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A new conifer from the Upper Triassic of southern Poland linking the advanced voltzialean type of ovuliferous scale with *Brachyphyllum-Pagiophyllum*-like leaves

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ABSTRACT

The Triassic is an exceptionally interesting period from the point of view of conifer evolution. The oldest representatives of some modern families appear in the fossil record in the Upper Triassic and all recent conifer families probably originated during this time. The stages whereby the primitive Voltziales transformed into the evolutionarily advanced families of modern conifers in the Triassic are yet to be fully documented. A newly discovered Upper Triassic (Norian) locality in Patoka (SW Poland, Upper Silesia) with a unique fossil record offers us a rare opportunity to fill this gap. In this paper, we describe the very well preserved remains of a new conifer from this locality. We have been able to reconstruct the whole plant and propose a new taxon, *Patokaea silesiaca* gen. et sp. nov., on the basis of organic attachment and similar cuticular details on leaves, ovuliferous cones, seed scale-bract complexes, ovules and mature seeds as well as polliniferous cones containing pollen grains of the *Enzonalasporites* type in situ. This plant combines shoots bearing *Brachyphyllum-Pagiophyllum*-type leaves with a new type of seed scale-bract complex clearly derived from evolutionary advanced Voltziales and polliniferous cones somewhat similar to the Cheirolepidiaceae (*Classostrobus*) type. Based on this distinctive and hitherto unique combination of features, a new conifer family – Patokaeaceae – has been proposed. The ovuliferous cones of this conifer are lax and borne singly at the end of leafy twigs. Ovule-bearing scales are stalked and trilobate with two lateral oval lobes, each bearing one ovule, and one sterile reduced lobe between them, all in one plane. The bract is small and leaf-like. Polliniferous cones are simple with helically arranged microsporophylls. Five to seven pollen sacs are arranged around the microsporophyll stalk. Polliniferous cones are borne singly at the end of leafy twigs. This is also the first evidence of a relationship between *Enzonalasporites* pollen and the parent plant. The pollen occurs in the polliniferous cones, in the micropyle inside the ovule and in the micropylar region inside the seed of this new conifer. This plant expands our view of voltzialean conifer diversity at the roots of modern conifer families.

1. Introduction

The Triassic is especially interesting from the point of view of conifer evolution (Miller, 1977; Grauvogel-Stamm, 1978; Rothwell et al., 2012). Modern conifer families originated at this time, as shown by the fossil record and phylogenetic data (Quinn et al., 2002; Rothwell et al., 2012). Older, evolutionary less advanced conifers, traditionally referred to as Voltziales, reached their peak of diversity in the Triassic, in terms of both taxa number and their wide adaptation to different environments (e.g., Rothwell et al., 2000; Taylor et al., 2009). Ovuliferous scale-bract complexes in ovuliferous cones were very diversified among Triassic conifers, but one general evolutionary tendency is identified in most taxa – the flattening of seed scales and reduction of their lobes (Florin, 1938–1945, 1951; Schweitzer, 1963). At this same time, polliniferous cones were probably more diverse, varying from simple to compound cones, than at any other period in conifer history (Roselt, 1956; Schaarschmidt and Maubeuge, 1969; Grauvogel-Stamm, 1969, 1972,

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1978; Grauvogel-Stamm and Grauvogel, 1973; Grauvogel-Stamm and Schaarschmidt, 1979; Meyen, 1987; Grauvogel-Stamm and Galtier, 1998). The stages of transformation from the primitive Voltziales to evolutionary advanced families of modern conifers in the Triassic have been insufficiently documented to date (Miller, 1977, 1982, 1988; Rothwell et al., 2012). Such families as the Podocarpaceae have uncontested representatives in the Triassic, but the occurrence of members of other families, e.g. the Pinaceae, is still open to question (Delevoryas and Hope, 1973, 1987; Miller, 1976; Rothwell et al., 2012).

The Triassic conifers described thus far from Poland are poorly preserved and still imperfectly known (Goeppert, 1845, 1846; Kunisch, 1886; Raciborski, 1890; Reymanówna, 1986; Brzyski and Heflik, 1994; Dzik and Sulej, 2007; Pacyna et al., 2013; Pacyna, 2014). Some newly discovered localities provide an exceptional opportunity to supplement this scanty information. Krasiejów, Patoka, Poręba, Marciszów-Zawiercie, Woźniki, Lipie Śląskie-Lisowice (all in South Poland and Upper Silesia), contain yet to be described well-preserved floras rich in conifer taxa, with forms which can shed new light on conifer evolution during the Late Triassic (Brzyski and Heflik, 1994; Szulc et al., 2006; Dzik and Sulej, 2007; Dzik et al., 2008; Racki, 2010; Sulej et al., 2011, 2012; Sadlok and Wawrzyniak, 2013; Kubik et al., 2015; Philippe et al., 2015; Racki and Szulc, 2015). The material is from the Patoka locality, which is Norian in age, and contains a flora that is not diverse, but very well-preserved and dominated by conifers. It is worth noting that worldwide Norian plant fossils are extremely rare (Dobruskina, 1988, 1994; Mader, 1990; Petti et al., 2013). Nearby localities provide older (Carnian – Krasiejów) and younger (upper Norian?–Rhaetian – Lipie Śląskie-Lisowice) floras together with exceptional vertebrate assemblages containing dinosaurs and dicynodonts (Dzik, 2001, 2003; Dzik et al., 2008; Wawrzyniak, 2010; Sulej et al., 2011, 2012; Niedźwiedzki et al., 2012; Pacyna et al., 2013; Pacyna, 2013, 2014).

The purpose of this paper is to describe the very well preserved remains of a new conifer from Patoka (Fig. 1). The whole plant has been reconstructed on the basis of organic connections and cuticle details on leaves, ovuliferous cones, seed scale-bract complexes, ovules and developed seeds as well as polliniferous cones with pollen grains of the *Enzonalasporites* type in situ (Fig. 2). Such fully documented plants have been used successfully for developing phylogenetic hypotheses about fossil-conifer relationships (Rothwell et al., 2005).

2. Geological setting, materials, and methods

2.1. Geological setting

The specimens described in this study were collected in the northern, lowest part of the Patoka clay pit (northern part of Upper Silesia, Fig. 1). Fossil bearing strata belong to uppermost part of the marly mudstone-sandstone Patoka Member of the Grabowa Formation (Szulc and Racki, 2015; Racki and Szulc, 2015; Szulc et al., 2015a, 2015b). This formation is the main lithostratigraphic unit of the Upper Silesian Keuper and a lateral equivalent of the German Weser and Arnstadt formations within the Triassic Germanic Basin, which extends from France in the West across Germany to Poland in the East (Mader, 1997; Szulc et al., 2006; Szulc and Becker, 2007; Franz, 2009; Racki, 2010; Lucas, 2015). The first description of Upper Triassic strata in the Patoka region was provided by Römer (1870), but plant remains were observed for the first time by Znosko (1955) in a currently-flooded old clay pit. The plant fossils described here derive from greenish-yellowish, sometimes grey, layers of mudstone and siltstone with sandstone lenses and occur in few very thin layers containing mainly new, leafy conifer twigs. Small fern fragments and sporadic leaves of other gymnosperms have also been found. Numerous associated tree trunks preserved as coalified remains and charcoal fragments have already been described (Philippe et al., 2015).

Palynological data were used to determine the age of the Patoka Member as Norian, the local Polish *Corollina meyerana* Palynozone, Subzone b (Orłowska-Zwolińska, 1983, 1985; Fijałkowska-Mader et al., 2015), which is correlated with the Middle European *Granuloperculatipollis rudis* zone (Cirilli, 2010; Kürschner and Herngreen, 2010; Fijałkowska-Mader et al., 2015). The nearby Patoka 1 borehole probably failed to penetrate the fossil-bearing level exposed in the pit, but it has been well documented palynologically (Fijałkowska-Mader et al., 2015). Unfortunately, in the locality where the fossils have been found, clay pit works have strongly disturbed the section. Palynological analysis of samples containing macrofossils of the new conifer shows that the miospore assemblages are taxonomically impoverished in comparison with the *Corollina meyeriana* b Subzone and mainly consist of *Ovalipollis*, *Vallasporites* and *Corollina*. It is difficult to correlate these spectra with the subzones (within the *Corollina meyerana* Zone) distinguished by Orłowska-Zwolińska (1983, 1985) as she did not mention *Vallasporites*. According to Pacyna (2014), the flora from Patoka can be correlated with the German Stubensandstein-Burgsandstein Flora of Kelber (1998) and he referred it to the local *Brachyphyllum* Assemblage Zone.

2.2. Material

The plant remains are preserved as coalified compressions with well-preserved cuticles. Leafy shoots (up to 50 mm long) predominate in the material associated with ovuliferous scale-bract complexes, ovuliferous and polliniferous cones, ovules, mature seeds and dispersed pollen grains. All organs undoubtedly belong to the same plant species. Ovuliferous and polliniferous cones were found attached to leafy shoots. One seed was found attached to a seed-scale. Vegetative and reproductive structures have cuticles of the same type. The pollen grains found in the polliniferous cone are the same as those observed in the micropylar canal of the ovule, in the micropylar region inside the seed and dispersed in the source sediment.

The specimens are stored at the Institute of Botany, Jagiellonian University, under the palaeobotanical collection number KRA-PALEO 104.

2.3. Methods

The compressed remains were separated from the sediment by treatment with 40% hydrofluoric acid for one to several days, then washed with distilled water. Prepared remains are partly stored in water containing thymol and partly in the dry state in test tubes. Bulk samples were examined in water using a Leica stereomicroscope and individual specimens were selected for further study.

Some leaves, ovule and seeds were macerated in Schulze solution (Schulze, 1855) and then washed with 3% KOH after which permanent slides were prepared. These were examined using Nikon Eclipse E 600 and Axio Scope A1 Carl Zeiss light and fluorescent microscopes. Some specimens (separate seeds, polliniferous cone cuticles, polliniferous cone fragments with pollen sacs, pollen grains) were only treated with hydrofluoric acid (and some were macerated afterwards in Schulze solution) for SEM examination. They were sputter-coated with gold and observed with a Hitachi S-2360N scanning electron microscope at 22 kV accelerating voltage and secondary electron detection.

For the pollen wall ultrastructure investigation, pollen grains were soaked with propylene oxide, 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.

3. Results

3.1. Systematics

Division - Pinophytina
Class - Pinopsida
Order - Voltziales

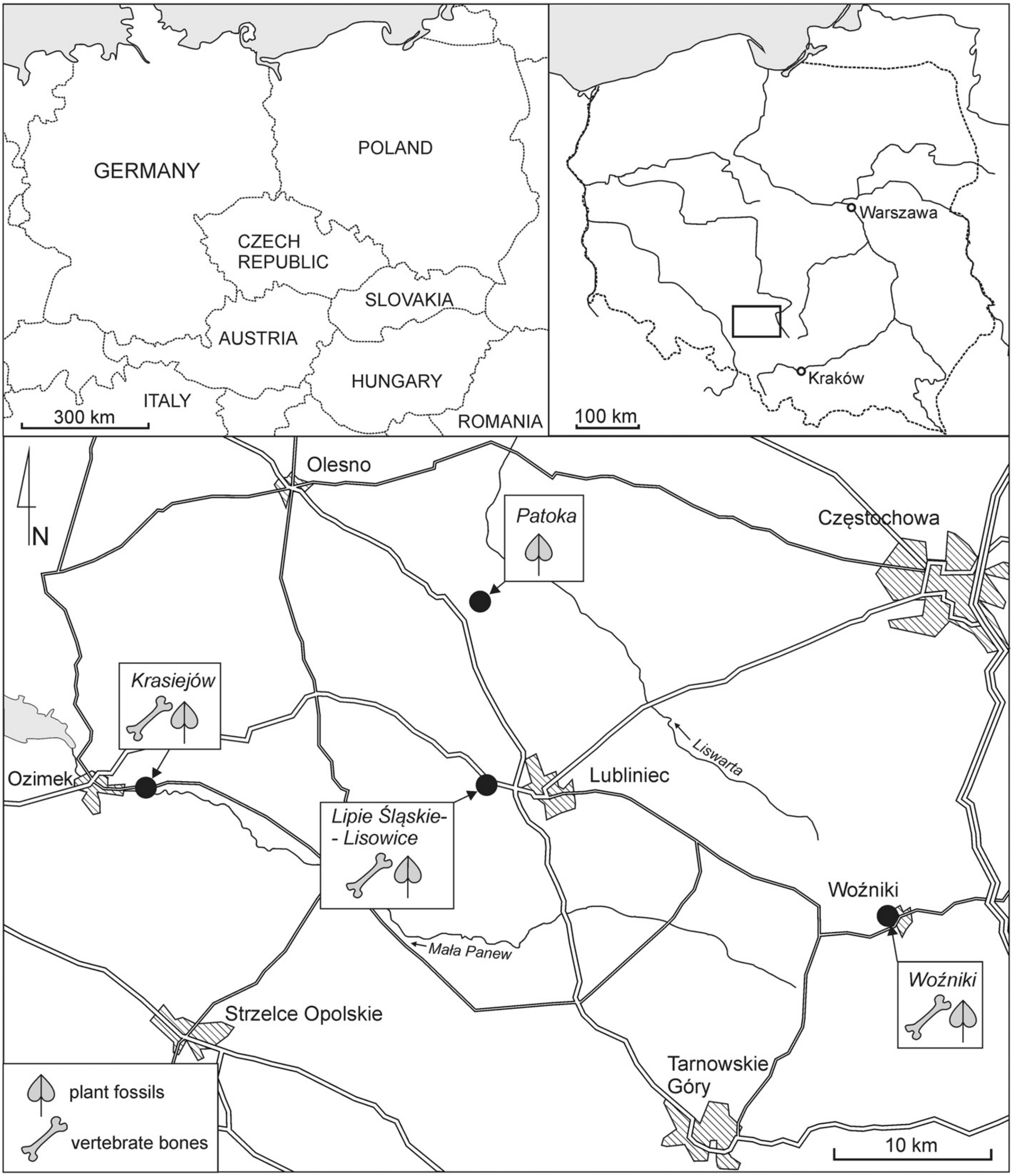


Fig. 1. Geographic location of the Patoka locality.

Family: **Patokaeaceae** Pacyna, Barbacka et Zdebska, *fam. nov.*

Type genus: *Patokaea* Pacyna, Barbacka et Zdebska, *gen. nov.*

Family diagnosis: Coniferous plant with *Brachyphyllum*- to *Pagiophyllum*-type leaves. Leafy shoots branching at acute angles in one plane, leaves helically arranged. Ovuliferous cones lax. Ovuliferous scales stalked, trilobate, with lobes in one plane, two lateral, oval in shape, bearing one ovule each, and sterile reduced lobe (lobes) situated between them. Ovules oval in outline, with micropylar beak directed basipetally. Bract small, leaf-like, merged with ovule-bearing scale stalk in part. Polliniferous cones simple, oval in outline, born at the end of the leafy

