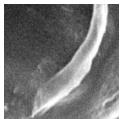


Cuticles of *Paripteris* Gothan, 1941 (Pteridospermopsida) from the Westphalian of Poland

ZBYNĚK ŠIMŮNEK



Leaf cuticles of two Carboniferous trigonocarpalean “medullosan” pteridosperms of the genus *Paripteris* Gothan are described. *P. gigantea* (Sternberg) Gothan and *P. linguaefolia* (Bertrand) Laveine have strikingly similar cuticles. The adaxial cuticles have elongated tetragonal cells orientated parallel to the veins. The cells of the abaxial cuticle are probably polygonal with only faintly discernible anticlinal walls. The haplochelic stomata are deeply sunken in the case of *P. linguaefolia* as revealed under SEM. Putative proximal papillae seen light-microscopically appear to be structures encased by sunken stomata. The differences between *P. gigantea* and *P. linguaefolia* are restricted to the presence of trichomes respectively trichome bases and differences in stomatal density values. There are two concepts of the intrageneric classification of *Paripteris*. In contrast to the widely used traditional binomial classification, Zhang *et al.* (1993) preferred to provisionally interpret all the so far described species assigned to *Paripteris* as formae of *P. gigantea*. The new information on cuticular structures neither confirms, nor fully disproves either one of the above-mentioned classifications. • Key words: *Paripteris*, cuticular analysis, Westphalian.

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The genus *Paripteris* Gothan, 1941 is very well known thanks to the work of J.-P. Laveine. Since his first comprehensive description (Laveine 1967), he studied the distribution and migration of this genus from Asia to Europe and North America (Laveine *et al.* 1993, 2003; Zhang *et al.* 1993) and published a reconstruction of the plant and its frond and deciphered its frond architecture as “pseudopinnate” (Laveine *et al.* 1993, Laveine 1997). Fronds disintegrated very rapidly, loosing their pinnules after they broke off the plant, which explains the quantity of isolated pinnules often found on bedding surfaces. His studies in China (Laveine *et al.* 1993, 2003) resulted in a new classification of *Paripteris*. He studied localities of Viséan and Namurian age and found an assemblage of isolated paripterid pinnules exhibiting great variability. Zhang *et al.* (1993) detected four to five *Paripteris* “species” in the same locality and argued that it is not tenable to have so many closely related species on the same bedding surface. Moreover, Laveine *et al.* (1993) also found a large frond with pinnules that could be assigned to at least three different *Paripteris* species. Therefore, they reclassified the species of the genus *Paripteris*. Only *P. gigantea*, the genus type, was retained; the other species were regarded as formae of *P. gigantea*. Not all palaeobotanists accepted this classification, e.g. Cleal & Shute (1995), Migier *in Brzyski et al.* (2001) and Cleal (2008) and others. Laveine *et al.*’s (1993) classifi-

cation fits better to Asian than to European representatives of *Paripteris*. European representatives of *Paripteris* do not show such great variability as seen in the Asian ones. For instance, *Paripteris* (*P. gigantea* f. *acuminatisima*) acute pinnules do not occur in Europe, whereas they are common in Asia. In Europe, in the Chockerian and Yeadonian, only *P. gigantea* occurs. This species is widespread in the Langsettian. However, *P. pseudogigantea* and *P. linguaefolia* first appear at the end of the Langsettian. These “species” or “forms” became more dominant in the Duckmantian and Bolsovian, where *P. linguaefolia* is an index species for the *P. linguaefolia* Zone (Wagner 1984). *P. gigantea* is locally still common in the Duckmantian and becomes very rare in the Bolsovian and then rapidly disappeared. *P. linguaefolia* is common throughout the Bolsovian and had its last occurrence at the end of the Bolsovian. Even though these species sometimes occur in the same localities, it is difficult to explain the very long stratigraphic occurrence of *P. gigantea* and relatively short occurrence of *P. pseudogigantea* and *P. linguaefolia*. The stratigraphic ranges of these “species” overlap only in the Duckmantian and in part of the Bolsovian (Table 1).

In this paper the problem as to whether *P. linguaefolia* and *P. pseudogigantea* are true species, or only forms of *P. gigantea* is addressed by means of cuticular analysis. Barthel (1961) was the first author who studied the cuticles

Age	<i>Paripteris</i>	Geographical distributions of <i>Paripteris</i> species																
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Duckmantian-Bolsovian	<i>P. gigantea</i>	x	x	x	x	(x)		(x)	x	x							x	
	<i>P. pseudogigantea</i>	x	x	x	x	x	x					x						
	<i>P. linguaefolia</i>		x	x		x	x	x	x	x	x	x	x	x	x	x		
	<i>P. linguaenova</i>					x												
Langsettian	<i>P. schuetzei</i>					x			x							x		
	<i>P. gigantea</i>	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x
	<i>P. pseudogigantea</i>								(x)									
C-Y	<i>P. linguaefolia</i>					(x)			(x)									
	<i>P. gigantea</i>	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x

