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LATE JURASSIC PLANT FOSSILS FROM WÓLKA BAŁTOWSKA (HOLY CROSS MOUNTAINS, POLAND)

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Abstract: Plant fossils were studied in samples from the Upper Jurassic (lowermost Kimmeridgian) locality at the village of Wólka Bałtowska in the Holy Cross Mountains (Góry Świętokrzyskie), collected in the 20th century by Jerzy Liszkowski. Eight macrofossil taxa were recognized: an indeterminate sphenophyte, a fern cf. *Gleichenites cycadina*, seed fern *Ptilozamites cycadea*, conifers, *Brachyphyllum mamillare* with female cone scales and male cones, containing *Araucariacites* and *Callialasporites* pollen grains *in situ* in pollen sacs, *Brachyphyllum crucis* and probably its male cone, *Pagiophyllum araucarinum,* an unassigned conifer male cone, and the gymnosperms *incertae sedis Pseudotorellia solida* sp. nov. and *Taeniatus elongatus.* The latter was for the first time found with a preserved cuticle, enabling emendation of the generic and specific diagnosis. Additional data, from the palynological analysis of six samples that yielded organic-walled dinoflagellate cysts (dinocysts) and sporomorphs, as well as rich phytoclast assemblages, including large cuticle remains, complement the vegetation picture and allow reconstruction of the palaeoenvironmental conditions. Palynological analysis confirms that the plant-bearing limestones were deposited in a nearshore, presumably shallow-marine sedimentary setting. Interpretation of the macroremains indicates that nearby land (probably an island) was covered by vegetation, typical for a nearshore marine-influenced zone, while some sporomorphs were probably transported (from inland or the vicinity).

Key words: Kimmeridgian, macroflora, gymnosperms, pollen *in situ*, *Araucariacites*, *Callialasporites,* palaeoenvironment.

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INTRODUCTION

A unique Upper Jurassic site with macroflora at the village of Wólka Bałtowska in the northern surroundings of the Holy Cross Mts. (Góry Świętokrzyskie; Fig. 1) was discovered by Jerzy Liszkowski in 1967 (Liszkowski, 1972, 1976), but since then, there has been no comprehensive study of the fossil plants from this site, except for preliminary taxonomic determinations made by Maria Reymanówna (*in* Liszkowski, 1972, 1976). The Wólka Bałtowska site is one of the very few known sites with Late Jurassic plant remains in Poland (e.g., Premik and Zabłocki, 1925; Liszkowski, 1972; Gutowski, 1998; Wierzbowski, 2023b), in contrast to the numerous known sites with Early Jurassic (e.g., Makarewiczówna, 1928; Wcisło-Luraniec and Ichas-Ziaja, 1990; Wcisło-Luraniec, 1992; Pacyna, 2013) and Middle Jurassic plants (e.g., Raciborski, 1894; Reymanówna, 1963a, b, 1973, 1987; Wcisło-Luraniec, 1989; Jarzynka and Pacyna, 2015). To fill that gap, the authors of this account present updated taxonomic descriptions of the macroflora assemblage, including one new taxon, supported by an environmental interpretation, based on microfossil and palynofacies analysis. Additionally, on the basis of ammonites (Wierzbowski, 2023a, b) and dinocysts (Gedl and Ziaja, 2004; this study), the present authors suggest that the plant-bearing strata in question accumulated most likely during the early Kimmeridgian.

Fig. 1. Map with the Upper Jurassic locality, Wólka Bałtowska marked with a red dot.

GEOLOGICAL SETTING

The Upper Jurassic land-plant-bearing limestone, exposed at the village of Wólka Bałtowska, represents the lower part of the Skarbka Oolite Limestone (Wierzbowski, 2023a, b), an informal lithostratigraphic unit, distinguished by Gutowski (1998; as the Skarbek Oolitic Limestone) in the Jurassic succession of the north-eastern surroundings of the Holy Cross Mts. The precise age was difficult to determine, due to a lack of ammonites, which generally and typically are scarce in the strata at this level in this area. Their absence most likely results from the nature of the sedimentary setting, which was nearshore, very shallow-marine to partly continental (e.g., Pieńkowski and Niedźwiedzki, 2005); the richer ammonitic fauna that occurs in the underlying middle Oxfordian and overlying younger Kimmeridgian reflects a more offshore-marine setting.

Accumulation of oolitic and platy limestone was associated with a transgressive sedimentary phase, which left conglomerates and subsequently oolitic-bioclastic grainstone and laminites in the north-eastern margin of the Holy Cross Mts., distinguished by Wierzbowski (2023a, b) as a shallow-water carbonate megafacies (I), accumulated during the late Oxfordian–early Kimmeridgian (correlated with Bifurcatus – the upper part of the Hypselocylum ammonite zones). The exposure studied at Wólka Bałtowska represents the second (I-2) sequence of the megafacies (Fig. 2) underlain in the vicinity of Wólka Bałtowska by massive coral limestone and organodetrital limestone, which represent the basal sequence (I-1) of the shallow-water carbonate megafacies. Deposition of the I-1 sequence took place during the middle to late Oxfordian (the coral limestone is correlated with the uppermost ammonite Transversarium to Hypselum zones); they rest upon deep-water middle Oxfordian micritic limestone, correlated with the Transversarium Ammonite Zone (Wierzbowski, 2023a). The overlying third sequence (I-3) is represented mainly by oolitic limestone. The topmost sequence of this megafacies (I-4) is the first that yielded ammonites, allowing their correlation with the upper part of the Hypselocylum Ammonite Zone, and limiting the upper age of the barren strata (I-2, 3).

On the basis of collected fauna, especially an ammonite of the genus *Discosphinctes*, Liszkowski (1972) interpreted the age of this sediment as late Oxfordian. However, due to the lack of specific determination as well as some questions of the true taxonomic affinity and stratigraphic validity of this taxon in Europe (e.g., Brochwicz-Lewiński, 1975), this interpretation should be treated with caution (see Wierzbowski 2023a, for taxonomic re-interpretations). Gutowski (1998, fig. 3) followed Liszkowski's interpretations and placed this exposure in the same upper Oxfordian position, on the basis of lithological correlation, since this lithostratigraphic unit lacks good age indicators.

However, Wierzbowski (2023a, b), on the basis of analysed and restudied ammonites of Liszkowski from the vicinity of Wólka Bałtowska, concluded that this transgressive sequence I-2, exposed in the section, originated during the earliest Kimmeridgian, the Bimammatum Chron, just after the Hypselum Chron (see Wierzbowski *et al*., 2023, fig. 14 for correlation).

An early Kimmeridgian age of the studied outcrop was also indicated on the basis of dinoflagellate cysts (Gedl and Ziaja, 2004). The age estimate was concluded from the co-occurrence of species like *Amphorula dodekovae* Zotto, Drugg et Habib, *Atlantodinium jurassicum* Zotto, Drugg et Habib, *Cribroperidinium venustum* (Klement) Poulsen and *Dichadogonyaulax chondra* (Drugg) Courtinat. *Amphorula dodekovae*, originally described from the lower Kimmeridgian of the North Atlantic (Zotto *et al*., 1987), also found in Poland in lower Kimmeridgian strata (ammonite Hypselocyclum Zone, Poulsen, 1996; it should be noted that ammonites from this zone were found in the overlying Ożarów Oolite and Platy Limestones, Gutowski, 1998, fig. 3). *Amphorula dodekovae* was also described from the Kimmeridgian–lower Tithonian of northern Bulgaria by Dodekova (1992), while Brenner (1988) reported the stratigraphic range of this species as late Oxfordian–early Kimmeridgian. The range of the morphologically similar species, *Amphorula metaelliptica* Dodekova is limited to the Kimmeridgian (Monteil, 1990; Poulsen, 1996).

Atlantodinium jurassicum was also described from the Hypselocyclum Ammonite Zone of Poland (Poulsen, 1996). A longer stratigraphic range of this species, but also limited to the Kimmeridgian, was given by Zotto *et al*. (1987), whereas Dodekova (1992) reported an even younger range: late Kimmeridgian–early Tithonian. *Cribroperidinium venustum*, the most frequent species at Wólka Bałtowska, was described from the lower Kimmeridgian of Poland (ammonite Planula–Divisum zones, Poulsen, 1996).

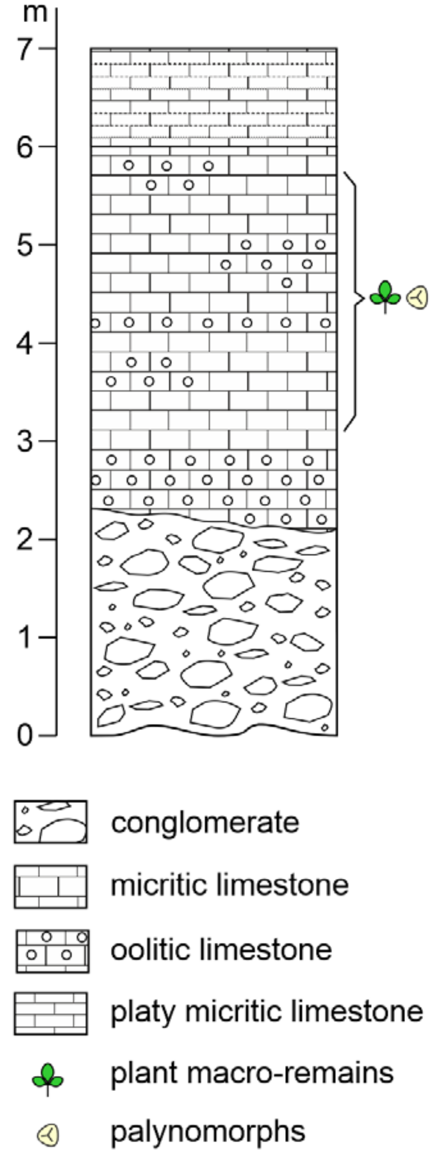

Fig. 2. Part of sequence I-2 exposed at Wólka Bałtowska, with source strata of macro- and microflora marked (based on Liszkowski 1972, 1976; Wierzbowski, 2023a).

MATERIAL AND METHODS

The samples, used for the palaeobotanical research presented in this paper, were collected from the exposure at Wólka Bałtowska by Jerzy Liszkowski, who subsequently gave them to Maria Reymanówna for macrofloristic investigation (see Liszkowski, 1972). This collection is housed at the Herbarium of the W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, Poland, Palaeobotanical Collection, Palaeozoic and Mesozoic (KRAM P, PM).

Liszkowski's material from Wólka Bałtowska contains many specimens (nearly 80), but only some of the collected objects are suitable for macrofloristic examination. The plant remains are preserved in limestone as small fragments of leaves or shoots; most of them are incomplete without base or apex; cone fragments or separate scales are also frequent. Many remains are deep imprints only, which in the case of conifer shoots are clearly visible, giving a 3D effect; thin leaf fragments are almost unrecognizable. In contrast to the poorly preserved gross morphology, the cuticles, where present, are rather well preserved, weakly- or not coalified, light brown or yellow, and often suitable for investigation without maceration. In many specimens, only one (abaxial or adaxial) cuticle was preserved, which, if adaxial only, made identification difficult or doubtful.

Cuticle pieces were usually cleaned in HCl (for 2 hours) and, when necessary, gently macerated in nitric acid (HNO_3), followed by 3% KOH. Slides were examined with a Carl Zeiss Axio Scope A1 transmitted light and fluorescence microscope. Photographs were taken with an AxioCam 305 colour camera. Cuticles for SEM observations were sputter-coated with gold and observed with a Hitachi SU8600 scanning electron microscope in the Scanning Electron Microscopy and Microanalysis Laboratory, Institute of Geological Sciences, Jagiellonian University, Kraków. Pollen *in situ* for SEM observations was sputter-coated with gold and observed with a Hitachi S-2360N scanning electron microscope at 22 kV accelerating voltage and secondary electron detection, at Eötvös Lorand University in Budapest.