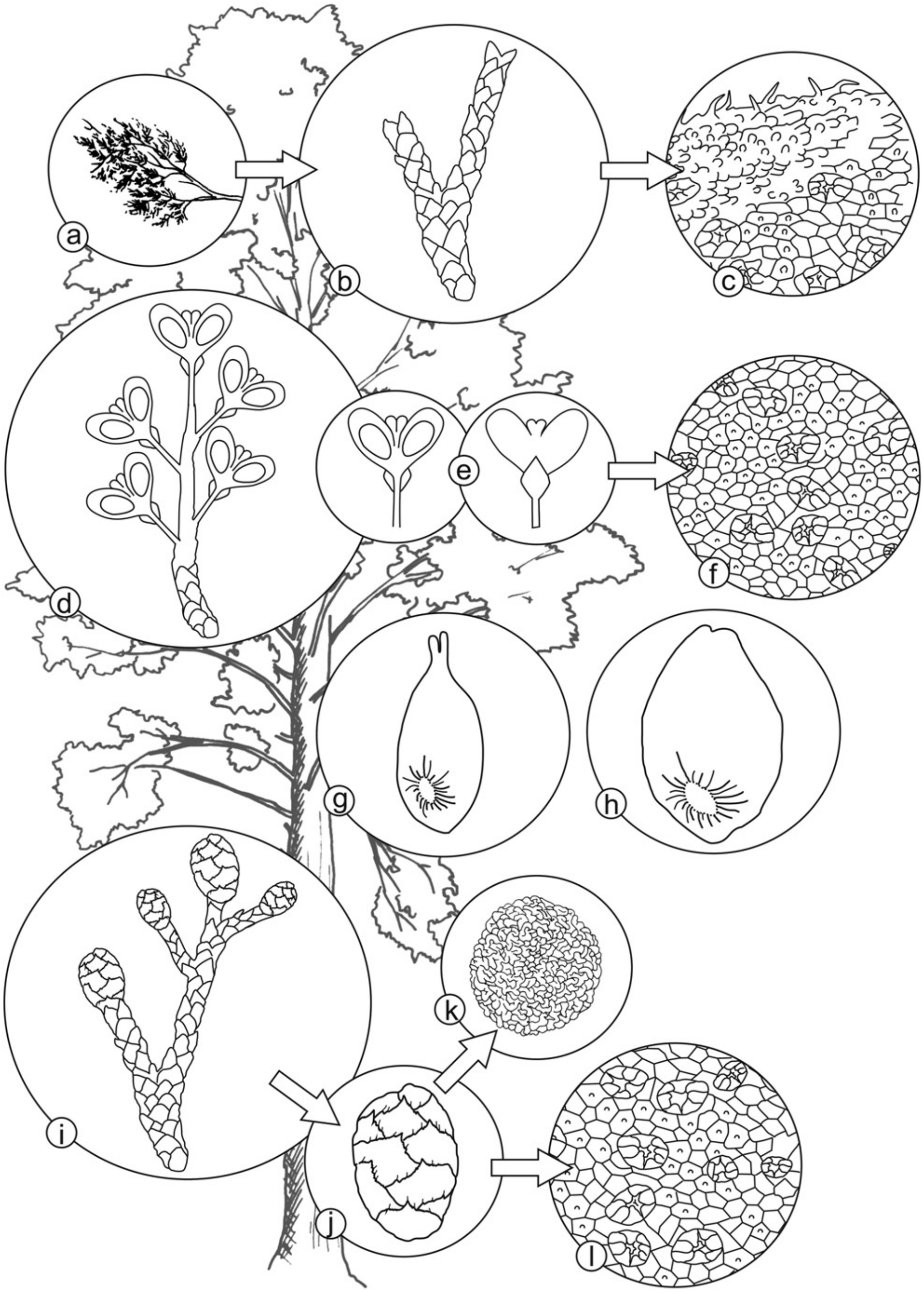


Fig. 2. A reconstruction of *Patokaea silesiaca* gen. et sp. nov., a – branch fragment; b - leafy twig (based on specimen figured on Plate I, 4A); c – cuticle of leaf (Plate I, 11); d – ovuliferous cone (Plate II, 1); e - seed scale – bract complex from adaxial (left) and abaxial (right) sides; f - adaxial cuticle of lobe (Plate III, 3); g – ovule (IV, 8); h – seed (Plate VI, 1A); i - twig fragment with terminal polliniferous cones (Plate VIII, 3); j - polliniferous cone (Plate VIII, 4); k – pollen grain (Plate XII, 1); l - cuticle of free blade of microsporophyll; tree habit hypothetical; not to scale (drawing by A. Sojka).

twigs. Microsporophylls helically arranged, consisting of a stalk and a distal free blade. Pollen sacs attached in a whorl around the microsporophyll stalk. Pollen grains circular in polar view to oval in equatorial or oblique view. Exine surface rugulate (folded irregularly). Surface of folds smooth.

Patokaea Pacyna, Barbacka et Zdebska, *gen. nov.*

Type species: *Patokaea silesiaca* Pacyna, Barbacka et Zdebska, *sp. nov.*
Generic diagnosis: Shoots branching at acute angles in one plane, bearing leaves helically arranged, distalmost branches with decussate leaves. Leaves rhomboidal or elongated-rhomboidal in shape with basal cushion and short, free part, but sometimes forming extended apex. Ovuliferous cones lax, easily disintegrate. Seed scale-bract complex stalked, seed scale trilobate, with two oval lateral lobes, each bearing one ovule, and one sterile lobe in between, strongly reduced, all lying in one plane. Bract small, leaf-like, merged with ovule-bearing scale stalk in part. Ovules large, laterally attached to the adaxial side of the lobes, partly hidden by the folded margin of the lobes. Ovules oval in outline, with prominent micropylar beak directed basipetally. Seeds broad and oval in outline, with slightly expanded micropylar end. Simple polliniferous cones borne singly at the end of the leafy twigs, small, oval in outline. Microsporophylls helically arranged, consist of stalk and distal free blade. Pollen sacs arranged in a whorl around the

microsporophyll stalk. Pollen grains circular in polar view to oval in equatorial or oblique view. Exine surface rugulate on whole specimen. Surface of folds smooth.

Etymology: The genus is named after the locality where the plant remains were found – the Patoka clay pit. Genus gender feminine.

Patokaea silesiaca Pacyna, Barbacka et Zdebska, *sp. nov.*

Holotype: KRA-PALEO 104/43 - twig fragment with terminal ovuliferous cone (Plates I, 12; II, 1).

Paratypes: twigs: KRA-PALEO 104/55 (Plate I, 4, A), 104/103 (Plate I, 5); ovule scale-bract complex: 104/3 (Plates II, 5, D; IV, 4, A), 104/20 (Plate II, 3–4), 104/62-104/65 (Plates III, 1–6; IV, 1–3, 6); ovule: 104/36 (Plates IV, 8; V, 1–6; XII, 6); seeds: 104/24 (Plates VI, 5; VII, 1–2; XII, 7–8), 104/26 (Plates VII, 4–6; VIII, 1–2), 104/37 (Plates VI, 1, A–B, 2–4; VII, 3); polliniferous cones: 104/40 (Plate VIII, 3), 104/67 (Plates VIII, 5; XI, 3; XII, 1–2), 104/100 (Plates IX, 4–6; X, 2–6; XI, 1–2, 4–7), 104/199 (Plates X, 1; XII, 3–5).

Referred material: Twigs: KRA-PALEO 104/43 (Plate I, 1), 104/45-104/54 (Plate I, 2–3, 4, C), 104/61 (Plate I, 4, B), 104/66 (Plate I, 6–7), 104/103-106 (Plate I, 8–11), 104/7 (Plate II, 5, C), 104/108, 104/111, 104/114; Ovule scale – bract complex 104/1 (Plate II, 5, I), 104/2, 104/4-104/18 (Plate II, 5, E, G–H; Plate IV, 4, B), 104/35, 104/39, 104/41, 104/42, 104/70 (Plate II, 5, F), 104/115 (Plate IV, 7), 104/197 (Plate II, 5, A),104/198 (Plate II, 5, B); Ovuliferous cone 104/196 (Plate II, 2) Seeds: 104/19, 104/21 (Plate VI, 1, C), 104/22 (Plate VI, 1, D), 104/23, 104/25, 104/27-104/34, 104/38, 104/71; Polliniferous cones: 104/68 (Plate VIII, 4, A–B), 104/101 (Plate IX, 1–3), 104/102; Microsporophyll free blade with stalk 104/150 (Plate IX, 4); Isolated pollen grains: 104/201 (Plate XII, 9–11).

Repository: Jagiellonian University, Institute of Botany, palaeobotanical collection number KRA-PALEO 104.

Type locality: Patoka clay pit, Upper Silesia, South Poland.

Type horizon and age: Grabowa Formation, Patoka Member, *Brachyphyllum* Assemblage Zone, Norian, Upper Triassic (Pacyna, 2014; Szulc and Racki, 2015; Racki and Szulc, 2015; Szulc et al., 2015a, 2015b).

Etymology: The species is named after the Latin name of the region where the fossils were found – Silesia.

Specific diagnosis: Leaves amphistomatic, cells irregular with rounded corners, uniform on the whole leaf blade, sometimes with central papillae. Stomata scattered, 5–7 subsidiary cells with or without papillae directed towards stomatal pit. Leaves margins entire, scarious, often turning into fringes which form microscopic, unicellular teeth near the apex. Ovules smaller than lobes, oval in outline. Seeds almost as large as lobes, broad oval in outline, with slightly expanded micropylar end. Bract's top reaches to the basal parts of ovuliferous scale lobes. Microsporophyll distal blade nearly rhomboidal in shape, with a sharp apex and scarious margins. Pollen grains circular in polar view to oval in equatorial or oblique view. Exine surface rugulate.

3.1.1. Description

3.1.1.1. Leafy shoots. The leafy shoots branch in one plane at acute angles. The preserved branches are short, up to 50 mm long and 3 mm wide (Fig. 2, a–c; Plate I, 1–5). They often end in rounded leaf buds (Plate I, 4, C, 6). Leaves are helically arranged. They are rhomboidal or elongated-rhomboidal in shape (Plate I, 5). The total length of the leaves (basal cushion plus free part) ranges from 4 to 6 mm. Elongated basal cushion tapers into the small free part, which is 0.45–0.70 mm long. Leaf apex in surface view is commonly acute, sometimes obtuse, rarely rounded when curved inwards, sometimes forming an extended sharp apex. Free leaf parts may be adhering, straight or bend outwards. Leaf margins are entire, scarious, often turning into fringes which form microscopical, unicellular teeth near the apex (Plate I, 6–7). The leaves are amphistomatic, and their cells are irregular or isodiametric with rounded corners, uniform on the greater part of the leaf blade, 11 × 10 to 20 × 20 μm, only becoming elongated at the leaf margin cells (about 30 × 11 μm). Occurrence of central papillae on the cells varies considerably. They occur on both the adaxial and abaxial surfaces or on one of them. Sometimes they are lacking, also on the subsidiary cells (Plate I, 8–13). Stomata are scattered randomly in equal numbers of both lower and upper cuticles, but they are rarer near the apex and along the margins. The stomatal apparatus is nearly circular with a diameter of 46–77 μm; 5–7 subsidiary cells possess large papillae directed towards stomatal pit in papillate leaves.

3.1.1.2. Ovuliferous cones. Ovuliferous cones are probably lax, and easily disintegrate (fragments of cone preserved with three or four cone scale-bract complexes range from 15 mm long and 14 mm wide) (Fig. 2, d; Plate II, 1, 2).

3.1.1.3. Ovuliferous scales. Ovuliferous scale-bract complexes are 4.6–13 mm long with a stalk (Fig. 2, e, f; Plate II, 5). The end of the complex stalk is slightly recurved. The ovuliferous scale consists of three lobes lying in the same plane. Two lateral fertile lobes are tongue-shaped to oval (c.1.8–4 mm wide), each bearing one ovule that almost occupies the whole width and length of the lobe (Plate II, 3–5; Plate III, 1–5). The fertile lobes are smooth on the abaxial side (Plate III, 5). On the adaxial side, the distal margins bend inwards forming an envelope partly overlapping the ovule from its chalazal end (Plates III, 4; IV, 2). The margin of the envelope bends to form a flounce-like thin edge around the place of ovule attachment (Plate III, 2–3). The place where the ovule attaches to the scale is a 0.8–2 mm long depression in the distal third of the lobe (Plate III, 1–2). Its surface shows a different structure than the other parts of the scale (amorphic, cell outlines unrecognizable, non-fluorescent, Plate IV, 2). One sterile, tongue- or heart-shaped lobe, strongly reduced compared to the neighbouring fertile lobes (1–3 mm wide). It reaches half the length of the fertile lobe (Plate III, 6). On the abaxial surface of the reduced lobe, a central line is sometimes observed (Plates II, 5, A–G; IV, 4, A–B). The cuticle of the ovuliferous scales shows cells with straight anticlinal walls and low papillae. Numerous stomata are scattered across all of the adaxial and abaxial scale surfaces except for narrow non-stomatal zone at the margin of the lobes. Stomatal pits are surrounded by 6–7 subsidiary cells possessing large papillae overarching the aperture (Plate IV, 1, 3).

3.1.1.4. Bract. Bracts are small, leaf-like, decurrent on the stalk, at the base fused with stalk along the greater part, with a free part ending just below the joint of the lobes (Plate IV, 4, A–B). They are 5–7 mm long and 2–3 mm wide. The free part of bracts is rhomboidal. The apex varies in shape from sharp to obtuse, margins are straight or slightly arched, with prominent fringes (Plate IV, 5–6). Cuticle on the abaxial surface shows irregular cells with thin and straight anticlinal walls, generally without papillae; small papillae appear only towards the bract base. Stomata are scattered, mainly in the middle part of the blade, and consist of 6–7 subsidiary cells, each bearing a large papilla. On the adaxial surface of the free part, stomata are similarly distributed as on the abaxial side. The part fused with the ovuliferous scale stalk is stomata-free (Plate IV, 7). Fringes are numerous at the margin, they are up to 170 μm long (Plate IV, 5–6).

3.1.1.5. Ovule. Ovules are directed basipetally, almost as large as the fertile lobes (4.5 × 2 mm), attached to the adaxial side of the lobes, partly hidden by the folded margins (up to 1/5 of the ovule) (Plates II, 3–4; IV, 8). Ovules are oval in outline, with a prominent, 1 mm long micropylar beak with forking ends (Fig. 2, g; Plates IV, 8; V, 1–3). The surface of the ovule is wrinkled. The ovule is laterally attached to the fertile lobe at the chalazal end. The place of attachment is 1.5 mm long, non-fluorescent like the corresponding place on the scale lobe (Plate V, 6). The outer cuticle of the integument is thick; cells are small, isodiametric or slightly elongated (from 35 × 30 to 70 × 30 μm). Near the chalaza, the cuticle becomes thinner, and cells, more elongated (35 × 18 μm). The surface of the cuticle is wrinkled. Sometimes trichome bases are observed on the outer cuticle of the integument, which consists of a ring of 6–7 thickened cells with a cavity in the center. The anticlinal walls have thickenings around the cavity that remain after breaking off the trichome. The inner cuticle of the integument or nucellus is very thin, rather poorly preserved and difficult to identify; the cell outlines are not recognizable. The cells of the micropylar canal are thicker and stronger cutinised than in other parts of the ovule. Some pollen grains were observed inside the micropylar canal and adhered to the inner cuticle of the integument or nucellus (Plate V, 4–5). They are of the same type as those observed in the pollen sacs of the polliniferous cones.

3.1.1.6. Seeds. Seeds are 6–8.5 mm long and 5.0–7.0 mm wide, broad oval in outline, flattened, slightly narrowing towards the somewhat expanded micropylar end and with a rounded chalazal end (Fig. 2, h; Plate VI, 1, A–D). The flattened edge of the seed forms a rim 0.5–0.8 mm wide (Plate VI, 2). The outer cuticle of the integument (seed coat) shows small, irregular cells from 26 × 23 to 67 × 38 μm. The anticlinal walls are straight (Plate VI, 2). Rare and irregularly arranged trichome bases consist of 6–7 cells surrounding the central cavity (Plate VI, 3). Their walls are thickened around the cavity. The cuticle of the integument (seed coat) becomes thinner at the edges of the seed. The inner cuticle of the integument is thinner than the outer one, and the cell pattern is similar to that of the outer integument (Plate VI, 5). The place of the seed attachment to the fertile lobe is well visible on the seed side and comprises one fifth of the seed length. It is an oval cavity without an integument (seed coat) being present, about 1 mm wide and 2 mm long, surrounded by integument (seed coat) that is wrinkled and curls up into the inside (Plates VI, 1, 4; VII, 5–6). Part of the megaspore membrane lying inside the seed is sometimes visible in this cavity (Plates VI, 1, A, 1, D; VII, 4–5). This cavity corresponds in size (about 2 mm long) and shape with the place of attachment observed in the ovule and fertile lobes of the scale. The cuticle of the integument around the cavity is very delicate and is often destroyed during maceration. The very thin cuticle of the nucellus is only observable at the micropylar end and shows large, rectangular cell outlines (Plates VII, 1; VIII, 1). The megaspore membrane forms a large sack inside the integument, the surface of this cuticle is finely grained (Plates VI, 5; VII, 3). On the SEM images, wavy lines are visible (state of preservation?, Plates VII, 4; VIII, 2). The surface of many seeds is slightly pitted and wrinkled with longitudinal and crosswise wrinkles, probably an effect of seed compression during the fossilization process (Plate VI, 1, A–D). In one seed at the micropylar end, some pollen grains were found adhering to the internal cuticles (Plate VII, 1–2). They are of the same type as found in situ in the ovule and polliniferous cones.

3.1.1.7. Polliniferous cones. Polliniferous cones are simple and borne singly at the end of the leafy twigs (Fig. 2, i; Plate VIII, 3). They are oval in outline and 3.8–6.0 mm long and 1.8–4.0 mm wide. Microsporophylls are helically arranged, c. 14 per cone (Fig. 2, j, l; Plate VIII, 4, A–B, 5). Their distal blade (scutellum) is triangular with a sharp apex and margins with large fringes (over 100 μm long). The apex of the distal blade is stomata free, elongated cells are arranged in rows and papillae occur only sporadically. The rest of the blade is covered by cells forming short rows, each cell bears prominent papillae. Stomata are randomly scattered on the abaxial side. Subsidiary cells, 6–7 in number, possess large papillae directed towards the stomatal pit. Long (up to 95 μm) unicellular trichomes (fringes) are randomly scattered on the lower part of distal blade (Plate VIII, 5). The adaxial cuticle is frequently destroyed, being pulled out just above the apex (Plate IX, 1–6). Microsporophyll stalk attached at the center of the adaxial side of the distal blade (Plate IX, 4). Pollen sacs, about 5–7 per sporophyll, probably sessile, arranged in a whorl around the central stalk as suggested by the indistinct compressed material (Plate X, 1–6). They are probably elongate, but their exact shape is indefinable because of strong cone compression. Groups of pollen sacs from the neighbouring microsporophylls are so crowded that they deform each other. In compressed state, pollen sacs are triangular or subtriangular to wedge-shaped, and reach 1–1.2 mm in length and 0.5–1 mm in width (Plate X, 3–4). Their wall is very thin with elongated cells (Plate XI, 2). Pollen sacs are filled by large numbers of pollen grains (Plate XI, 1, 7).

