting fossil plant assemblages for the purposes of reconstructing the vegetation of past environments is hampered by the strongly biased nature of the fossil record. Fossilised plants present a very incomplete record, and the composition of the fossil assemblage might not be an accurate reflection of the composition of the “original” vegetation, either in terms of the whole plant or the environment in which it grew. However, the plant fossils researched for this study are used for:

1) Filling gaps in the information about the Upper Triassic vegetation of Poland.
2) An attempt at palaeoecological and palaeoclimatological reconstructions.

2. Geological setting

The researched fossil flora originates from two regions with Upper Triassic exposed rocks: Upper Silesia (Zawiercie-Marciszów and Lipie Śląskie-Lisowice; Grabowa Formation) and the Tatra Mountains (Czerwone Żlebki; Tomanowa Formation; Fig. 1). These two regions belong to different geological units - German Basin and Tatricum, and they will be described in separate subsections.

2.1. German Basin - Upper Silesia Upper Triassic belt

Upper Silesia during the Late Triassic was located in the south-eastern-most region of the German Basin, known also as the Central European Basin. This subtropical, low-relief continental basin spread from what is today western France and Germany to eastern Poland (e.g., Beutler and Nitsch, 2005; Feist-Burkhardt *et al.*, 2008; Bachmann *et al.*, 2010; Fig. 2).

2.1.1. General lithology

The successions consist of variegated mudstone and claystone intercalated with sandstone and conglomerate and locally developed carbonates known as the Keuper Group. In Silesia, these deposits are about 400 m thick, but they thicken up to 2000 m towards the northern parts of the basin (Deczkowski *et al.*, 1997; Jewuła *et al.*, 2019).

The general succession of the Upper Triassic in the Upper Silesia area is typical for the German Basin with characteristic lithofacies changes matching climatic conditions of the Western Thetys domain throughout Carnian-Rhaetian (Feist-Burkhardt *et al.*, 2008). The Carnian begins with arid conditions, reflected in the evaporates of the Chrzanów Formation (Fm), which corresponds to the Grabfeld Formation (Lower Gypsum Beds) in NW Germany. In the middle Carnian the climate became more humid. The so-called Mid-Carnian Pluvial Event was responsible for the deposiotn of the fluvial facies of the Schilfsandstein (Stuttgart Fm, “Bolesław” Fm; Jewuła *et al.*, 2019; Fijałkowska-Mader *et al.*, 2021).

The Grabowa Variegated Mudstone – Carbonate Formation Fm starts with the basal Ozimek Member (Mbr.). The formation is equivalent to the Arnstadt Fm (Steinmergelkeuper) of the German lithological scheme (Szulc *et al.*, 2015a, 2015b). In the late Carnian the climate changed again to drier conditions that would last throughout the early Norian. Characteristic for that period are the evaporite-bearing red beds of the Ozimek Member (Mbr.),

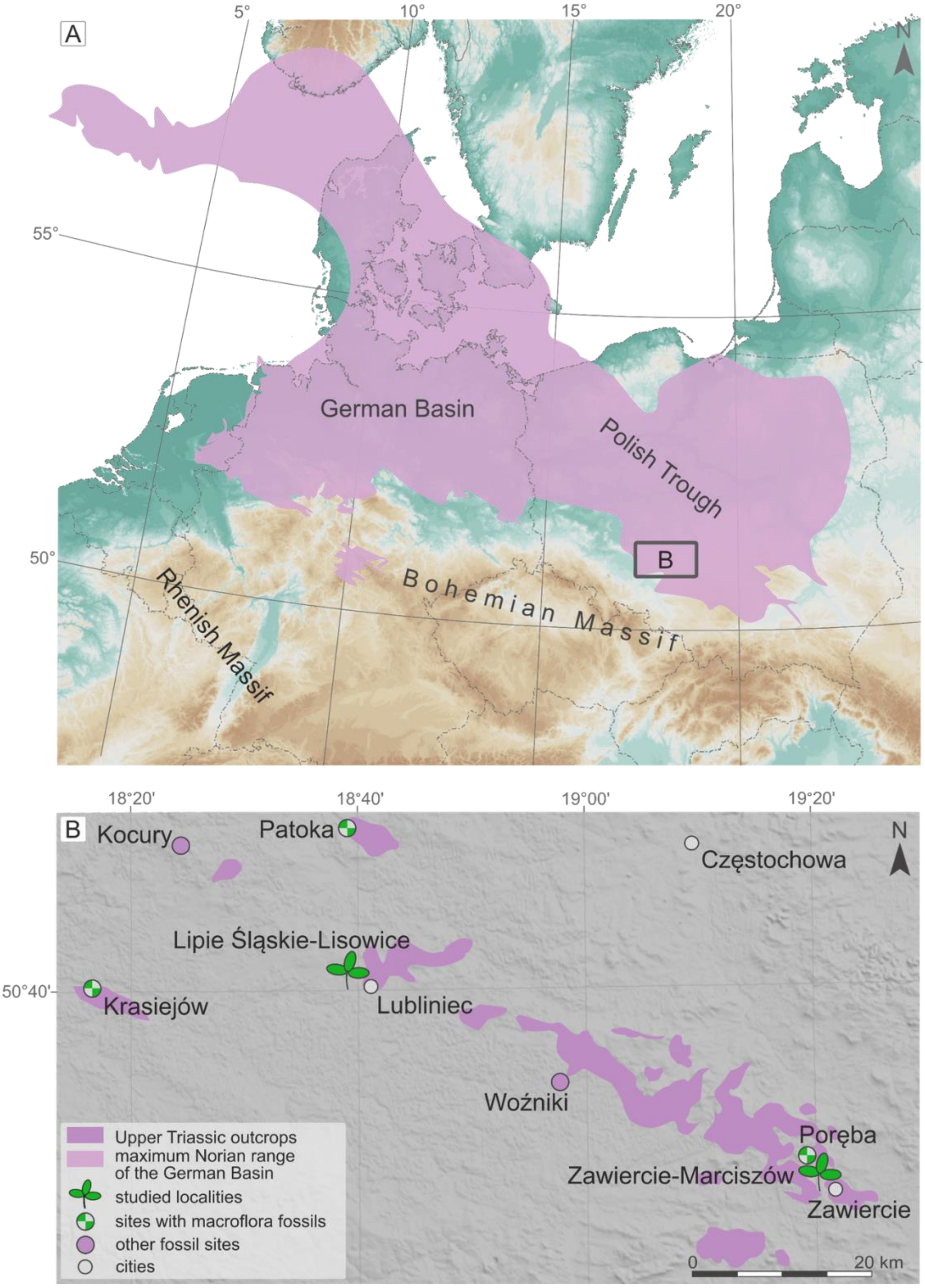

Figure 2. A. Generalized palaeographic map of the Germanic Basin in the Late Triassic with the Upper Silesia Upper Triassic fossil sites (rectangular) (after Feist-Burkhardt *et al.*, 2008). B. Simplified location of the Upper Triassic fossil sites in Upper Silesia (modified from Szulc *et al.*, 2015a; shaded relief from SRTM).

correlated with the Upper Gipskeuper of the German division. From the middle Norian climatic variations between humid and dry conditions (Jewuła *et al.*, 2019) left vertical and lateral facies variation. The mudstone-evaporite succession is replaced by the marly mudstone and sandstone of the Patoka Mbr which contains two bone-bearing levels: Krasiejów and Lisowice. In the upper part of the Grabowa Fm dark grey mudstone and sandstone are accompanied by micritic limestone and travertine with gypsum-rich and cherty horizons of the Woźniki Member (Szulc *et al.*, 2015a, 2015b). The Grabowa Fm is equivalent to the Arnstadt Fm (Steinmergelkeuper) of the German lithological scheme (Szulc *et al.*, 2015a, 2015b). The start of the Rhaetian is characterised by humid climatic conditions. The Upper Silesian Keuper succession is topped with Rhaetian conglomerate and coarse-grained sandstone of “Połomia Formation” (Szulc *et al.*, 2015a, 2015b; Fig. 3).

2.1.2. Lithostratigraphy and biostratigraphy of the Upper Silesia Upper Triassic belt

Due to the relatively scarce biostratigraphic indicators in the monotonous lithology and diachronous character of the terrigenous Keuper deposits of the German Basin, it is difficult to establish a definite chronostratigraphic order of the Upper Triassic continental succession of Upper Silesia (see summary in Bilan, 1991; Szulc and Racki, 2015). Dominated by fluvial siliciclastic deposits, intercalated with evaporates and freshwater carbonates, only a few outcrops are exposed at the surface, but are famous for yielding remains of Upper Triassic vertebrate biotas: Krasiejów, Woźniki, Patoka, Poręba, Zawiercie – Marciszów and Lipie Śląskie-Lisowice (e.g., Dzik *et al.*, 2008a, Dzik *et al.*, 2008b; Niedźwiedzki and Sulej 2008; Budziszewska *et al.*, 2010; Sulej *et al.*, 2012; Sadlok and Wawrzyniak, 2013; Niedźwiedzki *et al.*, 2014; Pieńkowski *et al.*, 2014; Bodzioch, 2015; Zatoń *et al.*, 2015; Szczygielski, 2017; Joyce, 2017; Racki and Lucas 2018; Sulej and Niedźwiedzki 2019; Szczygielski and Sulej 2019; Szczygielski *et al.* 2018; Bajdek *et al.* 2019; Fig. 2B).

The regional correlation of lithostratigraphic units is problematic because of the generally uniform lithology. Lithostratigraphy schemes for the Upper Silesian Keuper was previously proposed by i.a. Dadlez and Kopik (1963), Grodzicka-Szymanko and Orłowska-Zwolińska (1972), Kotlicki (1974), Bilan (1976a, b), Deczkowski *et al.* (1997), and Szulc and Racki (2015). The local lithostratigraphic divisions can be correlated with the classic divisions of the German part of the basin (Fig. 2), with an acceptance that the sedimentation was diachronous throughout the area (Franz, 2008; Szulc *et al.*, 2015a, Jewuła *et al.*, 2019).

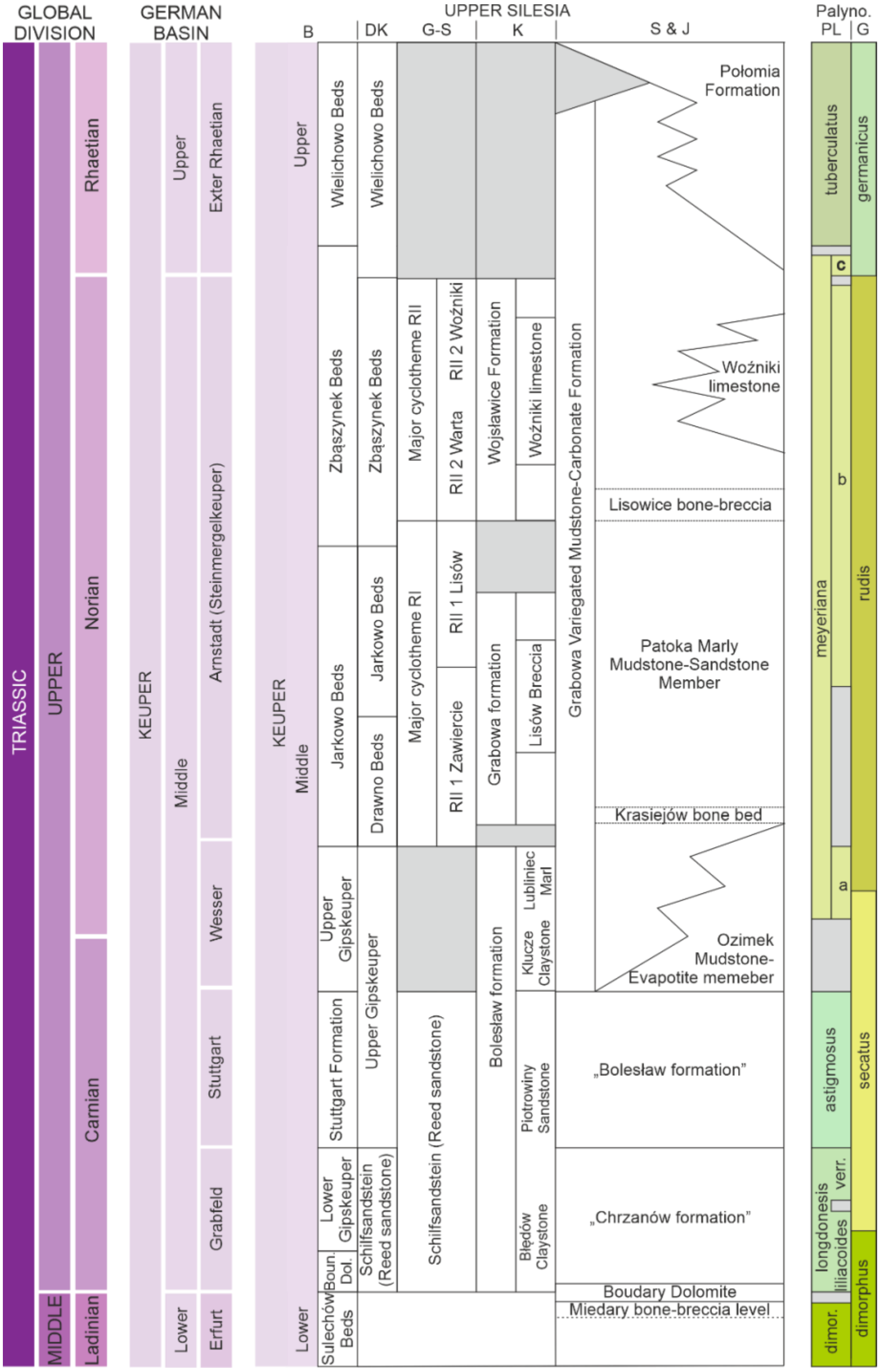

Figure 3. Comparison of the selected geochronological, lithostratigraphic and palynological subdivisions of Upper Triassic and the Upper Silesian Keuper. Abbreviations: B - Becker *et al*. (2008); D&K - Dadlez and Kopik (1963); G-S - Grodzicka-Szymanko (1978); K - Kotlicki (1995); S & J - Szulc *et al*. (2015) and Jewuła *et al*. (2019). Boun. Dol. - Boundary Dolomite, Palyno. - Palynostratigraphy; PL - Polish; G - GTS standard; dimor. - dimorphus; verr. - verrucata.

Despite there being only a few Upper Triassic outcrops in the Upper Silesia region, tremendously rich in fossilised plants and animals, the record of guide taxa is rather scarce and often limited to particular facies or lithostratigraphic units. Available biozonations are based on palynomorphs and conchostraca, with a limited record of the latter (e.g., Kozur and Weems, 2010; Pieńkowski *et al*., 2014; Skawina and Dzik, 2011; Zatoń *et al*., 2015; Niedźwiedzki and Budziszewska-Karwowska, 2018).

Conchostracans occur at the Krasiejów and Lipie Śląskie-Lisowice sites, and recently described from Woźniki (Sulej *et al*., 2020). Conchostracans from the Woźniki clay-pit determined as Laxitextella cf. laxitexta, suggest the deposits are middle to late Carnian (from the Anyuanestheria fimbriata–Laxitextella laxitexta Zone to the Laxitextella freybergi Zone in the German Basin; Sulej *et al*., 2020). At Lipie Śląskie-Lisowice two conchostracans horizons were identified: the lower horizon with Shipingia sp. and Euestheria sp., and the upper horizon with Gregoriusella polonica, indicating the deposits are of the latest Norian and early Rhaetian in age (Kozur and Weems, 2010; Pieńkowski *et al*., 2014).

Miospore-based palynology has been the most comprehensive tool for stratigraphic determination of the Upper TriassicUpper Silesian deposits (see Grodzicka-Szymanko and Orłowska-Zwolińska, 1972; Orłowska-Zwolińska, 1983, 1985). Three miospore assemblages are defined: Porcellispora longdonensis in the "Chrzanów" Fm, Aulisporites astigmosus in the Stuttgart Fm, and Classopollis (= Corollina) meyeriana in Woźniki-Cynków area. Orłowska-Zwolińska (1985) also stressed that establishing a decisive chronostratigraphic correlation of the Upper Triassic epicontinental successions is difficult because of the similarity of the upper Norian and Rhaetian floras and discrepancies in the setting of the boundary between the two stages. Palynological examination by Hennig (in Szulc *et al*., 2006) of the Woźniki Limestone assigned recognised miospore assemblage as subzone IVb Classopollis meyeriana zone suggesting that the age of the deposits is Norian. The Lipie Śląskie-Lisowice site has undergone some palynological investigations. Staneczko (2007b) found a miospores assemblage showing a strong resemblance to Subzone IVb Classopollis meyeriana Zone. Later Dzik *et al*. (2008a, 2008b) recorded the presence of *Brachysaccus neomundanus* and *Monosulcites minimus* and postulated a Rhaetian age for this site. Świło *et al*. (2014) listed miospore taxa from Lipie Śląskie-Lisowice and based on that determined strata as upper Norian – early Rhaetian (cf. Subzone IV c). That age was upheld by Pieńkowski *et al*. (2014). At the Zawiercie-Marciszów site, the preliminary palynological examination by Wawrzyniak (in Sadlok and Wawrzyniak, 2013) showed the presence of miospore assemblage probably representing meyeriana IVb Subzone. In the nearby Poręba site, the recognised palynological assemblage was identified as the characteristic for Subzone IVb of the Classopollis meyeriana Zone (Niedźwiedzki *et al.*, 2014). A more complex palynological investigation was conducted by Fijałkowska-Mader *et al.* (2015). Here, three palynological zones were distinguished: longdonensis veruccata Subzone in the "Chrzanów Fm", astigmosus in the Stuttgart Fm, and meyeriana in the Patoka Mbr of the Grabowa Fm, both from meyeriana b Subzone. Research indicates that the Grabowa Variegated Mudstone-Carbonate Formation belongs to the C. meyeriana IVb Subzone and is of the Norian age. The above data are compiled on Figure 3.

Megaspores were first used to determine Keuper sediment age by Fuglewicz and Śnieżek (1980). In Lipie Śląskie-Lisowice a miospore spectrum containing *Radosporites planus* and *Horstisporites imperfectus* was used to assign the age to the early Rhaetian. A second analysis of the previously described material by Marcinkiewicz (1981) undermined the previous results and determined that the only zone the described assemblage fits is Carnian.

Another approach used for determining the chronostratigraphic timing of the Upper Triassic fossil sites from Upper Silesia is a comparison of the composition the vertebrate fauna in a phylogenetic context. Sulej *et al.* (2020) points to similarities between the vertebrate assemblage of Krasiejów and Woźniki. In both sites are capitosaur (*Cyclotosaurus* sp.), *Ozimek* sp., a silesaurid dinosauriform, phytosaur remains (Phytosauria indet.), are present and evident is the lack of more advanced dinosaurian taxa (e.g., basal saurischians, sauropodomorphs, neotheropods), pointing to both sites as late Carnian in age. Woźniki fossil assemblage differs from older locality at Miedary – late Ladinian (Pawlak *et al.*, 2022; Sulej *et al.*, 2020), and the younger Zawiercie-Marciszów and Lipie Śląskie-Lisowice, which is considered by Sulej *et al.* (2020) to be late Norian – early Rhaetian, following Dzik *et al.* (2008a, 2008b), Niedźwiedzki *et al.* (2012), and Pieńkowski *et al.* (2014). Niedźwiedzki (in Niedźwiedzki and Budziszewska-Karwowska, 2018) favour the Sulej *et al.* (2020) concept suggesting that Lipie Śląskie-Lisowice and Zawiercie-Marciszów could be the same age (late Norian – early Rhaetian) and younger than the Poręba, Woźniki and Krasiejów sites.

2.1.3. Detailed geological setting of researched plant localities

Zawiercie-Marciszów

A locality preserving Upper Triassic plant remains is situated in the western district of Zawiercie-Marciszów (Fig. 4A). The material was recovered from a sediment pile that remained after excavating a site for a new city dump (Fig. 4B). Before the site was refilled, an exposed section was investigated by Joachim Szulc in 2000, and presented in 2006 (Szulc *et al*., 2006; Fig. 5A). As a consequence, all the findings from samples researched here are ex situ.

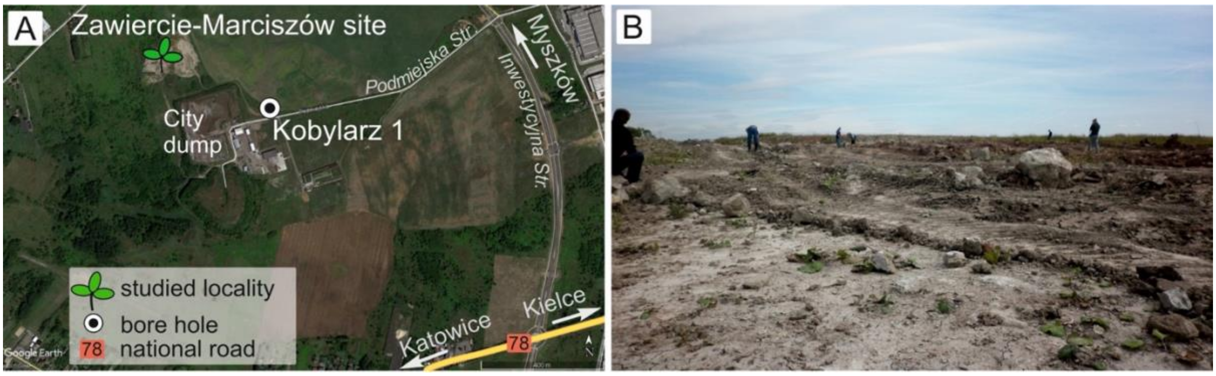

Figure 4. A. Localisation of the Zawiercie-Marciszów site. B. View of the dump site surface.

In 2012 drilling on Kobylarz Hill near the dump allowed for the extension of the previous profile (Fig. 5B). The core from Kobylarz 1 borehole is 55 m thick and consists of red and grey mudstone (Fig. 5C) representing middle Keuper strata, with defined levels of debris-flows, pedogenic levels, and intercalations of carbonate nodules, bivalve-oncoidal limestone conglomerates and plant debris (Fig. 5D). The Woźniki limestone base is above the core top and was poorly exposed in the nearby road cut (Szulc *et al*., 2015a).

Zawiercie-Marciszów indicates a relatively diverse terrestrial ecosystem with preserved microbial structures, plant remains (Fijałkowska-Mader *et al*., 2015; Kubik *et al*., 2015; Philippe *et al*., 2015; Szulc *et al*., 2015b), invertebrates – bivalves (Skawina and Dzik, 2011), ostracods and conchostracans (Niedźwiedzki and Budziszewska-Karwowska, 2018), as well as vertebrate remains including carnivorous *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; Tab. 1A).

Sediments exposed in Zawiercie-Marciszów represent fluvial facies developed as grey fine-grained clastics along with red mudstone and siltstone with sporadic pedogenic nodules. Present at the site are conglomerates containing the remains of microbial structures (oncoids and stromatolites), plant fragments including charcoalified wood, freshwater bivalves, and vertebrate remains like bones, teeth, and tetrapod traces. Fossilized remains are often associated with pyrite concentrations. Some carbonate concretions contain plant remains.

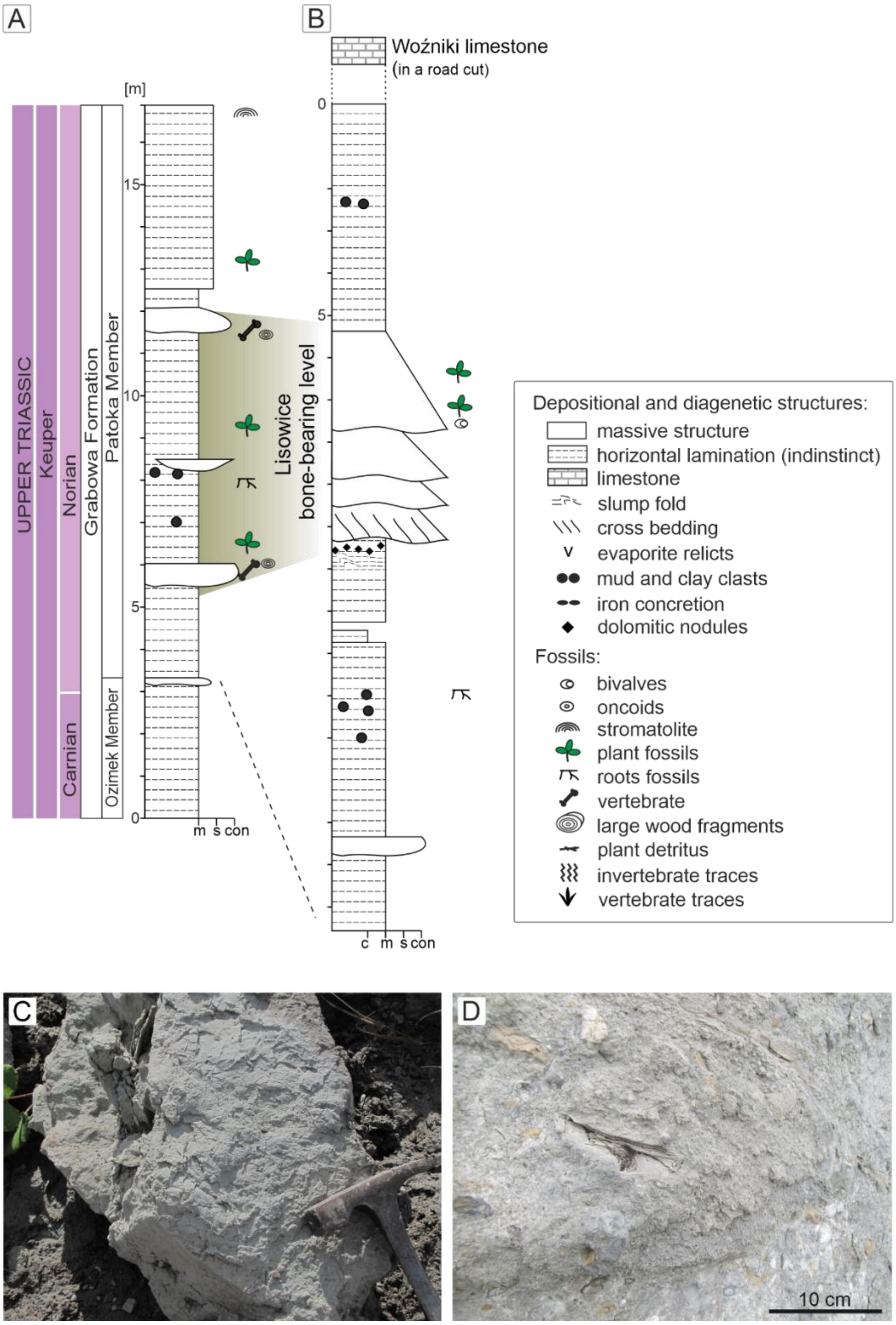

Figure 5. Lithology of the Zawiercie-Marciszów site. A. Lithological section of the strata exposed in the niche of the new city dump (after Szulc *et al.*, 2006; 2015a). B. Kobylarz 1 bore hole log (after Szulc *et al.*, 2015a). C. Grey mudstone block *ex situ* on the pile of sediment. D. *Ex situ* lime conglomerate with fragments of wood.

Preliminary research by Sadlok and Wawrzyniak (2013) showed a miospore assemblage with palynomorphotypes well-known from the Polish Upper Triassic (Orłowska-Zwolińska, 1985; Fijałkowska-Mader *et al.*, 2015), e.g., *Classopollis meyeriana, Ovalipolis ovalis, Brachysaccus neomundanus, Enzonalasporites* sp. It corresponds to the earlier findings of Szulc *et al.* (2006; Tab. 3B), that the clastic and carbonate deposits in the Zawiercie-Marciszów area are of the middle Norian age, based on the assignment to Classopollis meyeriana IVb Subzone (Fijałkowska-Mader *et al.*, 2015).

In the section presented by Szulc *et al.* (2006, 2015a, 2015b; Fig. 5D.) two conglomerate horizons occur that could be the main source of the ex situ fossil material found on the pile. In the lower parts of the section playa deposits are visible with evaporates. The top of the section comprises mudstones and siltstones with stromatolites and conglomerates (Szulc *et al.*, 2006; Szulc *et al.*, 2015a). The bone-bearing section is thought to be an equivalent to the age of the fossil-bearing horizons exposed at the Lipie Śląskie-Lisowice clay-pit ("Lisowice bone-bearing level"; Szulc *et al.*, 2015).

Table 1. A. A list of animal taxa described or mention from the Zawiercie-Marciszów site and adjacent area.

Taxon	Group	Fossil type	References
Vertebrates			
Dicynodontia indet.	Synapsida	bones	Budziszewska *et al.,* 2010
?Archosauromorpha indet.	Sauropsida	toothmarks/bitemarks	Budziszewska *et al.,* 2010
?Archosauromorpha indet.	Sauropsida	footprints	Sadlok and Wawrzyniak, 2013
?Dicynodontia indet.	Synapsida	footprints	Sadlok and Wawrzyniak, 2013
Archosauria indet.	Sauropsida	footprints	Sadlok and Wawrzyniak, 2013
Tetrapoda indet.	?	footprints	Sadlok and Wawrzyniak, 2013
Smok sp.	Sauropsida	bones, teeth	Niedźwiedzki and Budziszewska-Karwowska, 2018
Archosauria indet.	Sauropsida	bones	Malinowska 2015, after Piechowski (interview)
Coelacanthiformes indet.	Osteichthyes	bones	Malinowska 2015, after Piechowski (interview)
Dipnoi indet.	Osteichthyes	teeth	Malinowska 2015, after Piechowski (interview)
Dipnoi indet.	Osteichthyes	teeth	Personal observations Z.W.
Invertebrates			
Tihkia silesiaca	Bivalvia	imprints or casts of the shell surface	Szulc *et al.,* 2015 a, Niedźwiedzki and Budziszewska-Karwowska, 2018; personal observations Z.W.
Ostracoda indet.	Crustacea	imprints or casts of the shell surface	Niedźwiedzki and Budziszewska-Karwowska, 2018
Conchostraca indet.	Crustacea	imprints or casts of the shell surface	Niedźwiedzki and Budziszewska-Karwowska, 2018
Unionites posterus	Bivalvia	imprints or casts of the shell surface	Dadlez and Kopik, 1963; Grodzicka-Szymanko, 1971

Table 1. B. A list of micro- and macrofloral taxa described or mention from the Zawiercie-Marciszów site and the adjacent area.

Taxon	Group	Fossil type	References
Microflora			
Classopollis meyeriana	Coniferales	pollen	Sadlok and Wawrzyniak, 2013; Fijałkowska-Mader *et al.,* 2015
Ovalipolis ovalis	Coniferales	pollen	Sadlok and Wawrzyniak, 2013
Brachysaccus neomundanus	Coniferales	pollen	Sadlok and Wawrzyniak, 2013; Fijałkowska-Mader *et al.,* 2015
Brachysaccus sp.	Coniferales		Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop and Kobylarz 1 bore hole
Enzonalasporites sp.	Coniferales	pollen	Sadlok and Wawrzyniak, 2013; Fijałkowska-Mader *et al.,* 2015
Ovalipollis sp.	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop and Kobylarz 1 bore hole
Granuloperculatipollis rudis	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Labiisporites sp.	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Alisporites sp.	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Parillinites sp.	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop; Kobylarz 1 borehole
Platysaccus sp.	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Falcisporites sp.	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
aff. *Pinuspollenites* sp.	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Protodiploxypinus sp.	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Minutosaccus sp.	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Cedripites sp.	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Classopollis simplex	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Classopollis torosa	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Geopollis zwolinskae	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Duplicisporites granulatus	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Monosulcites sp.	Cycadales, Bennettitales	pollen	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Cycadopites sp.	Cycadales, Bennettitales, Pteridosperm	pollen	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Todisporites sp.	Pteridopsida	spore	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
aff. *Conosmundasporites* sp.	Pteridopsida	spore	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Cyclotriletes sp.	Pteridopsida	spore	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Verrucosisporites sp.	Pteridopsida	spore	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Densosporites sp.	Lycopodiales: Selaginellaceae	spore	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop and Kobylarz 1 bore hole
Nevesisporites sp.	Lycopodiales	spore	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Taurocusporites sp.	unknown affinity	spore	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Reticulatisporites sp.	Lycopodiales	spore	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Deltoidospora sp.	Pteridopsida	spore	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Calamospora sp.	Equisetales	spore	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Carnisporites sp.	Pteridopsida	spore	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Anapiculatisportes sp.	Lycopodiales	spore	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Uvaesporites sp.	Pteridopsida, Lycopodiales: Pleuromeiaceae	spore	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Foveolatitriletes sp.		spore	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Corrugatisporites sp.	unknown affinity	spore	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Baculatisporites sp.	Pteridopsida	spore	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Porcellispora sp.	Bryophyta	spore	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Polycingulatisporites sp.	Pteridopsida	spore	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Microreticulatisporites sp.	Lycopodiales	spore	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Neoraistrickia sp.	Lycopodiales	spore	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Pseudoenzonalasporites summus	Coniferales	spore	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop
Vallasporites ignacii	Coniferales	spore	Fijałkowska-Mader *et al.,* 2015: Zawiercie outcrop

fungal spores	Fungi	spore	Fijałkowska-Mader *et al.*, 2015: Zawiercie outcrop
Schizosporis sp.	Algae	spore	Fijałkowska-Mader *et al.*, 2015: Zawiercie outcrop
Lunatisporites sp.	Coniferales	pollen	Fijałkowska-Mader *et al.*, 2015: Kobylarz 1 borehole
Cedripites sp.	Coniferales	pollen	Fijałkowska-Mader *et al.*, 2015: Kobylarz 1 borehole
Anapiculatisporites sp.	Lycopodiales	spore	Fijałkowska-Mader *et al.*, 2015: Kobylarz 1 borehole
aff. *Todisporites* sp.	Pteridopsida	spore	Fijałkowska-Mader *et al.*, 2015: Kobylarz 1 borehole
Densoisporites sp. reworked	Lycopodiales: Pleuromeiaceae	spore	Fijałkowska-Mader *et al.*, 2015: Kobylarz 1 borehole
Macroflora			
Agathoxylon keuperianum	Coniferales	charcoal and fossil wood	Philippe *et al.*, 2015
charcoal	Gymnosperm	charcoalified wood	Kubik *et al.*, 2014

Lipie Śląskie-Lisowice

The Lipie Śląskie-Lisowice clay-pit is situated in Lisowice village near the city of Lubliniec (Fig. 6A). The strata exposed at the Lipie Śląskie-Lisowice clay-pit is dominated by grey calcareous mudstones and siltstones (Fig. 6B). The entire observed stratigraphic section in this locality is approximately 15 m thick and is very rich in plant and animal fossils including two intervals with vertebrate bones (Fig. 7A). Exposed deposits belong to the Patoka Member of the Grabowa Formation (Szulc and Racki, 2015) consisting of calcareous siltstone and claystone, intercalated with sandstone, carbonate conglomerate, marlstone, and limestones. According to Szulc *et al*. (2015a, 2015b) deposits exposed at the Lipie Śląskie-Lisowice outcrop are equivalent to the middle Norian Middle Grey Series within the Steinmergelkeuper known from Germany (the Mittlere Grauer Steinmergelkeuper; the Arnstadt Formation and the Middle Löwenstein Fm).

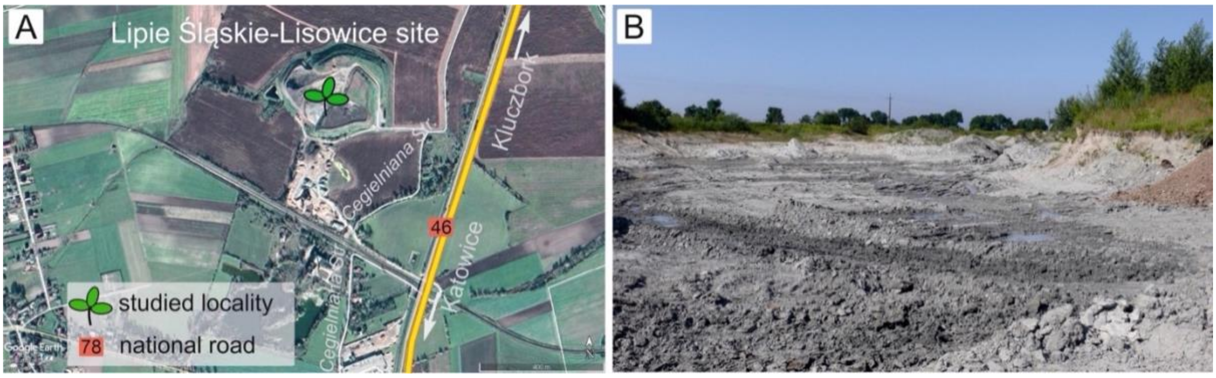

Figure 6. A. Localisation of the Lipie Śląskie-Lisowice site. B. Overview on the clay-pit in Lipie Śląskie-Lisowice.

The lower bone-bearing interval consists of grey sandstones intercalated with carbonate conglomerate. This interval is also rich in plant remains, including charcoalified wood fragments (Marynowski and Simoneit, 2009), as well asinvertebrates (Dzik *et al*., 2008a, 2008b; Niedźwiedzki and Sulej, 2008, 2010; Pieńkowski *et al*., 2014; Niedźwiedzki *et al*., 2015, Zatoń *et al*., 2015).

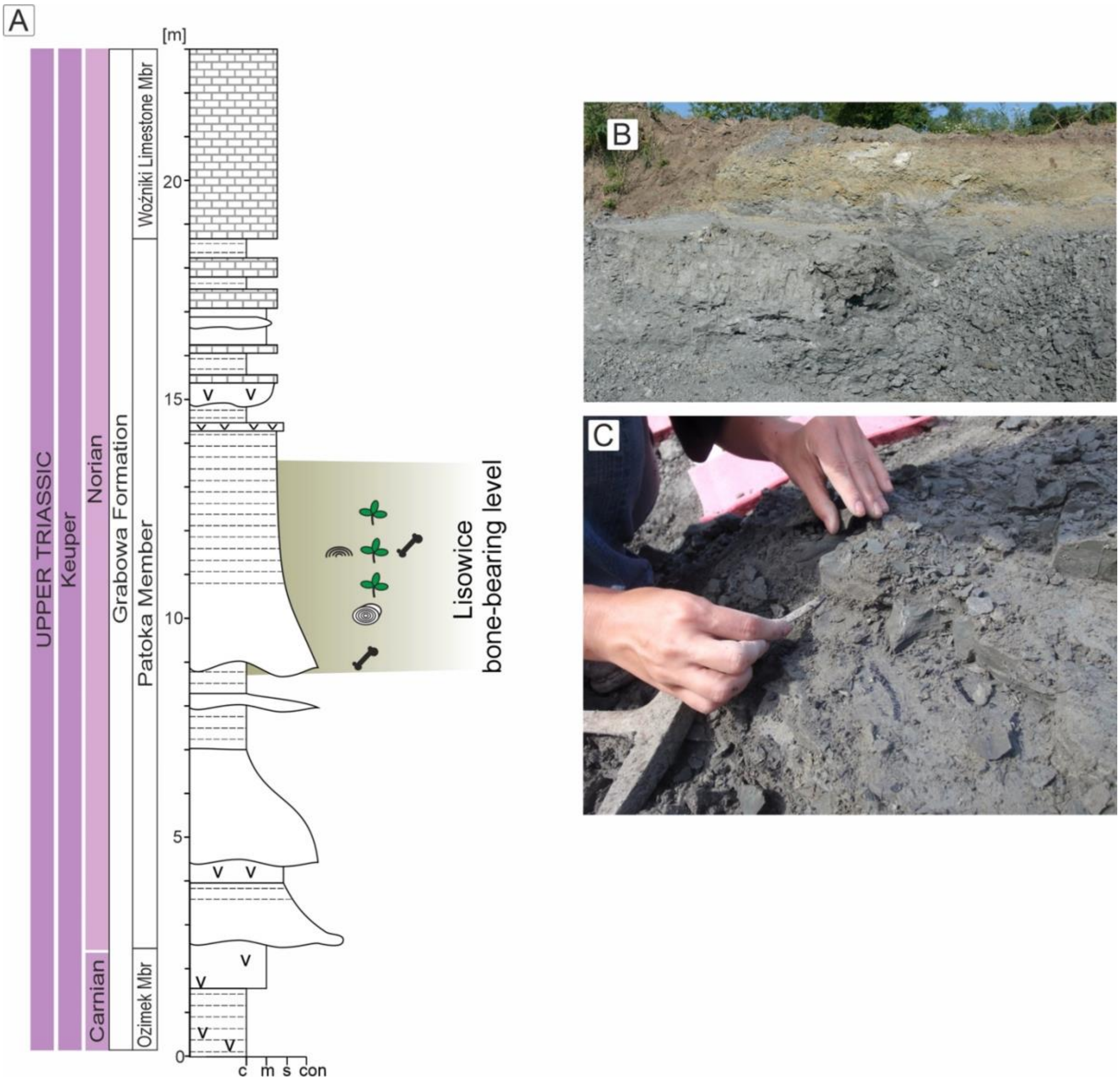

Figure 7. Lithology of the Lipie Śląskie-Lisowice site. A. Lithological section of the strata from Lipie Śląskie-Lisowice (after Szulc *et al*., 2015a; Racki & Lucas, 2018). B, C. Fossil rich grey claystones containing remains of Upper Triassic plants and animals.

The upper bone-bearing interval is composed of dark grey siltstone and claystone and includes invertebrate remains, plant debris, carbonate nodules, stromatolites and oncolites (Szulc and Racki, 2014; Szulc *et al*., 2015a, 2015b; Tab. 2A, Tab. 2B).

There are discrepancies in the biostratigraphic determination of the Lipie Śląskie-Lisowice deposits. According to Dzik *et al*. (2008a, 2008b), Świło *et al*. (2013) and Pieńkowski *et al*. (2014) palynological analysis identified the exposed strata as Subzone IVc of the meyeriana and Ricciisporites tuberculatus zones, suggesting correlation of the deposits with the uppermost Zbąszynek beds and lower Wielichowo beds (uppermost Norian – lower Rhaetian; Fig. 2). Fijałkowska-Mader *et al*. (2015) assigned the miospore spectrum from Lipie Śląskie-Lisowice to the Subzone IVb meyeriana representing middle Norian age. Recent lithostratigraphical considerations by Szulc and Racki (2015), Szulc *et al*. (2015a, 2015b) assigned the bone-bearing Lisowice level to the re-defined Grabowa Formation of Norian age (Fig. 3).

Recently Kowal-Linka *et al*. (2019) recovered single zircon grain from a sandstone bed from below the Lisowice bone-bearing level in the Lipie Śląskie-Lisowice outcrop. An absolute age of 211±3 Ma was returned, indicating that fossils recovered from Lisowice bone-bearing levels in the Lipie Śląskie-Lisowice as well as in Zawiercie-Marciszów are almost certainly not younger than the late Norian (Kowal-Linka *et al*., 2019; Racki and Lucas, 2018).

Table 2. A. A list of animal taxa described or mention from the Lipie Śląskie-Lisowice site

Taxon	Group	Fossil type	References
Vertabrates			
?Anura indet.	Amphibia	bones	Niedźwiedzki *et al.,* 2015;
?Cynodontia indet.	Synapsida	bones	Dzik *et al.,* 2008a
Actinopterygii indet.	Osteichthyes	bones	Pieńkowski *et al.,* 2014; Niedźwiedzki *et al.,* 2015; Zatoń *et al.,* 2015
Archosauria indet.	Sauropsida	bones	Niedźwiedzki and Sulej 2008; Niedźwiedzki and Sulej 2010
Archosauriformes indet.	Sauropsida	bones	Niedźwiedzki *et al.,* 2015
Ceratosauria aff. *Coelophysis*	Sauropsida	teeth	Dzik *et al.,* 2008a
Choristodera indet.	Sauropsida	bones	Pieńkowski *et al.,* 2014; Zatoń *et al.,* 2015
Coelacanthiformes indet.	Osteichthyes	bones	Niedźwiedzki and Sulej 2008; Niedźwiedzki and Sulej 2010; Pieńkowski *et al.,* 2014; Zatoń *et al.,* 2015
Coelophysoidae indet.	Sauropsida	bones	Dzik *et al.,* 2008b; Niedźwiedzki and Sulej 2010
Cyclotosaurus sp.	Amphibia: Cyclotosauridae	bones	Dzik *et al.,* 2008a; Dzik *et al.,* 2008b; Niedźwiedzki and Sulej 2008; Niedźwiedzki and Sulej 2010; Pieńkowski *et al.,* 2014; Zatoń *et al.,* 2015
Dinosauria indet.	Sauropsida	bones	Niedźwiedzki and Sulej 2010
Gerrothorax sp.	Amphibia: Plagiosauridae	bones	Dzik *et al.,* 2008a; Dzik *et al.,* 2008b; Niedźwiedzki and Sulej 2008; Niedźwiedzki and Sulej 2010; Pieńkowski *et al.,* 2014; Zatoń *et al.,* 2015
Hallautherium sp.	Synapsida	bones	Pieńkowski *et al.,* 2014; Świło *et al.,* 2014 Zatoń *et al.,* 2015
Hybodontoidea indet.	Chondrichthyes	bones	Dzik *et al.,* 2008a; Dzik *et al.,* 2008b; Niedźwiedzki and Sulej 2008; Niedźwiedzki and Sulej 2010; Pieńkowski *et al.,* 2014; Zatoń *et al.,* 2015; Niedźwiedzki *et al.,* 2015
Kannemeyeriiformes indet.	Synapsida	bones	Zatoń *et al.,* 2015
Lisowicia bojani	Synapsida: Placeriinae	bones	Dzik *et al.,* 2008a; Dzik *et al.,* 2008b; Niedźwiedzki and Sulej 2008; Niedźwiedzki and Sulej 2010; Niedźwiedzki *et al.,* 2011; Bajdek *et al.,* 2014; Pieńkowski *et al.,* 2014; Zatoń *et al.,* 2015; Bodzioch *et al.,* 2015; Racki and

			Lucas, 2018; Sulej and Niedźwiedzki, 2018; Niedźwiedzki and Budziszewska-Karwowska, 2018
Mammaliformes indet.	Synapsida	teeth	Niedźwiedzki *et al.,* 2015
Palaeonisciformes indet.	Osteichthyes	bones	Dzik *et al.,* 2008a; Dzik *et al.,* 2008b; Niedźwiedzki and Sulej, 2008; Niedźwiedzki and Sulej, 2010; Pieńkowski *et al.,* 2014
Poposauridae indet.	Sauropsida: Poposauridae	bones	Pieńkowski *et al.,* 2014; Zatoń *et al.,* 2015
Pterosauria indet.	Sauropsida	bones	Dzik *et al.,* 2008a; Dzik *et al.,* 2008b; Niedźwiedzki and Sulej 2008; Niedźwiedzki and Sulej 2010; Pieńkowski *et al.,* 2014; Zatoń *et al.,* 2015; Niedźwiedzki *et al.,* 2015
Ptychoceratodus sp.	Osteichthyes	bones	Dzik *et al.,* 2008a; Dzik *et al.,* 2008b; Niedźwiedzki and Sulej 2008; Niedźwiedzki and Sulej 2010; Pieńkowski *et al.,* 2014; Zatoń *et al.,* 2015; Niedźwiedzki *et al.,* 2015
Reptilia cf. *Lepidosauria*	Sauropsida	bones	Dzik *et al.,* 2008a
Rhynchosauria indet.	Sauropsida	bones	Pieńkowski *et al.,* 2014; Zatoń *et al.,* 2015
Silesauridae indet.	Sauropsida	bones	Zatoń *et al.,* 2015
Smok wawelski	Sauropsida	bones	Dzik *et al.,* 2008a; Dzik *et al.,* 2008b; Niedźwiedzki and Sulej 2008; Niedźwiedzki and Sulej 2010; Niedźwiedzki *et al.,* 2011; Bajdek *et al.,* 2014; Pieńkowski *et al.,* 2014; Zatoń *et al.,* 2015; Niedźwiedzki and Budziszewska-Karwowska 2018
Sphenodontia indet.	Sauropsida	bones	Zatoń *et al.,* 2015; Niedźwiedzki *et al.,* 2015
Temnospondyli indet.	Amphibia	bones	Niedźwiedzki *et al.,* 2015
Invertebrates			
Euestheria sp.	Crustacea: Conchostraca	imprints or casts of the shell surface	Dzik *et al.,* 2008a; Kozur and Weems, 2010; Skawina and Dzik, 2011; Zatoń *et al.,* 2015
Tihkia silesiaca	Bivalvia	imprints or casts of the shell surface	Skawina and Dzik, 2011
Gregoriusella polonica	Crustacea Conchostraca	imprints or casts of the shell surface	Kozur and Weems 2010; Pieńkowski *et al.,* 2014; Kozur and Weems, 2010; Skawina and Dzik, 2011; Zatoń *et al.,* 2015
Darwinula sp.	Crustacea: Ostracoda:	imprints or casts of the shell surface	Dzik *et al.,* 2008a; Kozur and Weems, 2010; Skawina and Dzik, 2011; Zatoń *et al.,* 2015
Rhombocythere sp.	Crustacea: Ostracoda	imprints or casts of the shell surface	Dzik *et al.,* 2008a; Kozur and Weems, 2010; Skawina and Dzik, 2011; Zatoń *et al.,* 2015
Shipingia sp.	Crustacea Conchostraca	imprints or casts of the shell surface	Dzik *et al.,* 2008a; Kozur and Weems, 2010; Skawina and Dzik, 2011; Zatoń *et al.,* 2015

Table 2. B. A list of micro- and macrofloral taxa described or mention from the Lipie Śląskie-Lisowice site

Taxon	Group	Fossil type	References
Microflora			
aff. *Conosmundasporites* sp.	Pteridopsida	spore	Fijałkowska-Mader *et al.,* 2015
aff. *Pinuspollenites* sp.	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015
aff. *Todisporites* sp.	Pteridopsida	spore	Fijałkowska-Mader *et al.,* 2015
Alisporites sp.	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015
Alisporites toralis	Coniferales; Pteridosperm	pollen	Świło *et al.,* 2013
Anapiculatisporites sp.	Lycopodiales	spore	Fijałkowska-Mader *et al.,* 2015
Anapiculatisporites spiniger	Lycopodiales	spore	Świło *et al.,* 2013
Anapiculatisportes telephorus	Lycopodiales	spore	Fijałkowska-Mader *et al.,* 2015; Świło *et al.,* 2013
Baculatisporites sp.	Pteridopsida	spore	Fijałkowska-Mader *et al.,* 2015; Świło *et al.,* 2013

Brachysaccus neomundanus	Coniferales	pollen	Dzik *et al.,* 2008a; Dzik *et al.,* 2008b; Fijałkowska-Mader *et al.,* 2015; Świło *et al.,* 2013
Brachysaccus sp.	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015
Calamospora sp.	Equisetales	spore	Fijałkowska-Mader *et al.,* 2015
Carnisporites sp.	Pteridopsida	spore	Fijałkowska-Mader *et al.,* 2015
Cedripites sp.	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015
Cedripites sp.	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015
Cedripites microreticulatus	Coniferales	pollen	Świło *et al.,* 2013
cf. *Carnisporites megaspiniger*	Pteridopsida	spore	Świło *et al.,* 2013
Classopollis classoides	Coniferales	pollen	Świło *et al.,* 2013
Classopollis meyeriana	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015; Świło *et al.,* 2013
Classopollis simplex	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015
Classopollis torosa	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015
Corrugatisporites sp.	unknown affinity	spore	Fijałkowska-Mader *et al.,* 2015
Cycadopites sp.	Cycadales, Bennettitales, Pteridosperm	pollen	Fijałkowska-Mader *et al.,* 2015
Cyclotriletes sp.	Pteridopsida	spore	Fijałkowska-Mader *et al.,* 2015
Deltoidospora sp.	Pteridopsida	spore	Fijałkowska-Mader *et al.,* 2015
Densoisporites sp. reworked	Lycopodiales: Pleuromeiaceae	spore	Fijałkowska-Mader *et al.,* 2015
Densosporites sp.	Lycopodiales: Selaginellaceae	spore	Fijałkowska-Mader *et al.,* 2015
Duplicisporites granulatus	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015
Echitriletes prerussu	Lycopodiales: Selaginellaceae	megaspore	Fuglewicz and Śnieżek, 1980; Marcinkiewicz 1981; Staneczko, 2007
Enzonalasporites sp	Coniferales	pollen	Świło *et al.,* 2013
Enzonalasporites vigens	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015
Eucommiidites sp	Cycadales	pollen	Świło *et al.,* 2013
Falcisporites sp.	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015
Foveolatitriletes sp.	Lycopodiales	spore	Fijałkowska-Mader *et al.,* 2015
Foveolatitriletes crassus	Lycopodiales	spore	Świło *et al.,* 2013
fungal spores	Fungi	spore	Fijałkowska-Mader *et al.,* 2015
Geopollis zwolinskae	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015
Granuloperculatipollis rudis	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015; Świło *et al.,* 2013
Horstiisporites imperfectus	Lycopodiales: Selaginellaceae	megaspore	Fuglewicz and Śnieżek 1980; Marcinkiewicz 1981; Staneczko 2007
Horstisporites bertelseni	Lycopodiales: Selaginellaceae	megaspore	Fuglewicz and Śnieżek, 1980; Marcinkiewicz, 1981; Staneczko, 2007
Labiisporites sp.	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015
Labiisporites triassicus	Coniferales	pollen	Świło *et al.,* 2013
Lunatisporites sp.	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015
Microreticulatisporites sp.	Lycopodiales	spore	Fijałkowska-Mader *et al.,* 2015
Minutosaccus sp.	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015
Monosulcites sp.	Cycadales, Bennettitales	pollen	Fijałkowska-Mader *et al.,* 2015
Monosulcites minimus	Cycadales, Bennettitales	pollen	Dzik *et al.,* 2008a; Dzik *et al.,* 2008b; Świło *et al.,* 2013
Neoraistrickia sp.	Lycopodiales	spore	Fijałkowska-Mader *et al.,* 2015
Nevesisporites sp.	Lycopodiales	spore	Fijałkowska-Mader *et al.,* 2015
Nevesisporites limatulus	Lycopodiales	pollen	Świło *et al.,* 2013
Ovalipolis ovalis	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015
Ovalipollis sp.	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015 ; Świło *et al.,* 2013
Parillinites sp.	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015
Platysaccus sp.	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015
Polycingulatisporites sp.	Pteridopsida	spore	Fijałkowska-Mader *et al.,* 2015
Porcellispora sp.	Bryophyta	spore	Fijałkowska-Mader *et al.,* 2015
Porcellispora longdonensis	Bryophyta	spore	Świło *et al.,* 2013
Protodiploxypinus sp.	Coniferales	pollen	Fijałkowska-Mader *et al.,* 2015
Pseudoenzonalasporites summus	Coniferales	spore	Fijałkowska-Mader *et al.,* 2015

Radosporites planus	Pteridopsida	megaspore	Fuglewicz and Śnieżek, 1980; Marcinkiewicz, 1981; Staneczko, 2007
Reticulatisporites sp.	Lycopodiales	spore	Fijałkowska-Mader *et al.,* 2015
Rhaetipollis germanicus	Coniferales	pollen	Świło *et al.,* 2013
Ricciisporites tuberculatus	Bryophyta, Gymnosperms, Coniferales	spore	Świło *et al.,* 2013
Schizosporis sp.	Algae	spore	Fijałkowska-Mader *et al.,* 2015
Taurocusporites sp.	unknown affinity	spore	Fijałkowska-Mader *et al.,* 2015
Taurocusporites verrucatus	unknown affinity	spore	Świło *et al.,*2013
Todisporites minor	Pteridopsida	spore	Świło *et al.,*.2013
Todisporites sp.	Pteridopsida	spore	Fijałkowska-Mader *et al.,*2015
Todisporites cinctus	Pteridopsida	spore	Świło *et al.,* 2013
Triadispora sp.	Coniferales	pollen	Świło *et al.,* 2013
Triadispora polonica	Coniferales	pollen	Świło *et al.,* 2013
Trileites cf. *pinguis*	Lycopodiales: Selaginellaceae	megaspore	Fuglewicz and Śnieżek 1980; Marcinkiewicz 1981; Staneczko, 2007
Uvaesporites sp.	Pteridopsida, Lycopodiales: Pleuromeiaceae	spore	Fijałkowska-Mader *et al.,* 2015
Vallasporites ignacii	Coniferales	spore	Fijałkowska-Mader *et al.,* 2015
Verrucosisporites sp.	Pteridopsida	spore	Fijałkowska-Mader *et al.,* 2015; Świło *et al.,* 2013
Macroflora			
Agathoxylon keuperianum	Coniferales	charcoal and fossil wood	Philippe *et al.,* 2015
charcoal	Gymnosperm	charcoalified wood	Kubik *et al.,* 2014; Marynowski and Simoneit, 2009
Stachyotaxus septentrionalis	Coniferales	twigs	Dzik *et al.,* 2008b; Pieńkowski *et al.,* 2014
Stachyotaxus sp.	Coniferales	twigs	Dzik *et al.,* 2008a
Hirmeriella muensteri-like	Coniferales	twigs	Dzik *et al.,* 2008b
Lepidopteris cf. *L. ottonis*	Pteridospermophyta	cuticle	Staneczko, 2007; Dzik *et al.,* 2008b

2.2. Tatricum – Tomanowa Formation

The Tatra Mountains represent the highest mountain range in the whole Carpathian Belt. The Tatras are a fold-and-thrust belt with a Palaeozoic crystalline core covered by autochthonous Permo-Mesozoic sedimentary succession and a series of over-thrusted nappes (Nemčok *et al*., 1994; Fig. 8). The so-called Tomanowa Formation (know also on the Slovakian side as the Tomanová Fm) contains Upper Triassic plant remains, and belongs to autochthonous sedimentary succession.

2.2.1. Lithology and lithostratigraphy

During Rhaetian, the Tatric region was located in the NW Palaeotethys, within a shelf-to-shoreline zone, 300-500 km from the deep oceanic basin called the Meliata (Michalik, 1993). Upper Triassic sinistral large-scale faulting resulting from the opening of the Peninic Ocean to the west (Mandl, 1999), portioned the shelf into the Tatric, Fatric, and Hronic units (Michalik, 1993). These global tectonic events also resulted in local block movements, causing marine transgression onto a local morphological depression (Jaglarz and Warchoł, 2009). Hence the Tatric Rhaetian facies are diverse from clastic to marine (Michalik, 1976; Fig. 9).