One specimen, KRAM P, PM 56/37, was unusually preserved with cells filled with calcium carbonate and visible in 3D as ovoid structures. The cuticle, preserved in some places and covering cells, occurs as a thin yellowish-brown layer. There are clearly visible spaces between cells; this explains how they were filled by the intruding cuticle, which created characteristic thickenings at the narrower sides of the cells.

Six samples of two different lithologies were studied for palynomorphs: four (KRAM P, PM 56/20, KRAM P, PM 56/57/II, KRAM P, PM 56/114/II, KRAM P, PM 56/135/I) are pale beige, platy limestone with frequent land-plant remains, and two (KRAM P, PM 56/48/II, 56/82) represent pale beige oolitic limestone without macrofossils.

Samples were processed in the Micropalaeontological Laboratory of the Institute of Geological Sciences, Polish Academy of Sciences, Kraków, following a palynological procedure that included 38% hydrochloric acid (HCl) treatment, 40% hydrofluoric acid (HF) treatment, heavy liquid ($ZnCl_2$ + HCl; density 2.0 g/cm^3) separation, and 15 μm nylon-mesh sieving. The quantity of rock processed approximates 100 g for each sample. Two slides were made from each sample, using glycerine jelly as the mounting medium. The rock samples, palynological residues and slides are stored in the collection of the Institute of Geological Sciences, Polish Academy of Sciences, Kraków.

In situ pollen grains were obtained by macerating coalified fragments of cone scales isolated from a cone, processing in HCl, HF (for pollen sacs) and Schulze's solution ($KClO_3$ + HNO_3) and 3% KOH (for the isolation of pollen clusters and single pollen grains), washing in distilled water and centrifuging after each stage of preparation.

Hand specimens, slides of cuticles and *in situ* pollen grains are housed at the Herbarium of the W. Szafer Institute of Botany, Polish Academy of Sciences, Kraków, Poland, Palaeobotanical Collection, Palaeozoic and Mesozoic (KRAM P, PM).

For observations of pollen wall ultrastructure, the pollen grains were soaked with propylene oxide and infiltrated and embedded in Durcupan resin. Ultrathin sections (70 nm) were cut with a Reichert-Jung Ultracut E ultramicrotome. Sections stained with uranyl acetate and lead citrate (Reynolds, 1963) were observed with a Hitachi 7100 transmission electron microscope at 75 kV accelerating voltage, at the Eötvös Lorand University in Budapest.

The botanical affinity of the palynomorphs was determined mainly according to basic palaeobotanical studies (Couper, 1958; Van Konijnenburg-van Cittert, 1971; Filatoff, 1975; Balme, 1995; Abbink, 1998; Kelber and Van Konijnenburg-van Cittert, 1998).

All described macroflora remains and their cuticles are shown in Figures 3–9.

SYSTEMATIC PALAEONTOLOGY

Division Tracheophyta Sinnott, 1935
Subdivision Monilophyta Pryer, Schuelttpelz, Wolf, Schneider, Smith et Cranfill, 2004
Class Equisetopsida Agardh, Holmberg et Lundstrom, 1825 *sensu* Chase and Reveal, 2009

Genus et species indet.
Fig. 3A

Material: Three (four) specimens of poorly preserved fragments of stems, without leaf sheaths or free leaves and with poorly visible nodi. Largest fragment 125 mm long.
Hand specimens: KRAM P, PM 56/49, 56/31, 56/61.
Description: Stem fragments 8–25 mm wide. Nodi thin, ill defined, no leaf scars visible. Internodia, where observable ~50 mm long. Surface of impression smooth, one incomplete specimen showing longitudinal ribs spaced 4 mm apart.
Remarks: Probably these specimens were labelled as *Equisetites* sp. by Reymanówna and mentioned by Liszkowski (1972, 1976), but the state of preservation and lack of diagnostic features do not allow determination, even to the genus.

Class POLYPODIOPSIDA Cronquist, Takhtajan et Zimmermann, 1966
Order GLEICHENIALES Schimper, 1869
Family Gleicheniaceae Presl, 1825
Genus *Gleichenites* Göppert, 1836

Type species: *Gleichenites porsildi* Seward, 1926.

cf. *Gleichenites cycadina* (Schenk 1871) Seward, 1926
Fig. 3B

1871 *Alethopteris cycadina* sp. nov. – Schenk, p. 218, pl. 27, figs 6, 6a, pl. 31, fig. 2.

1911 *Gleichenites cycadina* comb. nov. – Seward, p. 664, text-fig. 5; pl. III. figs 48–54A; pl. V, figs 87–89, 92–96.

1984 *Gleichenites cycadina* (Schenk) Seward – Van der Burgh and Van Konijnenburg-van Cittert, p. 365, pl. II, figs 1, 2.

2002 *Gleichenites cycadina* (Schenk) Seward – Van Konijnenburg-van Cittert, pl. 2, fig. 5.

Material: Deep impression of two small fragments of pinnae with unknown venation.
Hand specimens: KRAM P, PM 56/126, 56/89? (including part and counterpart)
Description: Sterile pinnae fragment from apical part, pinnate, with 7 pairs of pinnules. Pinna almost linear but gradually narrowing at apex, 6.5 mm wide at widest point. Pinnules subopposite, with parallel margins and obtuse/rounded apices, attached to rachis along whole width and overlapping it.
Remarks: *Gleichenites* is a fossil genus, of which different species are known from the Triassic (Moisen *et al.*, 2010) to the Paleocene (Liu *et al.*, 1996). Usually, this fern is fragile and preserved as small fragments (Van Konijnenburg-van Cittert, 2002). The typical venation consists of a midvein and forking secondary veins, but in the present specimen the pinnule surface was deeply wrinkled, probably dried before fossilization. This type of wrinkle, in the opinion of the authors, might occur on rather thick, fleshy blades, which is the case of *Gleichenites cycadina*. Although the present fragment is small and preserved without details of venation

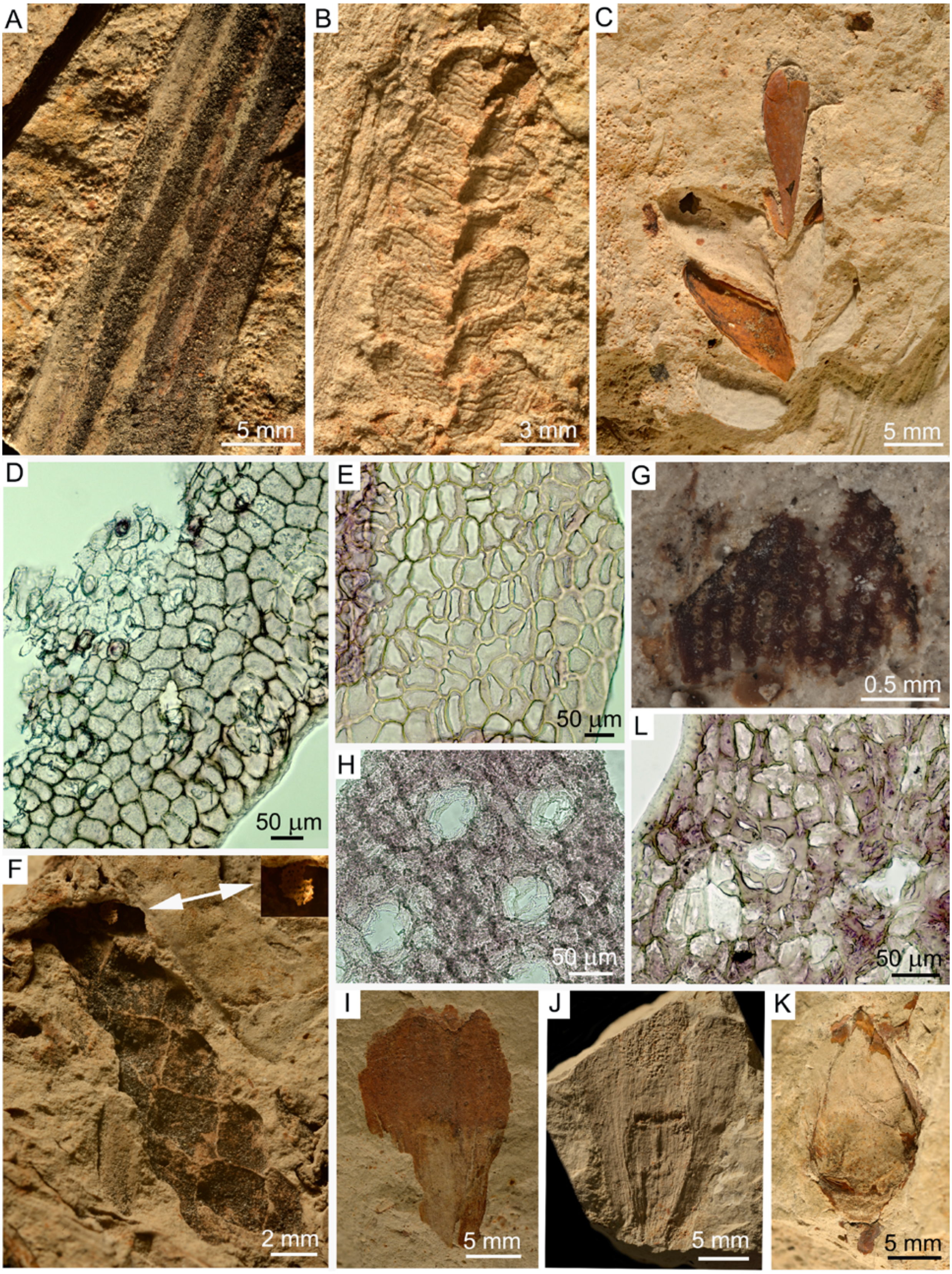

Fig. 3. Sphenopsids, ferns, seed ferns and conifers from Wólka Bałtowska. **A**. Equisetopsida gen. et sp. indet., fragment of stem, specimen KRAM P, PM 56/50. **B**. cf. *Gleichenites cycadina* (Schenk) Seward, fragment of frond, specimen KRAM P, PM 56/126. **C–E.** *Ptilozamites cycadea* (Berger) Möller, specimen KRAM P, PM 56/3 I; C – fragment of leaf; D – abaxial cuticle with stomata and hair bases; E – adaxial cuticle. **F–H.** *Brachyphyllum mamillare* Brongniart; F – fragment of shoot, in the corner magnified leaf fragment showing stomata rows, KRAM P, PM 56/31; G–H – specimen KRAM P, PM 56/23; G – separate leaf with visible stomata rows; H – cuticle with stomata. **I–L**. Female cone scales; I – specimen KRAM P, PM 56/113; J – scale showing single seed imprint, KRAM P, PM 56/128; K–L – specimen KRAM P, PM 56/125; K – scale probably from cone base; L – the cuticle with stomata.

or sori, the authors assigned it to *G. cycadina* on the basis of the similarity of leaf size and the shape and size of pinnules and their bases to previously described specimens of it. This taxon was common in the Upper Jurassic strata of Sutherland, where it occurred in large numbers (Seward, 1911), as well as in the Cretaceous strata of Greenland (Seward, 1927).

Class PTERIDOSPERMOPHYTA Oliver et Scott, 1904
Order and Family *incertae sedis*
Genus *Ptilozamites* Nathorst, 1886 emend. Popa and McElwain, 2009

Type species: *Ptilozamites nilssonii* Nathorst, 1878.

Ptilozamites cycadea (Berger, 1832) Möller, 1902
Fig. 3C–E

1887 *Ctenozamites cycadea* Berger – Schenk, pl. 3, figs. 11–16a; pl. 4, fig. 18; pl. 6, fig. 30; pl. 7, fig. 36; pl. 8, fig. 43; pl. 9, fig. 54.