3.1.1.8. In situ pollen. Pollen grains were found inside the micropylar canal of the ovule (Plates V, 4–5; XII, 6), at the micropylar end of the seed (Plate XII, 7–8), in one pollen cone attached to the microsporophyll blade outside the pollen sac (Plate XI, 3), and in the pollen sacs (Plates X, 1–6; XI, 1–2, 7) of several polliniferous cones and dispersed in sediment surrounding the macrofossils (Plate XII, 9–11). They are circular in polar view to oval in equatorial or oblique view (Fig. 2, k). Exine surface rugulate (folded irregularly) on whole specimen. Surface of folds smooth. Ectexinal folds are visible in LM (Plates XI, 4–6; XII, 6–11), SEM (Plate XII, 1–2) and TM (Plate XII, 3–5). An alveolate infrastructure is not visible between the exine layers (Plate XII, 3–5) and no distinct apertures are visible. Due to dense packing in the pollen sack, pollen grains are generally more or less deformed by dents of different shape (Plate XI, 1, 3). Some specimens are concave or possess one or more exinous ridges raised towards (or crossing over) the grain. Dimensions: The diameter of pollen varies from 26 to 37 μm. The average size is 32–35 μm. The diameter of the central part is 21–34 μm and the height of ectoexinal folds in a polar view, 2–3,5 μm.

4. Discussion

4.1. Reconstruction of the plant

The basis of the whole plant reconstruction is the organic connection of different organs of the new plant. Ovuliferous and polliniferous cones were found attached to leafy shoots. One seed was found attached to the seed-scale. The integument cuticles of the ovule and seed correspond with each other. The place of attachment at the chalazal end has the same side position, shape and cell pattern in ovule and seeds. All vegetative and reproductive structures have cuticles of the same type. The cell patterns, stomata, papillae and fringes present on each organ are of the same type and structure. The pollen grains found in the polliniferous cone are the same as those observed in the micropylar canal of the ovule and inside the seed. Woody trunks, recognized as *Agathoxylon keuperianum* (Unger) Phillipe (Philippe et al., 2015), are also known from Patoka (more than 0.5 m in diameter). If they belong to the *Patokaea* plant, this could be a huge tree in growth form.

4.2. General comparisons

4.2.1. Shoots

The *Brachyphyllum*-*Pagiophyllum*-type leaves were mainly characteristic of Jurassic and Cretaceous conifers. This type of leaf is thus far known for four families: Araucariaceae, Cheirolepidiaceae, Podocarpaceae and Cupressaceae (Meyen, 1987; Taylor et al., 2009). This type of leaf was rare in the Triassic and probably signalled the appearance of a new type of conifers, the ancestors of modern families. *Patokaea* leaves are morphologically similar to those of *Brachyphyllum*. Some leaves with an extended free part, probably belonging to young shoots, resemble the *Pagiophyllum*. Similar specimens from the European Triassic (Carnian) were referred to *Widdringtonites keuperinaus* Heer. Some of this species' twigs were described according to their gross morphology, but without cuticle details (Heer, 1865). Later, Kräusel (1923, 1955) re-described specimens of this species collected from the type locality, and emended the description through the addition of cuticle details. They are similar to the cuticles of *Patokaea* with the same arrangement of stomata, and variable occurrence of papillae around the stomatal pit and on the cells. The same species was reported by Kelber and Hansch (1995) from the Keuper of Germany without cuticle data, but recognized as being of the *Brachyphyllum*- and *Pagiophyllum*-type. Other similar shoots determined as *Pagiophyllum peregrinum* were described by Schenk (Schenk, 1889) from the Triassic-Lower Jurassic of northern Italy (Lake Como). None of the Triassic shoots with leaves of the brachyphyllous-pagiophyllous type from Europe were found with cones in organic attachment. In the Upper Triassic of North America, *Brachyphyllum* and *Pagiophyllum* were more widespread than in Europe (e.g., Ash, 1973, 1989, 1999). Some of these taxa are similar to *Patokaea* in cuticular structure (e.g., *B. hegevaldia* Ash, 1973, *B. comancheanum* Ash, 1999), but they usually differ in gross morphology from *Patokaea*.

Although the aforementioned remains resemble the shoots of *Patokaea*, brachyphyllous-pagiophyllous-leaf species generally only slightly differ in morphology, even when produced by different conifer families. The differences between species are observable in the cuticular structure, but their real taxonomical affiliation is determined by the attached cones. The leaves of *Patokaea* show high variability both in shape and in the structure of leaf margins being scarious or with more or less developed fringes, of variable number and length. According to Harris' study (Harris, 1979), the presence of such structures is a feature of taxonomical value, but the degree of their development can probably change even at a population level (see also Watson, 1977; Archangelsky, 1963). Fringes were found in the following brachyphyllous-pagiophyllous taxa: *Brachyphyllum comancheanum* Ash (Ash, 1999), *B. crucis* Kendall (Kendall, 1947; Harris, 1979), *Pagiophyllum fragilis* (Bose) Harris (Harris, 1979), *Pseudofrenelopsis parceramosa* (Fontaine) Watson (Watson, 1977), *B. bretti* Archangelsky, *B. mirandai* Archangelsky and *B. irregulare* Archangelsky (Archangelsky, 1963). The leaves of *Patokaea* cannot be attributed to a new taxon exclusively on the grounds of their macro- or micromorphology without taking into consideration the attached cones. The leaves are most similar to *B. crucis* (Harris, 1979) with stomata scattered randomly on the upper and lower cuticles, while in most other species stomata are arranged in files or bands.

4.2.2. Ovuliferous cones

The most important diagnostic features regard the reproductive organs of *Patokaea*. The ovuliferous scale-bract complex of *Patokaea* appears unique with its three lobes, from which one, the middle, is sterile. Some hitherto known genera of ovuliferous cones from the Permian to Cretaceous are potentially comparable with *Patokaea*

Plate I. *Patokaea silesiaca* sp. nov., morphology and anatomy of twigs.

1-4. Variability of leafy twigs:
1. KRA-PALEO 104/43,
2. KRA-PALEO 104/47,
3. KRA-PALEO 104/50,
4A KRA-PALEO 104/55 (paratype),
4B KRA-PALEO 104/61
4C KRA-PALEO 104/54 with terminal bud.
5-13. Cuticular details of the leaves:
5. Twig fragment, LM, paratype, KRA-PALEO 104/103.
6. Twig with bud (b) visible, SEM, KRA-PALEO 104/66.
7. Leaf margin with fringes KRA-PALEO 106/66, detail from Fig. 6.
8. Abaxial leaf cuticle, LM, KRA-PALEO 104/105.
9. Leaf surface with papillate epidermal cells, FM, KRA-PALEO 104/103.
10. Leaf surface with scattered stomata, FM, KRA-PALEO 104/103.
11. Leaf margin, stomata and fringes visible, abaxial side, FM, KRA-PALEO 104/103.
12. Leaf cuticle of shoot bearing ovuliferous cone, FM, holotype KRA-PALEO 104/43.
13. Leaf cuticle of shoot bearing polliniferous cones, FM, paratype KRA-PALEO 104/40.

Plate II. *Patokaea silesiaca* gen. et sp. nov., ovuliferous cone (1, 2) and seed scale-bract complexes (3–5). (see on page 36)

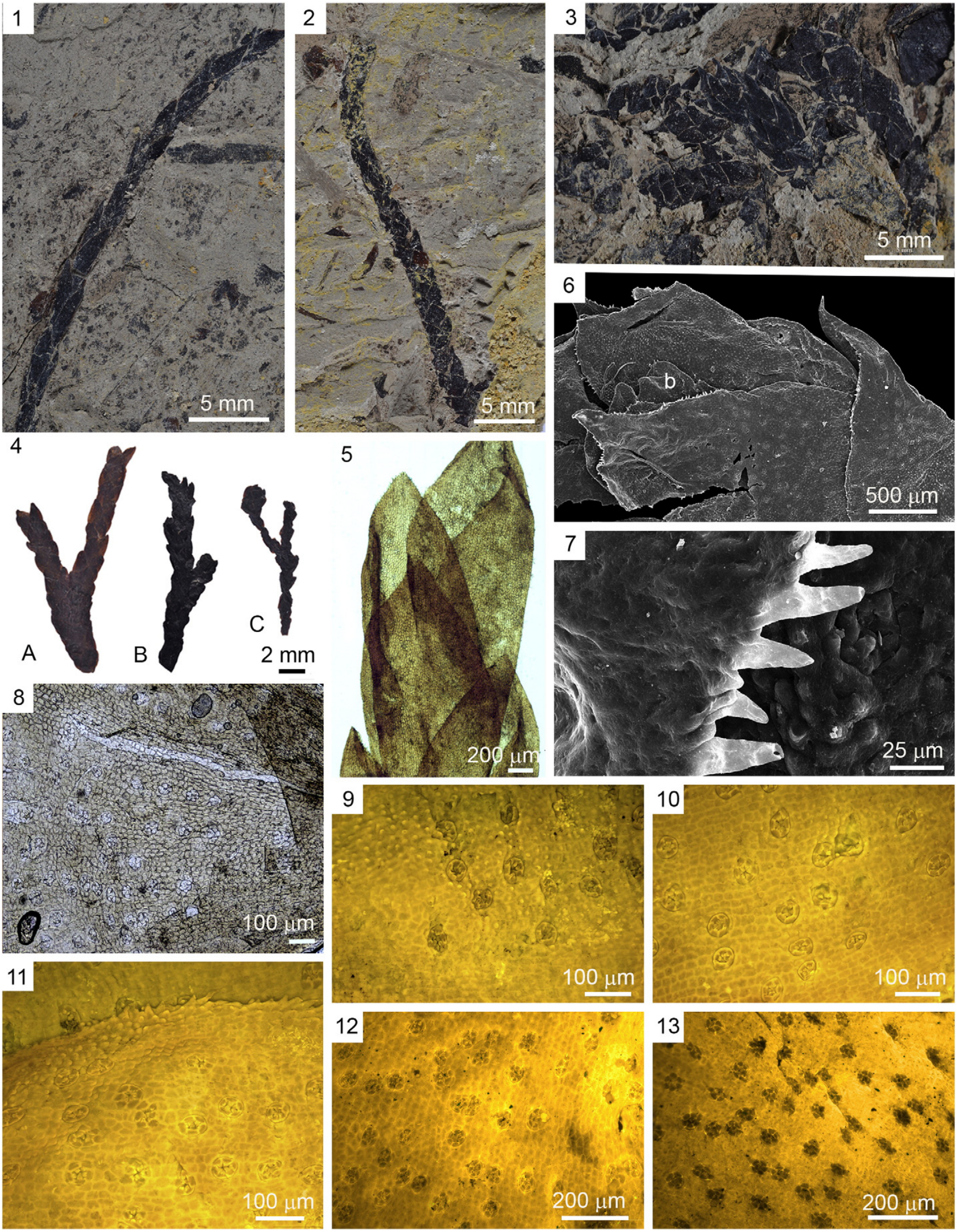
1. Leafy twig with terminal ovuliferous cone, holotype, KRA-PALEO 104/43.
2. Isolated fragment of ovuliferous cone, axis with two ovuliferous scale-bract complexes, KRA-PALEO 104/196.
3. Fragment of seed scale-bract complex with seed still attached from abaxial side, b - apical part of bract, sl - sterile lobe, fl – part of fertile lobe with seed (s) still attached, paratype, KRA-PALEO 104/20.
4. Fragment of seed scale – bract complex with seed still attached from adaxial side, b - apical part of bract, sl - sterile lobe, fl – part of fertile lobe with seed still attached (s), paratype, KRA-PALEO 104/20.
5. Variability of ovuliferous scale-bract complexes, A-D - with stalk preserved, E-I – with stalk missing, A - KRA-PALEO 104/197, B- KRA-PALEO 104/198, C – KRA-PALEO 104/7, D – KRA-PALEO 104/3 (paratype), E – KRA-PALEO 104/4, F – KRA-PALEO 104/70, G – KRA-PALEO 104/12, H – KRA-PALEO 104/8, I – KRA-PALEO 104/1.

Plate III. *Patokaea silesiaca* gen. et sp. nov., details of seed scale-bract complexes. (see on page 37)

1. Fragment of fertile lobe with place of ovule attachment, HF treated, paratype, KRA-PALEO 104/62.
2. Fragment of fertile lobe with place of ovule attachment, HF and Schulz treated, paratype, KRA-PALEO 104/63.
3. Detail of Fig. 2, adaxial cuticle of lobe, flounce-like margin of ovule envelope, paratype, KRA-PALEO 104/63.
4. Fragment of fertile lobe from adaxial side with place of ovule attachment, SEM, paratype, KRA-PALEO 104/64.
5. Abaxial side of fertile lobe SEM picture, paratype, KRA-PALEO 104/65.
6. Middle sterile lobe with middle dividing line well visible, SEM, paratype, KRA-PALEO 104/65.

Plate IV. *Patokaea silesiaca* gen. et sp. nov., details of seed scale-bract complexes (1–7) and ovule (8). (see on page 38)

1. Margin of fertile lobe, SEM picture, paratype, KRA-PALEO 104/65.
2. Fragment of fertile lobe with amorphic place of ovule attachment, HF treated, SEM picture, paratype, KRA-PALEO 104/64.
3. Stomatal apparatus, detail from Plate III, 5.
4. Seed scale-bract complexes from abaxial side, b – bract, A – KRA-PALEO 104/3 (paratype), B – KRA-PALEO 104/9 (one fertile lobe missing).
5. Free part of bract, detail from Fig. 6.
6. Stalk with decurrent bract of seed scale-bract complex, SEM, paratype, KRA-PALEO 104/64.
7. Free part of bract, cuticle, KRA-PALEO 104/115.
8. Isolated ovule, HF treated, paratype, KRA-PALEO 104/36.


1
5 mm
2
5 mm
3
5 mm
4
A
B
C
2 mm
5
200 µm
6
b
500 µm
7
25 µm
8
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9
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10
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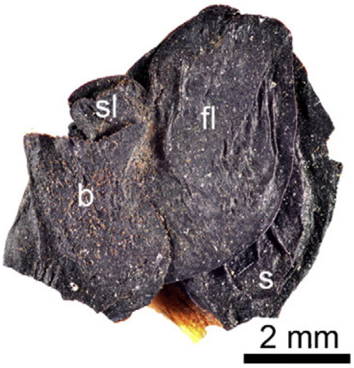
11
100 µm
12
200 µm
13
200 µm

Plate I.