Table 1. Geographical and stratigraphical distribution of European species of *Paripteris*. x – presence in the interval according to Cleal & Shute (1995), Polish data corrected according to Brzyski *et al.* (2001), (x) – very rare and usually at the base or top of the interval, C-Y – Chokierian-Yeadonian. 1: S-W United Kingdom, 2: Pennines, 3: Franco-Belgian Basin, 4: NW Germany, 5: NE Germany, 6: Lublin, 7: Saar-Lorraine, 8: Central Bohemia, 9: Intrasudetic, 10: Upper Silesia, 11: Alps, 12: Pyrenees, 13: NW Spain, 14: S. Spain, 15: Svojte, 16: Turkey, 17: Donets, 18: N. Caucasus.



Figure 1. *Paripteris gigantea* (Sternbrg) Gothan, borehole Jastrzębie 25, depth 371.5 m, Załęz Member, Langsettian. • A – detail of a pinnule, scale bar = 5 mm. • B – part of the ultimate pinna, scale bar = 1 cm.

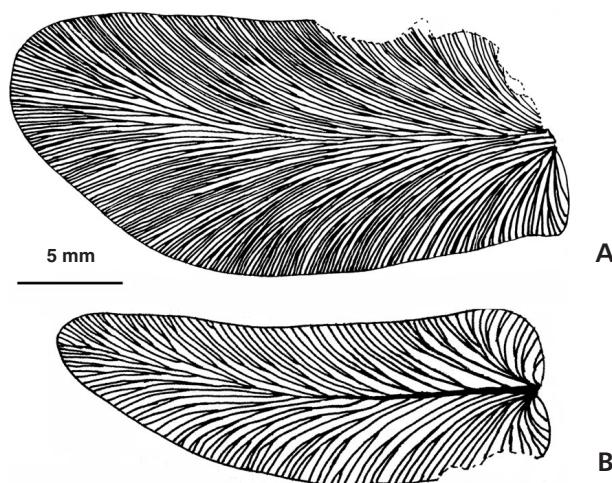


Figure 2. Venation form of *P. linguaefolia* (A, see Fig. 4B) and *P. gigantea* (B, see Fig. 1A).

of *P. gigantea* from the Langsettian of the Upper Silesian Basin, Poland. The abaxial cuticles show papillate stomatal complexes orientated parallel to the veins; the adaxial cuticle has oblong to longitudinal polygonal cells also orientated in one direction. Šimůnek (2007) published a figure of abaxial cuticle belonging to *P. linguaefolia* with strongly papillate stomatal complexes from the Bolsovian of the Kladno-Rakovník Basin (Czech Republic). Cuticles of *P. gigantea* from the Duckmantian of the Intrasudetic Basin (Czech Republic) were reinvestigated by Šimůnek (2009). The present paper deals with cuticles of the *P. linguaefolia* and *P. gigantea* from the Upper Silesian Basin (Poland). The cuticles of *P. linguaefolia* are very well preserved and reveal important new information, particularly when studied using scanning electron microscopy.

Systematic palaeobotany

Material and methods. – The macerated specimens are stored in the Polish Geological Institute, Upper Silesian Branch in Sosnowiec, Poland. They are from Teresa Migier's collection from the Upper Silesian Basin and the collection numbers are 4 *P. gigantea* (originally identified as *P. pseudogigantea*, borehole Jastrzębie 25, depth 371.5 m, Załęz Member, Langsettian, Westphalian A) and 472/239 *P. linguaefolia* (Suszec, borehole IG 9, depth 813.5 m, Orzesze Member, Duckmantian, Westphalian B). The method of cuticle preparation is that used by Šimůnek (2009, p. 120).

Class Pteridospermopsida
Order Medullosales (Trigonocarpales)

Genus *Paripteris* Gothan, 1941

Type species. – *Paripteris gigantea* (Sternberg, 1821) Gothan, 1941.