1902 *Ptilozamites cycadea* Nathorst, comb. nov. – Möller, p. 19.

1964 *Ctenozamites cycadea* (Berger), Schenk – Harris, pl. 4, figs 3, 7; text-figs 41, 42 [with synonymy].

1997 *Ctenozamites cycadea* (Berger) Schenk – Barbacka, figs 1–9, text fig. 1.

2021 *Ptilozamites cycadea* (Berger) Möller – Barbacka *et al.*, p. 706, fig. 3F–H [with synonymy].

Material: The most nearly complete specimen is a 10-mm-long fragment of a pinnate leaf with seven pinnules, rather atypical, possibly due to part damage. Also, some small fragments with few (one or two) pinnules, partly preserved as impressions, partly as compressions with pieces of preparable cuticle, mostly adaxial. Abaxial cuticle frequently damaged.

Hand specimens: KRAM P, PM No: 56/4, 56/8, 56/11, 56/22, 56/31 I, II, 56/32, 56/7; separate pinnules: 56/1, 56/21 56/69, 56/78, 56/64, 56/8.

Description: Pinnules slightly rhomboid or oval, ~10 mm long and 6 mm wide at base. Pinna rachis 1.5 mm wide, striated longitudinally. Pinnules attached along the whole width to rachis, at ~45°. Veins inconspicuous, entering from whole width of base, forking once or twice. Apex subacute. Leaf hypostomatic, adaxial cuticle shows irregularly polygonal cells, without other structures. On abaxial cuticle cells, nearly rectangular or square with rounded corners, forming rows. Stomata randomly arranged over whole abaxial side of pinnule, consisting of 6–7 subsidiary cells forming a thickened ring, with a small cavity above sunken guard cells. One-celled hair bases frequent.

Remarks: The gross morphology and cuticle structure, especially the characteristic stomata of the described specimens, agree with the diagnosis of the genus *Ptilozamites.* Although the specimens are fragmented, the size and shape of pinnules, as well as the cuticle correspond with *Ptilozamites cycadea* (Möller, 1902; Harris, 1964; Barbacka, 1997; Barbacka *et al.*, 2021), which in Poland occurred in the Middle Jurassic of Cianowice (Barbacka *et al.*, 2021).

Class PINOPHYTA Cronquist *et al.*, 1966
Family Araucariaceae Henkel et W. Hochstetter, 1865
Genus *Brachyphyllum* Brongniart, 1828, emend. Harris, 1979

Type species: *Brachyphyllum mamillare* Brongniart ex Lindley and Hutton, 1836.

Brachyphyllum mamillare Brongniart ex Lindley and Hutton, 1836
Figs 3F–L, 4A–F

1828 *Brachyphyllum mamillare* sp. nov. – Brongniart, p. 109.

1836 *Brachyphyllum mamillare* Lindley and Hutton, p. 188.

1947 *Brachyphyllum mamillare* Brongniart – Kendall, p. 230, text-figs 1, 2.

1949 *Brachyphyllum mamillare* Brongniart – Kendall, p. 152, text-figs 2b, c, e, f, 4.

1979 *Brachyphyllum mamillare* Lindley et Hutton – Harris, p. 4, pl. 1, figs 1–14, text figs 1–3.

Leafy shoots
Fig. 3F–H

Material: Small shoot fragments (one with short branch fragments), preserved mainly as deep impressions, with small, poorly preserved cuticle fragments on some leaves. One branched twig, with apically attached male cones.

Hand specimens: 56/3, 56/22/I, 56/17A, C, D (part) 56/23 A, C, D (counterpart), with two male cones attached, 56/124.

Description: Shoots branching in one plane, 3–4 mm wide, leaves helically arranged, 2.5–4 mm wide and 2–4 mm long. Free part of leaf ~1 mm, apex subacute. Leaf amphistomatic, but on adaxial surface stomata rarer. Epidermal cells almost isodiametric, forming longitudinal files, stomata in regular longitudinal rows one-stoma wide. Stomatal pit surrounded usually by 6 subsidiary cells. Papillae not observed.

Remarks: Details of shoots and leaves are barely observable because the material is preserved as three-dimensional impressions, deeply sunken in the rock. Cuticle very fragile, but without maceration the arrangement of stomata and some details are visible. The specimens best fit *Brachyphyllum mamillare*, described by Harris from Yorkshire (Harris, 1979), both in gross morphology and in cuticle structure.

Female cone scales
Fig. 3I–L

Material: Three separate scales: two preserved as imprints without cuticle, one with well-preserved abaxial cuticle.

Hand specimens: KRAM P, PM 56/80 (counterpart), 56/113 (part), 56/125, 56/128.

Description: Scales drop-shaped, 20–25 mm long and 10–17 mm wide at widest point, apex obtuse with pointed tip. Base gradually tapers to a point. In central part near base, single seed imprint observed, 8 mm long. Seed apex obtuse with small incision in middle, base narrows to 1 mm.

Preserved cuticle shows irregularly polygonal cells with well-marked straight cell walls. Stomata forming short rows, consisting of small guard cells, surrounded by rim of 5–6 subsidiary cells, often slightly bulging. Encircling cells triangular to rectangular, radially arranged around stomata.

Remarks: The scales with a single seed are characteristic of the genus *Araucarites* (Harris, 1979; Kunzmann, 2007), which can be related to the fossil genus *Brachyphyllum* (Harris, 1979; Kunzmann, 2007). The described scales may belong to a cone of *B. mamillare*, in the case of the Yorkshire material (Harris, 1979).

The scales correspond with the species *Araucarites phillipsii* Harris (Harris, 1979) from Yorkshire in their general form and size, but differ in cuticle structure. The first difference is that stomata are present on the adaxial cuticle, but not on the abaxial cuticle in *A. phillipsii*, while in the scale from Wólka Bałtowska the abaxial cuticle shows numerous stomata. This might be expected, because the outer side of the scale has more opportunity for photosynthesis than the inner side, which is less exposed to sunlight during most of its development. The second difference is in the structure of stomata, which in *A. phillipsii* have occasional unspecialised encircling cells; in the present specimen they are always present and belong to stomatal complex. The cuticle of *A. phillipsii* corresponds with cuticle of *Brachyphyllum mamillare* Lindley et Hutton (Harris, 1979). The cuticle of the scale from Wólka Bałtowska is similar in its isodiametric cell shape and the short longitudinal files it forms; also similarly, the stomata have 6 subsidiary cells without papillae. The scales differ slightly in shape and size. These differences agree with the usual variability between scales, placed in different positions within the cone. Those having the narrowest base indicate their position at the base of the cone (basal scales have very narrow bases), while two others probably were in the middle part of the cone.

Male cone
Fig. 4A–F

Material: Ten cones preserved in different states as surface impression and in section. Impressions of two cones attached to tips of once-branched twig.

Hand specimens: KRAM P, PM 56/1, 56/17 (part) 56/23 (counterpart), two cones attached, 56/118, 56/53, 56/70/I (preserved as transversal section), 56/92/I, 56/110, 56/116 (preserved as longitudinal section).

Description: Male cones singly borne terminally on leafy twigs. Small, ovoid, ~10 mm long, 9 mm wide near base. Axis conical, at widest point as wide as length of microsporophylls (on longitudinal section ratio 1:1:1). Microsporophylls crowded, helically arranged (high parastichy), with narrow stalk, distal lamina triangular, imbricate, 1 mm long, 0.75 mm at base, with acute tip, ~30 visible on exposed half of cone. Pollen sacs ~3 mm long, arrangement of pollen sacs on sporophyll unknown. Two types of pollen grains were isolated from the cone.

Pollen grains type 1 (Figs 4G–K, 5A, B): in light microscopy, pollen grains almost circular in outline, without apertures. Exine ~1.7 μm thick with various secondary folds, scabrate to finely granulate, in SEM visible as microechinate or microgranulate. Sculpture elements densely distributed. Exine folded. In section (TEM) exine ~1.7 μm thick, distinctly layered. Outer layer (ectexine) 0.6–1.1 μm thick, consisting of irregularly shaped granular elements, 0.1–0.2 μm in diameter. Inner layer (endexine I) ~0.5 μm thick, lamellate. Lamellae 0.045–0.09 μm thick; 8–12 lamellae can be distinguished within endexine I. Innermost layer (endexine II) homogenous, ~0.2 μm thick (Fig. 4K).

Dimensions: Diameter (in LM) 52.2–76.1 μm (41 specimens measured from cone KRAM P, PM 56/116), 58.7–78.3 μm (5 specimens measured from cone KRAM P, PM 56/118), 37.0–65.2 μm (10 specimens measured from cone KRAM P, PM 56/120).

Dimensions: Diameter (in SEM) 39.5–45.9 μm (4 specimens measured from cone KRAM P, PM 56/116).

Pollen grains type 2 (Fig. 6A, B): in light microscopy, pollen grains without apertures. Central body usually distinct, circular or roundly triangular 50–60 μm in diameter. Ectexine ~0.6 μm thick, finely granulate, separated from endexine, forming a saccus-like structure, similar to velum.

Dimensions: Diameter of whole pollen grain: 54.3–65.2 μm (2 specimens measured from cone no KRAM P, PM 56/116), 52.2–73.9 (6 specimens measured from cone KRAM P, PM 56/118), 43.5–47.8 μm (2 specimens measured from cone KRAM P, PM 56/120).

Remarks: The described specimens agree with the male cones of *Brachyphyllum mamillare* (found in organic connection with shoots), described by Kendall (1949) and Harris (1979), also containing *Araucariacites australis* Cookson ex Couper pollen grains of araucarialean affinity (Couper, 1958). The cones from Wólka Bałtowska have the same terminal position on the shoots, but are more spherical, and the pollen sac is twice as long as in the Yorkshire cones. Kendall (1949), studying the same cones that Harris (1979) examined later, maintained that the cones from Yorkshire were juvenile, which could explain the size differences. It also could explain the width of the cone axis, which is wider and more conical than in the material, illustrated by Kendall or Harris. The difference in the section plane is also relevant. Since the present material is also connected to the shoots, there are no doubts as to the determination.

Pollen grains type 1, separated from cones KRAM P, PM 56/116, 56/118 and 56/120 from Wólka Bałtowska are similar to the dispersed *Araucariacites australis* pollen grains, described by e.g., Couper (1953), while type 2 resembles dispersed *Callialasporites* (mainly *Callialasporites dampieri* (Fig. 6A) and *Callialasporites segmentatus* (Fig. 6B). Dispersed araucariaceous pollen grains were observed in the latest Lower Jurassic to Lower Cretaceous sediments (Filatoff, 1975). In north-western Europe, *Araucariacites* was noted from the ?Rhaetian and Hettangian and *Callialasporites* from the late Toarcian (Batten and Koppelhus, 1996), although Orłowska-Zwolińska (1983) reported *Araucariacites australis* from the Late Triassic of Poland.