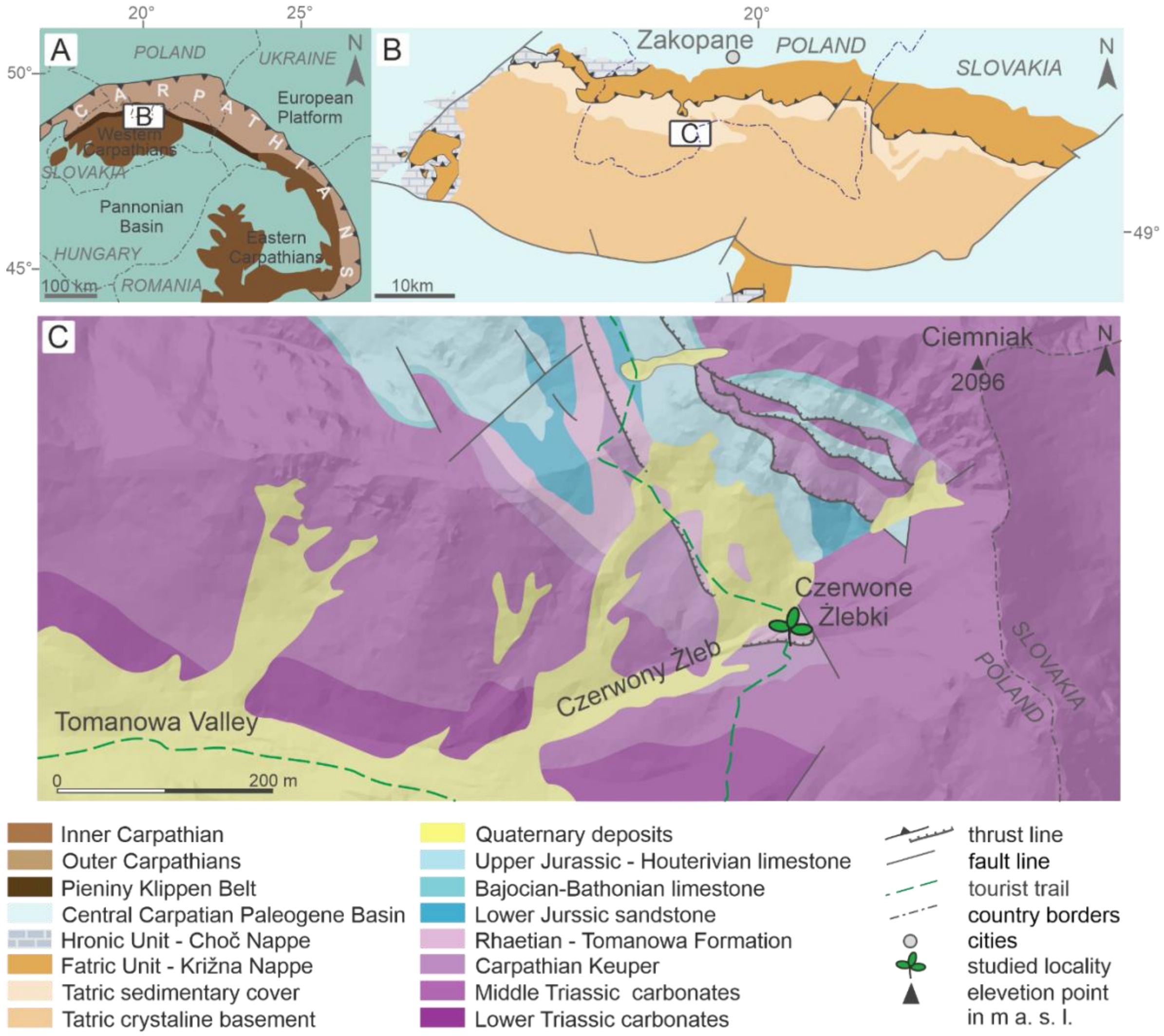

Figure 8. A. Localisation of the Tatra Mountains in the Carpathian Belt (white rectangular shows location of B). B. Geological sketch of the Tatra Mts (after Nemcok *et al.*, 1994; white rectangular shows location of C). C. Surface geological map with position of the Tomanova Formation and Czerwone Żlebki site (after Piotrowska *et al.*, 2008).

The Tomanowa Fm differs from the Carpathian Keuper in its terrestrial (freshwater) origin. In overall, Carpathian Keuper is developed as reddish claystone deposited more proximaly and grey-purple claystone intercalated with dolomite as a result of episodic ingressions (Rychliński, 2008; Michalik *et al.*, 2013). The exact age of the Tomanowa Fm has been discussed since Raciborski (1890) who described it as Rhaetian. Uhlig (1897) considered the Earliest Jurassic age. Kotański (1959) pointed out the possibility of the upper Norian to lower Rhaetian interval, based on lithostratigraphic position.

Fossil research from under- and overlaying strata led Radwański (1968) to assign these layers to the Rhaetian stage. Michalik *et al.* (1976, 1988) consider the uneven bottom of Tomanowa Fm as an indicator of a differentiation of the Tomanowa Fm sedimentation in space and time, suggesting the deposition period as from lower Norian to the base of the Liassic. The lower boundary of Tomanowa Fm varies from depositional with the Carpathian Keuper, to erosive (probably transgressive) with Middle Triassic limestone or Lower Triassic Campilian (Olenekian) claystone (Kotański, 1961; Radwański, 1968). The Tomanowa Fm beds are topped by Lower Jurassic limestone conglomerate (Radwański, 1968; Piotrowska *et al.*, 2009).

The complex geological structures of Tatra Mountains are a result of two major tectonic phases: Late Cretaceous folding and thrusting, and Neogene exhumation. This impedes paleogeographic reconstruction (Szaniawski *et al.*, 2012). Some of the Carpathian formations, are considered analogous to Alpine orogeny (e.g. Kotański, 1965), which was supposed to facilitate interpretation. However, in the case of the Uppermost Triassic of the autochthonous series, this analogy is missing. The Tomanowa Fm is diachronic unit and laterally turns into bioclastic limestone, deposited in a shallow marine environment, hence Radwański (1968) interpreted the clastic Tomanowa Fm also as shallow marine, close-shore sediments. However, lithosomes cyclicality and geometry, as well as varied erosive bottom surface indicate the terrestrial origin of the Tomanowa Fm (Michalik *et al.*, 1988; Lintnerová *et al.*, 2013). An important argument for such an interpretation are the discoveries of dinosaur trace fossils (Michalik *et al.*, 1976; Niedźwiedzki, 2005; 2011; Tab. 3A). Sandstones were deposited in rivers, while mudstone facies represent the flood plain environment (Michalik *et al.*, 1976; 1988; Jaglarz and Warchoł, 2009). After regression plant remains were deposited in remnant ponds and swamps (Michalik *et al.*, 1988; Lintnerová *et al.*, 2013; Tab. 3B). Jaglarz and Warchoł (2009) suggested that Tomanowa Fm was deposited in a proximal part of an estuary.

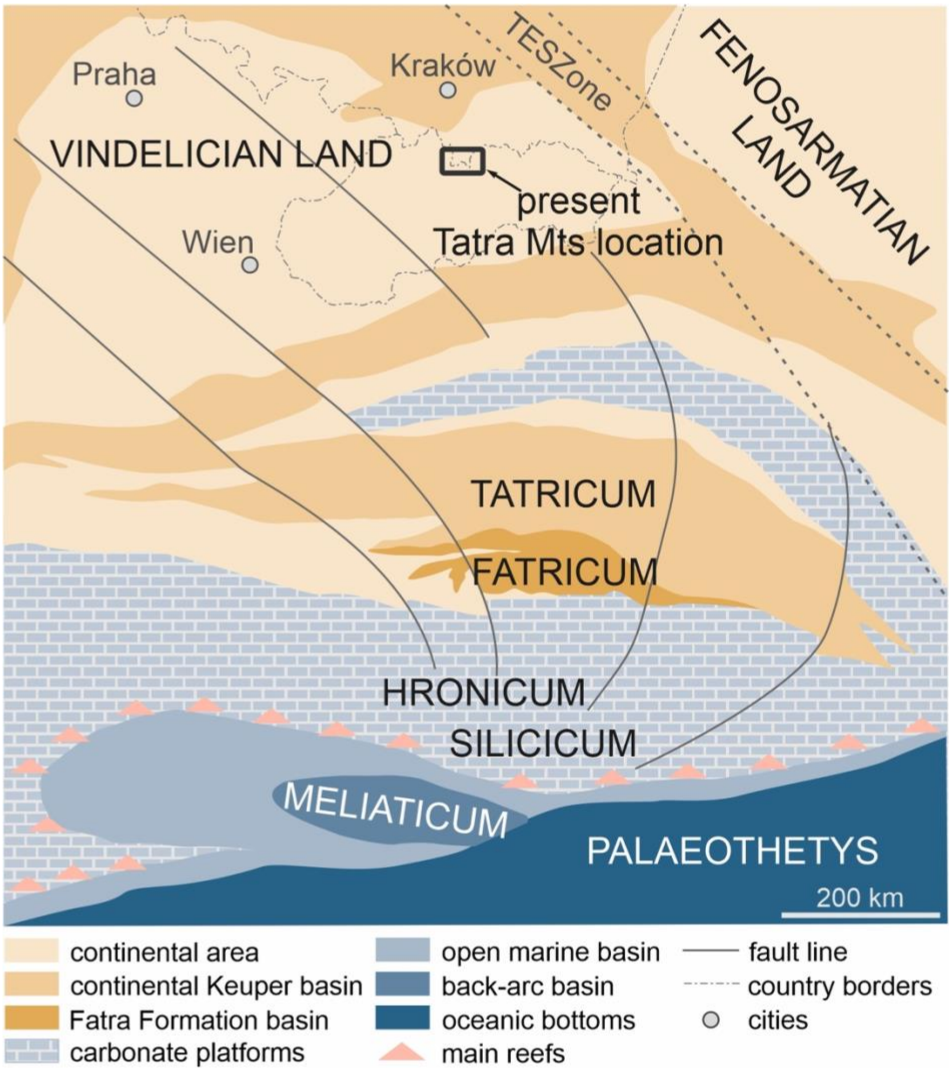

Figure 9. Palaeogeographic map showing position of the Taricum unit during the Late Triassic (after Michalik, 1982).

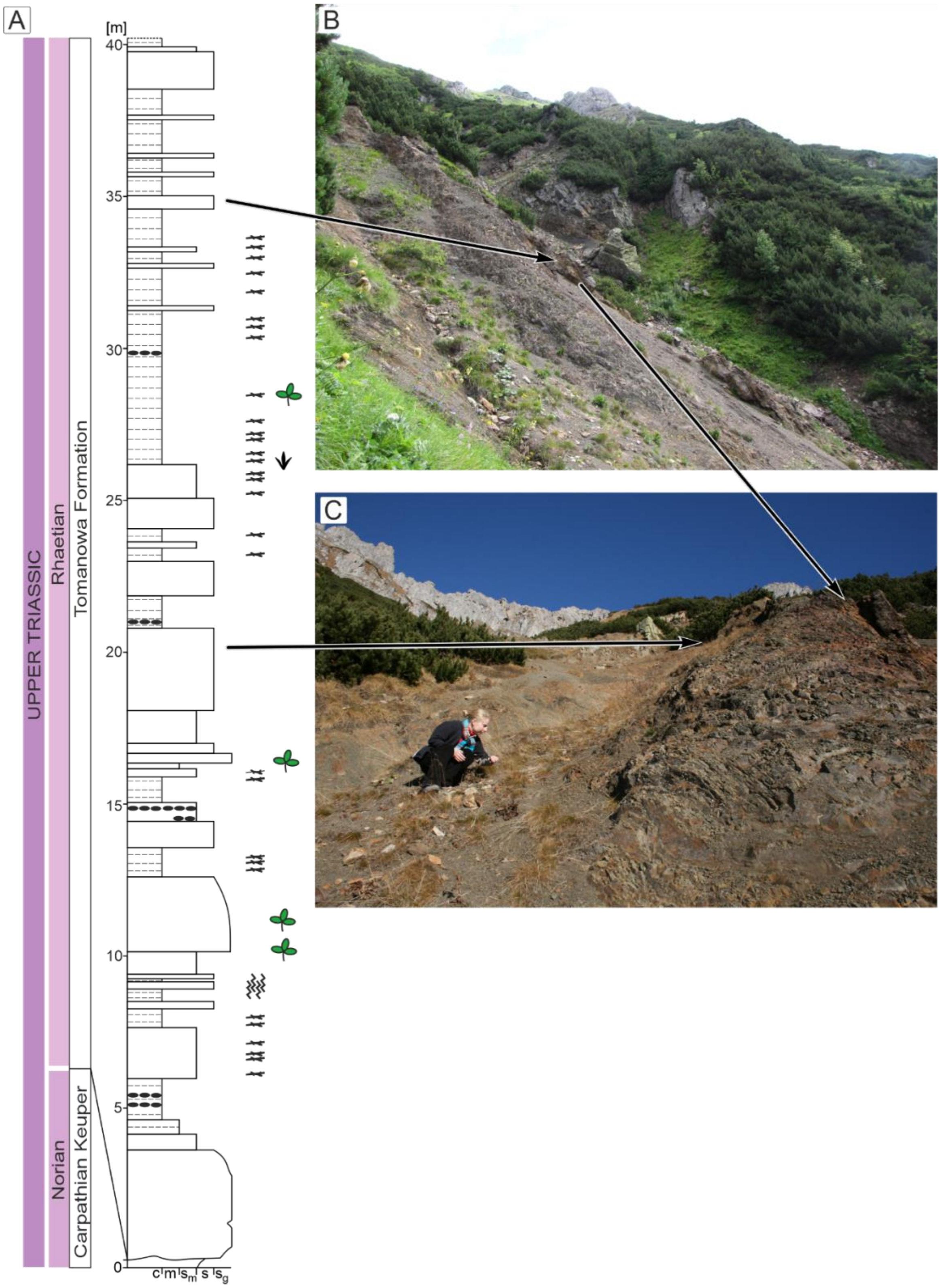

Figure 10. Lithology of the Czerwone Żlebki site. A. Lithological section (after Radwański, 1968; Lintnerova *et al*., 2013). B, C. Exposure of the Tomanowa Fm, arrows pointing sandstones beds.

Czerwone Żlebki

The Tomanowa Fm outcrops only in a few places, and is usually poorly exposed because of the resistance to erosion of the overlying sediments. Only three sites are accessible for detailed research: Czerwone Żlebki and Tomanowski Twardy Upłaz on the Polish side of the Tatra Mountains, and Ćerveny Uplaz on Slovakian side. The Tomanowa Fm is best exposed at the Czerwone Żlebki site in upper part of the Tomanowa Valley in the Czerwone Wierchy massif (Fig. 8). The Tomanowa Fm in the Czerwone Żlebki section starts with quartz sandstone and continues as claystone with plant detritus, intercalated with medium-grained sandstone comprising siderites ores. The middle part of the section is dominated by sandstone and clay sandstone with local erosive surfaces and locally poorly visible lamination. The upper part is represented by fine-grained deposits, mostly claystone with rare sandstone interbeds. (Radwański, 1968; Michalik *et al*., 1976). Quartz sandstone, locally found with gravels in the bottom, forms wide lenses up to 5 m thick. Lithosomes are characterized by a fining-upward succession, but also normal grading occurs within individual layers. Horizontal as well as cross-lamination is poorly preserved (Jaglarz *et al*., 2014; Fig. 10).

At the Ćerveny Uplaz, Tomanowa Fm is overlaid by Dudzieniec Fm developed as a transgressive sequence, gradually transitioning from shoreline to shelf marine environment with benthic foraminifera indicating the late Rhaetian age (Lintnerová *et al*., 2013). That would constrict Tomanowa Fm age to not younger than Rhaetian.

Table 3. A. A list of animal taxa from Czerwone Żlebki locality

Taxon	Group	Fossil type	References
Vertabrates			
Coelurosaurichnus tatricus	Sauropsida: Theropoda	footprints	Michalik *et al.,* 1988
Kayentapus sp.	Sauropsida: Theropoda	footprints	Niedźwiedzki, 2005, 2011
cf. *Anomoepus* isp.	Sauropsida: Ornithischia	footprints	Niedźwiedzki, 2005, 2011
Anchisauripus isp.	Sauropsida: Theropoda	footprints	Niedźwiedzki, 2011
cf. *Grallator* sp.	Sauropsida: Theropoda	footprints	Niedźwiedzki, 2011
?cf. *Moyenisauropus* sp.	Sauropsida: Ornithischia	footprints	Niedźwiedzki, 2011
Sauropodomorpha indet.	Sauropsida	footprints	Niedźwiedzki, 2011

Table 3. B. A list of micro- and macrofloral taxa from Czerwone Żlebki locality

Taxon	Group	Fossil type	References
Microflora			
Taeniaesporites sp.	Coniferales	pollen	Michalik *et al.,* 1976, 1998
Protohaploxypinus sp.	Pteridosper; Coniferales	pollen	Michalik *et al.,* 1976, 1998
Classopollis sp. (=*Gliscopollis* sp.)	Coniferales	pollen	Michalik *et al.,* 1976, 1998
Camarozonosporites sp.	Lycopodiales	spore	Michalik *et al.,* 1976, 1998
Cedripites sp.	Coniferales	pollen	Fijałkowska and Uchman, 1993
Dictyophyllidites harrisii	Pteridopsida	spore	Michalik *et al.,* 1976, 1998
Distalanulisporites punctus (=Annulispora)	Bryophyta	spore	Michalik *et al.,* 1976, 1998
Distanulisporites tomanovae (=Distalanulisporites=Annulispora)	Bryophyta	spore	Michalik *et al.,* 1976, 1998
Enzonalasporites cf. *tenuis*	Coniferales	pollen	Michalik *et al.,* 1976, 1998
Eucommiidites troedssonii	Cycadales	pollen	Michalik *et al.,* 1976, 1998
Eucommiidites major	Cycadales	pollen	Fijałkowska and Uchman, 1993
Granuloperculatipollis sp.	Coniferales	pollen	Fijalkowska and Uchman, 1993
cf. Infirmisporites fragilis	Pteridopsida	pollen	Michalik *et al.,* 1976, 1998
Leiotriletes mesozoicus	Pteridopsida	spore	Michalik *et al.,* 1976, 1998
Lunatisporites rhaeticus	Coniferales	pollen	Fijałkowska and Uchman, 1993
Maratiopsis hoerensis (=Marattisporites sp. = *Marattiopsis* sp.*)*	Pteridopsida	spore	Michalik *et al.,* 1976, 1998
Retusotriletes mesozoicus	Equisetales; Lycopodiales; Bryophyta	spore	Michalik *et al.,* 1976, 1998
Sporites indet.	indet.	spore	Michalik *et al.,* 1976, 1998
Toroisporis auritorius	Pteridopsida	spore	Michalik *et al.,* 1976, 1998
Toroisporis mesozoicus	Pteridopsida	spore	Michalik *et al.,* 1976, 1998
?*Triadispora* sp.	Coniferales	pollen	Michalik *et al.,* 1976, 1998
Bianulisporites badius	Pteridopsida	spore	Michalik *et al.,* 1976, 1998
Cyathitides sp.	Pteridopsida	spore	Michalik *et al.,* 1976, 1998
Cyathitides australis rimalis	Pteridopsida	spore	Michalik *et al.,* 1976, 1998
Gliscopollis meyeriana=Classopollis meyeriana	Coniferales	pollen	Michalik *et al.,* 1976, 1998; Fijałkowska and Uchman, 1993
Classopollis torosus	Coniferales	pollen	Michalik *et al.,* 1976, 1998
Classopollis zwolinskai	Coniferales	pollen	Fijałkowska and Uchman, 1993
Cycadopites follicularis	Cycadales, Bennettitales, Pteridosperm	pollen	Michalik *et al.,* 1976, 1998
Monosulcites cf. *minimus*	Cycadales, Bennettitales	pollen	Michalik *et al.,* 1976, 1998
Monosulcites sp.	Cycadales, Bennettitales	pollen	Fijałkowska and Uchman, 1993
Ovalipollis ovalis	Coniferales	pollen	Michalik *et al.,* 1976, 1998
Ovalipollis sp.	Coniferales	pollen	Fijałkowska and Uchman, 1993
Praecirculina granifer	Coniferales	pollen	Michalik *et al.,* 1976, 1998
Praecirculina tersa	Coniferales	pollen	Michalik *et al.,* 1976, 1998
Protohaploxypinus subcarpathicus	Pteridospem; Coniferales	pollen	Michalik *et al.,* 1976, 1998
Macroflora			
Schizoneura hoerensis	Equisetales	imprints, coalified stems	Raciborski, 1890; Michalik *et al.,* 1988
Equisetum chalubinskii	Equisetales	imprints, coalified stems	Raciborski, 1890
?Equisetum bunburyanum	Equisetales	imprints, coalified stems	Raciborski, 1890
Clathropteris platyphylla	Pteridopsida	imprints, coalified stems	Raciborski, 1890
Dictyophyllum aff. dunkers	Pteridopsida	imprints, coalified stems	Raciborski, 1890
Cladophlebis roessertii	Pteridopsida	imprints, coalified stems	Raciborski, 1890
Pecopteris lobata	Pteridopsida	imprints, coalified stems	Raciborski, 1890
Palissya braunii	Coniferales	imprints, coalified stems	Raciborski, 1890
Widdringtonites sp.	Coniferales	imprints, coalified stems	Raciborski, 1890

Equisetites sp.	Equisetales	imprints, coalified stems	Michalik *et al.,* 1988
Neocalamites sp.	Equisetales	imprints, coalified stems	Michalik *et al.,* 1988
Pagiophyllum sp.	Coniferales	imprints, coalified twigs	Michalik *et al.,* 1988
Palissya sp.	Coniferales	imprints, coalified twigs	Michalik *et al.,* 1988
charcoal			Lintnerova *et al*., 2013

3. Materials and methods

3.1. Materials

The investigated fossil plants come from two separate paleogeographical regions representing two different geological units and two different stratigraphical units: Norian Upper Silesia (Zawiercie-Marciszów, Lipie Śląskie-Lisowice) and Rhaetian Tatra Mts (Czerwone Żlebki).

3.1.1. Upper Silesia Zawiercie-Marciszów

All specimens were collected during excavations organised by the Faculty of Earth Sciences UŚ and Museum of the Faculty of Earth Sciences UŚ from 2009 to 2014, but also from individual fieldwork in 2015 to 2019 carried out by the author of this thesis.

Plant fossils at the Zawiercie-Marciszów locality are ex situ as the outcrop is gone and all remains were found on a sediment pile that remained after the preparation of a city waste-dump. Lithologies containing fossil plant remains can be divided into five types: 1) calcareous concretions with rare plant fossils, 2) calcareous concretions with mostly compressed plant remains arranged horizontally, occasionally cover with microbial structures, 3) fragments of mudstone with plant remains of different sizes disoriented within the matrix, 4) flat, thin fragments of mudstone densely packed with accumulated plant remains of the similar size, mainly cuticles, and 5) separated fragments of three-dimensionally preserved stems.

1) Type 1. Calcareous concretion without plant remains or scarce plant remains. Nodular concretions of micritic limestone are relatively rare on the site. Concretions are shaped irregularly. The average size is ca. 10 x 5 x 8 cm. The outer surface of concretion is smooth (Pl. 1.A). Occasionally concretions contain isolated plant remains, i.e., roots (Pl. 1B), but usually, they lack macroscopic fossils. In thin section bioturbations are visible (Pl. 1C, D). Microscopic observations of the micritic matrix revealed the presence of detritic grains of quartz and voids with quartz crystals. Concretions contain fragments of ostracods shells (Pl. 1E) and scarce plant cuticle fragments. Microflora is poorly preserved.
2) Type 2. Calcareous concretions with abundant plant macro-remains. Concretions containing abundant plant remains were found on site relatively often. The size of these concretions varies from ca. 10x5x10 cm up to 30x15x45 cm, they are round and flattened in one plane. The outer surface can be covered with microbial structures but not in all cases (Pl. 1F). Concretions contain plant remains in different proportions. Plants are fragmentary,

compressed (Pl. 1G, H), and occasionally preserved in three-dimension, i.e., stems filled with sediment (Pl. 1I). Plants are usually coalified, and sometimes the epidermal pattern is recognisable, but less often they are charcoalified. Plant cuticles are abundant, as are microflora. The concretions often contain Sphenophyta fossils (Pl. 1G, I). Compressed plant remains are oriented horizontally to longest axis of the concretion (i.e., parallel to the flattened surface). Concretions are composed of micritic limestones containing a small amount of pyrite. Small voids are often filled with quartz grains. Microfacial analyses revealed the presence of bioturbations (Pl. 1K). Also present in the sediment are crumbled, smooth-shelled ostracods (Pl. 1J, K) and fragments of phosphorous fossils, which are most likely to be fish elements.

3) Type 3. Mudstone with plant macro-remains. Light-grey calcareous solid mudstone is the most common lithology on site. It contains plant fragments of different sizes, including the largest plant remains found so far, such as sphenophyte stems and woody gymnosperms stems (Pl. 2B, C). Besides macrofossils, miospores, cuticles, fragments of leaves and twigs were also found within the mudstones. This mode of preservation is the most diverse in terms of plant body parts and taxonomical content. Intraclasts and bioclasts show no specific orientation within the mudstone matrix. Thin section observations showed the presence of fragmented ostracods and bivalves shells, detritic quartz grains, and pyrite. Along with plant remains, cuticles of arthropods, fish elements, and bone fragments were found.
4) Type 4. Mudstone with a dense accumulation of plant remains. Approximately 15 kg laminated calcareous mudstone comprising of fragmented layers 1 – 2 cm in thickness, densely packed with organic remains were collected on-site. Calcareous, light-grey coloured mudstone is interbedded with 1 – 2 mm thick laminas of plant detritus (Pl. 2F – H). A major component of the accumulation is plant cuticles (Pl. 2I, J), coalified to a varying degrees, with a smaller accumulation of charcoalified woody particles. Microflora, including megaspores is present. Remains are mixed without any particular orientation within the mudstone, are fragmented, and no larger than 1 cm^2.
5) Type 5. Three-dimensionally preserved stems. Plant stems found separately on site with pith filles with micritic limestone are rare. Only three were found so far (Pl. 3 and Pl. 7). Stems are fragmentary with partially petrified tissues remains. Thin sections showed traces of charcoalification (Pl. 3D, E, H). The inner pith is filled with neomorphized micritic limestone. Detritic quartz grains, pyrite and fragments of smooth-shelled ostracods are present (Pl. 3G). The terminology used in the description follows the IAWA Committee

(2004) and the key for identifying coniferous morphogenera by Philippe and Bamford (2008).

Investigated specimens are stored at the Institute of Earth Sciences of the University of Silesia in Katowice and the Museum of Earth Sciences of the University of Silesia in Katowice. There are 30 specimens with working numbers and ca. 15 kg of mudstone with plant detritus, held at the Institute of Earth Sciences, not included in the Museum of Earth Sciences collection. Working number starting with prefix “Z”; Z01–Z25, ZK1–ZK2, ZST1–ZST4 (mostly macrofossils preserved in concretions and on rock slabs), ZCD_A–ZCD_D (cuticulae dispersae), ZM01 (megaspore). As all specimens from this locality are ex situ they were grouped according to the preservation mode they represent and the plant morphotype of main interest in a particular piece and not any specific layer or strata. Cuticulae dispersae were retrieved in bulk maceration of mudstone with the dense accumulation of plant detritus (Preservation mode 4). Slabs of mudstone are not oriented and were collected on a loose pile at the site, but with certainty, they represent one stratum. Therefore, macerated cuticles are sorted accordingly to the morphotype, following the procedures for all cuticulae dispersae researched in this thesis (see Methods). Each group is described with a capital letter (five morphogroups, from ZCD_A–ZCD_E).

Specimens at the Museum of Earth Sciences at the US in Katowice are held under the collection acronym WNoZ_S_7. Only three specimens were selected for this research: WNoZ_S_7_159, WNoZ_S_7_193 and ZSTMuseum_no_number_ZST5_working_no.

3.1.2. Upper Silesia Lipie Śląskie-Lisowice

Fossil plants from the Lipie Śląskie-Lisowice locality were collected during excavations organised by the Institute of Palaeobiology, Polish Academy of Sciences (PAS), Warsaw, Poland, from 2006 to 2014. Upper Triassic strata are rich in plant fossils, such as charcoalified tree trunks, coalified compressions of shoots, and separated plant parts (i.e., cones, leaves, seeds). Sediment also contains dispersed cuticles (cuticulae dispersae), sometimes forming thin layers of highly concentrated plant detritus.

Plant remains were also preserved in three coprolites of a giant herbivore animal. They consist of wood fragments, higher plant cuticles, disaggregated higher plant tracheids, and black amorphous organic particles. Higher plant cuticles are the most numerous components of the coprolites. Coprolites are stored in the collection of the Institute of Paleobiology PAS and have the following numbers: 1 - ZPAL V.33/1101, 2 - ZPAL V.33/1106, 3 - ZPAL V.33/1107.

Hand specimens housed at the Institute of Earth Sciences (UŚ) are part of the Institute of Paleobiology PAS collection (collection acronym ZPAL V.33). Researched specimens have been given working numbers (L/I/_–L/X/_) for organizational reasons.

3.1.3. Tatra Mountains Czerwone Żlebki

Revised material consists of 119 specimens from the collections stored in the Geological Museum of the Institute of Geological Sciences, Polish Academy of Sciences, Research Centre in Kraków (collection acronym ZNG PAL A-III-31; 96 specimens), Tatra Museum in Zakopane (prefix "G"; 10 specimens) and Swedish Museum of Natural History in Stockholm (prefix "S", 13 specimens).

Specimens illustrated in the 1890 monograph were not numbered by Raciborski and illustrations are often presented with an idealised interpretation, therefore tracking the original specimens was difficult.

Plant fossils are preserved in black claystone and dark-brown sandstone as carbonised (charcoalified) compressions, casts and imprints. Some specimens are stained with yellowish limonite crust. On some specimens a thin layer of white-translucent calcite is present. Despite being preserved in fine-grained sediment the fossils do not show preservation of fine-structural details, except for the sporadic presence of epidermal pattern impressions.

Plant parts are fragmented and isolated, often dispersed without showing any particular order, or are densely accumulated. Maceration for retrieving plant cuticles from macrofossils was unsuccesfull, but bulk maceration revieled minute cuticle fragments.

3.2. Methods

3.2.1. Extraction and preparation

Macrofossils preparation

Surface preparation. Macro specimens collected during fieldwork in recent years (Zawiercie-Marciszów and Lipie Śląskie-Lisowice) often needed a proper preparation technique before data could be obtained in as much detail as possible. Yet, the procedures must be applied with caution to prevent damaging specimens and losing information. Fossils preserved in concretions, i.e., in Lipie Śląskie-Lisowice, are often broken along a fracture passing through the organic remains leaving a cleaved compression (see Chaloner, 1999). Under, often loose and fragile coaly tissue, are impressions of the plant surface in form of microrelief. Removing coaly film with soft brush or gentle air stream can result in highlighting e.g., anticlinal cell walls, surface structures, cell shape and cell organisation. This kind of effect is present in some of the specimens from Zawiercie-Marciszów, where plant remains are covered with coaly layer that is fragile and easy to remove, but often there is a faint cell impression underneath. When needed a portion of sediment was removed to unveil plant remains. A dissecting needle was used in that process.

Specimens from the Tatra Mountains did not undergo any preparation due to the historical status of the collection. Small pieces that had become naturally chipped from specimens were used for bulk maceration. To remove dust from the surface of some specimens a very soft brush was used or a gentle air stream.

Thin sectioning. 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 later grinded and polished with Logitech PM5 precision lapping and polishing systems, using abrasive diamond powder of 3, 1 and 0.25 µm and 0.04 µm silicon powder.

Cuticles from macrofossils. To remove sediment the plant remains were treated with 10% hydrochloric acid HCl and 20% hydrofluoric acid HF. Later, cuticles were macerated using Schulze's reagent (25% nitric acid HNO_3 with a few crystals of potassium chlorate $KClO_3$) and subsequently treated with a 5% potassium hydroxide KOH. After each step residue was rinsed with water. Macerated cuticles were washed with distilled water and dehydrated in pure glycerine. Each cuticle is kept in an Ependorph tube in pure glycerine with a few drops of thymol to prevent fungal growth (Kerp and Bomfleur, 2011).

Cuticulae dispersae

From each fossil site, sediment samples were macerated to retrieve dispersed cuticle material. Basic procedures were employed followed standard bulk maceration techniques described in Wellman and Axe (1999), Batten (1999), Pearson and Scott (1999), Reymanówna (1960), Worobiec (2003) and Florian and Worobiec (2016). Personal training with Prof. Hans Kerp from the Institute for Geology and Palaeontogy at the University of Muenster, Germany and Dr Jadwiga Ziaja from the Institute of Botany Polish Academy of Science, helped the author of this thesis to gain skills and fluency in using maceration techniques.

The protocol followed was modified slightly each time accordingly to the sample lithology and fossil preservation to ensure the best results. Samples ca. 1 x 1 cm in size were washed and left to naturally dry, later inserted in a glass beaker of 250 ml volume. The next steps were conducted under a fume hood. 10% HCl was added to every beaker in an amount that allowed the acid to completely cover the sample. After the reaction stopped and residuum sank the acid was gently decanted. 10 % HCl acid was added again and decanted after the reaction stopped. Next, 38% HCl acid was added, and after the reaction 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 neutral pH was achieved (tested using pH universal paper indicator). Every following decantation was conducted after ca. 12 to 24 hours, for certainty that the whole content sunk. Neutralised residuum was transferred to polypropylene containers and allowed to use in contact with HF acid. Ca. 24 hours later, after the residuum completely sunk to the bottom of the container, the remaining water was removed using a pipette. Later to every container 20 ml of 40% HF acid was added. After one to 24 hours, samples were neutralised with distilled water and after material sunk it was decanted. This step was repeated until residuum was completely neutral.

Macerated cuticles are stored in glass containers in pure glycerine with a few drops of thymol to prevent fungal growth.

3.2.2. Photography and documentation

Fossil plants that were subject of this researched are presented on Plates 1–42 at the end of this dissertation.

Macrophotography

Hand specimens were photographed using Canon 350D system with objective Canon EFS 18-55 and Canon Macro Lens EF 100 mm 1: 2.8 USM for macrophotography. The exceptions are specimens from NHM Sweden, which were photographed on-site using Canon EOS 5D Mark III. The camera was installed on a photography rack with an adjustable horizontal positioning of the camera and four LED lamps on adjustable holders for different angles of incident light to enhance the surface details. Fine detailed, bigger specimens were photographed in sections and merged in Adobe Photoshop software to obtain a high-resolution image.

Microphotography

Very fine details of hand specimens (ca. < 5 mm), thin sections, and megaspores were photographed using a Leica Wild M10 compound microscope equipped with NikCam Pro 1 camera and NIS D Elements software. Objects were illuminated from different angles with a gooseneck dual illuminator.

Translucent and smaller objects like cuticles and spores were photographed using Nikon Eclipse 50i transmitted light microscope with an integrated DS-Fi2 digital camera and NIS D Elements software.

SEM (scanning electron microscopy)

Selected macro- and microfossils were analysed and photographed under an environmental scanning electron microscope (ESEM) Philips XL 30 electron microscope with Element Energy Dispersive Spectroscopy (EDS) Sapphir EDAX and Quanta 250 ESEM with EDS Ultra Dry Thermo Fisher Scientific. The microscopes are housed at the Institute of Earth Sciences, Faculty of Natural Sciences, University of Silesia in Katowice (UŚ) in Sosnowiec. Low vacuum settings of the SEMs were used. Specimens were coated with gold before being inserted into the microscope chamber. Analysis was done in secondary electrons (SE) and Backscattered electrons (BSE) modes with large field detector (LFD) on Quanta 250 ESEM and CENtaurus Detector on Philips XL 30 SEM.

Measurements

Hand specimens were measured in two and three dimensions when possible, using a Vernier calliper. Measurements of cuticles microscopic specimens were taken using a NIS D-Elements software. The length of the cuticle was measured accordingly to the arrangement of epidermal cells, that indicate the top and base of an organ (i.e., leaf, seed etc.), between the most distal ends. The width of the cuticles was measured perpendicular to epidermal cells rows and the length. Because of the irregular shapes of the cuticles, surface area was estimated using a NIS D-Element tool „ellipse” for measuring surface area.

Cuticulae dispersae description

The term cuticle relates here to the extracellular layer which overlies the plant epidermis and other cutinised plant parts (i.e., cutinised megaspore membrane). The character of the material that can be considered as dispersed plant cuticle limits the description to the structure of the cuticle. Since the gross morphological features could not be determined, in most cases taxonomical determination is difficult. Therefore, cuticles were grouped into morphotypes and when possible, identified to the lowest taxonomical level. Cuticles retrieved in bulk maceration were grouped into morphotypes on the basis of combination of cuticle characters that are considered to have taxonomical importance among gymnosperms (e.g., Harris, 1935; Oldham, 1976; Kerp, 1990; Karasev, 2013): the differentiation of adaxial and abaxial leaf side, the presence of stomata, the orientation, arrangement and density of stomata, the shape and structure of stomata complex, the shape and arrangement of other epidermal cells, the ornamentation of epidermal cells and the presence of trichomes. Firstly, the most complete specimens were selected and described, preferably with upper and lower cuticle preserved and the shape complete enough to determine which body plant it represents, and if possible determining leaf shape. Specimens that are more fragmentary were later compared and assigned into morphotypes. The types are characterized by the following alphabet letters.

Database

Collected quantitative and qualitative data are organized in Microsoft Office Excel software.

4. Systematic description of fossil plants from researched localities

4.1. Zawiercie-Marciszów

Systematic description of fossil plants from Subchapter 4.1. Zawiercie-Marciszów is presented in Wawrzyniak, Z. & Filipiak, P., 2023. Fossil floral assemblage from the Upper Triassic Grabowa Formation (Upper Silesia, southern Poland). *Annales Societatis Geologorum Poloniae,* 93: 1–30, in press.

4.1.1. Macrofossils

Sphenophyta

Class Equisetopsida Agardh, 1825
Order Equisetales de Candolle ex von Berchtold & Presl, 1820
Family Equisetaceae Michaux ex de Candolle, 1804

Specimens show 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 *Phylloteca*. The most reliable feature that distinguishes respective forms is the shape of 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 *Phylloteca* 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; Grauvogell-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 speculations.

Genus *Equisetites* Sternberg, 1833

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

Equisetites sp.

Plates 4 & 5

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

Description. Stems leafless. Incomplete internodes. Nodes preserved; no nodal diaphragms. Stems straight, no tapering. No swelling at the nodes. Stems 3.0–52.9 mm wide in compression, and 5.1–130.0 long. Surface with longitudinal grooves. Grooves every 0.9–1.5 mm. Smooth exterior cortex surface and underlying ridged cortex layer; ridges every 2.1 mm (Pl. 6A). Delicate striae on ridges and alternating grooves surface. At the nodes vascular strands of the following internodes mostly alternating (Pl. 5D–G), less often opposite (Pl. 5H). No branch scars or lateral branching.

Remarks. No leaves or leaf-sheaths were found that could be associated with the specimens, which would provide distinction between main Triassic sphenophytes. Most specimen represents a decorticated internal cylinder, covered with longitudinal grooves corresponding to vascular strands. Fragment of the surface on the widest stem shows a cellular pattern probably representing an endodermis (Pl. 5B). Cells are isometric to elongated longitudinally, oblique and arranged in rows. 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* (Goeppert, 1846) Weber, 1968; Wilmsdorf, Landsberg, Silesia (today Gorzów Śląski, Poland), Rhaetian, Upper Triassic

Neocalamites sp.

Plate 6

Material. Two incomplete impressions of stems with fragments of charcoalified; specimens Z24, Z25.

Description. Leafless stems, 35.6–36.3 mm wide, 107.8–108.6 mm long, respectively; straight, no tapering (Pl. 6A, C). Internodal region, no nodes. Ridges every 3.1–3.4 mm alternated with flat grooves. Surface of the grooves with longitudinal striae 50.0 μm wide (Pl. 6B). Charcoalified cortical tissue with occasionally preserved longitudinally oriented tubular structures 10.0–12.0 μm wide (Pl. 6D).

Remarks. Due to the absence of leaves and leaf-sheaths associated with the stems assigning specimens to either *Equisetites* or *Neocalamites* is difficult. However, prominent ridges ("costae"; Pl. 6A, C), have been previously shown in i.e. *Neocalamites 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.

Plate 3 & 7

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

Description. Stems leafless*;* straight, no tapering or slight narrowing on one end. No nodes. Incomplete internodes (Pl. 3A, B, Pl. 7A, B). Stems from round in transverse section (Pl. 7C, E) to fusiform, compressed (Pl. 3C, D). Round stems 12.5 mm in diameter and 26.5–63.4 mm long, fusiform specimen 36.0 x 15.4 mm wide and 73.5 mm long. Preserved internal cylinder with degraded tissues. Layer of tissue remnants in round specimen 0.5–1.0 mm wide (Pl. 7C, E), in fusiform specimen 0.53–3.5 mm (Pl. 3E–G). Ribs discernible; distance between ribs ca. 1.5 mm in round specimen (Pl. 7A, B), 2.0 mm in fusiform specimen (Pl. 3C).

Remarks. All three specimens are different from each other in terms of dimensions, but they represent the same type of preservation. Stems are isolated, with hollow pith, filled with calcareous mudstone. They do not show characters that would allow to assign them with certainty to a particular genus, and even the sphenophyte origin is doubtful. The central canal must have been filled with sediment shortly after plants death, so the remains could have held their cylindrical shape. The most common plants with cylindrical pith inside the stem of that time were horsetails. Surface of the specimens bears traces of charcoalification. Longitudinal ribbing visible on specimen ZST2 (Pl. 7E) resembles the structure of *Neocalamites* sp. outer layer, that is considered to be characteristic of *Neocalamites* (Kustatscher and Van Konijnenburg-van Cittert, 2008).

Gymnospermophyta

Class Pinopsida
Order Pinales
Family ?Araucariaceae Henkel & Hochstetter, 1865
Genus *Agathoxylon* Hartig, 1848
Type species *Agathoxylon cordaianum* Hartig, 1848; Coburg, Germany, Triassic.

Plates 8–12

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

Description. Stem diameter 24.5 mm; stem length 66.8 mm. Secondary xylem, cortex, periderm and bark not preserved; outer surface smooth (Pl. 8A, B). Pycnoxylic; wood homoxylous. Pith circular, slightly elongated, 289.0 µm in diameter (Pl. 8C, E). Secondary xylem with discernible growth rings (Pl. 8C, Pl. 9). Early wood tracheids squarish to rounded in transverse section (Pl. 9D), 9.85–33.08 µm in diameter (mean 22.4 µm, n=207). Late wood tracheid rounded in cross section, 7.39–33.71 µm in diameter (16.91 µm, n=200). Tracheids in transverse section irregularly arranged or in loose rows. The transition from early to late wood rapid (Pl. 9B–D). Intracellular spaces irregular. Rays 14.03–19.19 µm wide in transverse section, separated by 2–15 rows of tracheids (mean seven rows; Pl. 9E–G). Radial tracheid pitting uniseriate, araucarian (Pl. 10A–C, I); radial pits mostly contiguous, sometimes separated (Pl. 10A,B). Bordered pits adjacent or separated by small distances (Pl. 10C), circular; Sanio rims absent; pore pit round to elongate. Size of the pit aperture 3.0–5.0 mm. Cross-fields with one to six circular pits (Pl. 10D, E), araucaroid, cupressoid oculipores (Pl. 10G, H). Pit pore ellipsoidal; 4.0–5.0 µm in diameter; longer axis of the pit pore oriented uniformly (Pl. 10E, G, H). Axial parenchyma undetermined. Resin canals absent.

Remarks. Terminology used in the description follows the IAWA Committee (2004) and the key for identifying coniferous morphogenera by Philippe and Bamford (2008).

Agathoxylon keuperianum was recorded from Zawiercie-Marciszów previously (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. Especially measurements of anatomical elements, i.e., tracheid radial and cross-fields pitting, could be biased by taphonomical processes; crystallisation is influencing the size and shape of pit pores, making them sometimes rhomboidal in outline (Pl. 12A, B).

In the observed sample, tracheids represent araucarian type; spotted were only uniseriate chains of round pits (Pl. 10A–C, 12C, D). 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 the transverse section, irregularities in wood development are visible. Growth rings became eccentric, and reaction (compression) wood has formed (Pl. 8A, 9A), probably in response to mechanical stress. Growth rings are superficially marked. From overall view, the late wood is darker than early wood. The lumen of late wood tracheids is slightly smaller than early wood (16.91 vs. 22.4 µm in tangential diameter). Presence of late wood is sometimes expressed by a few rows (2–3 rows) of tangentially creased cells. Spaces between cells are sometimes discernible, their irregular size can be connected with wood preservation (Pl. 9D, H). Eccentric growth rings and presence of compression wood along with changes resulting from fossilisation processes, makes tracing late-early wood more difficult. It cannot be excluded that some of them are actually false rings. Helical thickening sporadically observed only in transmitted light (Pl. 12J, K) might be an artefact caused by wood degradation or mineralisation processes (Philippe *et al.*, 2019; Boura *et al.*, 2021). They were observed only in regions where tracheids are damaged and disturbed (Pl. 12E, F). No such characters were observed under the SEM. Pith cavity cells contain roundish structures (Pl. 11C–F), 25.0–50.0 µm in diameter. They can represent secretory cells, but some possess a round operculum (Pl. 11G–I) which might indicate their fungal affinity (fungal spores?).

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

Gymnospermae *Incertae sedis*

Stem A

Plate 13

Material. Three permineralised stems; WNoZ_S_7_159, WNoZ_S_7_193, ZST5.

Description. Stems unbranching, straight. 81.1–100.0 mm long, 21.8–82.5 mm wide. Bark and cortex is not preserved.

Remarks. Three-dimensionally preserved stems with the massive inner structure were found as separate, isolated fragments or entombed in calcareous mudstone (Pl. 3H). Unfortunately, the specimen with the widest diameter (82.5 mm; WNoZ_S_7_159; Pl. 13A) is a very short fragment (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 (Pl. 9B) or bulging with branch scars and wrinkles (Pl. 13D, E). Specimen WNoZ_S_7_159 shows a thin (2.5 mm) darker layer resembling bark, partially surrounding the stem (Pl. 13A). All specimens inner structure forms a concentrating tissue arrangement from the central pith through the stem radius (Pl. 13A, C, F). Although specimens show the same preservation mode, they could be three different genera or even different class of gymnosperm. General appearance makes the specimen resemble *Agathoxylon*, but further identification is doubtful without thin section preparation and analysis of anatomical structure.

Stem B

Plate 14

Material. Impression of two stems on one rock slab with cuticle and charcoalified tissue preserved in mudstone; specimen Z21.

Description. Stems 107.2 mm long and 44.5 mm wide, and 83.9 mm long and 18.8 mm wide; bigger fragment straight, smaller widening on one end (Pl. 14A, B). Branch scars round (Pl. 14D) to rhomboidal (Pl. 14C), 6.0 mm wide. Patches of cuticle preserved on stem. Cuticle thick; no stomata; no epidermal cells; longitudinal parallel striae (10 per 100 μ width; Pl. 14E, F, H).

Remarks. Observed holes and brakes in the cuticle surface sometimes resemble stomata (Pl. 14F, G), but no features confirming that can be observed. Branch scars (bundle scar) found on both specimens are round to rhomboidal (Pl. 14C, D); they show resemblance to a scar found on permineralised specimens with gymnosperm anatomy (Pl. 13F, G). Fragment of charcoalified tissue shows longitudinal striae on the surface but has a completely homogenised internal structure. Cuticle obtained from the specimen is very brittle and prone to mechanical damage. Although the fossil is preserved in diverse modes, to classify it with certainty to any particular group was not possible. Based on size, the stem could also represent a sphenophyte. Retrieved cuticle also shows some resemblance to 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.

Incertae sedis

Root A

Plate 15A–D

Material. Compression of isolated root fragment preserved in a calcareous concretion; specimen ZR1.

Description. Isolated root fragment with secondary order of branching (Pl. 15A). The main root is 79.6 mm long and 3.3–3.6 mm wide. Three secondary roots emerge from one side of the main axis (Pl. 15A) and are irregularly spaced. They are 9.9–31.0 mm long and 0.9–1.9 mm wide, slightly narrowing towards the tip, and with delicate bulging close to the main axis (Pl. 15D).

Remarks. One outgrowth (Pl. 15A, D) is much broader than the others, 2.8–3.3 mm wide, and might be a branching of the main axis. Secondary root tips are rounded (Pl. 15B, C). Along the main root axis there is a region 1.8–2.0 mm wide of coalified layer differentiating in colour and structure, most probably representing a vascular cylinder surrounded by cortical tissue (Pl.

15D). Vascular cylinder is emerging into the rootlets (Pl. 15E) but is less visible in thinner branches.

Root B

Plate 15E–J

Material. Nine fragments of isolated root compression and petrification preserved in a calcareous concretion; specimens ZR2.1–ZR2.9.

Description. Isolated root fragments of secondary and tertiary branching. The main root axis is 2.1–3.3 mm wide. Specimens are tangled together, and determination of roots length is hard to measure (Pl. 15F, G, H, J); the longest distinguishable main axis is 46 mm. Secondary roots 1.1–1.7 mm wide; emerging from the main axis at a 70–80° (Pl. 15F, G, H). Tertiary order branches 0.3–0.56 mm wide and 1.1–1.3 mm long; emerging at an 80–90° (Pl. 15H). The root tip rounded.

Remarks. Tree dimensionally preserved roots in transversal section show a vascular strand ca. 2.5 mm in diameter surrounded by lightly colour mineralisation of cortical region and darker circle probably representing root epidermis (Pl. 15I). They are 1.4–1.7 mm in diameter. The surface of the roots is smooth (Pl. 15K).

Discussion. 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 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 represent a gymnosperm or herbaceous lycophyte.

Isolated rooting systems are sometimes assigned to a morphogenus *Radicites* known from late Palaeozoic and Mesozoic localities, i.e., 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 *Radicites* 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.

4.1.2. Cuticulae dispersae

Morphotype A

Plate 16

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. Cuticle thick. The largest fragment is 25 mm long and 5 mm wide; straight. Leaf margins smooth (Pl. 16A). Apex acute (Pl. 16B); base unknown. Epidermal cells arranged loosely in longitudinal rows. Cells polygonal, sometimes rectangular to isodiametric. Anticlinal walls thick and straight, evenly cutinized. Periclinal walls smooth or bearing a faint, hollow papilla (Pl. 16C). Cuticle amphistomatic. Stomata evenly distributed on both cuticles (Pl. 16A) in rows, more or less regularly (Pl. 16A, C, D). Stomata complex round, 40–65 μm in diameter. Guard cells deeply sunken, orientated irregularly, rarely visible. Usually, six subsidiary cells bearing a solid papilla directed towards the stomata pit, overarching the aperture (Pl. 16E). Anticlinal walls of subsidiary cells are strongly cutinised but not thicker than normal epidermal cells (Pl. 16F). Encircling cells unspecialised, but sometimes forming a discernible circle of secondary cells (Pl. 16E–H).

Remarks. Cuticles from morphotype A show resemblance to conifer cuticles. The size and shape of the largest fragments suggests that 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 than 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

Plate 17

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 of elongated flattened leaves, straight (Pl. 17A–C). No base. Tip rounded (Pl. 17D). Margins 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 in loose longitudinal rows. Epidermal cells rectangular to polygonal, isodiametric to slightly elongated in rows between stomata rows (Pl. 17B). Anticlinal walls thick and well-marked. Periclinal walls with round shallow papillae in the middle or slightly in the upper part of the epidermal cell (Pl. 17E). Cuticle amphistomatic. Stomata distributed evenly on whole surface of the cuticle. Stomata in longitudinal rows, single stomata wide. Stomata complex round, 40–55 μm in diameter. In rows stomata distributed more or less regularly. Adjacent stomata not sharing subsidiary cells. Stomata are sunken. Stomata complex is round, comprising of thinly cutinized guard cells surrounded by 5–6 subsidiary cells equipped with prominent papillae overarching the stomata aperture (Pl. 17F, G). Papillae are straight, sometimes slightly swollen at the tip. A faint groove in the middle of the papilla, along its longer axis (Pl. 17G). Outer anticlinal walls of stomata are thicker than other epidermal cells anticlinal walls. No additional encircling cells present.

Remarks. The overall shape of the leaf suggests it might come from *Elatocladus*-type foliage. Leaf attachmentcannot 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 close resemblance, especially in details comparison. Type A cuticles have more robust appearance, the cuticle is thicker, anticlinal walls of epidermal cells are wider (thicker). Leaf tip of type A is acute whereas of type B is rounded and blunt. 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 stomatalsurround 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

Plate 18

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 (Pl. 18A). A cuticle of leafy twig 43 mm long with elongated lanceolate leaves attached with the whole leaf base (Pl. 18A). Leaves 9.0–12.0 mm long and 3.0–4.0 mm wide. Leaves attached alternatively. Leaves linear, slightly lanceolate. Base wide, ending with a deccurent leaf cushion attaching to a stem. Leaf tip acuminating but leaf tip not preserved. Margins smooth. Cuticle moderately thick. Epidermal cells in longitudinal, loose rows. Epidermal cells from rectangular, isodiametric to strongly elongated. Anticlinal walls evenly cutinized, sometimes gently undulating. Periclinal walls 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 triangular to rounded. Stomata present on both adaxial and abaxial sides. Stomata in rows single stomata wide, more or less evenly distributed along. Stomata complex round, 50.0–60.0 μm in diameter. Guard cells indiscernible. Stomata pore encircled by 5–6 subsidiary cells (Pl. 18E). Subsidiary cells possess a short hollow papilla directed toward the pore. Outer anticlinal walls of subsidiary cells not thicker than ordinary epidermal cells (Pl. 18E). No specialised encircling cells.

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 (Pl. 18B, C). Lower leaves cuticle consists of cells arranged similarly, but cells are shorter with sharper corners and equipped with triangular papillae (Pl. 18E). Heteromorphy in cuticle development within a single plant is connected more to pre-adaptations to biotic and abiotic environmental conditions and plant ontogeny than taxonomical affinity (Kerp, 1990; Bomfleur *et al.*, 2011; Webster *et al.*, 2022). A similar specimen was previously described 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 – 1.7–2.0 mm long and 0.8–1.2 mm wide (Ash, 1970).

Morphotype D

Plate 19

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 elongated, ensiform to falcate, laterally flattened (Pl. 19A, B); 5–7 mm long and 2–3 mm wide. Leaf tip acute, incurved from the lateral view (Pl. 19A, B), leaf base unknown. Adaxial and abaxial sides evenly cutinised. Cuticle relatively thick. Epidermal cells are arranged irregularly. Cells are rectangular to elongated in outline. Anticlinal walls between epidermal cells slightly thickened. Periclinal walls are bearing an elongated triangular papilla, probably hollow, 5.0–55.0 μm high (Pl. 19C, G). Papillae on marginal cells are longer, up to 70.0 μm and spiky. Stomata scattered on adaxial and abaxial sides evenly. Stomata complex consists of sunken guard cells (Pl. 19E–G) and 5 to 6 subsidiary cells (Pl. 19D), between 30.0 to 50.0 μm in diameter. Subsidiary cells are 4-sided with rounded distal and proximal anticlinal walls and straight radial walls (Pl. 19E). Proximal walls are thickened, sometimes with faint papillae pointing towards the aperture (Pl. 19E–G). Encircling cells form an indistinctive ring of cells equipped with long papillae with blunt tip directing toward the centre of stomata (Pl. 19H–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

Plate 20

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 comprised of helically arranged scale-like leaves (Pl. 20A–C). The longest preserved twig is 4 cm long, unbranching, comprising of 19 leaves. Twigs between 3 and 8 mm wide. Twigs branching at a 20°. Leaves tightly pressed to the axis, except free leaf tip. Leaves scale-like, wider than longer, sometimes isodiametric, widest in approximately middle of their length. Leaves from 2 mm wide and 1.8 long, up to 10 mm wide and 10 mm long. Leaves in distal view rhomboidal in outline (Pl. 20D–G) tapering towards the apex. Leaf tip acute to obtuse. In lateral view leaf tip is incurved. Leaf base broad, usually round. Leaf margins with wavy fringes (Pl. 20E), sometimes ending with spines elongated towards the leaf tip. Fibrous tissue is on the upper cuticle’s inner side, between stomata rows (Pl. 20D, F). Some specimens possess fibrous tissue on the inner side of the upper cuticle, between stomata rows (Pl. 20F, H). Surface of adaxial cuticle is smaller than abaxial.

Epidermal cells are isodiametric, slightly elongating in rows between stomata rows (Pl. 20H, J). Epidermal cells with strongly cutinised anticlinal walls, periclinal walls rather smooth, without thickenings and papillae. Papilla on periclinal walls sometimes appear near the leaf tip. Leaves amphistomatic. Stomata in rows (Pl. 20H, J). Rows continuing from leaf base towards the apex (Pl. 20G). Stomata in rows scattered irregularly. Orientation of stomata irregular (Pl. 20K). Stomata sunken. Cuticle of guard cells very thin, unrecognisable most of the times. Stoma complexes consists of guard cells and 5–7 subsidiary cells. Prominent papilla present on subsidiary cell directing toward the stomata aperture. Subsidiary cells papillae possess a shallow groove parallel to the papillae longer axis (Pl. 20I, J). Tip of the papilla slightly swollen. Subsidiary cells papillae sometimes show a shallow groove parallel to the papillae longer axis (Pl. 20I, K, L). Sometimes subsidiary cells completely cover stomata pore. Anticlinal walls of subsidiary cells are heavily thickened (Pl. 20G, I, J). Adjacent stomata do not share subsidiary cells.

Remarks. All cuticles from Type E are representing a *Brachyphyllum*-like foliage. *Brachyphyllum*-foliage is a leaf morphogenera recognised from Triassic to Cretaceous and associated with different conifer groups: Cupressaceae, Podocarpaceae, Araucariaceae, Cheirolepidiaceae (Meyen, 1987; Stockey, 1994) and Patokaeceae (Pacyna *et al.*, 2017). Type E cuticles show gross characters of Cheirolepidiaceae family (i.e. random orientation of stomata, 4–6 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. Particular cuticles show diverse characters, but still within a *Brachyphyllum*-like genera. Due to that and because it is documented that *Brachyphyllum*-like foliage can be accompanied by other foliage type i.e., *Pagiophyllum*-like (Pacyna *et al.*, 2017) within one fossil plant, cuticles are not classified as *Brachyphyllum* sp., but as a separate *cuticulae dispersae* morphotype.

4.1.3. Megaspores

Striatriletes ramosus Marcinkiewicz, 1985

Plate 21

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. Diameter 400–500 µm. Trilate mark with ridges 60–70 µm high. Ridges ca. 80% of the megaspore radius (Pl. 21A, D, G). Trilate mark ridges crested with wavy margin, occasionally topped with granular to spiky ornamentation (Pl. 21B, C, E). Proximal and distal surfaces 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 (Pl. 21H, I). Ridges are 20–30 µm tall and ca. 6–10 µm thick at the base. On some specimens area between trilete mark arms is covered with shorter ridges (Pl. 21B, E). Megaspore surface is composed of fine mesh (Pl. 21F).

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. Documented specimen of macrospores fit to the description of *Striatriletes ramosus* Marcinkiewicz (Marcinkiewicz and Orłowska-Zwolińska, 1985). *S. ramosus* Marcinkiewicz was first described from boreholes (*Erlansonisporites sparassis* Marcinkiewicz 1960, later changed for *Erlansonisporites ramosus* Marcinkiewicz 1969; Marcinkiewicz and Orłowska-Zwolińska 1985; Marcinkiewicz *et al.,* 2014). It was found in the Upper Triassic Zbąszynek Beds. Subzone Striatrileites 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).

4.2. Lipie Śląskie-Lisowice.

4.2.1. Macrofossils

Sphenophyta

Class Equisetopsida Agardh, 1825
Order Equisetales de Candolle ex von Berchtold & Presl, 1820
Family Equisetaceae Michaux ex de Candolle, 1804
Genus *Equisetites* Sternberg, 1833
Type species *Equisetites muensterii* Sternberg, 1833, Abtswind, Bavaria, Germany, Carnian, Upper Triassic
Equisetites sp.

Plate 22

Material. 11 compressed stems with coalified tissues; specimens L/V/1–11.

Description. Straight, unbranching, leafless stems. Incomplete internodes; no nodes preserved (Pl. 22). Internodes straight; up to 69.3 mm long, 5.9–33.2 mm wide. Surface with longitudinal grooves; grooves flat; 0.8 mm wide. Delicate striae on ridges and alternating grooves surface (Pl. 22C).