1

2

3



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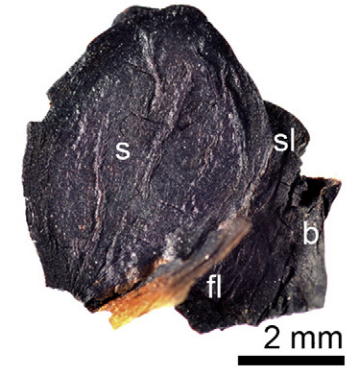

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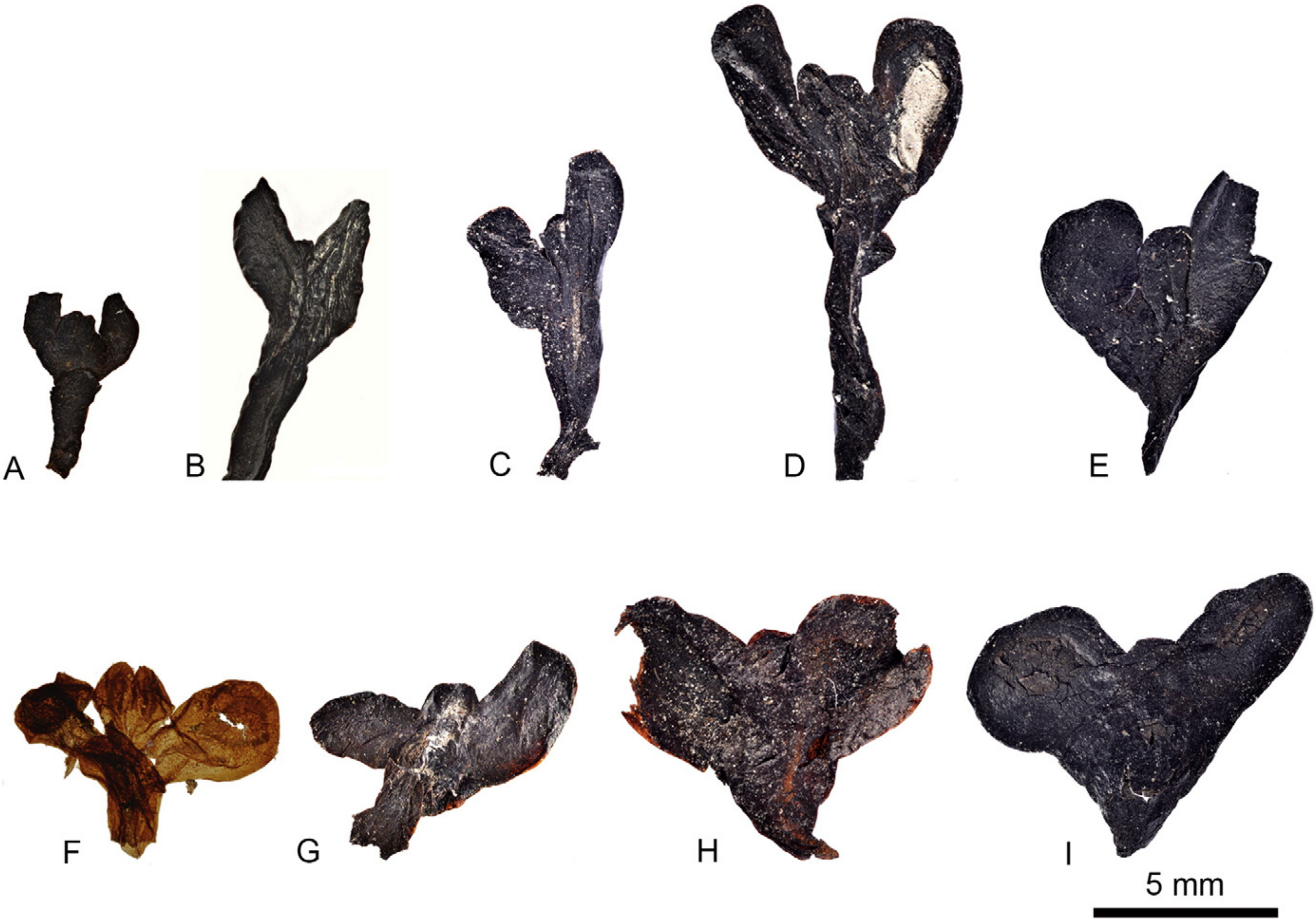

Plate II *(caption on page 34).*

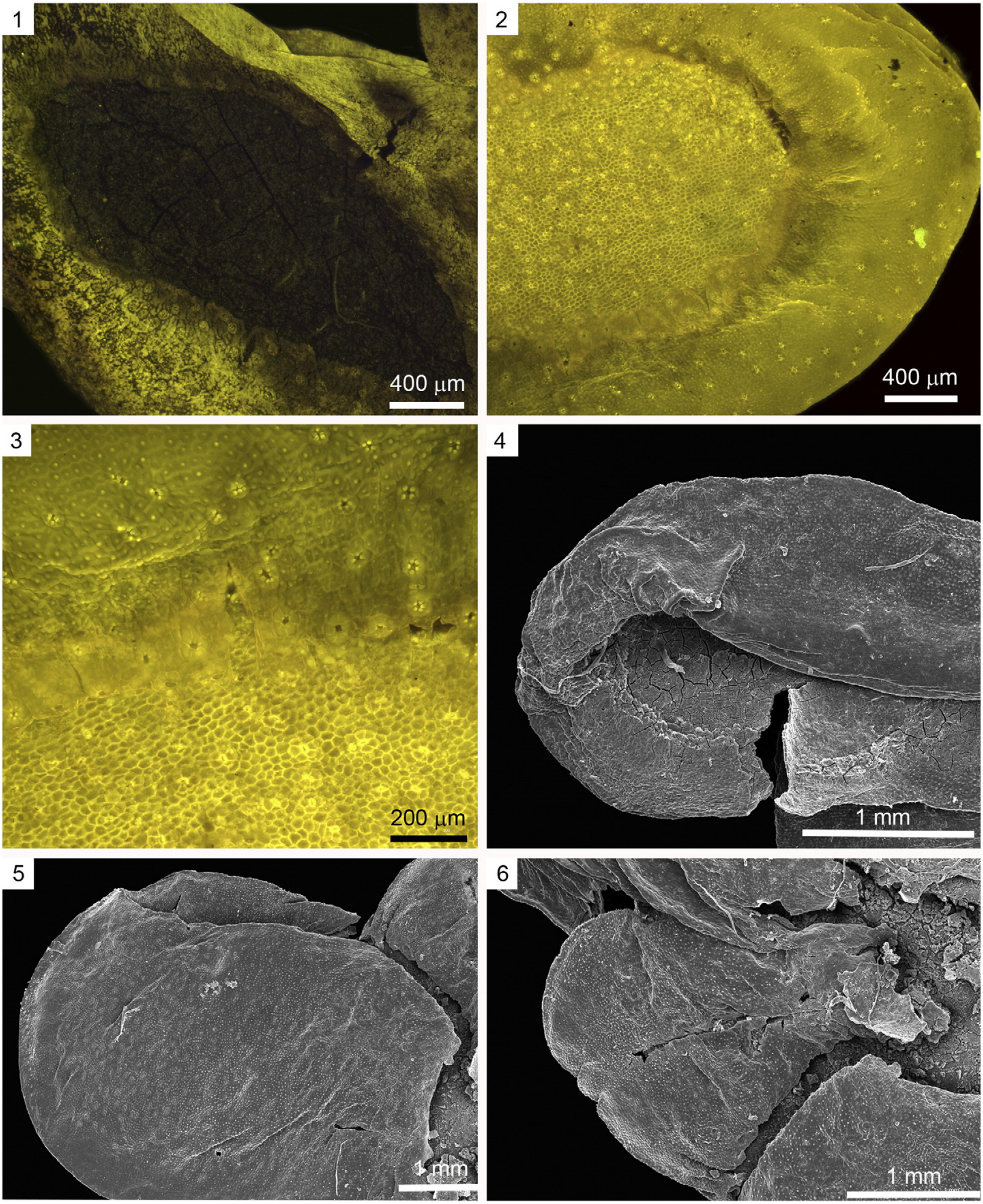

Plate III *(caption on page 34)*.

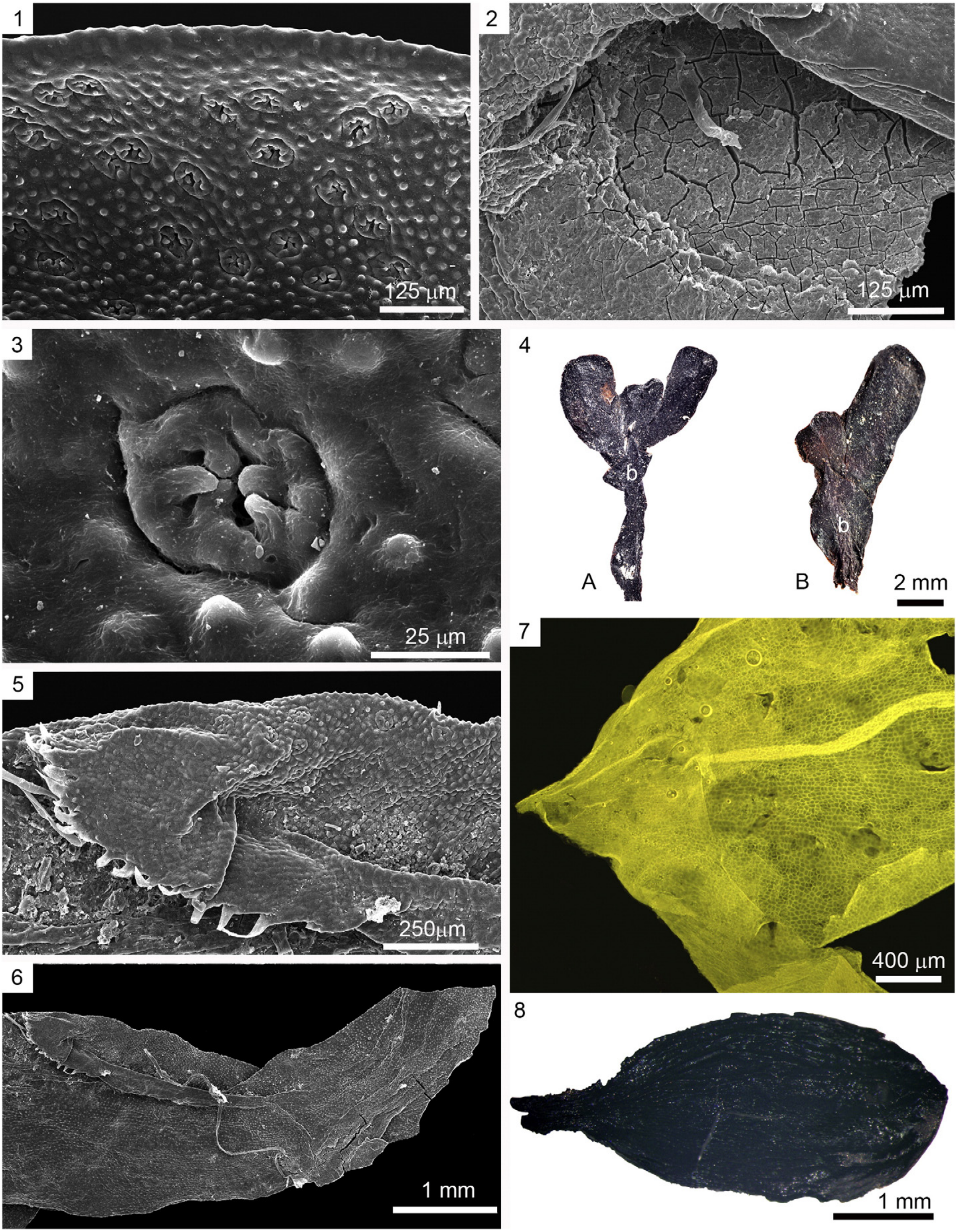

Plate IV *(caption on page 34)*.

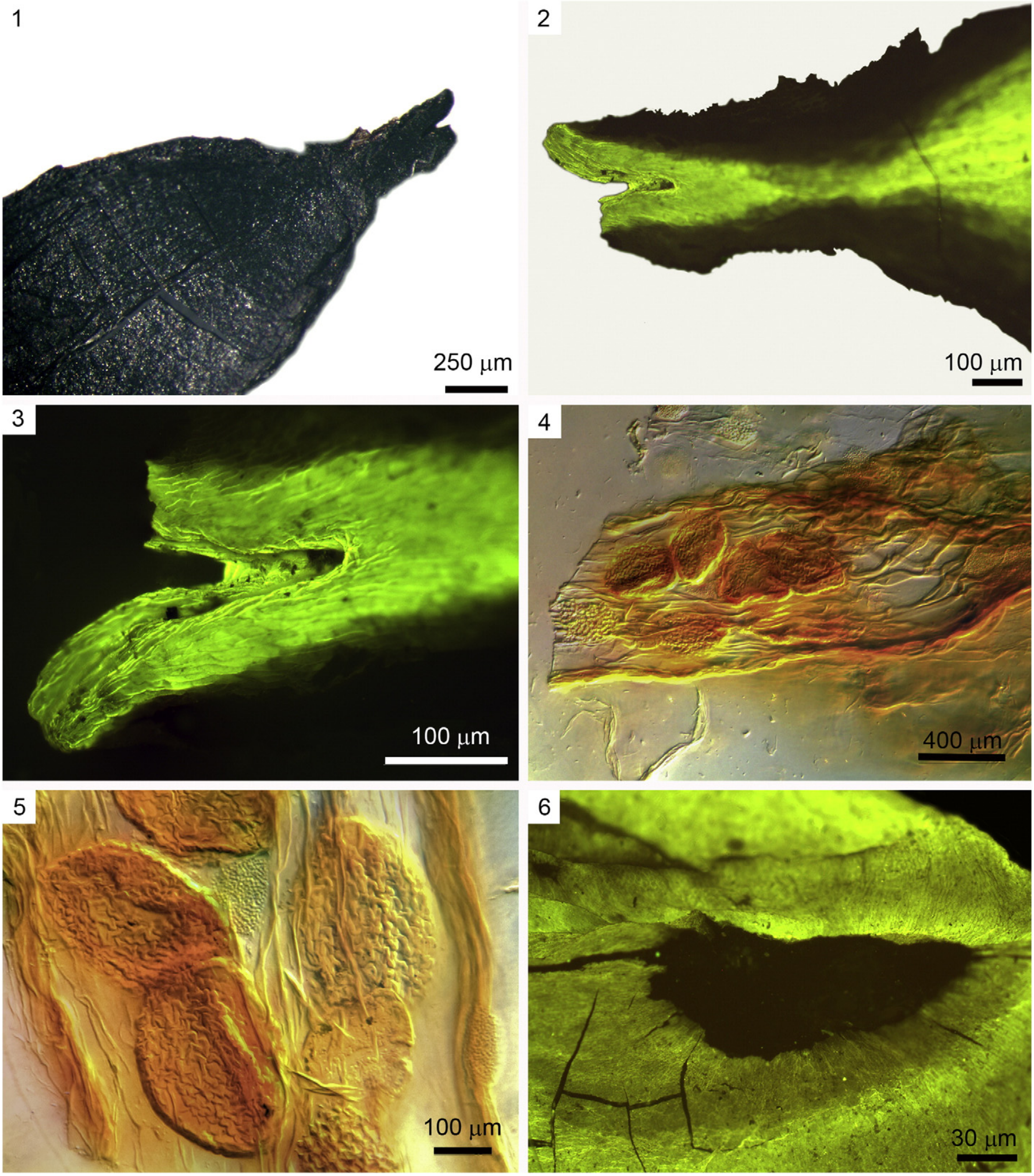

Plate V. *Patokaea silesiaca* gen. et sp. nov., details of ovule morphology and anatomy.

1. Micropylar end of ovule, paratype, KRA-PALEO 104/36.
2. Micropylar beak, FM, paratype, KRA-PALEO 104/36.
3. Forking ends of micropylar beak, FM, paratype, KRA-PALEO 104/36.
4. Pollen grains inside micropylar canal, LM, paratype, KRA-PALEO 104/36.
5. Detail of Fig. 4.
6. Chalazal end of ovule with place of attachment, FM, paratype, KRA-PALEO 104/36.

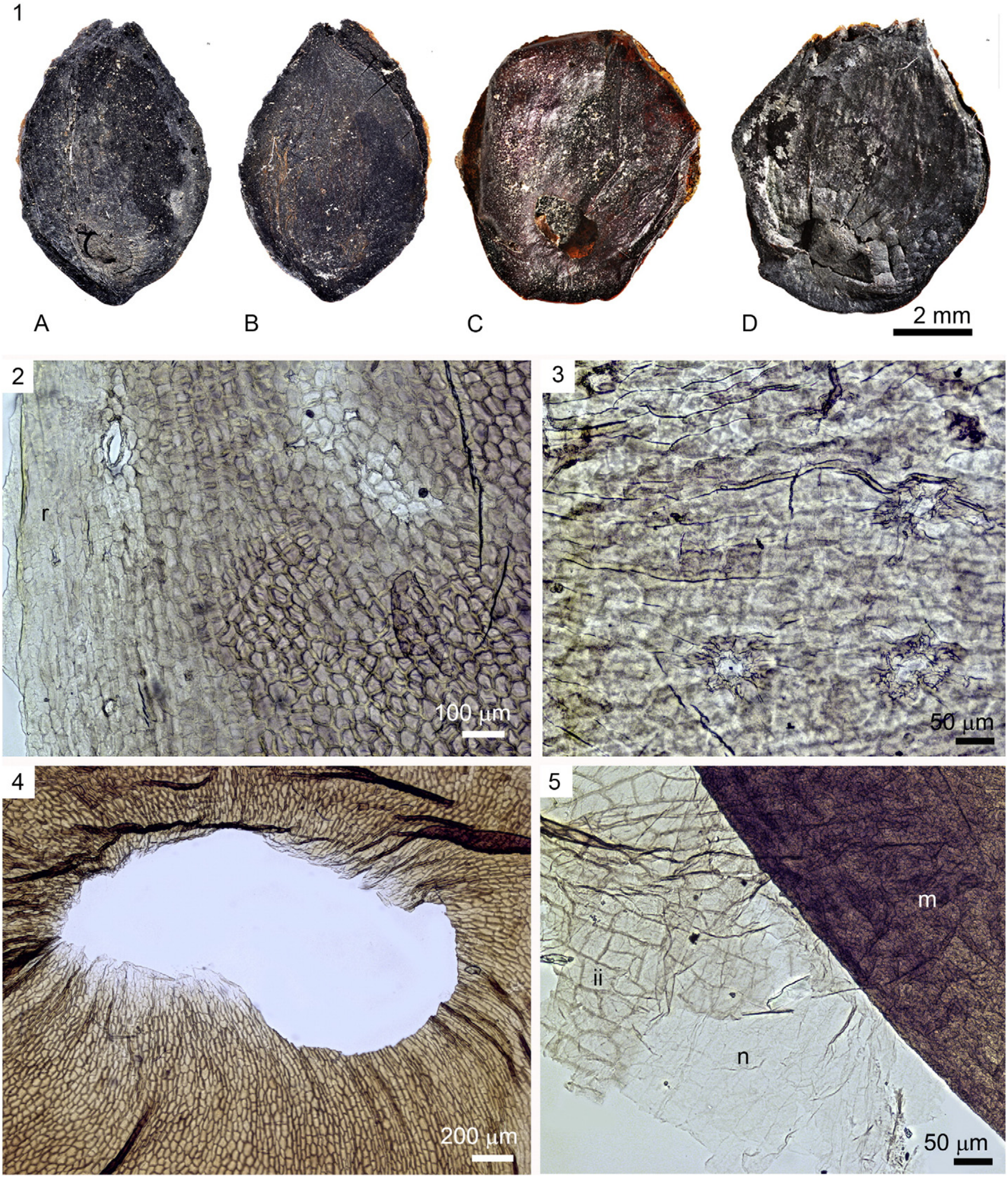

Plate VI. *Patokaea silesiaca* gen. et sp. nov., morphology and anatomy of seeds.