Both *Araucariacites* and *Callialasporites* pollen grains, found *in situ* inside the same cones, were found in male cones, associated with *Brachyphyllum mirandai* (Archangelsky, 1963), in cones attached to or associated with *Brachyphyllum mamillare* from the Middle Jurassic

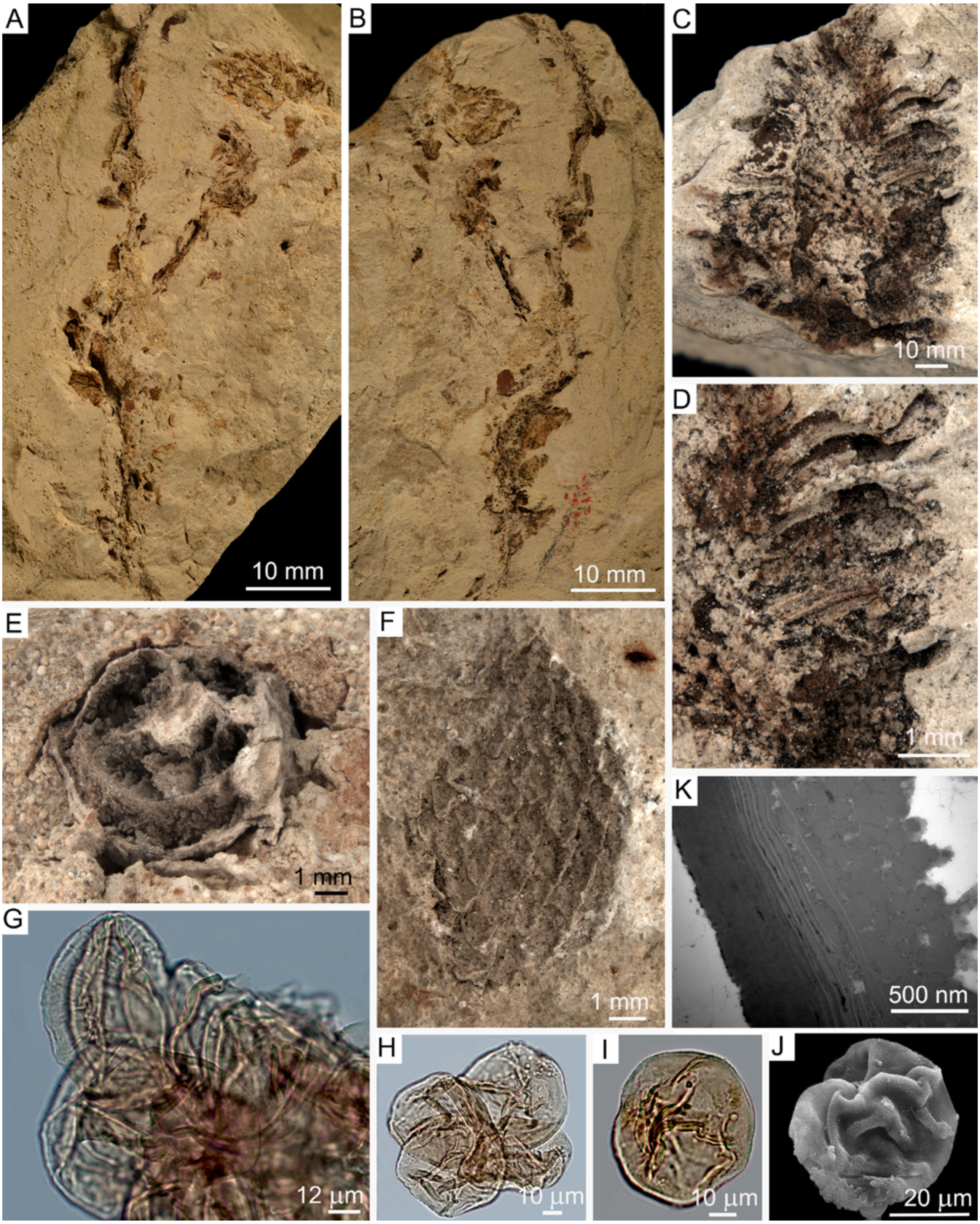

Fig. 4. Araucariacean conifers from Wólka Bałtowska. **A–F.** *Brachyphyllum mamillare* Brongniart, male cones; A–B – shoot with distally attached cone (part and counterpart) KRAM P, PM 56/17, 56/23; C – cone in longitudinal section, KRAM P, PM 56/116; D – magnified part of C, showing microsporophylls; E – cone in transverse section KRAM P, PM 56/70; F – cone with outer surface preserved, distal blades of microsporophylls are visible KRAM P, PM 56/56. **G.** Cluster of pollen grains type 1 and 2 (similar to dispersed *Araucariacites australis* and *Callialasporites dampieri*), isolated from cone KRAM P, PM 56/116, slide KRAM P, PM 56/116/P/2 [R 37/4], scale bars = 20µm. **H–K.** Pollen grains type 1 (similar to dispersed *Araucariacites australis* Cookson ex Couper), isolated from cone KRAM P, PM 56/116; H – tetrad of pollen grains slide KRAM P, PM 56/116/P/2 [F 41/3]; I – single pollen grain, KRAM P, PM 56/116/P/2 [E 48/3]; J – the surface of pollen grain in SEM; K – ultrastructure of pollen wall, TEM picture.

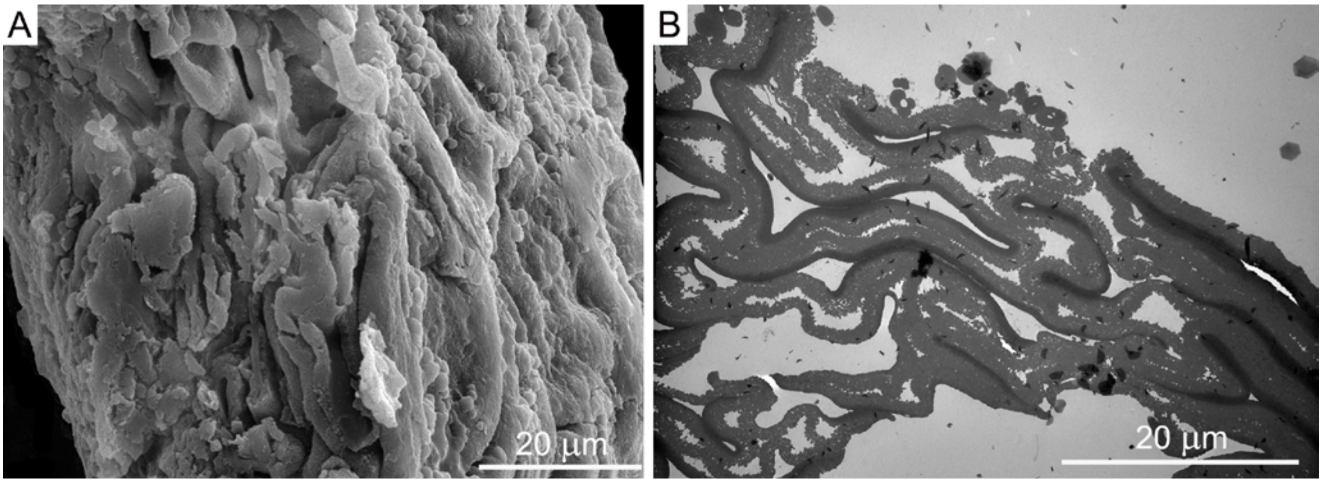

Fig. 5. Pollen grains of *Brachyphyllum mamillare* male cone. **A.** Concentration of compressed pollen grains in pollen sack, isolated from the cone KRAM P, PM 56/116, SEM picture. **B.** The same cone as A, section of pollen sack and pollen grains inside, TEM picture.

of England (Van Konijnenburg-van Cittert, 1971), in separated *Masculostrobus graiterensis* Allenbach et Van Konijnenburg-van Cittert cones from the Late Jurassic of Switzerland (Allenbach and Van Konijnenburg-van Cittert, 1997), inside a single separated *Upatoia barnardii* Leslie, Herendeen et Crane cone from the Late Cretaceous of Georgia, USA (Leslie *et al.*, 2009) and in a single dispersed *Callialastrobus sousai* J. Kvaček et Mendes pollen cone from the Early Cretaceous of Portugal (Kvaček and Mendes, 2020; Tekleva *et al.*, 2022). These two types of pollen have also been observed in cones of modern *Araucaria araucana* (Molina) K. Koch (Van Konijnenburg-van Cittert, 1971) and *Araucaria excelsa* (Lamb.) R. Br. (Courtinant, 1987).

The percentage of *Callialasporites* pollen grains in relation to *Araucariacites* pollen grains in the material from cones of *Brachyphyllum mamillare* from Poland (16% *versus* 84%) is lower than that reported by Van Konijnenburg-van Cittert (1971) for material from England (49% *versus* 51%), perhaps due to different degrees of cone maturation.

The wall ultrastructure of dispersed *Araucariacites* pollen, observed in TEM, was described by Kedves and Pardutz (1974), Zavada (1992), Archangelsky (1994), Batten and Dutta (1997), and of those *in situ* by Del Fueyo (1991) and Tekleva *et al.* (2022). All of these studies confirm the presence of an outer granular layer (called the sexine or ectexine), a lamellar layer (outer layer of the nexine or ectexine I) and a homogeneous layer (inner layer of the nexine or ectexine II). Del Fueyo (1991) presented the ultrastructure of *Araucariacites* pollen grains from *Nothopehuen brevis* Del Fueyo cones, attached to branches with leaves of *Brachyphyllum* type, from the Early Cretaceous of Argentina, and Tekleva *et al.* (2022) described and illustrated it from a *Callialastrobus sousai* cone. The ultrastructure of *in situ Araucariacites* pollen grains with an affinity to *Brachyphyllum mamillare* is presented here for the first time. The ultrastructure of *in situ Callialasporites* from the cones of *Brachyphyllum mamillare* from Poland was not studied.

Family Hirmeriellaceae Harris, 1979
Genus *Brachyphyllum*, Brongniart, 1828, emend. Harris, 1979

Type species: *Brachyphyllum mamillare* Brongniart ex Lindley and Hutton, 1836.

Brachyphyllum crucis Kendall, 1947
Fig. 6C–G

1947 *Brachyphyllum crucis* sp. nov. Kendall, p. 240, text figs 5, 6.
1971 *Brachyphyllum crucis* Kendall – Van Konijnenburg -van Cittert, p. 59, pl. 14, figs 3–6; pl. 15, figs 1, 2, 4; pl. 16, fig. 1; text figs 8, 9.
1972 *Brachyphyllum crucis* Kendall – Van Konijnenburg -van Cittert, p. 98, pl. 1, fig 3.
1979 *Brachyphyllum crucis* Kendall – Harris, p. 16, text figs 6, 7.
1999 *Brachyphyllum crucis* Kendall – Van Konijnenburg -van Cittert and Morgans, p. 114, pl. 19, fig. 4.
2006 *Brachyphyllum crucis* Kendall – Barbacka *et al.*, p. 41, pl. II, figs 5–6.

Leafy shoots
Fig. 6C–F

Material: Small shoot fragments ~15 mm long, one of them branching, preserved mainly as deep impressions, with cuticle on some leaves.

Hand specimens: KRAM P, PM No: 56/4A, 56/ 17B (part), 56/23 B (counterpart), 56/27, 56/29, 56/31A, B, 56/42, 56/47, 56/50, 56/57, 56/59, 56/61, 56/68, 56/73, 56/75/IV, 56/76, 56/101, 56/102, 56/104, 56/121/I.

Description: Shoot fragments 3–4 mm wide, densely covered with leaves. Leaves coriaceous, arranged spirally, usually 3 x 3 mm. Free part of leaf usually ~1mm, occasionally up to 2.5 mm, truncate in section. Apex acute or subacute. Lower surface of leaf bears a keel. Leaf margins entire.