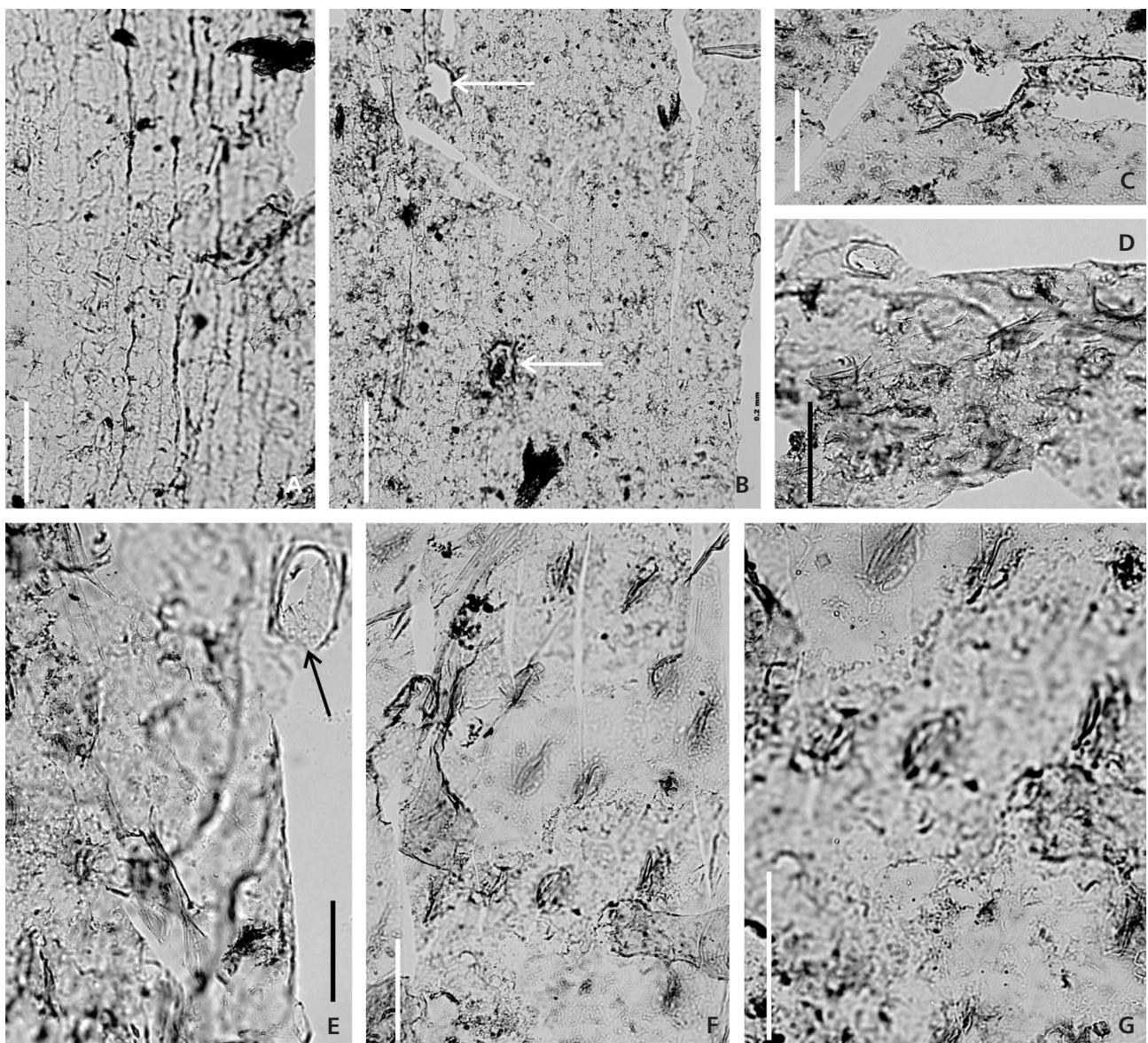


Figure 3. Cuticles of *Paripteris gigantea* (Sternberg) Gothan from Fig. 1. • A – adaxial cuticle, slide 515/1, scale bar = 50 µm. • B – adaxial side probably in the area of the midrib with two structural holes (trichome bases, arrows), slide 515/1, scale bar = 100 µm. • C – detail of a structural hole from Fig. 3B, scale bar = 50 µm. • D – a fragment of abaxial cuticle with stomata in the intercostal field and a structural hole (trichome base, arrow) in the costal field, slide 515/5, scale bar = 100 µm. • E – detail of stomata and a structural hole from Fig. 3D, scale bar = 50 µm. • F – stomata in the intercostal field, slide 515/6, scale bar = 50 µm. • G – detail of stomata from Fig. 3F, scale bar = 50 µm.

Paripteris gigantea (Sternberg, 1821) Gothan, 1941 Figures 1, 2B, 3

For comprehensive synonymy see Šimůnek (2009) and Laveine (1967).

Description of the hand specimen. – Five pinnules are preserved on the left side of the ultimate pinna (Fig. 1B). The pinnules are tongue-shaped, slightly falcate with a cordate base and blunt apex. The pinnules are 22–24 mm long and 7–8 mm wide. The venation density is 25–30 veins per

1 cm on the pinnule margin. The midvein is prominent up to around half the pinnule length (Fig. 2B). The lateral veins arise obliquely from the midvein, divide up to three times and reach the pinnule margin at an angle of 50 to 65°.

Description of cuticles (slides 415/1–6). – Pinnule adaxial cuticle (Fig. 3A): Costal and intercostal fields can not be clearly differentiated. Anticlinal cell walls are thinly cutinised and difficult to observe (Fig. 3A); they are longitudinally tetragonal (oblong or trapezoidal), 40–100 µm long and 8–16 µm wide.

