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Cuticular characteristics of *Neuralethopteris jongmansii* LAVEINE (medullosalean foliage, Westphalian, Intrasudetic Basin, Poland)

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Abstract

Foliar cuticles are described for the first time from the medullosalean pteridosperm *Neuralethopteris jongmansii* LAVEINE. This species is not as common, either in abundance or distribution, as *Neuralethopteris schlehanii* (STUR) CREMER, the abaxial cuticle of which has paracytic (in morphological sense) and anomocytic stomata. In contrast, the stomata of *Neuralethopteris jongmansii* occur on both abaxial and adaxial cuticles and are anomocytic, monocyclic with prominent proximal papillae and sometimes paracytic. The epidermal cells of *N. jongmansii* are papillate and partly differ from *N. schlehanii* cuticles. However, there is a striking similarity between the foliar cuticles of *N. jongmansii* and *Neurodontopteris auriculata* (BRONGNIART) POTONIÉ. Although *N. auriculata* is a much younger fossil-species with pinnules that are more robust and of a different shape than *N. jongmansii,* their epidermal structures are practically the same – polygonal papillate cells, anomocytic, monocyclic stomata with prominent proximal papillae. Even their stomatal densities are equivalent. Despite this, there is a marked difference in the frond architecture of both genera. *Neuralethopteris* has „alethopterid" bifurcate-pinnate frond architecture, *Neurodontopteris* has quite a different bifurcate-semi-pinnate frond architecture. Based on comparison of the cuticles, *Neuralethopteris jongmansii* and *Neurodontopteris auriculata* appear very similar and it may reflect common palaeoenvironmental demands.

1. INTRODUCTION

The fossil-genus *Neuralethopteris* CREMER is characterised by neuropteroid pinnules that have cordate bases and alethopteroid venation (GOUBET et al., 2000). Representatives of *Neuralethopteris* are widespread in the Euramerican Realm, and are important biostratigraphic indicators in upper Namurian and lower Westphalian strata. *Neuralethopteris schlehanii* (STUR) CREMER, the type and most common species of *Neuralethopteris*, occurs in Euramerica, although 10 other fossil-species are known (five each from Europe and North America) (CLEAL & SHUTE, 1995, GOUBET et al., 2000 TENCHOV & CLEAL, 2010). To date, *N. schlehanii* is the only member of the fossil-genus for which cuticles have been studied (CLEAL & SHUTE, 1992). During a visit to Wrocław University in Poland to study the type material of *Cordaites palmaeformis* (GÖPPERT) WEISS (ŠIMŮNEK, 2015), some pinnules of *Neuralethopteris* were found on the same slab as one of the syntypes of *C. palmaeformis* and sampled for maceration. The pinnules were identified as *Neuralethopteris jongmansii* LAVEINE, which is relatively rare in the Intrasudetic Basin and has yet to be determined in the Czech part of the basin. In this paper, a detailed cuticular analysis is presented for *N. jongmansii*, which represents only the second species of *Neuralethopteris* for which cuticles are known.

2. MATERIAL AND METHOD

The syntype of *Cordaites palmaeformis*, from which the pinnules of *Neuralethopteris jongmansii* were collected, came from the Wałbrzych locality, Intrasudetic Basin, Poland. The syntype slab is stored in Wrocław University under no. 1667p. Although the exact horizon and stratigraphic level from which the syntype slab was collected is not known, the fact that other occurrences of *N. jongmansii* in Europe are in Langsettian (Lower Pennsylvanian) strata (CLEAL et SHUTE, 1995) suggests that it probably came from the lower part of the Žacléř Formation (Table 1).

The cuticles were prepared by a standard maceration method using Schulze's Reagent, as described by KERP (1990), KRINGS & KERP (1997) and KERP & KRINGS (1999).

3. GEOLOGICAL SETTING

The Intrasudetic Basin extends from the north-eastern Czech Republic into south-western Poland, where the Wałbrzych locality is located (Fig. 1). Mississippian strata of the Intrasudetic Basin are largely coarse-grained siliciclastics that reach 5 km in thickness. Sedimentation changed at the end of the Mississippian, after which the coal-bearing Wałbrzych Formation was deposited. It reaches up to 250 m thickness, and is of Serpukhovian and earliest Bashkirian (lower Namurian) age. The overlying coal-barren Biały Kamień Formation is up to 380 m thick and largely comprises sandstones and conglomerates. In the Polish part of the Intrasudetic Basin, the lower part of the overlying Žacléř Formation (upper Bashkirian, Langsettian and Duckmantian) is coal-bearing. The study samples probably come from this stratigraphic level, a conclusion supported by the fact that coals of the Žacléř Formation were mined in the vicinity of Wałbrzych. The uppermost Bashkirian (Duckmantian) part of the formation only contains a few workable coal seams in the Polish part of the basin. The Moscovian and Kasimovian (upper Westphalian and lower Stephanian) Glinik Formation, which reaches 850 m in thickness, is practically devoid of workable coal seams. The uppermost formation in the Polish part of the basin is the Ludwikowice Forma-

Table 1. Stratigraphy of the polish part of the Intrasudetic Basin with emphasize to the Pennsylvanian strata.