Remarks. Specimens are preserved as impressions of inner vascular cylinder. Specimen L/V/6 represent a compression of inner vascular cylinder (Pl. 22A). Surface is covered with patches of thin coalified organic layer, accentuating longitudinal rows (Pl. 22). Stems show diverse width, from 5.8 to 33.2 mm. Five categories could be distinguished: the narrowest stem of width 5.9 mm, stems of width 14.5–16.8 mm (mean 15.6 mm, n=5), 19.9–21.3 mm, 23.7–24.0 mm, and the widest stem of 33.2 mm. All specimens show similar structure of the outer surface and are preserved in the same manner in the same type of sediment. Identification of the remains impedes lack of stem nodal regions, leaf scars or branch scars, but also absence of any other remains that could relate to Sphenophyta. Straight and ribbed fragments of possible *Equisetites* are rare in the Lipie Śląskie-Lisowice outcrop. Analysed specimens are preserved in the light grey mudstone, sometimes accompanied by plant debris, mostly conifer foliage.

Cycadophyta

Class Cycadopsida Brongniart 1843
Order Cycadales Persoon ex von Berchtold et Presl 1820
Family Cycadaceae Persoon 1807
Genus *Dioonitocarpidium* Rühle von Lilienstern 1928
Type species *Dioonitocarpidium pennaeformis* (Schenk 1864) Rühle von Lilienstern 1928, Erfurt Formation, Würzburg, Bavaria, Germany, Ladinian, Middle Triassic
Cf. *Dioonitocarpidium* sp.

Plate 23

Material. Single, incomplete specimen; L/III/62.

Description. Pinnatifid (pinnatisect) leaf blade, triangular in outline; tapering towards the apex (Pl. 23A); 11.6 mm long and 9.5 mm wide. Axis width from 2.2 mm at the base, to 0.48 mm at the apex area. Apex not preserved; leaf-base not preserved. Pinnae 3.1–3.7 mm long and 0.7–0.8 mm wide; decreasing towards the apex. Pinnae opposite to sub-opposite. Pinnae arising from the axis at an angle from ca. 80° in the proximal part, gradually decreasing to 50°. Pinnae apex acute to slightly obtuse. Hispid indumentum covering whole leaf blade; hairs ca. 0.4 mm long and 0.16 mm wide.

Remarks. Upper, sterile part of a cycadalaen ovule-bearing sporophyll. Lower part where seeds were attached is missing. The general impression of the remains suggests some stiffness of the sporophyll. Although compressed, the middle part of the leaf blade, the axis, is slightly convex. Pinnae are attached to the axis at an almost right angle in the basal part of the leaf blade. Closer to the apical part of the leaf blade, the angle of pinnae attachment is decreasing up to 50°. Pinnules lanceolate, margin entire. Pinnules are opposite to subopposite; due to the incompleteness of the specimen the number of the pinnules on both sides of the axis is different (seven and eighth). Following pinnae are adjoin with their bases. No venation is visible on the axis nor on the pinnules. Surface of the leaf blade is covered with indumentum (Pl. 23B, C). Hairs cover the whole leaf blade, including axis and pinnules. Unfortunately, specimen was glued after excavating, and cuticle could not be obtained. There is no indication of number of the seeds attached to the sporophyll. Incomplete and small specimen from Lipie Śląskie-Lisowice shows structure distinctive for cycad megasporophylls known from the Middle and Upper Triassic European localities (e.g. Lunz, Austria, Pott 2019; Ilsfeld, Germany, Rozynek

2008; Dolomites, Italy, Kustatscher *et al*., 2004). *Dioonitocarpidium* is a genus erected by Rühle von Lilienstern (1928) for fertile megasporophylls similar to extant Cycas. Before, Schenk (1864) recognised in the Ladinian material from Wurzburg (Germany) cycad megasporophylls, *Dioonites pannaeformis* Schenk 1864, but it was changed by Lilienstern to *Dioonitocarpidium* (Lilienstern, 1928). *Dioonitocarpidium pennaeformis* (Schenk 1864) Rühle von Lilienstern 1928 was described from Ladinian deposits of southern and eastern Germany (Franconia; Schenk, 1864; Kelber and Hansch, 1995; Badenia, Thale am Harz in Saxony-Anhalt, Kustatscher and van Konijnenburg-van Cittert, 2010; Apolda in Thuringia, Compter 1918, 1922). The sterile part is up to 65 mm long and 20 mm wide (Kustatscher and van Konijnenburg-van Cittert, 2010). Pinnate leaf blade possesses a central axis 3.5 mm wide at the basis and its decreasing to 1–2 mm, therefore it is wider than L/III/62 specimen (2.2–0.48 mm). Pinnae at the apical region of *D. pennaeformis* are 4.0–6.0 mm long and 0.5–1.0 mm wide (Kustatscher and van van Konijnenburg-van Cittert, 2010), what makes them about twice the size of pinnae of the L/III/62 specimen (3.1–3.7 mm long and 0.7–0.8 mm wide). Pinnae of *D. pennaeformis* are covered with fine hairs (Rühle von Lilienstern, 1928) but are not always preserved (Kustatscher and van Konijnenburg-van Cittert, 2010). *Dioonitocapidium moroderi* (Leonardi, 1953) Kustatscher, Wachtler et van Konijnenburg-van Cittert 2004 is another Ladinian representative of the genus, but from the Dolomites, Italy. Sterile part of the megasporophyll is ca 90 mm long, and ca. 25 mm wide. Pinnae are up to 20 mm long and 2 mm wide and attached to a rachis 5–10 mm wide (Kustatcher *et al*., 2004). It is much bigger than currently analysed specimen. From the Carnian of Lunz, Austria known are two species: *Dioonitocarpidium titzei* (Krasser, 1917) Pott and *Dioonitocarpidium liliensternii* Kräusel 1953, emend. Pott (Pott, 2019). *D. titzei* is up to 192 mm long and at its maximum 24 mm wide. Specimens from Lunz have preserved both sterile and fertile part with probably 2–3 ovules attached (Pott, 2019). Specimen from Lipie Śląskie-Lisowice represents only incomplete apical part of the leaf-blade, but it's general appearance and arrangement of the pinnules show resemblance to the sterile part of *D. titzei* sporophyll. The maximum pinnule length of the megasporophyll from which the specimen L/III/62 originated, cannot be determined. The pinnules of *D. titzei* are up to 11 mm long, however pinnules are decreasing in length towards the apical part of the leaf-blade (Pott, 2019). Distal parts with shorter pinnae of Lunz specimens can be compared with Polish specimen that possess longest pinnae of 3.7 mm. The stiff appearance and indumentum with long hairs (0.5–0.7 mm long in *D. titzei,* ca. 0.4 mm long in L/III/62) are a shared feature for Lunz and Polish specimen. *D. liliensternii* specimens are up to ca. 130 mm long, sterile part up to 87 mm; the sterile part consists of a lanceolate pinnules attached to a thick and robust central area, 6 mm wide at its basal part. The longest pinnules of *D. liliensternii* are 12 mm, their length decreases towards the apical region and disappear completely at the apex of the leaf blade, leaving the tip entire (Fig. 3e, Pott, 2019). In *D. liliensternii* pinnules are covered with long thin hairs, ca. 0.7 mm long. Both Lunz species are bigger than Polish specimen (max. pinnae length x width in mm: *D. titzei* 11x3, *D.liliensternii* 12x2 - from plate, L/III/62 3.7x0.8). Although the L/III/62 specimen has incomplete tip of the leaf blade, the arrangement of pinnules suggest that the axis was pinnatifid up to the tip, more like *D. titzei* than *D. liliensternii*. *Dioonitocarpidium-liliensternii*-type macrosporophyll was described also from Anisian of the Dolomites (Broglio Loriga *et al*., 2002). Ovule-bearing sporophylls are gathered in almost complete fructification. Sterile part is up to 40.0 mm long (Broglio Loriga *et al*., 2002). It comprises of wide central axis and lanceolate pinnae attached at an angle of ca. 70–80°; longest pinnae are ca. 12 mm long (from the illustration Pl. 1, fig.7; Broglio Loriga *et al*., 2002). Observations by Pott (2019) confirmed similarity to *Dioonitocarpidium liliensternii*, apart from the absence of indumentum, present in Lunz specimens. *Schozachia donaea* Rozynek 2008 from Ladinian of Baden-Württemberg, southern Germany (Rozynek, 2008) differs from *Dioonitocarpidium* in structure of the fertile part. The whole megasporophyll has total length up to ca. 100 mm; sterile pinnate lamina is ca. 55 mm long and 21.0 mm wide at most. The central axis is 4.0 mm wide near the base and decreases to less than 1.0 mm in the apical part. On each side of the axis there are 35 pinnae. Pinnae are 10–15 mm long and 2–3 mm wide in the basal and middle part of the leaf-blade, but they are becoming shorter in one-fourth of the lamina length to ca. 2–3 mm. In terms of size and arrangement of the most distal pinnae of *S. donaea* can be compare in with specimen L/III/62 from Lipie Śląskie-Lisowice (pinnae length 3.1–3.7 mm, width 0.7–0.8 mm). However, *S. donanaea* is lacking hairy indumentum (Rozynek, 2008) present in Polish specimen, and shows longitudinal strands of vascular system along the axis and in the middle of each pinna (Rozynek, 2008) of which there is no indication in L/III/62. Fossils resembling *Dioonitocarpidium* and cycad megasporophylls are reported also from Early Permian of USA (DiMichele *et al*., 2004) and Early Jurassic of Hungary (Bodor, 2015). The youngest *Dioonitocarpidium* is reported by Bodor (2015; unpublished thesis) from the Mescek Coal Formation, Hettang, Early Jurassic, in Hungary.

Table 4. Comparison of cf. *Dioonicarpidium* sp. from Lipie Śląskie-Lisowice with cycad megasporophylls from the Middle and Upper Triassic Europe.*Measured from plates/published data

Taxa	Age	Locality	Sterile lamina length (mm)	Pinnae				Indumentum	Remarks	References
				length (mm)	width (mm)	shape	angle			
Dioonitocarpidium sp.	Hettangian	Mescek Mts., Hungary	9.0	–	–	–	–	na	sterile part simple, entire	Bodor, 2015
Dioonitocarpidium titzei	Carnian	Lunz, Austria	60-70*	Up to 11	Up to 3	apex acute; straight triangular, tapering	40-45*	Y	megasporophyll at least up to 150 mm	Kräusel, 1949; 1953; Pott, 2019
Dioonitocarpidium liliensternii	Carnian	Lunz Austria	Up to 87	Up to 12	Up to 2*	apex acute; lanceolate; base constricted	70-90*	Y		
Schozachia donaea	Ladinian	Ilsfeld,Baden-Württembeg, Germany	50-55*	10-15	2-3	apex acute, straight slightly curved; leaf base overlapping	45	N	megasporophyll ca. 100 mm long; pinnae with single vein	Rozynek, 2008
Dioonitocarpidium pennaeformis	Ladinian	Franconia, Germany		up to 10.0		apex acute; linear; leafbase deacrising				Schenk, 1864; Frentzen, 1922;Rühle von Lilienstern, 1928; Kelber and Hansch, 1995; Kustatscher and van Konijnenburg van-Cittert, 2010
	Ladinian	Badenia, Germany					45			Frentzen, 1922
	Ladinian	Thale, Saxony, Germany	65	4.0-11.0	0.5-1.5	lanceolate, slightly falcate	60-80*	N	only sterile part	Kustatscher and van Konijnenburg-van-Cittert, 2010
	Ladinian	Thuringia, Germany		4-11, 14	1.0-2.5	acuminate; tapering, straight	45	Y		Rühle von Lilienstern, 1928
Dioonitocarpidium moroderi	Ladinian	Dolomites, Italy	90	20	2		70		only sterile part	Wachtler and van Konijnenburg-van Cittert, 2000; Kustatscher *et al.*, 2004
Dioonitocarpidium-liliensternii-type	Anisian	Dolomites, Italy								Broglia Loriga *et al.*, 2002; Kustatscher and van Konijnenburg-van-Cittert, 2010; Pott, 2019
Dioonitocarpidium sp.	Permian	King County, Texas, USA		1.5-7.5*	1.0-1.5*	lanceolate	45-70*	Y		DiMichele *et al.*, 2001

Comparison of specimen L/III/62 from Norian of Lipie Śląskie-Lisowice with sterile parts of other Triassic genera showed that described specimen is smaller, but its general appearance follows descriptions of fossil cycad-megasporophylls. The most distinctive features of sterile megasporophylls used for comparison are the presence of indumentum and size and arrangement of pinnae (length, width, attachment angle, shape; Table 4). Presence of venations is in my opinion strongly dependent on preservation. Specimen could be also considered to represent a needle-leaf conifer, such as *Elatocladus*, but thickness and robustness of the axis and surface covered with relatively long hair make the cycad megasporophyll affinity more reliable.

Gymnospermophyta

Order Coniferales sensu Farjon 2010
Family Cheirolepidiaceae (Takhtajan 1956) Doludenko 1978
Genus *Brachyphyllum* (Brongniart 1828) Harris 1979
Type species: *Brachyphyllum mamillare* Lindley et Hutton 1837, Haiburn Wyke, Yorkshire, UK, Middle Jurassic
Brachyphyllum sp.

Plate 24

Material. Isolated fragments of sterile shoots; L/XI/1–96.

Description. Shoots isolated, single or branching two–three times twigs. The longest twig 72.0 mm long, 9.8 mm wide. Leaves scale-like, rhomboidal in outline, arranged spirally, shorter than the width of leaf cushion. Leaf tip acute to obtuse. Leaf base broad, rounded. Cuticle thick. Stomata, arranged in longitudinal, irregular rows, distributed more or less evenly. Stomata are unevenly arranged in rows, rarely sharing subsidiary cells. Distance between stomata 3–4 epidermal cells, 120.0–145.0 µm). The number of stomata in rows decreases towards the edges of the cuticle. Stomata round, ca. 60x50 µm; 4–5 subsidiary cells with strongly cutinised walls on the side of the stomata opening, additionally provided with papillae. Surrounding cells large, not specialised. Epidermal cells isodiametric, slightly elongated, arranged in longitudinal rows; cells ca. 30.0 µm wide. The anticlinal walls of the cells thickened, straight, with rounded corners. Wall thickness 2.0–8.0 µm. Periclinal walls thickened in the middle, sometimes forming a poorly formed papilla.

Remarks. The genus *Brachyphyllum* includes plants with mostly pinnately compound branches and usually flat stems (Pl. 24A-E). Leaves are arranged spirally (Pl. 24I), leaf cushions are rhomboid or hexagonal, tapering into the free part of the leaf (the upper surface outside the leaf cushion). The total length of the leaf, including the leaf cushion, is equal to the width of the leaf, sometimes less (Harris, 1979). *Brachyphyllum* cuticles are always thick. Stomatal complexes occur above the leaf cushion and lower parts of the leaf (Pl. 24G). Stomata are round (Pl. 24H), arranged in elongated rows that converge at the top of the leaf. Each row is one stomata wide. Between the rows of stomata are rows of elongated epidermal cells. Adjacent stomata never share subsidiary cells and are usually separated by additional epidermal cells. Rows of stomata do not show any depression in relation to the surface of the cuticle, but individual stomata seem to be sunken. Stomata are irregularly oriented. Around the aperture is a ring of 4–6 large subsidiary cells equipped with a papilla. Rectangular and relatively short epidermal cells form rows that converge at the top of the leaf. The epidermal cells between the rows of stomata are less regular. The anticlinal walls of epidermal cell walls are straight. The hairs and papillae do not occur on cells other than the subsidiary cells of the stomata (Kendall, 1947).

Order Pinales Dumortier 1829

Family Palissyaceae Florin 1958

Genus *Elatocladus* (Halle 1913) Harris 1979

Type species: *Elatocladus heterophylla* Halle 1913, Hope Bay, Antarctica, Early Jurassic

Elatocladus sp.

Plate 25

Material. Isolated fragments of sterile shoots; L/III/1–81.

Description. Shoot fragments 11.0–24.0 mm long and 5.0–20.0 mm wide. Shoot axis 0.7–1.2 mm thick. Leaf blade entire, equatorial to lanceolate; twisted to opposite; 25º–70º to the axis. Leaves 6.0–9.5 mm long, 1.1–1.5 mm wide. Leaves separate, sometimes leaf base overlapping.

Leaf petiole twisted. Leaf apex acute or pointed. Leaf base tapering or cuneate. Stomata complex 30.6–51.48 µm long, elongated; stomat aperture 13.50–19.61 µm long; 4–5 subsidiary cells 7.83–11.55 wide. Stomata in loose rows, single stomata wide. Epidermal cells isodiametric to slightly elongated. Apertures oriented regularly.

Remarks. Sterile shoots fitting *Elatocladus* definition from researched locality show some variation, and it is probable that more than one species of *Elatocladus* is present. The leaf blade is darker in the central part, with a distinct nerve running through the middle, often darker than the marginal parts of the leaf (Pl. 25D, F, H, I). Cuticles are not preserved on each shoot. Some specimen possess elongated papillae arranged in a single row on the lower part of the leaf margin (Pl. 25E). Stomata complex comprises of 4–5 subsidiary cells, thickened in the central part of the periclinal wall (Pl. 25G). Epidermal cells are thickened in the central part of the cell wall, with hollow papillae (Pl. 25E–G). *Elatocladus* was erected by Halle (1913) to describe “sterile coniferous branches of the radial or the dorsiventral type, which do not show any characters that permit them to be included in one of the genera instituted for more peculiar forms". Seward (1919) agreed with Halles arguments, and pointed that the genus could be used for sterile shoots presenting distinctive heterophylly, like *Elatocladus heterophylla* Halle 1913 possessing both linear and scale-like leaves. From the Upper Triassic of Scoresby Sound Greenland Harris (1935) described as *Elatocladus* "sterile conifer twigs with small needles". Harris distinguished particular species using cuticular characters (Harris, 1935). Later, Harris narrowed *Elatocladus* definition: "shoot bearing leaves spirally (rarely opposite). Leaf elongated, dorsiventrally flattened, diverging from stem; at base strongly contracted and forming a short petiole attaching it to basal cushion. Lamina with a single vein" (Harris, 1979). In The Yorkshire Jurassic Flora. Vol. V, Harris emended *Elatocladus* definition justifying that it was "too narrow". Emendation made by Harris (1979) defined the form-genus *Elatocladus* as "Fossil conifer shoot bearing elongated, dorsiventrally flattened leaves with a single vein. Leaves divergent from stem." and Jurassic of Yorkshire (1979), but gross morphological characters are overlapping with Lipie Śląskie-Lisowice specimens.

Incertae sedis

Genus *Carpolithes* Brongniart, 1822

Type species: *Carpolithes thalictroides* Brongniart, 1822, Isle of Wight, UK, Paleogene

Fossilised isolated seeds lacking morphological characters that would enable generic identification (Wang, 2011).

Carpolithes sp.

Plate 26 & 27

Material. 19 specimens of isolated fructifications; charcoalified, compressions, cutinised; L/I/1–19.

Description. Seeds flattened (Pl. 26A–I, P–T, 27G) or preserved three-dimensionally (Pl. 27A, B). Seed body round to triangle in outline (Pl. 26, Fig. 11), 6.8–10.8 mm long, 5.0–7.6 mm wide. Micropylar end acute to blunt, chalazal end rounded to truncate. Attachment point oval to roundish, at the chalazal end, centrally (Pl. 27A) or more laterally (Pl. 26C–E). Integument cuticle around scar folding to the inside (Pl. 26D). Integument cuticle very thick (Pl. 26M–O, 27D). Cells isodiametric, sometimes elongated, polygonal, ca. 19x21–37x25 μm in size (n=20); arranged irregularly; anticlinal walls thick, 3.82–7.53 µm (n=20), periclinal walls smooth, slightly granulated, no papillae, no stomata. Nucellus cuticle visible at the micropylar end of the megaspore (Pl. 27H, I). Nucellus cuticle thin; cells rectangular, elongated in outline, ca. 23x39x29x68 μm in size (Pl. 27I). Megaspore membrane non-cellular, reticulate (Pl. 27J).

Remarks. Majority of described seeds are platyspermic, thickly cutinised compressions. Some are only represented by a compression with charcoalified fractured tissue (Pl. 26A), without any morphology preserved. A few specimens are preserved three-dimensionally, presenting a pear-like shape (Pl. 27A, B, specimen L/I/17). Seeds outline change from roundish to more triangular (Fig. 11). This is rather an effect of different phylogenetic affinity of particular seeds than intraspecific variability. Seeds were probably attached laterally to the ovule-bearing scale. Attachement point is localised, in most specimen, on side (Pl. 26C–F), only in some cases at the central part of the chalazal end (Pl. 27A).

Figure 11. Schematic drawing of length/width ratio changes in *Carpolithes* sp. from Lipie Śląskie-Lisowice. Shape of the seeds spread from more rounded (left) to triangle (right).

Gymnosperm ovules/seeds possess cutinised multi-layered cover composed of outer integument, inner integument (after fertilisation integument developed into sarcotesta, sclerotesta, endotesta of the seat coat; Simpson, 2019), nucellus and megaspore membrane The outermost layer with distinctive cell pattern received through the maceration is probably an outer integument cuticle. Probable inner integument cuticle is visible only at the edges of the outer integument edges and was thinner (Pl. 26N). Outline of the nucellus cuticle cells can be recognised only on one specimen (L/I/12; Pl. 27H, I) in the micropylar area of the megaspore. Megaspore membrane forms a sac triangular in outline (Pl. 27G, H). Megaspore is empty, however occasionally visible are miospores trapped in the membrane folds (Pl. 27K–M).

All described seeds are isolated, preserved in a mudstone containing other fragmented plant remains in different volume. The most recognisable and at the same time most common are isolated leaves of *Brachyphyllum*- and *Pagiophyllum*-type foliage. However, those are though the most abundant plant remains dispersed in the Lipie Śląskie-Lisowice, and the organic connection with described specimen has not been found so far. Generic identification of isolated seeds is limited by general similarities in gymnosperms seed anatomy (Harris, 1935). There is a strong resemblance between Lipie Śląskie-Lisowice seeds and *Patokea silesiaca* Pacyna, Barbacka et Zdebska 2017. *P. silesiaca* producing wingless seeds with characteristic attachment place (pl. VI, Pacyna *et al.*, 2017) like in the seeds currently described. Also size of *P. silesiaca* seeds and *Carpolithes* from Lipie Ślaskie-Lisowice is comparable (6–8.5 mm long and 5.0–7.0 mm wide vs. 6.8–10.8 mm long, 5.0–7.6 mm wide respectively).

4.2.2. Cuticles macerated from coprolites

Morphotype A

Plate 28A – B

Material. Cuticle fragments bulk-macerated from coprolites; coprolite 1- ZPAL V.33/1101, cuticle: 04, 08, 09, 13–16, 20, 21, 27–30, 35, 36, 38, 46, 47, 49, 50, 52, 55, 59, 69, 71, 74; coprolite 2- ZPAL V.33/1106, cuticle: 02–04, 12, 16–19, 26, 27, 33, 35, 38, 39, 48, 50; coprolite 3- ZPAL V.33/1107, cuticle: 01–04, 06–08, 10, 16, 17, 25–27.

Description. Leaves lanceolate in shape, slightly incurved on adaxial side; apex tapering acute. Leaf base not preserved or incomplete. The biggest and most complete leaf cuticle is 4.1 mm long and 2.5 mm wide, but the biggest cuticle fragment is 8.0 mm long and 3.6 mm wide. Short wing on a ridge formed by elongated marginal cells (Pl. 28A). Epidermal cells rectangular to polygonal, arranged in longitude rows, shorter, isodiametric in stomata rows. Anticlinal walls of epidermal cells straight, evenly cutinised, slightly rounded in corners. Periclinal walls bear solid papillae in the centre of a cell or closer to the acroscopic side. Cuticle amphistomatic. Stomatal complexes arranged irregularly in parallel longitudinal rows, single stomata wide, separated with ca. 1–7 rows of epidermal cells (Pl. 28B). Stomata complexes circular to oval in outline, composed of a pair of sunken guard cells and 4–6 subsidiary cells. The size of stomata complexes 46–74 mm in diameter. Apertures randomly orientated. Subsidiary cells cutinised stronger than epidermal cells. Subsidiary cells with a solid papilla on the inner edge, overarching the stomatal pit. Anticlinal walls of subsidiary cells thickened, forming a ridge (Pl. 28C). Outer parts of periclinal walls with fine striations. Encircling cells inconspicuous.

Remarks. Cuticles of Type A probably belong to the family Cheirolepidiaceae due to the presence of the thickened rim with papillae surrounding the stomatal pore. Type A specimens resemble *Pagiophyllum* Heer 1881, a foliage morphogenus use for sterile leaves/shoots of conifers from Late Triassic to Upper Cretaceous. Isolated awl-shape leaves fit to the description of *Pagiophyllum* in Harris (1979), Kendall (1948), Cantrill *et al*. (1995). Fragmentary cuticles classified into type A differ between each other, but all show characters of the genus. Differences might indicate presence of more than one species of *Pagiophyllum* or be a result of heterophylly in *Pagiophyllum*. Nevertheless, the dispersed and fragmentary nature of the material do not allow more accurate determination of the cuticles.

Morphotype B

Plate 28D – F

Material. Cuticle fragments bulk-macerated from coprolites; coprolite 1- ZPAL V.33/1101, cuticle: 01–03, 10–12, 23, 24, 33, 37, 42–45, 48, 51, 53/54, 58, 62, 65, 77; coprolite 2- ZPAL V.33/1106, cuticle: 09–11, 13–15, 20, 23–25, 29–32, 34, 36, 37, 40–47, 49; coprolite 3- ZPAL V.33/1107, cuticle: 05, 12–14, 19, 21–24, 28, 29, 35, 37.

Description. Leaves ovate in proximal view, almost as wide as long. Apex acute to obtuse (Pl. 28D). Leaf base not preserved. The biggest most complete leaf cuticle 5.2 mm long and 5.8 mm wide. The smallest complete leaf cuticle 1.5 mm long and 1.6 mm wide. Epidermal cells in longitudinal rows converging toward the apex (Pl. 28D), rectangular to polygonal, isodiametric. Anticlinal walls thick and straight. No papillae on periclinal walls. Epidermal cells elongated closer to the leaf margin, forming a scarious, dentate edge on the free part of a leaf (Pl. 28E). Towards the leaf tip area epidermal cells are getting elongated and are equipped with long papillae forming a "hairy" apex cover. 3–4 epidermal cell rows between stomata rows. Stomata complexes round, aligned in rows single stomata wide; guard cells sunken, surrounded by 5–7 subsidiary cells. Stomata separated by 3–4 epidermal cells, adjacent stomata never share a subsidiary cell (Pl. 28F). The stomata complex size 50–90 mm in diameter. Subsidiary cells strongly cutinised, forming a ridge; each subsidiary cell with a solid papilla pointed towards the centre of stomatal complex.

Remarks. The most complete cuticles assigned to type B morphotype have preserved upper and lower cuticle. Despite differences in shape of an apex within individual cuticles and incomplete preservation, type B cuticles show similarities to *Brachyphyllum* Lindley & Hutton ex Brongniart, a morhogenus possessing features characteristic for Cheirolepidiaceae family. Isolated cuticles correspond with the description of Kendall (1947), Watson (1988) and Ash (1999). The presence of macrofossils with cuticles preserved assigned to genus *Brachyphyllum* identified from the Lipie Śląskie-Lisowice sediments (Wawrzyniak, 2010), makes the diagnosis more reliable.

Morphotype C

Plate 28G – I

Material. Cuticle fragments bulk-macerated from coprolites; coprolite 1 - ZPAL V.33/1101, cuticle: 07, 18, 19, 26, 32; coprolite 2 - ZPAL V.33/1106, cuticle: 28; coprolite 3 - ZPAL V.33/1107, cuticle: 20.

Description. No leaf tip and leaf base. The biggest cuticle preserved is 5.5 mm long and 4.5 mm wide. Cells arranged loosely in longitudinal rows. Epidermal cells rectangular, elongated in rows between stomata and more isodiametric in stomata rows. Marginal cells form a slightly scarious leaf ridge. Anticlinal walls are thickened with rounded corners, sometimes irregular pitting and gentle bulging is present. Periclinal walls smooth, occasionally striae is visible. Stomata organised in loose rows single stomata wide (Pl. 28G). Stomata in rows more or less regularly spaced; adjacent stomata never shear a subsidiary cell (Pl. 28H). Stomata aperture and guard cells sunken. Stomata orientated randomly. 4–7 rounded subsidiary cells from (usually 5 or 6) form a "flower" shape stomatal complex. Stomata complexes size is 45–85 mm in diameter. Subsidiary cells tapering to an aperture of stomata . Subsidiary cells anticlinal walls slightly more cutinised than epidermal cells, thicker towards the stomatal pit. A small, prominent papillae on subsidiary cells pointing toward the centre of the complex, overarching the aperture (Pl. 28I). Encircling cells inconspicuous, but if recognizable they do not form a complete circle.

Remarks. Cuticle fragments representing only one side of a leaf. Cuticles of type C are most probably representing Coniferales. They are similar to type A and B in construction of the stomata complex and general pattern of the epidermis. They show characters that would correspond with the description of *Brachyphyllum* and *Pagiophyllum* from Harris (1979) and Kendall (1948). Despite that, cells of type C are slightly bigger and do not possess any papillae on periclinal walls as in type A. Also, the distribution of the stomata seems to be looser than in types A and B. From the shape of the cuticles, it might be assumed that leaf was wider at the base and was tapering towards apex resembling *Brachyphyllum*. Similar cuticles were found in the dispersed material from this locality previously (Wawrzyniak, 2010).

Remarks on types A, B and C. Cuticles of the same characteristics as assigned to morphotypes A, B and C are also found dispersed in the same strata at Lipie Śląskie-Lisowice clay-pit, and the most complete leaves can be correlated with leafy shoots of two conifer genera – *Pagiophyllum* and *Brachyphyllum*, abundant in the Upper Triassic sediments of this locality. Foliage of these types is known from the Upper Triassic and has been recognized in Cupressaceae, Podocarpaceae, Araucariaceae, Cheirolepidiaceae (Meyen, 1987; Stockey, 1994) and Patokaeceae (Pacyna *et al*., 2017). The morphogenus *Pagiophyllum* includes the remains of plants with stems with leaves growing spirally, set on a leaf cushion. Leaves triangular with a broad base. The free part of the leaf is equal to its width or much longer. The lower surface is convex, the upper concave or slightly convex. The smooth and sharp edges of the leaf converge to a sharp apex (Harris, 1979). *Pagiophyllum*- and *Brachyphyllum*-type foliage can as well originate from the same species of plant, i.e. in Patokea Pacyna, Barbacka et Zdebska, leaves are morphologically variable, some leaves have extended free part, showing similarity to *Pagiophyllum*, whereas other are in *Brachyphyllum*-type (Pacyna *et al*., 2017). Unfortunately, fragmented nature of the specimens and lack of organic attachments with reproductive structures unable the definite identification. Majority of the cuticles from Lipie Śląskie-Lisowice, show similarities to Cheirolepidiaceae family (i.e. random orientation of stomata, 4–6 subsidiary cells and distinctive papillae on them) (Watson, 1988; Ash, 1999; Bomfleur *et al*., 2011).

Morphotype D

Plate 28J – L

Material. Cuticle fragments bulk-macerated from coprolites; coprolite 1- ZPAL V.33/1101, cuticle: 22

Description. Leaf fragment 1.8 mm long and 1.7 mm wide, margin smooth (Pl. 28J). Epidermal cells polygonal to rectangular, arranged in longitudinal loose rows. In stomata rows epidermal cells shorter. Anticlinal walls irregularly cutinised, with thickenings, granulations and pitting.

Striae and reticulate pattern on periclinal walls, no distinctive papillae present. Stomata placed irregularly in longitudinal, loose rows. Stomata complexes round to oval in outline, 45–65 mm in diameter. Stomata guard cells sunken and strongly cutinised, orientated more or less parallel to cell rows (Pl. 28K). The guard cells surrounded by 4–6 (usually 5) subsidiary cells. Subsidiary cells strongly cutinised than other epidermal cells. A solid papillae on subsidiary cells, overarching stomata aperture; outer margin of the cell thickened and elevated above epidermal level (Pl. 28L). Adjacent stomata do not share subsidiary cells. Encircling cells present, but rarely forming a complete circle.

Remarks. No resin bodies were found. Leaf fragment with partially preserved upper and lower cuticles. Leaf was probably tapered, one natural margin preserved. Both surfaces of a leaf are similar, but stomata are more dense on one side (abaxial?). It can originate from elongated entire leaf or from a pinnate compound leaf. It is hard to distinguish costal/intercostal zones, or any feature that could indicate possible venation. The density of stomata seems to be higher closer to the narrowing part of the cuticle. The general outline of the cuticle features show some similarities to Coniferales, but the incomplete preservation and so far lack of similar cuticles identified from the macrofossils of that locality makes diagnosis unreliable.

Morphotype E

Plate 28M – O

Material. Cuticle fragments bulk-macerated from coprolites; coprolite 1- ZPAL V.33/1101, cuticle: 40, 41, 64, 67, 72, 75, 76; coprolite 2- ZPAL V.33/1106, cuticle: 21, 22; coprolite 3- ZPAL V.33/1107, cuticle: 34.

Description. Leaves elongated, linear to lanceolate. Leaf tip acute to obtuse (Pl. 28M). Leaf base not preserved. The most complete leaves are: 4.3 mm long and 2.3 mm wide and 3.6 mm long and 1.4 mm wide. The biggest cuticle is 4.4 mm long and 3.3 mm wide. Leaf margin entire, occasionally minute teeth or marginal cells forming a scarious edge (Pl. 28N). Cuticle moderately thick. Epidermal cells quadratic and isodiametric, with slightly rounded corners. Epidermal cells arranged in loose rows. Epidermal cells in rows alternating stomata rows slightly more elongated. Anticlinal walls straight, evenly cutinised, sometimes with bulging projections. Periclinal walls bear a solid papillae in the centre of a cell. Papillae prominent, round and short to longer and pointed, even hair-like. Longer papillae show striae from tip of the papillae to its base. 4–7 epidermal cells rows separate stomata rows. Stomata distributed irregularly in rows, single stomata wide. Adjacent stomata never share a subsidiary cell. guard cells sunken, irregularly orientated, thinly cutinised. 4–6 subsidiary cells, with a papilla pointing towards centre of a pit (Pl. 28O), rarely overarching it completely. Encircling cells present, forming an incomplete ring. Sometimes incomplete second ring of encircling cells is visible.

Remarks. The shape of the most complete cuticles indicate that the leaves were elongated, presumably needle-like shape. Unfortunately, the lack of leaf base precludes reliable leaf shape reconstruction. Additionally, leaves are broadening slightly from the apex. Also, the cuticle pattern is not differentiating towards the leaf base, whereas it is usually at least slightly different closer to the leaf end. Therefore, the cuticle might have been part of a much longer leaf blade. The biggest fragmented cuticle assigned to this type is indicating that the leaves could be much bigger than the ones already found. Cuticle of this type show resemblance to needle-like Coniferales macrofossils, found previously in the Lipie Śląskie-Lisowice sediments (Wawrzyniak, 2010), but the cuticle could not be obtained.

Morphotype F

Plate 29A – C

Material. Cuticle fragments bulk-macerated from coprolites; coprolite 1 - ZPAL V.33/1101, cuticle: 05, 68, 73; coprolite 2 - ZPAL V.33/1106, cuticle: 05, 06, 08.

Description. The biggest fragment is 3.1 mm long and 2.8 mm wide. Epidermal cells polygonal, differentiated into costal and intercostal fields (Pl. 29A, B). Cells in the costal fields elongated and aligned in longitudinal rows, cells in the intercostal fields shorter to isodiametric and arranged more irregularly. Corners of epidermal cells slightly rounded. Anticlinal walls straight or gently sinuous (undulated; Pl. 29C). Prominent papillae on periclinal walls of shorter cells; longer cells show a darkening in the middle where the cuticle was probably thicker. No stomata.

Remarks. Stomata are the most important feature in the taxonomical identification of cuticles. Hypostomatic (stomata only on abaxial leaf side) and epistomatic (stomata only on adaxial leaf side) plant taxa is not a feature characterizing any particular group among gymnosperms. In addition, in amphistomatic plants number of stomata on upper and lower cuticle can differ. Usually there is a greater number of stomata on the abaxial leaf side, therefore, it cannot be excluded that the cuticles are coming from the adaxial leaf side, because of their fragmentary preservation, and it cannot be defined if the plant was amphi-, hypo-, or epistomatous. The curved alignment of cell rows visible in some specimens might indicate that the cuticle could be coming from other parts of the plant, i.e. cone, seed, stem, and not necessarily from the leaf.

Morphotype G

Plate 29D – F

Material. Cuticle fragments bulk-macerated from coprolites; coprolite 1 - ZPAL V.33/1101, cuticle: 25, 31; coprolite 3 - ZPAL V.33/1107, cuticle: 09, 11, 32.

Description. The biggest cuticle is 4.3 long and 3.3 wide. Cuticle moderately thick. Epidermal cells polygonal in longitudinal rows, sometimes rectangular to isodiametric (Pl. 29D). Anticlinal walls are thick and straight, evenly cutinised. Periclinal walls occasionally bearing a central, hollow papillae (Pl. 29E). Stomata in loose rows or scattered. The size of stomata complex 40–65 mm in diameter. Guard cells deeply sunken, orientated irregularly. Usually 5 subsidiary cells bearing a solid papillae, directed inwards the stomata pit, often overarching the aperture. Anticlinal walls of subsidiary cells strongly cutinised (Pl. 29F). Encircling cells unspecialised.

Remarks. All cuticles are similar in the general pattern of epidermis and type of stomata complex. They show resemblance to conifer cuticles, but their affinity cannot be determined.

Morphotype H

Plate 29G – I

Material. Cuticle fragments bulk-macerated from coprolites; coprolite 2 - ZPAL V.33/1106, cuticle: 07; coprolite 3 - ZPAL V.33/1107, cuticle: 36.

Description. Fragments of thick cuticle. Generally uniformed cuticles are similar in size, with length equal 2.4 mm and width 2.3 mm. Cells arranged in longitudinal rows, stomata rows intercalated with epidermal cells rows. On one cuticle discernible is a band of slightly elongated, polygonal epidermal cells arranged in ca. 14 rows without stomata (Pl. 29G). Polygonal epidermal cells are isodiametric, but single row of elongated, narrow cells is separating stomata rows. Anticlinal walls of epidermal cells thick and straight, mostly evenly cutinised, sometimes small bulging is present. Periclinal walls show a delicate granulation, papillae are rare and faint, if present they are placed closer to the one side of a cell. Resin bodies absent, but masses of resin can be spotted between epidermal cells. Stomata arranged irregularly in longitudinal rows (Pl. 29H). In stomata complex sunken guard cells surrounded by 5–6 subsidiary cells. Subsidiary cells do not show stronger cutinisation than epidermal cells, except for their inner margin that usually is ended with flat papillae pointing towards centre of the stomata pit (Pl. 29I). Subsidiary cells vary in shape and size within single stomata. Stomata orientated irregularly. Encircling cells not specialized.

Remarks. Only one side of the cuticle is present. No apices, bases or margins are preserved. The intercostal field without stomata might mark the area of cuticle over venation, otherwise cuticles have rather uniformed outline. It indicates that cuticles must be a part of a much bigger leaf blade. The general structure of cuticles show resemblance to conifer type cuticles, but because of lack of natural margins enabling the reconstruction of the natural leaf shape the reliable diagnosis is not possible. This is also the first time this type of cuticle has been recognized in the Lipie Śląskie-Lisowice sediment.

Morphotype I

Plate 29J – L

Material. Cuticle fragments bulk-macerated from coprolites; coprolite 1 - ZPAL V.33/1101, cuticle: 39; coprolite 3 - ZPAL V.33/1107, cuticle: 15.

Description. Fragments of moderately thick cuticle. Epidermal cells are arranged in longitudinal rows. No venation could be distinguished from cell arrangement. Epidermal cells rectangular and elongated, more elongated between stomata rows, some twice as long as wide

(Pl. 29J). Anticlinal walls thick, irregularly cutinised with pitting, bulging and granulation (Pl. 29K). Periclinal walls smooth, shorter cells show a faint hollow papillae and sometimes granulation occurs. Stomata arranged in vague rows, irregularly distributed within them. Stomata complexes have elliptical shape. Thinly cutinised guard cells are sunken, orientated transversely to obliquely. Guard cells surrounded by 4–5 subsidiary cells. Subsidiary cells more cutinised than other epidermal cells, especially their inner margin (Pl. 29K, L). Anticlinal walls between subsidiary cells thinner and sometimes hard to distinguish. There is no papillae on subsidiary cells. Sometimes striae is visible overspreading from the centre of the pit towards the outer edge of a cell. Adjacent stomata never share a subsidiary cell. Encircling cells not specialized or form an incomplete circle, but cells are never more cutinised than ordinary epidermal cells.

Remarks. Two cuticles are similar in general cuticle arrangement. They might originate from the same plant or plant family. Unfortunately, fragmentary character and lack of natural margins that would allow the reconstruction of the original leaf shape unable the reliable diagnosis. Tentatively, cuticles are assigned to Coniferales, as they show features described before by Harris 1979, Stockey 1994, Jansson *et al.*, 2008 and Bosma *et al.*, 2009.

Morphotype J

Plate 30A – C

Material. Cuticle fragments bulk-macerated from coprolites; coprolite 1 - ZPAL V.33/1101, cuticle: 06, 17, 60, 61, 66; coprolite 3 - ZPAL V.33/1107, cuticle: 18, 30, 33.

Description. Cuticle fragments and nearly complete cuticles. All cuticles non-cellular. Shape of the most complete specimens and the characteristic structure indicates that this morphotype might in fact represent cutinised megaspore membrane (Pl. 30A). Cuticles surface is sculptured, sometimes with discernible reticulate pattern (Pl. 30B). The presence of a thin membrane on one cuticle suggests that this might be (fused?) megaspore membrane with the nucellar cuticle (Pl. 30C). On the thin nucellar cuticle visible are outlines of elongated tetragonal cells with straight anticlinal walls, arranged in longitudinal rows.

Remarks. Because cuticles are isolated and incomplete exact affinity is hard to define, and this type can be assigned to different gymnosperm lineages. Similar structures were also recognized in the carnivorous coprolites from Lipie Śląskie-Lisowice (Zatoń *et al*., 2015).

Morphotype K

Plate 30D – F

Material. Cuticle fragments bulk-macerated from coprolites; coprolite 1 - ZPAL V.33/1101, cuticle: 56, 63, 70; coprolite 3 - ZPAL V.33/1107, cuticle: 31.

Description. Almost complete cuticle and cuticle fragments. The cuticle has an ellipsoidal shape, slightly pointed on one side and more round on the other. Cuticle is thick and robust. Margins of the cuticle are smooth and entire. There are characteristic dark strips formed by sclerotic fibres on the underside lengthwise of the cuticle (Pl. 30D). Both cuticles have similar character. Epidermal cells are rectangular, isodiametric with corners rounded, arranged in longitudinal rows. Cells in rows with stomata bigger and more quadratic than cells in alternate rows (Pl. 30E). Anticlinal walls very thick. Periclinal walls sometimes show granular ornamentation and small papillae. Stomata arranged in rows. Guard cells deeply sunken surrounded by 6–7 subsidiary cells forming a round stomata complex (Pl. 30F). Subsidiary cells usually have the same size and shape. They are strongly cutinised with a solid papilla on every cell, directed towards the pit. Encircling cells unspecialised.

Remarks. Epidermal features including shape of the stomata show resemblance to Coniferales. The shape and general layout of the cuticle suggest it might come from the pollen cone scale.

4.3. Tatra Mts.

Marian Raciborski described nine species of fossils plants from the Czerwone Żlebki in the Tatra Mountains, where the Tomanova Formation is exposed. The collection was originally presented in 1890 as a monography in Polish, "Flora retycka w Tatrach" (eng. "Rhaetic flora in the Tatra Mts"; Raciborski, 1890; *fig.* 1; Pl. 31), and although a few specimens were distributed across some foreign institutions, i.e. the Swedish Museum of Natural History in Stockholm, it is not known to the broad group of palaeontologists. Michalik et al. (1976) was interested in the stratigraphy and palaeogeographic position of the Tomanova Fm, and presented microfloristic findings, later supplemented with sedimentological analysis and recontruction of the plant bearing section (Michalik *et al.*, 1988). The fossil plant assemblage was revisited by Reymanówna (1984) and mentioned by Pacyna (2013). XIX century descriptions need a modern revision and a taxonomical update. Some of the species need to be synonymised or renamed due to a change in definitions of particular taxa since they were first described by Raciborski (1890). Preservation of the material did not allow many new techniques to be applied, apart from the scanning electron microscope (SEM), but with poor results. Tatra Mts. collection was published in 1890 and was deposited first in the archive of Polska Akademia Umiejętności (eng. Polish Academy of Arts and Sciences). Later collection was relocated to Jagiellonian University, and finally ended up at the Geological Museum of the Institute of Geological Sciences, Polish Academy of Sciences, Research Centre in Kraków. Some specimens from the collection were distributed among other facilities, i.e. Museum in Zakopane and Swedish Museum of Natural History. Raciborski did not numbered specimens, he only add loose labels ("Figs 1B, C") to some of them. Under many specimens number a couples of fragments were gathered. During revision particular specimen were reorganised because fragments assigned as one specimen were presenting completely different characters. Because of the collection primary organisation and its 131-year-old history, finding some specimens, figured and described by original collector and author, was difficult. Also, observation techniques are different now, and what could have been primary observed as fossil plant, observed under modern optical equipment appear to be i.e., a sedimentary structure – an artefact.

4.3.1. Macrofossils

Sphenophyta

Order Equisetales de Candolle 1804
ex von Berchtold et Presl 1820
Family Equisetaceae Good 1975
Genus Equisetites Sternberg 1833
Type species *Equisetites muensterii* Sternberg 1833, Abtswind, Bavaria, Germany, Carnian
Equisetites chalubinskii Raciborski 1890

Plates 32 – 35

Material. Isolated fragments of stems, leaf sheaths, diaphragms and strobili: ZNG PAN A-III-31/0.2, 0.3, 0.4, 1, 2, 3, 4, 6, 7, 8, 9, 10, 11, 12, 13, 14b, 15a, 15b, 16, 17, 18, 19, 20, 22, 23, 24, 26, 29, 37, 38, 39, 43, 48, 49, 51, 52, 53, 56, 57, 61, 66, 71, 72, 74, 78, 79, 83 (Pl. I. fig. 3 – 16), S083113, S083126, S083117, S083119, S083120, S083121, S083122, S083123, S083124, S083125.

Description. Stems straight, unbranched, up to 85.0 mm long and between 5.5 and 28.0 mm wide (most around 15.0 mm), no tapering visible. Stems leafless or leaf sheath covering nodal region (Pl. 32B–F). Internodes smooth or with flat ridges, every 2.0–3.0 mm, sometimes faint longitudinal striae visible (Pl. 32A, E). The nodal regions indistinct. An internode gradually transiting into a leaf-sheath (Pl. 32B–F); no or very subtle swelling (Pl. 32C). Nodal diaphragms circular, 3.9 – 11.1 mm (mostly 8.0 mm) in diameter. Central part surface pitted and surrounded with a ring, ca. 1 mm wide, of slightly square to round pits (probably vallecular canals; Pl. 33A–D, F). Sometimes diaphragms surrounded by attached leaf sheath (Pl. 33E). Leaves linear to slightly lanceolate in shape. Leaves fused in 70–85% leaf length, forming a leaf sheath. Two types of leaf sheaths – wider, with shorter free part (Pl. 34A, D–G) and thinner, slender, with free part longer (Pl. 34B, C). Width of wider leaf sheaths between 13.0 and 20.5 mm and consistent with width of stems found on site. Between 6 and 8 leaves in a leaf sheath (on the compressed half of a stem). Leaves up to 17.0 mm long and between 2.0 and 3.5 mm wide, with free part 2.0–4.0 mm long (ca. less than 20% of the entire leaf length). Leaf tips broken most along a straight or gently convex cut line. Smaller specimens up to 12.0 mm long and 1.5–2.0 mm wide; free part ca. 20–30% of the entire leaf length. Midrib invisible. Leaves separated from each other by commissural furrows emerging from the leaf base, forming a wedge with sharp edges. Commissural furrows wider towards the base of a free leaf tip (Pl. 34F, I). Preservation of leaf surface variable. Leaves surface in some specimens with preserved epidermal pattern impression (Pl. 34I–J), or hair-like ornamentation (Pl. 34H). One specimen with projections on a leaf surface, round to gently oval in outline (Pl. 34K, L), 50.0–55.0 µm in diameter. Projections gathered in two bands separated by a strip of leaf surface cover with square epidermal cells (Pl. 34K). Within bands structures distributed in loose rows. Strobili incomplete; overall shape of the structure undetermined. Preserved fragments 19.9 mm long x 10.0 mm wide and 15.0 mm long x 9.5 mm wide; elongated. Imprints of hexagonal sporangiophores discs with dimensions 2.0–2.2 x 0.8–1.3 mm. Sporangiophores slightly elongated in one direction. A hexagonal umbo in the middle of the sporangiophore disc (Pl. 34B, E, F). Umbo usually well-marked, reflects shape of the sporangiophore, slightly convex with delicate depression in the middle. Thin grooves separating an umbo area from the marginal flange of the sporangiophore disc. Sometimes faint grooves extending from an umbo to the disc margins corners (Pl. 34B, C). Two specimens slightly differ from each other. Specimen A-III-31/21.1 (Pl. 34D) with sporangiophores more widely separated, whereas specimen A-III-31/1.1 (Pl. 34A) with sporangiophores tightly spaced. No spores retrieved. Sporangiophore surface with delicate impression of cellular pattern, but no stomata recognizable (Pl. 34C, F). Pattern is more discernible on disc margins than on the umbo surface. Sporangia not recognized.

Remarks. *Equisetites chalubinskii* is the most common fossil plant in the Czerwone Żlebki. Raciborski was comparing new Tatras sphenophyte specimens with a common Late Triassic–Middle Jurassic *Equisetites muensterii* Sternberg 1833. Raciborski (1890) justified establishing *Equisetites chalubinskii* a new species with preservation of leaf tips and differences in surface and size of sporangiophore discs. Raciborski compared Tatras specimens with descriptions of *E. munsterii* in Saporta (1873), Schenk (1864, 1867) and Nathorst (1878), in which leaf tips are rounded or obtuse but never cut straight as in *E. chalubinskii*. Moreover, in his work on the Rhaetian Flora of the Holy Cross Mountains, Raciborski (1891) described specimens of *E. muensterii* and compared them with *E. chalubinskii* pointing to the later having more robust leaf sheaths and internodes. Raciborski described and emphasize the difference in surface of sporangiophore discs of *E. chalubinskii* with *E. muensterii*. Raciborski (1890) noted that sporangiophores in specimens from the Tatra Mts do not possess a papillae or any protruding structure, as opposed to of *E. muensterii* (Raciborski 1890). The size of *E. chalubinskii* sporangiophores was also an argument used by Raciborski for separating Tatras specimens from *E. muensterii.* Sporangiophores of *E. chalubinskii* are smaller than in e.g. *E. muensterii* illustrated in Schenk (1867) to which it was compared (Raciborski, 1890). Strobili in the Raciborski's collection are incomplete. However, the remaining impressions are longer than wide. That might indicate that strobili were oval in outline or elongated. Two most complete specimens slightly differ between each other with arrangement of sporangiophores. One specimen shows sporangiophores tightly adjacent (specimen A-III-31/1.1; Pl. 34A), in the other sporangiophores are more widely separated (specimen A-III-31/21.1; Pl. 34D). This is probably connected with the developmental stages of strobili before burial or taphonomy. Specimen A-III-31/21.1 was probably more “ripe”. Raciborski (1890) recognised two types of leaf sheaths in *Equisetites chalubinskii*. According to his observations thinner leaf sheaths represent younger, undeveloped plants. In the current studies a diversity of leaf sheaths was also spotted. Leaf sheaths with leaves more slender and thinner are found often along with more robust and wider specimens. There are no distinctive differences in leaves number or surface details that could suggest that they belonged to separate sphenophyte species (Pl. 34). Both types show surface projections that could represent stomata in bands separated by a midrib. Other authors, i.e. Harris (1931, 1961), Schweitzer *et al*. (1997), Barbacka (2009) also noted intraspecific diversification in *Equisetites* genus. The general habit of *Equisetites chalubinskii* cannot be determined with certainty. The exact length of the internodal region is unknown, because no specimen has preserved two following nodal regions. However, the longest preserved piece of stem is 85.0 mm, therefore it can be assumed that internodal region of *Equisetites chalubinskii* was at least that long. There is no evidence of lateral branching in the form of scars on main stems.

Comparison with most common Equisetites species from Triassic to Middle Jurassic of Northern Hemisphere. Raciborski (1890, 1891) found *Equisetites chalubinskii* most similar to a common Northern Hemisphere Upper Triassic–Middle Jurassic horsetail *Equisetites muensterii*. *E. muensterii* has been reported from Rhaetian of Greenland (Harris, 1926, 1931), Liassic of Hungary (Barbacka, 2009) and the lower Liassic of Franconia (Germany; Sternberg, 1833; Schenk, 1886). General size range of both species is similar, including width of stem and number of leaves in a leaf sheath. The main difference is in details of leaf sheaths. Raciborski (1980) found breaking of the leaf tips to be a character separating *E. chalubinskii* from *E.*

muensterii. Tatras specimens have leaf tips broken along the straight line, whereas representatives of the *E. muensterii* had leaf tips rounded or opaque. Harris (1931) also described *E. muensterii* from Greenland with leaf tips "often injured or broken". *Equisetites muensterii* from Hungary has leaf tips acute or subacute (Barbacka, 2009). Damage of the leaf tips might be a feature strongly dependent on taphonomical processes and connected with delicate anatomy of leaf tips. This could be a secondary character in taxonomical divagations or be a feature used as an indirect indication of leaf tip shape. However, the straight cut line of free leaf tips in *E. chalubinskii* is so common and characteristic that could be an effect of leaves internal morphology occurring in this particular species that influenced desiccation of free leaf tips and breaking off along a straight line. Leaves in *E. chalubinskii* do not have a midrib (apart for one specimen, no indications of midrib has been found; Pl. 33K) as in *E. muensterii* described by Harris (1926, 1931) or Barbacka (2009), although it is not a feature used as characteristic for that species, for example leaves of *E. muensterii* illustrated by Sternberg (1833), Saporta (1873) or Halle (1909) were smooth. Most of the *E. chalubinskii* specimens have leaves more robust and straighter than in *E. muensterii*. In *E. chalubinskii* leaves are tapering to acuminate tip from the free leaf level and edges have a characteristic concave shape. Another difference between these two taxa are dimensions of sporangiophores. *Equisetites chalubinskii* has sporangiophore disc ca. 2 mm in diameter, whereas Harris (1931) reports for Greenland specimen 2.5 mm. Isolated fragments of strobili described by Barbacka (2009) from Hungary has similar dimensions to *E. chalubinskii*, but was not assigned to any species, though it was found with vegetative remains of *E. muensterii* on the same site.

One of the most abundant sphenophyte of the Middle to Upper Triassic is *Equisetites arenaceus* (Jaeger) Schenk 1864. *E. arenaceus* was a cosmopolitan species known from sediments from i.e., Buntsandstein of Vosges, France (Grauvogel-Stamm, 1978), late Ladinian of Thale, Germany (Kustatcher and van Konijnenburg-van Cittert, 2008), Ladinian of the Dolomites, Italy (Kustatscher, 2004), early Carnian of Lunz, Austria (Pott *et al.*, 2008). Stems of *Equisetites arenaceus* are 40–120 mm wide (Pott *et al.*, 2008). Leaf sheaths consists of large number of leaves (up to 32, Kustatcher and van Konijnenburg-van Cittert, 2008; >100, Kelber and van Konijnenburg-van Cittert, 1998) showing a prominent vascular bundle in the central part of a leaf (Pott *et al.*, 2008). Free leaf tips had tendency/to fold adaxially (Pott *et al.*, 2008). Leaf tip, if present, is acuminate (Kustatcher and van Konijnenburg-van Cittert, 2008). Although, *E. arenaceous* is considered to be one of the biggest Triassic horsetails, but it was also identified to have a smaller, slender form, probably strobili bearing stem (Kelber and van Konijnenburg-van Cittert, 1998). Smaller stems of *E. arenaceous* are 4.5–6.0 mm wide. Leaf sheaths are 3.5–5.0 mm long, composed of 12–15 leaves, 0.7–1.2 mm wide, separated by indistinctive commissural furrows. Free leaf tip can be acuminate, triangular or slightly blunt. Diaphragms are 2.0–-2.5 mm in diameter and possesses granular central area (Kelber and van Konijnenburg-van Cittert, 1998). Size range of *Equisetites chalubinskii* stems overlap with dimensions of smaller *Equisetites arenaceous* form. Nevertheless, details of leaf sheaths are differentiating these two species – *E. chalubinskii* possess up to 8 leaves, 1.5–3.0 mm wide.

Equisetites conicus Sternberg 1833 is another common Triassic horsetail. This species is known from early Carnian of Lunz (Pott *et al*., 2008), Keuper of southern Germany (Kelber and Hansch, 1995) and Norian of Iran (Schweitzer *et al*., 1997). It is however different than specimens assigned to *Equisetites chalubinskii.* Stems of *E. conicus* are wider than *E. chalubinskii* (35–77 mm wide vs 5.5–28.0 mm) and possess more leaves within leaf sheaths (25–30 leaves in a leaf sheath vs 6–8 leaves on compressed stem), leaves are also bigger (5.7–6.1 mm wide and 27.0–29.0 long vs 1.5–3.5 mm wide and 12.0–17.0 mm long; Pott *et al*., 2008; Schweitzer *et al*., 1997).

Equisetites columnaris (Brongniart 1828) Phillips 1875 is a species known mostly from Jurassic sites: Bajocian of Yorkshire, UK (Harris, 1961), Hettangian of Mescek Mts., Hungary (Barbacka, 2009) and upper Liassic of Iran (Scheweitzer *et al*., 1997). Specimens similar to *E. columnaris* were found also in the Middle Jurassic of Grojec, Poland (Jarzynka and Pacyna, 2015). Tatras specimens show some general similarities to *Equisetites columnaris*. Stems of *E. columnaris* are up to 50 mm wide, but smaller forms from Hungary are 5–10 and 12–25 mm wide (Barbacka, 2009). Harris reported stems 40–50 mm wide, but also slender stems 4–9 mm wide, probably fertile (Harris, 1961). Width of *E. chalubinskii* internodes (5.5–28.0 mm) fits within Hungary wider form and smaller stems have similar dimentions as slender stems from UK. Leaf sheaths are 20 mm long, in small Hungarian form 5–-11 mm, 11–12 in big Hungarian form. Commissural furrows are very distinct and continue 10–20 mm below the node.The acute leaf teeth can be up to 10 mm and sinuses between them are acutely rounded. Leaf number varies between 9 and 16 (on flattened surface; up to 29 in total; Barbacka, 2009). In Yorkshire specimens 50–80 in the lower parts of the stem, ca. 25 in the upper part of the stem (Harris, 1961). Surface of *Equisetites columnaris* on the internodes and leaf sheaths is covered with pits, connected with stomata (Harris, 1961) or hair bases (Schweitzer *et al*., 1997; Barbacka, 2009).

Diaphragms are 5–7 mm in smaller Hungarian form and 20–25 mm in bigger (Barbacka, 2009), they are slightly grained. Hexagonal sporangiophores heads are from 2.5 (Schweitzer *et al*., 1997) up to 3.0 mm wide (Harris, 1961) with concave central area. There is no clear pitting on the internodes of *Equisetites chalubinskii*. Rare ornamentation on the leaf sheath of *E. chalubinskii* lack details to confirm whether they are remnants of stomata. Leaf tips of *E. columnaris* of Iranian specimen are long and generally preserved. The general shape of leaf sheaths is slenderer than in *E. chalubinskii* and there are much more leaves in leaf sheaths.