1. Seeds, A-B seed from both sides, KRA-PALEO 104/37 (paratype), C-D - seeds from side with place of attachment, C – KRA-PALEO 104/21, D - KRA-PALEO 104/22.
2. Outer integument of the seed with thinner marginal rim (r), paratype, KRA-PALEO 104/37.
3. Outer integument of the seed with trichome bases, paratype, KRA-PALEO 104/37.
4. Outer integument of the seed with hole at the attachment place, paratype, KRA-PALEO 104/37.
5. Inner cuticle of integument (ii), probably cuticle of nucellus (n) and megaspore membrane (m), paratype, KRA-PALEO 104/24.

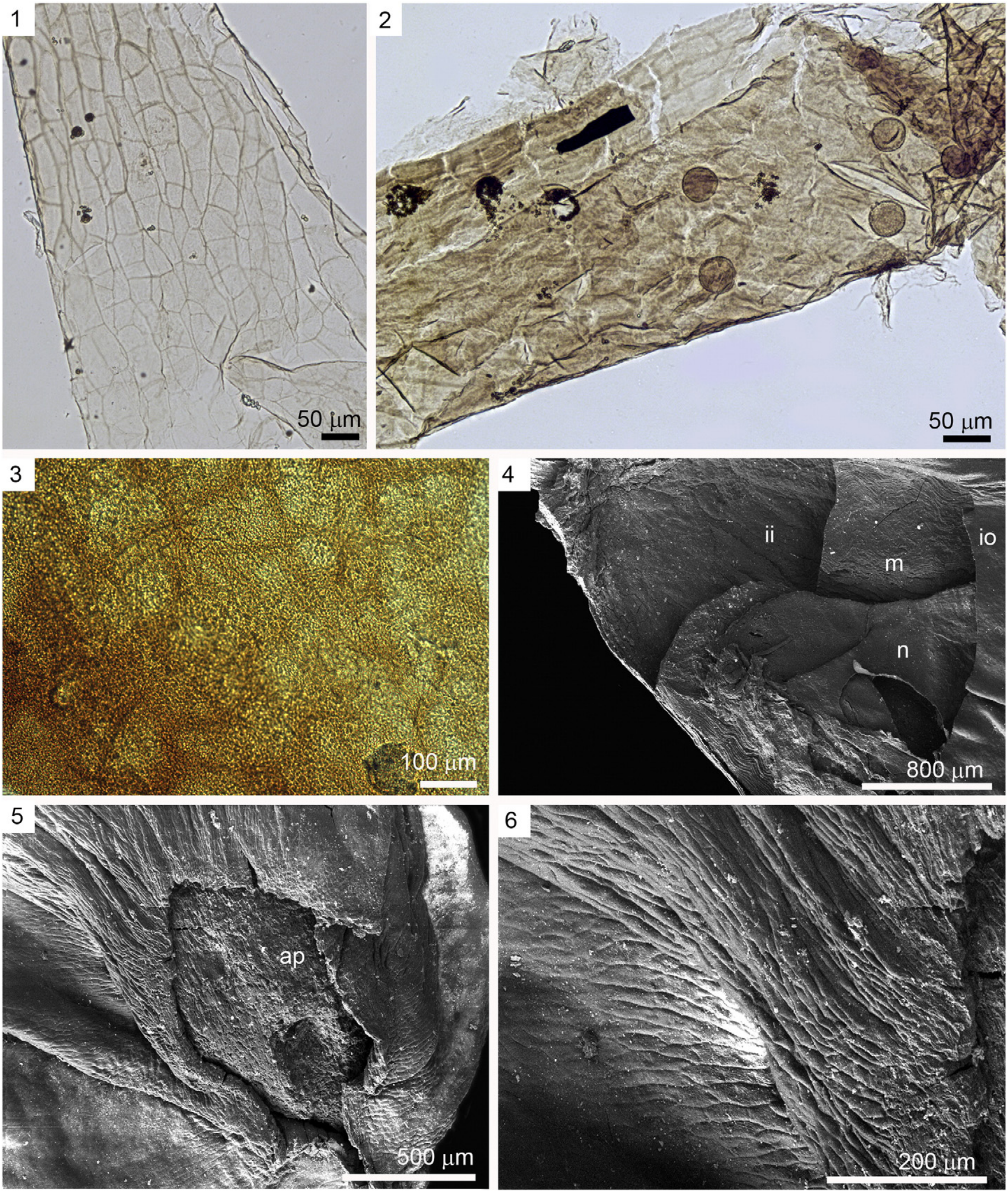

Plate VII. *Patokaea silesiaca* gen. et sp. nov., anatomy of seeds.

1. Cuticle of nucellus, paratype, KRA-PALEO 104/24.
2. Cuticles from the micropylar end of seed with adhering pollen grains, KRA-PALEO 104/24.
3. Megaspore membrane, paratype, KRA-PALEO 104/37.
4. Micropylar part of seed, io – integument from outside, n – nucellus, m – megaspore membrane, ii – integument from inside, paratype, KRA-PALEO 104/26.
5. Chalazal end of seed with attachment place (ap), paratype, KRA-PALEO 104/26.
6. Cell pattern of the integument at the margin of attachment place, detail of Fig. 5.

(Table 1) and could settle its systematic position. Late Palaeozoic and early Mesozoic conifers *Glyptolepis* Schimper, *Voltziopsis* Potonié, *Voltzia* Brongniart, *Tricranolepis* Roselt, *Schizolepidopsis* Doweld, *Swedenborgia* Nathorst, *Aetophyllum* Brongniart, *Pachylepis* Kräusel, *Hirmeriella* Jung and *Tomaxiella* Archangelsky are here taken into consideration for comparison. Unfortunately, some Permian and Triassic conifers described in the 19th and early 20th centuries were misinterpreted (e.g., *Glyptolepis*, Florin, 193–1945, 1951), therefore the phylogenetic interpretations based on them are doubtful. Revisions of these are only just beginning (Axsmith and Taylor, 1997; Axsmith et al., 2004; Arndt, 2002) and the results could change our perception of Triassic conifers. A useful graphic comparison of ovuliferous scale-bract complexes of Permian and Mesozoic conifers was recently presented by Herrera et al. (Herrera et al., 2015, Fig. 8). Based on this figure, it is apparent that *Patokaea* is generically different from the Permian–Mesozoic conifers described thus far. The ovuliferous cones of extant families like Araucariaceae, Cephalotaxaceae, Cupresaceae, Phyllocladaceae, Pinaceae, Podocarpaceae, Sciadopityaceae, or Taxaceae differ so much that they are not compared here (Page, 1990). In Walchian Voltziales (Carboniferous–Permian, Rothwell et al., 2005), ovuliferous ovulate cones consist of prominent three-dimensional ovuliferous dwarf shoots axillary to the bract. Voltzian Voltziales (Permian–Cretaceous, Taylor et al., 2009) have more or less developed flat seed scales. Voltzialean bract-scale complexes are multi-lobate (from eleven-lobed *Conewagia longiloba* Axsmith) through many five-lobed forms (e.g., *Voltziopsis*, some *Swedenborgia* species, *Aethophyllum*, *Pachylepis*) to three-lobed in *Swedenborgia tyttosperma* (Stanislavsky, 1976; Herrera et al., 2015). In all these forms, ovules are attached on the lobes or below the lobes. Generally, voltzialean ovule-bearing scales may be classified by having: (1) only sterile lobes at the distal part of the ovule-bearing scale and seeds on the central part of this structure; (2) all lobes fertile with ovules on them, or (3) more or less reduced sterile lobes between fertile lobes with ovules (see Table 1). Of the Cheirolepidiaceae, *Tomaxellia biforme* Archangelsky (Archangelsky, 1968) has a bract-scale complex in which there are six sterile lobes in relation to only two ovules placed in the central part of the complex (Archangelsky, 1968). *Patokaea* is exceptional with regard to the structure of the ovule-bearing scale, the number of lobes and ovules and the position of the ovules. Due to the morphology of ovuliferous scale-bract complex, *Patokaea* somewhat resembles the genus *Schizolepidopsis* (=*Schizolepis*) (Wang et al., 1997; Zhang et al., 2011), in which the seed scale possesses two lobes each bearing an ovule (Leslie et al., 2013). Some species of *Schizolepis* with trilobate seed scales, e.g., *Schizolepis hoerensis* (Antevs, 1919), have been described and referred to another genus, i.e. *Tricranolepis* as *T. hoerensis* (Roselt, 1958). However, it has three ovules, partly situated on each lobe. The Early Cretaceous *Schizolepidopsis canicularis* Leslie et al. published a few years ago (Leslie et al., 2013) clearly shows details of the cone and ovuliferous scales. This form is two-lobed, ovules are attached near the base of the lobe (no noticeable fold overlapping the ovule like in *Patokaea*) and the seeds are winged like in modern Pinaceae. In *Patokaea* seeds are not winged and attached distally. The form of seed scale-bract complex in *Patokaea* seems to be derived from voltzialean three- or more-lobate forms (like *Voltzia* or *Glyptolepis*) and could be transitional between them and the bilobate *Schizolepidopsis*.

4.2.3. Seeds

Seeds associated with conifer ovuliferous organs have been described from some European Triassic localities. However, most of these were interpreted as cycad seeds even though they closely resembled seeds still attached to associated seed scales (Compter, 1883, 1903; Mägdefrau, 1956). In gross morphology some of these seeds are similar to the seeds of *Patokaea*, but their internal structure is almost unknown. Only Compter (1883) has macerated some seeds and illustrated the integument cuticles. In fact, the internal cuticles of the seeds (cuticle of integument, nucellus and megaspore membrane) are very similar in most gymnosperms. Opportunities to compare *Patokaea* seeds with other previously described Upper Triassic conifer seeds are therefore limited. Only the Triassic seeds described by Harris (1935) from the Upper Triassic–Lower Jurassic flora of Greenland are relatively well known, but their coniferous affinity has not been determined unequivocally. In addition, they were neither associated by their leafy shoot nor by ovuliferous cones being similar to *Patokaea* (Harris, 1935). More taxa of coniferous seeds have been described form the Upper Triassic of North America but, as a rule, only their gross morphology is known (Ash, 1999). The distinguishing feature of seeds from Patoka, which makes them different from other coniferous seeds described thus far is the attachment place on their sides.

4.2.4. Polliniferous cones

During the Triassic, conifer polliniferous cones were very diverse. Simple to compound cones have been identified (Roselt, 1956; Grauvogel-Stamm, 1969, 1972, 1978; Grauvogel-Stamm and Grauvogel, 1973; Grauvogel-Stamm and Schaarschmidt, 1979; Meyen, 1987; Grauvogel-Stamm and Galtier, 1998). A useful summary of conifer polliniferous cones was presented by Meyen (Meyen, 1987, Fig. 67, 1997). Clearly, polliniferous cones of *Patokaea* could not be referred to any type distinguished by him. The majority of Triassic coniferous polliniferous cones were proportionally large, with numerous microsporophylls (e.g., *Willsiostrobus* and *Masculostrobus* are several cm long). The large number of microsporangia on particular microsporophylls is also characteristic of some Triassic forms (Grauvogel-Stamm, 1969, 1972; Grauvogel-Stamm and Álvarez Ramis, 1996; Grauvogel-Stamm and Galtier, 1998). The *Patokaea* polliniferous cone differs from those of other Triassic Voltziales mainly in size, being much smaller than most described species. This may therefore be regarded as a progressive feature (see also Table 2). One prominent feature of the *Patokaea* polliniferous cone is the comparatively small number of pollen sacs (about 5–7 per microsporophyll), which are probably sessile, arranged in a whorl around the central stalk. However, the location and attachment of the pollen sacs is difficult to interpret due to strong compression. In *Darneya*, the pollen sacs are attached to the microsporophyll stalk with thin branching stalks; in *Masculostrobus* they are connected to the adaxial side of the microsporophyll (Schaarschmidt and Maubeuge, 1969). The pollen grains of these two genera are bisaccate. Ash (1999) described a new polliniferous cone, *Masculostrobus lafonii*, from the Upper Triassic of New Mexico (USA), of which the distal blade cuticle details are similar to those of the cone described here, i.e. similar cell shapes, stomata, fringes. He also found similar pollen grains (*Pseudoenzonalasporites*, *Enzonalasporites*) associated with this cone. However, the gross morphology of this cone is different from the *Patokaea* polliniferous cone, it is larger (4–4.5 cm long and 0.8–1.4 cm in diameter), and the pollen sacs are attached to the lower half of the distal lamina of the microsporophyll, extending perpendicularly to the distal lamina. The small size and helical arrangement of the microsporophylls of the *Patokaea* polliniferous cone resembles Jurassic or later forms, e.g., *Classostrobus* and the polliniferous cone of *Hirmeriella muensteri* (Cheirolepidiaceae) (Hörhammer, 1933; Jung,