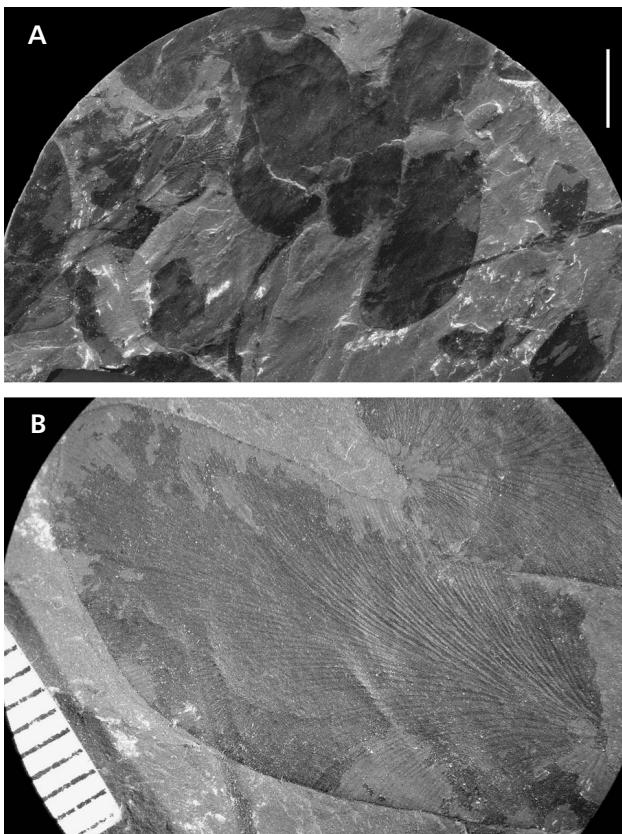


Figure 4. *Paripteris linguaefolia* (Bertrand) Laveine, loc. Suszec, bore-hole IG 9, depth 813.5 m, Orzesze Member, Duckmantian. • A – a few isolated pinnules, scale bar = 1 cm. • B – detail of a pinnule, scale bar in mm.

Pinnule abaxial cuticle (Fig. 3B–G): The anticlinal walls are also very thinly cutinised and cell outlines are difficult to trace. The costal and intercostal fields differ in the presence of stomata in the intercostal fields and trichome bases in the costal fields. The intercostal cells are polygonal, mostly elongated, clearly visible only in part of the cuticle; they are 20–30 µm long and up to 20 µm wide. Monocyclic, deeply sunken stomata, 23–30 µm long and 10–14 µm wide, are orientated parallel to veins; 5 to 6 elongated polygonal to trapezoidal subsidiary cells surround each stoma. The stomatal density is approximately 260 stomata per mm². The stomatal index could not be determined. The cells of the costal fields are similar to those on the adaxial cuticle but smaller. Oval pore-like structures representing trichome bases (Fig. 3D, E), 45–50 µm long and 25–30 µm wide, occur rarely among these cells.

Cuticle of the midrib (Fig. 3B, C): This cuticle with elongated tetragonal cells is too wide for costal fields, it probably represents the abaxial cuticle of the midrib. Oval to elliptical pores, 45–50 µm long and 25–30 µm wide, with more strongly cutinised, mostly irregular outlines, as in papillae, are present, probably they are trichome bases (Fig. 3C). Only small pinnule fragments were macerated; therefore the results are not as good as in the case of the Žacléř specimen (Šimůnek 2009).

***Paripteris linguaefolia* (Bertrand, 1930) Laveine, 1967**
Figures 2A, 4–6

For comprehensive synonymy see Laveine (1967).

Description of the hand-specimen. – Only isolated pinnules in a slab (Fig. 4) are preserved. The pinnules are large, broadly lingulate, with a faintly cordate base and round apex. The pinnules are 26–28 mm long and 10–12 mm wide. The pedicel is positioned asymmetrically. Either there is no midrib or only a very short midrib. Lateral veins maybe diverging in a fan-shaped manner from the pedicel or arising at a very sharp angle from the short midrib; the midrib consists of very narrowly spaced lateral veins (Fig. 2A). The lateral veins run in a slightly oblique direction through the blade, divide 3 to 7 times and reach the pinnule margin at angles of 55–70°. The venation density is 42 to 50 veins per 1 cm on the pinnule margin.

Description of the cuticles. – The cuticles are very well preserved thus enabling light and scanning electron microscopic studies.

Pinnule adaxial cuticle (Figs 5A, B, D, 6E, H): Costal and intercostal fields can not be clearly differentiated. Anticlinal cell walls are thinly cutinised, as can be seen in the SEM pictures (Fig. 6E, H). The cells are longitudinally tetragonal (oblong or trapezoidal), 50–130 µm long and 10–20 µm wide.