There are some similarities between Tatras *Equisetites chalubinskii* and *Equisetites laevis* Halle 1908. This species has been previously confused with *Equisetites muensterii* (Schweizter *et al*., 1997). It is also known from Upper Triassic sediments, i.e., Rhaetian of Bjuv, Sweden (Halle, 1908), Upper Rhaetian of Iran (Schweitzer *et al*., 1997) and Greenland (Harris, 1926; 1931), but according to Schweitzer *et al*. (1997), *E. laevis* from Greenland did not belong to this species. Stems of *Equisetites leavis* are max 25 mm wide in specimens from Iran (Schweitzer *et al*., 1997), and up to 40 mm wide in Sweden (Halle 1908) which is in the same size range as *E. chalubinskii* (5.5–28.0 mm; Table 5). Both species have internodes with smooth surface. *Equisetites leavis* was a sphenophyte with small number of leaves within leaf sheath, similarly to *Equisetites chalubinskii.* Specimens described by Schweitzer *et al*., (1997) possess 12 leaves at the node (on the compressed specimen 5–6 leaves; from photo). Shape and size of leaves differ however from *E. chalubinskii. Equisetites leavis* had leaves up to 6.0 mm long, 1.3–1.4 mm wide at the base, whereas leaves of *E. chalubinskii* are between 12.0 and 17.0 mm long and 1.5–3.5 mm wide. *E. leavis* leaves start tapering from the middle, and they taper conically towards the apex. *E. chalubinskii* leaves have more robust appearance and are more linear and straight in outline.

Summarizing, *Equisetites chalubinskii* is an endemic species, known only from Late Triassic of Tatra Mountains. Current observations of leaf sheaths morphology and general appearance of the plant remains support Raciborski's decision of separating a part of *Equisetites* specimens from the Tomanowa Fm as a new species.

Equisetites sp.

Plate 36

Material. Leaf sheaths: ZNG PAN A-III-31/8.4, 12.1, 12.2, 12.11, 16.1, 19, 21.1, 26.2, 26.5, 32, 33. 35.3, 37.1 (Pl. I, Pl. 1, 2).

Description. Stems straight, no branching. Internodes between 6.0 and 14.0 mm wide; smooth (Pl. 36A, B). Nodes covered by leaf sheaths; no swelling or swelling indistinctive. Leaf sheaths up to 16.0 mm wide. Leaves lanceolate; leaf tip acute; commissural furrows between leaves narrowing down towards the leaf base (Pl. 36). 8–9 leaves in a leaf sheath (on the compressed half of a stem). Free tip for ca. 30–40% of a leaf length. Leaves between 1.0-1.5 mm wide, 5–10.5 mm long. No midrib on leaves, or midrib faint (Pl. 36F, G). Some specimens with surface covered by elliptical projections 60–75 µm long and 30–40 µm wide (Pl. 36D, E), sometimes with a shallow elongated depression in the middle, possible stomata (Pl. 36E).

Remarks. Raciborski found five specimens of incomplete leaf sheaths that were different from specimens he ascribed to *Equisetites chalubinskii* (Raciborski, 1890). He noticed some similarities between Tatras specimens and Liassic *Equisetites bunburyanum* described by Zigno (1856) from Italy. But due to incomplete and poor preservation Raciborski only pointed to a resemblance to the Italian species (Raciborski, 1890). *Equisetites bunburyanum* Zigno 1856 was also mentioned by Heer (1877) from Jurassic of Svalbard, but these specimens possess no leaf sheaths, and stems are covered with rows. No more specimens were found that could confirm *E. bunburyanum* affinity in the Tomanova Fm Specimens assigned in this work to *Equisetites* sp. differ from specimens described as *Equisetites chalubinskii* mainly in the shape of a leaf and construction of a leaf sheath. Leaves of *E. chalubinskii* are straight and generally robust and have distinctive concave shape of free leaf parts, whereas *Equistetites* sp. have lanceolate leaves with acute leaf apex. It is however possible that they represent *E. chalubinskii* younger, undeveloped stems and differences are caused by taphonomical processes or interspecies diversity. Although even smaller, underdeveloped leaves of *E. chalubinskii* show distinctive shape of free leaf parts and possess a broken leaf tip (Pl. 33B, C).

Comparison of the diagnostic features of selected *Equisetites* species from Late Triassic – Middle Jurasic sites of Northern Hemisphere the most similar to *Equisetites chalubinskii* and *Equisetites* sp. in terms of size and number of leaves in leaf sheath is presented in Table 5.

Table 5. Comparison of *Equisetites chalubinskii* and *Equisetites* sp. from the Upper Triassic Tomanova Fm in the Tatra Mountains with selected *Equisetites* species from Late Triassic–Middle Jurassic Northern Hemisphere localities.

Equisetites taxa	Internode width (mm)	Diaphragm (mm)	Leaf sheath			
			N° of leaves (compressed specimen)	Leaf width (mm)	Leaf shape	Free tip shape
E. bunburyanum	6.0–14.0 (MR); 6.0–16.0 (Z); 8.0 (H)	–	8–9 (ZW; from plate)	1.0 (MR)	lanceolate (Z)	acute (MR)
E. leavis	25.0–40.0 (HJS)	25.0 (HJS)	5–6 (ZW; from plates); 12 (HJS; not compressed)	1.3–1.4 (HJS)	lanceolate (HJS)	acute (HJS)
E. musensterii	6.0–28.0 (TH); 13.0–27.0 (smooth), 15.0–20.0 (ribbed; MB); 12.0–20.0 (MR1)	3.0–8.0 (TH); 6.0–15.0 (MB)	6 (TH); 10–12 (smooth), 6–7 (ribbed; MB)	0.8–2.5 (smooth), 2.0–4.0 (ribbed; MB)	subacute – acute (smooth), rounded – subacute (ribbed; MB)	acute or bland (TH)
*E. chalubinskii**	28 (MR); 5.5–28.0 (ZW)	4.0–18.0 (MR); 3.9–11.1 (ZW)	6–8 (ZW)	1.5–3.5 (ZW)	linear (MR; ZW)	straight (MR; ZW)
Equisetites sp.*	6.0–14.0 (ZW)	–	8.0– 9 (ZW)	1.0–1.5 (ZW)	lanceolate (ZW)	acute (ZW)

Abbreviations: H – Heer, 1877; MR – Raciborski, 1890; MR1 – Raciborski, 1891; ZW – Wawrzyniak, this study;

MB – Barbacka, 2008; TH – Harris, 1931; HJS – Schweitzer *et al.*, 1997; Z – Zigno, 1856; * – this study

Family *Incertae sedis*

Genus *Neocalamites* (Halle 1908) Bomfleur *et al*., 2013

Type species *Neocalamites lehmannianus* (Goeppert 1846) Weber 1968 (=*Neocalamites hoerensis* (*Schimper* 1869 sensu Halle 1908), Wilmsdorf,
Landsberg, Silesia (today Gorzów Śląski, Poland), Rhaetian, Upper Triassic

Neocalamites lehmannianus (Goeppert 1846) Weber 1968

Plate 37

1846 *Calamites lehmannianus* Goeppert, p. 143, pl. I, pl. 1–3.
1856 *Calamites lehmannianus* Goeppert: Zigno, p. 43.
1867 *Schizoneura hoerensis* Schimper, pp. 283–284.
1881 *Schizoneura hoerensis* Hisinger, Heer: pp. 1–2, pl. I, II.
1894 *Schizoneura hoerensis* Schimper: Raciborski, pp. 95–98 in part
1908 *Neocalamites hoerensis* (Schimper) Halle, pp. 6–13, taf. 1–2.
1931 *Neocalamites hoerensis* (Schimper) Halle: Harris, pp. 22–25, 29, text-pl. 4A, B.
1961 *Neocalamites hoerensis* (Schimper) Halle: Harris, pp. 30–33, text-Pl. 8.
1968 *Neocalamites lehmannianus* (Goeppert) Weber, pp. 31–39, pl. 1, Pl. 17–23, pl. 2, pl. 5–27, Abb. 4–5.

Material. ZNG PAN: A-III-31\35, 36 (pl. I, fig. 23)

Description. Straight, unbranching, leafless stems, 24.0–30.5 mm wide, up to 63.5 mm long. Internodes straight; no internode complete. Nodes slightly swollen. Fine ribs present, but not well marked, densely covering stems surface; ca. 6–8 ribs per 10 mm stem width (Pl. 37C). Ribs opposite at node, sometimes alternating. Nodal regions poorly preserved (Pl. 37A, B); leaf scars hard to determine. No leaves found. One specimen with a branch scar below the node (Pl. 37D). Scar round, 6.4 mm in diameter.

Remarks. Raciborski classified two specimens as *Schizoneura hoerensis* (Hisinger 1840) Schimper 1869 after comparing them with specimens from Sweden that he had received from Nathorst (Raciborski, 1890). Later, Raciborski identified as *Schizoneura hoerensis* similar specimens from Holy Cross Mts. (Raciborski, 1891,1892) and Middle Jurassic Grojec clays (Raciborski, 1894). The generic name *Schizoneura* was later changed by Halle (1908) to *Neocalamites* (*Schizoneura hoerensis* = *Neocalamites hoerensis*), as the *Schizoneura* is characterized by possessing leaves grouped in leaf sheaths of at least two leaves fused for almost entire length and *Neocalamites* has leaves generally free (Halle, 1908; Willis, 1910; Grauvogel-Stamm, 1978; Kelber, 1983; Bomfleur *et al*., 2013). Further classification changes were made by Weber in 1968, who synonymised *Neocalamites hoerensis* described by Halle in 1908 with *Calamites lehmanianus* created by Goeppert in 1846 (*Neocalamites hoerensis* = *Neocalamites lehmanianus*; for details see Pott and Mcloughlin, 2011; Barbacka *et al*., 2014). Raciborski's specimens from Grojec were revised by Jarzynka and Pacyna (2015) and reasigned as *Neocalamites lehmannianus* (Goeppert 1846) Weber 1968, *Neocalamites grojecensis* Jarzynka et Pacyna 2015 and *Neocalamites* sp. Raciborski found also similarities of investigated Tatra specimens with *Schizoneura meriani* (Brogniard 1828) Heer 1877 from Late Triassic flora from Lunz, Austria, (that species was also transitioned to *Neocalamites meriani* by Halle in 1908) up to a point where he found distinguishing one species from another difficult (Raciborski, 1890). Weber (1986) and Pott and Mcloughlin (2011) also emphasised that *N. hoerensis* and *N. meriani* are within the same size range and morhphology of those two species is resembling one another. According to Schweitzer *et al*., (1997) *N. meriani* can be distinguished from *N. hoerensis* (Schweitzer *et al*., 1997 uses *Neocalamites hoerensis*) by possessing smaller number of ribs and their wider distrubiution within the stem width.

All preserved in Tatra Mts. specimens are representing compressions of inner vascular cylinder. More complete specimens of *Neocalamites lehmanianius* (i.e. Barbacka *et al*., 2014, Jarzynka and Pacyna, 2015), possess a circular leaf scars on the node, distributed every second to third rib. *N. lehmanianus* has long linear leaves; in the Tatra material leaves are not preserved. One of the specimen found by Raciborski bears a round scar too big to be a leaf scar (6.4 mm diameter), but could be a trace left by a secondary branch. The preserved specimen might represent a rhizomatic fragment of the plant, what could explain the lack of leaf scars at the nodal region. Also, if *Neocalamites lehmanianus* was closely related to *Neocalamites meriani* and share similar morphological features and general habit, than the reconstruction of the *N. meriani* (Frentzen, 1934; Pott *et al*., 2008) suggest that the secondary branches emerged from the leafless main stem and were much thinner.

Stems dimensions, ribbing and general appearance are resembling *N. lehmannianus.* All identified specimens are preserved on rock slabs that probably were part of the same rock layer, due to similarities of the sediment and accompanied plant detritus. Therefore they are considered to belong to the same species, and might share the same habitat during growing season or even be part of the same plant. No reproductive structures were found in close proximity of the specimens. Because of the poor preservation of the researched specimens it cannot be excluded that specimens assigned to *Neocalamites lehmanianus* belonged to a different species, i.g. *Neocalamites meriani.* However, considering lackness of other features that would determine different taxonomical affinity of the specimens the author decided to remain with original diagnosis by Raciborski (1890).

Neocalamites lehmanianus was also found in Upper Triassic (Rhaetian) of Poland (Barbacka *et al*., 2014), Portugal (Heer, 1881), Greenland (Harris, 1926; 1931) and Sweden (Pott and McLoughlin, 2011), Jurassic of Yorkshire (Harris, 1961) and Lower Jurassic of Poland (Barbacka *et al*., 2010; Barbacka *et al*., 2014), Middle Jurassic of Poland (Raciborski, 1894; Jarzynka and Pacyna, 2015).

Pteridophyta

Order: Osmundales
Family: Osmundaceae
Genus: *Cladophlebis* Brongniart 1849
Type species: *Cladophlebis albertsii* (Dunker) Brongniart 1849, northern Germany, early Cretaceous

Cladophlebis roessertii (Schenk 1867) Saporta 1873

Plate 38

1838 *Alethopteris roessertii* Presl: p. 145, pl. 33, pl. 14a, b.
1867 *Asplenites roessertii* Schenk, p. 49, pl. 7, pl. 7, pl. 10, Pl. 1–4.
1873 *Cladophlebis roessertii* (Schenk) Saporta, p. 301, pl. 31, Pl. 4.
1878 *Cladophlebis* (*nebbensis* var.) *roessertii* Presl: Nathorst, p. 42, pl. 2, Pl. 1–3.
1890 *Cladophlebis roessertii* (Presl) Saporta: Raciborski, p. 11, pl. 3, Pl. 26–29.
1894 *Cladophlebis subalata* Raciborski, p. 85, pl. 10, Pl. 11C, pl. 24, pl. 14 (non pl. 24, pl. 15, 16).
1894 *Cladophlebis whitbiensis* Brongniart: Raciborski, p. 73, pl. 21, Pl. 1, 2 (non pl. 20, Pl. 23, pl. 21, Pl. 8, 9).

1919 *Cladophlebis roessertii* Presl: Antevs, p. 18, textPl. 2, pl. 8, Pl. 1.
1922 *Cladophlebis roessertii* (Presl) Saporta: Johansson, p. 18, pl. 5, Pl. 4–9.
1926 *Cladophlebis roessertii* (Schenk) Saporta: Harris, p. 57, text-Pl. 3A–D.

Material. Fragments of sterile fronds: ZNG PAN A-III-31/0.1, 0.2, 0.3, 0.4, 2, 3, 4, 6, 7, 8, 9, 10, 11, 12, 13, 14b, 15a, 15b, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 34, 37, 38, 39, 41, 42, 43, 47, 48, 49, 50, 51, 52, 53, 54, 56, 57, 58, 59, 61, 62, 63, 64, 65, 67, 68, 70, 71, 72, 73, 74, 75, 77, 78, 79, 80, 83, 85, 86, S083113, S083115, S083117, S083118, S083119, S083120, S083121, S083122, S083125, S083126.

Description. Fragments of sterile bipinnate fronds, with maximum length of 63.0 mm and up to 35.0 mm wide. Fragmented pinnae between 15.0 and 60.0 mm long, and 12.0–27.0 mm wide. Pinnae 2.0–3.0 mm wide, arise from the smooth rachis, at 55–75° angle. Pinnules entire, triangular, in some specimen oblong, falcating closer to the apex. Pinnules arise from axis at 45–75° angle, oppositely or suboppositely (Pl. 38A, B, C, E). Pinnules 5.0–12.0 mm long, 3.0–6.0 mm wide, length/width ratio 1.1–2.6. Apex acute, slightly rounded tip. Leaf base wide and straight (Pl. 38F). The following bases attached to one another. Pecopterid type of venation. Midrib grows to the pinnule apex (Pl. 38F). Secondary veins inserted on midrib at 60° angle fork usually once or twice.

Remarks. *Cladophlebis* is a widespread osmundaceous genus known from Upper Palaeozoic and Mesozoic (Taylor *et al*., 2009). The usually bipinnate fronds show variability in pinnae attachment which can be opposite, subopposite, alternate or subalternate (Harris, 1961). Pinnules are lanceolate with slightly wider base (Taylor *et al*., 2009) but observed is some multivariousness of shape within the same frond (Harris, 1931, 1961; Barbacka and Bodor, 2008; Jarzynka, 2016). Morphological characters of the Tatras specimens like triangular, sometimes oblong pinnules with entire margins and secondary veins forking once or twice are consistent with *Cladophlebis roessertii* (Schenk 1867) Saporta 1873 descriptions from Late Triassic–Early Jurassic of Germany (Schenk, 1867), Jurassic of France (Saporta, 1873), Late Triassic–Jurassic of Sweden (Nathorst, 1878; Antevs, 1919; Johansson, 1922), Early Jurassic of Greenland (Harris, 1926), Early Jurassic of Hungary (Barbacka and Bodor, 2008) and Late Jurassic–Early Cretaceous of Antarctica (Gee, 1989). *Cladophlebis roessertii* was also described from Poland, from Middle Jurassic of Grojec (Jarzynka, 2016). Apart from *C. roesertii* Raciborski separated also *C. roessertii* forma *parvifolia*, but Raciborski did not exclude the possibility that it is a completely separate species (Raciborski, 1890). Current research did not confirm presence of forma *parvifolia.* Specimens distinguished by Raciborski do not possess features that could explain establishing a new species or subspiecies. *Cladophlebis* is a genus with well-preserved morphological variations. Specimens of *Cladophlebis rosertii* from the Tatra Mts. also show high level of diversification, i.e. in leaf size and shape. But the influence of ontogeny state/developmental stage or inta-specific variation reflecting on plant morphology cannot be disregarded. Blanco-Moreno and Buscalioni (2021) noticed that the number of veins at the margin could be affected by pinnule size. Barbacka and Bodor (2008) pointed towards the influence of environmental conditions like light and soil on development of such features like pinnules base, apex and margin shape.

Order Gleicheniales Schimper 1869

Family Dipteridaceae Seward et Dale 1901

Genus *Clathropteris* Brongniart 1828

Type species: *Clathropteris meniscoides* (Brongniart 1825) Brongniart 1828

Clathropteris meniscoides (Brongniart 1825) Brongniart 1828

Plate 39A – D

1825 *Filicites menisciolides* Brongniart, p. 218; pl. 11.
1828 *Clathropteris meniscoides* (Brongniart) Brongniart, p. 62.
1838 *Clathropteris meniscoides* Brogniart, Sternberg, p. 169.
1867 *Clathropteris platyphylla* Brongniart: Schenk: pp. 81–86, pl. 16, pl. 2–9, pl. 27.
1883 *Clathropteris platyphylla* var. *expansa* Fontaine, p. 54; pl. 31, pl.. 3, 4; pl. 32, pl. 1; pl. 34, pl. 1; pl. 35, pl. 2.
1907 *Clathropteris meniscoides* Seward, p. 20; pl. 6, pl. 49, 50; pl. 8, pl. 75, 76.
1914 *Clathropteris platyphylla* Goeppert: Gothan: p. 107.
1922 *Clathropteris* cf. *meniscoides* Yabe, p. 11, text-Pl. 8.
1925 *Clathropteris meniscoides* Kawasaki, p. 10; pl. 13; pl. 14, pl. 46–49; pl. 15, pl. 50–52.
1931 *Clathropteris meniscoides* Brongniart: Harris, pp. 88–93, pl. 15, pl. 1, 9, pl. 16, l. 9–10, pl. 13, pl. 3, 5, 12, text-pl. 32–34.
1936 *Clathropteris meniscoides* Brongniart: Oishi and Yamasita, p. 158.

Material: 11 isolated fragment of frond lamina covered with reticulate venation; ZNG PAL A–III-31\45.

Description. The largest fragment of frond lamina 49.4 mm long and 19.3 mm wide. Main vain 0.7 mm wide. Veins depressed. Secondary venation forms a net of rectangular/square to polygonal mesh. Tertiary and quaternary veins emerging at a 90°. More regular, square mesh ca. 2.5 x 2.5 mm. The smallest mesh 0.3 x 0.3–0.5 x 0.5 mm. The tertiary veins sometimes end blind. No sporangia found.

Remarks. Preservation of frond fragments makes it hard to reconstruct leaf shape. The biggest preserved specimen (ZNG PAL A-III-31/45) has irregular shape (Pl. 39A). It shows a fragment of a lamina with two veins spreading from one point at the angle of 30°, veins are 0.7 mm wide. Venation between them is branching, forming a net of mainly square and isodiametric polygonal meshes (Pl. 39B–D). Type of venation and shape of the fragment (Pl. 39A) show a resemblance to lower parts of the pinna and leaf fragment close to the base of the frond of *Clathropteris meniscoides* Brongiard 1828 (i.e., Harris, 1931; Choo *et al*., 2016; Barbacka *et al*, 2019).

Fragmentary preservation of described specimens and therefore lack of possibility to address all the diagnostic features (morphology of primary segments, tooth shape, angle of secondary veins spreading, size and shape of sporangia) neccecery to establish a species makes current diagnosis rather ambiguous. Nevertheless, *Clathropteris* has highly distinctive orthogonal venation pattern. Type of venation showed in Tatra specimens is showing strong resemblance to *Clathropteris* genus. Raciborski (1890) described *Clathropteris* from Tatra Mts.., as *Clathropteris platyphylla* Goeppert 1841. However, *C. meniscoides* and *C. platyphylla* were later recognised as conspecific, with priority of *C. meniscoides* (Johansson, 1922; Harris, 1931). *Clathropteris meniscoides* is a wide distributed species, abundant in Late Triassic: Greenland (Harris, 1931), Iran (Farahimanesh *et al*., 2021), Early Jurassic: Argentina (Choo *et al*., 2016), Sweden (Brongniard, 1925, 1928), Antarctica (Bomfleur and Kerp, 2010), Hungary (Barbacka *et al*., 2019), Japan (Oishi and Yamasita, 1932).

Some reservation is however needed in terms of definite classification of the remains. These particular fragments are representing Dipteridiaceae ferns with certainty, due to a characteristic venation pattern. However, as previously some authors pointed (i.e. Pott, 2014; Pott and Jiang, 2017) when dealing with fragments of the leaf lamina without preserved features like frond or pinna/pinnule shape, presence of sori etc., determining taxonomical identity can be difficult.

Oder *Clathropteris* similar to *C. meniscoides* is *C. obovata* Oishi 1932 (Pott, 2014). The character considered to be the most distinctive between the two taxa is the general coarseness appearance of the leaf surface connecting with thickness of the veins and details of the veins distribution (Schweitzer *et al*., 2009; Pott, 2014). Venation in *C. meniscoides* is more incisive and the whole leaf blade has a thicker appearance than *C. obovata* Secondary veins in *C. obovata* emerge at a more acute angle from the midvein and tertiary and quaternary veins form mesh less regular than in *C. meniscoides* (Schweitzer *et al*., 2009; Pott, 2014).

Clathropteris vs Dictyophyllum: Clathropteris and *Dictyophyllum* show very similar general appearance. Up to a poin where some authors suggestet that these two genere should be merged (Choo *et al*., 2016; Herbst, 1992). The most discriminating features are size and number of sori and sporangia, and the venation pattern. Ortogonal venation patern is characteristic for *Clathropteris*. Veins of higher order in *Dictyophylllum* form less regular pattern. The specimen is not coming from *D. muensterii*, cause *D. muensterii* has deeply cut pinnae; in this specimen the leaf blade between pinnae is very narrow, almost absent, like if leaf blade surface started on the rachis and pinae don’t touch each other like in Schweitzer (2009).

Order Gleicheniales Schimper 1869
Family Dipteridaceae Seward et Dale 1901
Genus *Dictyophyllum* Lindley and Hutton 1834
Type species: *Dictyophyllum rugosum* Lindley and Hutton, 1834 Jurassic; Yorkshire, England.
Dictyophyllum exile (Brauns 1862) Nathorst 1878

Plate 39E – I

Selected synonymy
1862 *Camptopteris exilis*; Brauns, p. 54; pl. 13, pl. 11.
1878a *Dictyophyllum exile* Brauns; Nathorst, p. 14, pl. 1, pl. 9.
1878b *Dictyophyllum exile* Brauns; Nathorst, p. 39, pl. 5, pl. 7.
1902 *Dictyophyllum acutilobium* (Brauns) Schenk; Moeller, p. 41, pl. 4, pl. 5.

1906 *Dictyophyllum exile* Brauns; Nathorst, p. 7, pl. 4, pl. 1; pl. 5, pl. 1–8; pl. 6, pl. 1–22; pl. 7, pl. 2–11; text-pl. 1–3.
1922 *Dictyophyllum* cf. *exile* (Brauns) Schenk; Johansson, p. 8, pl. 1, pl. 1–6; pl. 5, pl. 45–52.
1931 *Dictyophyllum exile* (Brauns) Nathorst; Harris, p. 80, pl. 18, pl. 15–16.

Material: 12 isolated fragments of frond lamina covered with reticulate venation; ZNG PAL A-III-31\40, 46, 82, 85

Description. Triangular leaf lamina; thick midrib in the centre, from the wider part to the tip (Pl. 37E, H). Apex obtuse, base absent. Tertiary veins form polygonal mesh.

Remarks. Triangular in shape fragments with a centrally placed thick vein, extending to the tip (Pl. 39E, H) were classified as genus *Dictyophyllum*. Fragments represent pinnules from a bigger pinnae. *Dictyophyllum exile* is known from Upper Triassic (Norian) to Middle Jurassic sites (Pott, 2012). Although, *Dictyophyllum exile* shows similarities to other Rhaetian *Dictyophyllum* genera, the leaf anatomy is rather characteristic. The main difference is in the attachment of lobes. Leaf lamina is long and deeply cut, so that the part between adjacent lamina is narrow (Schweitzer *et al*., 2009; Pott and McLoughlin, 2011).

Dictyophyllum nathorstii Zeiler 1903 in general view is similar to *D. exile*, however pinnae of *D. exile* have shorter lobes (Zhou *et al*., 2016) and are basally free (Harris, 1931), whereas *D. nathorstii* has pinnae basally adnate (Pott, 2012).

Many similarities were also noticed between *D. exile* and *Dictyophyllum nillsonii* (Brogniart 1836) Goeppert 1846. *D. nillsoni* is a widely spread genus, known from Upper Triassic to Lower Jurassic deposits of Germany (i.e., Goeppert, 1846; Schenk, 1867; Gothan, 1914; Weber, 1968), France (Saporta, 1873), East Greenland (Harris, 1926, 1931), Sweden (Moller,1902; Nathorst, 1906; Johansson, 1922), Romania (Popa, 2000), Japan (Oishi and Yamasita, 1936), Iran and Afghanistan (Kilpper, 1964; Fakhr, 197; Schweitzer *et al*., 2009) and China (i.e., Sze, 1933; Zhou,1983; Guinard *et al*., 2009). Shape of lobes allow to distinguish *D. nillsonii* from *D. exile*, respectively, falcate lobes *vs*. triangular (Schweitzer *et al*., 2009). *D. nillsonii* pinnae base is decurrent and following lobes are adjacent, in *D. exile* pinnae are free to the base (Pott and McLoughlin, 2011), also mesh in *D. nillsoni* is more irregular than in *D. exile* (Bodnar *et al*., 2018).

Dipteridiaceae were a wide spread group of ferns from the Middle Triassic to the Middle Jurassic (Bodnar *et al*., 2018; Choo and Escapa, 2018). Geographical range of the group is wide in the early and middle Mesozoic, but starts to decline in the Cretaceous when diversity of genera where reduced to *Hausmania* (Guinard *et al*., 2009; Choo and Escapa, 2018). The general homogeneity of the most foreground character as venation pattern visible on the leaf blade can cause arduousness in determining particular genera. *Dictyophyllum* share so many similarities of the leaf blade gross morphology with on other dipteridiaceous fern *Thaumatopteris* that the most reliable feature to distinguished the two genera is the organisation of sori along with size and number of sporangia (Schweitzer, 2009). Nathorst in 1875 moved *Thaumatopteris muensteri* created by Gothan in 1841 to genus *Dictyophyllum* (Nathorst, 1875), leaving the *Thaumatopteris* genus without type species (Barbacka *et al*., 2019). Herbst (1992) pointed that many attempts of different researchers of classification of Dipteridiaceae on the basis of different characters including reproductive structures failed to produce conclusive results. Harris (1931) considered sori to not to be used as a "basis classification" because of the limited information available on the development of sori in fossil Dipteridiaceae. Before, Thomas (1922) proposed to use *Dictyophyllum* to describe species with sporangia not arranged in sori, but he also proposed to retain the name *Dictyophyllum* for the specimens with discernible sori, as it was erected for Yorkshire specimen of *D. rugosum* (Lindley and Hutton, 1834) and that there should be a new generic name for "continental species". Oishi and Yamasita (1936) called *Thaumatopteris* as "a type of *Dictyophyllum* in which the arms are extremely reduced". The similarities between *Dictyophyllum* and *Thaumatopteris* were emphasised again by Harris (1931) when showing that sterile *D. muensteri, D. fuchsi* and *D. dunkerii* resembling *T. brauniana*. Pinnules of *T. brauniana* are wider than *D. dunkerii,* have more narrow bases than in *D. fuchsi* and lamina connection between adjacent pinules is narrower than in *D. muensteri*. Harris later (1961) suggested that because the similarities between *Thaumatopteris* and *Dictyophyllum* are so great the specimens without sori should be classified as *Dictyophyllum*. Oishi ad Yamasita (1936) found the available data on Dipteridiaceae soral characters not sufficient and based classification on the frond structure (frond division, pinnae disposition, laminae dissection) with regard to the information about sori and sporangia when available. Herbst (1992) proposed a key for distinguishing Depteridiaceae genera based on the frond organisation.

Due to the lack of fertile specimens of Dipteridiaceae in the Tarta Mts. collection classification was made using the sterile fronds characters, i.e., shape of the pinnae and venation pattern. Among the most discernible differences between *Dictyophyllum* and *Thaumatopteris,* is dissection of pinnae, more deep in the later (Guinard *et al*., 2009).

Another genus difficult to recognize from *Dictyophullum* is *Geoppertella* (Oishi and Yamasita, 1936), especially when only small part if the leaf blade is preserved. *Geoppertella* is bi-pinnate, whereas *Dictyophyllum* (and *Thaumatopteris*) are once-pinnate, but the characteristic for Dipteridiaceae vein mesh can be confusing (Rees and Cleal, 2004).

Order: *Incertae sedis*
Family: *Incertae sedis*
Genus: *Spiropteris* Schimper, 1869
Type species: *Spiropteris miltonii* (Brongniart) Schimper, 1869
Spiropteris sp.

Plate 40

Material. One specimen preserved as coalified compression; part and counterpart; ZNG PAN A-III-31/0.5.1, 0.5.2

Description. Frond coiled in one plane, circular in outline; diameter 16 mm. Frond rachis 2.5 mm wide, slightly decreasing towards the tip (Pl. 40).

Remarks. Emerging fronds of extant ferns are tightly circinate, forming a crozier-shaped bud. Undeveloped frond found in the Tomanova Fm has smooth rachis. Although the specimen is preserved along *Cladophlebis roesertii* pinnae, there are no features that could allow to substantiate its affinity with this species, or any other species at all. It is common to assign isolated juvenile fossil fern fronds to morphogenera *Spiropteris* (Schimper 1869, Vaez-Javadi and Mirzaei-Ataabadi, 2006; Bomfleur *et al*., 2011; van Konijnenburg-van Cittert *et al*., 2020).

Raciborski in his description of the Tatra Rhaetic flora (1890) have not mentioned *Spiropteris* or any similar form associated with juvenile fern fronds. Information on the specimen label is scarce, only gives a collection date 1935. The most probable is that Raciborski did not found this specimens.

Gymnospermophyta

Order Pinales Dumortier 1829

Family Palissyaceae Florin 1958

Genus *Elatocladus* (Halle 1913) Harris 1979

Type species: *Elatocladus heterophylla* Halle 1913, Hope Bay, Antarctica, Early Jurassic

Elatocladus sp.

Plate 41

Material: Fragments of sterile shoots; ZNG PAL A-III-31/0.1, 0.6, 15b.1, 15b.2, 38a, 40, 41, 43, 60, 66.2, 71.3, 71.4, 71.6

Description. Material consists only of sterile shoots; no fructifications were found. Shoots between 13.0–44.5 mm long. Shoots branching once (Pl. 41A, F, H) to twice (Pl. 41B) times, in an opposite manner. Angle between branches between 30–35°. Bifacial leaves born spirally, rather sparsely; leaves in the lower parts of branch addressed to the axis (Pl. 41A, B); towards the apex leaves spread at an angle 30–50° from the axis; angle is slightly narrower near the apex. Some leaves are bended and twisted near the base (Pl. 41D). Leaves are flat with well-marked midrib extending from a base to a leaf tip (Pl. 41D). Leaves are linear, awl-like, acuminating. Leaf entire, leaf margin smooth. Leaf base slightly contracted; petiole not discernible. Leaf base deccurent (Pl. 41C, D). Leaf cushions not recognisable. Laves are between 3.0–9.0 mm long and 0.5–1.0 mm wide in the widest part; the same size along the axis. Cuticles not preserved.

Remarks. Raciborski compared sterile leafy twigs found in Czerwone Żlebki with descriptions of *Palissya braunii* from Germany and Sweden (Raciborski, 1890). He found similarities in his specimens and sterile twigs i.e., in Braun (1843; *Cunninghamites sphenolepis*) and Schenk (1867). Schenk described twigs of spirally arranged, alternating lanceolate leaves with a vein in the middle, associated with fertile specimens. Similar diagnosis to Raciborski was made by Nathorts (1878) and Heer (1881). Nathorst (1878) found similarities between specimens from Palsjö (Sweden) and specimens from Franconia described by Schenk (1867), except that among Swedish specimens one represented a cone with *Palissya* leaves attached (Nathorst, 1878). However, later Nathorst (1908) revised his first diagnosis and transferred the specimens to genus *Schizolepis* Braun 1847. Heer (1881) described a few sterile twigs from Rhaetian of Portugal. Heer's specimens show similarities to those described by Raciborski. Heer illustrated a few leaves with a midrib in the centre of each one. Leaves are opposite to slightly alternate; elongated and depart at an angle of ca. 40–70°. Later, Raciborski (1891) described similar twigs in Holy Cross Mts (1891). However, he only classified them to genera *Palissya*, due to a poor state of preservation.

Described first by Endlicher (1847) from Early Jurassic of Germany, *Palissya braunii* was later corrected by Nathorst (1908) to *Palissya sphenolepis* Braun (1843) considering the rule of priority. Nathorst (1908) and later other authors (Hirmer, 1936; Florin, 1958; Hill, 1974; Parris *et al*., 1995; Schweitzer and Kirchner, 1996; Arndt, 2002; Wang *et al*., 2012; Pattermore *et al*., 2014; Pattermore *et al*, 2019) considered *Palissya* as a taxon of an ovule scale complex, and often described specimens were not associated with any sterile foliage. Halle (1913) and Seward (1919) both concluded that sterile specimens without reproducing structures but showing generic similarities to *Palissya* should be refeed as *Elatocladus* Halle 1913. Harris (1931) described *Elatocladus* as a "sterile conifer twigs with small needles". He described/selected particular species based on their cuticular characters. As the cuticle is not preserved in the Tatra Mts. specimens, it is difficult make comparison with most of the *Elatocladus* species described by Harris from Triassic–Jurassic of Greenland (1931) and Jurassic of Yorkshire (1979), but gross morphological characters are overlapping with Tatras specimens. Hill (1974) illustrated and described from Middle Jurassic of Yorkshire fertile specimens of *Palissya harrissi* with leafy twigs associated of *Sewardiodendron laxum* (Phillips) Florin (=*Elatocladus laxus* (Phillips) Harris; Harris, 1979). Iranian *Palissya oleschinskii* Schweitzer and Kirchner (1996) from Late Triassic–Early Jurassic is also considered to be associated with *Elatocladus*-type foliage (Schweitzer and Kirchner, 1996).

Other taxa resembling *Palissya* in terms of affinity is *Stachyotaxus* Nathorst 1886. Stomata in *Stachyotaxus* are in two parallel longitudinal zones on the abaxial surface as in *Palissya* (Nathorst, 1908; Pattermore, 2014). *Stachyotaxus* is a conifer with single-veined leaves, known from Rhaetian of Greenland (Harris, 1931) and Sweden (Pott and McLoughlin, 2011). However, it has fertile as well as sterile parts preserved.

Pott and McLoughlin (2011) described sterile shoots with univeined lanceolate leaves from Rhaetic of Sweden as *Elatocladus* sp. *Palissya* (*Elatocladus*) *sphenolepis* (Braun). During revision, Tatra Mts. specimens described by Raciborski (1890) as *Palissya braunii*, due to a recent changes in definition of the *Palissya* taxa (Pattermore, 2014), as genera concerning fertile organs, and lack of such structures in research material, are transferred to *Elatocladus* sp. Attributing *Elatocladus* specimens to any particular species would be dubious. The material is very fragmentated and generally poorly preserved, lacking characteristics that would link it to particular *Elatocladus* species. Also, it is not uncommon for conifers to show heterophylly and fossils of short fragments of shoots might be misleading.

Coniferophyta *incertae sedis*

Plate 42

Material. Shoot fragment; ZNG PAN A-III-31/44

Description. Sterile shoot; branching two times. Main shoot length 62.2 mm, width 1.8 mm; branchlets length 23.0–41.0 mm, width 1.0–1.5 mm. Maximum leaf width 1.8 mm, length 3 mm. Leaves longer than wider.

Discussion. ZNG PAN A-III-31/44 specimen is the only specimen in the Tatra Mts Rhaetian collection described by Raciborski preserved in sandstone intercalating mudstones (Raciborski, 1890). He found the specimen similar to "short-leaf form of *Cheirolepis munsteri* Schenk" (translated from Polish; Raciborski, 1890) and even more to *Widdringtonites keuperianus* Heer 1865. Raciborski (1890), however had dooubts about the specimen affinity, due to the poor preservation and lack of details. Apart from conifer Raciborski considered lycophyte or bryophyte origin. But because the specimen is preserved in an unfavorable sandstone Raciborski regarded delicate lycophyte and bryophytes as less probable. Created by Endlicher (1947) *Widdringtonites* defines fossil shoots similar to extant *Widdringtonia* Endlicher 1942 with spirally arranged leaves that are more elongated, needle-like in juvenile plants and scally and appressed when growing older (Endlicher, 1847). *W. keuperianus* was first described from the Keuper of Basel. However, Heer himself admitted that he had only very incomplete shoots (Heer, 1865). More sterile fragments were found in the Keuper of Frankonia, Germany (Schenk, 1864). Schutze (1901) revised *W. keuperianus* and extended species description; he observed alternate position of the secondary branches on the main branch, leaves on older branches more dense, mean leaf length 4.0–5.0 mm and 1.5–3.5 mm width.

Many authors had doubts concerning *Widdringtonites* affinity and even justification of using this generic name to describe some fossils (Seward, 1919; Potonie and Gothan, 1921). According to Nathorst (1878-86) *Widdringtonites* from Keuper of Europe should be moved to *Cyparassidium* Heer 1877 as well as some Liassic examples. Seward stated that many authors including Shutze (1901) and Heer (1865) used generic name *Widdringtonites* without discussing similarieties of described specimen to *Widdringtonia* and noticed that *Widdringtonites* show close resemblance to other common conifer sterile foliage genera i.e. *Brachyphyllum* (Seward, 1919). Potonie and Gothan (1921) noted that systematic position of *Widdringtonites* is uncertain, and doubted its Cupressaceae affinity. Harris (1979) compared *W. keuperianus* with *Genitzia rigid*a (Phillips) Harris 1979 from the Jurassic of Yorkshire, but dismissed potential synonymy due to the longer leaves length of *G. rigida* and presence of papillae on *W. keuperianus* stomata.

Very poor preservation of Tatra specimen makes precise identification impossible. Branches are barely discernible (Fig. 42A, B). Separate leaves are in gross unrecognizable (Fig. 42C, D). Preservation in different sediment than the rest of the described fossils from the site, particularly other conifer *Elatocladus* sp. is making further conclusion even harder. The robustness of conifers shoots comparing to other plants representing similar habit like lycophytes and bryophytes indeed makes conifer origin of the remains more reliable, as well as branching pattern. But due to the lack of other characters I decided to leave this specimen as Coniferophyta *incertae sedis*.

5. Reconstructions of studied plant communities

5.1. Comparison of studied floras composition

Discrepancies in the taxonomical composition of researched Late Triassic floral assemblages reflect differences in regional environmental conditions during specific time periods. Norian deposits of the Grabowa Fm developed when the Upper Silesia region (Zawiercie-Marciszów, Lipie Śląskie-Lisowice) was influenced by climate fluctuations, dry to semi-dry, and represents the most south-east peripheries of the Central European Basin (e.g., Szulc *et al.*, 2006, 2015). The depositional environment of the Grabowa Fm was controlled in gross by fluvial processes, and the studied floral assemblages correspond with more wet conditions during the mid-Norian pluvial episode recorded in the Lisowice Bone-Bearing Level (Szulc *et al.*, 2015). During Norian in the Tatricum (Czerwone Żlebki, Tatra Mts) carbonate-dominated sedimentation took place (Jaglarz, 2010) and the whole region was part of the northern rim of the Alpine–Carpathian limestone shelf (Michalik *et al.*, 1988). Tomanowa Fm is a product of sedimentation in the palustrine environment during the Rhaetian (Michalik, 2011; Litnerová *et al.*, 2013).

The Norian fossil assemblages of the Zawiercie-Marciszów and the Lipie Śląskie-Lisowice represent the different architecture of plant community than the Tatra Mts Tomanowa Fm. The most explicit is the proportion of conifer, horsetails and fern fossils. Upper Silesia localities are distinctly dominated by conifer fossils, whereas in the Tatra Mts they are rather rare. Ferns are completely absent in the Zawiercie-Marciszów and the Lipie Śląskie-Lisowice but are the most dominating plant group in the Tatra Mts along with horsetails that by contrast are scarce in the Norian localities.

Sphenophyta are present in both studied regions. However, Tatra Mts flora shows a much higher abundance of horsetail remains, including sterile and fertile organs. The relatively low diversity of Sphenophyta (genera limited to *Equisetites* and *Neocalamites*) is common, i.e., in Lunz (Austria), there are "only" *Equisetites arenaceous*, *E. conicus* and *Neocalamites myerianii* (Pott *et al.*, 2008). Sphenophyta can form a monotypic community, which is connected with vegetative reproduction common in this plant group (Taylor *et al.*, 2009). The dominance of Sphenophyta remains in the Tomanowa Fm deposits might be a remnant of such a community, reproducing vegetatively, but also developing strobili. The Norian Zawiercie-Marciszów Sphenophyta have poor representation compared to Tatra Mts but show higher diversification than in the Lipie Śląskie-Lisowice (Tab. 6).

Table 6. Comparison of the macrofloral composition of researched localities. Cut. * - data from *cuticulae dispersae;* Cut. ** - data from cuticles from coprolites.

Plant group	Localities		
	Upper Silesia		Tatra Mts
	Zawiercie-Marciszów	Lipie Śląskie-Lisowice	Czerwone Żlebki
Sphenophyta			
	Equisetites sp.	*Equisetites* sp.	*Equisetites chalubinskii*
	Neocalamites sp.		*Equisetites* sp.
	Cf. *Neocalamites* sp.		*Neocalamites lehmannianus*
Pteridophyta			
	–	–	*Cladophlebis roessertii*
	–	–	*Clathropteris meniscoides*
	–	–	*Dictyophyllum exile*
	–	–	*Spiropteris* sp.
Cycadophyta			
	–	*Dioonitocarpidium* sp.	–
Coniferophyta			
	Agathoxylon keuperianum	*Brachyphyllum* sp.	*Elatocladus* sp.
	Pagiophyllum sp. Cut. A*	*Elatocladus* sp.	cf. *Widdringonites* sp.
	Pagiophyllum sp. Cut. C*	*Pagiophyllum* sp. Cut. A**	
	Pagiophyllum sp. Cut. D*	*Brachyphyllum* sp. Cut. B**	
	Elatocladus sp. Cut. B*	*Brachyphyllum* sp. Cut. C**	
	Brachyphyllum sp. Cut. E*	*Elatocladus* sp. Cut. D**	
		Elatocladus sp. Cut. E**	
		cf. Coniferales Cut. H**	
		cf. Coniferales Cut. I**	
Rooting structures			
	Root A		
	Root B		
Dispersed *seeds*			
	–	*Carpolithes* sp.	–

The presence of Pteridophyta remains at the Tatra Mts makes the main difference between the studied localities of the Tomanowa Fm and the Grabowa Fm There is no indication of fern presence in the macrofossil record of Zawiercie-Marciszów and Lipie Śląskie-Lisowice. Fern diversity from Tatra Mts is limited to three genera (*Cladophlebis, Clathropteris, Dictyophyllum*) and juvenile morphotaxa *Spiropteris*.

Conifers, so abundant in the Grabowa Fm have a marginal position in the Tomanowa Fm assemblage. Macrofossils of needle-like leaves of *Elatocladus* are represented by isolated sterile twigs. The second conifer taxa, a single specimen of Coniferophyta *incertae sedis* shows no morphological details that could allow its definite identification.

There is much greater morphological and taxonomical diversity present among dispersed cuticles, not available at the Tatra Mts. A major component of *cuticulae dispersae* in both assemblages from the Upper Silesia are conifer cuticles. Separated scale leaves and shoot fragments of *Pagiophyllum, Brachyphyllum* and *Elatocladus* are very abundant, moreover, they show a bigger variance in cuticle morphological details than what can be observed from macrofossils. Analysis of *cuticulae dispersae* from Grabowa Fm show more diversified dispersed conifer cuticles in the Lipie Śląskie-Lisowice than in Zawiercie-Marciszów in terms of morphological characters, which could imply the higher taxonomical variability of the plant assemblage. A comparison of researched assemblage macrofloral composition is presented in Table 6.

Macroremains of other plant groups (lycophytes, ferns, seed ferns, ginkgophytes, and cycads) are not discernible at the studied localities and their presence is only recorded in the palynological record (Tab. 1B, 2B, 3B). Quantitative compillation of genera and species representing different plant groups is presented in Table 7.

Table. 7. Representation of different plant groups in micro- and macrofloral record at studied localities (microflora references in Table 1B, 2B, 3B). *Cycadales and Ginkgoales are presented here together due to the uncertain affinity of some miospores; ** only Cycadales macrofossils are considered in the table, as no Ginkgoales were identified so far at any of the researched localities.

Plant group No of (morpho)genera/species	Localities		
	Upper Silesia		Tatra Mts
	Zawiercie-Marciszów	Lipie Śląskie-Lisowice	Czerwone Żlebki
Equisetales			
Microflora	1/1	1/1	1/1
Macroflora	2/3	1/1	3/2
Pteridopsida			
Microflora	7/7	9/12	6//8
Macroflora	0/0	0/0	4/4
Cycadales, Ginkgoales*			
Microflora	2/2	3/4	3/5
Macroflora **	0/0	1/1	0/0
Coniferales			
Microflora	18/22	18/31	8/13
Macroflora	4/4	4/9	2/2

5.2. Plants ecology and taphonomy bias in the reconstruction of plant communities from researched localities.

Although Late Triassic sediments of Grabowa Fm and Tomanowa Fm are very resourceful in plant fossils of different types (macrofossils, *cuticulae dispersae*, coprolites, miospores), a comprehensive reconstruction of the floral community is still ambiguous. Small fragments like cuticles, often preserved with minute morphological details, cannot provide enough data for precise taxonomical determination, as well as isolated macrofossils, whether they are vegetative or generative. Data from different types of fossil plant material complement environmental reconstructions, however, each fossil type is taphonomical biased. Plant fossils have a huge tendency to represent disarticulated plant body parts. Each plant organ can have a different composition characterised by a different preservation potential and can be produced by a plant in different quantities, i.e., one tree trunk and hundreds of thousands of leaves per plant in plant life. During transport shape, size, density and structure of plant parts together with transport conditions influence fossil plant community composition (Greenwood, 1991) and in consequence palaeoecological reconstructions.

The fragmentation of the plant material suggests that the plants were transported over a considerable distance. Different types of lithologies containing plant remains provide insights into distinct taphonomic processes. Of particular interest are the accumulations of plant debris. A dense concentration of small plant particles (leaves, megaspores, twigs, etc.) measuring less than 3-5 cm, represents a mixture of plants growing along the river and materials collected from floodplain areas during flood events. The selectivity of transport may explain the reduced diversity of plant remains. Delicate fern fronds would have been torn into tiny fragments during water transport by currents, while sphenophyta stems would disarticulate, and secondary axes and leaves would detach from the main axis. In contrast, the thicker main axis of sphenophyta, woody gymnosperm shoots, and highly cutinized organs possess better preservation potential (Sweetman and Insole, 2010; Kustatscher *et al.*, 2017).

Macrofossils and *cuticulae dispersae*

Conifer dominance visible in the Norian localities of the Grabowa Fm can be an effect of (1) selective preservation due to a relatively long transport that resulted in completely damaged and/or shredded into small pieces delicate leaves of ferns, long leaf blades of cycads/Bennettitales and ginkgophytes; (2) true plant diversity was low, and conifers utterly dominated the environment with no or minimal participation of other plant groups. In comparison, the Upper Silesian floras and other Norian sites in Europe (i.e., Seefeld, Austria; Kustatscher *et al.*, 2017), the homogenous composition is typical and conifer domination is very clear. Because conifer remains in the Grabowa Fm are preserved as different types of plant fossils (pollen, cuticles, leaves, trunks, etc.), it is possible that this plant group was indeed exceedingly abundant and the fossil record under study represents a floristic true trend characteristic for the Norian of Europe. If conifers would dominate only in one fossil type, i.e., macrofossils or palynomorphs, that could indicate a biased fossil record.

Conifers are considered well-adjusted to environments and climates with occasional problems with water deficiency (Farjon, 2010). That could explain their high abundance during the generally drier Norian period. However, fragmentation of the material and the presence of isolated sterile and fertile conifer organs suggest that the plant remains were transported from their growing sites. Conifer remains found in other Norian European localities are also strongly fragmented (Seefeld, Austria; Kustatscher *et al.*, 2017; Dolomites and Pre-Alps; Dalla Veccia, 2000). The Rhaetian Tomanowa Fm conifer record is poor compared to Norian Grabowa Fm deposits.

Norian Grabowa Fm completely lack fern macrofossils in contrast to the Tatra Mts. A high abundance of delicate structures like fern stems, fronds, pinnae with pinnules, and croziers (*Spiropteris* sp.) indicate that the growing area could not be distant from the deposition site. Isolated and fragmented, brittle fern fronds are not shredded, suggesting that the water current transporting remains was not so destructive. However, disarticulated plant remains still suggest an allochthonous character of the assemblage.

Plant cuticle hosting a protective function against water loss, UV radiation and pathogens is a resistant extracellular hydrophobic layer (Arya *et al.*, 2021; Fernandez *et al.*, 2017; Yeats and Rose, 2013) with great potential for preservation (Greenwood,1991). Cuticles can be collected from macrofossils from Lipie Śląskie-Lisowice and Zawiercie-Marciszów, so far preparing cuticles from the Tatra Mts specimen was unsuccessful. Sediments of Grabowa Fm at researched Upper Silesia localities are abundant in isolated cuticles.

In both Upper Silesia localities layers of densely accumulated plant litter were found. Such debris layers are composed of disarticulated plant parts, often fragmented and of similar size. Cuticles macerated from debris accumulation are relatively well preserved in terms of morphology even when they are shredded. The similar size of plant debris suggests it was deposited in an environment with a stable, low water current (Blanco-Moreno *et al.*, 2022). Most cuticles are fragmentary, i.e., cuticles of needle-like conifers very rarely have preserved leaf base, making it difficult to reconstruct their attachment to a stem (a feature used for taxonomical recognition; Kerp, 1990). Yet still, their presence might indicate a short-distance transport, like leaves of conifer *Pseudofranelopsis parceramosa* at the Early Cretaceous Wessex Fm (Sweetman and Insole, 2010).

Observations of *cuticulae dispersae* from the Lipie Śląskie-Lisowice sediments revealed the presence of cuticles resembling ginkgoes, cycads, and seed ferns, not recognised in macrofossils. A few cuticles resembled *Lepidopteris ottonis* (Staneczko, 2007; Wawrzyniak, 2010), the seed fern characteristic of Rhaetian (Dzik *et al*., 2008), but the cuticles are rare and very incomplete, which makes identification somewhat ambiguous.

Coprolites

Herbivorous and carnivorous coprolites are another source of plant remains. Investigated coprolites were found at the Lipie Śląskie-Lisowice, in the strata rich in plant fossils like charcoalified tree trunks, coalified compressions of shoots, and separated plant parts (i.e., cones, leaves, seeds; Fig. 7). Coprolites can be a good medium on the dietary and behavioral habits of extinct animals. Analysed coprolites were left by a big herbivore, presumably a rhino-elephant size dicynodont (Bajdek *et al*., 2014; Sulej and Niedźwiedzki, 2019). Such a big plant eater was probably feeding on a big territory or migrating, therefore, the content of coprolites does not necessarily represent the vegetation of the place where they were left. Also, post-deposition transport needs to be considered. However, coprolites represent a mix of plant remains from limited areas, and therefore can be an additional source of ecological information.

For this research already macerated residuum was available containing plant cuticles (see Chapter 4.2.2). Cuticles retrieved from coprolites are in good shape. The surface is smooth, and the morphology is clear and identifiable. Proportions of distinguished cuticle types are similar in all three coprolites (Tab. 8; Fig. 12). It could be expected that gastric juices and the digesting process if it would not damage cuticles completely, would leave some marks. In some cases, coprolite's cuticles are in better condition than cuticles macerated from macroremains and sediment, except that they are more fragmented. Vajda *et al*. (2016) pointed out that pollen, spores and cuticles found in predatory dinosaur coprolites, were enclosed in a phosphatic cement protecting them from further mechanical and chemical degradation.

Table 8. Properties of cuticles macerated from coprolites.

Cuticle type	Frequency	% of all	Mean area (mm^2)
A	54	34	3,38
B	60	38	3,49
C	7	4	3,22
D	1	1	1,71
E	10	6	2,11
F	6	4	4,21
G	5	3	2,91
H	2	1	2,56
I	2	1	3,13
J	8	5	1,45
K	4	3	6

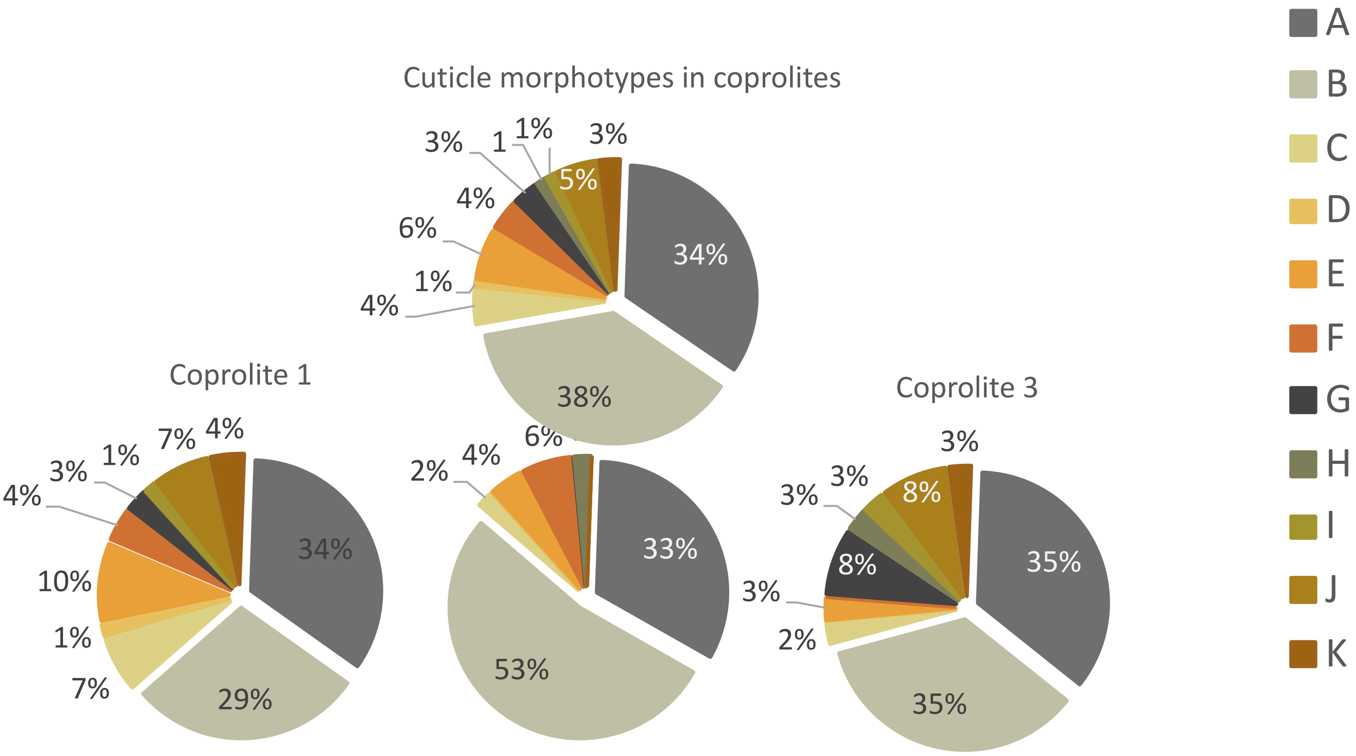

Figure 12. Proportions of cuticle morphotypes A–K macerated from coprolites (description in Chapter 4.2.2). Morphotypes A–C are in *Brachyphyllym*/*Pagiophyllum* type.

Content analyses might indicate whether a producer was a bulk or selective feeder. On the other hand, coprolites are more of a "snapshot" of the dietary habits of an extinct animal, yet they remain a valid source of additional palaeoecological information.

If the content of coprolites is monotypic regarding plant parts and/or composition is generally monospecific in terms of plant taxa, then it might indicate that an animal would feed on one plant part or a single species. This might be connected with dietary preferences or vegetation seasonality, the animal was feeding on what was ripe at the time (Sander *et al.*, 2010). Another possibility is that the components that were the real basis of an animal diet have been completely dissolved during feeding and digesting. During pasture herbivores like dicynodont could intake a big amount of different plant food. Delicate cuticles of i.e., fern, could get digested entirely, and only the most resistant material remained. The majority of retrieved cuticles belong to conifers (Figure 12). Extant conifers have different leaf shedding habits, some lose leaves annually (*Larix, Metasequoia*), others every couple of years (i.e., *Pinus sylvestris* every 3–6 years; Pensa and Jalkanen, 2005). The longer leaves stay on the plant the more metabolites can accumulate in a leaf (Hatcher, 1990). Conifers also produce essential oils to protect from herbivory. Therefore, dicynodonts would have to be specialized plant eaters. However, the Late Triassic environments were dominated by conifers so a big size herbivore might be adapted to feed on them. Also, according to *in vitro* fermentation method, conifers, i.e., *Araucaria* foliage is attractive as an energy-efficient food source, due to their high energy content over a long retention time (Hummel *et al*., 2008). *Pagiophyllum/Brachyphyllum* foliage abundant in Lipie Śląskie-Lisowice sediments and coprolites overlap features of araucarias (Harris, 1979; Kendall, 1948; Stockey, 1982), then it might have been a designated dicynodont feeding area. Even though Araucariaceae and Cheirolepidiaceae are considered to be tall trees, a giant dicynodont with a beak at approximately 1.5–2.0 m high and a body mass of ca. 9000 kg (Sulej and Niedźwiedzki, 2019) would not have a problem to knock over a tree, like extant elephants and rhinos. The high abundance of conifer cuticles in the coprolites makes accidental ingestion, e.g., when drinking water (Perez Loinaze *et al*., 2018), less possible. Previously investigated carnivorous coprolites from Lipie Śląskie-Lisowice reviled some plant cuticles and tracheids. Apart from being shredded, cuticles are not much degraded, and some morphological features can be observed. A few cuticles show similarities to *L. ottonis* and *Podozamites* leaves (Zatoń *et al*., 2015).