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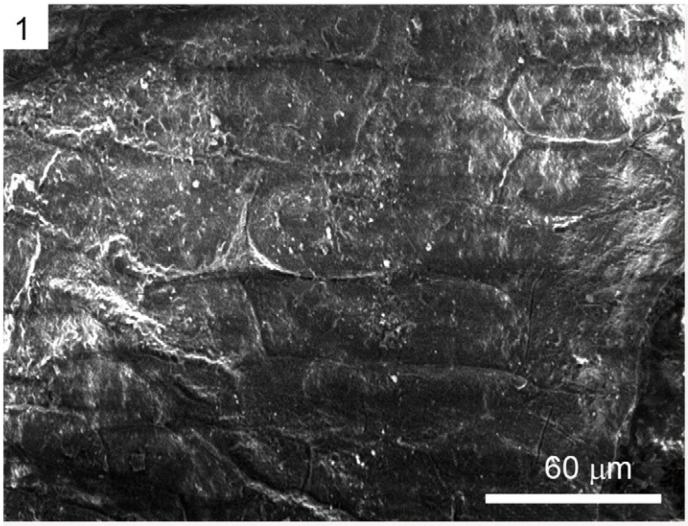
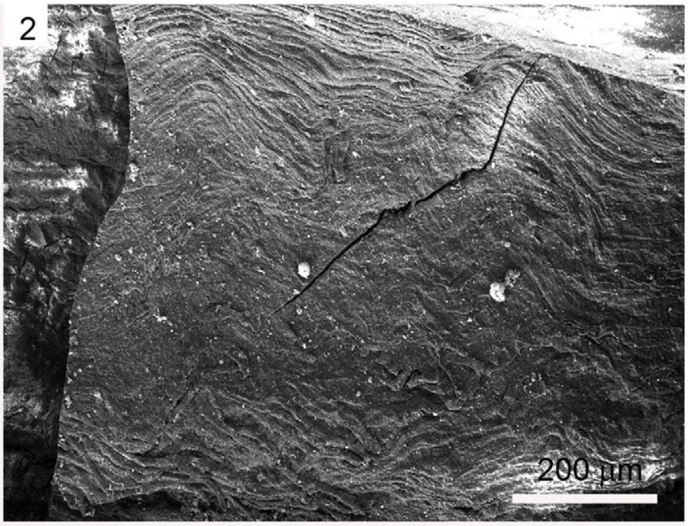
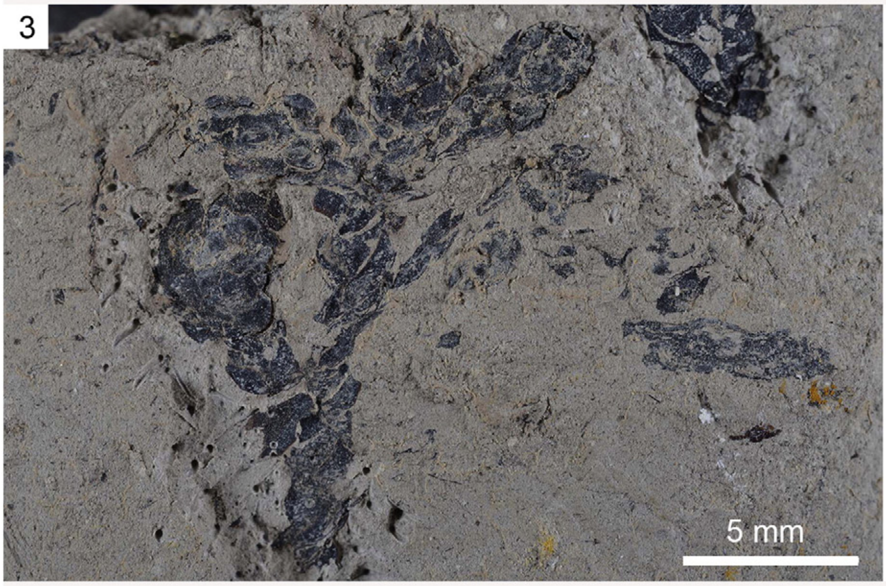
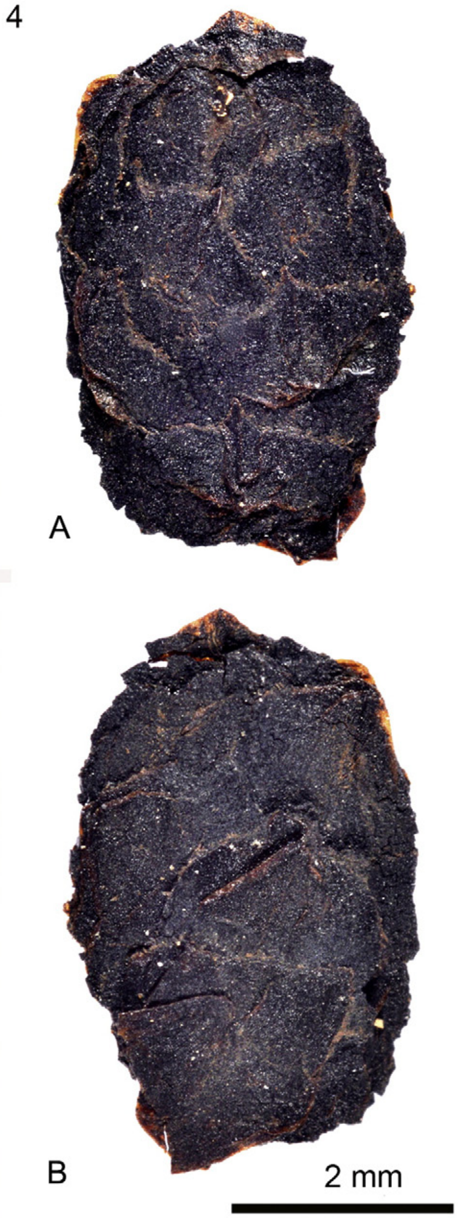
Plate VIII. *Patokaea silesiaca* gen. et sp. nov., anatomy of seeds (1, 2), morphology of polliniferous cones (3–5).

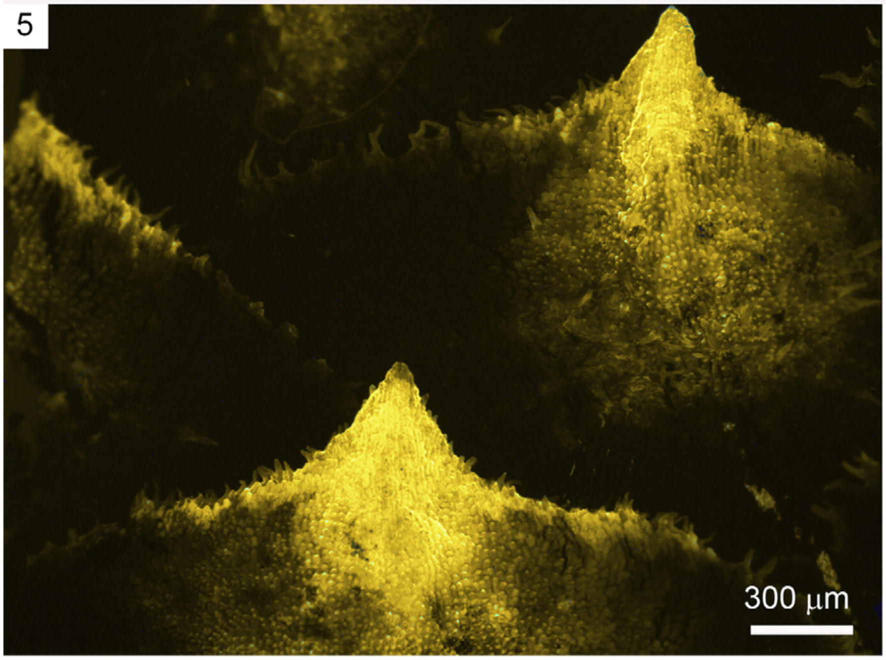
1. Pattern of cells of nucellus, detail of VII, 4, paratype, KRA-PALEO 104/26.
2. Fragment of megaspore membrane, detail of VII, 4, paratype, KRA-PALEO 104/26.
3. Twig fragment with terminal polliniferous cones, paratype, KRA-PALEO 104/40.
4. Isolated polliniferous cone from both sides A – one side, B – the other side, KRA-PALEO 104/68.
5. Fragment of polliniferous cone with free blades of microsporophylls visible, FM, paratype, KRA-PALEO 104/67.


1
60 µm


2
200 µm


3
5 mm


4
A
B
2 mm


5
300 µm

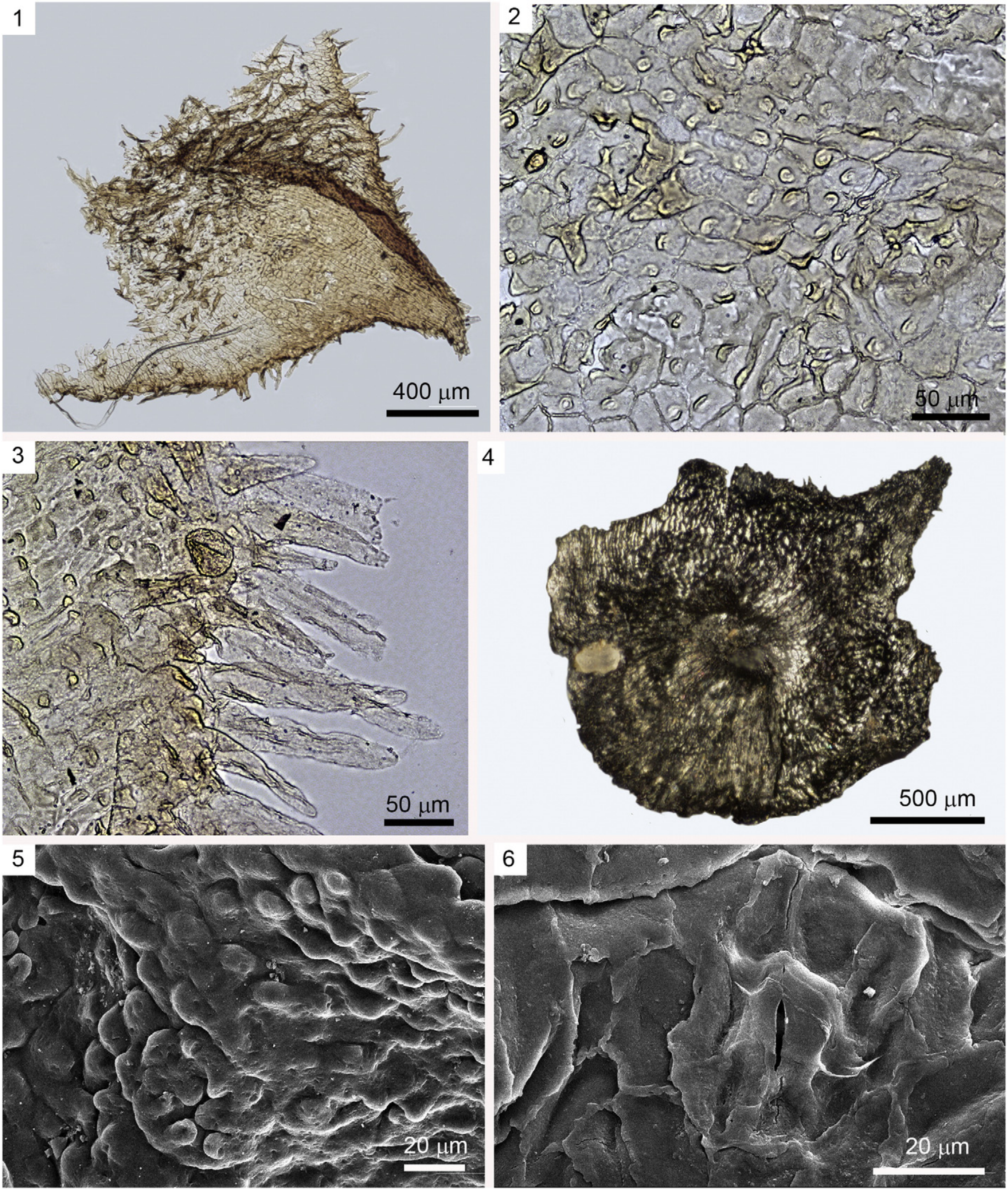


Plate IX. *Patokaea silesiaca* gen. et sp. nov., morphology and anatomy of microsporophyll free blades.

1. Cuticle of free blade of microsporophyll, LM, KRA-PALEO 104/101.
2. Fragment of cuticle of free blade of microsporophyll, detail of Fig. 1, LM, KRA-PALEO 104/101.
3. Margin of free blade of microsporophyll, detail of Fig. 1, LM, KRA-PALEO 104/101.
4. Microsporophyll free blade with stalk basis, KRA-PALEO 104/150.
5. Stomata of free blade of microsporophyll, detail of Fig. 4, SEM, paratype, KRA-PALEO 104/100.
6. Inner side of cuticle of free blade of microsporophyll with stomata, SEM, paratype, KRA-PALEO 104/100.

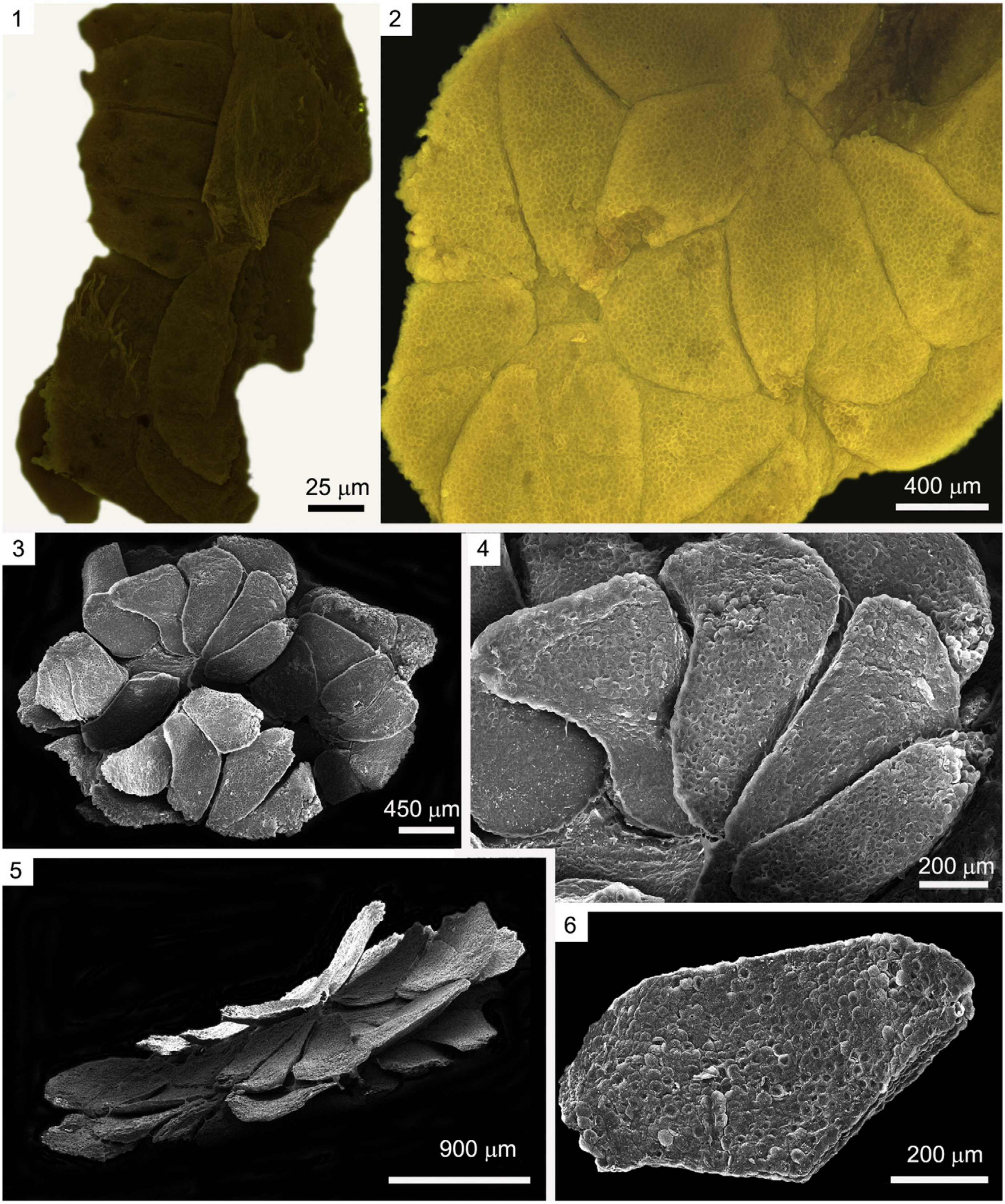


Plate X. *Patokaea silesiaca* gen. et sp. nov., polliniferous cones.

1. Fragment of polliniferous cone, crowded pollen sacs and two fragments of free blades of microsporophylls visible, FM, paratype, KRA-PALEO 104/199.
2. Fragment of polliniferous cone with whorls of pollen sacs, FM, paratype, KRA-PALEO 104/100.
3. Fragment of polliniferous cone with whorls (in spiral?) of pollen sacs, SEM, paratype, KRA-PALEO 104/100.
4. Part of one whorl of pollen sacs, detail of Fig. 3.
5. Compressed polliniferous cone with pollen sacs visible from the side, SEM, paratype, KRA-PALEO 104/100.
6. Isolated pollen sack, SEM, paratype, KRA-PALEO 104/100.

1968; Alvin, 1982; Watson, 1988; Clement-Westerhof and Van Konijnenburg-Van Cittert, 1991; Kirchner, 1992; Barbacka et al., 2007). However, the arrangement of the pollen sacs is different, being on a microsporophyll stalk which corresponds with those of primitive Permian and Triassic Voltziales. Hieger et al. (2015) described a silicified polliniferous cone, *C. elliotii*, from the Lower Jurassic of Antarctica in which the 4–7 sporangia are situated abaxially, as in most modern conifers. The same arrangement of sporangia was observed in *C. crossii* Rothwell (Rothwell et al., 2007). Sporangia situated on both sides of the stalk, interpreted as a primitive feature, were observed in *Kobalostrobus olmosensis* Serlin et al. (Serlin et al., 1981) from the Upper Cretaceous of Mexico, but the cone differs in structure from that of *Patokaea*. Modern conifer families also do not have polliniferous cones comparable with *Patokaea* (Page, 1990; Schulz et al., 2014). Pinaceae have polliniferous cones that are solitary or form terminally situated fasciculars of a completely different type in which there are only two microsporangia are situated abaxially on the microsporophylls. Taxaceae, whose simple cones also form fasciculars near the top of a branch, have 3–9 microsporangia per microsporophyll like *Patokaea*. They are positioned around the stalk, but arising from the scutellum. The simple cones of the Cupressaceae are terminal on small lateral branches, solitary, in fasciculars or clustered, and have 1–14 pollen sacs situated abaxially on the scutellum. However, in *Juniperus* and *Chamaecyparis* the sporangia are laterally attached to the stalk of the sporangiophore and not fused to the scutellum. The fossil taxodiaceous pollen cone, *Drumhellera kurmanniae* Serbet et Stockey, from the Upper Cretaceous of Canada possesses only two abaxial sporangia (Serbet and Stockey, 1991). The simple cones of the Araucariaceae form fasciculars situated terminally on lateral branches and have 2–20 microsporangia, which may arise in two rows, on the scutellum. Podocarpaceae have compound polliniferous cones, solitary or in clusters, terminal or axillary, with two microsporangia placed abaxially on the scutellum (Page, 1990). Cephalotaxaceae polliniferous cones are compound, clustered or fascicular and in the axils of leaves. Microsporophylls bear 2–8 microsporangia borne abaxially. Pollen grains are spherical and without saccae. Sciadopitiaceae cones are clustered and compound, with two microsporangia per microsporophyll. The polliniferous cones of the Phyllocladaceae are fascicular, each arising in the axil of the leafy bract with two microsporangia (Page, 1990).