GLOBAL SCALE		REGIONAL SCALE		FORMATION
PERMIAN	Asselian			Ludwikowice
PENNSYLVANIAN	Gzhelian	Stephanian	C	
	Kasimovian		B	Glinik
			Barruelian	
			Cantabrian	
	Moscovian	Westphalian	Asturian	
			Bolsovian	Žacléř ←
	Bashkirian		Duckmantian	
			Langsettian	
		Namurian	Yeadonian	Biały Kamień
			Marsdenian	
			Kinderscoutian	Wałbrzych
			Alportian	
			Chokierian	
MISSISSIPPIAN	Serpukhovian		Arnsbergian	
			Pendleian	
	Viséan			
	Tournaisian			

← Probable location of studied sample

Figure 1. A map of Poland showing the locality of Wałbrzych (black square).

tion, which reaches 440 m thickness and largely comprises coarse-grained redbeds of Gzhelian (late Stephanian) and Asselian (early Permian) age (Table 1.) (BOSSOWSKI et al., in ZDANOWSKI & ŻAKOWA, 1995).

4. SYSTEMATICS

Order Medullosales CORSIN, 1960

Family Alethopteridaceae CORSIN, 1960*

Fossil-genus *Neuralethopteris* CREMER, 1893 emend. LAVEINE, 1967

Type species: *Neuralethopteris schlehanii* (STUR, 1877) CREMER, 1893

*Family Alethopteridaceae is based on frond architecture that is an ancillary feature, however a natural botanical system should be based on fructifications. Such a family is the Trigonocarpaceae SEWARD, 1917 family, but plants with different frond architectures can have trigonocarpalean seeds. So the Alethopteridaceae family is an artificial family from this point of view.

Neuralethopteris jongmansii LAVEINE, 1967

1967 *Neuralethopteris jongmansii* LAVEINE: p. 107–112, pls. 2–4.

2010 *Neuralethopteris jongmansii* LAVEINE; TENCHOV & CLEAL: 2010, p. 303, pls. 1, figs. 5, 6.

Description: Two pinna fragments up to 35 mm long, together with several isolated pinnules are preserved on the edge of specimen 1667p. Pinnules are small, being 5–8 mm long and usually 2–3 mm wide, and have a cordate, asymmetric base and a thick midvein that nearly extends to the pinnule apex. Lateral veins arise oblique to the midvein and arch broadly to meet the pinnule margin at 80–90°. Each lateral vein generally forks twice, resulting in a high vein density of 60–80 veins per cm on the pinnule margin.

Adaxial cuticle: Stomata are present in the intercostal fields but absent in the costal fields. Ordinary cells are polygonal, 40–80 (100) mm long and 30–45 mm wide, and slightly elongated in the costal fields. A small papilla, up to 10 mm in diameter, is present in the middle of each cell. Stomatal complexes are 60–70 mm in diameter, and comprise two guard cells and five or six small polygonal subsidiary cells that are 25–40 mm long and 15–30 mm wide. Cutinisation of papillae on the subsidiary cells is stronger than Cutinisation of papillae on ordinary cells. These papillae are also longer, up to 15 mm wide, and oriented (bent) towards the guard cells (proximal papillae). Hydathodes (Pl. I/j) are 40–45 mm in diameter and situated at the edge of pinnules. Stomatal density varies from 40–50 stomata per mm^2 and the stomatal index ranges from 8–10.

Abaxial cuticle: Abaxial cuticles are very similar to adaxial cuticles. Stomatal complexes are generally monocyclic, anomocytic, but some stomata can be also paracytic in a morphological sense (Pl. II/i). Polygonal cells are 30–80 mm long and 20–40 mm wide, and stomata are practically the same as those on adaxial cuticles. Stomatal density varies from 50–65 stomata per mm^2 and the stomatal index is between 8–10, similar to the values for adaxial cuticles. Trichome bases, surrounded by six or seven ordinary cells, occur in the area that is presumed to correspond to the midvein (Pl. II/b,c,g,h). Trichome bases are circular to slightly oval and their margins are strongly cutinised. No hairs have been observed. Also occurring in these areas are stomata-like features (Pl. II/g,h), which are oval and surrounded by eight small cells, although no guard cells have been observed.