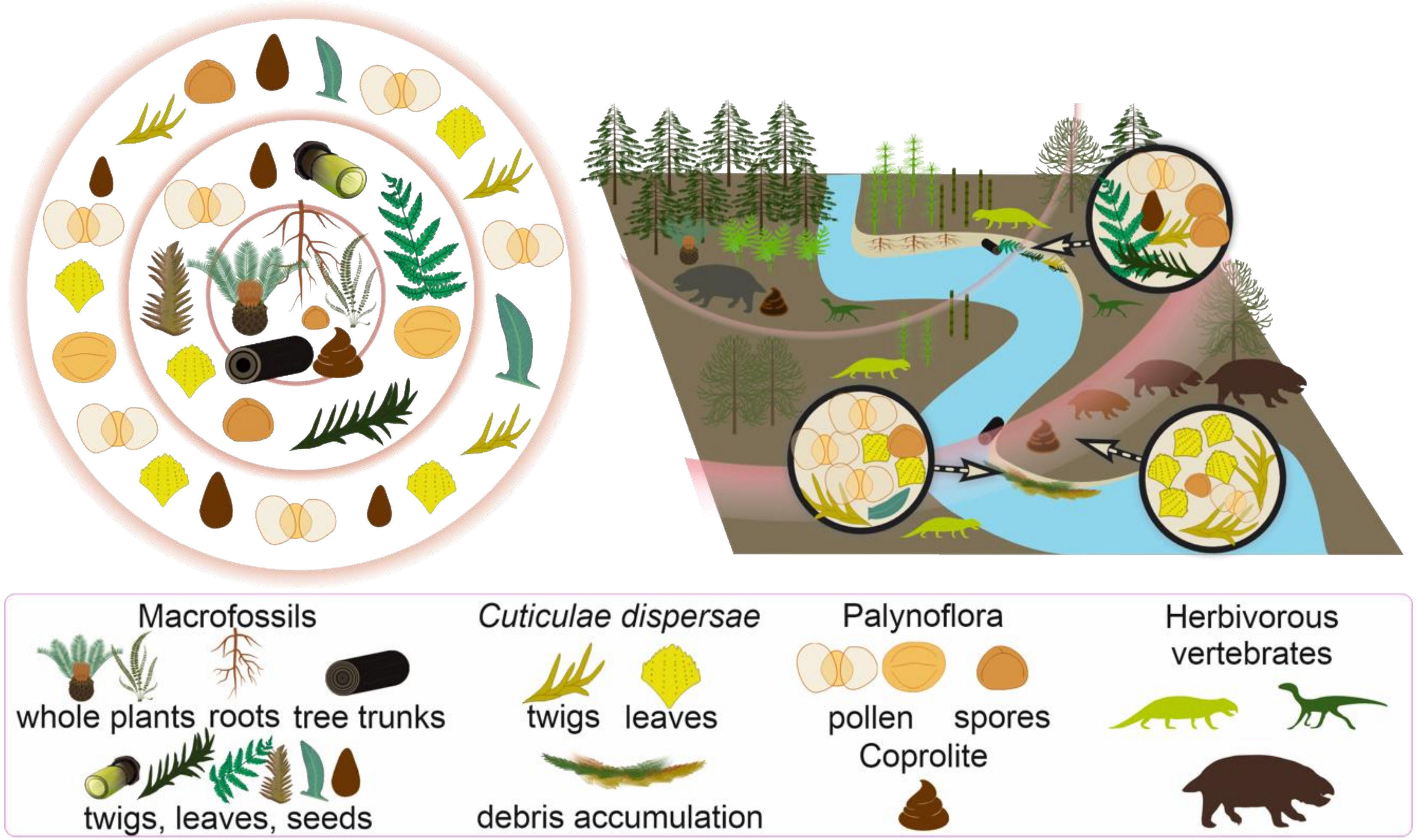

Figure 13. Simplified model of different plant fossil dispersal. Smaller plant particles are deposited further from the parent plant. Plant content found in coprolites can represent floral composition from distant areas (herbivorous vertebrates after Zatoń et al., 2015)

5.3. Palaeoecological implications of plant fossils from studied localities

Recent vegetation distribution and plants responses to changes in their surroundings over time provide valuable insights into past ecosystem dynamics. Plant functional traits represent adaptations to the environment and affect plant morphological and physiological, characteristics (Violle *et al.*, 2007; Chapin *et al.*, 2000). By understanding these traits, we gain valuable insights into the behavior and strategies of individual plant species and ecological groups. The integration of plant macrofossils and miospore data with environmental record allow for a more comprehend recontructions.

Conifers developed adaptations to grow in environments and climates that occasionally experience water deficiency (Farjon, 2010). This may explain their high abundance during the generally dry Norian period (Berra *et al*., 2010; Preto *et al*., 2010; Fijałkowska-Mader, 2015; Kustatscher *et al*., 2018; Bahr *et al*., 2020). Zawiercie-Marciszów and Lipie Śląskie-Lisowice are abundant in fossil foliage morphogenera of scale-leaf conifers, like *Brachyphyllum* and *Pagiophyllum*, together with long-leaf conifers of *Elatocladus*. Tightly pressed small leaves, thick cuticle, presence of papillae, and sunken stomata are adaptations that help reduce water loss through transpiration (Thevenard *et al*., 2005). Macrofossils, cuticles and miospores confirm the high presence of conifers in the Upper Silesia Grabowa Fm (Fijałkowska-Mader, 2015; Pacyna *et al*., 2017). Conifer pollen is the most abundant composite of the assemblage. *Classopollis meyeriana*, *Brachysaccus neomundanus*, *Ovalipollis* spp. Pollen genus *Classopollis* is hereby an argument for the presence of the Cheirolepidiaceae family in the Late Triassic of Lipie Śląskie-Lisowice, as it is considered to be characteristic of cheirolepidiaceous plants (Alvin, 1982; Watson, 1988; Clemence-Westerhof and Van Konijnenburg-Van Cittert, 1991; Ash, 1999; Barbacka *et al*., 2007). Pollen *Enzonalasporites*, recently found in the polliniferous cones of *Patokaea silesiaca* (Pacyna *et al*., 2017), might be an indication of the affinity of some *Pagiophyllum*-and *Brachyphyllum*-like leaves to a plant from the Patokaeceae family.

However, local conditions could also support the growth of hygrophilous plants like ferns (Pacyna, 2019), but it's important to note that the fossil record might be biased due to the preferential preservation of conifer remains.

Plant assemblage from Rhaetian Czerwone Żlebki (Tomanowa Fm) is strongly dominated by fern genera *Cladophlebis*, up to a point where it can be described as monospecific. *Cladophlebis*, a herbaceous fern, preferred riverbanks, lake shores, marshes, and brackish-water environments near the coastline, with warm and humid conditions (Barbacka *et al.*, 2019; Van Konijngenburg-Van Cittert, 2002; Harris, 1961; Blanco Moreno and Buscalioni, 2021). *Cladophlebis* occurs in localities with peat and coal formations, like Iran, Romania, and Hungary (Van Konijnenburg-van Cittert, 2002). Species *C. roessertii* present in the Tomanowa Fm is connected with much wetter conditions than other species like *C. denticulata* at the early Jurassic Mescec Mts deposits from Hungary (Bodor and Barbacka, 2008; Barbacka *et al.*, 2019). Fern family Dipteridiaceae, also observed at the Tomanowa Fm are associated with warm-temperate and humid subtropical climate (Van Konjingenburg-Van Cittert, 2002; Bomfleur and Kerp, 2010; Wang *et al.*, 2015; Guinard *et al.*, 2009; Barbacka *et al.*, 2019), flourishing in riverbanks like modern *Dipteris* Reinwardt 1825 (Choo and Escapa, 2018; Ouyang *et al.*, 2021). Dipteridiaceae could have spread from South-East China to Western Europe (Shuying, 1987) during elevated humidity periods in Carnian and Rhaeto-Liassic (Barale, 1990). *Clathropteris* and *Dictyophyllum* recognised in the Tatra Mts are considered less resilient to humidity stress genera than *Haussmania* (Van Konjingenburg-Van Cittert, 2002; Van Konijnenburg-Van Cittert and Van der Burgh, 1996).

The presence of Sphenophyta macrofossils (*Equisetites* and *Neocalamites*) at the studied locations suggests that the environment experienced increased humidity, which aligns with the findings of other authors based on palynological and lithological evidence (Szulc et al., 2006, 2015a, b; Fijałkowska-Mader, 2015; Fijałkowska-Mader et al., 2015; Jewuła et al., 2019).

The Sporomorph Ecogroup (SEG) model and Palyno-Palaeoclimatic (PPC) model developed by Fijałkowska-Mader (2015) indicate the development of conditions that are favorable for spore-producing horsetails, such as those found in riparian habitats, of the Grabowa and Tomanowa Formations.

The Sporomorph ecogroup (SEG) model describes the ecological characteristics of plant assemblages based on observations of extant plants' requirements (Abbink, 1998). The model links palynological taxa of known botanical affinities with ecological preferences of mother plants (e.g., Van Konijnenburg-Van Cittert, 2002; Kustatscher *et al.*, 2012; Baranyi *et al.*, 2019b; Li *et al.*, 2015; Li *et al.*, 2020; Li *et al.*, 2022; Li *et al.*, 2023; Krupnik *et al.*, 2014; Fijałkowska-Mader, 2015; Zhang *et al.*, 2021; Burgess *et al.*, 2022). To apply the SEG model quantitative data of sporomorphs with a relatively well-established affinity, are necessary (Abbink, *et al.*, 2004). In principle, the Sporomorph Ecogroup (SEG) is a reflection of plant community composition despite transport, sedimentation and preservation (Traverse, 2007; Abbink *et al.*, 2004).

Observations presented here are based on miospores genera described previously by other authors (Litnerová et al., 2013; Fijałkowska-Mader and Uchman, 1993; Fijałkowska-Mader, 2015; Fijałkowska-Mader *et al.*, 2015; Świło *et al.*, 2013; Staneczko, 2007). However, conclusions should be considered superficial, mostly due to scarce quantitative data. Nevertheless, a comparison of plant palaeocommunities inferred from macrofossils observation with sporomorph assemblages can result in supplementary remarks on palaeoecological and palaeoclimatological reconstruction. The most frequently occurring sporomorphs were assigned to C-coastal, LR - lowland river, U - upland ecogroups.

Deposits of the Upper Silesia localities, Zawiercie-Marciszów and Lipie Śląskie-Lisowice are determined as the Patoka Mbr of the Grabowa Fm and represent middle Norian meyeriana b Subzone (Szulc and Racki, 2015; Fijałkowska-Mader, 2015; Fijałkowska-Mader, *et al.*, 2015).

Table 9. SEG for Lipie Śląskie-Lisowice (after Fijałkowska-Mader, 2015; Fijałkowska-Mader *et al.*, 2015; Świło *et al.*, 2013; Staneczko, 2007)

Ecogroup	Plant group	Genus
Upland	Coniferales	*Alisporites* spp., *Brachysaccus* spp., *Cedripites* spp., *Enzonalasporites* spp., *Labiisporites* spp., *Lunatisporites* spp., *Minutosaccus* spp., *Ovalipollis* spp., *Parillinites* spp., *Rhaetipollis* spp., *Triadispora* spp.
Lowland/river	Pteridopsida	*Baculatisporites* spp., *Carnisporites* spp., *Cyclotriletes* spp., *Deltoidospora* spp., *Todisporites* spp., *Verrucosisporites* spp.
	Lycopodiales	*Anapiculatisporites* spp., *Nevesisporites* spp., *Uvaesporites* spp.
	Equisetales	*Calamospora* spp.
	Cycadales, Bennettitales, Pteridosperm	*Monosulcites* spp., *Eucommiidites* spp.
	Bryophyta	*Porcellispora* spp., *Ricciisporites* spp.
Coastal	Coniferales	*Classopollis* spp., *Duplicisporites* spp., *Granuloperculatipollis* spp., *Pinuspollenites* spp., *Protodiploxypinus* spp.

Table 10. SEG for Zawiercie-Marciszów (after Fijałkowska-Mader, 2015; Fijałkowska-Mader *et al.*, 2015).

Ecogroup	Plant group	Genus
Upland	Coniferales	*Alisporites* spp., *Brachysaccus* spp., *Cedripites* spp., *Enzonalasporites* spp., *Labiisporites* spp., *Lunatisporites* spp., *Minutosaccus* spp., *Ovalipollis* spp., *Parillinites* spp., *Rhaetipollis* spp., *Triadispora* spp., *Platysaccus* spp.
Lowland/river	Pteridopsida	*Baculatisporites* spp., *Carnisporites* spp., *Cyclotriletes* spp., *Deltoidospora* spp., *Todisporites* spp., *Verrucosisporites* spp.
	Lycopodiales	*Anapiculatisporites* spp., *Nevesisporites* spp., *Uvaesporites* spp. *Neoraistrickia* spp.
	Equisetales	*Calamospora* spp.
	Cycadales, Bennettitales, Pteridosperm	*Monosulcites* spp., *Cycadopites* spp., *Eucommiidites* spp.

	Bryophyta	*Porcellispora* spp., *Ricciisporites* spp.
Coastal	Coniferales	*Classopollis* spp., *Duplicisporites* spp., *Granuloperculatipollis* spp., *Pinuspollenites* spp., *Protodiploxypinus* spp., *Geopollis* spp.
	Lycopodiales	*Densoisporites* spp., *Densosporites* spp.

Table 11. SEG for Tatra Mts (after Litnerová et al., 2013; Fijałkowska-Mader and Uchman, 1993).

Ecogroup	Plant group	Genus
Upland	Coniferales	*Alisporites* spp., *Brachysaccus* spp., *Cedripites* spp., *Enzonalasporites* spp., *Labiisporites* spp., *Lunatisporites* spp. *Minutosaccus* spp., *Ovalipollis* spp., *Parillinites* spp., *Praecirculina* spp., *Rhaetipollis* spp., *Triadispora* spp., *Platysaccus* spp., T*aeniaesporites* spp.
Lowland/river	Pteridopsida	*Baculatisporites* spp., *Carnisporites* spp., *Cyclotriletes* spp., *Deltoidospora* spp., *Dictyophyllidites Leiotriletes* spp., *Marattisporites* spp., *Todisporites* spp., *Toroisporis* spp., *Verrucosisporites* spp.
	Lycopodiales	*Anapiculatisporites* spp., *Camarozonosporites* spp., *Nevesisporites* spp., *Uvaesporites* spp. *Neoraistrickia* spp.
	Equisetales	*Calamospora* spp.
	Cycadales, Bennettitales, Pteridosperm	*Monosulcites* spp., *Cycadopites* spp., *Eucommiidites* spp., *Protohaploxypinus* spp.
	Bryophyta	*Annulispora* spp., *Porcellispora* spp., Retusotriletes spp., *Ricciisporites* spp.
Coastal	Coniferales	*Classopollis* spp., *Duplicisporites* spp., *Granuloperculatipollis* spp., *Pinuspollenites* spp., *Protodiploxypinus* spp., *Geopollis* spp.
	Lycopodiales	*Densoisporites* spp., *Densosporites* spp.

For the purpouse of this work, all the taphonomical, taxonomical and ecological factors were used to create an idealised reconstructions of the researched floras and are presented on Figures 14 – 16.

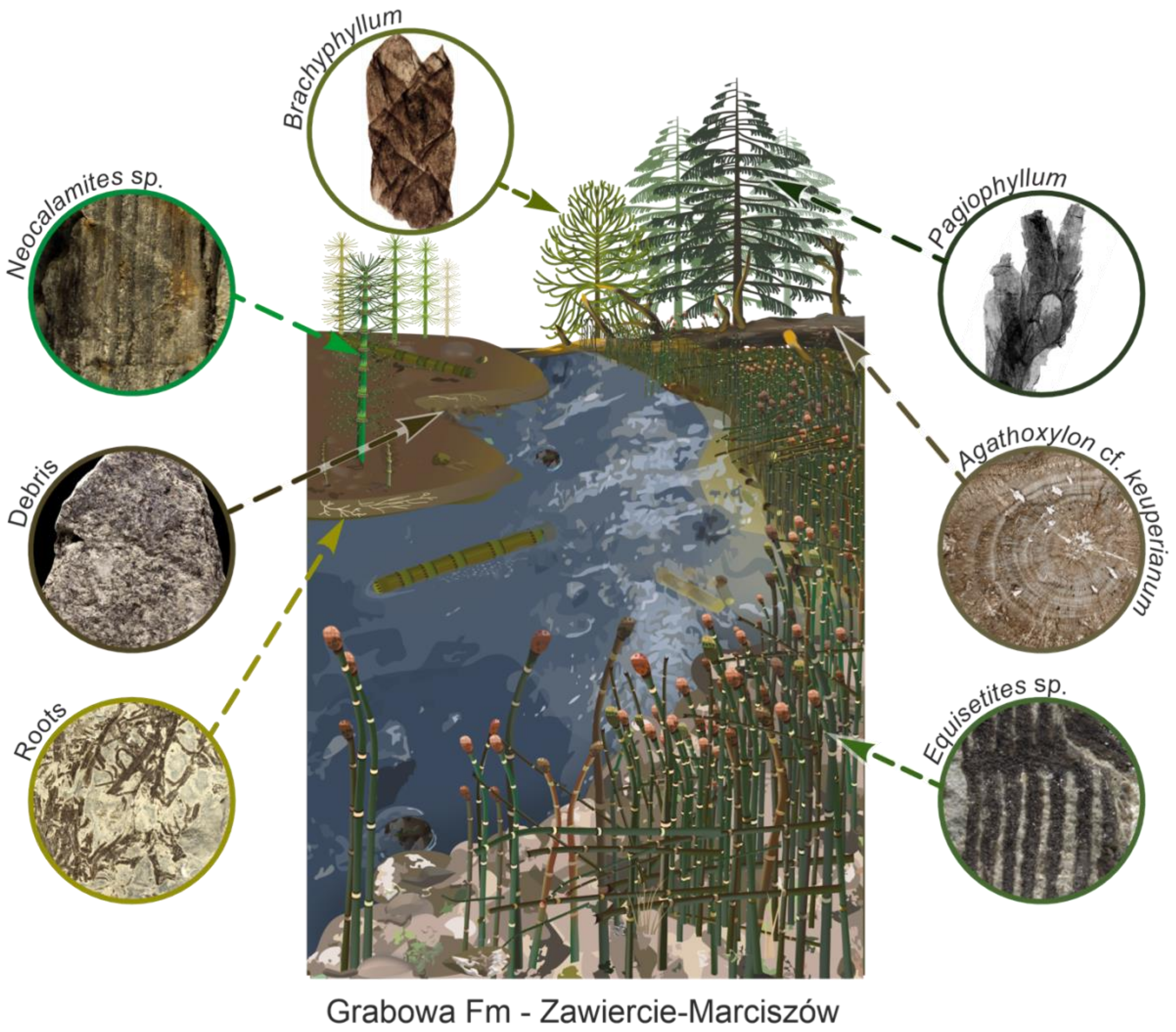

Figure 14. Idealised environment reconstruction of the Grabowa Formation at the Zawiercie-Marciszów.

Figure 15. Idealised environment reconstruction of the Grabowa Formation at the Lipie Śląskie-Lisowice.

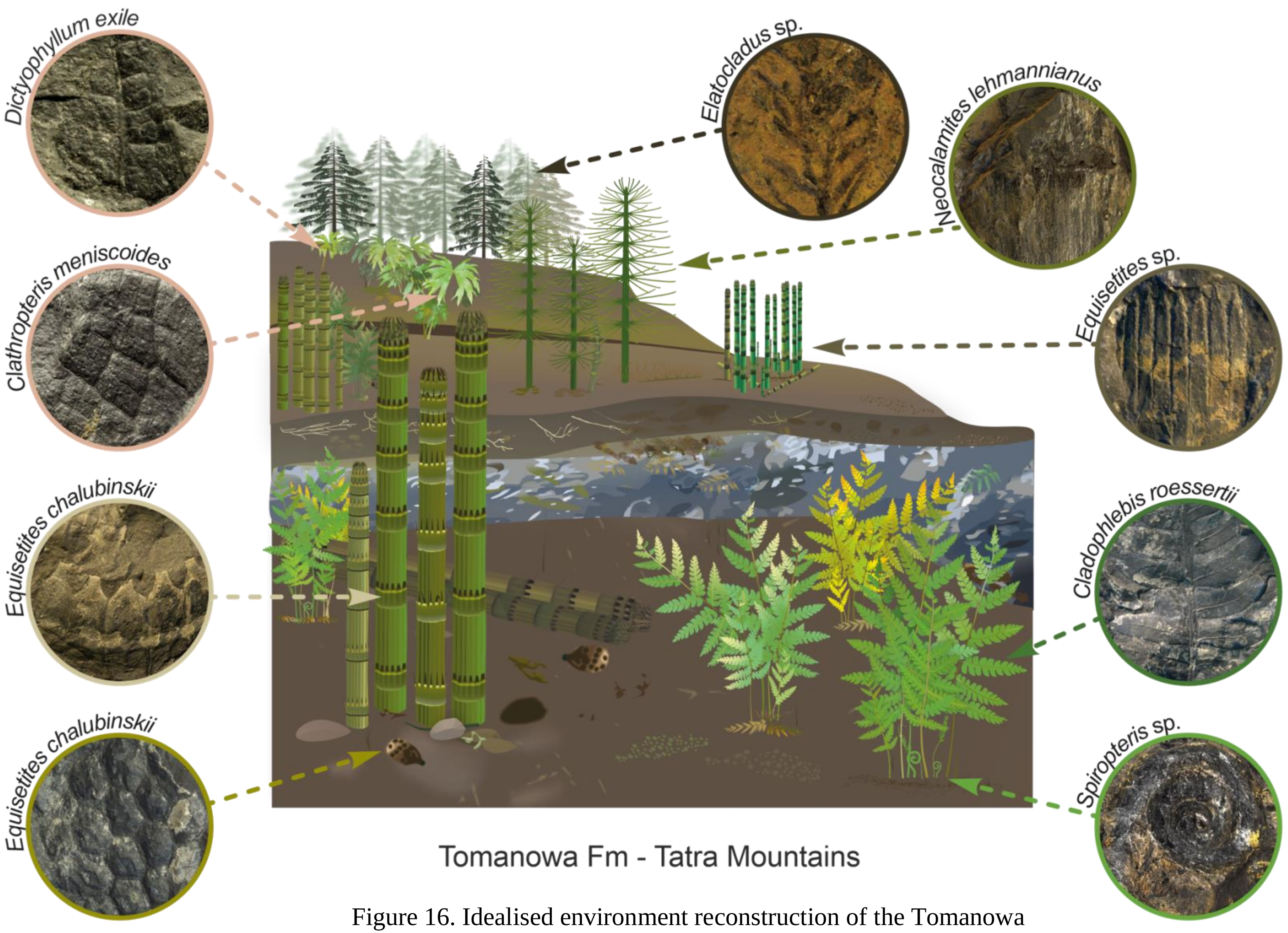

Figure 16. Idealised environment reconstruction of the Tomanowa Formation at the Czerwone Żlebki, Tatra Mountains.

6. Supraregional aspect of studied palaeofloristic assemblages.

6. 1. Phytogeographic significance of Polish macrofloras vs Floristic provinces in the North Hemisphere of Carnian, Norian and Rhaetian.

Because selected Polish localities are of Norian (Upper Silesia) and Rhaetian age (Tatra Mts) a short description only of palaeofloristic zonation from these two Triassic stages is presented here, with a focus on the Northern Hemisphere. That is for assessing the position of Polish assemblages in the phytogeographic pattern of Norian and Rhaetian accordingly. Carnian age localities are marked on the global reconstruction of the Late Triassic (Fig. 14), from which fossil plant taxa were used for comparison with remains found in Poland.

The consolidated land mass of Pangea, and the consequences it has for climate and environment after the end-Permian mass extinction, are reflected in less diversified plant provincialism than during the end of the Palaeozoic (Kustatscher *et al.*, 2018; Meyen, 1987). The fossil record shows plant assemblages spreading across two provinces coinciding with North Hemisphere – Laurussian Province (North America, Eurasia) and South Hemisphere – Gondwana Province (Antarctica, South America, Africa, South Asia, Australia; Kustatscher *et al.*, 2018; Dobruskina, 1994). Laurussian plant assemblages show higher variegation than those across Gondwana, and therefore a number of subprovinces established in the North Hemisphere is higher (Kustatscher *et al.*, 2018; Dobruskina, 1994).

Differences between analyzed floral assemblages from Upper Silesia and Tatra Mts are natural implications of the palaeoecological and palaeoclimatological conditions in which Grabowa Fm and Tomanowa Fm developed. Upper Silesia Norian flora composition is in agreement with the general trend across European floras of that stage – low diversity assemblages, dominated by conifers (Kustatscher *et al* 2017; Dobruskina 1994; Dalla Veccia, 2000).

When comparing with Carnian (e.g., Lunz, Pott, 2010) and Rhaetian (e.g., Wüstenwelsberg, Kelber and Van Konijnenburg-van Cittert, 1997), Norian floras of Europe are less diversified and relatively poorly preserved (Kustatscher *et al.*, 2018; Dalla Veccia, 2000). North American Laurussian subprovinces, as well as Asian ones, show higher taxonomical diversity (Meyer, 1988). Far more diversified floras of North America show however discernible dominance of conifers. So far, across the North American continent, Rhaetian deposits have not been documented (Kustatscher *et al.*, 2018). Three floristic subprovinces were established: the Chinle/Dockum on the southwest of the United States and north-western

Mexico, the Newark Supergroup on the west coast of the USA and Canada, and the Arctic Canada Subprovince. Norian floras of North America share many elements with their Carnian predecessors. The Carnian-Norian Chinle/Dockum flora is showing a wide variety of vascular plants but is particularly famous for the abundant petrified conifer wood – Petrified Forest Member (Ash, 1982). Conifers dominate plant assemblages and are represented not only by petrified wood but also by fossil foliage and fertile organs. Cycads, bennettitaleans, ferns and horsetails were also present in the Chinle/Dockum ecosystems, but the flora is impoverished with ginkgophytes and gnetopsids (Ash, 1969, 1975; Ash *et al.*, 1982). The Lockatong Formation flora of the so-called Newark supergroup is composed of all major vascular land plants groups; horsetails, ferns, ginkgophytes, cycads, and bennettitalean, together with many conifers occur at this locality (Ash, 1989; Fraser *et al.*, 1996).

Sharing characteristics between floras of the same and different subzones is common. For example, the presence of *Schizoneura* in the Chinle-Dockum and the Newark floras (Ash 1986, 2011; Axsmith *et al.*, 1997) suggests floral interchange between North America, Europe and Gondwana during the Late Triassic or earlier. The late Norian flora of the Sverdrup Basin (eastern Canadian Arctic Archipelago) reflects high-latitude vegetation that lived close to the border with Europe and Siberia and contains elements of both regions (Kustatscher *et al.*, 2018).

Europe is divided into two Late Triassic palaeofloristic subdivisions: North Atlantic/Central European Subprovince (southern Sweden, Eastern Greenland, northern Central Europe, including Poland) and Western Thetydean Subprovince (Alps, south Europe; Kustatscher *et al.*, 2017, 2018; Dobruskina, 1994). The most complete European macrofloral record of the Norian age was found in Seefeld, Austria (Kustatscher *et al.*, 2017). Fossils occur in the basin facies of the Seefeld Formation, formed by calcareous wackstones and mudstones alternating with calcareous laminates, that are organic-rich. This assemblage is dominated by conifer shoot fragments, female and male cones, isolated seed scales and bracts, leaf fragments, stem fragments and dispersed seeds. Conifer morphogenera *Brachyphyllum*, *Pagiophyllum*, *Peleurodea* and *Elatocladus* are the most common. Some putative cycadophytes, *Taeniopteris*-like are also present. Seefeld Formation also contains isolated male and female cones of obscured affinity, but connected with conifers. Other Norian plant localities, i.e., Dolomia di Forni Formation, Italy, have a very scarce floristic record, but avaiable remains suggest conifer dominance (Dalla Vecchio, 2000, 2012; Kustatscher *et al.*, 2013).

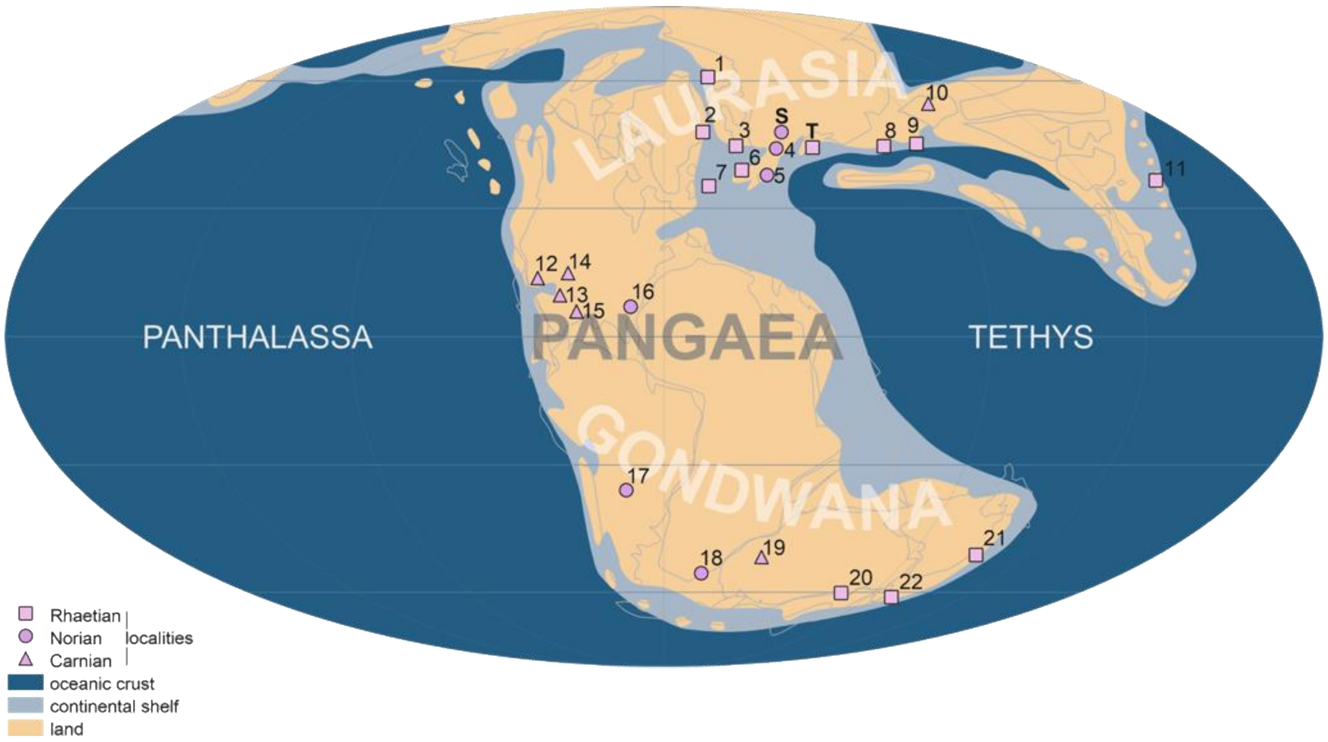

Figure 14. Palaeogeographic world map showing the distribution of major Upper Triassic plant assemblages including exemplary studies (1-21) and this study sites marked with stars: S – Upper Silesia, T – Tatra Mts, 1. Spitzbergen (Pott, 2014); 2. Greenland (Harris, 1926, 1931, 1935); 3. Scania (Pott and Mcloughlin, 2011); 4. Lunz (Pott *et al.*, 2008); 5. Southern Alps (Kustascher *et al.*, 2011); 6. German Basin (Van Konijnenburg-Van Cittert *et al.*, 2014); 7. UK (Harris, 1938a); 8. Iran (Vaezjavadi and Syooki, 2002); 9. Afganistan (Schweitzer *et al.*, 1997); 10. Northwestern China (Wan *et al.*, 2017); 11. Japan (Yukagawa *et al.*, 2020); 12. Arizona (Ash, 1970); 13. New Mexico (Ash, 1999); 14. Colorado Plateau (Ash, 1987); 15. Texas (Ash, 2011); 16. North Carolina (Delevoryas and Hope, 1973); 17. Argentina (Archangelsky and Brett, 1961); 18. South Africa (Anderson and Anderson, 2018); 19. East Antarctica (Cantrill *et al.*, 1995); 20. East Antarctica (Bomfleur and Kerp, 2010); 21. Western Australia (Barone-Nugent *et al.*, 2003); 22. New Zealand (Retallack, 1985; Pole and Raine, 1994); Base map: PALEOMAP Project, Scotese, 2014)

German Basin locality Seinstedt, Lower Saxony, Germany (Fig. 14, 15), contains delta plain deposits that were formed by fluvial processes (Barth *et al.*, 2014). According to palynostratigraphy and conchostracan stratigraphy, the age of this succession is determined to be upper Norian – lower Rhaetian (Barth and Kozur, 2011). The plant remains preserved in coarse sandstone at Seinstedt mostly consist of impressions, but they exhibit a higher taxonomic diversity compared to older Norian fossil floras in Europe.

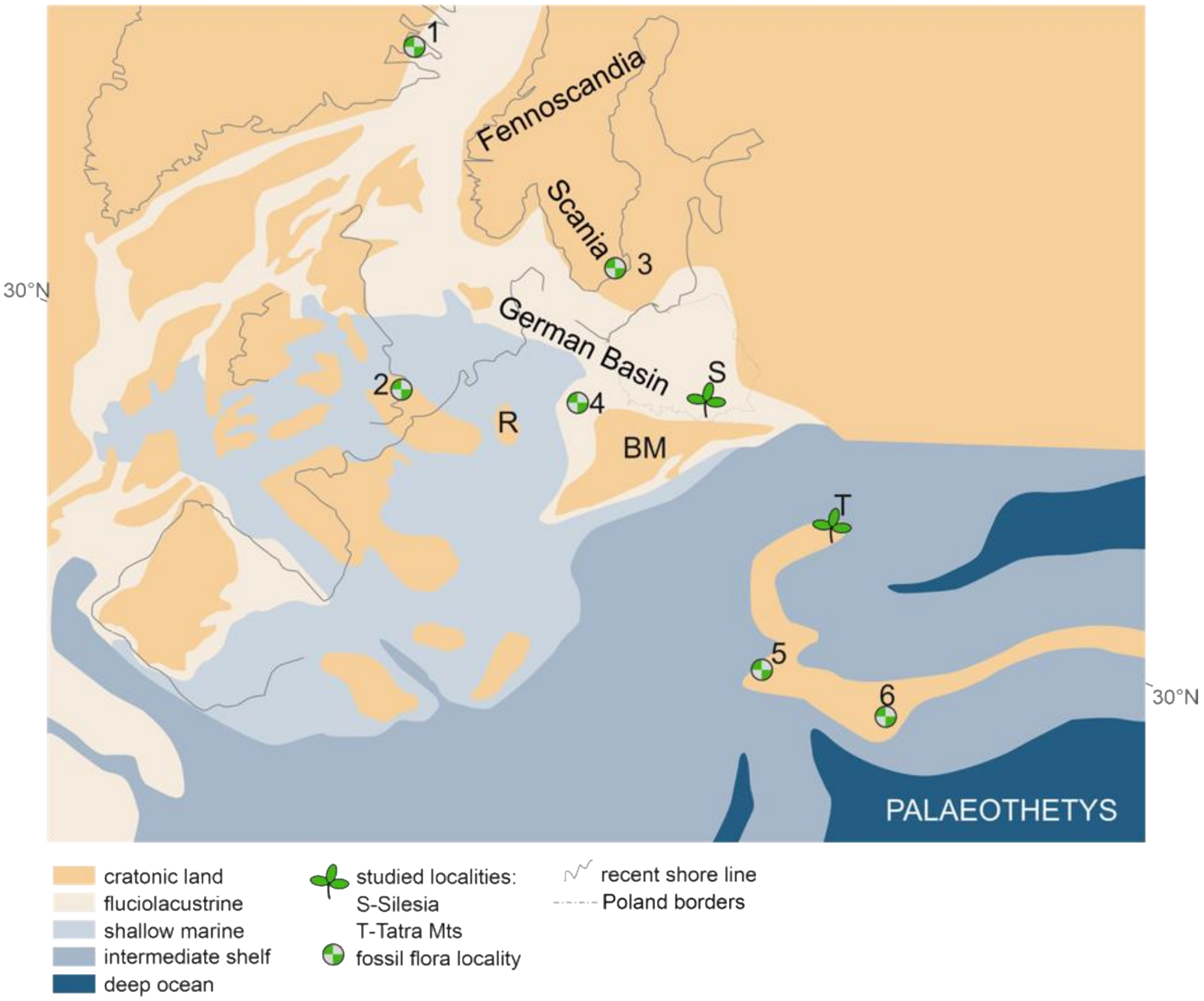

Figure 15. Palaeogeography of Europe in the Late Triassic showing Norian and Rhaetian fossil plants localities; 1 – East Greenland (Harris, 1931); 2 – UK; 3 – Southern Sweden (Pott and McLoughlin, 2011); 4 – Seinstedt, Germany (Barth *et al.*, 2014); 5 – Seefeld, Austria (Kustatscher *et al.*, 2017); 2 – Dolomiti and Southern Alps, Italy (Dalla Vecchia, 2012).(modified after Van de Schootbrugge *et al.*, 2009 and Schobben *et al.*, 2019).

Abundant at Seinstedt are Cycadophyta (*Nilssonia*, *Pterophyllum*), Pteridophyta (*Clathropteris*, *Dictyophylllum*, *Phlebopteris*), and Pteridospermophyta (*Ctenozamites*, *Lepidopteris*, *Ptilozamites*). The conifers present at Seinstedt are primarily represented by the scale-leaf species *Hirmeriella muensteri* (Cheirolepidiaceae), preserved as shoots and male cones. Common element shared with researched localities from Poland is the presence of *Neocalamites* (Sphenophyta). The fragmented and poorly preserved nature of the plant remains at Seinstedt is a result of material transportation from an upstream terrain (Barth *et al.*, 2014).

Grabowa Fm from the Upper Silesia shows the same characteristic conifer domination as North American fossil plant assemblages. Zawiercie-Marciszów and Lipie Śląskie-Lisowice are abundant in fossil foliage morphogenera of scale-leaf conifers, like *Brachyphyllum* and *Pagiophyllum*, together with long-leaf conifers of *Elatocladus*. Macrofossils, cuticles and miospores confirm the high presence of conifers (Fijałkowska-Mader, 2015; Pacyna *et al.*, 2017).

6. 2. Researched flora in the context of Late Triassic climate shifts and global events

World-wide environmental conditions of the Late Triassic were shaped by climate fluctuations together with direct and indirect effects of catastrophic events, like large-scale vulcanic eruptions and asteroid impacts.

The whole Triassic is consider a "hot house" period in the climatic history of Earth (e.g., Li *et al*., 2023; Scotese *et al*., 2021). Arid and semi-arid conditions were common, until in the latest Triassic climate shifted to more humid (Goddéris *et al*., 2014). Atmospheric CO^2 levels dropped Pangea northward drift resulted in enlarging humid, tropical zone forced changes in hydrology and temperature regimes. High atmospheric CO^2 level dropped from ca. 3000 ppmv in the End Permian to middle Triassic, to 800 ppmv in the late Triassic in connection to Pangea drifting North and an increase in silicate weathering. Plant growth is controllled by hydrology, temperature and avaiablity of habitable space (Gurung *et al*., 2022). Due to the Pangea northward drift from Carnian to Rhaetian more land surface got under tropical, humid zone influence (Godderis *et al*., 2014). Increase in land area with higher precipitation and high-moderate temperatures encouraged plant productivity in the late Triassic (Gurung *et al*., 2022). Polar regions were covered by foreststs insted of ice caps (Li et al 2023; Strullu-Derriene *et al*., 2012). Recent studies by Jin *et al*. (2022) and Scotese *et al*. (2021) have identified three distinct periods of humid climate shifts linked casually to different-sized Large Igneous Province (LIP) eruptions (Fig. 16). One well-documented humid interval during the Late Triassic is the Carnian Pluvial Event (CPE), link with volcanic activity from the Wrangelia Oceanic Province (Scotese *et al*., 2021). This climatic condition facilitated the expansion of moisture-loving plants, particularly ferns (Fijałkowska-Mader, 2015; Kustatscher *et al*., 2018). Another humid period, the Mid-Norian Pluvial Event, coincides with the Lisowice Bone-bearing Level (Kowal-Linka *et al*., 2019).

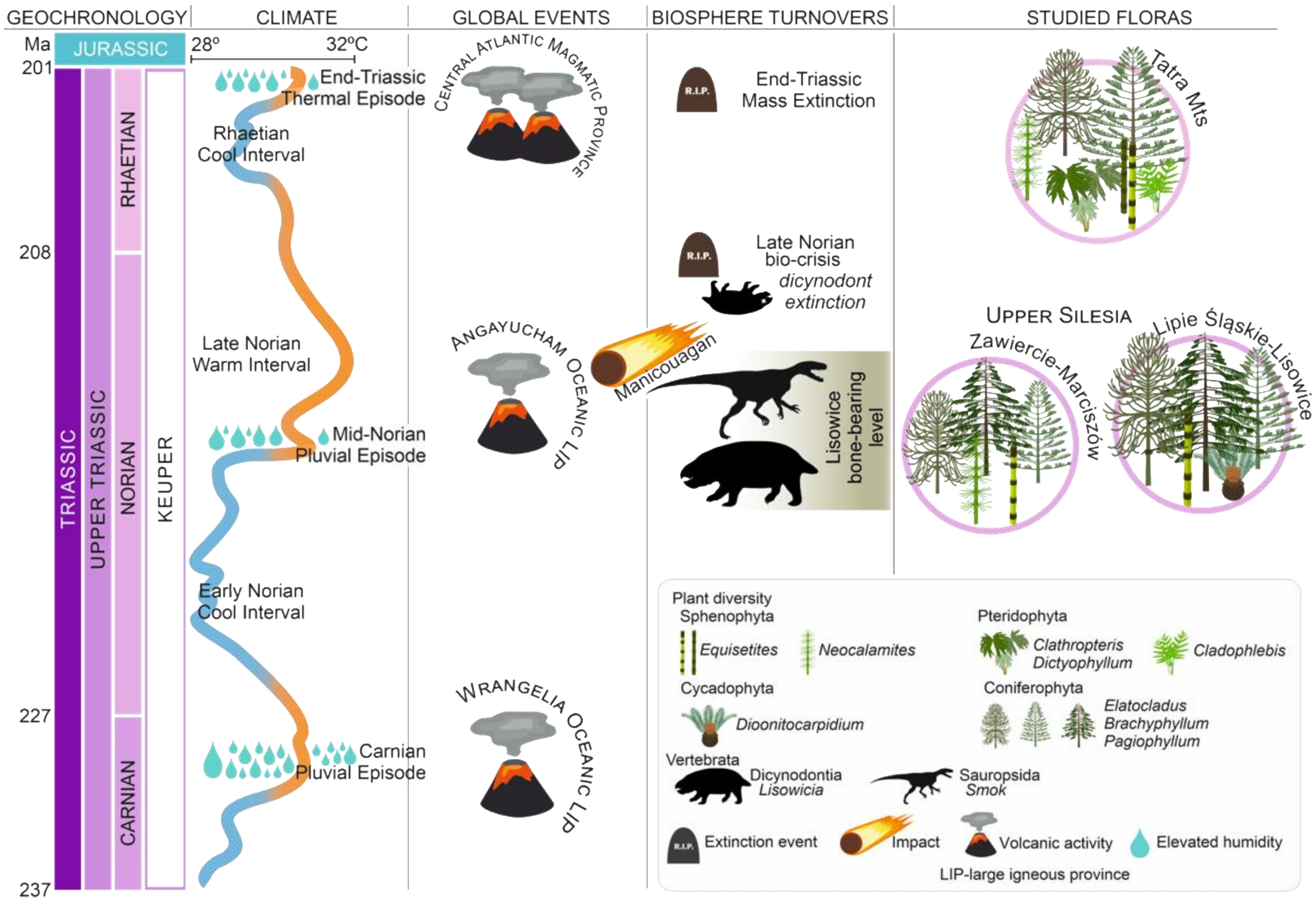

Figure 16. Late Triassic major geo- and bioevents correlated with climatic changes as a background for development of studied floral assemblages (compiled from Trotter *et al.*, 2015; Lucas, 2021; Scotese *et al.*, 2021; Jin *et al.*, 2022)

The Late Triassic was a dynamic period characterized by global environmental changes that influenced faunal and vegetation turnovers contribitung significantly to the decimation of the and finally extinction of Dicynodontia (Racki and Lucas, 2020). Notably, one of the "Big Five" mass extinctions occurred at the Triassic-Jurassic boundary, possibly linked to the cataclysmic flood basalt eruptions in the Central Atlantic Magmatic Province (CAMP; Wignall, 2019). The increasing activity of CAMP resulted in a global volcanic cataclysm by the end of the Triassic, with evidence of humidification in stressed land habitats, such as the Passaic fern spike in North America (Lucas, 2021). Similar climatic changes are also observed in the Tatra Rhaetian succession (Michalik *et al.*, 2010; Onouke et al., 2022).

Fluctuations in climate and turnovers in the biosphere during the Late Triassic are less likely to be caused by meteoritic impact events The most notable impact in the Late Triassic, which occurred near the research areas, took place in southwestern France, forming the Rochechouart impact structure. According to absolute dating, the recrystallization of minerals associated with this impact happened approximately 206 million years ago (Cohen *et al.*, 2017; Rasmussen *et al.*, 2020). However, the impact in this region was not severe enough to cause a catastrophic event. Another significant impact, Manicouagan in northeastern Quebec, Canada, dated at 215.5 Ma, as suggested by Cohen *et al.* (2017), may have influenced the evolutionary trends of Late Norian through Rhaetian biota. Figure 16 shows presents stratigraphic position of the researched floras against major Late Triassic biotic and abiotic events and climate fluctuations.

7. Conclusions

1) Upper Silesian Norian floras from Lipie Śląskie-Lisowice and Zawiercie-Marciszów were found within the Lisowice Bone-bearing Level of the Grabowa Formation. Both assemblages are dominated by Coniferophyta macrofossils. The main difference between the Lipie Śląskie-Lisowice and Zawiercie floras is the abundance of Sphenophyta remains, which are more common in Zawiercie-Marciszów. The Lipie Śląskie-Lisowice flora is better preserved, and palaeobotanical data were collected from dispersed cuticles, macrofossils, and coprolites.

2) Analysis of coprolite material from Lipie Śląskie-Lisowice provided insight into dietary habits of herbivorous tetrapods/dicynodontia (i.e. sinapsids like *Lisowicja bojani*). Plant remains macerated/retrieved from coprolites supplement information about floral composition showing higher taxonomical diversification than suggest by the macroremains.

3) Tatra Mts. Rhaetian Tomanowa Formation yielded plant fossils limited to macrofossils, without cuticles preserved. Flora is dominated by Sphenophyta and Pteridophyta with minimal participation of Conipherophyta. Spore producing plants are more water dependent than Gymnosperms.

4) Norian Grabowa Formation flora differs in taxonomic composition from Rhaetian Tomanova Formation. Disparities are an effect of different palaeogeographic location (Grabowa Fm-German Basin epicontinental basin; Tomanova Fm – Tatricum, north-east Thetys) and palaeoclimatic conditions (Grabowa Fm – dry to semi dry climate with humid episodes; Tomanova Fm – humid conditions).

5) Domination of ferns in the Tomanova Fm combined with general humidification during the latest Rhaetian might be controlled by end-Triassic ecosystems changes promoted by increased vulcanic activity (CAMP).

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Plates

Plate 1

Different modes of fossil plant preservation from the Upper Triassic of the Zawiercie-Marciszów, south Poland.

A – E. Micritic limestone concretion with rooting structures preserved.
  A. Outer surface of the concretions lacking microbial structures.
  B. Rooting structures entrap inside the micritic limestone concretion.
  C. Thin section of the micritic limestone concretion, from A, B.
  D. Bioturbations in the micritic limestone, magnification of C.
  E. Fragments of ostracods (Crustaceae) shells.
F – N. Micritic limestone concretion with plant remains.
  F. Outer surface of the micritic concretion covered with microbial structures.
  G. Inside of the micritic concretion with sphenophyta fossil compressions.
  H. Side view of the micritic concretion with fragments of compressed sphenophyta stems oriented horizontally.
  I. Thin section of the specimen from F showing charcoalified plant stems filled with sediment.
  J. Details of the thin section from I showing bioturbations, fragments of ostracods (Crustaceae) shells, dispersed cuticle fragments and quartz grains.
  K. details of thin section from I with partially preserved ostracods (Crustaceae) shells.

Abbreviations: b – bioturbations, c – cuticle, o – Ostracoda, pl – plant, q – quartz.
Scale bar: A, B, F – H 10 mm, C, I 5mm, D 500 µm, J, L, M, 200 µm, K, N 100 µm.
Specimen: A – E ZK1; F, I – K specimen ZC2; G, H, L – N specimen Z22.

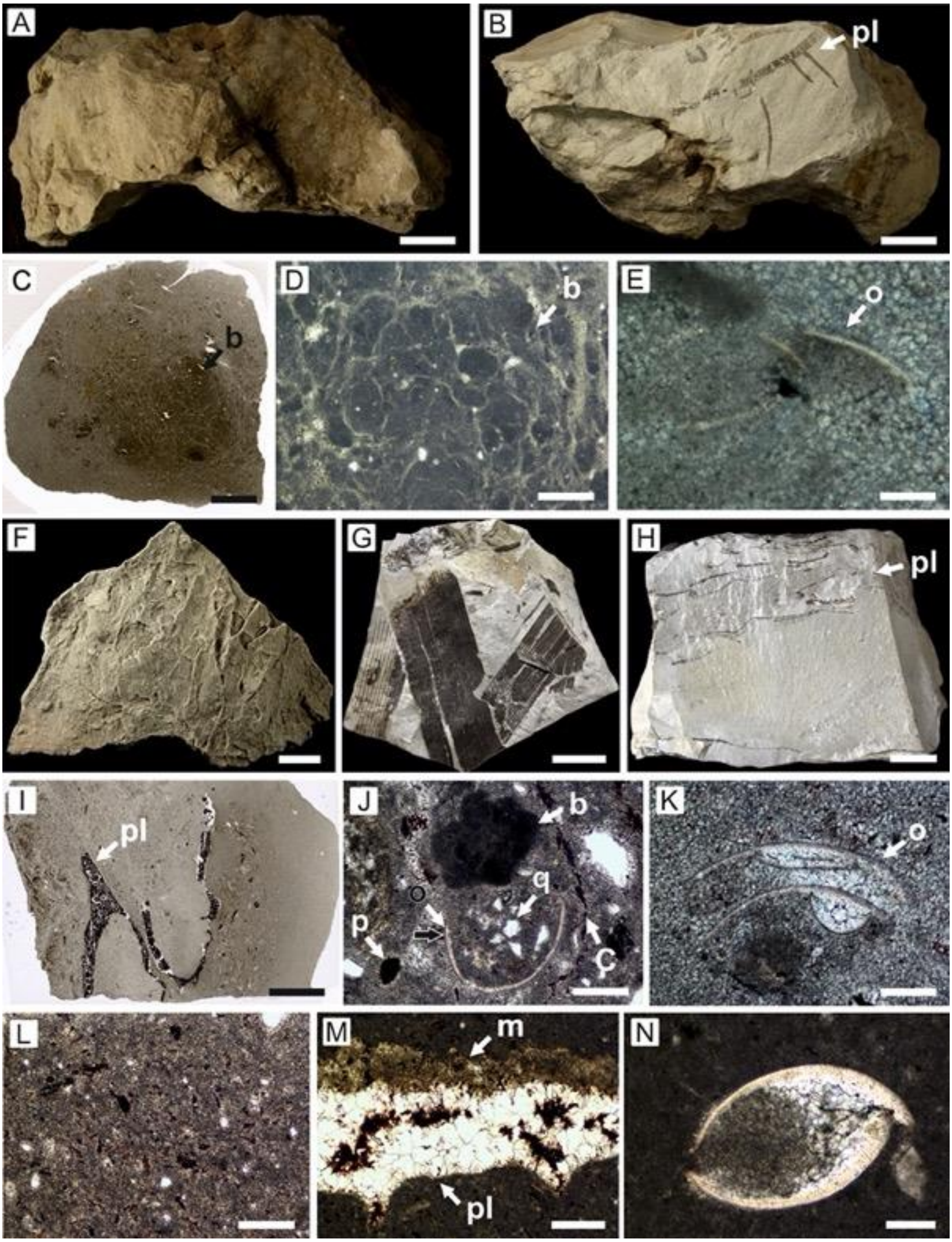
A
B
pl
C
b
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Plate 2

Different modes of fossil plant preservation from the Upper Triassic of the Zawiercie-Marciszów, south Poland.

A – E. Calcareous mudstone containing disoriented remains.

A, C. Fragments of light-grey mudstone yielding plant remains of different sizes, including fragments of gymnosperms stems. B. Thin section of mudstone with gymnosperm stem.

D, E. Details of B showing fragmented cuticles, animal remains (probable fish element), detrital quartz grains.

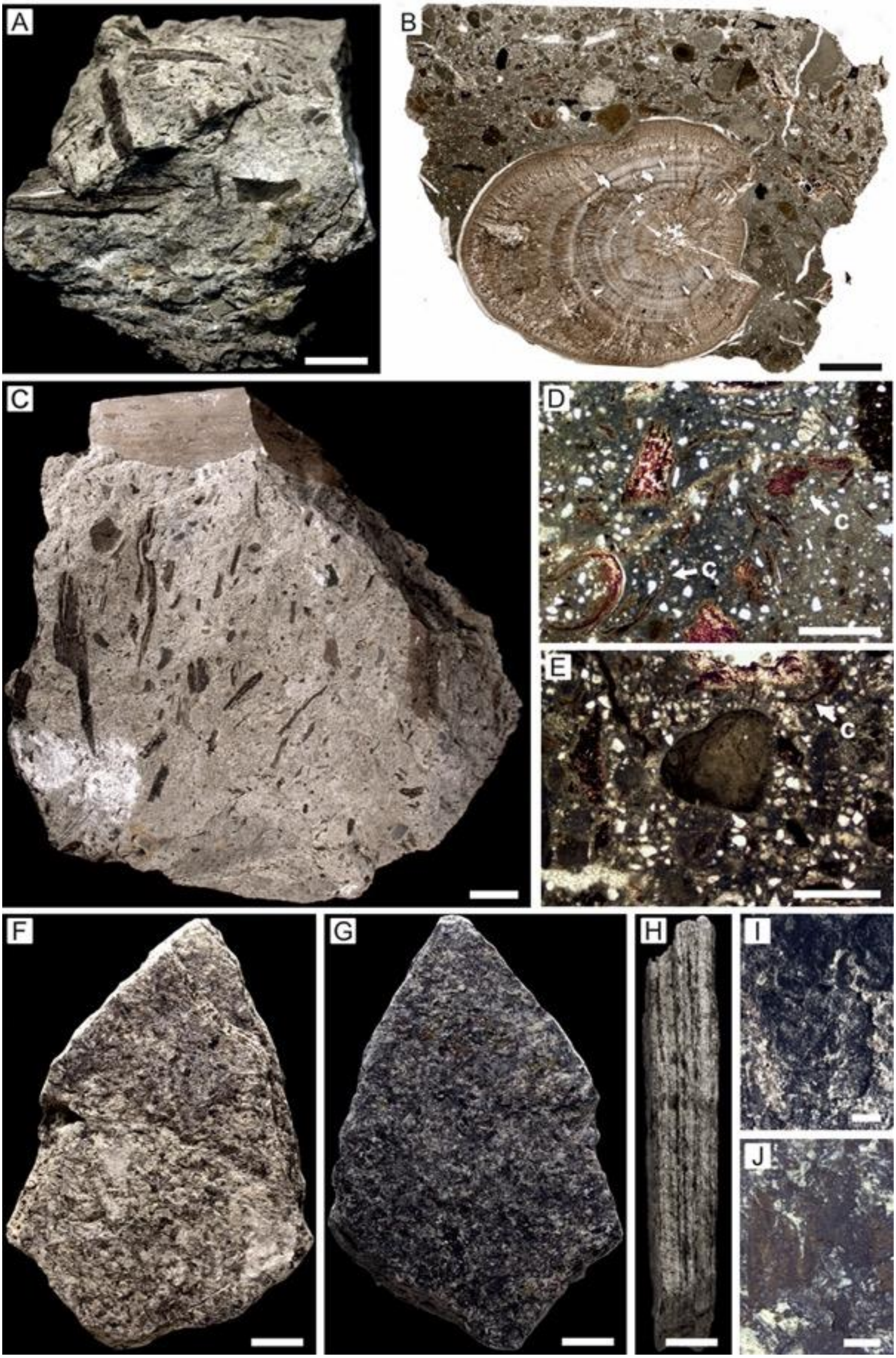
F – H. Piece of a mudstone densely packed with organic particles, mostly plant remains.

I. Fragment of dark cuticle from coniferous twig; J. Light brown leaf cuticle fragment.

Abbreviations: c – cuticle, f – fish scale, q – quartz.

Scale bar: A – C, F – H 10 mm; D 5 mm; E, I, J 100 µm.

Specimen: A – E ZR1; F – H ZC2.