4.2.5. Pollen

The pollen grains found in *Patokaea silesiaca* are most similar to the dispersed pollen grains of the following genera: *Enzonalasporites* Leschik emend. Scheuring, *Pseudoenzonalasporites* Scheuring, *Vallasporites* Leschik emend. Scheuring and *Patinasporites* Leschik emend. Scheuring. Schulz (1967) suggested that *Enzonalasporites* and *Vallasporites* were synonyms, but Scheuring (1970), after reexamination of the type and additional material from Leschik's type slides, treated these genera as separate. Detailed information about nomenclatural problems and diagnoses of *Enzonalasporites*, *Vallasporites*, *Patinasporites* and *Pseudoenzonalasporites* are given by Jansonius and Hills (1976).

Classifying these genera is problematic. Leschik (1955) described the genera *Enzonalasporites*, *Vallasporites* and *Patinasporites* as monosaccate pollen, in spite of the fact that the term “saccus” was not be used in their diagnosis. Mädler (1964a) when emending *Enzonalasporites* Leschik, 1955 used the term “velum”. Schulz (1967) described *Enzonalasporites* as monosaccate, saccizonate pollen, and also used the term “velum” rather than “saccus”. Scheuring (1970) classified *Enzonalasporites*, *Pseudoenzonalasporites* and *Vallasporites* as kryptoaperturate pollen, whereas *Patinasporites* was classified as monosaccate pollen. He neither used the term “saccus” nor “zone” in his description of the *Enzonalasporites* genus. Van der Eem (1983) classified *Enzonalasporites* and *Vallasporites* as monosaccate and monosaccoid pollen. Balme (1995) treated *Enzonalasporites* as a synonym of *Patinasporites* and classified it as asaccate pollen. Detailed TM investigations are needed to solve the problem of the presence or lack of a saccus formed by expansion of the exine of pollen grain at least partly filled with an alveolate infrastructure (Punt et al., 2007). As the pollen grains found in a *Patokaea silesiaca* polliniferous cone, show no alveolar structure in TM (Plate II, 3–5), they are probably asaccate.

The lack of a bulging proximal trilete mark differentiates *P. silesiaca* pollen grains from *Vallasporites*. The finer ornamentation, narrower and less distinct ectoexinal area (zona?) and lack of distal germinal area differentiate them from *Patinasporites*. The rugulate sculpture of the exine differentiates pollen grains of *Patokea* from *Pseudoenzonalasporites* Scheuring.

Pollen grains found in *Patokaea silesiaca* may also resemble those of *Cerebropollenites* Nilsson and *Zonalapollenites* Pflug in Thomson and Pflug (Thomson and Pflug, 1953; Nilsson, 1958). *Cerebropollenites*, however, has a coarser sculpture and the pollen grains are always hardly concave (Nilsson, 1958; Shang and Zavada, 2003), whereas *Zonalapollenites* possesses a broad collar (Stuchlik et al., 2002) in the equatorial area which is absent in *P. silesiaca* specimens.

Patokaea pollen grains are most similar to dispersed pollen assigned to *Enzonalasporites* because of the narrow ectoexinal zona, sculpture and relatively small dimensions of the whole specimens in polar view, although it is difficult to unambiguously classify the pollen of *P. silesiaca* as one species of *Enzonalasporites*.

The approximate time of occurrence of dispersed pollen grains referred to *Enzonalasporites*, *Vallasporites*, *Pseudoenzonalasporites*, *Patinasporites* in northwestern Europe is Late Triassic. *Enzonalasporites* spp., *Vallasporites ignacii* Leschik emend. Scheuring and *Patinasporites densus* Leschik ranges from the Carnian to early Rhaetian. These data are based on previously unpublished and published studies by, for example, by Leschik (1955), Mädler (1964a, 1964b), Schulz (1967),

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Plate XI. *Patokaea silesiaca* gen. et sp. nov., pollen sacs (1-2) and pollen grains in situ (3–7).

1. Compressed pollen grains within pollen sac, SEM, paratype, KRA-PALEO 104/100.
2. Densely packed pollen grains in the marginal part of the pollen sac, cuticle of pollen sac wall visible, LM, paratype, KRA-PALEO 104/100.
3. Pollen grains adhering to free blade of microsporophyll, FM, paratype, KRA-PALEO 104/67.
4. Pollen grains released during preparation of pollen sacs, LM, paratype, KRA-PALEO 104/100, slide 104/100/1.
5. Pollen grains released during preparation of pollen sacs, LM, paratype, KRA-PALEO 104/100, slide KRA-PALEO 104/100/2.
6. Pollen grains released during preparation of pollen sacs, LM, paratype, KRA-PALEO 104/100, slide KRA-PALEO 104/100/2.
7. Densely packed pollen grains in the marginal part of the pollen sac, SEM, paratype, KRA-PALEO 104/100.

Plate XII. *Patokaea silesiaca* gen. et sp. nov., pollen grains found in situ (1–8) and dispersed (9–11). (see on page 48)

1. Pollen grains from the pollen sac, rugulate surface of pollen exine visible, SEM, paratype, KRA-PALEO 104/67.
2. Details of pollen grain surface, SEM, paratype, KRA-PALEO 104/67.
3. Section through the pollen grains in the pollen sac, TEM, paratype, KRA-PALEO 104/199.
4. Detail of Fig. 3, TEM, paratype, KRA-PALEO 104/199.
5. Detail of Fig. 4, TEM, paratype, KRA-PALEO 104/199.
6. Pollen grain inside micropylar canal, detail of Plate V, 4 and 5, paratype, KRA-PALEO 104/36.

7-8. Pollen grains from micropylar end of the seed, paratype, KRA-PALEO 104/24/2.

9-11. Dispersed pollen grains from the sample containing remains of *Patokaea silesiaca* gen. et sp. nov., KRA-PALEO 104/201.

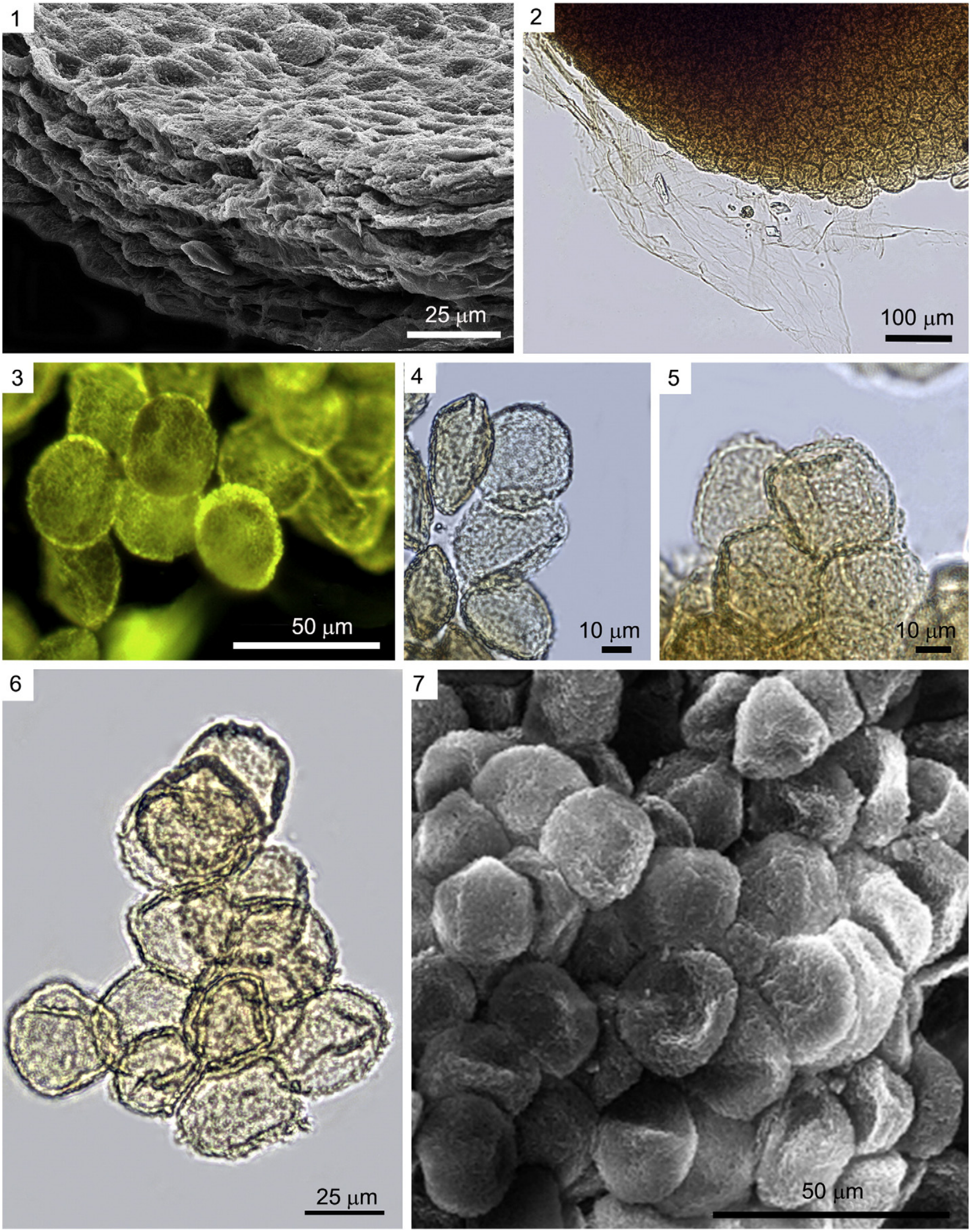

Plate XI.

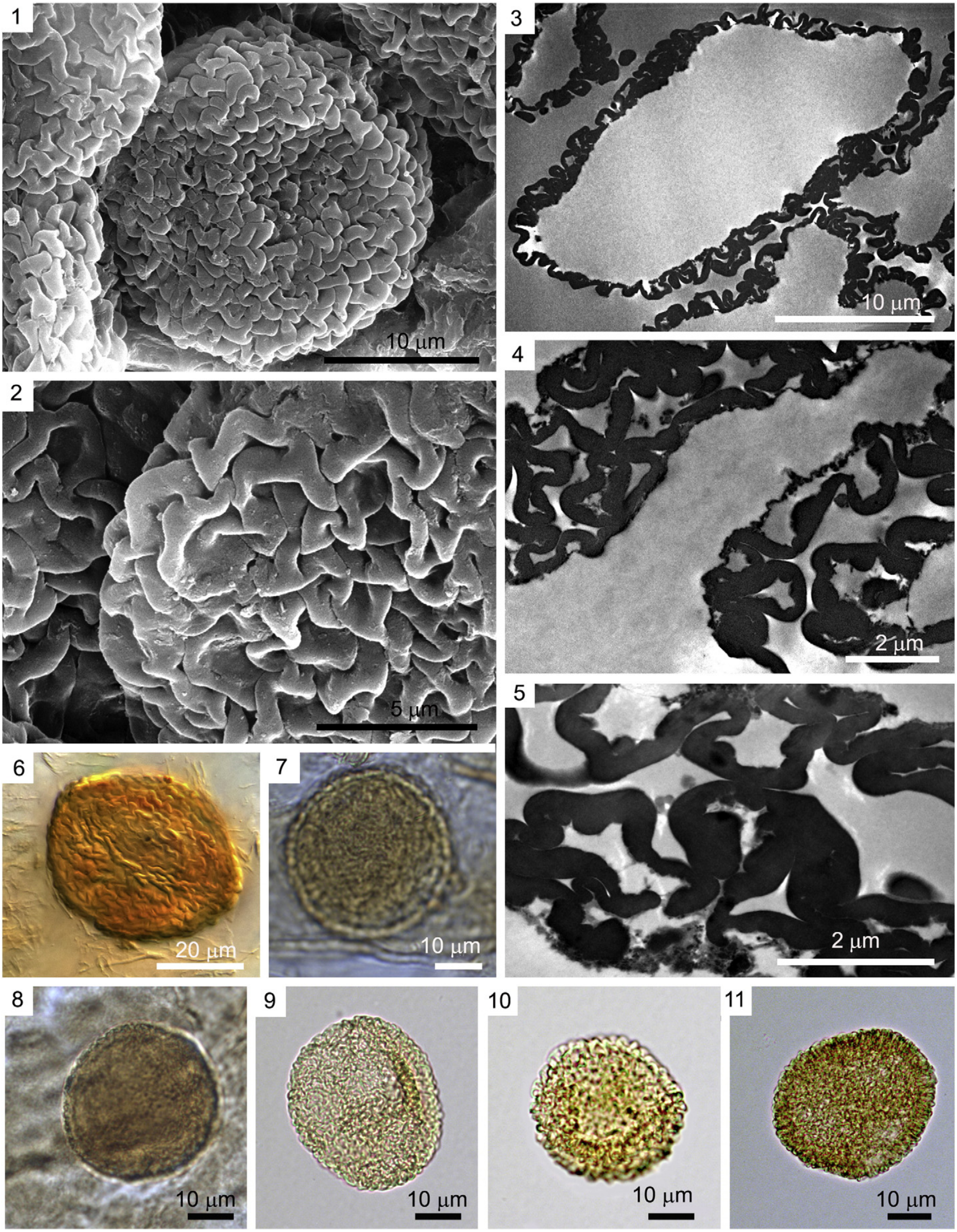

Plate XII *(caption on page 46).*

Table 1
Comparison of selected Permian and Mesozoic conifer ovuliferous cones.

Species	Ovule/seed scale-bract complex organization	Number of lobes of seed-scale	Position of ovules	Number of ovules/seeds per ovule/seed scale	Bract morphology	Age	Papers
Aetophyllum stipulare	Seed-scale flat	5 (all fertile)	Proximally, on lobes	5	Narrow, acuminate	Middle Triassic	Grauvogel-Stamm (1978)
Compsostrobus neotenicus	Flat, spatulate ovuliferous scale	1 (seed scale not divided)	Proximally, on the adaxial surface of seed scale	2	Acuminate, extend beyond the seed scale	Upper Triassic	Delevoryas and Hope (1973, 1987)
Conewagia longiloba	Seed-scale flat	11 (elongated, toothlike, fused basally, all identical)	?	?	Robust, expanded slightly below acute apex, basally fused with seed scale	Upper Triassic	Axsmith et al. (1998)
Eathiestrobus mackenziei	Seed-scale flat	1 (broadly ovate)	attached to the adaxial surface of seed scale	2	Broadly ovate	Upper Jurassic	Rothwell et al. (2012)
Florinostrobus andrewsii	Seed-scale flat	5 (partly fused)	Middle on three median lobes	3	Shorter than scale, with acute, free tip	Late Triassic	Delevoryas and Hope (1975, 1987)
"*Glyptolepis*" *keuperiana* sensu *Florin*	Seed-scale flat	7 (2 lateral fertile, 5 middle sterile)	On lobes	2	Probably leaf-like	Late Triassic	Florin (1938–1945, 1951), Mägdefrau (1963)
Glyptolepis richteri	Seed-scale flat	8	Unknown	Unknown	Diamond-shaped, base fused to seed scale stalk	Late Triassic	Axsmith and Taylor (1997)
Hirmeriella muensteri	Seed-scale flat, but not all lobes in one plane	6 (two lateral fertile scales, one round abaxial sterile scale, tree adaxial sterile scales)	Below lobes	2	Rhomboidal, width greater than length, apex acuminate	Lower Jurassic	Hörhammer (1933), Jung (1967, 1968), Clement-Westerhof and Van Konijnenburg-Van Cittert (1991), Kirchner (1992), Barbacka et al. (2007)
Krassilovia mongolica	Seed-scale flat, but not all lobes in one plane	5	Proximally, on lobes	3–5	Delicate, membranous, partially fused to the stalk of seed scale	Lower Cretaceous	Herrera et al. (2015)
Pachylepis quinquies	Seed-scale flat	5 (only fertile, fused)	On lobes	5	Narrow, base fused to seed scale stalk	Late Triassic	Linck (1950), Kräusel (1952)
Patokaea silesiaca	Seed-scale flat, both sterile and fertile lobes present	3 (2 lateral fertile, 1 middle reduced)	Distally, on lobes	2	Leaf-like, base fused to seed scale stalk	Late Triassic	This paper
Pseudohirmerella platysperma	Seed-scale flat	5 (2 lateral fertile, 3 middle sterile)	Proximally, on lobes	2	Unknown	Late Triassic	Mägdefrau (1956, 1963), Arndt (2002)
Pseudovoltzia libeana	Seed-scale flat, but not all lobes in one plane	5 (3 fertile – two lateral and middle, 2 sterile between fertile)	Proximally, on lobes	3	Narrow, base fused to seed scale stalk	Late Permian	Schweitzer (1963)
Schizolepidopsis liasokeuperianus	Seed-scale flat	2 (both fertile)	Proximally, on lobes	2	Broadly fan-shaped with rounded tip	Lower-Middle Jurassic	Harris (1979)
Schizolepidopsis canicularis	Seed-scale flat	2 (both fertile)	Proximally, on lobes	2	Small, laminar	Lower Cretaceous	Leslie et al. (2013)
Swedenborgia cryptomerides	Seed-scale flat, but not all lobes in one plane	5 (all fertile)	At the base of lobes	5	Fused for the most part to the seed scale	Lower Jurassic	Harris (1935)
Tomaxellia biforme	Seed-scale flat, but not all lobes in one plane	6	At the base of fertile scale	2	With wide base and long acute apex, near the base fused with the ovuliferous scale	Lower Cretaceous	Archangelsky (1968)
Tricranolepis monosperma	Seed-scale flat, but not all lobes in one plane	3	Located midway between the base of the seed scale and the apex of the middle lobe	1	Probably short and fused with seed scale	Middle Triassic	Roselt (1958)
Voltzia hexagona	Seed-scale tree-dimensional, somewhat flattened	5 (3 fertile – lateral and median, 2 sterile between fertile)	Proximally, on lobes	3	With acute apex, base fused to seed scale stalk	Middle Permian	Schweitzer (1996)
Voltziopsis africana	Seed-scale lobes at different levels	5–6 (all fertile)	Middle, on stalks adnate to lobes	5	Forked, narrow, as long as or longer than cone scale	Lower Triassic	Townrow (1967)

Scheuring (1970), Schuurman (1977), Orłowska-Zwolińska (1983, 1985), Fijałkowska (1994), Fijałkowska-Mader (1999) compiled by Batten and Koppelhus (1996) and also by Kürschner and Herngreen (2010).