Pinnule abaxial cuticle (Figs 5C–I, 6A–D, F, G, I, J): Costal and intercostal fields are clearly distinguishable. Costal cells are usually oblong to trapezoidal, 40–70 µm long and 8–12 µm wide. Rounded to oval pores, representing trichome bases, are present; unicellular bent trichomes have been observed (Fig. 5F, G). These trichomes are 125–150 µm long and 30–40 µm wide and widen towards their base, which is 80–90 µm in diameter. Two types of trichome bases occur; one type is broadly oval 45–55 µm long and 30–40 µm wide, whereas the other is narrowly oval 90–120 µm long and 30–35 µm wide. It is interesting to note that half of the margin around these pores is more strongly cutinized, whereas the other half of the margin shows the same cutinization as the rest of the cuticle (Figs 5H, 6A, B).

The intercostal cells are poorly discernible, only prominent stomata are clearly visible (Fig. 5C). Under SEM (Fig. 6A, I), the monocyclic stomata, deeply sunken (15–20 µm) below the epidermis level are clearly observable. The guard cells are elliptical, 22–34 µm long and 9–14 µm wide. The stomatal slit is usually 20–25 µm long (Fig. 6D). The stomatal density is 320–370 stomata per mm². The stomatal index is difficult to determine. The anticlinal walls of the ordinary cells are very weakly cutinized as can be seen under SEM (Fig. 6I). The cells are usually elongated, polygonal, 24–34 µm long and 10–15 µm wide. The outer surface of the cuticle is not