A
B
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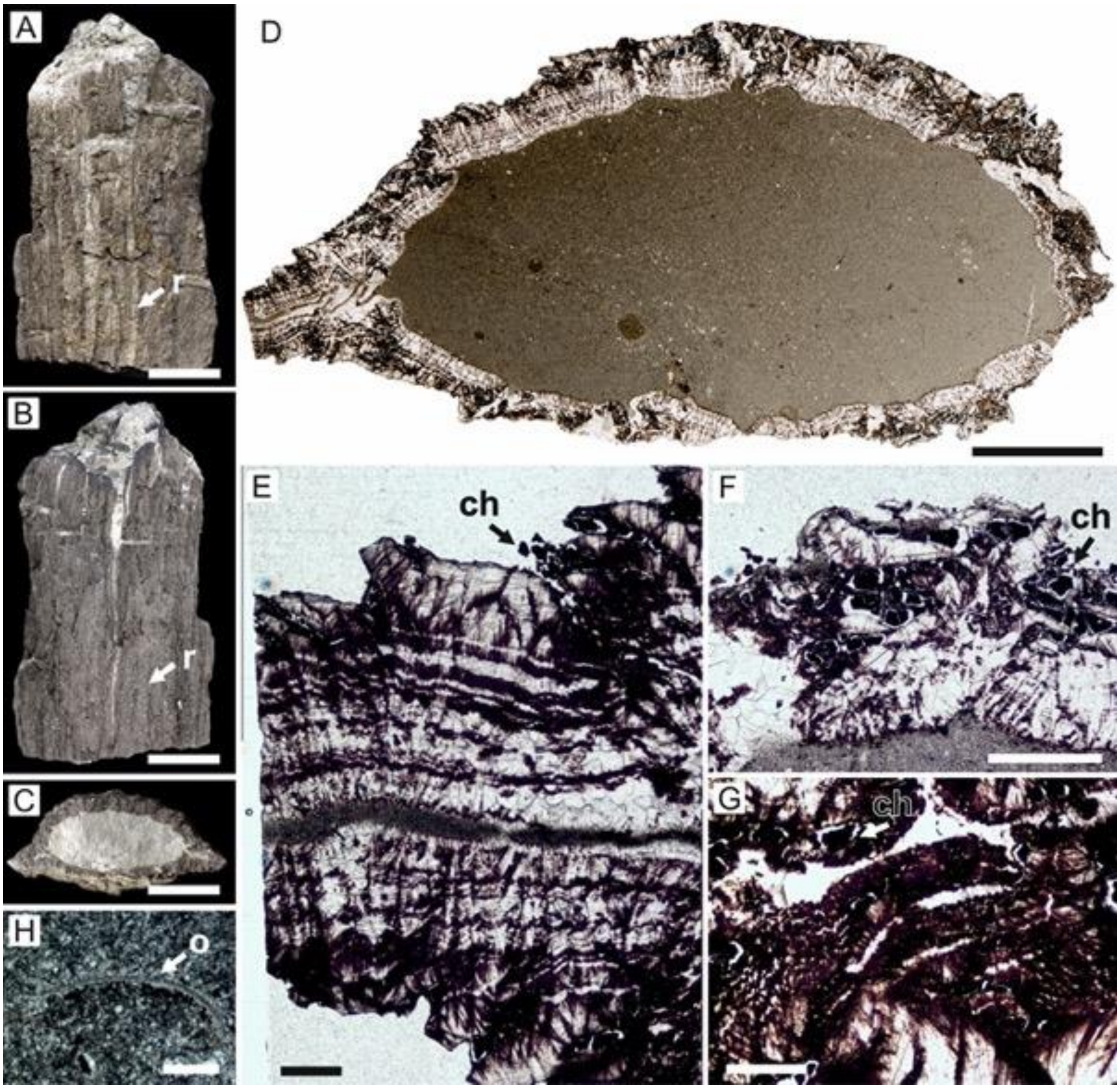
I
J

Plate 3

Different modes of fossil plant preservation found in Zawiercie-Marciszów. Separated three-dimensionally preserved stems with inner-cavities filled with sediment.

A – C. Outer surface of a stem, specimen.
D. Thin section of a stem showing stem pith filled with neomorphized micritic limestone.
E – G. Details of calcified plant tissue with fragments of charcoal.
H. Fragment of smooth-shell ostracoda (Crustaceae).

Abbreviations: ch – charcoal, o – Ostracoda, r – ribs.
Scale bar: A – C 10 mm; D 5 mm; E 1 mm; E, F 500 µm; G, H 100 µm.
Specimen: A – H ZST1


A
r
B
r
C
H
o
D
E
ch
F
ch
G
ch

4. Systematic description of fossil plants from researched localities

4.1. Zawiercie-Marciszów

Plate 4

Equisetites sp. from the Upper Triassic of the Zawiercie-Marciszów, south Poland.

A. Compressed stems of sphenophytes and the widest preserved stem.
B. Impression of epidermal pattern, probably of the outer layer of stem from A and C.
C. A counterpart of A.
D. Compressed stem of *Equisetites* sp. with preserved internodal regions and an internode between them.
E. Details of the node from D.
F. Stem with partially preserved node.
G. Internodal region separated with the node.
H. Stem with preserved internodal and nodal regions.

Abbreviations: n – node, v – vascular strand.
Scale bar: A, C 10 mm; B, D 15 mm; E, F 2 mm; G, H 1 mm.
Specimen: A, F Z01A; B, C Z01B; D, E Z22; G Z07; H Z02.

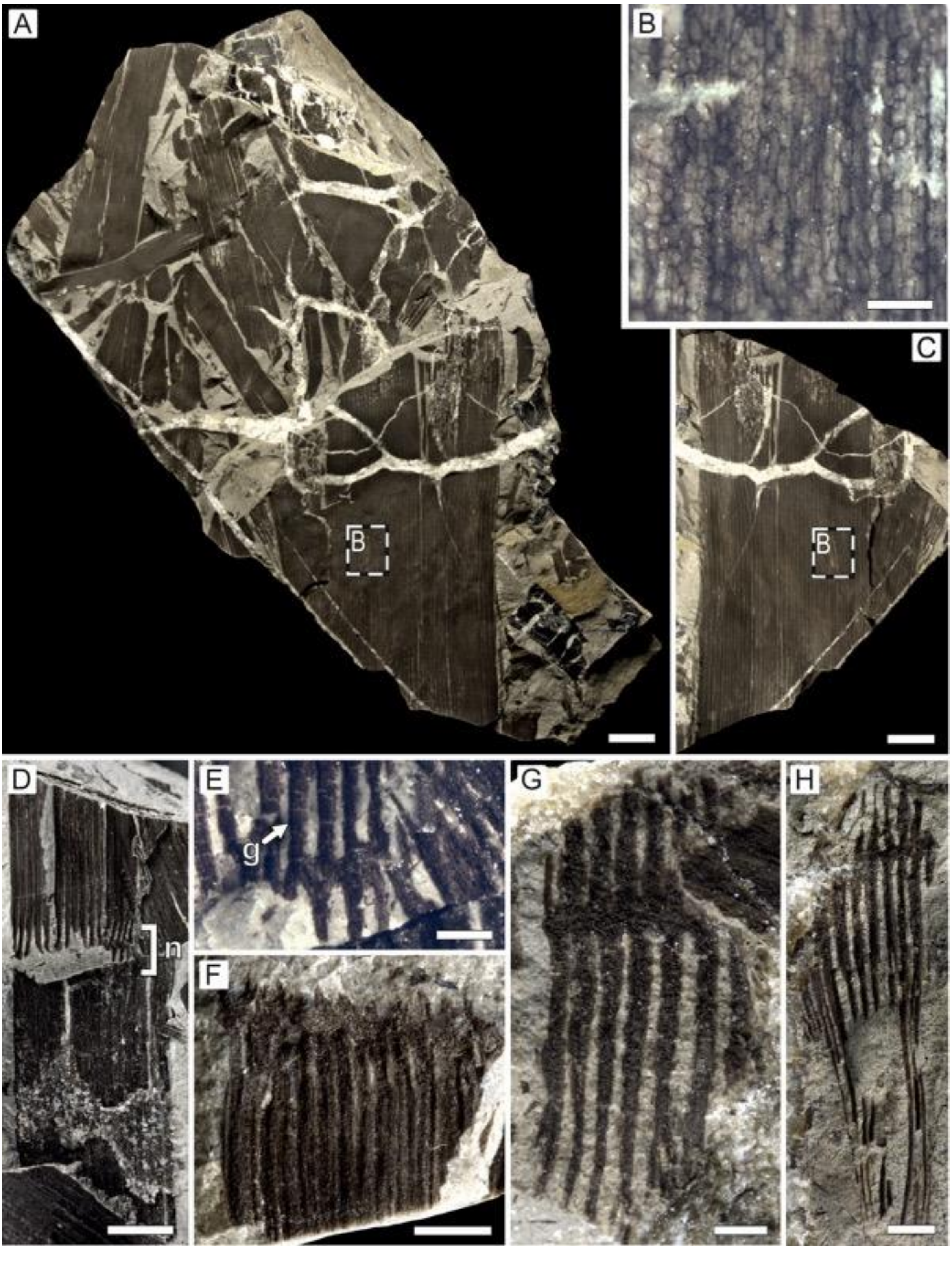

A
B
C
B
B
D
n
E
g
F
G
H

Plate 5

Equisetites sp. from the Upper Triassic of the Zawiercie-Marciszów, south Poland.

A. Stem with preserved outer smooth layer and exposed underlying ridged surface.
B. Internodal region of compressed stem.
C. Transverse view on specimen in A showing compressed stem filled with sediment.
D. Transversal view of the specimen from B showing stem filled with sediment.

Abbreviations: ec – external cortex, rg – ridge.
Scale bar: A – C 10 mm; D 1 mm.
Specimen: A, C Z02; B, D Z05.

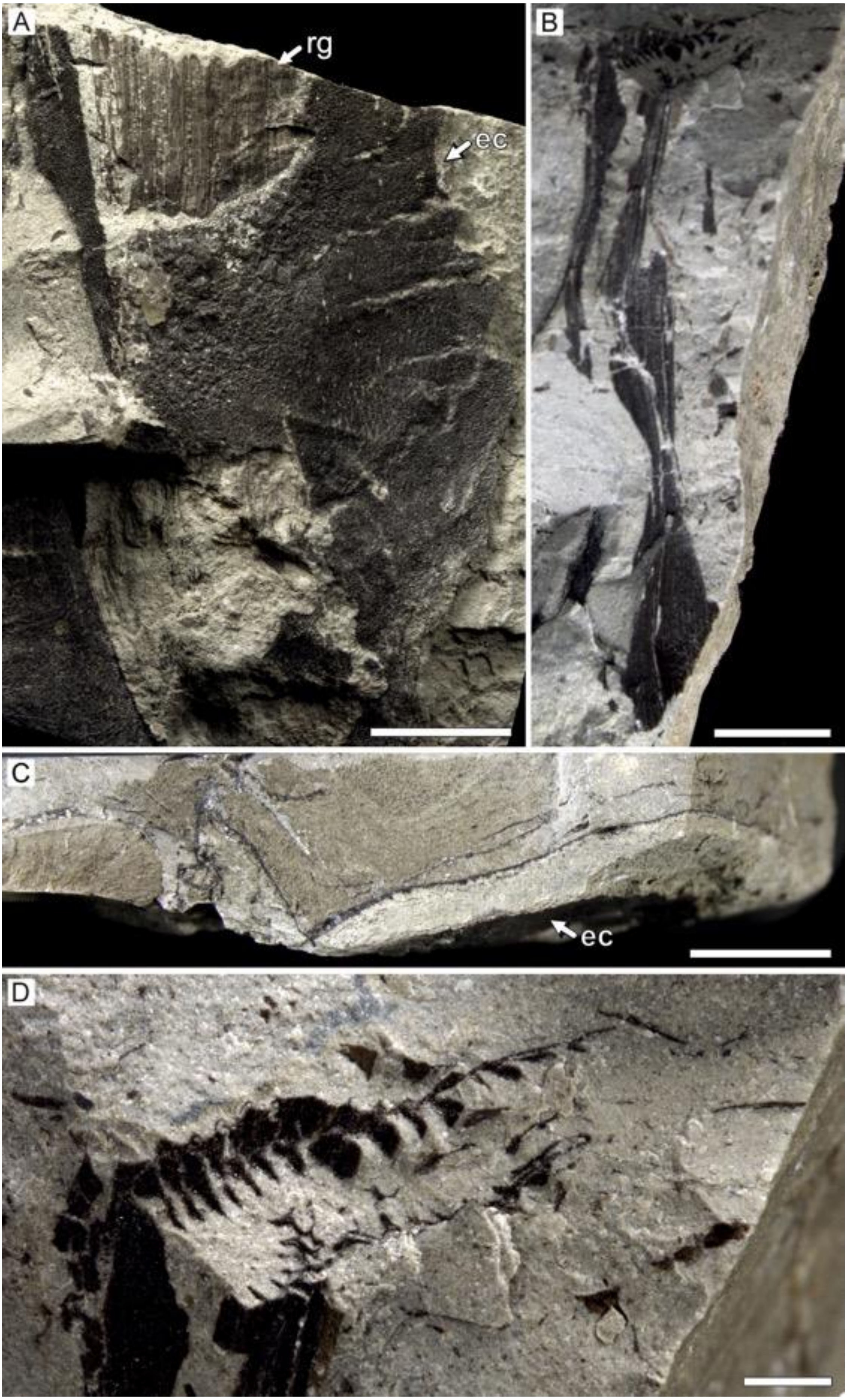

A
rg
ec
B
C
ec
D

Plate 6

Neocalamites sp. from the Upper Triassic of the Zawiercie-Marciszów, south Poland.

A. Impression of the sphenophyte stem with ridges and grooves well marked.

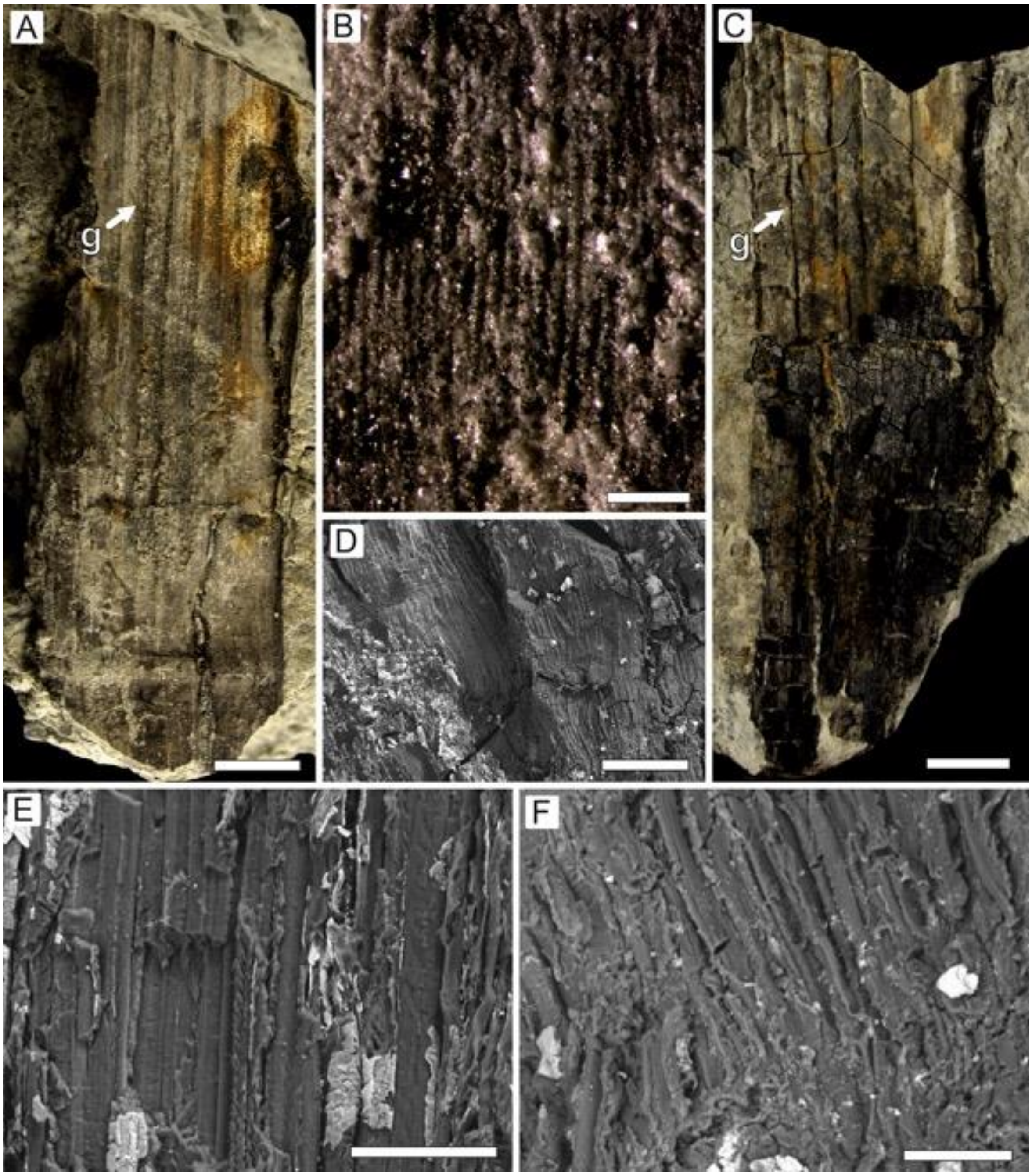
B. Details of the surface from A, thin longitudinal striae on the ridged surface.

C. Impression of the sphenophyte stem with ridges and partially preserved charcoalified tissue.

D – F. SEM photos showing details of charcoalified tissue from C.

Scale bar: A, C 10 mm; D 200 µm; E – F 50 µm.

Specimen: A, B Z24; C – F Z25.


A
g
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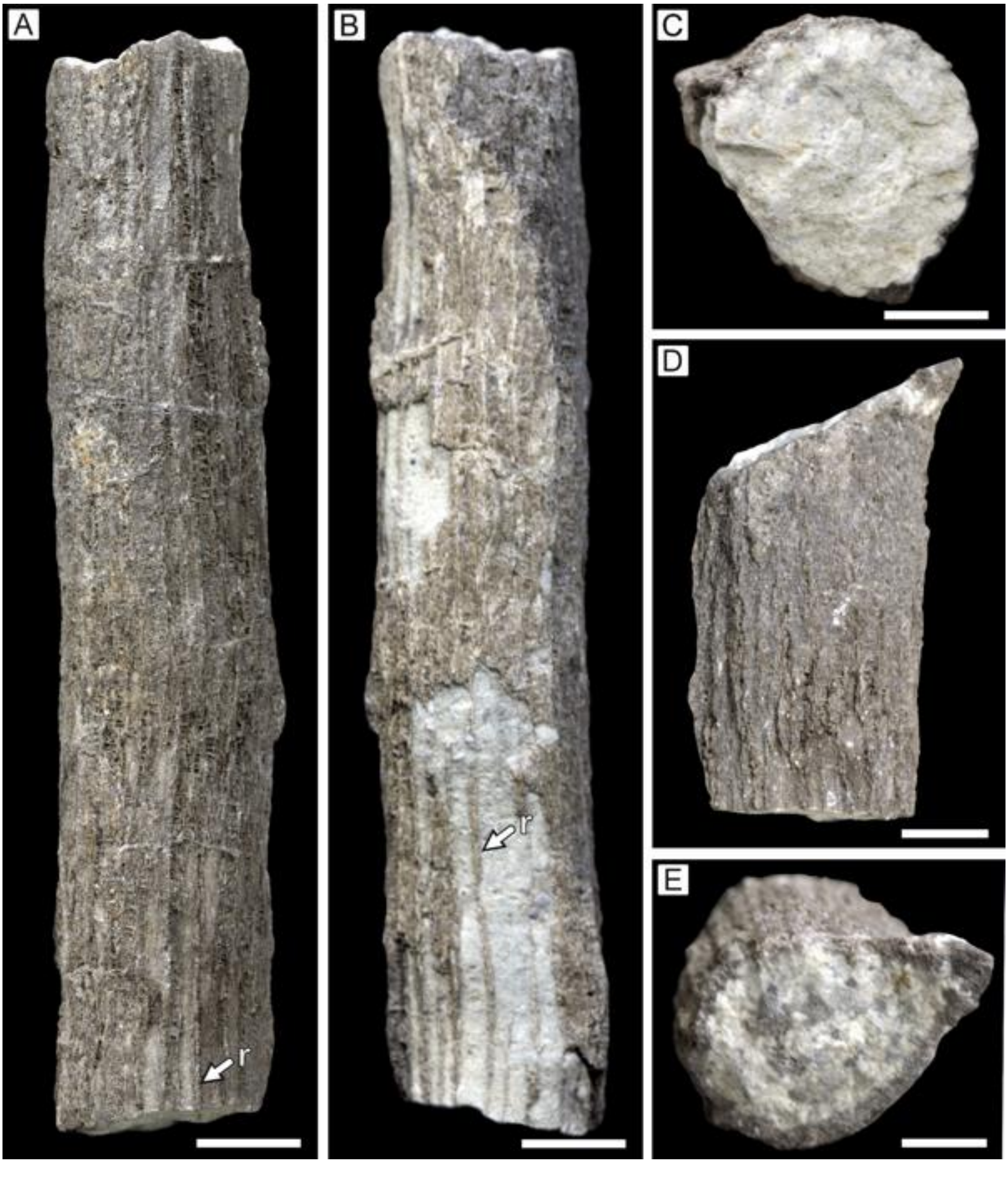
E
F

Plate 7

Cf. *Neocalamites* sp. from the Upper Triassic of the Zawiercie-Marciszów, south Poland.

Three-dimensionally preserved stems with permineralized and partially charcoalified tissue.
A, B. View on the outer surface of the stem showing damaged tissue and ribs.
C. A side view of the stem, pith is filled with micritic limestone.
D. Outer surface of a stem with less discernible ribs.
E. A side view on the stem in D showing a pith filled with micritic limestone.

Abbreviations: r – ribs.
Scale bar: 5 mm.
Specimen: A – C ZST2; D, E ZST3.



A
r
B
r
C
D
E

Plate 8

Agathoxylon cf. *keuperianum* (Unger) Philippe stem from the Upper Triassic of the Zawiercie-Marciszów, south Poland.

Permineralized, three-dimensionally preserved stem with preserved internal anatomy.

A, B. Outer surface of the stem.

A. Outer surface with rhomboidal branch scar.

C. Transverse view of the permineralized stem.

D. Transverse thin section of the stem.

E. Radial thin section of the stem.

Abbreviations: p – pith.

Scale bar: 5 mm.

Specimen: A – E ZST4

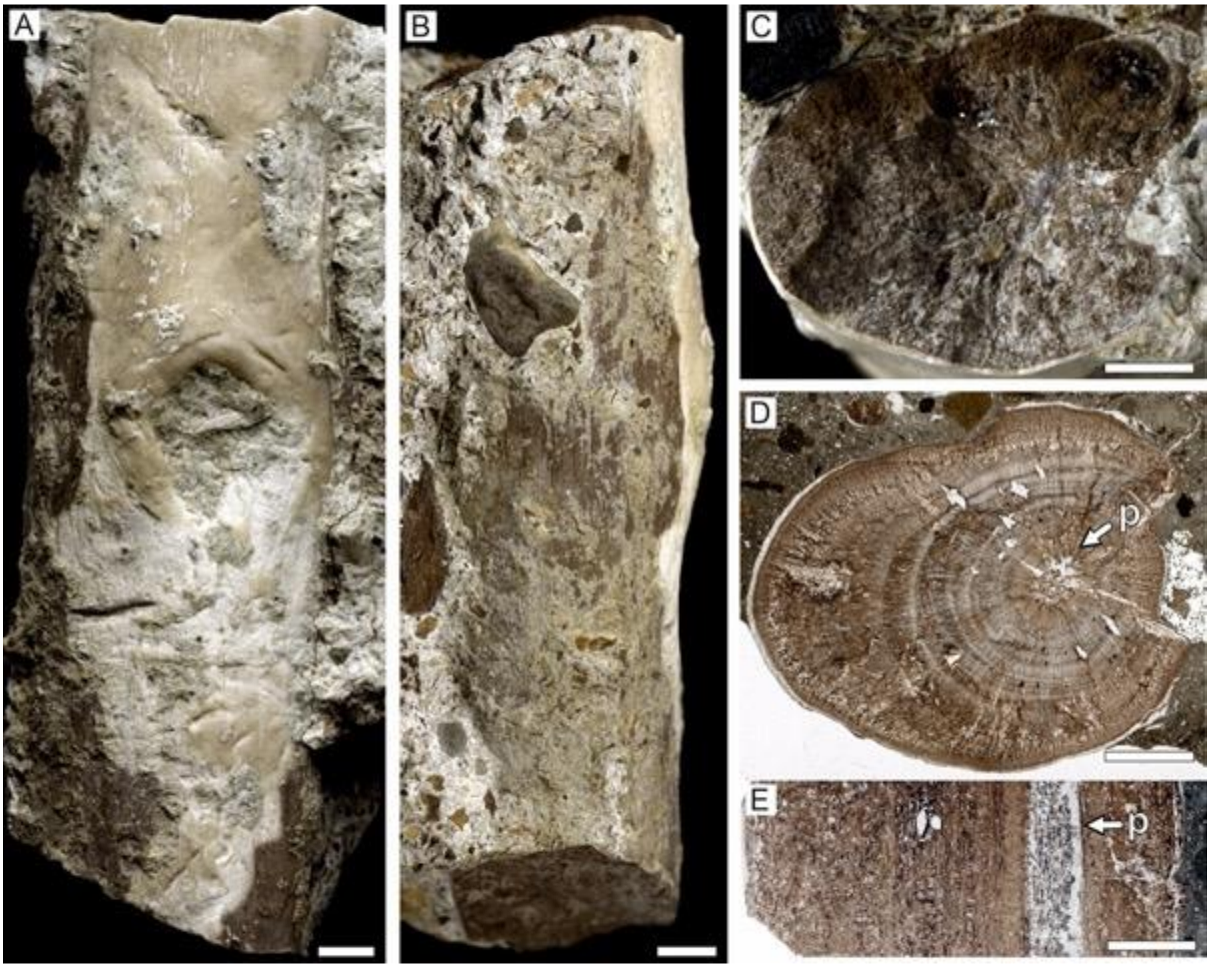

A
B
C
D
p
E
p

Plate 9

Agathoxylon cf. *keuperianum* (Unger) Philippe stem from the Upper Triassic of the Zawiercie-Marciszów, south Poland.

A. A cross thin section of the stem with permineralised tissue.
B. Transition between regular wood and reaction wood.
C. Transition between 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 bar: A 10 mm; B, E 500 µm; C, F, G 100 µm; D 25 µm; H 50 µm.
Specimen: A – H ZST4.

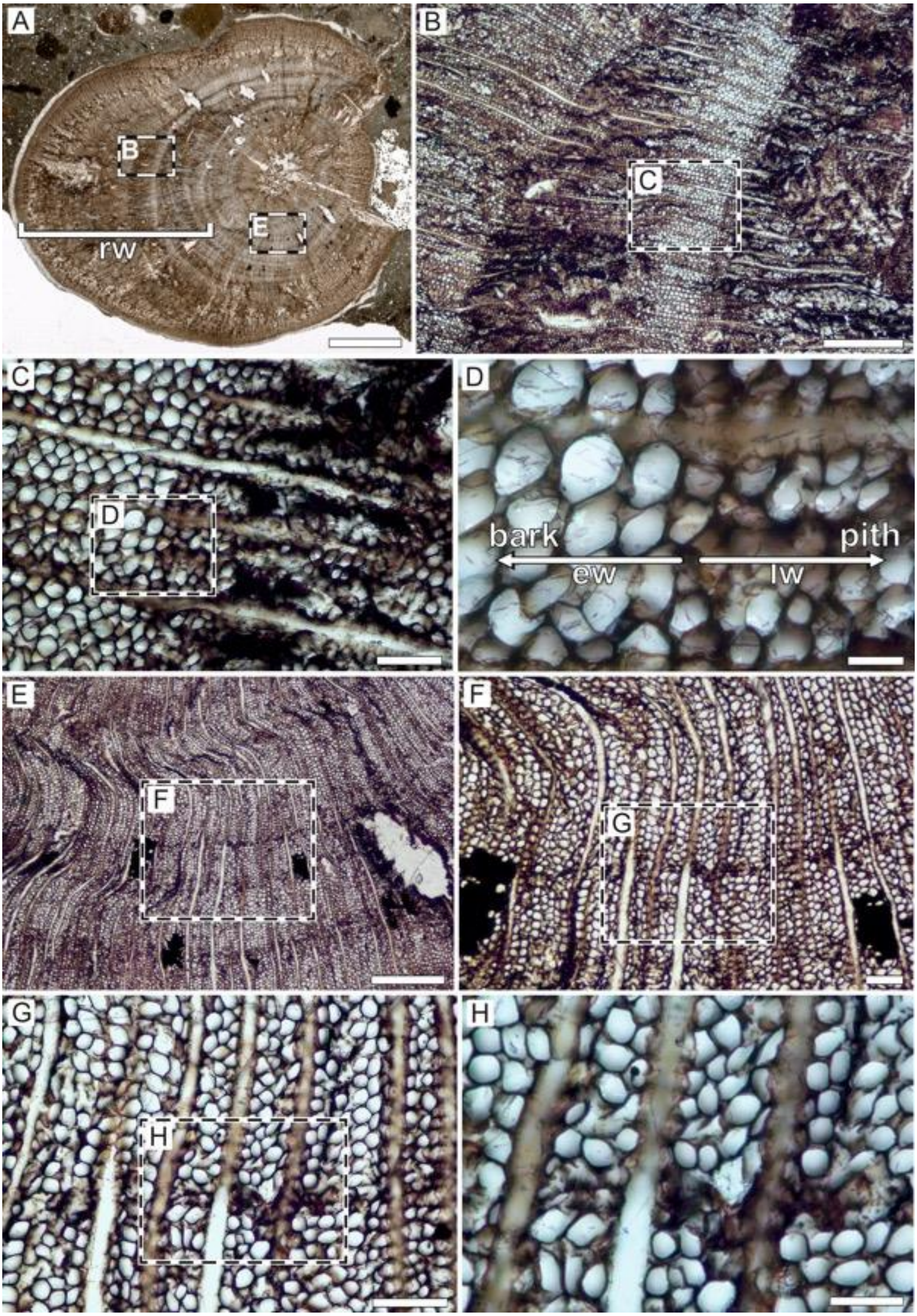
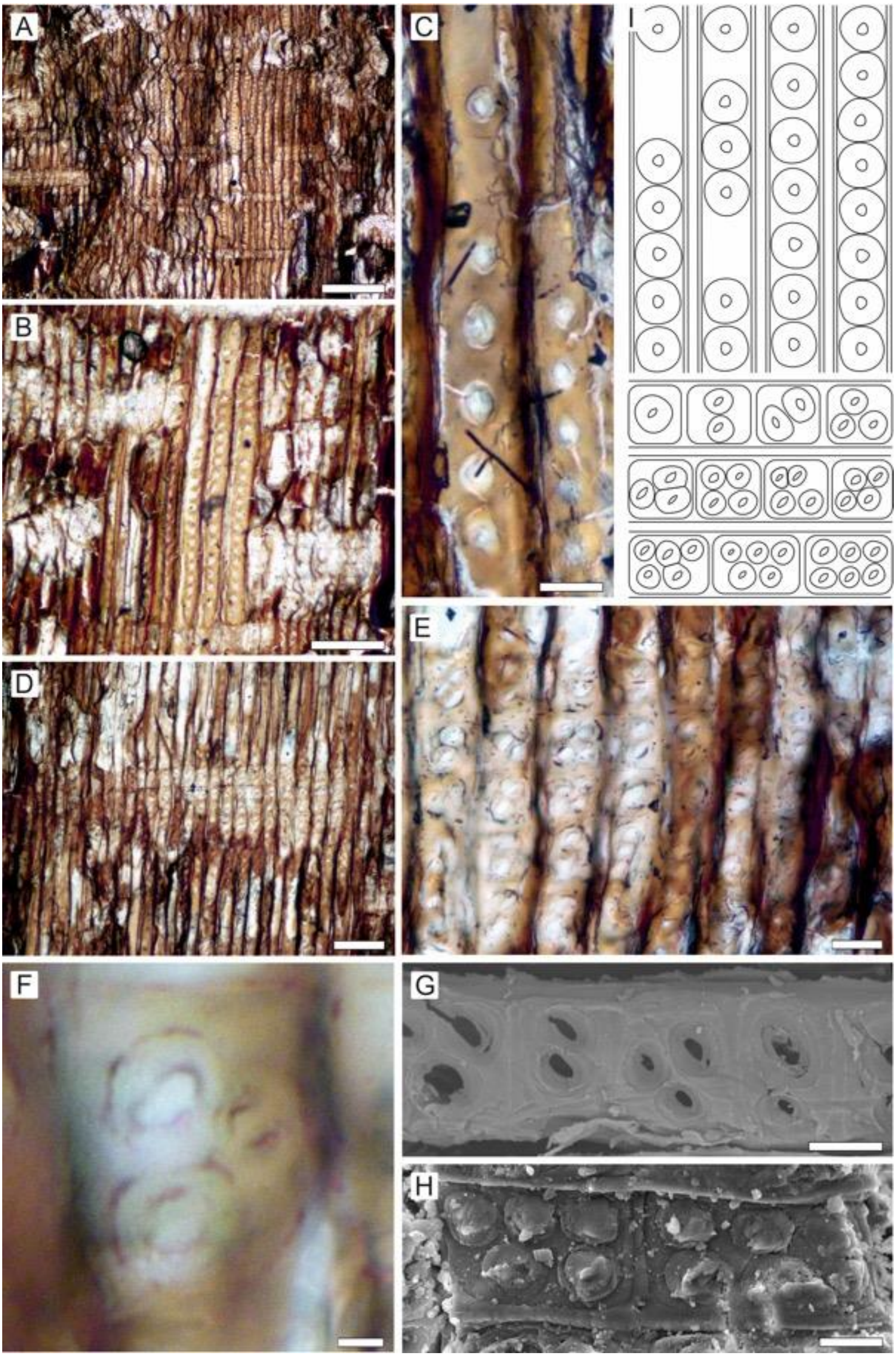

A
B
E
rw
B
C
C
D
D
bark
pith
ew
lw
E
F
F
G
G
H
H

Plate 10

Agathoxylon cf. *keuperianum* (Unger) Philippe stem from the Upper Triassic of the Zawiercie-Marciszów, south Poland.

A – C. Tracheids in radial section showing uniseriate pitting.
B. Tracheid radial pitting, uniseriate, araucarian, pits adjacent or separated by small distances.
C – F. Cross-fields in radial view.
G, H. SEM of araucaroid cross-fields with one to six circular pits, cupressoid oculipores.
I. A schematic drawing of radial pitting and cross fields variety.

Scale bar: A, B 100 µm; C – E 25 µm; F 50 µm; G, H 10 µm.
Specimen: A – I ZST4.


A
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D
E
F
G
H

Plate 11

Agathoxylon cf. *keuperianum* (Unger) Philippe stem from the Upper Triassic of the Zawiercie-Marciszów, south Poland.

A, C, E. Details of the pith in radial section.
B, D, F. Details of the pith in cross section.
G – I. Spherical structures in pith tissues.

Abbreviations: p – pith, o – operculum, s – spherical structures.
Scale bar: A, B 10 mm; G – I 25 µm.
Specimen: A – I ZST4.

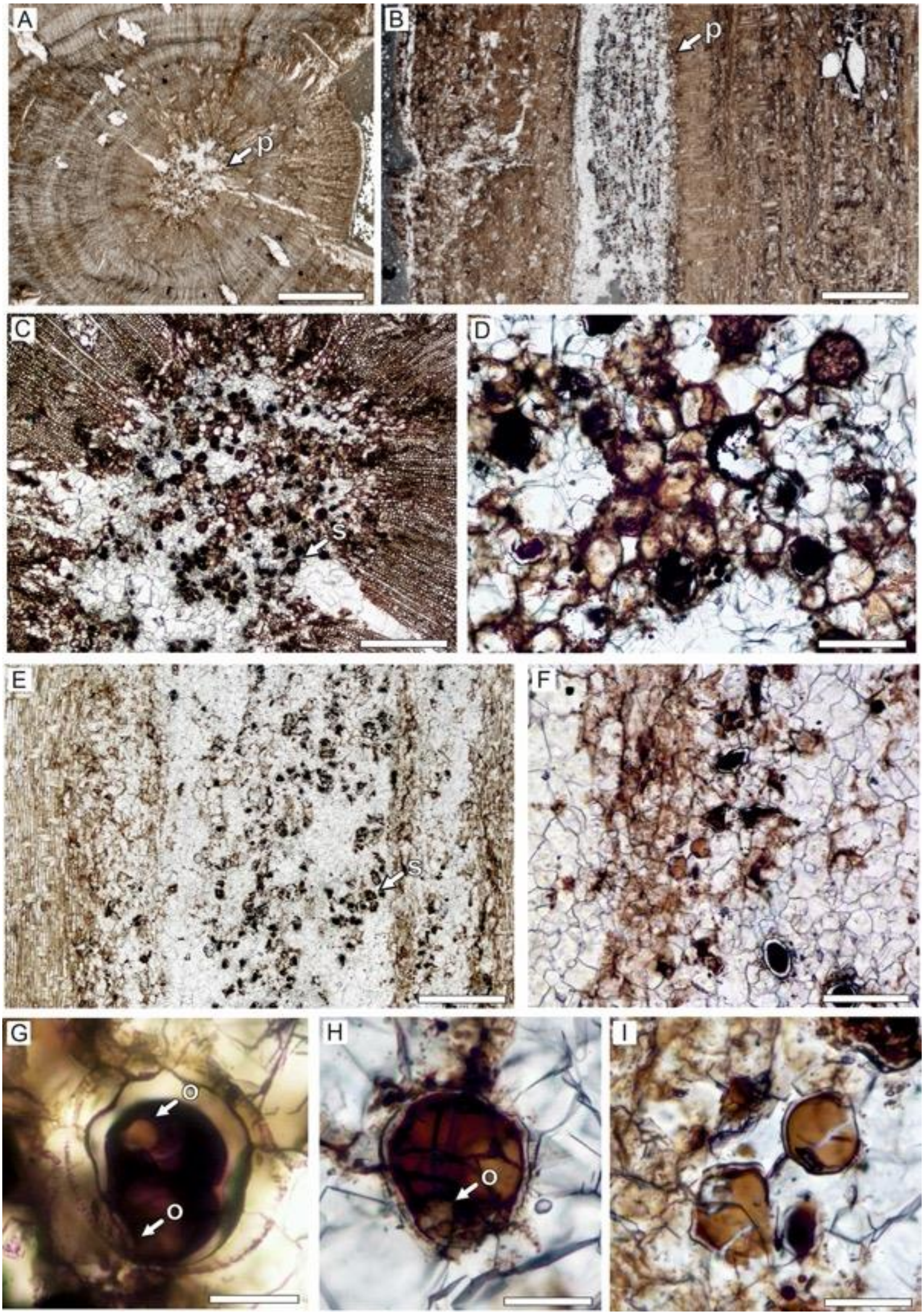
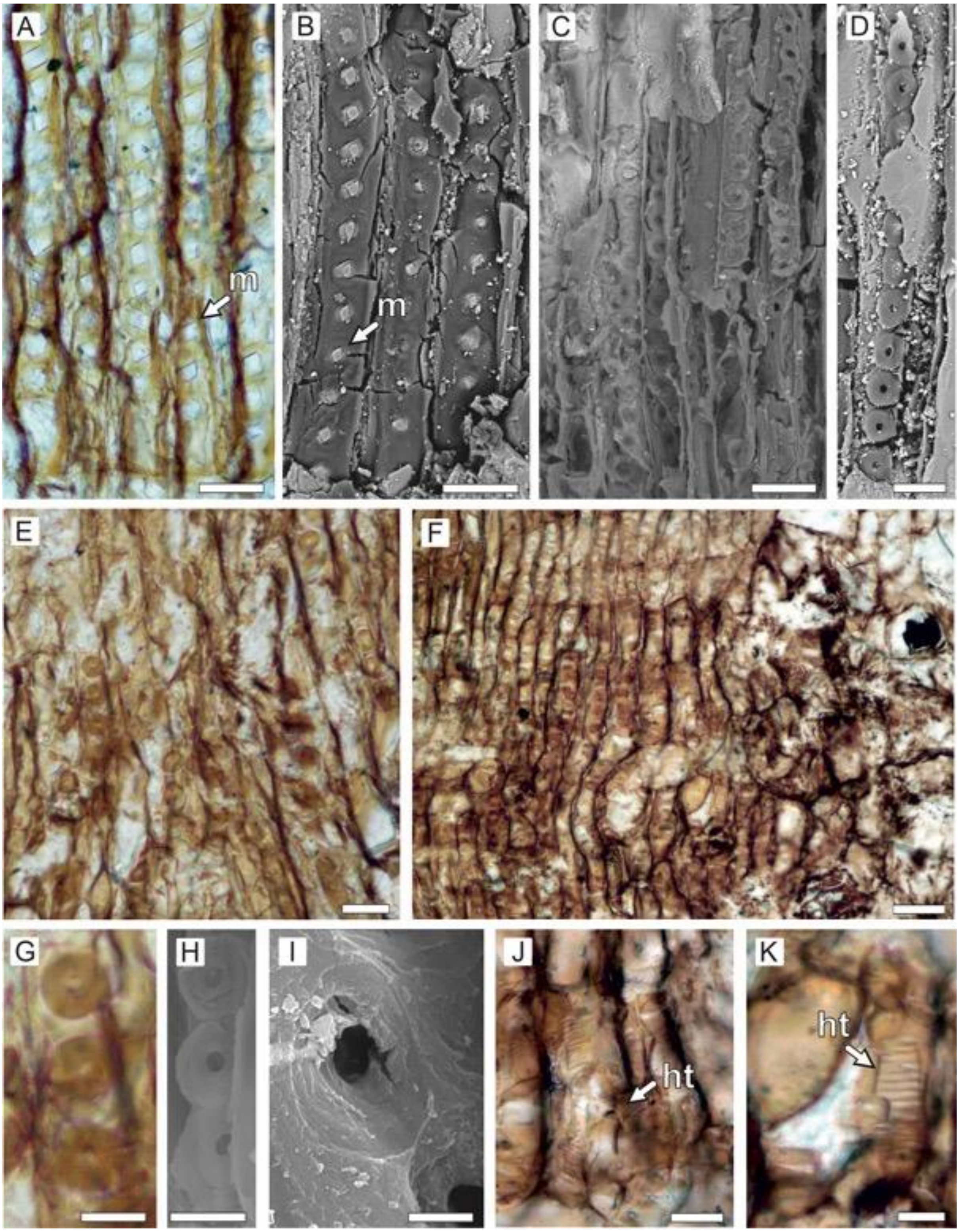

A
p
B
p
C
s
D
E
s
F
G
o
o
H
o
I

Plate 12

Agathoxylon cf. *keuperianum* (Unger) Philippe stem from the Upper Triassic of the Zawiercie-Marciszów, south Poland.

Details of tracheids preservation in radial view.
A. Tracheids with pit pores deformed by crystalising minerals in transmitted light.
B. Tracheids with pit pores deformed by crystalising minerals in SEM.
C, D. Tracheids in radial section showing uniseriate pitting.
E, F. Tracheid deformations in radial section.
G. Bordered pit deformations in transmitted light.
H. Bordered pit deformations in SEM.
I. Magnification of bordered pit in SEM.
J, K. Helical thickenings on the tracheids walls.

Abbreviations: ht – helical thickenings, m – mineralisation.
Scale bar: A – H, J, K 25 µm; I 10 µm.
Specimen: A – K ZST4.


A
m
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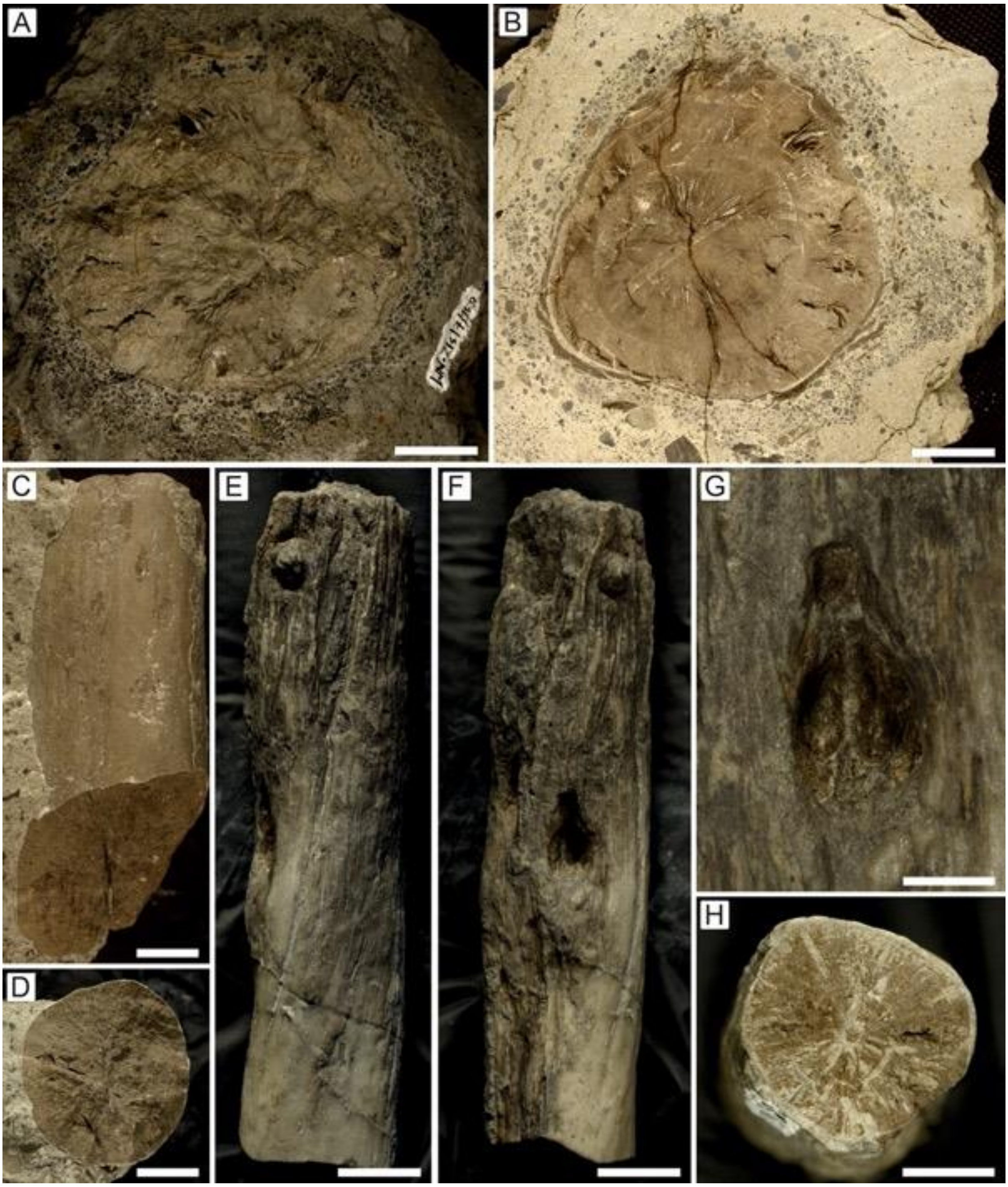
H
I
J
ht
K
ht

Plate 13

Incerte sedis Gymnospermae Stem A from the Upper Triassic of the Zawiercie-Marciszów, south Poland.

Permineralized, three-dimensionally preserved stems.
A, B. Transversal view of the stem preserved in calcareous mudstone; A – naturally preserved surface, B – polished surface.
C. Permineralized stem with smooth surface.
D. Transversal view of the specimen from C.
E, F. Permineralized stem.
G. Details of branch scar from specimen in E.
H. Transversal view of the specimen from E.

Scale bar: A – D 20 mm; E, F, H 10 mm; G 5 mm.
Specimen: A, B WNoZ/S/7/159; C, D ZST5; E – H WNoZ/S/7/193.


A
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E
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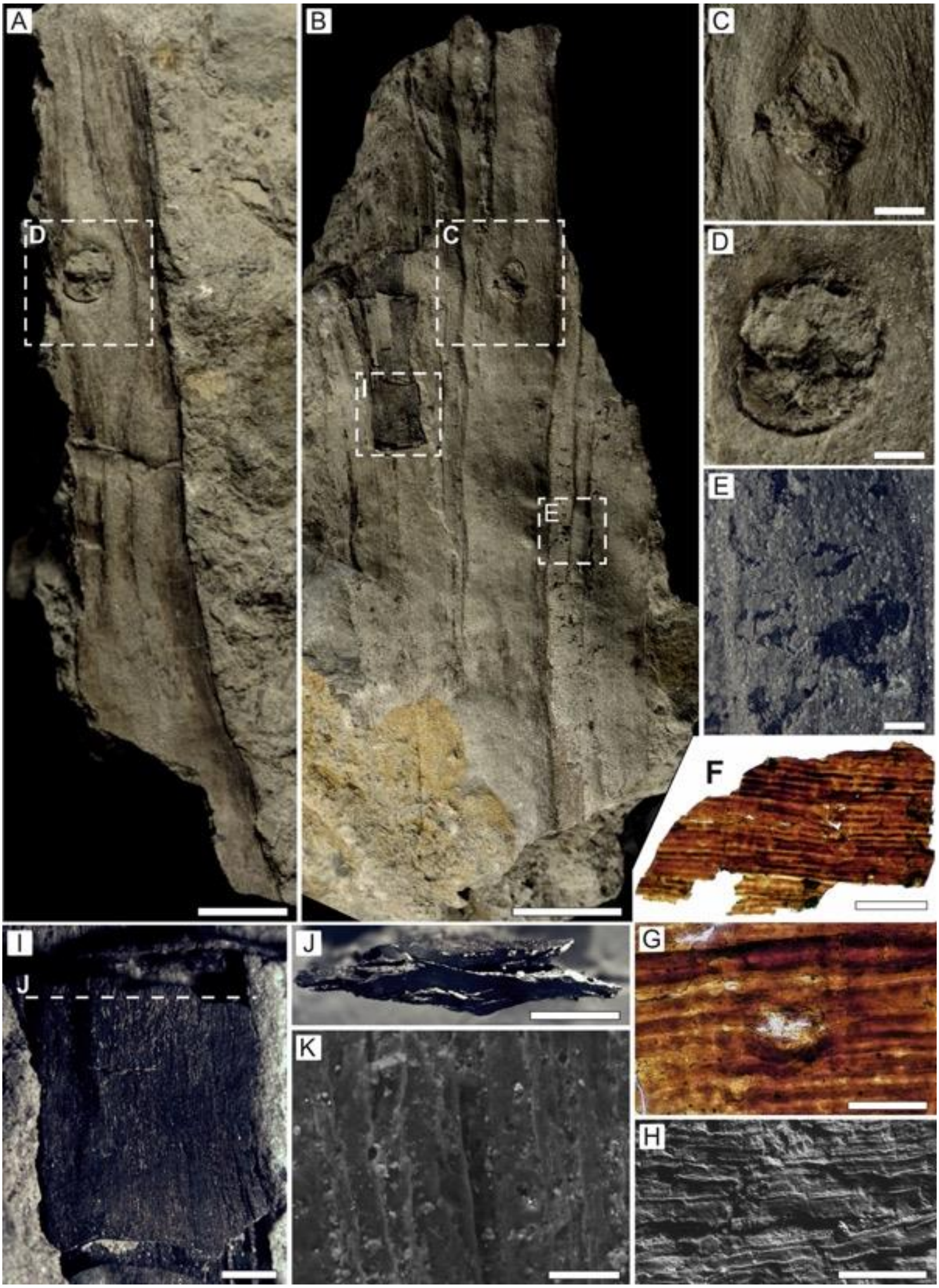
G
H

Plate 14

Incerte sedis Gymnospermae Stem B from the Upper Triassic of the Zawiercie-Marciszów, south Poland.

A. Negative impression of a stem with probable nodal region and branch scar.
B. Positive impression of a stem with preserved charcoalified tissue fragments and patches of cuticle, with branch scar.
C. Magnified branch scars from specimen in B.
D. Magnified branch scars from specimen in A.
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 charcoalified tissue from stem in B.
J. Transverse section of charcoalified fragment on I showing completely homogenized structure.
K. SEM photo of a charcoalified fragment from stem in B.

Scale bar: A – B 10 mm; C – D 2 mm; E, H – J 1 mm; F 100 µm; G 50 µm; K 50 µm.
Specimen: A – K Z21.


A
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C
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E
C
D
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F
I
J
J
K
G
H

Plate 15

Isolated rooting system from the Upper Triassic of the Zawiercie-Marciszów, south Poland.

A – E. An isolated fragment of Root A.
- 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.
- 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 bar: A, F, G, H, J 10 mm; B, C 500 μm; D 3 mm; E, I, K 1 mm.

Specimen: A – E ZR1; F – K ZR2.

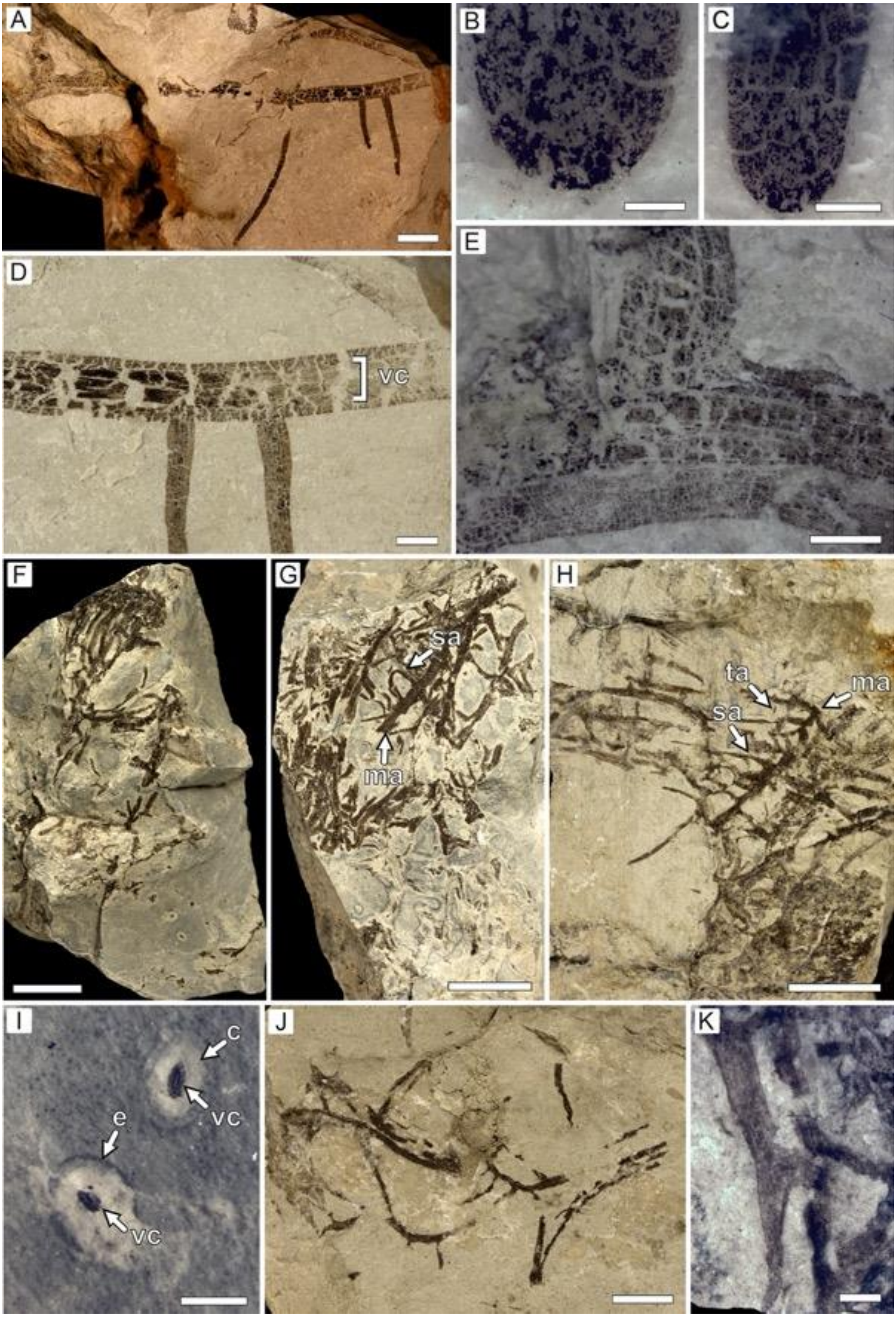

A
B
C
D
vc
E
F
G
sa
ma
H
ta
ma
sa
I
c
vc
e
vc
J
K

Plate 16

Cuticulae dispersae type A from the Upper Triassic of the Zawiercie-Marciszów, south Poland.

A. Cuticle fragment showing upper and lower cuticle and smooth margin; visible are rows of stomata evenly distributed.

B. Incomplete cuticle of a leaf tip.

C. Details of cuticle in A; epidermal cells differ in size and shape, from isodiametric to polygonal and elongated.

D. SEM photo of outer cuticle surface.

E – F. Details of stomata complex; stomata pore surrounded with subsidiary cells equipped with papillae.

F – H. SEM photo of inner cuticle surface.

Abbreviation: p – papillae.

Scale bar: A – B 10 mm; C – D 100 µm; E – H 50 µm.

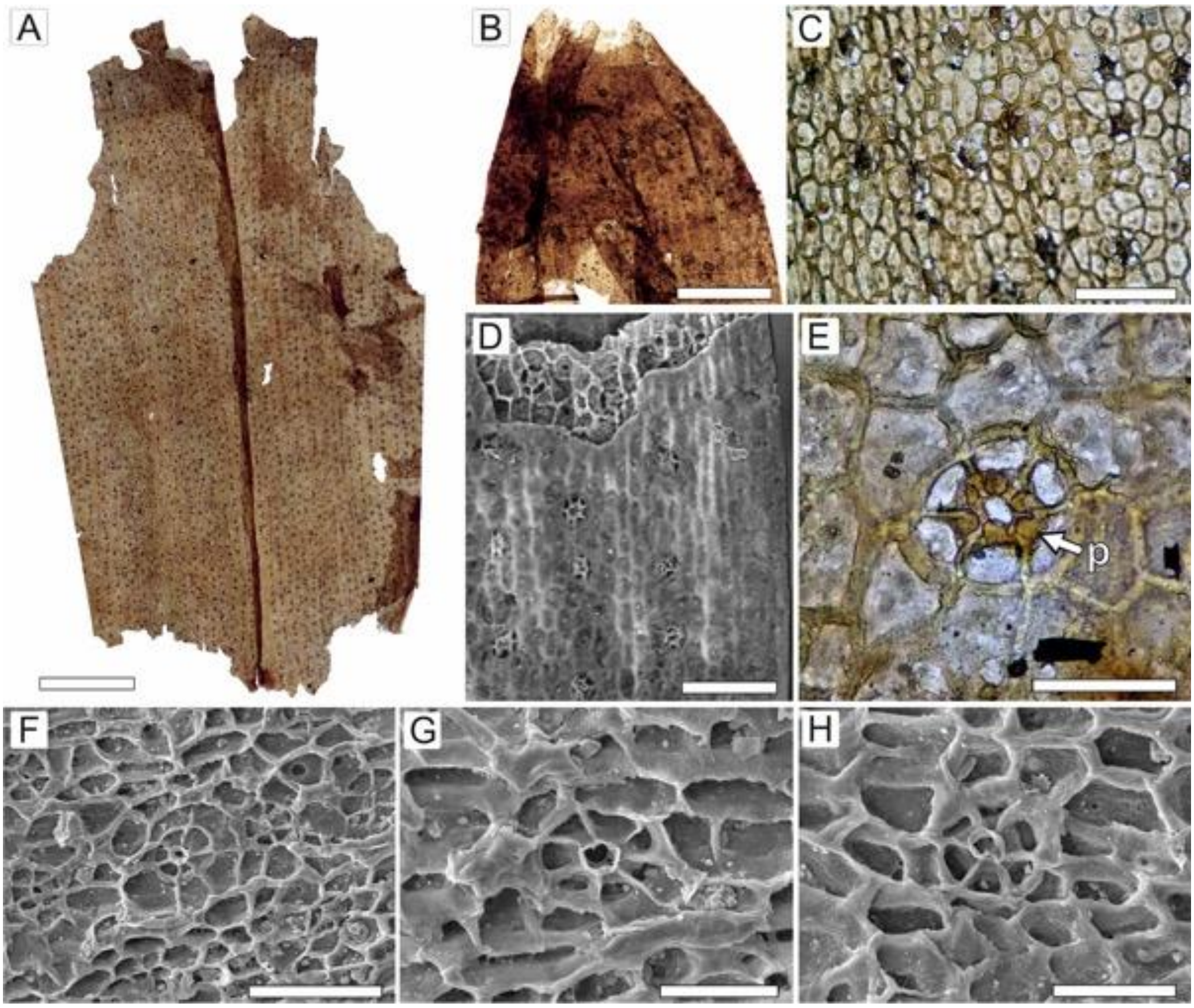

A
B
C
D
E
p
F
G
H

Plate 17

Cuticulae dispersae type B from the Upper Triassic of the Zawiercie-Marciszów, south Poland.

A, B. Cuticles of elongated linear leaves with rounded tips, transmitted light.