4.3. Systematic affinity

The new conifer *Patokaea* combines shoots with *Brachyphyllum*-*Pagiophyllum*-type leaves with a new type of seed scale-bract complex

Table 2
Comparison of selected Permian and Mesozoic conifer polliniferous cones.

Species	Systematic affinity within conifers	Cone position	Type of cone	Length of cone (mm)	Morphology of microsporophyll	Arrangement of microsporangia	Type of pollen grain	Ag	Papers
Aethophyllum stipulare	Voltziales	Lateral in axil of leaf	Compound	35–50	Linear, with bilateral keeled distal lamina, single apex	Abaxially on scutellum	Bisaccate	Triassic	Grauvogel-Stamm (1978)
Classostrobus crosii	Cheirolepidiaceae	Unknown	Simple	20	Stalked with distal lamina	Abaxial, surround the microsphorophyll stalk	*Classopollis*	Middle Jurassic	Rothwell et al. (2007)
Classostrobus elliotii	Cheirolepidiaceae	Unknown	Simple	5.5	Stalked with distal lamina	Annular cluster abaxial to the microsphorophyll stalk	*Classopollis*	Lower Jurassic	Hieger et al. (2015)
Darneya peltata	Voltziales	Terminal	Compound	30–100	Stalked with distal lamina, peltate	In pairs of double pairs on a branched pedicel, several pedicels occur on the adaxial side of microsphorophyll stalk	Bisaccate	Lower Triassic	Schaarschmidt and Maubeuge (1969), Grauvogel-Stamm and Schaarschmidt (1979), Grauvogel-Stamm and Galtier (1998)
Hercynostrobus digitatus	Voltziales	Terminal?	Compound	70	Linear	Adaxial	Monosaccate	Middle Triassic	Arndt (2002)
Hirmeriella muensteri	Cheirolepidiaceae	Terminal	Simple	3–9	Stalked with distal lamina	Up to 12 in ring around microsphorophyll head (?)	*Classopollis*	Lower Jurassic	Hörhammer (1933), Jung (1968), Clement-Westerhof and Van Konijnenburg-Van Cittert (1991), Kirchner (1992), Barbacka et al. (2007)
Kobalostrobus olmosensis	Coniferales	?	Simple	15–35	Stalked bilateral distal lamina without keel, single apex	Sessile, around the central stalk	?	Upper Cretaceous	Serlin et al. (1981)
Leastrobus fallae	Voltziales	?	Compound	6	Stalked with distal lamina	Attached to scutellum	Protosaccate	Middle Triassic	Hermsen et al. (2007)
Masculostrobus zeilleri	Coniferales	Lateral in axils of leaves	Simple	130	Stalked with distal lamina	Abaxially on scutellum	Spherical pollen grains without wings	Triassic–Cretaceous	Seward (1911), Grauvogel-Stamm (1969), Miller (1977)
Millerostrobus pekinensis	Voltziales	Terminal	Simple	10	Stalked with distal lamina	Abaxial	Bisaccate	Upper Triassic	Taylor et al. (1987)
Patokaea silesiaca	Voltziales	Terminal	Simple	3.8–6	Stalked bilateral distal lamina without keel, single apex	Probably sessile, around the central stalk	Asaccate	Upper Triassic	This paper
Pityanthus scalbiensis	Podocarpaceae?	Terminal?	Simple	8–10	Slender stalk with nearly vertical expanded keeled distal lamina	Two pollen sacs below the stalk	Bisaccate	Middle Jurassic	Van Konijnenburg-van Cittert (1971), Harris (1979)
Ruechleostachys pseudoarticulatus	Voltziales	Terminal	Simple	70–130	Peltate	Abaxially on scutellum	Bisaccate	Middle –Late Triassic	Roselt (1956), Arndt (2002), Hermsen et al. (2007)
Sertostrobus laxus	Voltziales	Terminal	Simple	70	Stalked with distal lamina, peltate	Several star-shaped clusters of four microsporangia each on adaxial surface of sporophyll stalk	Bisaccate	Lower Triassic	Grauvogel-Stamm (1969), Grauvogel-Stamm and Schaarschmidt (1979)
Tomaxellia biforme	Cheirolepidiaceae	Lateral and terminal	Simple	2–3	Unknown	In groups, probably forming synangium	*Classopollis*	Lower Cretaceous	Archangelsky (1968), Archangelsky and Gamerro (1967)
Uralostrobus voltzioides	Voltziales	Lateral in axil of leaf	Simple	About 50	Stalked with distal lamina	Abaxial	Bisaccate	Lower Permian	Naugolnykh (2014)
Willsiostrobus willsii	Voltziales	Terminal	Simple	100	Stalked with distal lamina, peltate	Abaxially on scutellum	Bisaccate	Middle Triassic	Grauvogel-Stamm and Schaarschmidt (1979), Grauvogel-Stamm and Álvarez Ramis (1996)
Voltzia hexagona	Voltziales	Terminal	Compound	90	With bilateral keeled distal lamina, single apex	?	?	Early Permian	Schweitzer (1996)

clearly derived from evolutionary advanced Voltziales. The ovuliferous scale-bract complex of *Patokaea* appears unique with its three lobes, from which one, the middle, is strongly reduced and sterile, while the two, much larger fertile lobes are placed laterally. On the abaxial surface of the reduced lobe, a middle dividing line is sometimes observed. This could suggest that the reduced sterile lobe originates from the fusion of two sterile lobes. This is not surprising as older Permian and Triassic Voltziales had numerous lobes of fertile scale which fused and reduced in number in more advanced taxa. The morphology of the ovuliferous scale-bract complex of *Patokaea* resemble *Schizolepidopsis*, which has been suggested by some authors to be an early representative of the Pinaceae (e.g., Leslie et al., 2013). The short shoots and leaves associated with *Schizolepidopsis* (*Pityocladus*, *Pityophyllum*) are similar to those in the Pinaceae (e.g., Harris, 1979). However, *Patokaea* ovuliferous cones are connected with *Brachyphyllum-Pagiophyllum* foliage which has never been recorded in any extinct or extant species of Pinaceae.

Brachyphyllum-Pagiophyllum foliage is typical for some Jurassic and Cretaceous conifers, belonging to families: Araucariaceae, Cheirolepidiaceae, Cupressaceae and Podocarpaceae. However, the morphology of the ovuliferous scale-bract complexes in these families differs from that of *Patokaea*. The gross morphology of the polliniferous cones of *Patokaea* resembles that of *Classostrobus*, the polliniferous cone of the Cheirolepidiaceae, but the arrangement of the pollen sacs on the microsporophyll (probably sessile, in a whorl around the stalk) corresponds more closely to that of Permian and Triassic Voltziales. The *Patokaea* polliniferous cone differs from other Triassic Voltziales in its size, being much smaller than in most described species, and the number of pollen sacs per microsporophyll, which is low (about 5–7). Both characters may be regarded as advanced features.

Pollen grains similar to dispersed *Patinasporites densus* have been found inside Triassic (Carnian) polliniferous cones associated with ovuliferous cones referred to *Glyptolepis* (Cornet, 1977). Reichgelt et al. (2013) discussed the affinities of *Patinasporites*, *Vallasporites* and *Enzonalasporites* and suggested they were all closely related to Volzialean conifers. However, pollen grains similar or identical to dispersed *Vallasporites*, *Pseudoenzonalasporites* and *Enzonalasporites* have thus far never been found in situ.

Among the recent genera, the morphologically most similar pollen grains have been described from *Tsuga* (Pinaceae), especially *Tsuga canadensis* (Linné) Carrière (Sivak, 1973). *Tsuga canadensis* pollen grains possess a smooth and folded ectexine surface similar to the pollen grains of *Patokaea silesiaca*, but they differ from our material with regard to the collar around the equator of the specimen. The ectexine is folded and separated from the endexine, but the structure of the folds is not clear. Some authors describe *Tsuga* pollen grains as monosaccate (Punt et al., 2007). From the morphological similarity of the *Tsuga* and *P. silesiaca* pollen grains, it can be assumed that *P. silesiaca* pollen, like that of *Tsuga*, was dispersed in the same way, by the wind.

4.4. Rationale for new family proposition

Family relationships among Voltziales are poorly resolved. Rothwell and collaborators (Mapes and Rothwell, 1991; Rothwell and Mapes, 2001, 2003; Rothwell et al., 2005) proposed a solution for this problem for the oldest Walchian Voltziales. Some of the families they established, e.g., the Thucydiaceae and Bartheliaceae, were and still are monotypic (Rothwell and Mapes, 2001; Hernandez-Castillo et al., 2001), like the new family Patokaeaceae proposed here. However, this approach leads to a much better understanding of the biodiversity of the oldest conifers (Rothwell et al., 2005). Only few Palaeozoic conifer families, e.g., the Emporiaceae and Majonicaceae, are sufficiently well known to incorporate several genera and species (Clement-Westerhof, 1987; Mapes and Rothwell, 2003; Looy, 2007; Hernandez-Castillo et al., 2009a, 2009b, 2009c). Among the younger Voltzian Voltziales the resolution on the family level is poorer (Rothwell et al., 2005). The Voltziaceae incorporates numerous taxa and lacks clearly defined synapomorphies. This problem needs to be solved, because new taxa of Triassic Voltziales have been described and previously described taxa have been revised (e.g., Delevoryas and Hope, 1975, 1987; Axsmith and Taylor, 1997; Axsmith et al., 1998; Arndt, 2002; Axsmith et al., 2004; Escapa et al., 2010). The proposal of the new family, Patokaeaceae, is a step in this direction. The new *Patokaea* plant combines *Brachyphyllum-Pagiophyllum*-type leaves that are rare in the Triassic, but characteristic of Jurassic and Cretaceous conifers with a new type of seed scale which may have evolved from primitive *Voltzia*-type scales with numerous unfused sterile and fertile lobes, polliniferous cones somewhat similar to the Cheirolepidiaceae (*Classostrobus*) type and pollen grains of the *Enzonalasporites* type. So far, such a combination of features has not been recognized in any fossil or recent conifer. The new genus *Patokaea* is well-documented and clearly defined. Incorporating such well-preserved and characterized material into the strongly artificial Voltziaceae family, along with numerous taxa of doubtful affinity and missing or unclear details, would increase the impact of this family's uncertain circumscription, creating the need for its diagnosis to be at least emended.

It cannot be ruled out that some species referred to *Glyptolepis*, with several sterile lobes among two larger, lateral, fertile lobes (e.g., Florin, 1938–1945; Cornet, 1977), could be affiliated with *Patokaea* and could even belong to the same family. It is easy to imagine that the numerous sterile lobes between two fertile lobes, as seen in some species referred to *Glyptolepis*, decreased in dimension and number to the condition visible in *Patokaea*. Such an evolutionary trend, reduction of the number of free, in particular sterile, elements in the seed scale is characteristic of the Voltziales (Florin, 1938–1945; Miller, 1977). Unfortunately, the concept of *Glyptolepis* is very confused. As revised by Axsmith and Taylor (1997), it should include only the type species *G. keuperiana*, and *G. richteri*. The species *G. longibracteata*, *G. windsheimensis* and *G. hungarica* as described by Florin (1938–1945), were misinterpreted as having lateral stalks bearing a terminal seed rather than having lateral seed-bearing lobes. These species probably need to be classified in new genera. Ovuliferous cone scales described by Cornet (1977) as *Glyptolepis* were associated with *Pagiophyllum*-type leafy shoots like *G. windsheimensis* (Kräusel, 1939). Unfortunately, associated foliage has not been recognized for other *Glyptolepis* material. Extending the newly proposed family Patokaeaceae to incorporate at least some species previously referred to as *Glyptolepis* requires future research, including the revision of original material and detailed phylogenetic analysis. These taxa are much more poorly documented than *Patokaea*, as details of ovules, seeds, polliniferous cones and foliage are all missing. We believe that the ovuliferous cone scales of *Voltzia* and *Patokaea* differ at the family level. Furthermore, *Voltzia* is associated with a markedly different type of leaf, shoot and polliniferous cone. Meanwhile *Patokaea* and some "*Glyptolepis*" are characterized by *Brachyphyllum-Pagiophyllum* leaves. The trend involving the reduction of the middle sterile lobe in *Patokaea* until it totally disappeared could lead to the condition visible in *Schizolepidopsis* that has only two fertile lobes. However, *Schizolepidopsis* cannot be included in the new family proposed here. Despite the fact that its systematic placement has been disputed (Rothwell et al., 2012), it has more features in common with the Pinaceae than with *Patokaea*, e.g., seed structure and associated foliage (Leslie et al., 2013).

Another feature of the new family Patokaeaceae proposed here, is the presence of *Enzonalasporites* or similar (*Pseudoenzonalasporites*, *Vallasporites*, *Patinasporites*) pollen. *Patinasporites* was isolated from the polliniferous cones associated with *Glyptolepis* and *Pagiophyllum* (Cornet, 1977). Ash (1999) noted that *Enzonalasporites* and *Pseudoenzonalasporites* pollen grains were probably produced by *Masculostrobus lafonii* – a polliniferous cone associated with *Brachyphyllum comancheanum* leaves. If this type of pollen grain is really only connected with this new family, the aforementioned polliniferous cones could also belong to it. Unfortunately, with the exception of the type genus, other putative representatives of the new Patokaeaceae family are poorly known, only preliminarily described or require revision. They should be the focus of further detailed research.

5. Conclusions

A new taxon, *Patokaea silesiaca* gen. et sp. nov. is described on the basis of organic connections and similar cuticular details of leaves, ovuliferous cones, seed scale-bract complexes, ovules and developed seeds as well as polliniferous cones containing *Enzonalasporites* pollen grains. This new conifer combines the *Brachyphyllum*-*Pagiophyllum*-type leaves with seed scale-bract complexes clearly derived from evolutionary advanced Voltziales. The gross morphology of the polliniferous cones resembles *Classostrobus*, the polliniferous cone of Cheirolepidiaceae, but the arrangement of the pollen sacs on the microsporophyll corresponds more closely with those of primitive Permian and Triassic Voltziales. This is the first opportunity to clearly define the relationship between *Enzonalasporites*, whose affinity has been widely determined as coniferous, and *Patokaea* polliniferous cones from which they were extracted. Such a combination of features has not previously been recorded in Mesozoic conifers. Based on this distinctive and hitherto unknown feature combination, the creation of a new conifer family – Patokaeaceae – is proposed. The new plant expands our view of the huge voltzialean conifer diversity at the roots of modern conifer families. The co-occurrence of features typical of Voltziales (ovuliferous cones) with those typical of modern families (foliage) strongly suggests that new feature combinations attempted to arise in Triassic conifers but, in this case, ultimately failed.

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