5. COMPARISONS

The first descriptions of cuticles of the fossil-genus *Neuralethopteris* were made by CLEAL & SHUTE (1992), who noted that cuticles of the type species *Neuralethopteris schlehanii* have an unusual type of paracytic stomatal structure that was previously unknown in the medullosaleans. But CLEAL (pers. com. 2016) admitted that the abaxial cuticle of *Neuralethopteris schlehanii* was fragmentary in preservation, and some stomata can be interpreted as anomocytic, the others as paracytic. A stoma of *Neuralethopteris jongmansii* figured on Pl. II/i resembles the paracytic type. Nevertheless, the cuticles of *Neuralethopteris jongmansii* differ from those of *N. schlehanii* (Table 2.), namely by the adaxial cuticle. In contrast to *Neuralethopteris schlehanii, N. jongmansii* also has stomata on the adaxial cuticle which represents amphistomatic foliage, a feature that, among the medullosaleans, is only known for the monotypic fossil-species *Neurodontopteris*

Table 2. Important diagnostic features of the *Neuralethopteris* species.

Species			*Neuralethopteris schlehanii*	*Neuralethopteris jongmansii*	*Neurodontopteris auriculata*
Pinnules		Authors	TENCHOV & CLEAL (2010)	TENCHOV & CLEAL (2010)	ŠIMŮNEK (1999)
		Length x width (mm)	(4-15)x(2-4)	(up to 13)x(4-5)	(36-42)x(15-18)
		Shape	Subtriangular, elongate linguaeform to subfalcate	Linguaeform	Tongue-shaped with basal lobe
		No. veins per pinnule margin	36-48	(50-60); (60-80)	35-40
Cuticle Authors			CLEAL & SHUTE (1992)	This paper	KRINGS (1999); ŠIMŮNEK (1999)
Pinnules			Hypostomatic	Amphistomatic	Amphistomatic
Adaxial cuticle		Costal cells	Elongate to subrectangular	±Elongate, polygonal	±Elongate, polygonal
		Size of costal cells (μm)	Up to 120 x up to 20	[40-80(100)]x (30-45)	Up to 100 x up to 45
		Intercostal cells	Irregularly polygonal	Irregularly polygonal	Irregularly polygonal
		Size of intercostal cells (μm)	Up to 80 x up to 30	(40-80) x (30-45)	Up to 45 in the diameter
		Form anticlinal walls	±Straight	±Straight	±Straight
		Palillae on periclinal walls	–	+	+
Abaxial cuticle		Costal cells	Elongate to subrectangular	±Elongate, polygonal	Elongate tetragonal to polygonal
		Size of costal cells (μm)	up to 70 x up to 5	(30-80)x (20-40)	(20-40) x (10-15)
		Intercostal cells	? Polygonal	Irregularly polygonal	Irregularly polygonal
		Size of intercostal cells (μm)	(up to 80) x (up to 20)	(30-80) x (20-40)	(30-50) x (10-25)
		Form anticlinal walls	? Slightly bent	±Straight	±Straight
		Palillae on periclinal walls	–	+	+
	Stomata	Distribution	Regularly arranged parallel to veins in the intercostal field	Mostly parallel to veins, some stomata random	Randomly oriented in the intercostal fields
		Type	?Paracytic, anomocytic; monocyclic	Anomocytic, ?Paracytic; monocyclic	Anomocytic; monocyclic
		Density per 1 mm2	ca. 300	40-50; 50-65	60-70
		Stomatal index	19	8-10	?
		Shape of guard cells	?	Reniform	Reniform
		length and width of guard cells (μm)	cca 30 x 3	cca 30 x 7	(20-25) x (4-6);(25-35) x (5-10)
		Dimension of stomatal complex (μm)	?	60-70 in the diameter	75-95 in the diameter
	Subsi-diary cells	Number and shape	2 or more; ±oblong (polygonal)	5-6; polygonal (oblong), poximal papilae	5-6; polygonal, proximal papillae
		Size (μm)	?	(25-40)x(15-30)	35-50 in the diameter
Trichome bases (shape and dimension in μm)				Circular; cca 25 in the diameter	Star-like; 40-55 in the diameter
Trichomes (shape and dimension in μm)			Unicellular; 120 x 15		
Hydathodes (shape and dimension in μm)				Rounded on the pinnule margin; 40-45 in the diameter.	

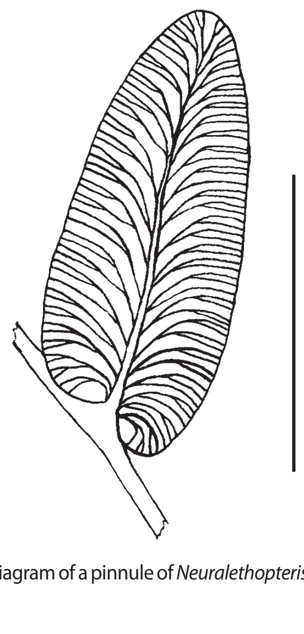

Figure 2. Venation diagram of a pinnule of *Neuralethopteris jongmansii* LAVEINE. Scale bar = 5 mm.

auriculata (BRONGNIART) POTONIÉ (KRINGS, 1999, ŠIMŮNEK, 1999). The cuticles of these two fossil-species are also strikingly similar.