C. Leaf from B in SEM photo showing a smooth margin and surface covered with papillae.

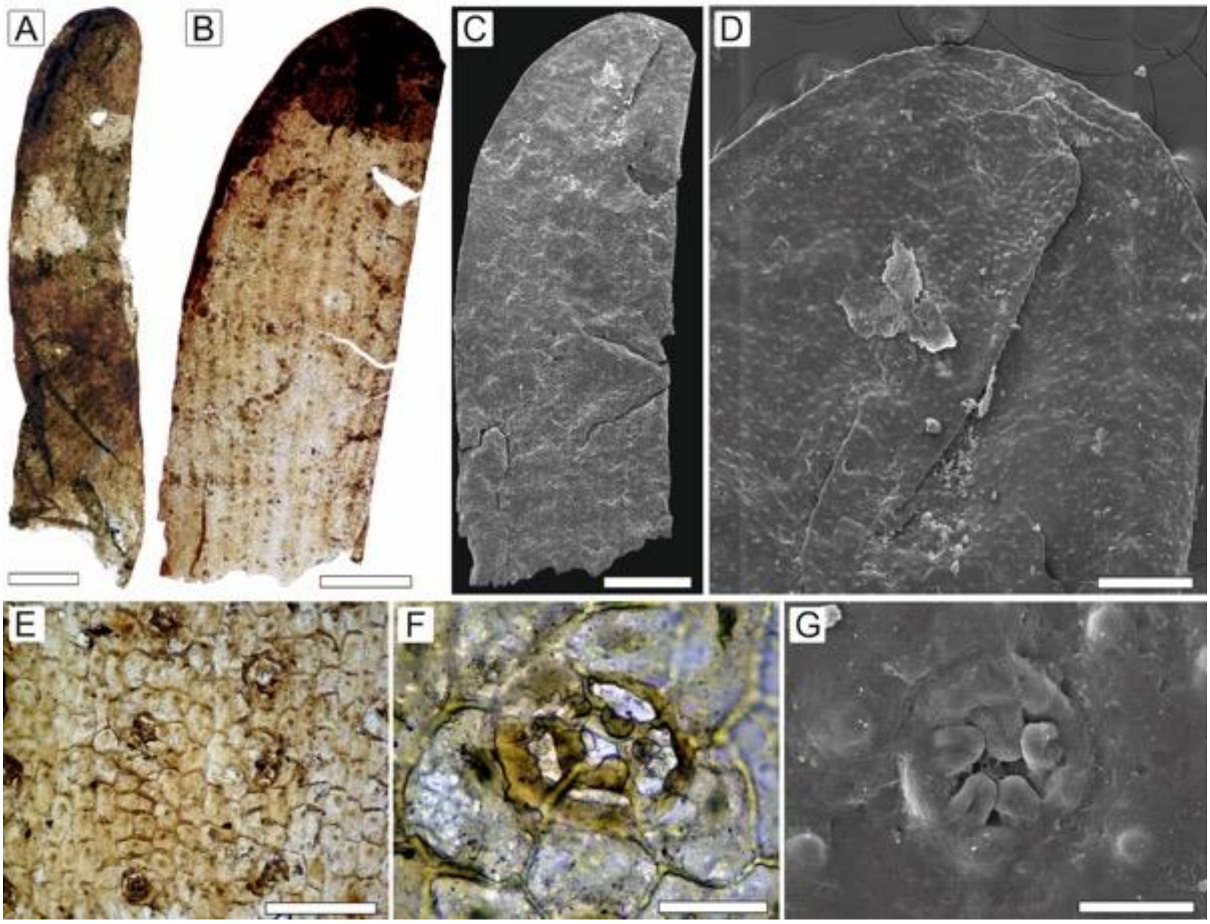
D. SEM photo of a leaf tip of C, papillae are covering entire leaf surface including the tip, stomata are present a the whole length of a leaf.

E. Magnification of stomata rows.

F. Details of stomata complex, outer anticlinal walls showing thickening, transmitted light.

G. SEM photo of stomata complex showing prominent papillae overarching the stomata aperture.

Scale bar: A – C 1 mm; D 200 μm; E 100 μm; F – G 20 μm.


A
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G

Plate 18

Cuticulae dispersae type C from the Upper Triassic of the Zawiercie-Marciszów, south Poland.

A. Cuticle of a partially preserved leafy twig with elongated leaves.

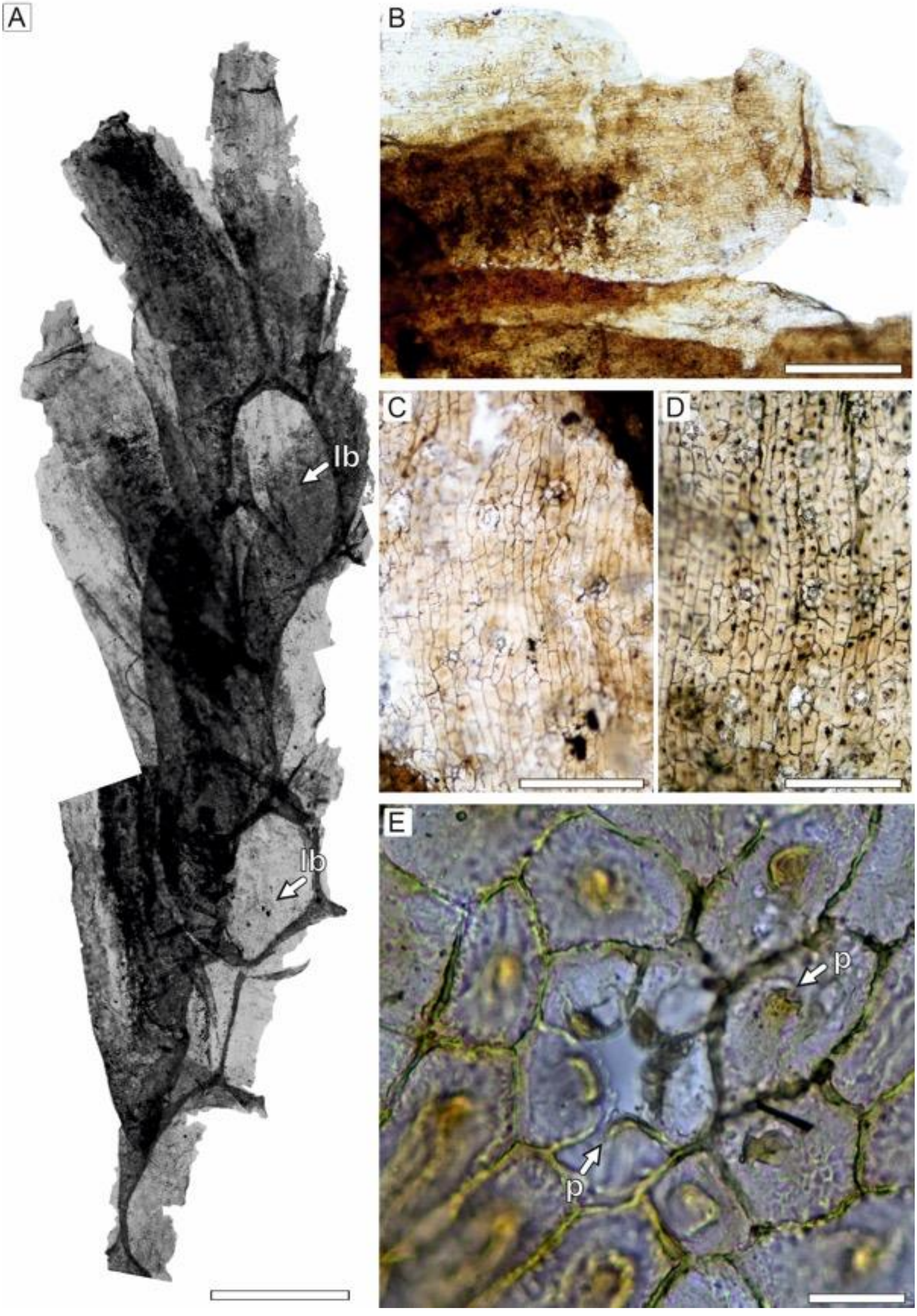
B, C. Cuticle fragments from upper part of the stem showing more elongated cells without papillae.

D. Fragment of cuticle from lower leaves with epidermal cells and stomata subsidiary cells equipped with papillae.

E. Details of stomata from lower part of the stem.

Abbreviations: lb – leaf base, p – papilla.

Scale bar: A 1 mm; B 500 µm; C – D 200 µm; E 20 µm.


A
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C
D
E
lb
lb
p
p

Plate 19

Cuticulae dispersae type D from the Upper Triassic of the Zawiercie-Marciszów, south Poland.

A, B. Elongated leaf with adaxial and abaxial cuticle evenly developed.

C, D. Epidermal cells equipped with papillae;

E – G. Details of stomata complexes.

F, G. SEM photos of stomata complexes.

Abbreviations: p – papilla.

Scale bar: A – B 500 µm; C 100 µm; D – 20 µm; E – G 20 µm.

z

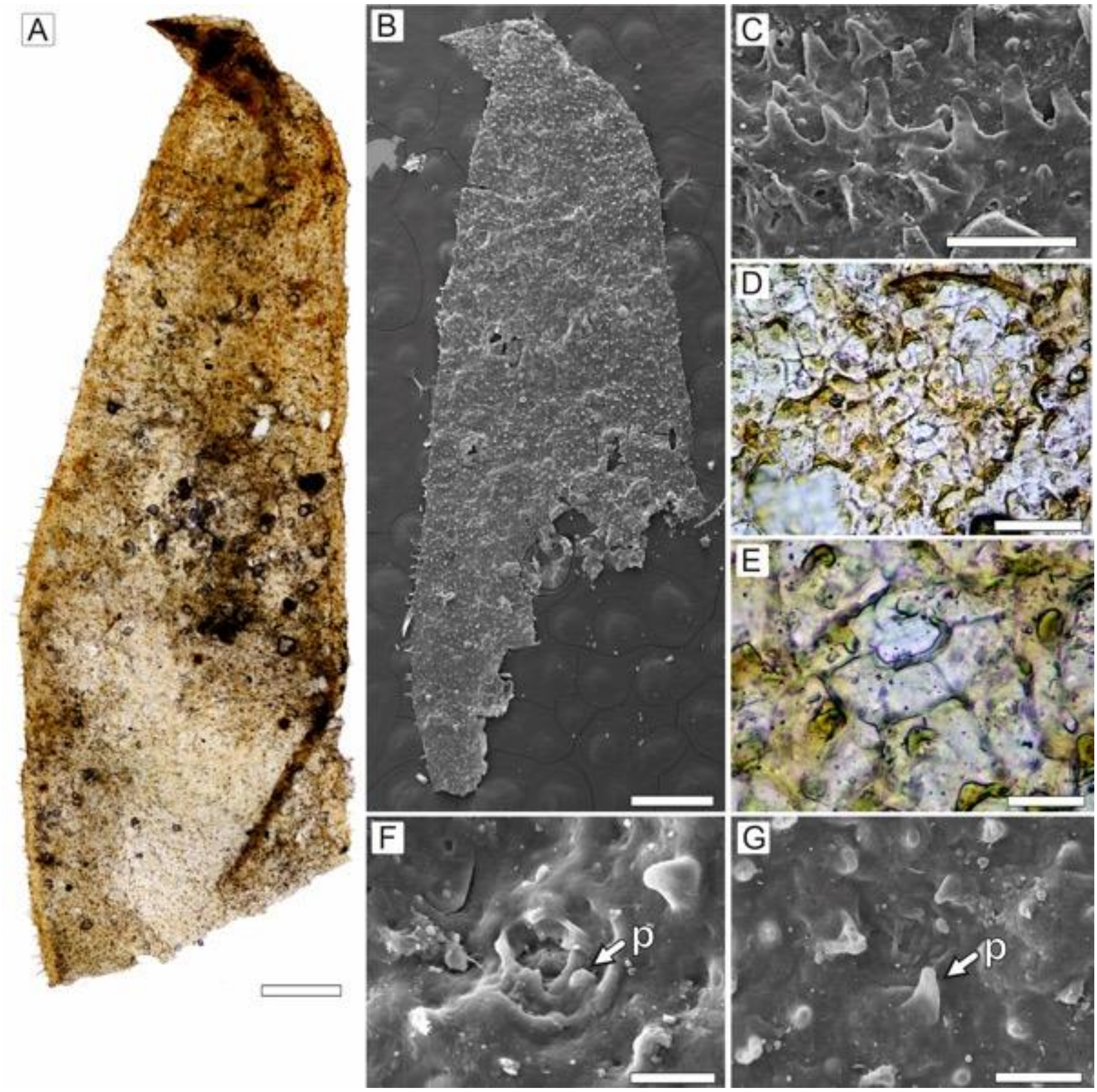


Plate 20

Cuticulae dispersae type E from the Upper Triassic of the Zawiercie-Marciszów, south Poland.

A. Fragment of a twig with helically arranged leaves.

B. Fragment of a twig with helically arranged twigs, leaves are smaller than in specimen in A.

C. SEM photo of a twig from B.

E. SEM photograph of fringed leaf margin.

D, F. Isolated, scale-like leaves of rhomboidal shape.

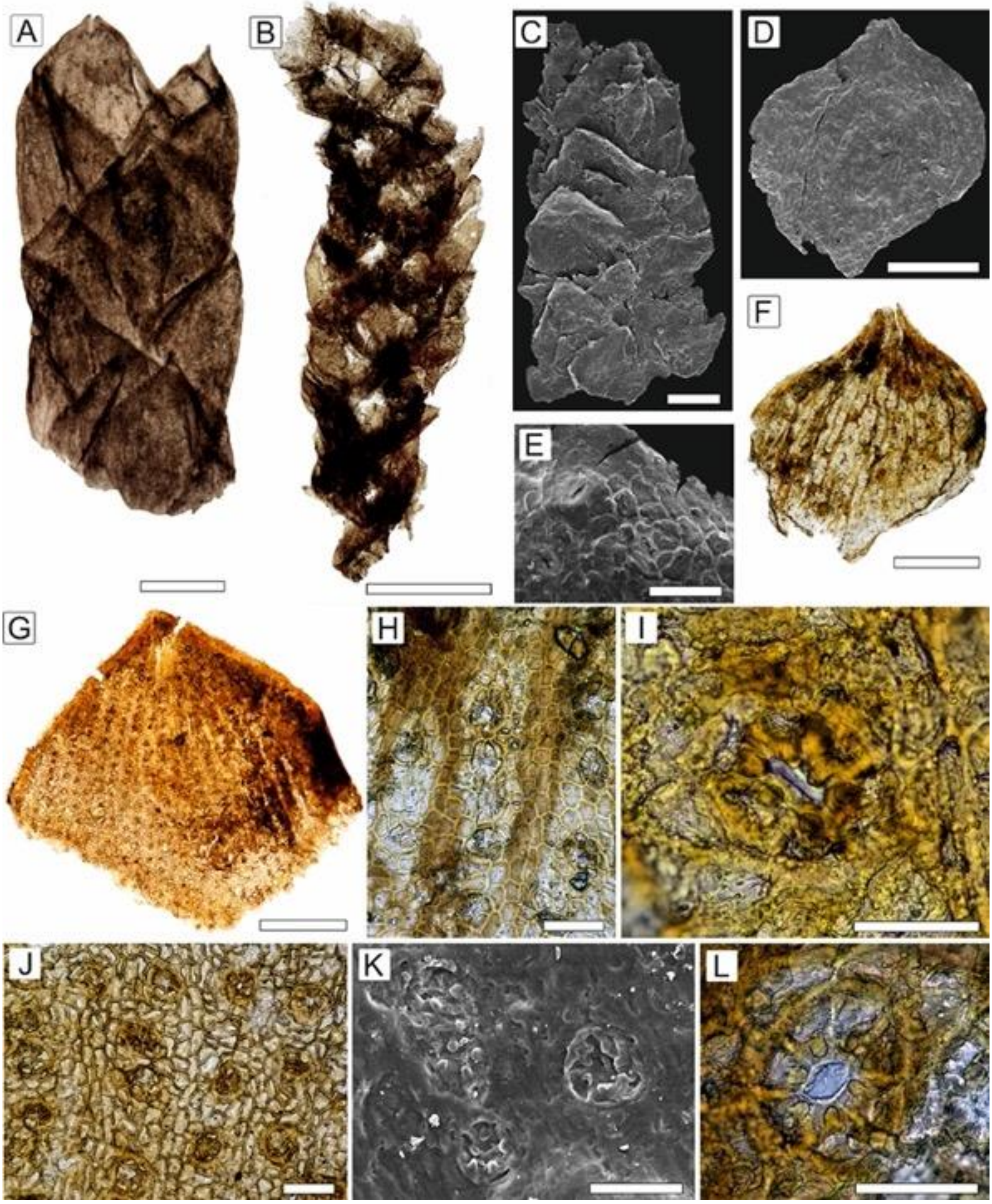
H, J, K. Stomata arrangement on abaxial cuticle.

H. Abaxial cuticle showing an underlying fibrous tissue between stomata rows.

K. SEM photo of stomata complexes on abaxial cuticle, stomata with prominent papillae on subsidiary cells.

I, L. Details of stomata complex with prominent papillae on subsidiary cells, directed towards the stomata pit.

Scale bar: A – D, F – G 10 mm; E, H – L 50 µm.


A
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G
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I
J
K
L

Plate 21

Striatriletes ramosus Marcinkiewicz 1985 from Upper Triassic of Zawiercie-Marciszów, south Poland.

A – H. SEM photographs of proximal side; G – proximal side in reflected light; H – I SEM photographs of distal 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.

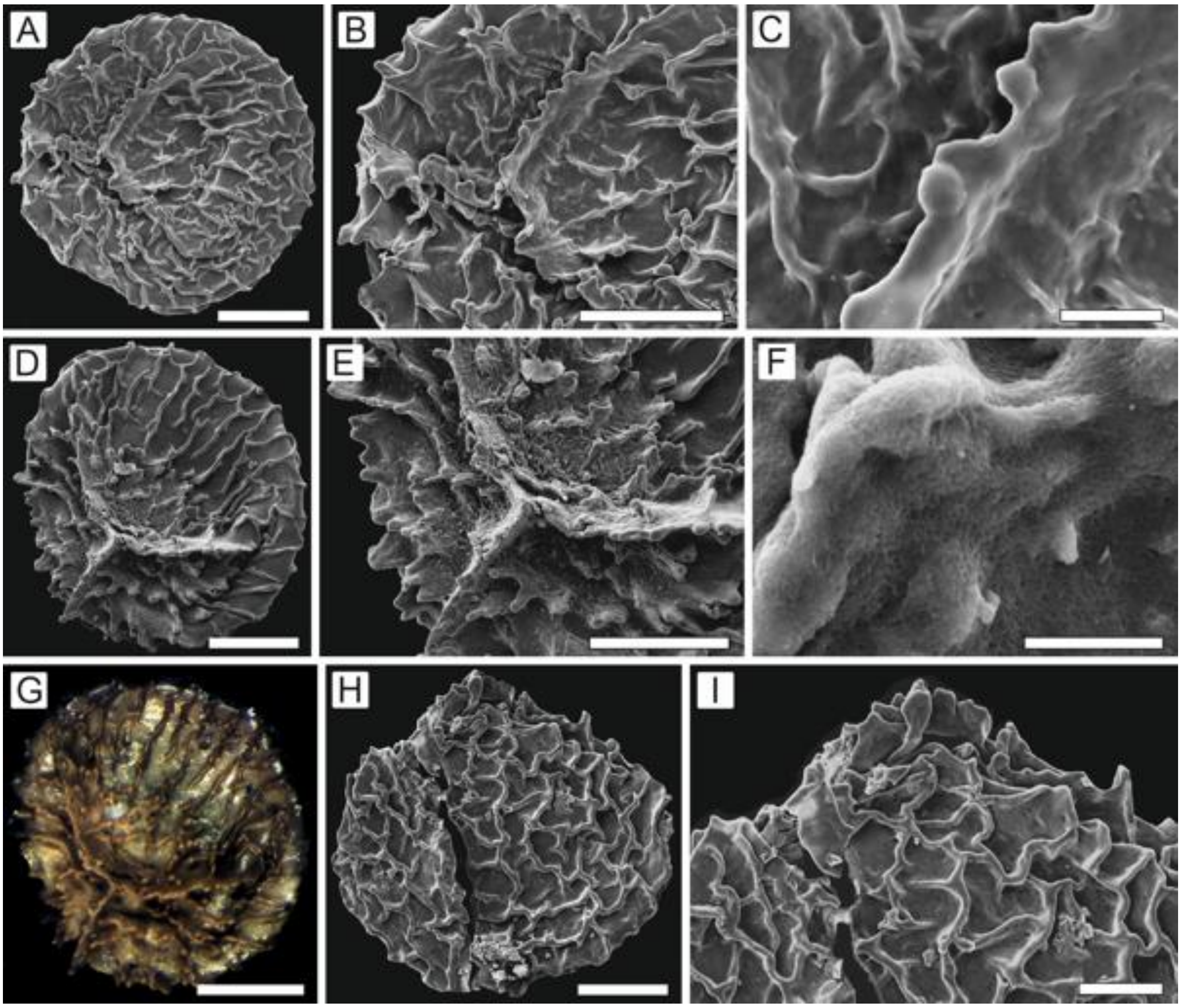
E. Magnification of trilete mark of megaspore in D.

I. Magnification of megaspore in H.

F. Higher magnification of megaspore surface in E showing a fine mesh structure.

Scale bar: A, D, G, H 200 µm; B, E, I 100 µm; C 20 µm; F 10 µm.

Specimen: A – C ZM01; D – I ZM02.


A
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4.2. Lipie Śląskie-Lisowice

Plate 22

Equisetites sp. from the Upper Triassic of the Lipie Śląskie-Lisowice, south Poland.

A. Inner vascular cylinder of compressed stem.

B. Impression of the internode preserved with fragment of scale-leaf conifer twig.

C. Striae on the surface of the ridges.

D. Fragment of a mudstone with accumulation of stems.

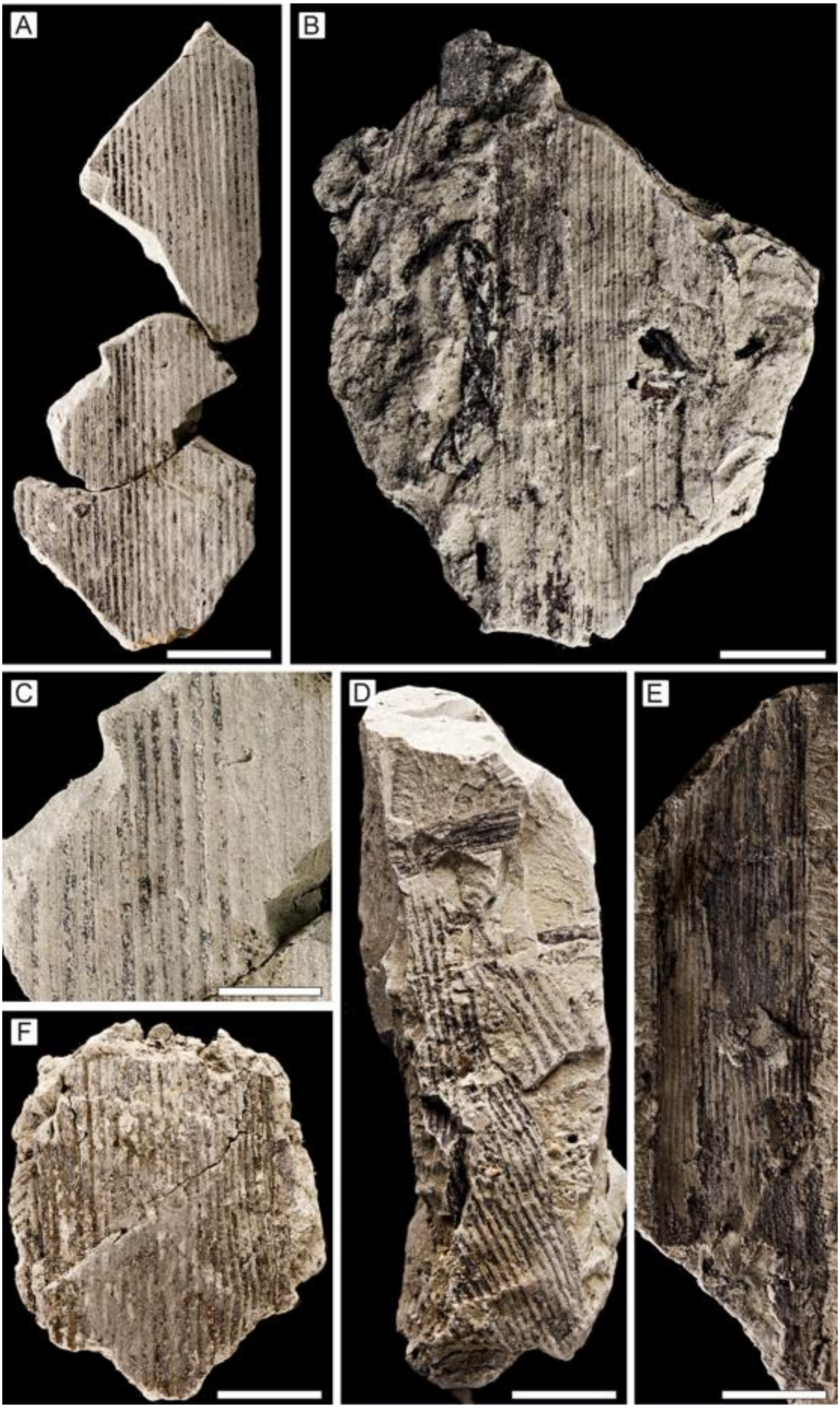
E. Internodal region cover with remnants of coalified tissue.

F. Fragment of the internodal region.

Abbreviations: rg – ridge.

Scale bar: A, B, D – F 1cm; C 5mm.

Specimen: A L/V/3; B L/V/8; C L/V/2; D L/V/6; E L/V/1; F L/V/9.


A
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F

Plate 23

Cf. *Dioonitocarpidium* sp. from the Upper Triassic of the Lipie Śląskie-Lisowice, south Poland.

A. Fragment of sterile part of the megasporophyll.
B. Hispid indumentum covering the main axis.
C. Hispid indumentum covering pinnae blade.
D. Schematic drawing of the specimen in A.
E. Extant female cone of *Cycas revoluta* with ovules. Marked is potential position of fossil megasporophyll.

Abbreviations: a – axis, f – fertile part of megasporophyll, h – hair, o – ovule, p – pinule, s – sterile blade of megasporophyll.
Scale bar: A 1 mm; B, C 200 µm.
Specimen: A – E L/III/62.

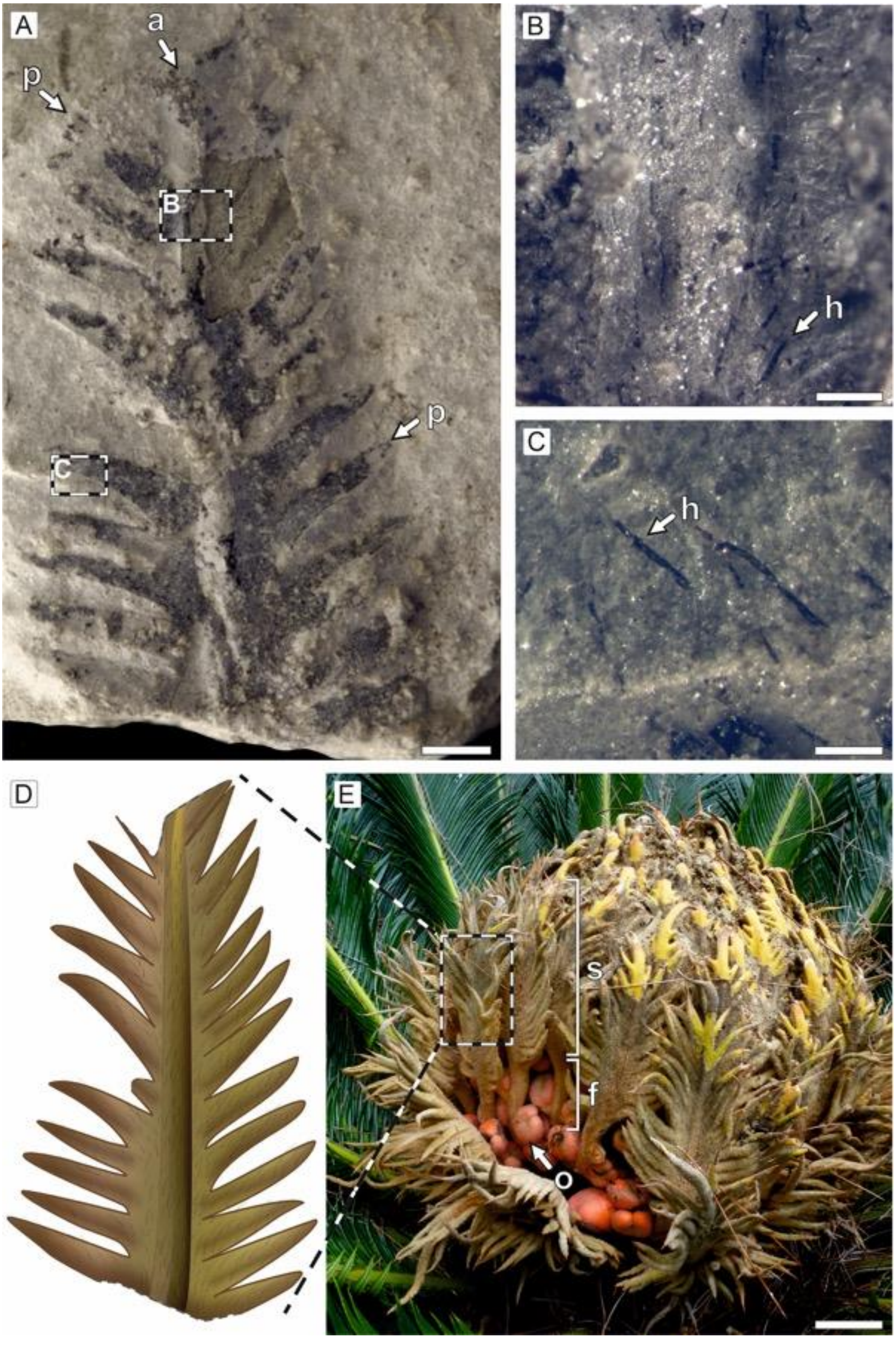

A
a
p
B
p
C
B
h
C
h
D
E
s
f
o

Plate 24

Brachyphyllum sp. from the Upper Triassic of the Lipie Śląskie-Lisowice, south Poland.

A, B. Sterile branch with opposite to sub-opposite lateral shoots.

C, D. Shoots fragments with primary axis and lateral shoots of the same width.

E. Fragment of a shoot with primary axis twice the width of the lateral shoots.

F. Small shoot with tightly appressed leaves.

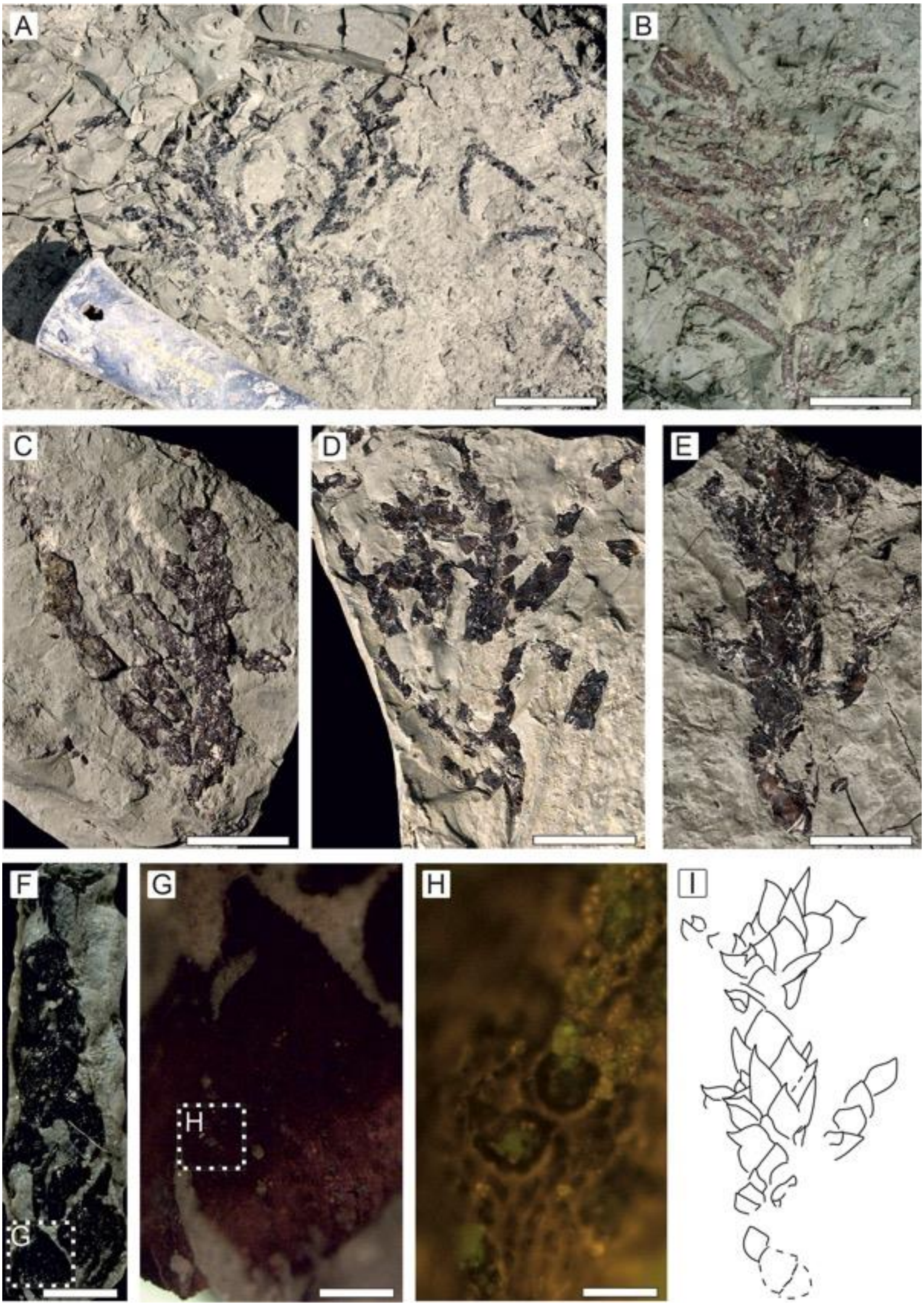
G. Magnification of the leaf from G in fluorescence light.

H. Adjacent stomata on the leaf from G.

I. Outline drawing of leaves arrangement in the shoot from E.

Scale bar: A, B 40 mm; C – E 10 mm; F 2 mm; B, G 200 µm; H 50 µm.

Specimen: A L/XI/3; B L/XI/4; C L/XI/2; D L/XI/1; E L/XI/57; F – G L/XI/97.


A
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G
H

Plate 25

Elatocladus sp. from the Upper Triassic of the Lipie Śląskie-Lisowice, south Poland.

A, B. Shoot fragments with spirally arranged leaves; leaf tip acute.

C. Shoot fragment with spirally arranged leaves.

D. Shoot fragment with leaves showing clear dark central vein area.

E. Cuticle showing papillae at the leaf margin; magnification from D.

F. Shoot with spirally arranged leaves showing clear dark central vein; fragment of C.

G. Details of stomata complexes; magnification from F.

H. Bifurkating shoot fragment.

I. Shoot fragment with clear dark central vein area.

J. Cuticle of a leaf showing stomata in loose rows; overlaping of the leves creates an impression of double venation; magnification from I.

Specimen: A, B L/III/36; C, F, G L/III/65; D, E L/III/60; H L/III/9; I, J L/III/55.

Scale bar: A, B 10 mm; C, F 1 mm; D, H, I 5mm; E 100 µm; G 50 µm; J 200 µm.

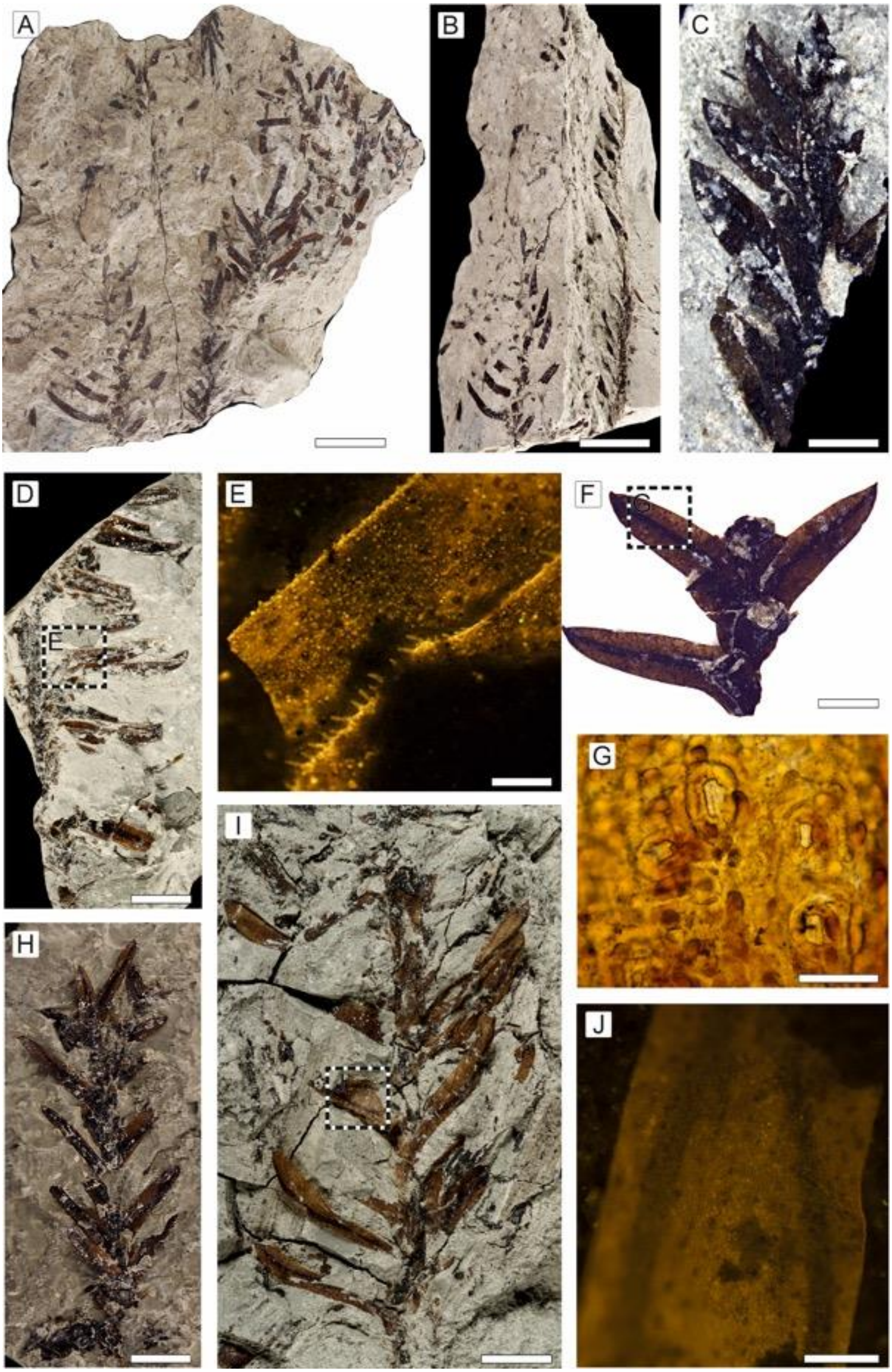
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Plate 26

Carpolithes sp. from the Upper Triassic of the Lipie Śląskie-Lisowice, south Poland.

A – J, P – T, flattened platyspermic seeds.

B – J, P – T, seeds with coalified outer layer.

A. Seed with charcoalified outer layer.

K. Specimen from J after after treating with Schulze reagent.

L. Specimen from H after treating with Schulze reagent.

M. Probable outer integument from specimen in K.

N. Probable outer integument from specimen in G after treating with Schulze reagent.

O. Probable outer integument from specimen in L;.

Abbreviations: ap – attachment point.

Scale bar: A – L, P – T 2 mm; M – O .

Specimen: A L/I/5; B L/I/7; C L/I/2; D L/I/1; E L/I/4; F L/I/16; G, N L/I/14; H, L, O L/I/13; J, K, M L/I/15; I. L/I/10; P L/I/9; R L/I/11; S L/I/8; T L/I/6.

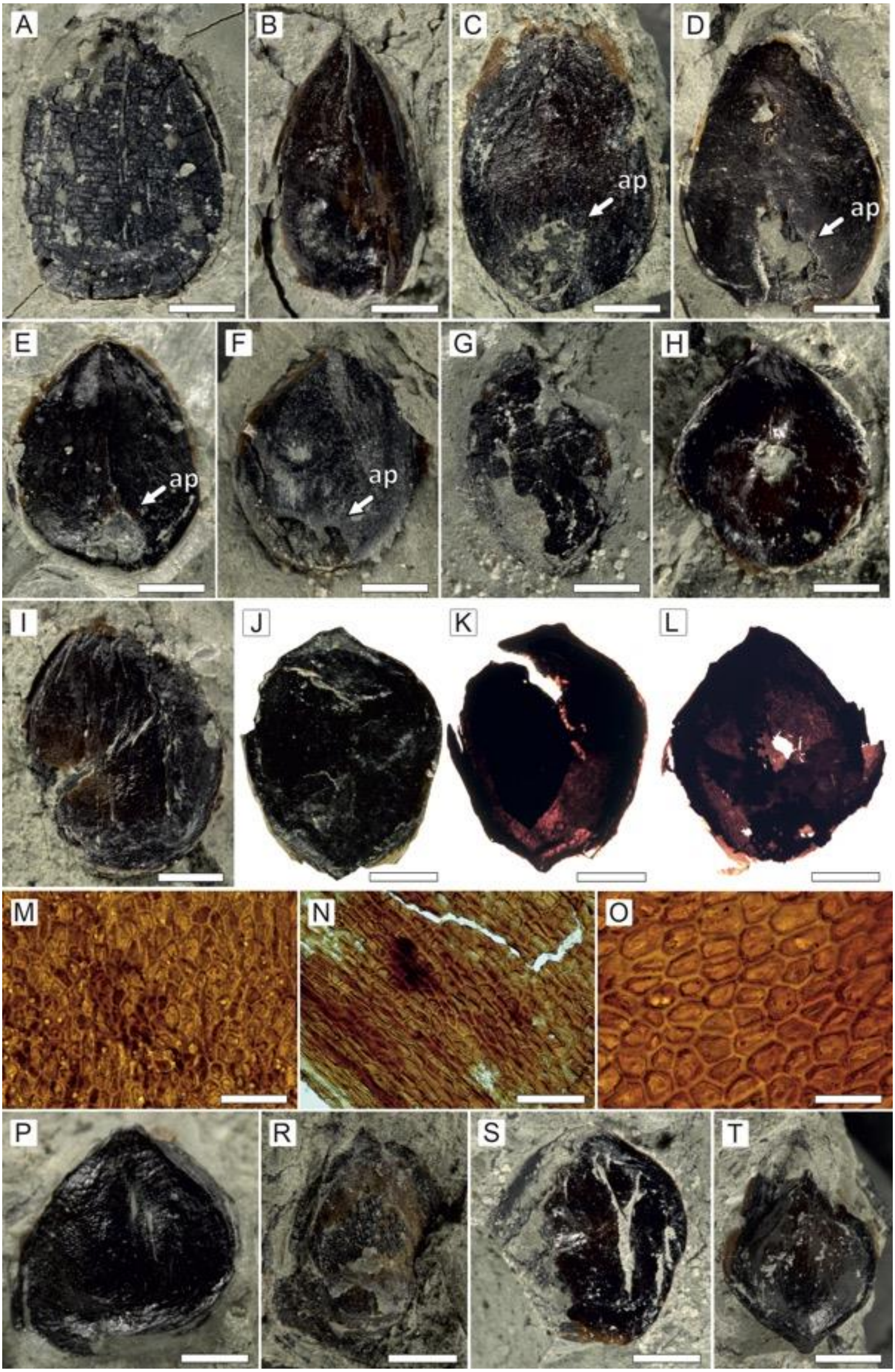
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Plate 27

Carpolithes sp. from the Upper Triassic of the Lipie Śląskie-Lisowice, south Poland.

A, B. Seed preserved three-dimensionally, attachment point in the center of the chalazal point.

C, D. Magnification of the surface of the specimen from A, cells outline visible in UV light, probably outer integument.

E, F. SEM observations of specimen from A, faint outline of cells visible on the surface, probably outer integument.

G. Specimen with preserved megaspore inside, remnants of the outer integument still present.

H. Megaspore from G after treating with Schulze reagent.

I. Micropylar peak of the megaspore from G, faint outline of nucellus cells visible.

J. Megaspore membrane reticulate structure.

K. Miospores trapped in the megaspore sac.

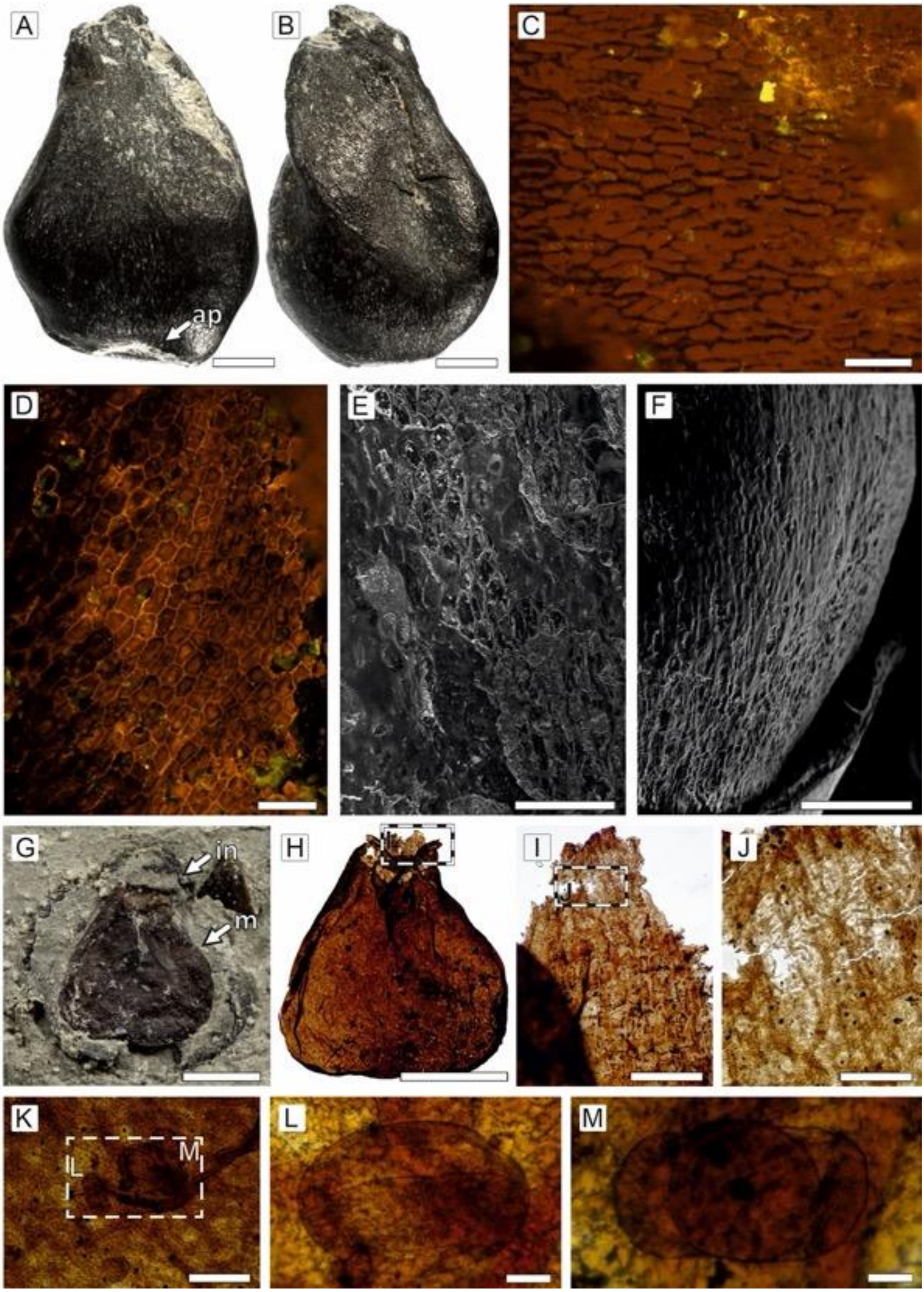
L. Miospore resembling conifer pollen *Ovalipollis ovalis* Krutzsch 1955.

M. Bisaccate pollen resembling *Tradispora* genus.

Abbreviations: ap – attachment point, in – integument, m – megaspore.

Scale bar: A, B, G, H 2 mm, D, E 200 µm, F 500 µm, I 100 µm, J, K 50 µm, L, M 10 µm.

Specimen: A – F L/I/17; G – M L/I/12.


A
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L
M

Plate 28

Cuticles macerated from coprolites from the Upper Triassic of the Lipie Śląskie, south Poland.

A – C. Cuticle type A.
  A. Almost complete leaf cuticle.
  B. Epidermal cells with papillae closer to the acroscopic side, cells in longitudinal rows with irregularly spaced stomata.
  C. Detail of stomata complex with strongly cutinised subsidiary cells.
D – F. Cuticle type B.
  D. Leaf cuticle without leaf base preserved.
  E. Lower cuticle showing longitudinal arrangement of epidermal cells and stomata.
  F. Stomatal complex with visible sunken guard cells surrounded by papillate subsidiary cells.
G – I. Cuticle type C.
  G. Cuticle with loose rows of cells. Stomatal complexes arranged in rows.
  H. Details of arrangement of epidermal cells and stomata complexes.
  I. Neighboring stomata with papillate subsidiary cells.
J – L. Cuticle type D.
  J. Lower and upper cuticle; fragmentary leaf margin.
  K. Stomata arranged in loose, discontinuous rows.
  L. Details of epidermal cells and stomata.
M – O. Cuticle type E.
  M. Upper and lower cuticle of the elongated leaf.
  N. Arrangement of epidermal cells and stomata.
  O. Stomatal complex with thickly cutinised subsidiary cells.

Scale bar: A, D, G, J, M 500 µm, B, E, H, K, N 100 µm, C, F, I, L, O 25 µm.

Specimen: A Cop2/17; B, C Cop1/08; D Cop1/03; E, F Cop1/02; G, H Cop1/18; I Cop 1/07; J – L Cop1/22; M Cop1/64; N, O 3/34.

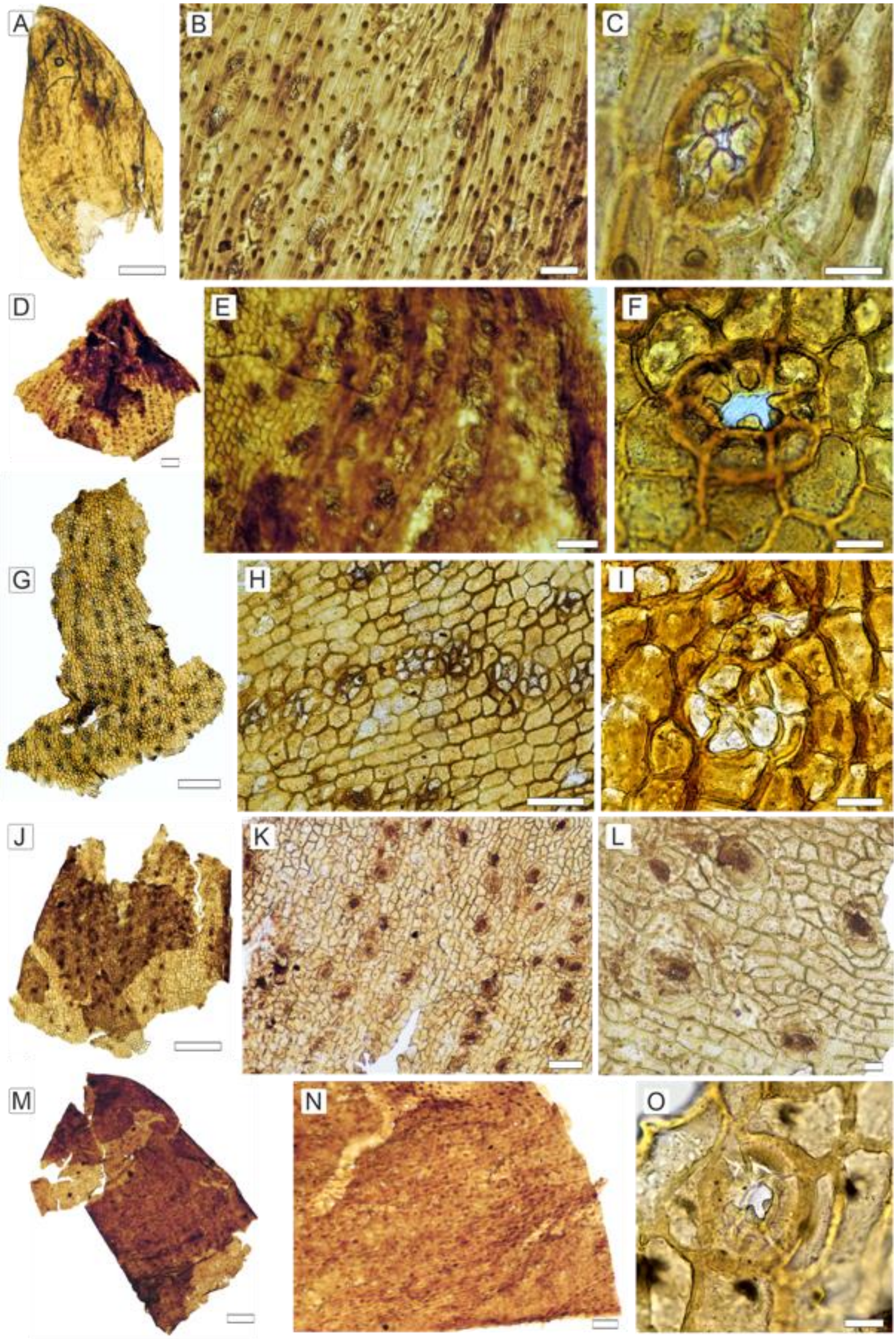
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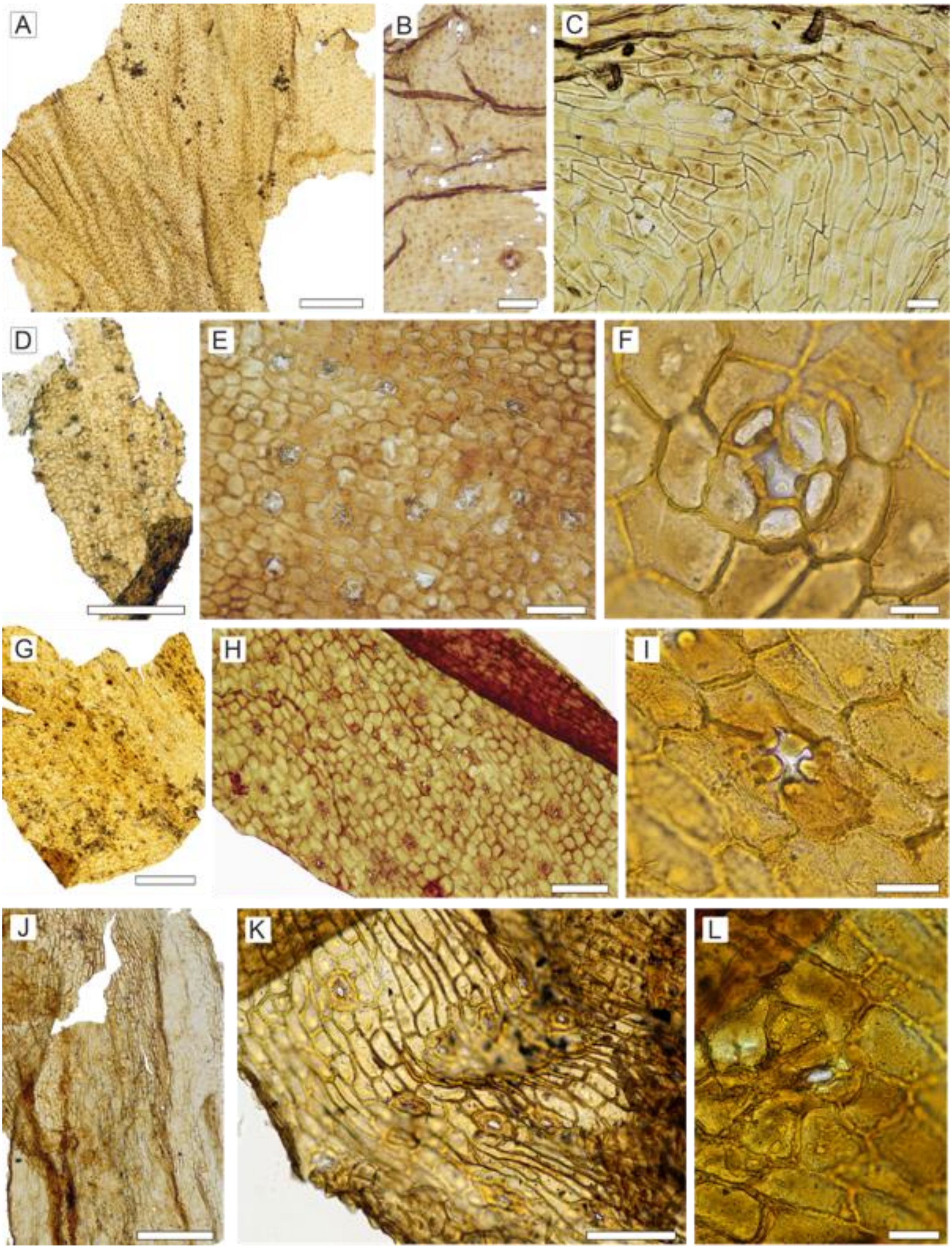
Plate 29

Cuticles macerated from coprolites from the Upper Triassic of the Lipie Śląskie south Poland.

A – C. Cuticle type F.
  A. Fragment with preserved epidermal cells divided into costal and intercostal zones.
  B. Short epidermal cell bearing a solid papilla.
  C. Anticlinal walls of epidermal cell with a shallow undulation.
D – F. Cuticle type G.
  D. Cuticle with polygonal to rectangular cell arranged in loose rows.
  E. Epidermal cells with hollow papillae located in the central part of a periclinal cell wall.
  F. Stomatal complex with strongly cutinised subsidiary cells anticlinal walls.
G – I. Cuticle type H.
  G. Cuticle with cells arranged in longitudinal rows.
  H. Stomata and epidermal cells arrangement; masses of resin visible between cells.
  I. Stomatal complex with developed flat papillae.
J – L. Cuticle type I.
  J. General layout of cells arrangement.
  K. Details of stomata.
  L. Ornamentation of cell walls and details of stomata.

Scale bar: A, D, G, J, M 500 µm, B, E, H, K, N 100 µm, C, F, I, L, O 25 µm.