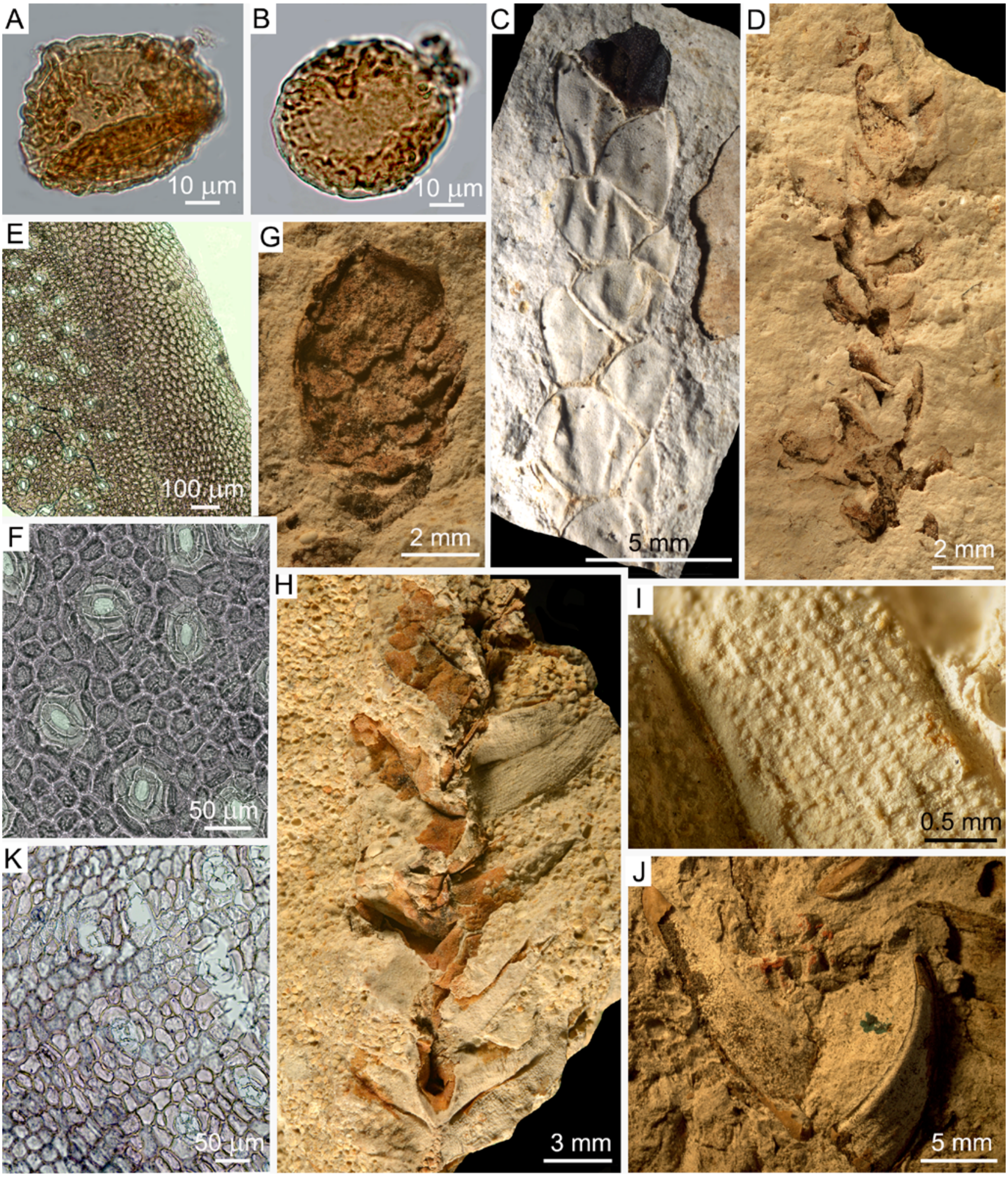

Fig. 6. Araucariacean and cheirolepidiacean conifers from Wólka Bałtowska. **A–B.** *Brachyphyllum mamillare* Brongniart, pollen grain type 2 (similar to dispersed *Callialasporites*; A – *Callialasporites dampieri* (Balme) Sukh Dev, isolated from cone KRAM P, PM 56/118, slide KRAM P, PM 56/118/P/1; B – *Callialasporites segmentatus* (Balme) Srivastava isolated from the cone KRAM P, PM 56/116, slide KRAM P, PM 56/116/P/2 [G 47/3]. **C–D.** *Brachyphyllum crucis* Kendall; C – specimen KRAM P, PM 56/17; D – KRAM P, PM 56/17a. **E–F.** Adaxial cuticle with randomly distributed stomata from KRAM P, PM 56/17B. **G.** Male cone, probably belonging to *Brachyphyllum crucis* KRAM P, PM 56/100. **H–J.** *Pagiophyllum araucarinum* (Pomel) Saporta; H – specimen KRAM P, PM 56/78 III; I – detail from H, imprint of stomata rows; J – specimen KRAM P, PM 56/4.

Cuticle thick, the abaxial showing irregular cells with thick, straight cell walls and slightly rounded corners. Periclinal walls striated. Stomata scattered on entire leaf surface, less frequent at apex, where they tend to form short rows. Guard cells slightly sunken, surrounded by regular oval or circular ring of 5–6 subsidiary cells. Their periclinal walls near stomatal pits slightly bulge, but do not form papillae. Encircling cells often triangular, radially arranged around stoma. Stomatal apparatus cells differ from ordinary cells, remaining dark in fluorescence microscopy.

Remarks: The characteristic features of this species are its relatively long free part of leaves, and the stomata, scattered on the whole abaxial surface. Because of the shape of the leaves and the expanded cushion, the adaxial surface in *Brachyphyllum* may be very small and not really characteristic (Kendall 1947), probably all the cuticles the present authors obtained from the rock were abaxial. The scattered stomata and striations on the periclinal cell walls, as well as the leaf shape, are characteristic for this species. The structure of stomata agrees with those described by Harris (1979) and Kendall (1947). *Brachyphyllum crucis* is known from Great Britain: Christian Malford (Wiltshire; Kendall, 1947), Oxfordshire (Kendall, 1952) and Hasty Bank, Yorkshire (Harris, 1979; Van Konijnenburg-van Cittert and Morgans, 1999). It was also described from Puale Bay, in Alaska (Barbacka *et al.*, 2006). All data on this species originate from localities with marine strata; it seems connected with a saline environment (Kendall, 1947, 1952; Harris, 1979), which also corresponds with the Wólka Bałtowska locality.

Male cone
Fig. 6G

Material: Three more or less complete cones without cuticle and pollen *in situ*.

Hand specimens: KRAM P, PM 56/26, 56/94, 56/100/ I, 56/100/II.

Description: Ovoid cone, 10 mm long and 5 mm wide, with subacute apex. Microsporophylls rather large, helically arranged with low parastichy, not crowded, 14 visible on one exposed side of cone. Distal lamina 1–1.5 mm long and 1 mm wide, widely rhomboid with obtuse to subacute apex. Position and number of pollen sacs unknown, pollen grains unknown.

Remarks: Morphologically, the cone resembles *Classostrobus rishra* (Barnard) Alvin, Spicer et Watson. The present material is also very similar to a cone described by Van Konijnenburg-van Cittert (1971) as strongly believed to belong to *B. crucis* (close association, but not attached to leafy shoot, see discussion on p. 61). She isolated pollen grains of *Classopollis* type, which after prolonged maceration were comparable to *Classopollis multistriatus*.

The low number of parastichies and the *Classopollis* pollen grains distinguish Hirmeriellaceae from Araucariaceae, which have their microsporophylls in higher (8 + 13) parastichies and have *Araucariacites* pollen grains (Cookson, 1947).

Since pollen grains were not found inside the cone from Wólka Bałtowska, the classification is based on cone morphology and co-occurrence with *B. crucis* at the locality.

Additionally, in the sediment there are numerous pollen grains from the genus *Classopollis* (if they originate from the present male cone, it may be classified as *Classostrobus* sp.).

Genus *Pagiophyllum* Heer, 1881

Type species: *Pagiophyllum circinicum* (Saporta, 1873) Heer, 1881.

Pagiophyllum araucarinum (Pomel, 1849) Saporta, 1879
Figs 6H–J, 7A

1981 *Pagiophyllum araucarinum* (Pomel) Saporta – Barale p. 172, pls 49–50, text fig. 45 [with references].

2003 *Pagiophyllum araucarinum* (Schimper) Barale – Thévenard *et al.*, p. 72, pl. 1, figs 6–10.

Material: Some small fragments of leafy shoots and separate leaves with coriaceous cuticle, frequently strongly pressed into rock matrix, making leaf bases barely recognisable.

Hand specimens: KRAM P, PM 56/4B, 78 I, III.

Description: Leafy shoots 12–15 mm wide. Leaves borne helically, free part up to or more than 20 mm long and up to 7 mm wide, widest at base, truncate to often falcate, depending on leaf morphotype. Two leaf morphotypes observed. One, narrow, linear or falcate, length 15–18 mm, width 2–6 mm with acute/subacute apex; second, truncate, 7–10 mm long, 2–7 mm wide, with subacute apex. Stomatal strips observable macromorphologically, in first morphotype 12 stomatal rows on surface, in second morphotype 2 x 12 stomatal strips separated by non-stomatal area in middle part of leaf. Cuticle coriaceous. Leaf probably amphistomatic, no cuticle without stomata found. Cuticle structure the same in both morphotypes. Cells with thick cell walls, square to elongated, sporadically irregular, uniform on whole surface, generally in regular longitudinal rows. Stomata in single rows, separated by 1–3 cell- wide non-stomatal bands. 4–5 subsidiary cells bearing papillae directed towards stomatal pit. Stomatal apparatus surrounded by 7 encircling cells.

Remarks: The species *Pagiophyllum araucarinum*, after extended revision by Barale (1981) was synonymised with three other species: *P. connivens* Kendall, *P. rigidum* Saporta and *P. kurri* Pomel, based on leaf size and shape (which may be quite varied), but mainly on strong similarity of cuticle structure. Specimens from Wólka Bałtowska in gross morphology are comparable with *P. araucarinum sensu* Barale (1981). Narrow leaves correspond with *P. kurri* (Harris, 1979; Barale, 1981); wide ones resemble *P. araucarinum* (Barale 1981), as far as could be observed in deformed fragments. Because the specimens are highly compressed, in most cases the leaf bases and their attachment to the shoots are not visible; nor was the square leaf. However, the cuticle well corresponds with descriptions and illustrations of *P. araucarinum*, for example in cell shape, stomata arrangement of and structure, including the presence and shape of papillae on subsidiary cells.

The difference is in the presence of encircling cells, which were not described in *P. araucarinum* but always visible in cuticles from Wólka Bałtowska. Despite this detail, the present authors regard the material from Wólka Bałtowska as *P. araucarinum.*

Unidentified conifer male cone
Figs 7B, C

Material: One specimen poorly preserved
Hand specimen: KRAM P, PM 56/96.
Description: Male cone, cylindrical, with widely rounded apex. Estimated size ~10 mm long and 4.5 mm wide. Axis linear, 1 mm wide. Microsporophylls 2.5 mm long, helical, crowded, distal blade a narrow triangle 1 mm long, 0.75 mm wide at base, with elongated acute apex. Pollen sacs and pollen grains unknown.
Remarks: The specimen probably represents an araucarialean type of male cone with crowded microsporophylls and small distal blades. It differs from another araucarialean cone from this locality, belonging to *Brachyphyllum mamillare,* in having a linear axis and cylindrical shape. The lack of preserved details prevents classification, even to the genus. A similar cone was illustrated by Barnard (1968, text fig. 2E, F) from the Stonesfield Slate, and classified as an "elliptical group 2 cone (possibly Araucarian male cone)" but the present specimen is half the size of Barnard's cone, which was 20 mm long and 10 mm wide.

Subdivision GYMNOSPERMAE Prantl, 1874
Gymnospermae *incertae sedis*
Family Pseudotorelliaceae Krassilov, 1972
Genus *Pseudotorellia* Florin, 1936

Type species: *Pseudotorellia nordenskioeldii* (Nathorst, 1897) Florin, 1936.