Pinnules of *Neuralethopteris jongmansii* and Neuralethopteris schlehanii have comparable dimensions, but their vein densities differ, with *N. schlehanii* having 36–48 veins per cm on the pinnule margin and *N. jongmansii* having 50–60 (TENCHOV & CLEAL, 2010). The studied samples had 60–80 veins per cm. These two species also differ in the course of the lateral veins and other features. Although *N. schlehanii* is hypostomatic and *N. jongmansii* is amphistomatic, they have anomocytic, monocyclic stomata. Some stomata can be interpreted as paracytic, as in CLEAL & SHUTE (1992). The abaxial cuticles of both species differ in the following features: stomatal densities of ca. 300 per mm^2 in *N. schlehanii* and ca. 50–65 mm^2 in *N. jongmansii*, and whereas the cells of *N. jongmansii* are papillate, the cells of *N. schlehanii* are not. It is debatable whether this is the result of the poor preservation of the second species. These features can be used by distinguishing of both species.

Even though the morphology of *Neuralethopteris jongmansii* and *Neurodontopteris auriculata* differ, their cuticles are surprisingly remarkably similar. *Neuralethopteris* fronds have an „alethopterid“ bifurcate-pinnate architecture (LAVEINE et al., 1992, fig. 3). The fronds can be several metres long and do not have intercalary elements. The fronds of *Neurodontopteris auriculata* are about 0.5 m long (LANGIAUX, 1984, fig. 233) and have a bifurcate-semi-pinnate architecture. Pinnules of *N. auriculata* have a basal lobe and are much larger and wider than pinnules of *N. jongmansii* (Table 2). Furthermore, *N. auriculata* occurs in much younger strata of Stephanian B to early Permian age. Nonetheless, these two fossil-species are the only amphistomatic taxa known to date in the Order Medullosales. Both have anomocytic, monocyclic stomata, strikingly similar papillate polygonal cells, stomata with proximal papillae, and similar adaxial and abaxial cuticles. Even though occurrences of the two fossil-species in the fossil record are separated by some 8 Myr, their stomatal densities are comparable: 50–65 stomata per cm for the abaxial cuticle of *N. jongmansii* and 60–70 for *N. auriculata* (Table 2.). In fact, the only distinguishing feature between the fossil-species is the presence of star-like trichome bases (ŠIMŮNEK, 1999) in *N. auriculata,* although the feature only occurs on a single (?adaxial) cuticle. On the whole, distinguishing these fossil-taxa would be very difficult if only dispersed cuticles were available and the age of the strata were not known. However, both genera differ in gross-morphology. The frond architecture of *Neuralethopteris* is mainly based on *Neuralethopteris schlehanii* (LAVEINE et al., 1992), because the occurrences of *Neuralethopteris jongmansii* specimens are rare and fragmentary. *Neurodontopteris auriculata* belongs to plants with small stature (ŠIMŮNEK, 1999). The dimensions of the *Neuralethopteris jongmansii* plant are not known. Due to the similarity of the cuticles with those of *Neurodontopteris auriculata*, it probably was also of small stature (similar palaeoecological demands of both plants) in contrast to *Neuralethopteris schlehanii.*

6. PALAEOBIOLOGY

The presence of amphistomatic pinnules in medullosaleans is exceptional. ŠIMŮNEK (1999) speculated that this feature, found in *Neurodontopteris auriculata*, could point to a small-statured plant, having fronds that were protected from direct sunshine. *Neuralethopteris jongmansii* also had some adaptation to living in the understory (stomata on both pinnule sides). Proximal papillae on subsidiary cells around guard cells could prevent watter drops to enter the stoma opening. The adaxial and abaxial cuticles have approximately the same stomatal densities. Both species are amphistomatic and have small papillae on periclinal cell walls. This probably helped the plant to get rid of water drops from the pinnule surface. *Neuralethopteris jongmansii* and *Neurodontopteris auriculata* probably lived in similar habitats.

7. CONCLUSION

(1) The morphology of *Neuralethopteris jongmansii* pinnules is similar to those of *Neuralethopteris schlehanii*, The latter is the type species of the fossil-genus *Neuralethopteris*, although *N. jongmansii* has denser lateral veins that follow a slightly different course.

(2) The pinnules of *Neuralethopteris jongmansii* are amphistomatic and the pinnules of *Neuralethopteris schlehanii* are hypostomatic. Abaxial cuticles of both species are similar in stomatal types. *N. jongmansii* have anomocytic, monocyclic stomata, some stomata morphologically resemble the paracytic type and resemble those of *N. schlehanii* stomata.

(3) Based on cuticles, *Neuralethopteris jongmansii* and *Neurodontopteris auriculata* are strikingly similar, and are the only medullosaleans known to date with amphistomatic foliage. Both fossil-species have the same type of stomata, cell shapes and stomatal densities, indicating life in similar environments. Both plants were probably of small stature and probably lived in undergrowth.