Specimen: A Cop2/06; B Cop1/68; C Cop2/05; D Cop3/09; E, F Cop3/32; G, I Cop2/07; H Cop3/36; J, K Cop3/15; L Cop1/39.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J
K
L

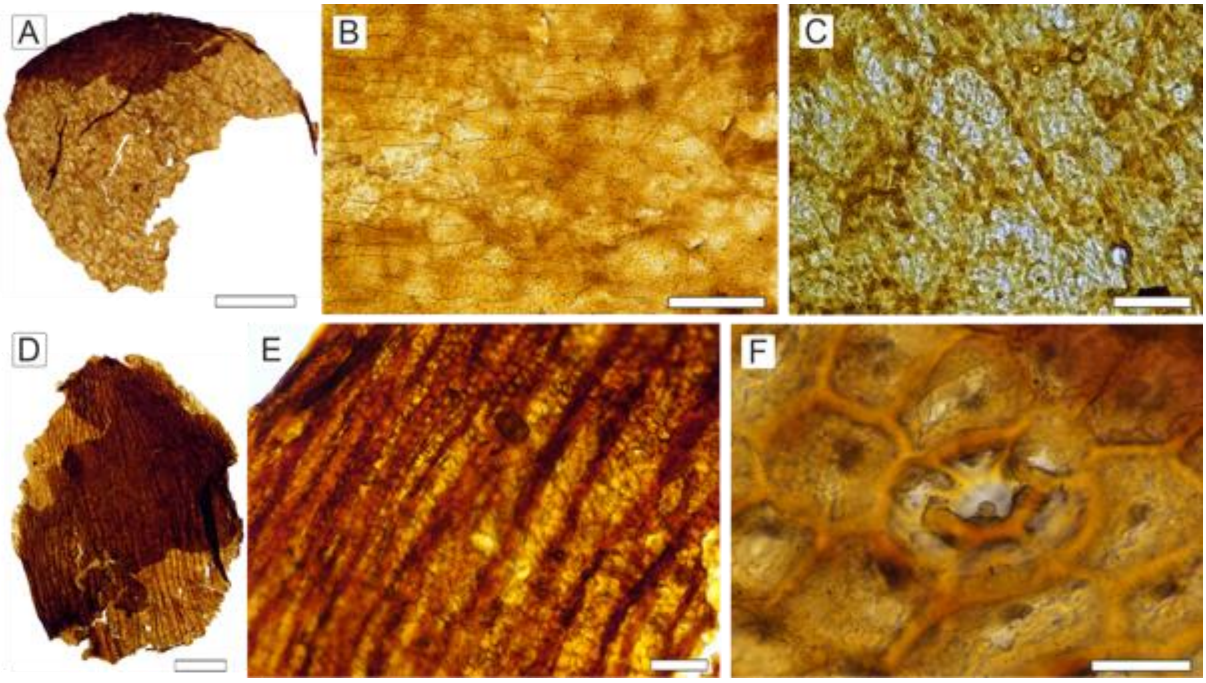
Plate 30

Cuticles macerated from coprolites from the Upper Triassic of the Lipie Śląskie, south Poland.

- A – C. Cuticle type J.
  - A. Ellipsoidal cuticle with partially preserved both sides cuticles.
  - B. probably fused megaspore membrane and nucellar cuticle.
  - C. Reticulate structure of the cuticle.
- D – F. Cuticle type K.
  - D. Ellipsoidal cuticle with sclerotic fibers.
  - E. Cell arrangement and fragment of smooth cuticle margin.
  - F. Details of stomata complex.

Scale bar: A, D 500 µm, B, E 100 µm, C 50 µm, F 25 µm.

Specimen: A, C Cop1/06; B Cop3/18; D, E Cop1/56; F Cop1/63.


A
B
C
D
E
F

4.3. Tatra Mountains

Plate 31

Marian Raciborskis (1890a) research monograph "Flora retycka w Tatrach".

A. Figure from original Raciborskis' work "Flora retycka w Tatrach"

B, C. Original specimen labels from Raciborskis' collection.

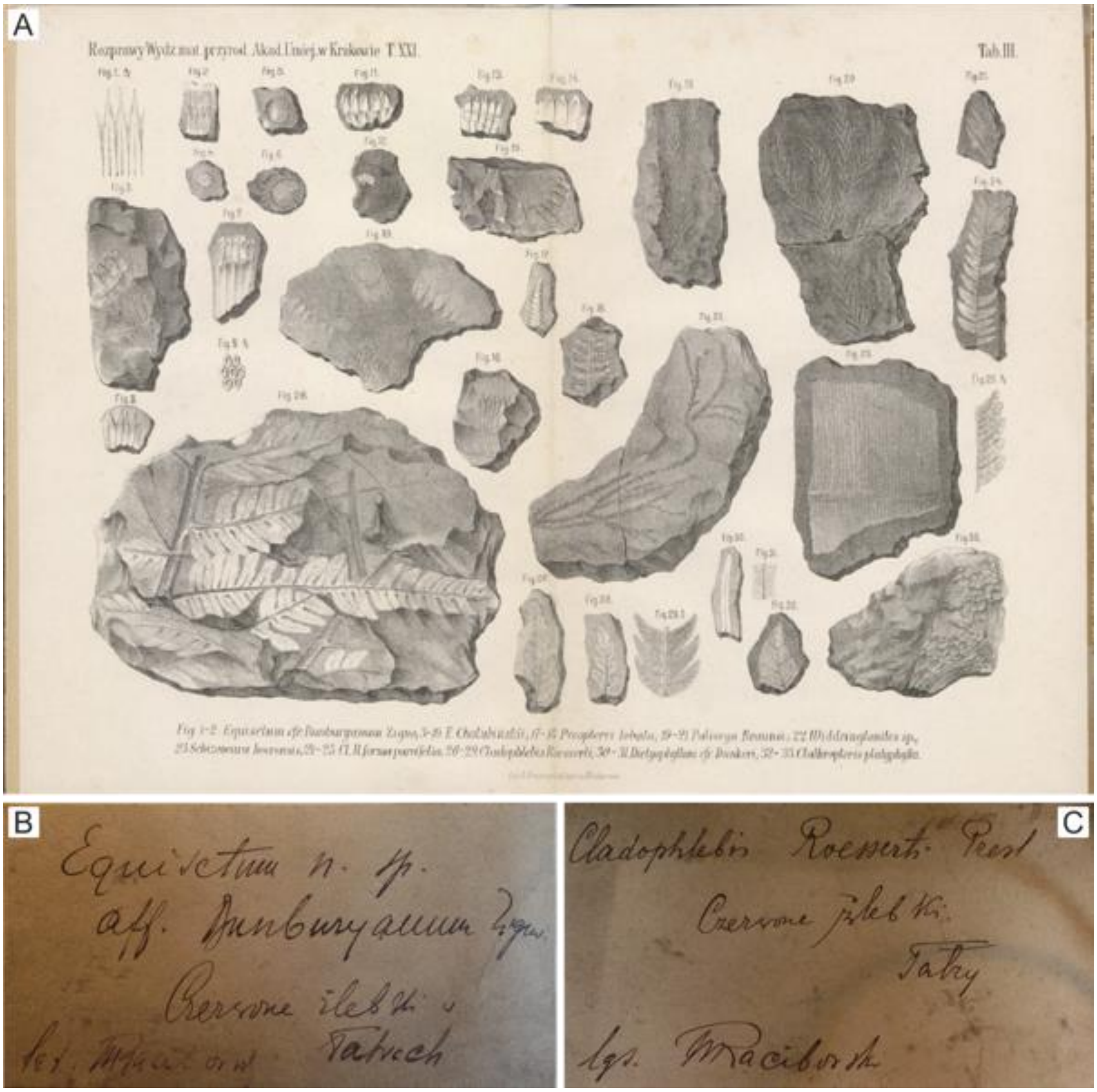

A
Rozprawy Wydz. mat. przyrod. Akad. Umiej. w Krakowie T. XXI
Tab. III
B
Equisetum n. sp.
aff. Bunburyanum Zign.
Czerwone żlebki w
Tatrach
C
Cladophlebis Roesserti Presl
Czerwone żlebki
Tatry
lgt. Raciborski

Plate 32

Equisetites chalubinskii from the Upper Triassic Tomanowa Fm in the Tatra Mountains, Poland.

A. Stem fragment representing an internode showing regularly placed ribs.
B – F. Stem fragments with leaf sheath and node.

Abbreviations: ls – leaf sheath, n – node.
Scale bar: 10 mm.
Specimen: A ZNG PAL A-III-31/0.3.2; B ZNG PAL A-III-31/0.3.1, C ZNG PAL A-III-31/0.3.4; D ZNG PAL A-III-31/20.1; E ZNG PAL A-III-31/56; F ZNG PAL A-III-31/64.2.

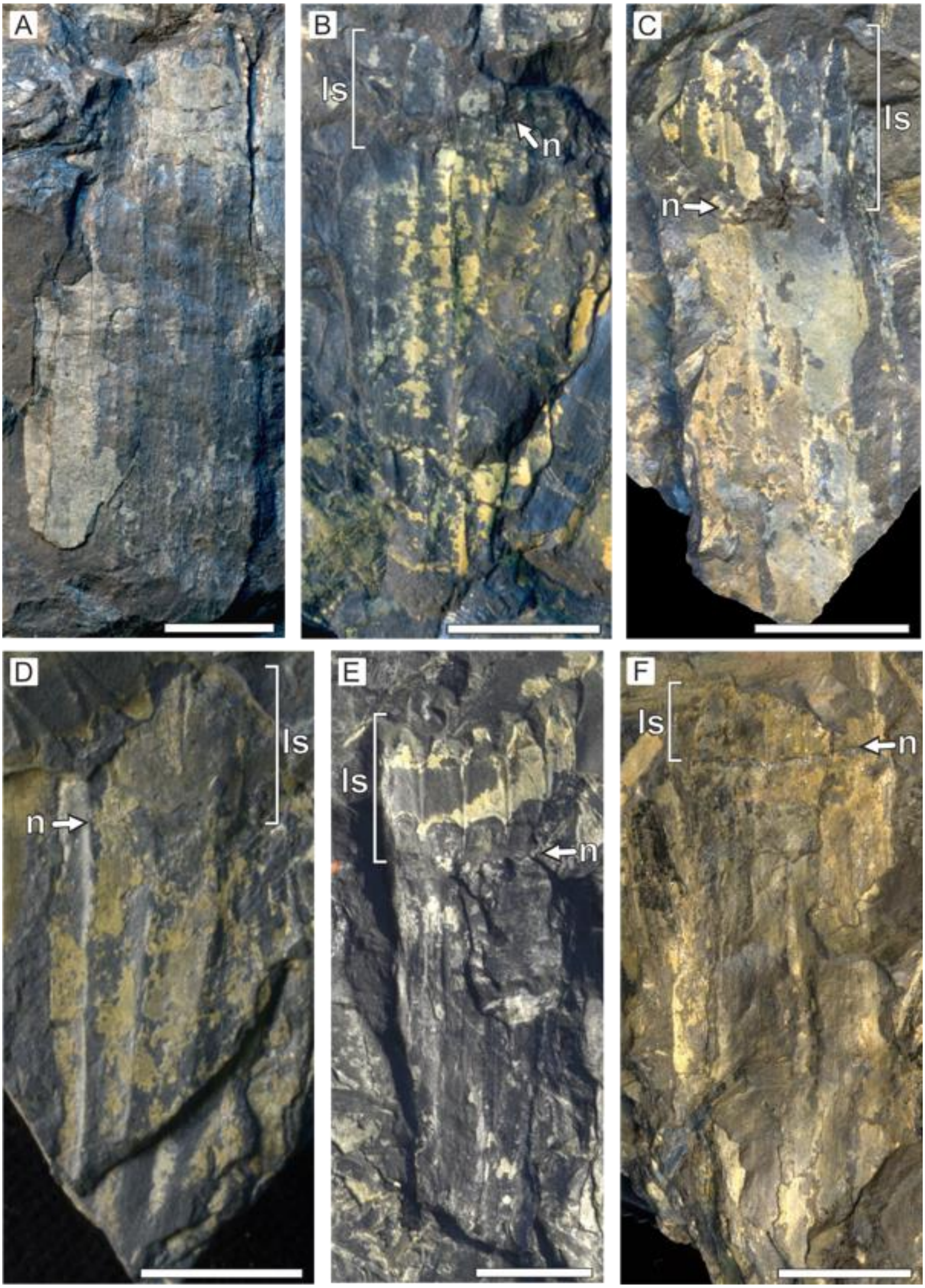

A
B
ls
n
C
ls
n
D
ls
n
E
ls
n
F
ls
n

Plate 33

Equisetites chalubinskii from the Upper Triassic Tomanowa Fm in the Tatra Mountains, Poland.

A – F. Pitted diaphragms.

E. Pitted diaphragm with partially preserved leaf whorl.

Abbreviations: c – cortex, cf – commissural furrow, ls – leaf sheath, pd – pitted diaphragm, vc - vallecular canal.
Scale bar: 5 mm.
Specimen: A ZNG PAL A-III-31/1.2; B ZNG PAL A-III-31/64.1; C ZNG PAL A-III-31/14a.1; D ZNG PAL A-III-31/70.3; E ZNG PAL A-III-31/60; F ZNG PAL A-III-31/21.2.

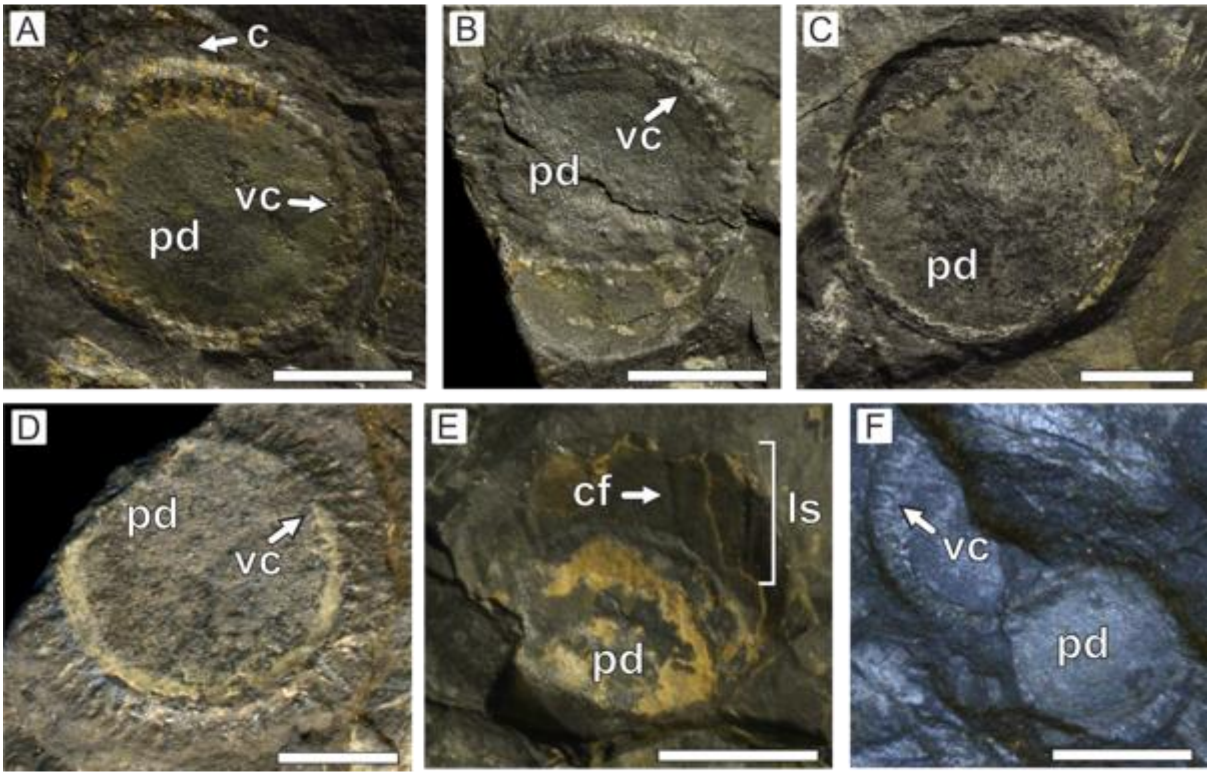

A
c
vc
pd
B
vc
pd
C
pd
D
pd
vc
E
cf
ls
pd
F
vc
pd

Plate 34

Equisetites chalubinskii from the Upper Triassic Tomanowa Fm in the Tatra Mountains, Poland.

A. Stem composed of free following nodes cover with leaf sheaths.
B – C. Leaf sheaths comprising smaller and slender leaves.
D – G. Leaf sheaths composed of wider leaves.
H – K. Details of leaf surface showing epidermal pattern and surface "ornamentation".
  H. Hair-like ornamentation on a leaf surface.
  I. Single leaffrom leaf sheath.
  J. Magnification of leaf surface shown in I.
  K. Leaf surface showing possible stomata distributed in bands, separated by a midrib.
  L. Details of stomata from K.

Abbreviations: blt – broken leaf tip, cf – commissural furrow, fl – free leaf, ls – leaf sheath, m – midrib. pd – pitted diaphragm, sb – stomata band, s – stomata.
Scale bar: A – G 10 mm; H – K 1 mm; L 100 μm.
Specimen: A ZNG PAL A-III-31/.21.1; B ZNG PAL A-III-31/1.2; C ZNG PAL A-III-31/19; D ZNG PAL A-III-31/21.1; E ZNG PAL A-III-31/54; F ZNG PAL A-III-31/0.3.4; G ZNG PAL A-III-31/12.13; H ZNG PAL A-III-31/32.1; I – J ZNG PAL A-III-31/21.1; K – L ZNG PAL A-III-31/37.5.

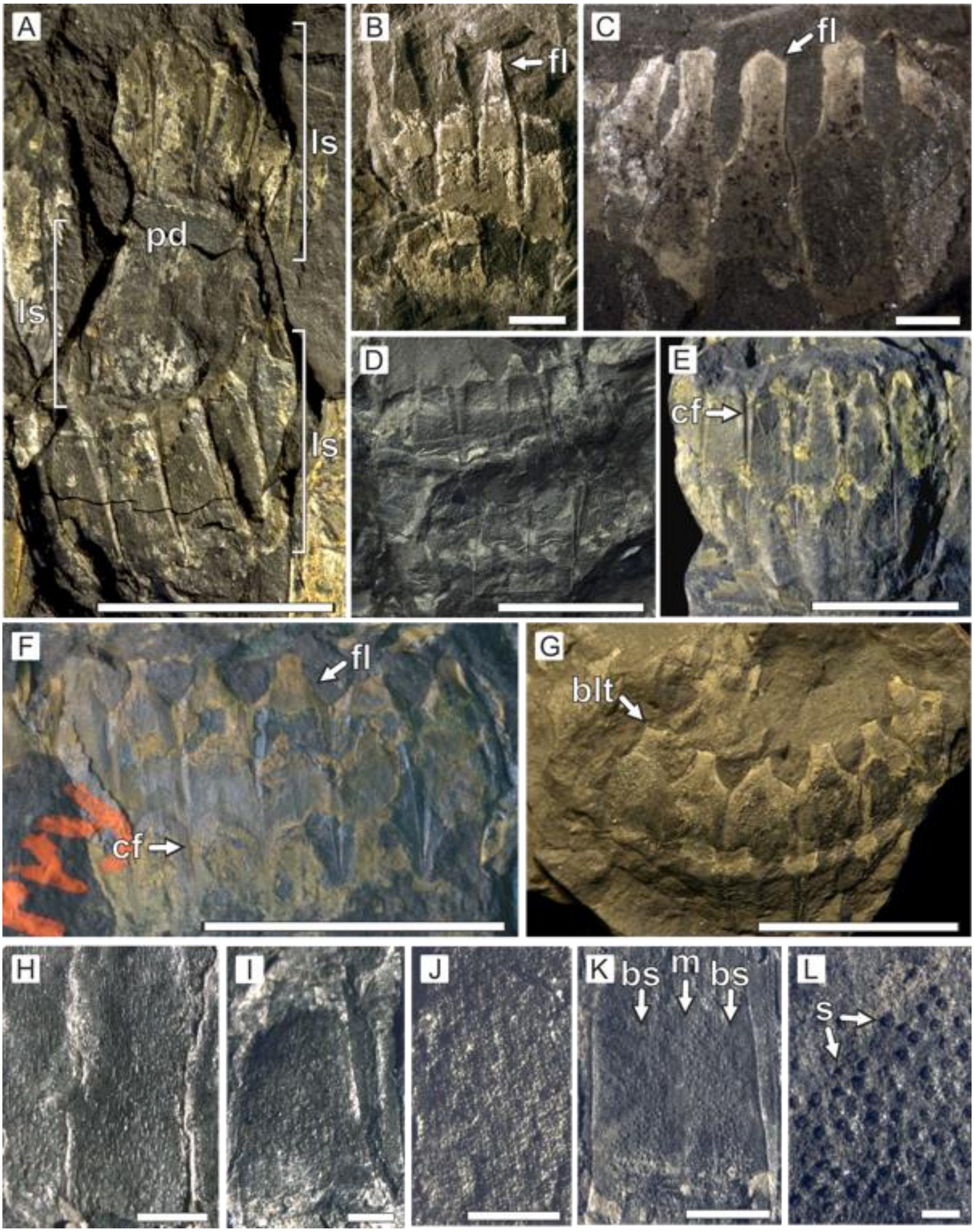

A
ls
pd
ls
ls
B
fl
C
fl
D
E
cf
F
fl
cf
G
blt
H
I
J
K
bs
m
bs
L
s

Plate 35

Equisetites chalubinskii from the Upper Triassic Tomanowa Fm in the Tatra Mountains, Poland.

Fragments of strobili with hexagonal sporangiophores.

A. Hexagonal sporangiophores tightly adjacent.

B. Magnification of one of the sporangiophores from A showing central umbo clearly separated from marginal flanges with thin grooves, faint grooves extend from margin corners towards the base of an umbo.

C. Details of sporangiophore surface from B with epidermal cells imprint.

D. Fragment of strobili with hexagonal sporangiophores.

E. Magnification of sporangiophore from D showing a central umbo.

F. An isolated sporangiophore slightly elongated in one dimension, with discernible epidermal cell pattern.

Abbreviations: u – umbo, mf – marginal flange, g – groove.

Scale bar: A, D 5 mm; B, D – F 500 μm; C 100 μm.

Specimen: A – C ZNG PAL A-III-31/1.1; D – E ZNG PAL A-III-31/21.1; F ZNG PAL A-III-31/83.1.

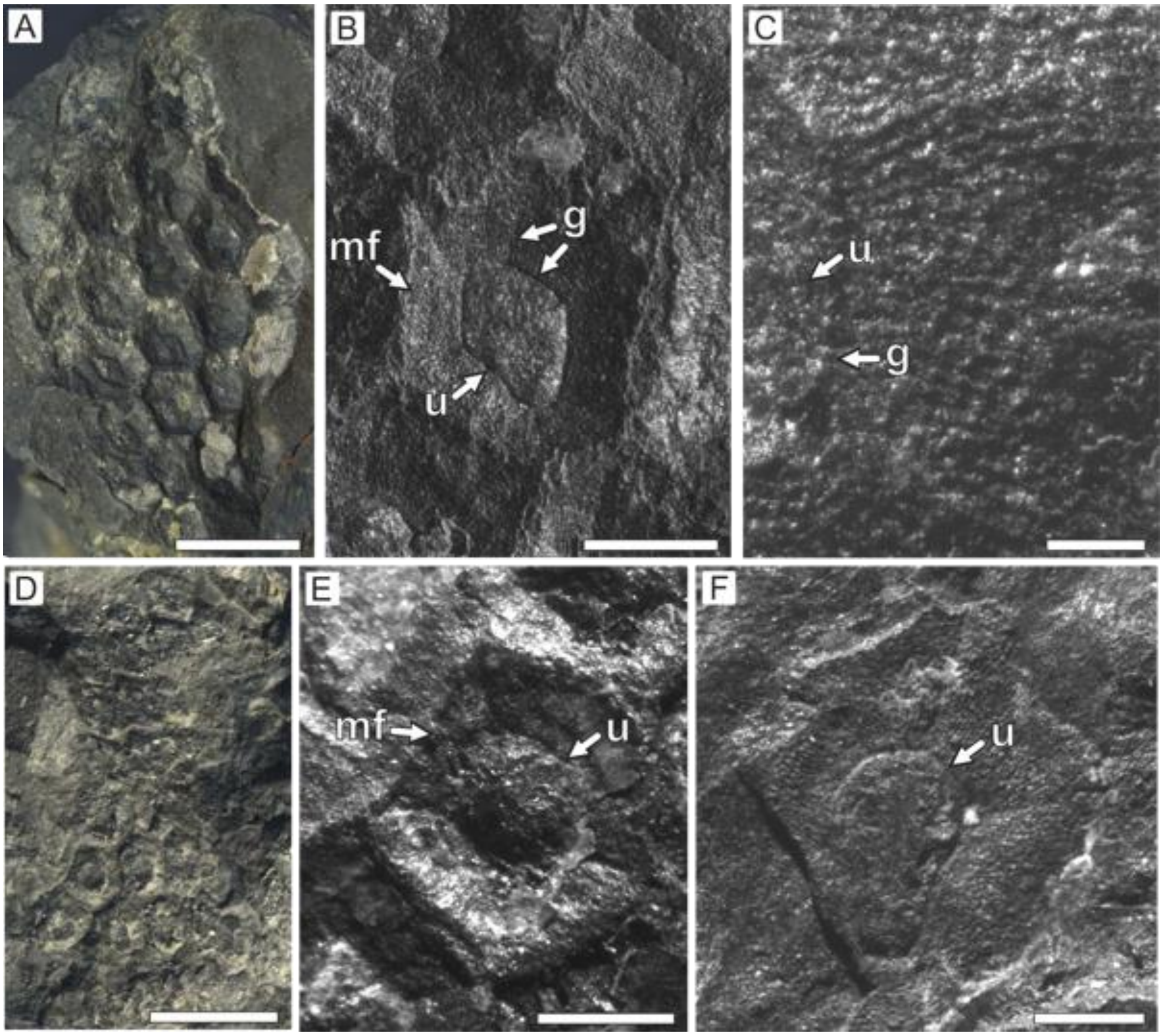

A
B
mf
g
u
C
u
g
D
E
mf
u
F
u

Plate 36

Equisetites sp. from the Upper Triassic Tomanowa Fm in the Tatra Mountains, Poland.

Leaf sheaths of *Equisetites* sp.

A, B. Stems with attached leaf sheaths.

C. Magnified leaf sheath from B.

D. Details of leaf surface from B.

E. Stomata on the leaf surface from B.

F. Two following leaf sheaths.

G. Magnified leaf fragment from F. showing remains of a midrib.

H. Stem with leaf sheath with discernible nodal region.

I – L. Leaf sheaths comprising of lanceolate leaves with acute tip.

M. Pitted diaphragm with leaf sheath attached.

Abbreviations: cf – commissural furrow, fl – free leaf, ls – leaf sheath, n – node, pd – pitted diaphragm, s – stomata.

Scale bar: A – C, F, H – M 5 mm; D, G 1 mm; E 100 µm.

Specimen: A ZNG PAL A-III-31/12.11; B - E ZNG PAL A-III-31/26.2; F - G ZNG PAL A-III-31/37.1; H ZNG PAL A-III-31/12.2; I ZNG PAL A-III-31/16.1; J ZNG PAL A-III-31/21.1; K ZNG PAL A-III-31/12.1; L ZNG PAL A-III-31/35.3, counter part of ZNG PAL A-III-31/12.1 in K; M ZNG PAL A-III-31/83.1.

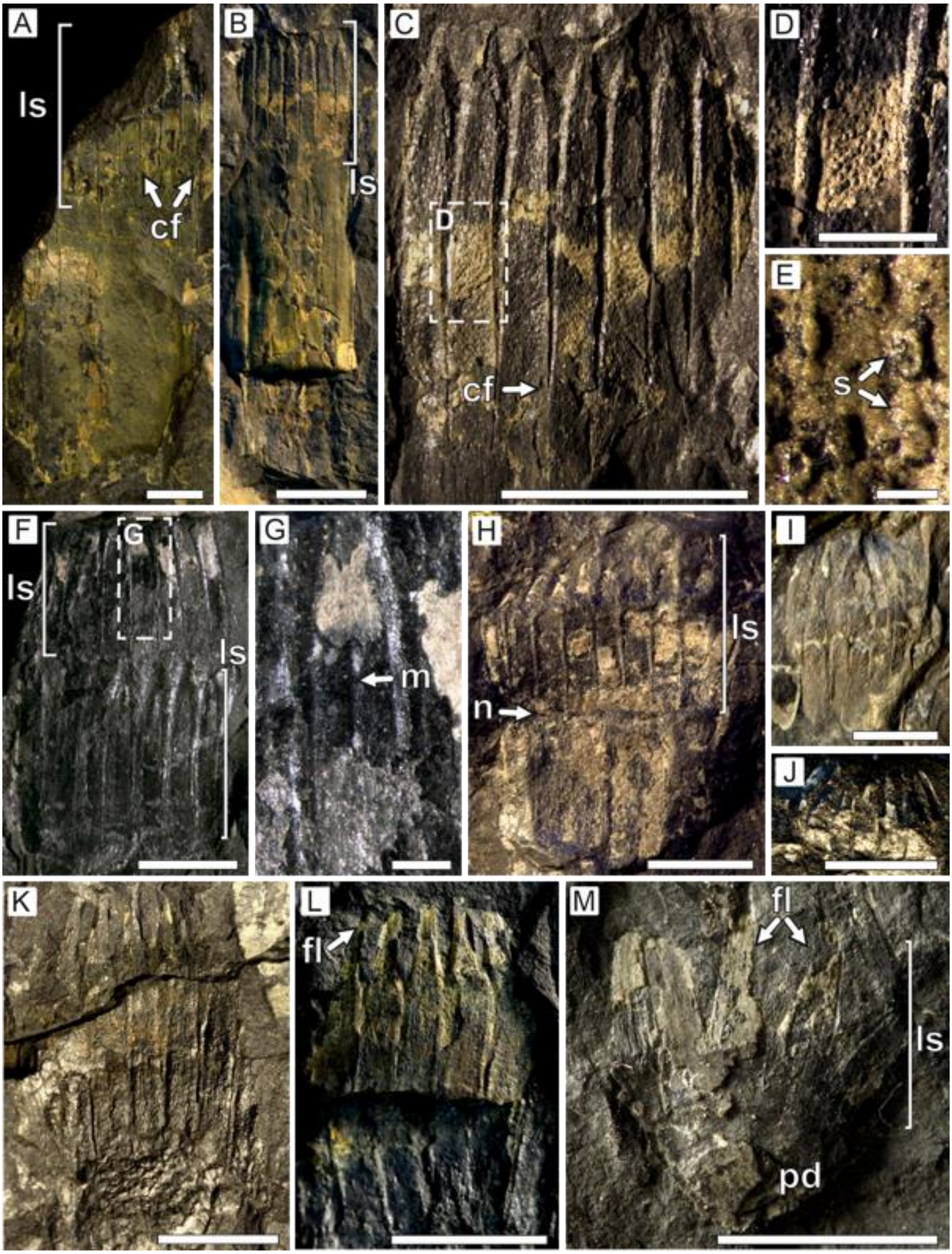

A
ls
cf
B
ls
C
D
cf
D
E
s
F
G
ls
ls
G
m
H
ls
n
I
J
K
L
fl
M
fl
ls
pd

Plate 37

Neocalamites lehmannianus (Goeppert) Weber from the Upper Triassic Tomanowa Fm in the Tatra Mountains, Poland.

A, B. Stem fragments with poorly preserved nodal regions.
C. Magnification of a stem surface.
D. Stem fragment with visible circular branch scar.

Abbreviations: bs – branch scar, n – node.
Scale bar: A – D10 mm.
Specimen: A ZNG PAL A-III-31/35.2; B ZNG PAL A-III-31/35.1; C ZNG PAL A-III-31/36.3; D ZNG PAL A-III-31.35.2.

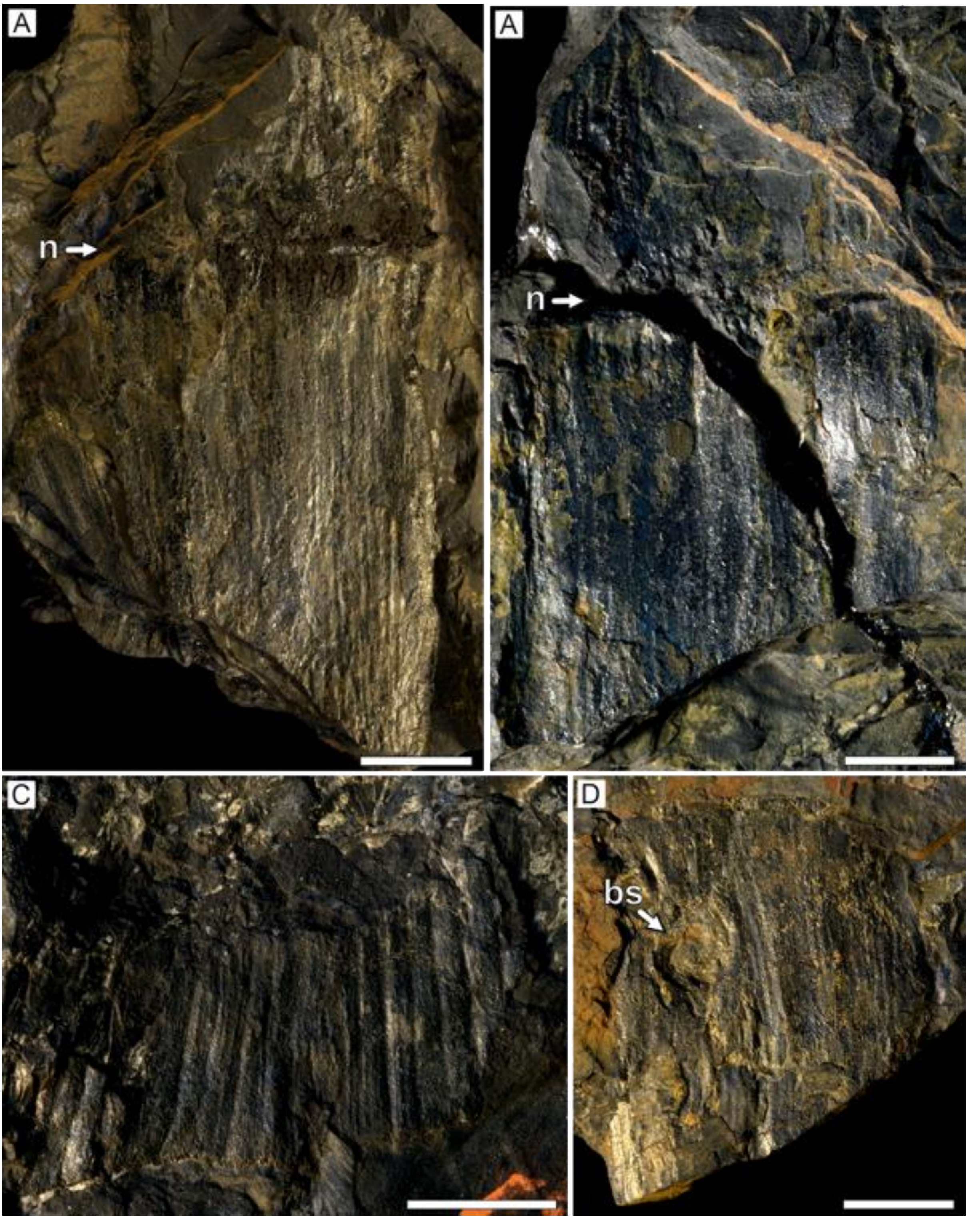

A
n
A
n
C
D
bs

Plate 38

Cladophlebis roessertii (Schenk) Saporta from the Upper Triassic Tomanowa Fm in the Tatra Mountains, Poland.

A – E. Pinnae with smooth rachis and pinnules arising oppositely to alternately.
F. Schematic drawing of pinnule from F.

Scale bar: A – F 10 mm.
Specimen: A ZNG PAL A-III-31/78; B ZNG PAL A-III-31/70.2; C ZNG PAL A-III-31/70.1; D ZNG PAL A-III-31/69.1; E – F ZNG PAL A-III-31/28.3.

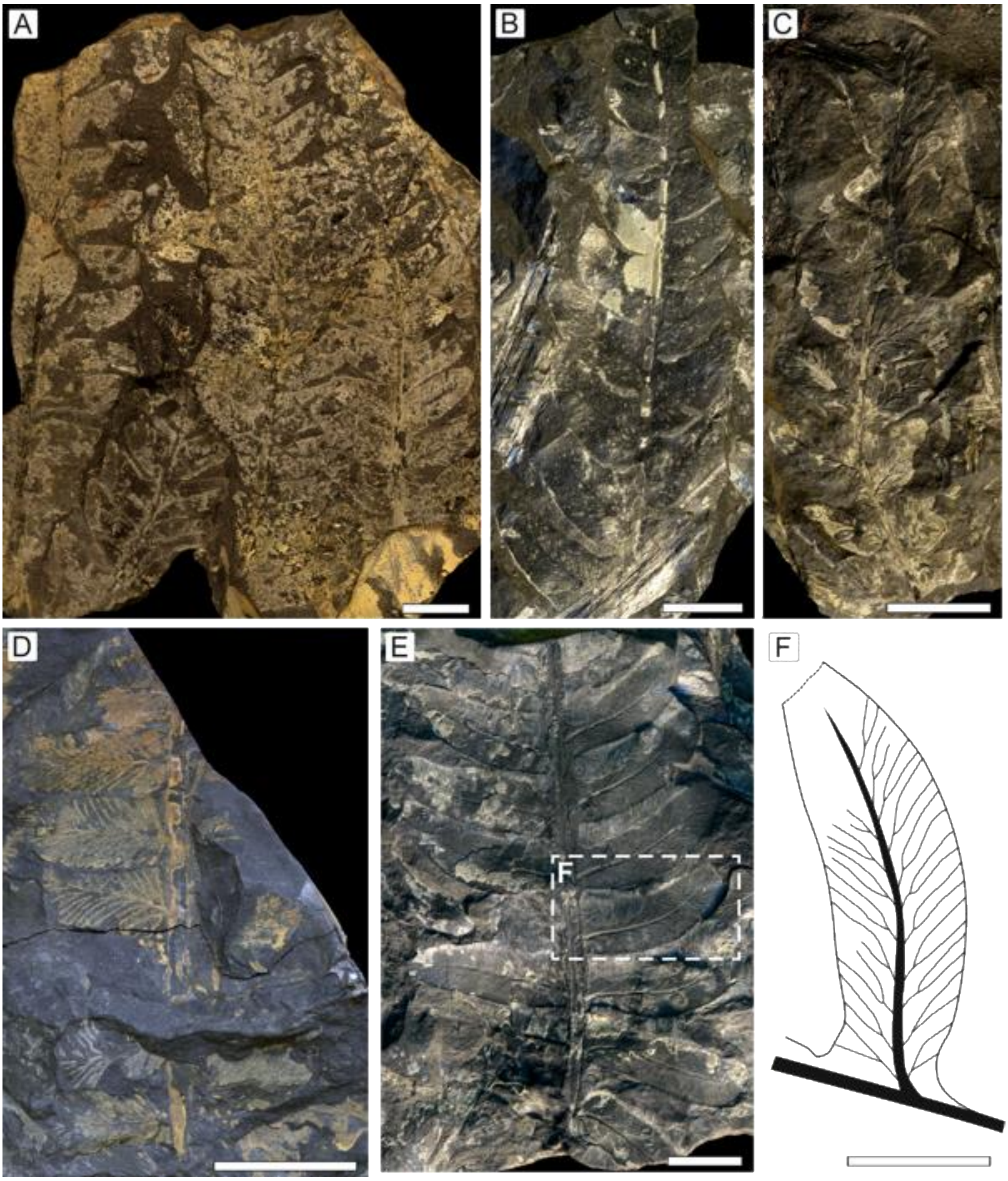

A
B
C
D
E
F
F

Plate 39

Dipteridaceae Seward et Dale 1901 from the Upper Triassic Tomanowa Fm in the Tatra Mountains, Poland.

A – D. *Clathropteris meniscoides* (Brongniart 1825) Brongniart 1828.

A. Leaf fragment with preserved two veins and lamina with orthogonal venation.
B. Magnification of the leaf blade showing orthogonal venation; magnification of A.
C. Schematic drawing of venation from B.
D. Details of venation from B.

E – I. *Dictyophyllum exile* (Brauns 1862) Nathorst 1878.
E, H. Triangular fragments of leaf lamina with midrib in the centre.
F. Schematic drawing of a leaf fragment from E.
G. Details of venation from E.
I. Schematic drawing of venation from a leaf fragment from H.

Abbreviations: v – vein.
Scale bar: A, B 10 mm; D – H 5mm.
Specimen: A – D ZNG PAL A-III-31/45; E – G ZNG PAL A-III-31/46; H – I ZNG PAL A-III-31/40.

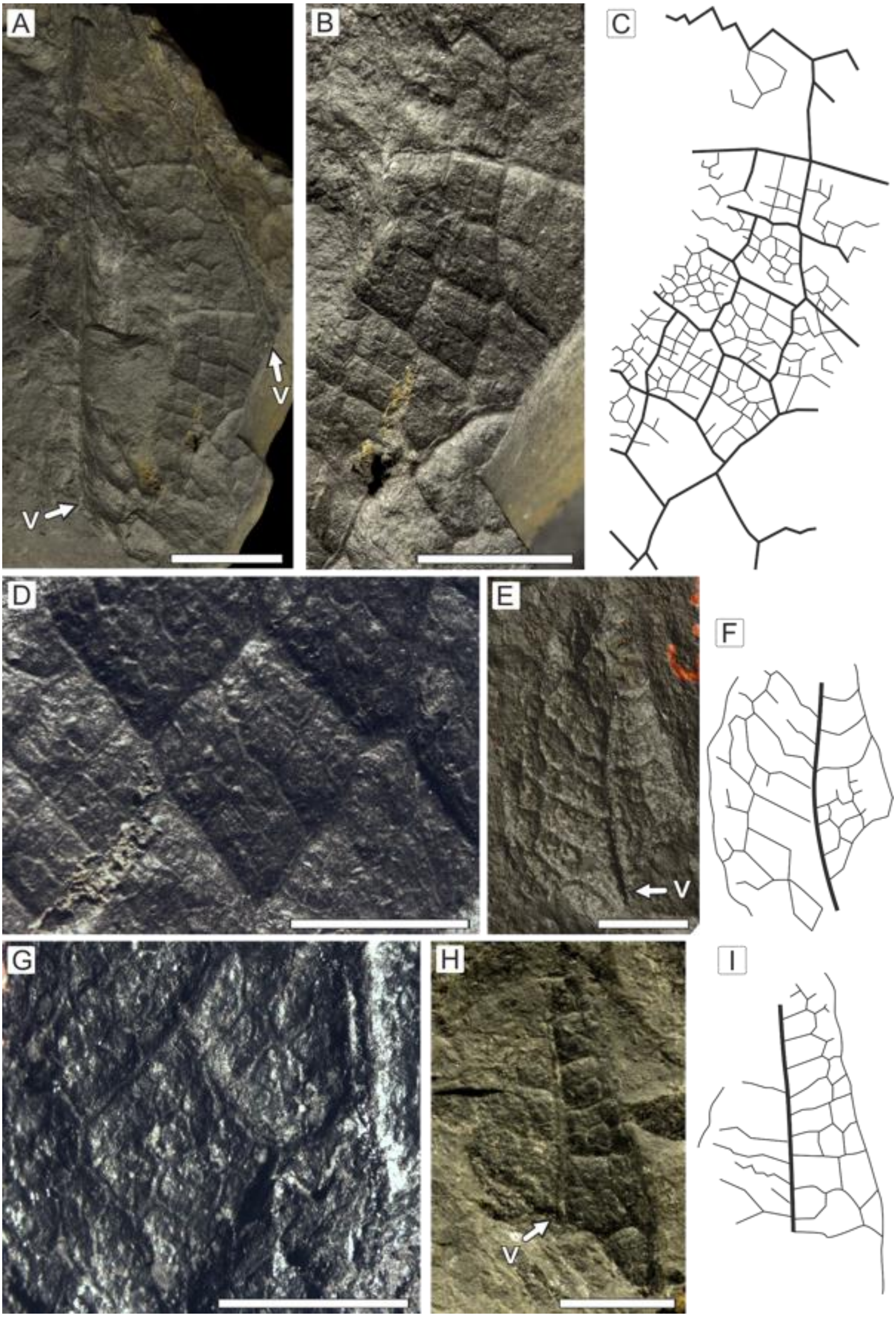

A
V
V
B
C
D
E
V
F
G
H
V
I

Plate 40

Spiropteris sp. from the Upper Triassic Tomanowa Fm in the Tatra Mountains, Poland.

A – B. Coiled juvenile fern frond.

Scale bar: A, B 10 mm.

Specimen: A ZNG PAL A-III-31/0.5.1; B ZNG PAL A-III-31/0.5.2.

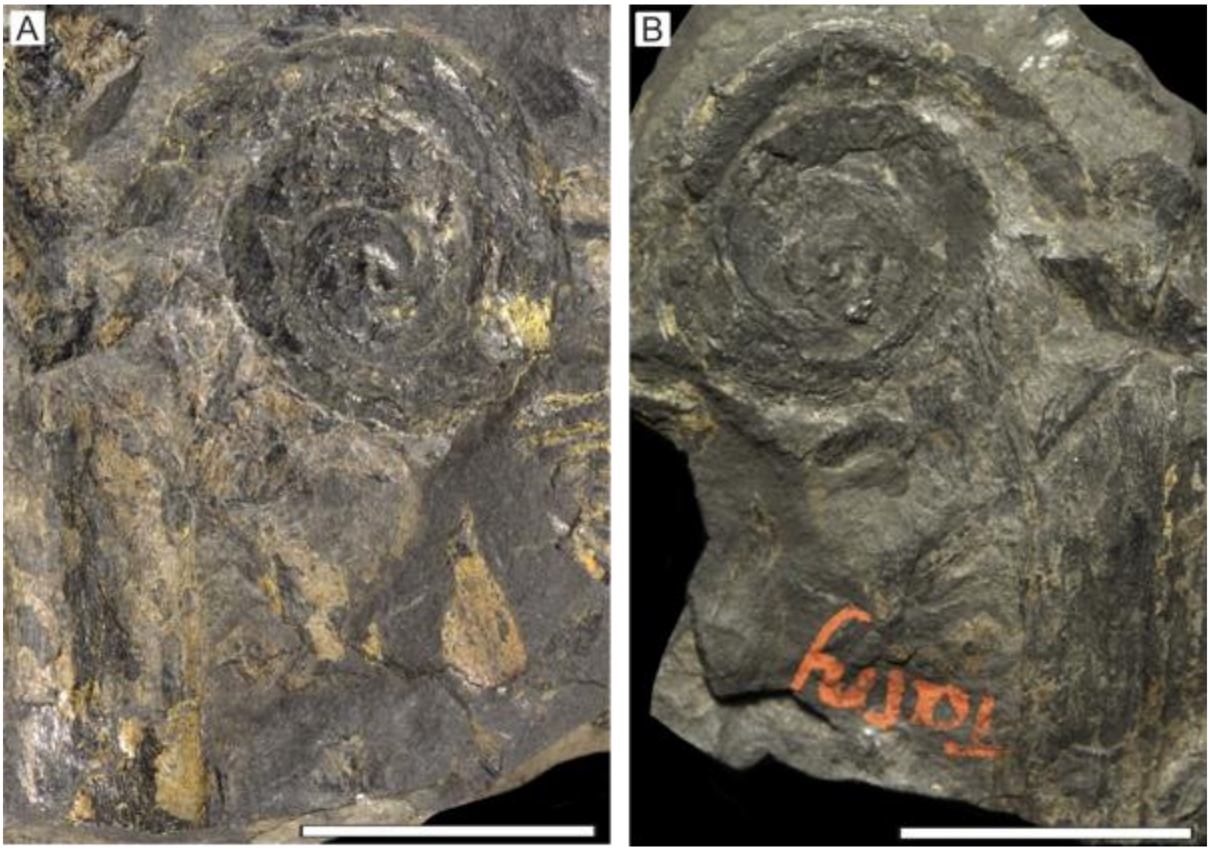

A
B

Plate 41

Elatocladus sp. from the Upper Triassic Tomanowa Fm in the Tatra Mountains, Poland.

A, B, F. Branching twigs.
C. Details of leaves; leaf base deccurent; magnification from B.
D. Midrib extending from a leaf base towards a tip; magnification from B.
E, G, H. Single twigs.

Abbreviations: m – midrib, s – leaf sheath
Scale bar: A, B, G, H 10 mm; C, D, E, F 5 mm.
Specimen: A ZNG PAL A-III-31/0.1; B – D ZNG PAL A-III-31/39; E ZNG PAL A-III-31/60; F ZNG PAL A-III-31/38; G ZNG PAL A-III-31/15b.1; H ZNG PAL A-III-31/15b.2.

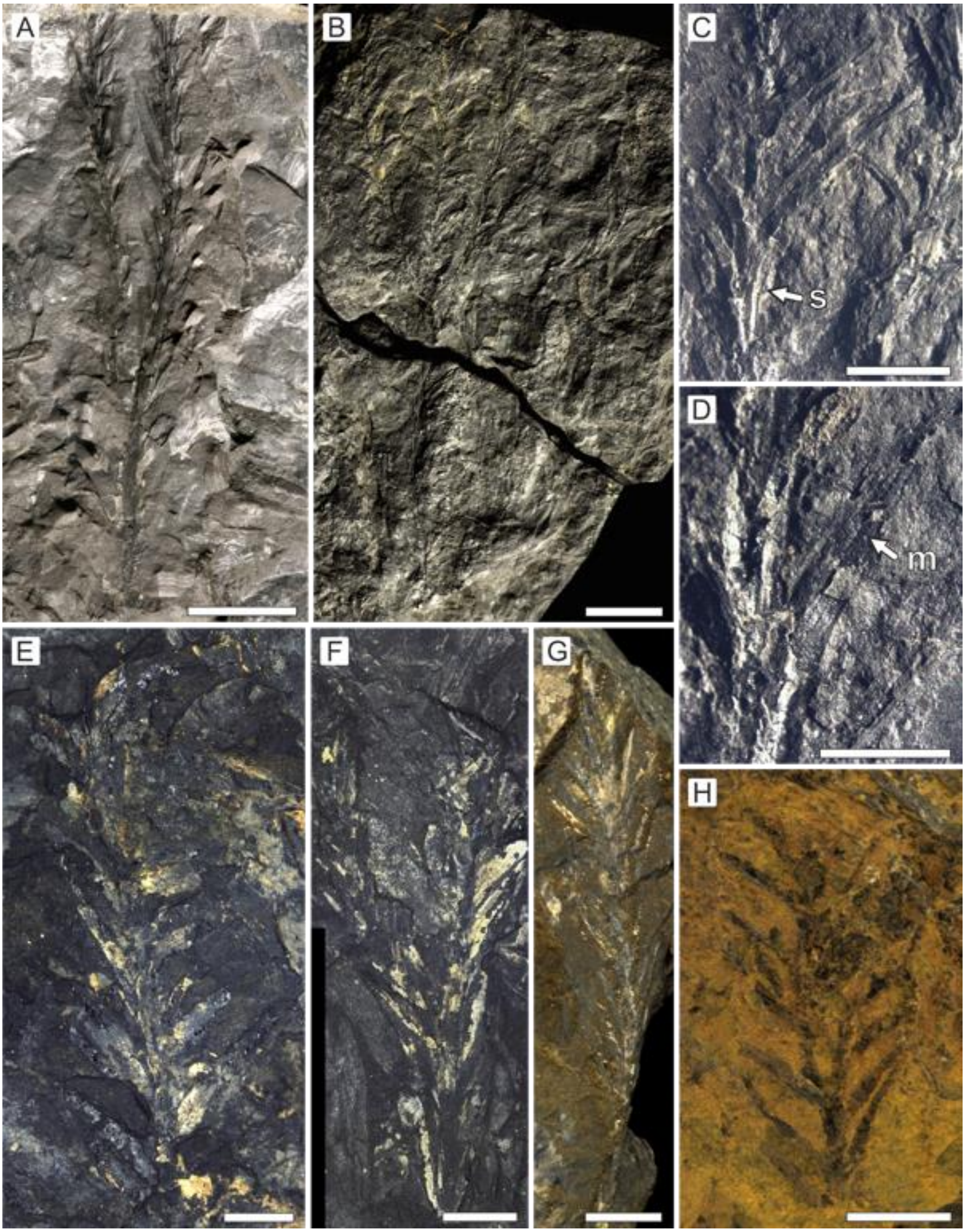
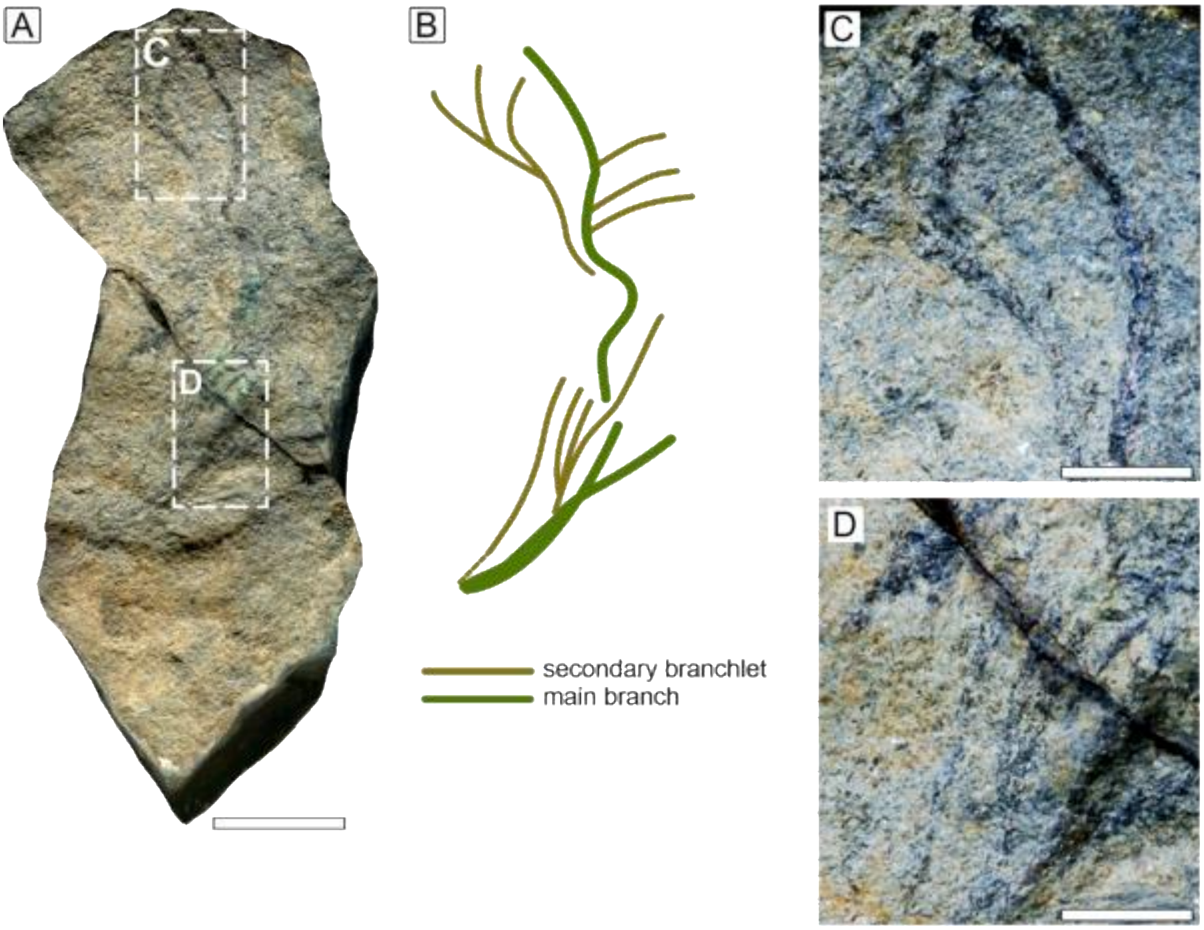

A
B
C
s
D
m
E
F
G
H

Plate 42

Coniferophyta *incertae sedis* from the Upper Triassic Tomanowa Fm in the Tatra Mountains, Poland.

A. Overall view of only specimen preserved in sandstone; shoot branching two times.
B. Schematic drawing of main shoot and secondary branches.
C, D. Magnification of the shoot; leaves barely recognisable.

Scale bar: A 20 mm; C, D 10 mm.
Specimen: ZNG PAN A-III-31/44.


A
C
D
B
secondary branchlet
main branch
C
D

Streszczenie

Przeprowadzone badania miały na celu uzupełnienie informacji paleobotanicznych o makroflorę pozyskaną z dwóch nowych stanowisk, z górnotriasowych utworów formacji grabowskiej z Górnego Śląska (Zawiercie-Marciszów i Lipie Śląskie-Lisowice) oraz przeprowadzenie rewizji historycznej kolekcji paleobotanicznej z tatrzańskiej formacji z Tomanowej. Głównym celem tarzańskiej rewizji było uzyskanie bardziej kompletnego obrazu zespołów z tego regionu, poprzez aktualizację opracowanej części kolekcji przez M. Raciborskiego oraz ustalenie pozycji taksonomicznej okazów znajdujących się w kolekcji Muzeum Geologicznego PAN w Krakowie, oraz Muzeum Tatrzańskiego w Zakopanem. Wyniki badań ujawniły nowe interesujące dane dotyczące flory noryku (Lipie Śląskie-Lisowice i Zawiercie-Marciszów). Flory te wykazały dominującą obecność roślin szpilkowych (Coniferophyta), podobnie jak w innych noryckich zespołach z terenów dzisiejszej Europy. W retyckich utworach formacji z Tomanowej (Tatry) zachowane są makroskamieniałości wykazujące dominację roślin skrzypowych (Sphenophyta) i paprociowych (Pteridophyta), podczas gdy reprezentacja szpilkowych jest tu minimalna. Różnice te są konsekwencją ich odmiennych lokalizacji paleogeograficznych. Dodatkowo inne warunki paleoklimatyczne przyczyniły się także do taksonomicznej rozbieżności. Flora z formacji grabowskiej kształtowana była głównie suchym lub półsuchym klimatem przeplatanym epizodami podwyższonej wilgotności, podczas gdy flora z formacji z Tomanowej występowała w stale wilgotnym środowisku. Dostępność materiału pozyskanego z koprolitów z Lipia Śląskiego-Lisowic pozostawionych przez dużych roślinożerców pozwoliła na podjęcie próby rekonstrukcji interakcji roślinno-zwierzęcych. W efekcie przeprowadzonych analiz otrzymane wyniki uzupełniają lukę w wiedzy na temat roślinności górnego triasu w Polsce. Dodatkowo pozyskane informacje przyczyniły się do próby rekonstrukcji warunków paleoekologicznych i paleoklimatycznych.

Contribution statement/oświadczenie współautora publikacji

Sosnowiec, 12.06.2023

Dr hab. Paweł Filipiak, prof. UŚ

Oświadczenie współautora publikacji wchodzącej w skład rozprawy doktorskiej

Jako współautor publikacji, pt. „Fossil floral assemblage from the Upper Triassic Grabowa Formation (Upper Silesia, southern Poland)" opublikowanej w czasopiśmie *Annales Societatis Geologorum Poloniae* w 2023 roku, oświadczam, iż wkład Pani mgr Zuzanny Wawrzyniak w jej powstanie wyniósł 85%.

Doktorantka odpowiada za zebranie materiału do badań, analizy mikroskopowe oraz interpretację uzyskanych wyników. Pani mgr Wawrzyniak jest autorką figur, plansz oraz zasadniczej treści manuskryptu.

Z poważaniem

Wawrzyniak, Z. & Filipiak, P., 2023. Fossil floral assemblage from the Upper Triassic Grabowa Formation (Upper Silesia, southern Poland). Annales Societatis Geologorum Poloniae, 93: 1-30. Doi: 10.14241/asgp.2023.02