Pseudotorellia solida Barbacka et Pacyna new species
Figs 7D–H, 8A–F, 9A–C

Holotype: KRAM P, PM 56/130, Figs 7D, 8A, B, E, F, Herbarium of the W. Szafer Institute of Botany, Polish Academy of Sciences, Cracow, Poland, Palaeobotanical collection, Palaeozoic and Mesozoic (KRAM P, PM).
Paratype: KRAM P, PM 56/37 Fig. 7F–H, Herbarium of the W. Szafer Institute of Botany, Polish Academy of Sciences, Cracow, Poland, Palaeobotanical collection, Paleozoic and Mesozoic (KRAM P, PM).
Etymology: From the solid, stiff leaves.
Referred material: Nine fragments on eight specimens, without base, with clearly visible venation details and cuticle, stored in the collection of the W. Szafer Institute of Botany, Polish Academy of Sciences, no KRAM P, PM 56/28, 56/37, 56/59, 56/73, 56/**77**, 56/68 I, II, 56/87, 56/115, 56/130, 56/134.
Diagnosis: Leaves linear, with rounded apex, margins entire. Veins distinct, parallel, 8 per leaf. Areas between veins 1.25 times wider than veins. Leaf hypostomatic, cuticle thick on both adaxial and abaxial sides. Cell pattern the same on both cuticles; cells elongated, above veins narrower than between veins, arranged in longitudinal rows. On abaxial side, cells in stomatal bands slightly shorter than between bands. Cell walls straight. Each cell with thickened ridge along its long axis. In stomatal bands, ridges running from stoma to stoma, their ends turning into papillae, surrounding stomatal pits. In non-stomatal bands and on adaxial cuticle, ridges run continuously, interrupted with slight incisions.

Stomata oriented longitudinally, forming single rows, arranged in wide bands. Rows separated by 2–3 files of ordinary cells. Stomata having 4–6 subsidiary cells including two polar cells, papillae directed towards stomatal pits.
Description: Leaves linear, 5–7 mm wide, with parallel, entire margins narrowing slightly to obtuse-rounded apex. Veins distinct, parallel, usually 8 per leaf, ~ 280 wide *versus* ~350 µm wide stomatal strips in between (ratio 1:1.25).

Cuticle thick, uniformly thick on both adaxial and abaxial sides. Cells similar on both sides, from rectangular between stomata to elongated above veins, forming longitudinal files. Cell walls straight; from outer side, periclinal walls of all cells with strongly thickened longitudinal ridge, most often in middle of cell, running continuously through more than one cell. Ridges at ~600 µm wide strip near leaf margin on both surfaces flat, slightly marked, then gradually become more developed. In stomatal bands, ridges running from stoma to stoma have spherically expanded ends, forming a type of papillae above stomatal pit. Ridges running near stomatal pit have papillae-like thickenings on their sides. Frequently, ridges within stomatal bands show a series of prominent cylindrical thickenings along them. In non-stomatal bands and on the outer side of adaxial cuticle, ridges longer, without additional thickenings, and with occasional interruptions every few cells. From the inner side of both cuticles, space between neighbouring cells at their transversal walls highly cutinised, forming more or less rectangular to square thickness at end of each cell, often with protruding edges.

Between stomata these thickenings less distinct. Generally, cuticle layer reaches deep between epidermal cells on whole leaf surface.

Stomata numerous, longitudinally oriented, sunken, arranged in single longitudinal files, 14 –20 per band. Stomatal files separated from each other by 2–3-celled rows of ordinary cells. Well-cutinised guard cells surrounded by 4–5(6) subsidiary cells: two polar cells and 2–3(4) side cells; edges of stomatal pit thickened; 4–5 papillae directed inwards.
Remarks: *Pseudotorellia* is a genus, widely distributed in the north-eastern parts of the globe, on the territory of Eurasia: Northern and Central Europe, Central Asia, Kazakhstan (most diverse), Siberia, the Far East and China (Bugdaeva, 1999). More than forty species were created on the basis of leaf morphology and cuticle structure. Generally, the genus is represented by small, single, elongated leaves. Individual species differ in leaf size, shape (narrower or wider, linear or tongue-shaped) or in the number of veins, which is not very variable, reaching in different species from 2 to 4, with some exceptions, such as *P. striata* (7–9) or *P. kiensis* (15–20) (Nosova and Golovneva, 2018). In cuticle structure, most differences are regarding the shape of cells (more or less rectangular), their arrangement (in rows or irregular), the distribution of stomata (in wider or narrower bands, and within them, in rows or scattered). The structure of stomata

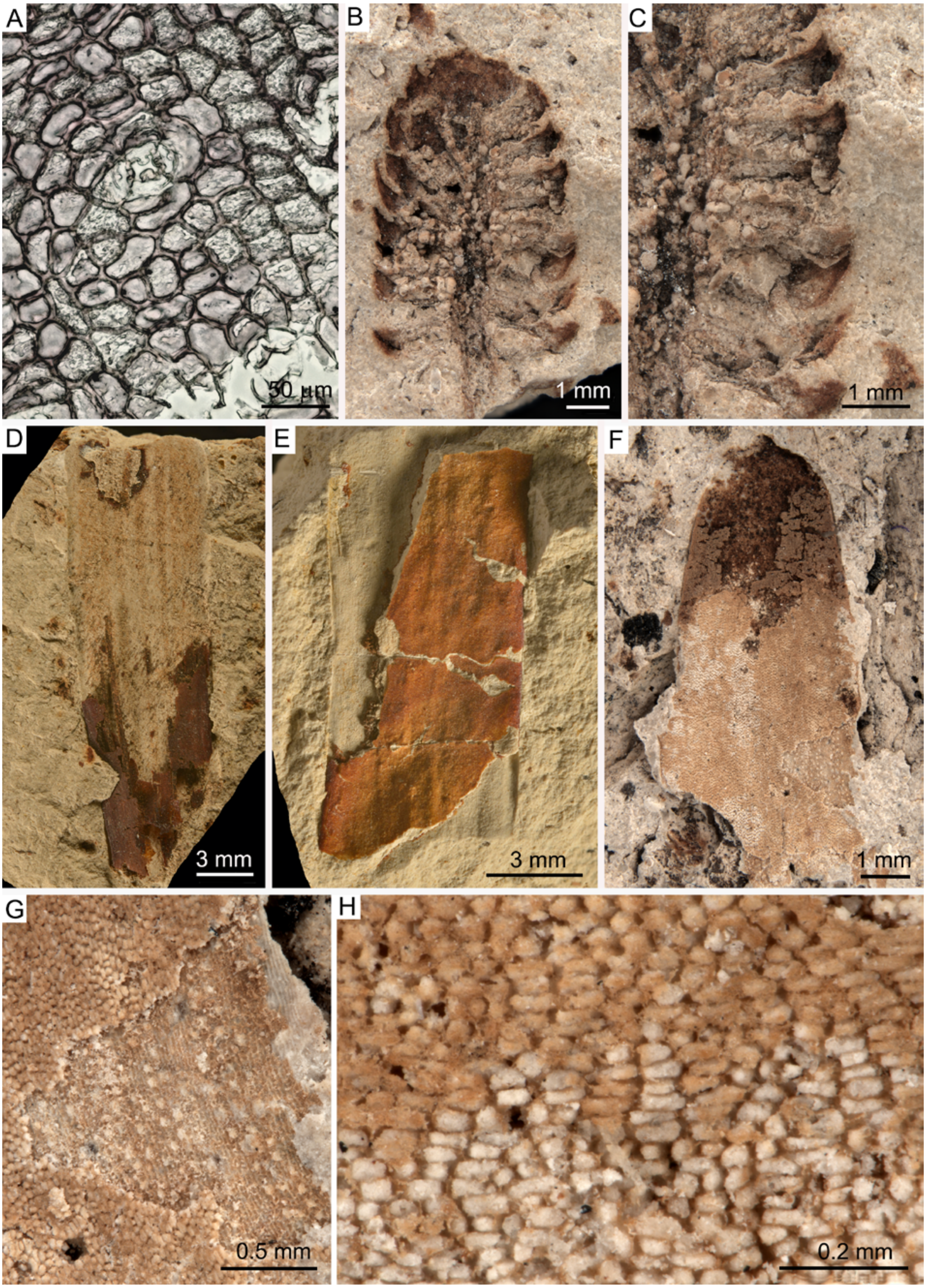

Fig. 7. Conifers and gymnosperm *incertae sedis* from Wólka Bałtowska. **A.** *Pagiophyllum araucarinum* (Pomel) Saporta, cuticle with papillate stomata. **B–C.** Unidentified conifer male cone, KRAM P, PM 56/96. **D–H.** *Pseudotorellia solida* Barbacka et Pacyna sp. nov.; D – specimen KRAM P, PM 56/130; E – specimen KRAM P, PM 56/87 I; F – specimen KRAM P, PM 56/37 unusually preserved with cells filled with calcium carbonate; G – detail of F with visible inner side of abaxial cuticle; H – detail from F with visible outer side of adaxial cuticle, thin yellowish-brown layer on the surface is remaining cuticle, visible spaces between cells, where the intruding cuticle created characteristic thickenings at the narrower sides of the cells.

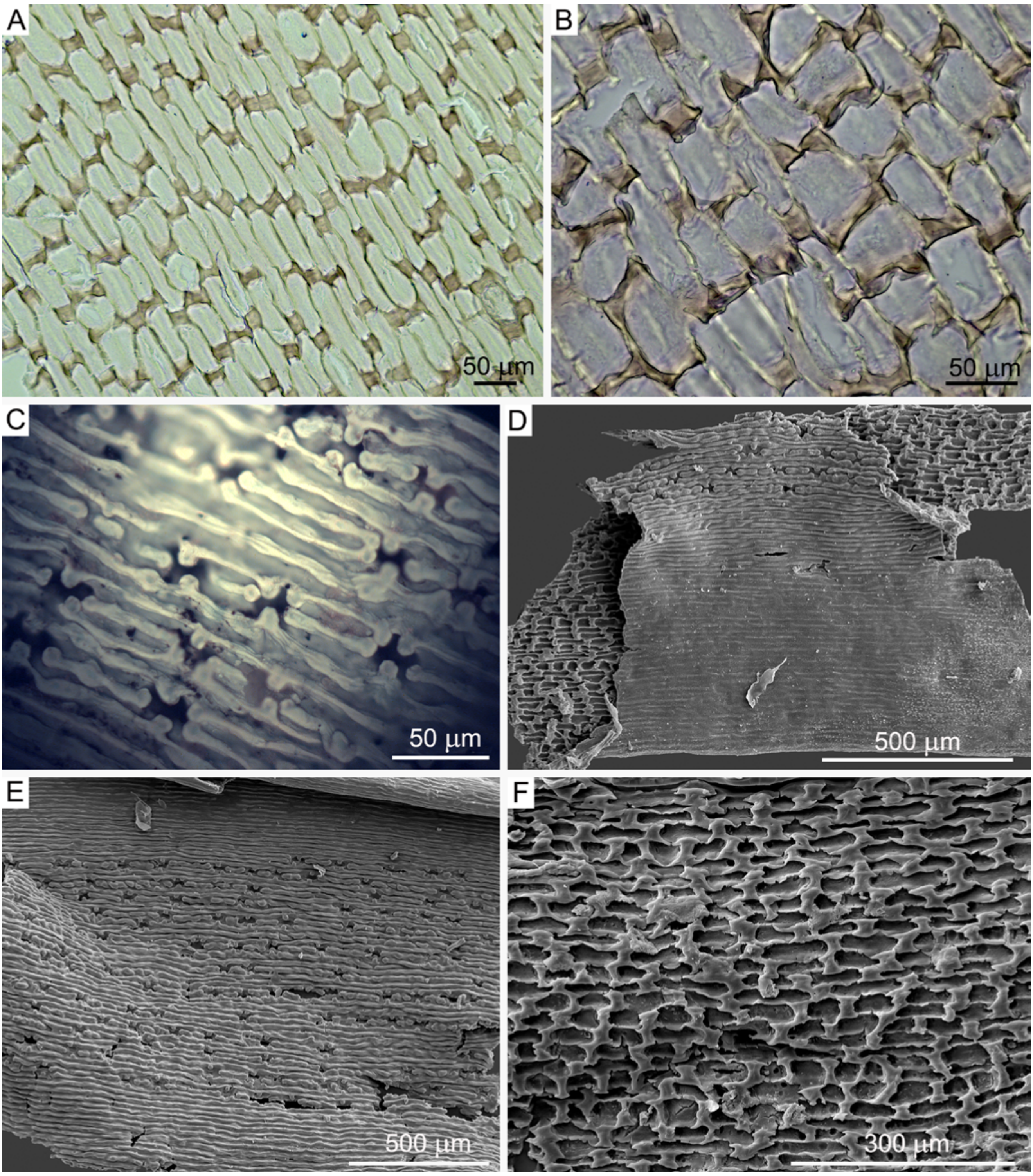

Fig. 8. Gymnosperms *incertae sedis* from Wólka Bałtowska. **A–F.** *Pseudotorellia solida* Barbacka et Pacyna sp. nov., cuticle structure; A–B – adaxial cuticle with characteristic thickenings of cuticle from outer side in light microscope KRAM P, PM 56/130; C – abaxial cuticle inner side with thickenings along cells and stomata in fluorescent microscope KRAM P, PM 56/125a; D – inner side of adaxial, and outer side of abaxial cuticle, noticeable gradual thickening of cuticle ridges from leaf margin towards middle, SEM picture KRAM P, PM 56/59B; E – outer side of abaxial cuticle, general view; F – thickenings on inner side of adaxial cuticle in SEM, both E, F KRAM P, PM 56/130.