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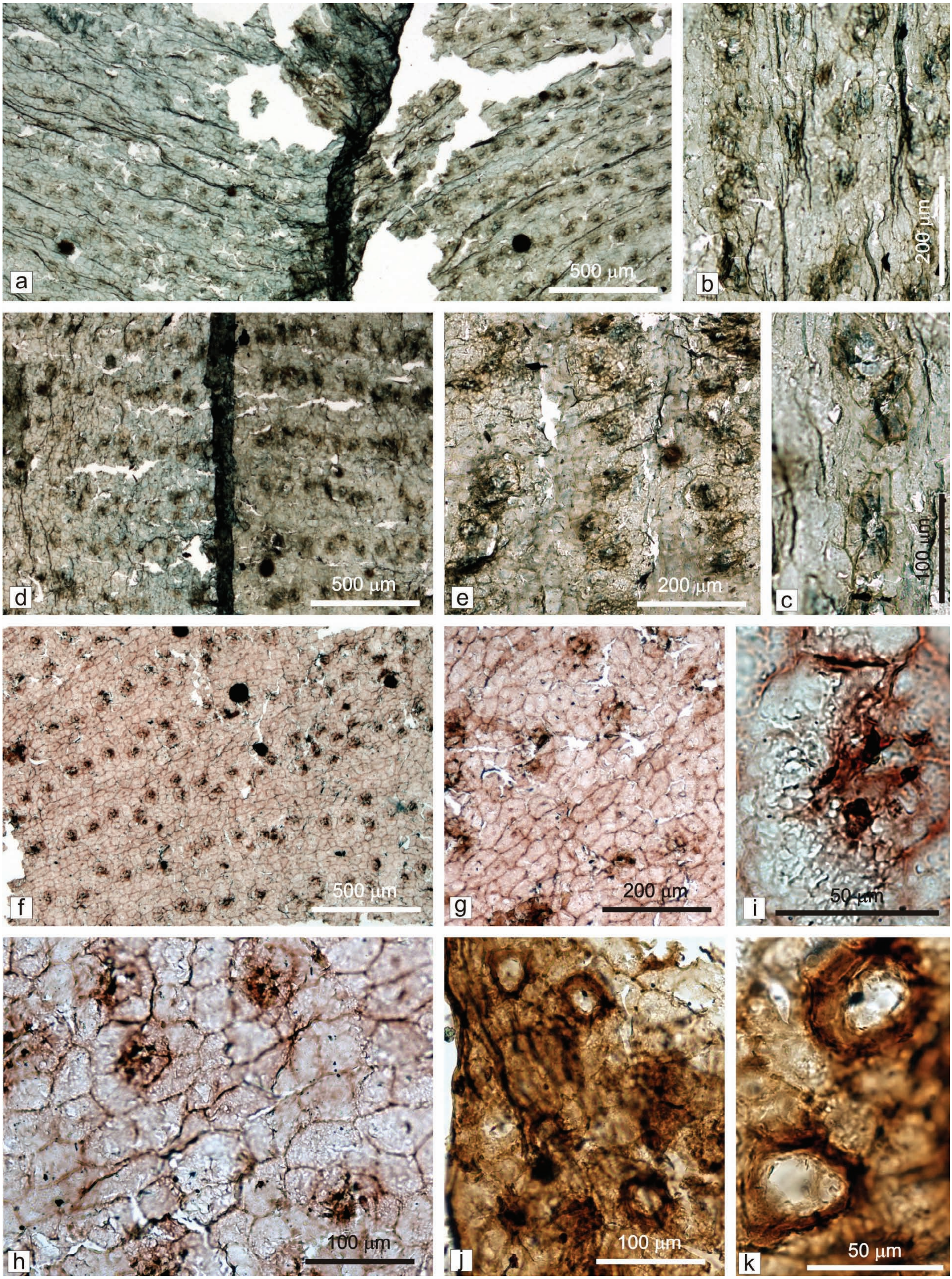
Plate 1

Neuralethopteris jongmansii LAVEINE. loc. Wałbrzych, „Langsettian?“, coll. GÖPPERT, Wrocław Univ., Inv. No. 1667 p.