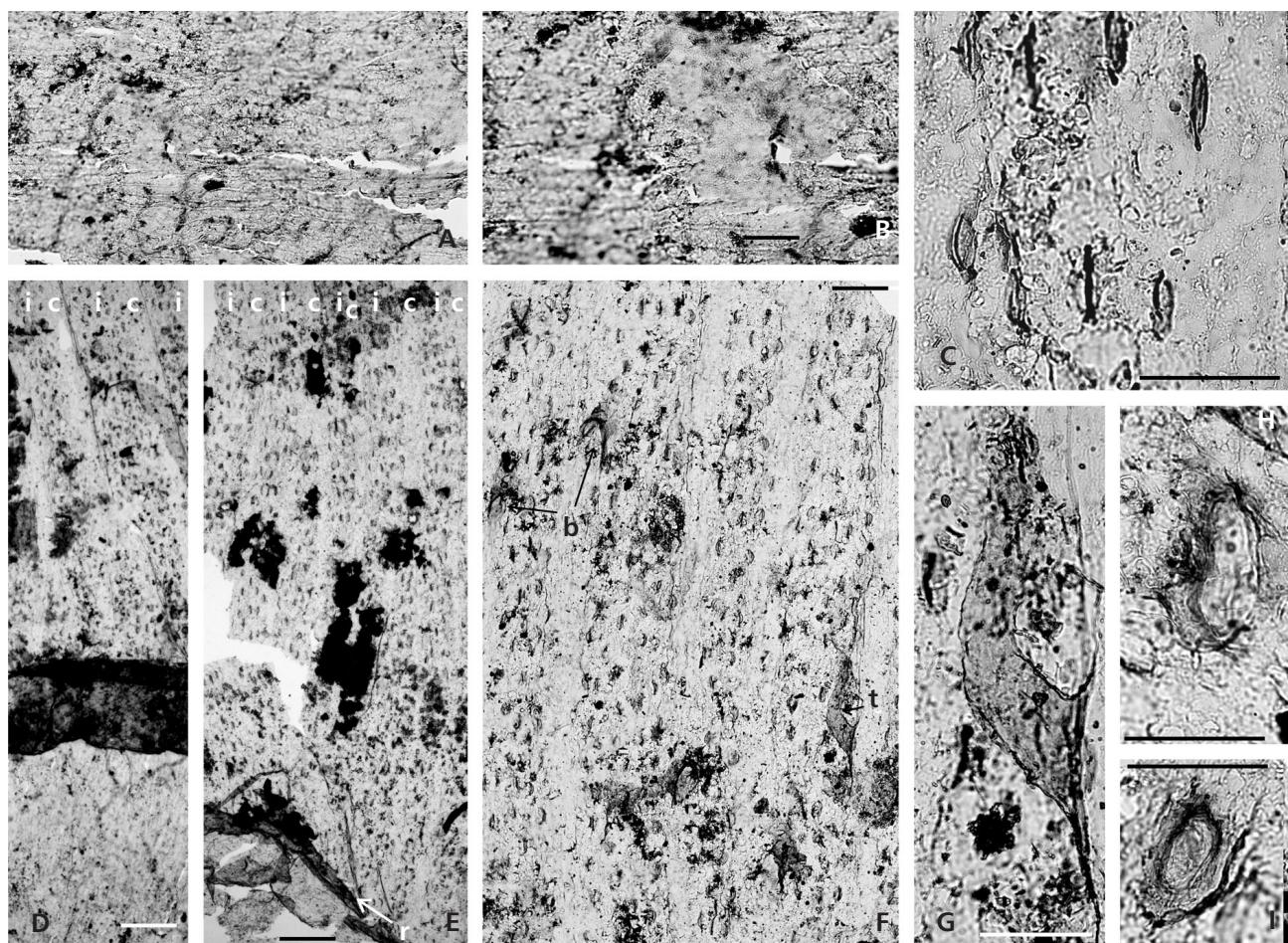


Figure 5. Cuticles of *Paripteris linguaefolia* (Bertrand) Laveine. • A – adaxial cuticle from Fig. 5D, scale bar = 100 µm. • B – detail from Fig. 5A, scale bar = 50 µm. • C – abaxial cuticle with stomata in the intercostal field from Fig. 5F, costal field is above and below, scale bar = 50 µm. • D – adaxial cuticle (below) and abaxial cuticle (above), i – intercostal fields with stomata, c – costal fields, slide 514/7, scale bar = 200 µm. • E – adaxial cuticle on the lower left corner and abaxial cuticle, r – rim between adaxial and abaxial cuticle, i – intercostal fields with stomata, c – costal fields, slide 514/5, scale bar = 200 µm. • F – abaxial cuticle with costal and intercostal fields, b – trichome bases, t – trichome, scale bar = 100 µm. • G – detail of a trichome from Fig. 5F, scale bar = 50 µm. • H, I – trichome bases from the costal field, H – slide 514/3, I – slide 514/7, scale bar = 50 µm.

smooth, but seems to be covered by tiny scales. Only closed stomatal pores were observed (Fig. 6D).

Cuticle of the pinnule rim (Fig. 5D, E): The rim between the adaxial and abaxial cuticle is strongly cutinised and 50–60 µm wide; trichome bases are absent.

Comparison of *Paripteris* species

P. linguaefolia differs from *P. gigantea*, *P. pseudogigantea* and *P. schuetzei* by the absence of a (markedly longer) midrib but presence of fan-shaped venation. *P. schuetzei* and *P. pseudogigantea* usually have smaller pinnules, a prominent, coarser venation, and often a vaulted pinnule blade. The midrib is always very distinct, in length up to $\frac{4}{5}$ of the pinnule length. *P. gigantea* has a prominent midrib in length at least $\frac{1}{2}$ of the pinnule length. *P. gigantea* and *P. linguaefolia* usually have relatively large pinnules. The venation

density does not appear significant for distinguishing individual species. The venation density can vary greatly between different specimens of the same species (Table 2).

Taken together available data, the adaxial cuticle of *P. gigantea* is very similar to *P. linguaefolia*. The cells are elongate tetragonal. The adaxial cuticles of *P. gigantea* figured by Barthel (1961) differ from the adaxial cuticles figured by Šimůnek (2009) and those illustrated here in having much wider cells. Barthel (1961) figured a very small fragment and it is difficult to say whether it is part of the abaxial or adaxial side of a midrib; it is definitely not typical adaxial cuticle. Abaxial cuticles of *P. linguaefolia* and *P. gigantea* are very similar in the specimens illustrated by Barthel (1961) and Šimůnek (2009, this paper). The stomata in the specimens studied by the present author are approximately 22–30 µm long, whereas they are only 15–20 µm long in the material studied by Barthel (1961). However, his illustrations show that they are 20–26 µm

Table 2. Some morphological and micromorphological features of the species *Paripteris gigantea* and *Paripteris linguaefolia*. Explanation: USB – Upper Silesian Basin, ISB – Intrasudetic Basin, West. – Westphalian, * – cuticle of midvein, ** – from Barthel (1961, pl. 4, fig. 1).

Species	<i>Paripteris gigantea</i>			<i>Paripteris linguaefolia</i>		
Author and locality	Barthel (1961)	Šimůnek (2009)	This paper	This paper		
	USB, Brzeszcze, West. A ISB, Žacléř, West. B		USB, Jastrzębie, West. A ISB, Suszec, West. B			
Cell shape	Longitudinal-polygonal*	Longitudinal, oblong, trapezoidal	Longitudinal, oblong, trapezoidal	Longitudinal, oblong, trapezoidal		
Adaxial cuticle	Cell dimensions	Length [µm]	50–100*	60–120	40–100	50–130
		Width [µm]	20–30*	12–20	8–16	10–20
Pinnule margin	Cell shape		?	Oblong, tetragonal, trapezoidal	?	Anticlinal cells not discernible
	Strongly cutinized rim [µm]			200–300		50–60
	Density of trichomes bases per mm ²			120–200		0
Costal	Cell shape	Longitudinal-polygonal, longitudinal-tetraedric	Oblong	Not preserved	Oblong	
	Length [µm]	About 80	60–80	Not preserved	(35) 60–90	
	Width [µm]	8–15	8–16	Not preserved	8–16	
Intercostal	Cell shape	Indistinct anticlinal walls	Polygonal, partly elongated	Polygonal, partly elongated	Polygonal, partly elongated	
	Length [µm]		22–35	20–35	18–30 (35)	
	Width [µm]		16–20	14–20	10–15	
Abaxial Stomata cuticle	Type	Haplocheilic, monocyclic	Haplocheilic, monocyclic	Haplocheilic, monocyclic	Haplocheilic, monocyclic	
	Length [µm]	15–20	22–30	23–30	22–34	
	Width [µm]	12–15	10–14	8–15	9–14	
	Stomatal density per mm ²	?	220–260	Around 260	320–370	
Trichomes	Length [µm]				125–150	
	Width [µm]				30–40	
Trichome base	Length [µm]	40**	25–30 in diameter	45–50	(26) 45–55; 90–120	
	Width [µm]	35**		25–30	(18) 30–40; 30–35 (70)	
	Density per mm ²		8–16		up to 6	
Pinnule	Length [mm]	24**	25–40	23–25	25–28	
	Width [mm]	8**	10–15	7–8	10–13.5	
Number of veins per cm on the pinnule margin			35–50	25–30	42–50	