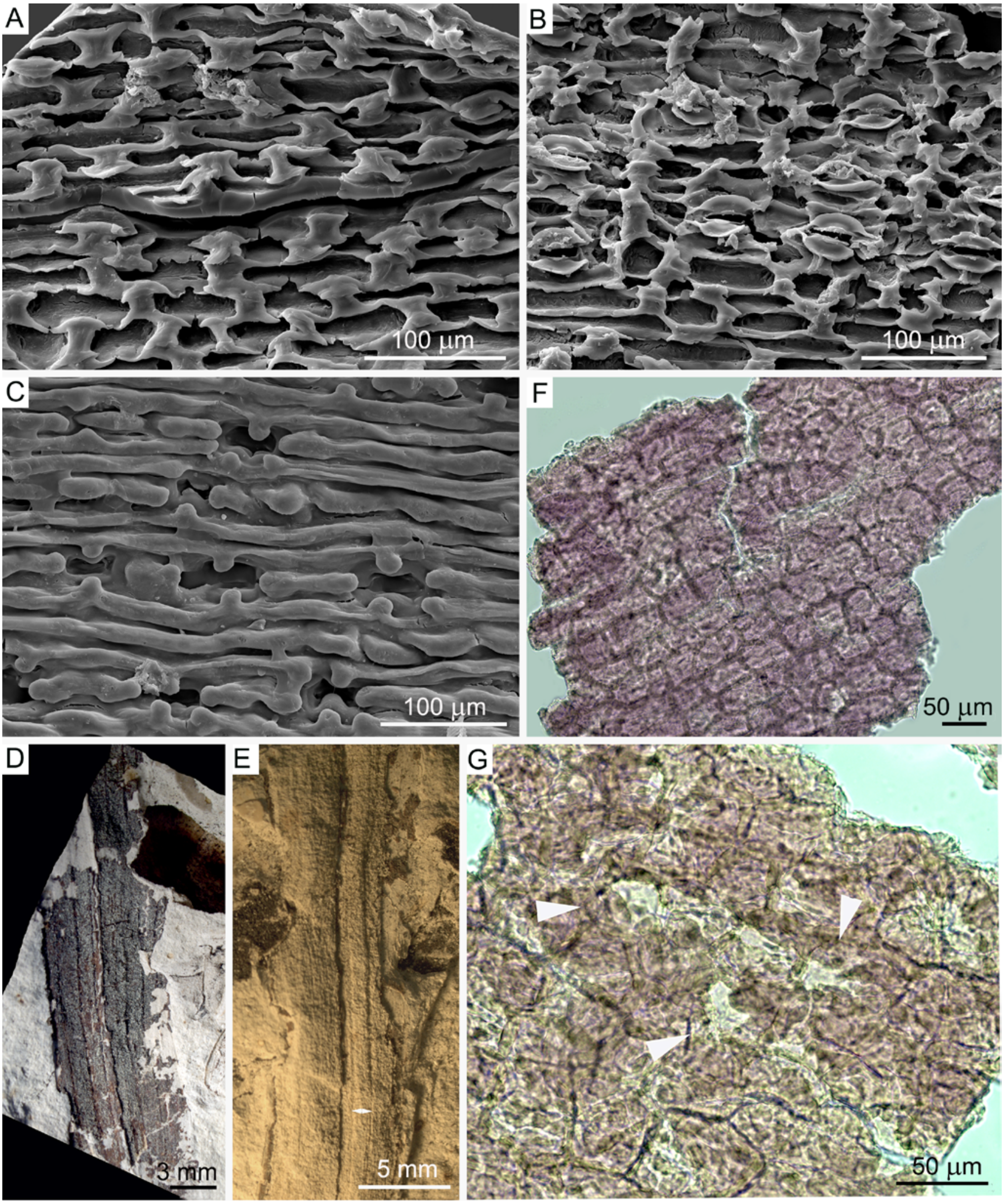

Fig. 9. Gymnosperms *incertae sedis* from Wólka Bałtowska. **A–C.** *Pseudotorellia solida* Barbacka et Pacyna sp. nov.; A – detail from Figure 8F; B – abaxial cuticle inner side with stomata and thickenings; C – Outer surface of abaxial cuticle with ridges and stomata. **D–G.** *Taeniatus elongatus* Takimoto, Ohana et Kimura; D – specimen KRAM P, PM 56/49; E – specimen KRAM P, PM 56/59A, double-sided arrow indicates width of the midvein; F – adaxial cuticle KRAM P, PM 56/49; G – abaxial cuticle with papillate stomata (arrows) KRAM P, PM 56/49.

is rather constant; differences lie in the presence or absence of papillae on subsidiary cells.

Although the specimens from Wólka Bałtowska are preserved only fragmentarily, mainly fragments of the middle part of leaves with one apex and no preserved leaf base, the cuticle is characteristic enough for the proposal of a new species. The constant number of veins and relatively wide stomatal bands are the main macroscopic features; in cuticle structure, the new species is recognizable by its very regular stomatal rows, longitudinal ribs and square thickening on the transversal cell walls on both cuticles. Similar ribs with papillae at their ends are observable only in *Pseudotorellia insolita* Nosova et Golovnevna (Nosova and Golovnevna, 2011), but there the ordinary cells are different in shape, have strongly sinusoid cell walls, and the stomata form narrow bands. Ridges in non-stomatal bands are not continuous but interrupted (ending within cells).

The thickenings at the ends of cells are characteristic exclusively for the proposed new species. In a few other species, like *P. angustifolia* Doludenko, or *P. gracilis* Kiritchkova, the transversal cell walls are about twice as thick as the longitudinal walls (Kiritchkova and Nosova, 2012), which is much less than in *P. solida* sp. nov.

The thickness of both cuticles, the system of longitudinal and transversal thickenings and the strong protection of stomata allow the authors to conclude that the plant was exposed to strong mechanical effects, such as wind, and the stiffening of the leaves is a response to unfavourable climatic conditions.

Type locality and horizon: Wólka Bałtowska,

Type level: Skarbek Oolitic Limestone, earliest Kimmeridgian.

Family *incertae sedis*

Genus *Taeniatus* Takimoto, Ohana et Kimura 2008, emend. Barbacka et Pacyna

Type species: *Taeniatus elongatus* Takimoto, Ohana et Kimura 2008.

Taeniatus elongatus Takimoto, Ohana et Kimura 2008
emend. Barbacka et Pacyna
Fig. 9D–G

2008 *Taeniatus elongatus* Takimoto, Ohana et Kimura, p. 138, fig. 6.

Material: Two fragments of middle part of leaves, cuticle present, poorly preserved, very fragile (impossible separation adaxial and abaxial cuticles), but some details visible.

Hand specimens: KRAMP, PM 56/49, 56/59A.

Emended generic and specific diagnosis: Leaves large, fasciculate, attached to short shoot-like organ. Leaf long and narrow; margins parallel-sided throughout with strong midvein. Leaves not branched (so far, original generic diagnosis Takimoto *et al.*, 2008). Venation longitudinal, parallel, thin, ~8 veins on half leaf width. Leaf hypostomatic. Cuticle thick. Adaxial, with irregularly polygonal cells arranged irregularly. Abaxial cuticle with nearly square cells, arranged in longitudinal rows. Cell walls straight. Stomata rare, round, with 5–7 subsidiary cells bearing papillae.

Description: Leaves linear, length unknown, width 8 mm. Prominent sunken midrib up to 0.8 mm wide. Venation longitudinal, parallel, thin, ~8 veins on half width from margin to midrib visible. Leaf hypostomatic. Cuticle thick on both surfaces. Adaxial with square to irregularly polygonal cells arranged irregularly, cell walls straight. Abaxial cuticle with nearly square cells arranged in longitudinal rows. Stomata rare, round, orientation unknown, probably random. Arrangement of stomata undefined but seeming to form groups. Guard cells probably sunken (not preserved), 5–7 subsidiary cells bordering quite large openings and bearing papillae.

Remarks: The fossil genus *Taeniatus* was created for long linear fasciculate leaves, attached to a short shootlike organ (Takimoto *et al.*, 2008). The type material, originating from the Upper Jurassic of Japan, was described on the basis of gross morphology (cuticle details were added above, in emendation). According to Takimoto *et al.* (2008), secondary veins were not visible, only a strong midvein was observed, in which *Taeniatus* differed from similar leaf forms like *Nilssonia*, *Taeniopteris* or *Nilssoniopteris.* Also, as a characteristic feature, the number of leaves in the fascicle is high, at least 10. The leaves are narrow, relative to their length. The specimens from Wólka Bałtowska were preserved without apex or base, as single fragments, and the manner of their attachment to shoots is unknown. However, the shape and size (width) of the leaf blade correspond with the diagnostic features of *Taeniatus*, as does the strong and relatively wide midvein. The leaf shape and size is so characteristic that the authors assign the material from Wólka Bałtowska to the same species. The same age of the Japanese and Polish localities favours this determination. Some additional details, such as longitudinal veins and cuticle structure, confirm the difference between *Taeniatus* and other genera, discussed by Takimoto *et al.* (2008). The stomata structure differs from that of cycads or bennettitaleans and is of a type, differing from that of conifers, being closest to those of seed ferns or ginkgophytes. On the other hand, the parallel venation and fasciculate leaves indicate rather a ginkgoalean affinity.

REMARKS TO TAXONOMIC COMPOSITION

Quantitatively, the macrofossil assemblage from Wólka Bałtowska is dominated by araucariacean (*Brachyphyllum mamillare*) and cheirolepidiacean (*B. crucis* and *Pagiophyllum araucarinum*) conifers. Less numerous were seed ferns (*Ptilozamites cycadea*), ferns (cf. *Gleichenites cycadina*) a gymnosperm of unknown affinity, *Pseudotorellia solida* sp. nov. The record of *Taeniatus elongatus* is the first for Europe.

The microfloristic record is dominated by coniferalean pollen grains from Araucariaceae (*Araucariacites australis, Callialasporites dampieri*, *Callialasporites trilobatus, Callialasporites* sp.) and Cheirolepidiaceae (*Classopollis torosus*). Also occurring are bisaccate pollen grains including those from seed ferns (*Alisporites*), Podocarpaceae (*Podocarpidites*), Pinaceae (*Pinuspollenites*) and taxodiaceous Cupressaceae (*Cerebropollenites mesozoicus* and *Perinopollenites elatoides*). Erdtmanithecales, an extinct order of gymnosperms, known from the Mesozoic (*Eucommiidites trodessonii*, *Eucommiidites minor* and *Eucommiidites* sp.), and *Cycadopites* and cf. *Monosulcites* gymnospermous pollen grains of uncertain affinity (Bennetttitales and/or Cycadales and/or Ginkgoales).