a – Pinnule margin with adaxial cuticle on the left and abaxial cuticle on the right. Slide 603/8.
b – Detail of abxial cuticle with stomata from Fig. a.
c – Close up of Fig. b with detail of stomata.
d – Adaxial cuticle on the left and abaxial cuticle on the right. Slide 602/10.
e – Detail of abaxial cuticle with stomata from Fig. d.
f – Adaxial cuticle with stomata. Slide 456/4.
g – Close up of Fig. f with stomata and cells with very small papillae.
h – Close up of Fig. f with details of stomata and cells of intercostal field with very small papillae.
i – Detail of s stoma from Fig. h. Note the papillae arising from subsidiary cells.
j – Margin of adaxial cuticle with hydathodes. Slide 456/5.
k – Close up of two hydathodes from Fig. j.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j
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k
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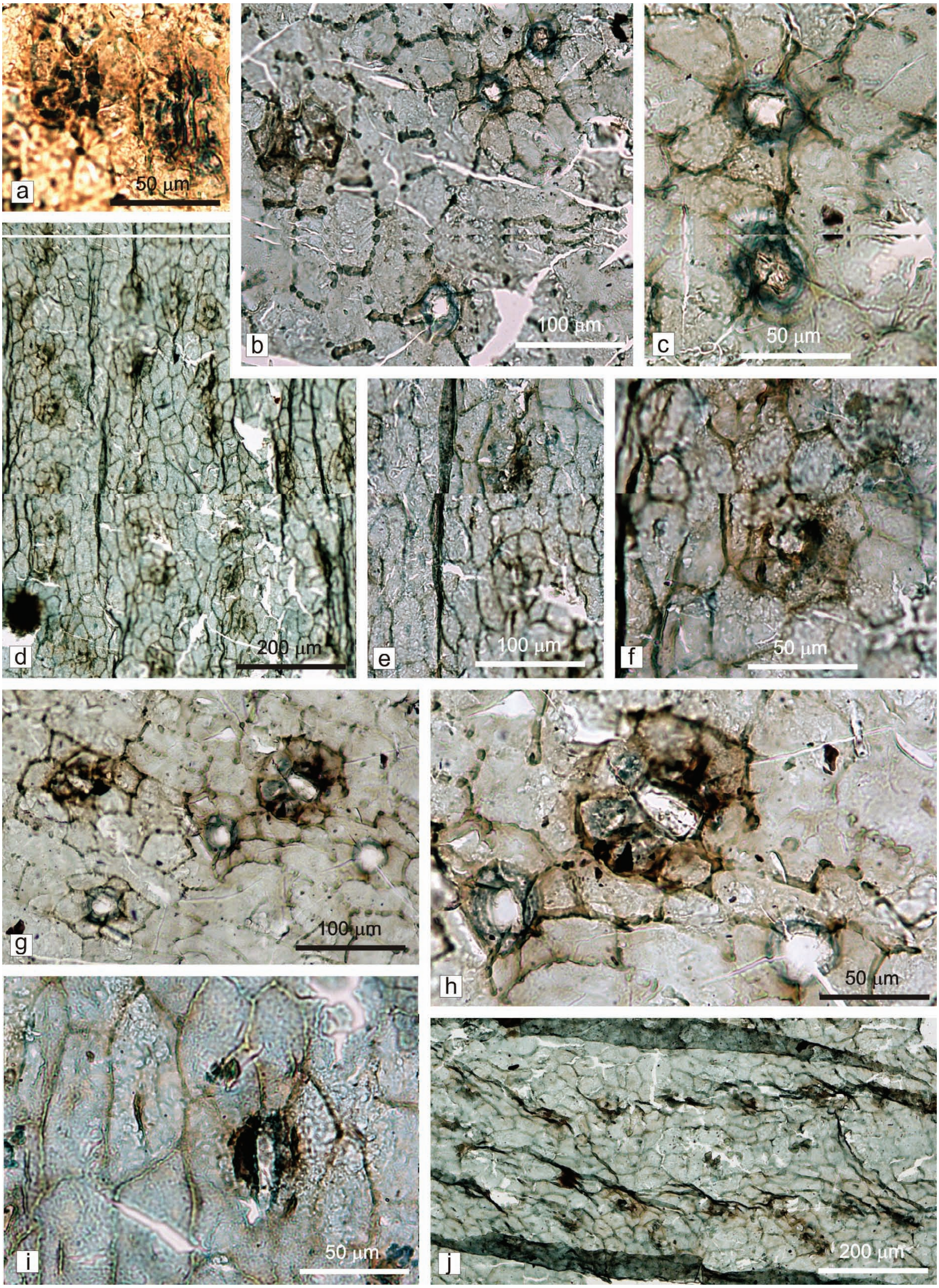
Plate 2

Neuralethopteris jongmansii LAVEINE. loc. Wałbrzych, „Langsettian", coll. GÖPPERT, Wrocław Univ., Inv. No. 1667 p. Abaxial cuticles.