long. Barthel (1961) mentioned the occurrence of proximal papillae on some subsidiary cells. Papillae also seemed to be present in the cuticles figured by Šimůnek (2009). However, observations under the scanning electron microscope revealed the true nature of this feature in *P. linguaefolia* (Fig. 6). The guard cells are deeply sunken and when the stomatal slit is closed, it looks as if proximal papillae, partly covering the guard cells, are developed (Fig. 5I). The small, 45–50 µm long and 25–30 µm wide, oval trichome bases in the costal field appear to be typical for all samples. Narrow, elongated oval trichome bases, 90–120 µm long, are only present in the costal fields of *P. linguaefolia* also the 125–150 µm long unicellular bent trichomes. This feature distinguishes *P. linguaefolia* from *P. gigantea*. The other

difference is the pinnule margin. The pinnule margin of *P. gigantea* (Šimůnek 2009) is formed by a 200–300 µm wide zone of specialised cells with numerous trichome bases. *P. linguaefolia* has only a 50–60 µm wide zone of more cutinized cells without trichome bases. Trichomes have not yet been observed in *P. gigantea*.

The stomatal density in the two species also differs. *P. gigantea* has a stomatal density of 220–260 stomata per mm², whereas *P. linguaefolia* has a stomatal density of 320–370 stomata per mm². These differences may be caused by differences in environmental and palaeo-atmospheric parameters, e.g. different CO₂ concentrations, but this needs to be tested by studying more samples from different stratigraphical levels.