Spores are less numerous and originate mainly from ferns Cyatheaceae and/or Dicksoniaceae (*Cyathidites minor*), Matoniaceae or Dicksoniaceae (*Concavisporites toralis*), Gleicheniaceae (*Gleicheniidites* sp.) and Schizaeaceae (*Klukisporites* sp.), from lycophytes (*Staplinisporites telatus* and *Sestrosporites pseudoalveolatus*) and probably from equisetaleans (cf. *Calamospora* sp.).

Some macrofossil taxa were reported by Liszkowski (1972, 1976), on the basis of Reymanówna's unpublished data. His list of determined plants includes one sphenophyte genus (*Equisetites* sp.), five gymnosperm species (*Ctenozamites* sp., *Pachypteris* sp., *Pseudotorellia* sp., *Pagiophyllum connivens* Kendall and *Brachyphyllum* aff. *crucis*) and some undeterminable fragments of bennettitaleans. He also mentioned trunks 120 cm long, currently lacking from the collection. The authors have reassigned some of his listed taxa. *Equisetites* sp., because of the lack of diagnostic features, was replaced by Equisetopsida, gen. et sp. indet.; *Ctenozamites cycadea* was renamed *Ptilozamites cycadea*, according to Popa and McElwain (2009). *Pachypteris* sp. was re-examined and on the basis of cuticle structure included in *Ptilozamites cycadea*. *Pagiophyllum connivens* is in this paper referred to *Pagiophyllum araucarinum* and *Brachyphyllum crucis* was confirmed under the original determination. Bennettitalean remains were not found in the collection; perhaps previously they were misdetermined due to poor preservation. Some additional taxa were described, such as *Gleichenites cycadea*, *Brachyphyllum mamillare*, *Pseudotorellia solida*, *Taeniatus elongatus* and male cones and female scales, associated with or accompanied by shoots of *Brachyphyllum*.

Liszkowski (1972) also mentioned the presence of *Classopollis* and *Araucariopollites* (probably a misspelled name for *Araucariacites*) pollen grains *in situ* in male cones, which is now confirmed, and dinoflagellate cysts in palynologically examined sediment samples.

REMARKS ON VEGETATION

Most of the species, occurring in the studied Wólka Bałtowska material, correspond with the suggested marine-influenced palaeoenvironment, reflected in their adaptive features. *Brachyphyllum crucis* was previously described from coastal zones and was interpreted as a possible halophyte (Harris, 1964, 1979; Van Konijnenburg-van Cittert and Morgans, 1999; Barbacka *et al.*, 2006). *Gleichenites cycadina* was found in shales, containing salt/brackish marsh vegetation (Van Konijnenburg-van Cittert and Van der Burgh, 1996). Fragments of *G. cycadina* were also found in Scotland as fusain; it was interpreted as dwelling in upland areas, often subjected to fire (Van Konijnenburg-van Cittert, 2002). The only seed fern in this locality, *Ptilophyllum cycadea*, is also thought to be adapted to the coastal zone, due to the xeromorphic character of its coriaceous cuticle with strongly protected stomata (e.g., Barbacka, 2011; Barbacka *et al.*, 2021). *Taeniatus elongatus* and *Pseudotorellia solida* showing an adaptation to windy conditions (stiffened leaves), could occupy exposed, elevated nearshore sites (cliffs?). The general picture of the Wólka Bałtowska island vegetation is comparable to that of today's New Caledonia in its dominance of a huge araucariacean conifer forest near the shore. The dominance of araucarian and cheirolepidialean pollen grains in the sediment corresponds with the dominance of these groups in the macrofossil record. The habitat of the gymnosperms, of which only pollen grains were found co-occurring with the described macroflora is unclear; their sporomorphs could have been transported over long distances, even from neighbouring islands or land. Spores of lycophytes and ferns, and pollen grains of some bennetttitales, cycadales and ginkgoales could have been transported both from inland (from moister and less disturbed areas) or from the coastal zone of near or distant areas. Various habitats are possible, because different plant species (precisely unrecognizable in the pollen record) may have been adapted to diverse conditions and could have occupied very different niches. Bisaccate pollen grains, found in the sediment, could have been transported by wind and/or water currents for long distances, much longer than other sporomorphs.

COMPARISON WITH COEVAL FLORAS

During the Late Jurassic, the greater part of Western and Central Europe was covered by epicontinental seas with numerous islands. The recorded vegetation of these islands was rather undiverse, often xeromorphic and dominated by conifers. Besides conifers only bennettialeans and seed ferns have been documented relatively frequently (Barale, 1981), whereas other plant groups are represented sporadically. The Late Jurassic islands with the best-known floras were located in modern-day Germany (Solnhofen, Nusplingen, Brunn), Switzerland (Basel, Röschenz Beds of Court and Charuque in Jura Mts.) and France (Armaille, Creys, Orbagnoux – late Kimmeridgian, Châtelneuf, Châteauroux and Besançon in Jura Mts. – late Oxfordian–early Kimmeridgian). The typical island flora in France was associated with late Kimmeridgian coral reefs formed from the late Oxfordian on continental platform (Barale, 1981). Flora best corresponding in age with those of Wólka Bałtowska (Châtelneuf – Oxfordian, Besançon – late Oxfordian Bifurcatus Zone, and beginning of Kimmeridgian, Bimammatum zone, Châteauroux – Bimammatum zone) was very poor, consisting of few ferns, *Ctenopteris* seed fern and *Pagiophyllum-Brachyphyllum-Araucarites* conifers indicating proximity to the coast.

Very poor coastal flora from Switzerland found in Röschenz Beds of Court, Jura Mountains, Vellerat Formation (middle to late Oxfordian; Allenbach and Van Konijnenburg-van Cittert, 1997) consisted of only three conifer taxa, preserved in a supratidal environment.

From the same formation, from Charuque (Péry-Reuchenette) four taxa, belonging to bennettitaleans and araucariacean and cheirolepidiacean conifers, have been described (Van Konijnenburg-van Cittert and Meyer, 1996), associated with a coastal zone.

The flora from Wólka Bałtowska suits these scenarios with its similar palaeogeographic latitude and habitat type. Vakhrameev (1991), on the basis of type of environment and shared taxa, included all these floras, German, French and Polish, to the South European province, proposed by him. Previous sporadic finds of Late Jurassic plant macroremains from Poland (mainly from the Holy Cross Mts) yielded only single fragments of bennetittalean leaves or indeterminate pieces of wood (Premik and Zabłocki, 1925; Liszkowski, 1972; Gutowski, 1998; Wierzbowski, 2023b). Only the flora from Wólka Bałtowska is diverse enough to be compared with some coeval sites. Barbacka *et al.*'s (2014) comparative analysis of European Jurassic floras indicated that all Late Jurassic European island floras were dominated by conifers, which formed about ~45% (Armaille, Creys, Orbagnoux, Jura) to 75% (Basel) of all taxa occurring. Among the sites, the flora from Basel was the least diverse (3 plant groups recorded). According to the present study (which increases number of plant groups known in 2014), the diversity of Wólka Bałtowska is the same as that of Solnhofen, both represented by seven plant groups, though with some differences (lack of macroremains of lycophytes, bennettitaleans and ginkgophytes in Wólka Bałtowska, and the presence of two taxa *incertae sedis Pseudotorellia* and *Taeniatus*, absent at other localities). The lack of bennettitaleans differentiates Wólka Bałtowska from other localities where, besides conifers, they were an important element of the floras (Barbacka *et al.*, 2014). On the other hand, the occurrence of the genera *Pseudotorellia* and *Taeniatus* indicates biogeographic connections with Eastern European and Asiatic floras that grew on the larger Ukrainian land (Vakhrameev, 1991) and Japan (Takimoto *et al.*, 2008), placing Poland in an intermediate position between the western and eastern floristic regions.

RECONSTRUCTION OF SEDIMENTARY SETTING

On the basis of lithological and sedimentary features and the described fossils, Liszkowski (1972) inferred a nearshore, shallow-marine environment in the Wólka Bałtowska succession. Liszkowski interpreted some changes in lithology as caused by basin deepening, from a very shallow (basal breccias and conglomerates) to a lagoonal environment (oolitic and platy limestone in the top of the succession). The palaeoenvironmental interpretation, based on palynology presented by Gedl and Ziaja (2004), cannot be precisely correlated with the one proposed by Liszkowski, due to uncertainty about the location of the studied samples within the profile. Nevertheless, palynofacies analysis points to a nearshore environment during deposition of the sediments, confirmed by a high ratio of terrestrial phytoclasts and palynomorphs as well as the low diversity of dinocyst assemblages. Lithological differences between the two studied samples (KRAM P, PM 56/48/II and KRAM P, PM 56/135/I) are reflected also in their palynofacies, confirming different sedimentary conditions. Black phytoclast dominance, the frequency of saccate pollen grains and relatively frequent dinocysts from oolitic limestone (sample KRAM P, PM 56/48/II) indicate that this part of the section was deposited in a more offshore setting, with stronger hydrodynamic conditions. Limestone with frequent macroflora remains (sample KRAM P, PM 56/135/I) was deposited during a period of increased influx of terrestrial material. On the basis of sedimentological data, the palaeoenvironment was interpreted as nearshore shallow-marine, with a transition to a lagoonal system, confirmed by non-pollen palynomorphs of green algae of the Chlorophyceae (*Botryococcus*) and Prasinophyceae (*Pterospermella*), found at the locality.

The low diversity of dinocyst assemblages from the sediment indicates stressed environmental conditions. It is hard to say whether the cause was land proximity, hydrodynamic factors, salinity, nutrient availability, or climatic disturbances. Poulsen (1996) described frequent records of *Subtilisphaera* from a nearshore Kimmeridgian dinocyst assemblage in Denmark. He also treated the genus *Cribroperidinium* as an inshore genus – represented in the present material by the dominant species, *C. venustum*. Another taxonomic composition characterises coeval dinocyst assemblages from offshore deposits and is characterized by high diversity (Gedl, 2000). From sporomorph analysis, the present authors conclude that their parent plants may have occupied nearby land areas.

The plant macroremains from Wólka Bałtowska are fragmented, very damaged, and commonly associated with undeterminable detritus, indicating their allochthonous origin from long transport or short high-energy transport. The present authors lean towards the latter. The fragments are small, the largest being undeterminable stem and branch fragments ~30 mm long, and the usual size being not more than 10–20 mm (except for one twig of *Brachyphyllum mamillare*, 100 mm long). The deep impressions in very fine sediment (conifer leaves, cone scales) with visible details of the cuticle (stomata) indicate fossilization in the undisturbed, very fine sediment of a lagoon, to which they were transported from shore.

CONCLUSIONS

1. Wólka Bałtowska is the first Upper Jurassic locality in Poland, for which a complex flora is described.
2. In the Late Jurassic, Poland was covered by an epicontinental sea, and the terrestrial plant remains most likely originated from islands.
3. The plant cover was dominated by conifers (Araucariaceae, Cheirolepidiaceae), other plant groups like sphenopsids, ferns and seed ferns, and non-coniferalean gymnosperms were rare.
4. The floristic composition (conifer-dominated) and xeromorphic features of the plants confirm a marine-influenced habitat and its island nature.
5. The flora from Wólka Bałtowska corresponds with the Late Jurassic island floras of Western Europe (France,

Germany, Switzerland), but shows a transition towards eastern floristic regions (*Pseudotorellia*, *Taeniatus*).

6. Sporomorphs complete the picture of the vegetation, with lycopsids, diverse ferns and some gymnosperms (cycadophytes, Erdtmanithecales, Podocarpaceae, Pinaceae, taxodiaceous Cupressaceae). They may have originated from transport from more or less distant habitats (other islands, mainland).

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