a – Two stomata with papillae on subsidiary cells. Slide 602/9.
b – ? probably an area of midrib with ?trichome basis. Slide 602/10
c – Close up of two trichome bases from Fig. b.
d – Abaxial cuticle with stomata. Slide 603/8 (cuticle from Pl. I, a).
e – Close up of two stomata from Fig. d.
f – Close up of a stomata from Fig. d. Note the papillae on subsidiary cells.
g – ? Probably midrib with trichome bases. Slide 603/9.
h – Close up of trichome bases? from Fig. g.
i – Close up of a stoma resembling the paracytic stomatal type. Slide 602/11.
j – Abaxial cuticle with stomata. Slide 603/7.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f
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g
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h
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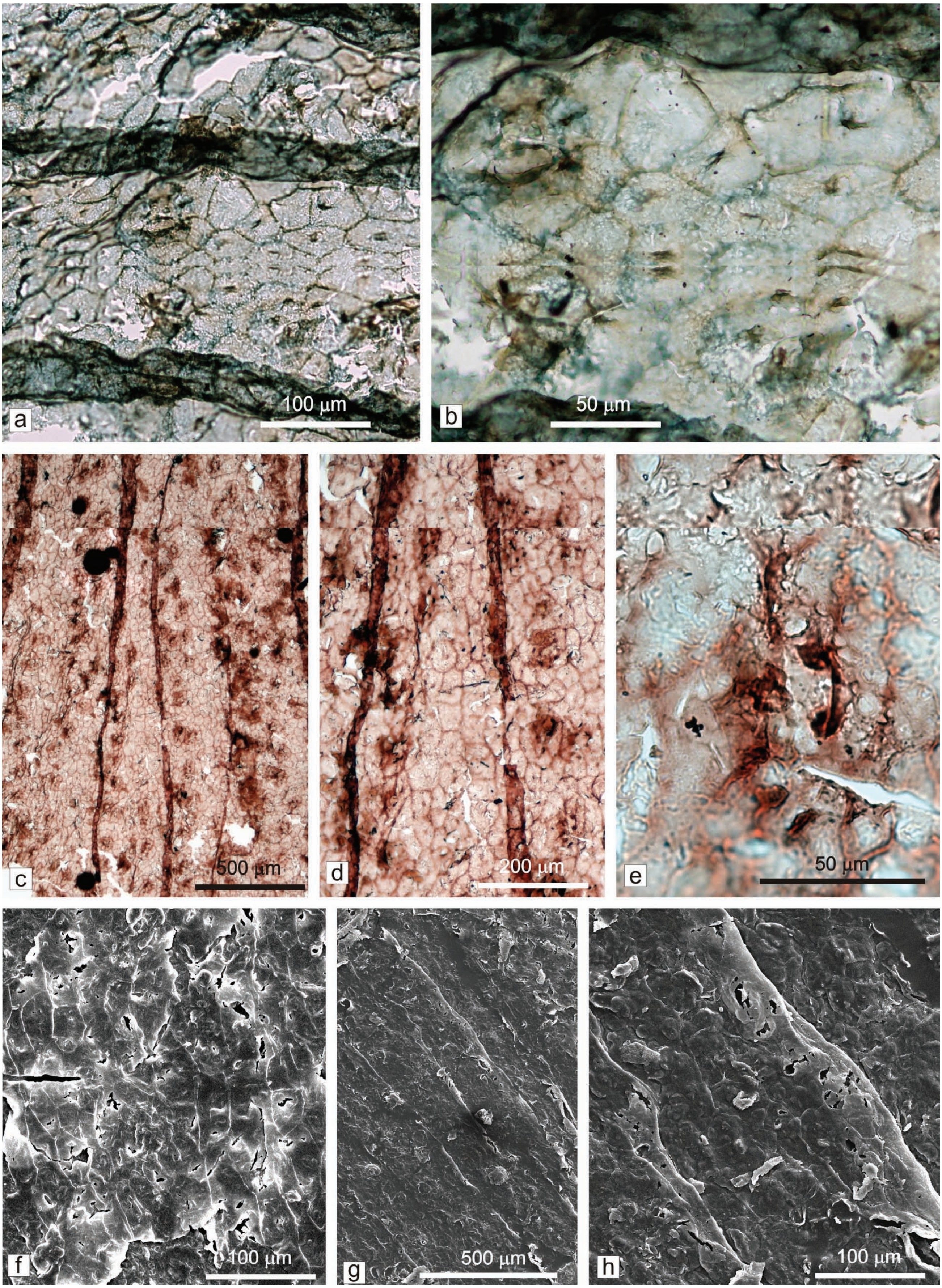
i
50 µm
j
200 µm

Plate 3

Neuralethopteris jongmansii LAVEINE. loc. Wałbrzych, „Langsettian", coll. GÖPPERT, Wrocław Univ., Inv. No. 1667 p. Abaxial cuticles and cuticles in SEM.

a – Abaxial cuticle with costal and intercostal fields; intercostal fields with stomata and small papillae on epidermal cells. Slide 603/6.
b – Close up of three stomata from Fig. b. Note the papillae on the subsidiary cells and normal epidermal cells.
c – Abaxial cuticle with stomata. Slide 456/3
d – Close up of abaxial cuticle with stomata and papillae on epidermal cells from Fig. c.
e – Close up of a stoma from Fig. d. Note the papillae on the subsidiary cells.
f – Cuticle under SEM. Stomata are not discernible. SEM stub 39.
g – Abaxial cuticle in SEM. SEM stub 84.
h – Close up of abaxial cuticle from Fig. g.