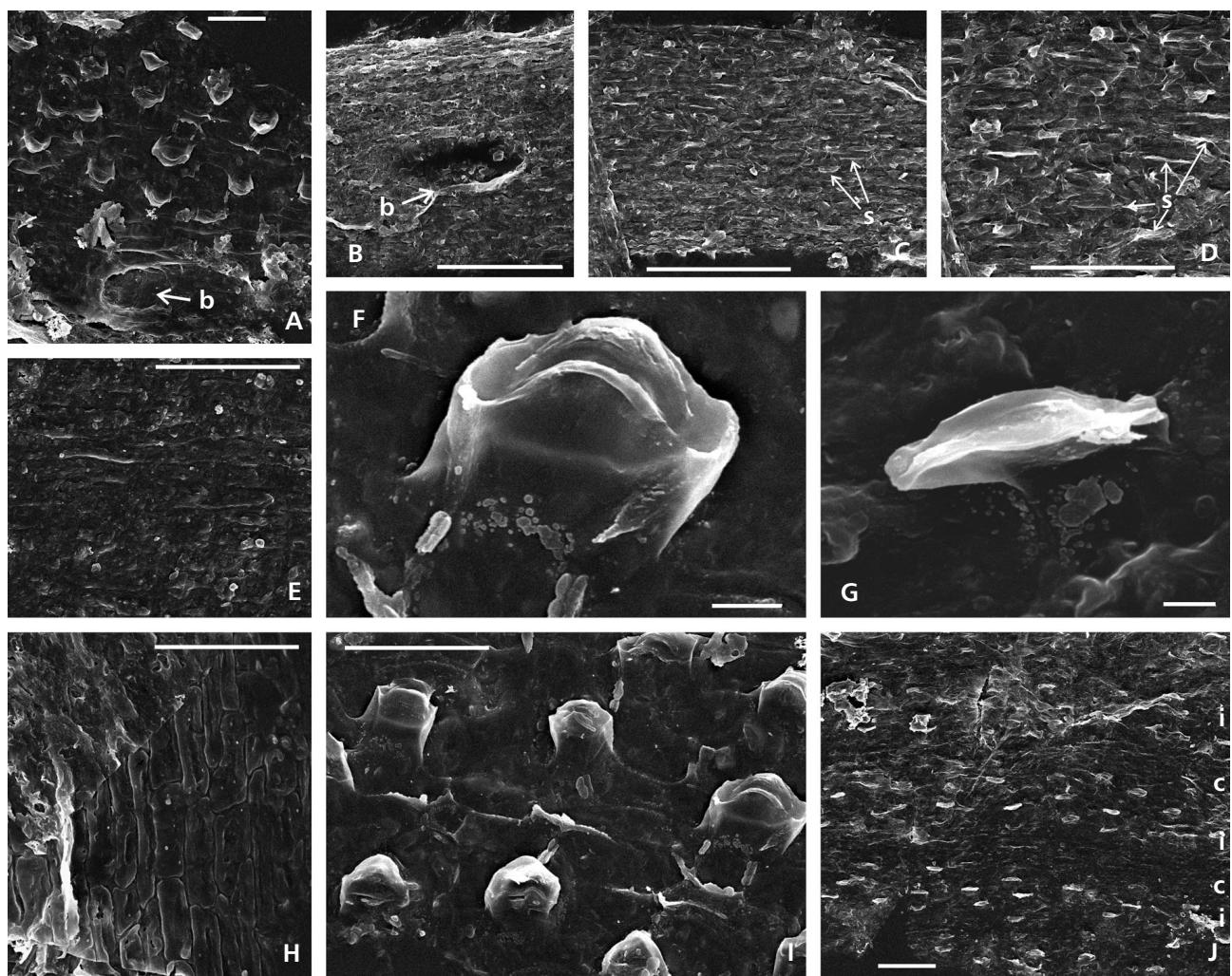


Figure 6. Cuticles of *Paripteris linguaefolia* (Bertrand) Laveine in SEM, stump No. 54. • A – abaxial cuticle from an internal view with stomata and a trichome base (b), scale bar = 50 µm. • B – abaxial cuticle from the outer side with a trichome base (b), scale bar = 100 µm. • C – abaxial cuticle from the outer side with stomata (s), scale bar = 100 µm. • D – detail from Fig. 6C with stomata (s), scale bar = 50 µm. • E – adaxial cuticle from an external view, scale bar = 100 µm. • F – detail of a stoma from Fig. 6I, scale bar = 10 µm. • G – detail of a stoma from Fig. 6J, scale bar = 10 µm. • H – adaxial cuticle from an internal view, scale bar = 50 µm. • I – detail from Fig. 6A, scale bar = 50 µm. • J – abaxial cuticle from the inner side with costal fields (c) and intercostal fields with stomata (i), scale bar = 100 µm.

Discussion

The basic question is: is *P. linguaefolia* an independent species or just a form of *P. gigantea*? This question is difficult to answer. The cuticles of above-mentioned species are very similar. They differ only in the pinnule rim and in the presence of trichomes in *P. linguaefolia*. New macerations will be necessary in order to verify how significant the pinnule rim is for distinguishing between *P. gigantea* and *P. linguaefolia*. In other words, whether the rim is a stable diagnostic feature or not, and whether trichomes also occur in *P. gigantea*. Nowadays, it is impossible to resolve this problem based on only cuticle structure.

If we look at the genus *Laveineopteris*, we can see that the species of this genus also have very similar cuticles,

e.g., *L. loshi* and *L. tenuifolia*. But these species differ in cell size, in the presence of small trichome bases near the midvein of *L. tenuifolia* (Cleal & Zodrow 1989), and in stomatal density. According to Cleal & Zodrow (1989) *L. loshi* has 200 stomata per mm² of pinnule blade, whereas *L. tenuifolia* has 300 stomata per mm² of pinnule blade. Cleal & Shute (1992) stated that *L. loshi* has a stomatal density of 325 stomata per mm² of pinnule blade. It thus seems that stomatal density is not significant in this particular species. It depends on the CO₂ concentration in the atmosphere which changed with time. Cleal *et al.* (1999) demonstrated changes in stomatal density of *Neuropteris ovata* over time.

In recent literature, the binomial classification of *Paripteris* is still commonly used, e.g., Migier *in Brzyski et*

al. (2001) and Cleal (2008). Therefore, I also use this classification here. Cuticular data from the two species of *Paripterus* do not support the “trinominal” classification proposed by Zhang *et al.* (1993), but it cannot be rejected either. It will be necessary to prepare cuticles from further material to answer this question.

Conclusion

Cuticular studies of *P. gigantea* and *P. linguaefolia* have not solved the classification problem regarding the taxa assignable to *Paripterus*, i.e. whether these taxa should be retained as separate taxa, or whether *P. linguaefolia* and other species traditionally assigned to *Paripterus* should be regarded as synonyms of *P. gigantea*, having the status of formae as was advocated by Zhang *et al.* (1993). The cuticles of *P. gigantea* and *P. linguaefolia* are very similar, but there are some differences. The main differences are the presence of trichome bases on pinnule margins of *P. gigantea* and presence of trichomes in *P. linguaefolia* cuticles (*P. gigantea* has only trichome bases). The two species have different stomatal densities. The degree of variability in these features within individual species is not known. It will therefore be necessary to verify cuticular variability of in more specimens before the problem can finally be solved.

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