a
100 µm
b
50 µm
c
500 µm
d
200 µm
e
50 µm
f
100 µm
g
500 µm
h
100 µm

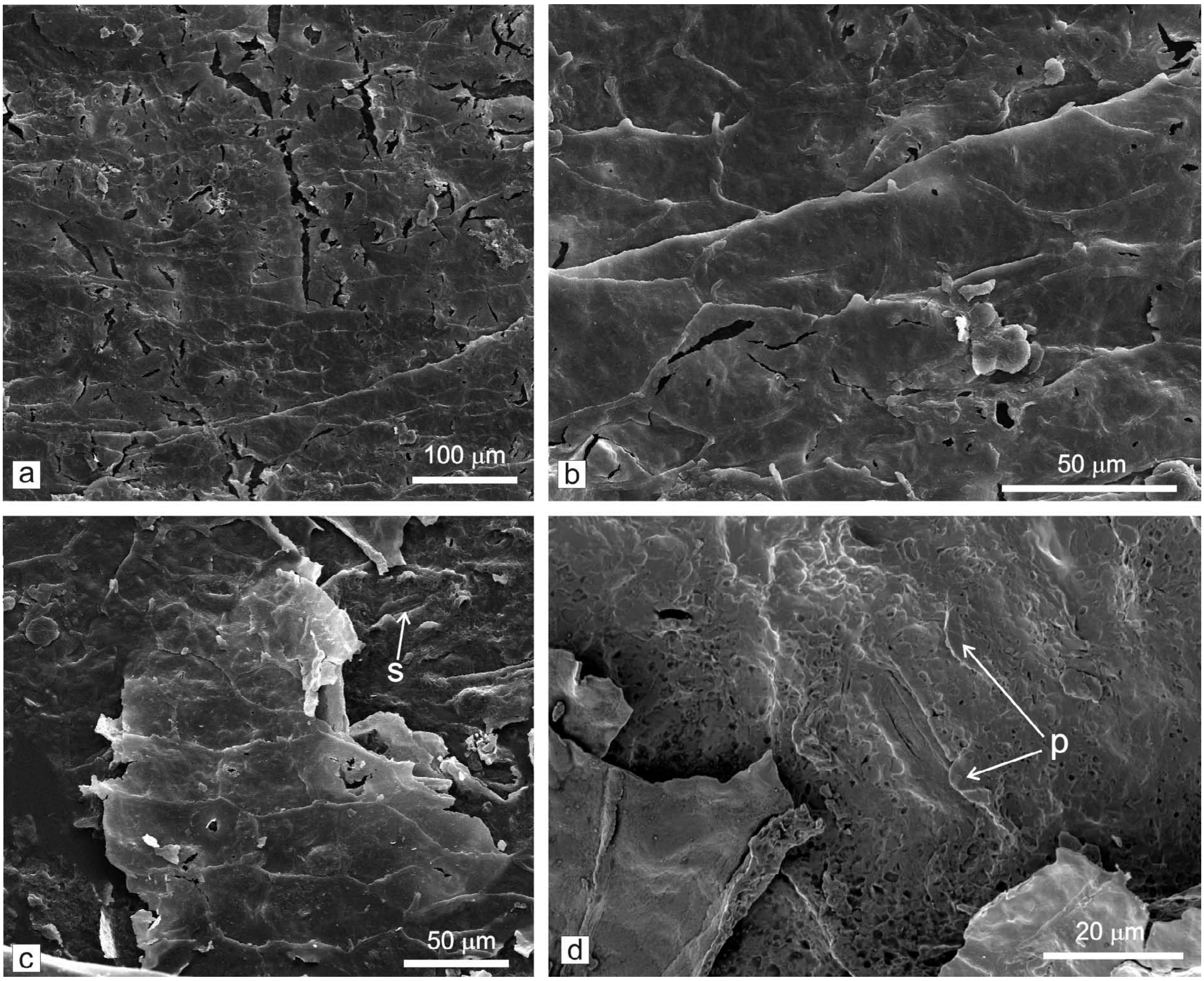


Plate 4

Neuralethopteris jongmansii LAVEINE. loc. Wałbrzych,„Langsetian", coll. GÖPPERT, Wrocław Univ., Inv. No. 1667 p. Cuticles under SEM.

a – Cuticle in inner view with discernible anticlinal walls. SEM stub 84.

b – Detail of Fig a., with discernible anticlinal cell walls and small papilla-like projections on the corners of cells.

c – Cuticular fragment from the inner side with clearly discernible cells (lighter) and a stoma (s) on the cuticle in background in the upper right corner. SEM stub 84.

d – Detail of the stoma from Fig. c. Note the papillae (p).