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Leaf cuticles from the Pennsylvanian-aged medullosalean *Odontopteris cantabrica* Wagner

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ABSTRACT. Examples of *Odontopteris cantabrica* Wagner from early Stephanian (latest Moscovian) macrofloras of the Canadian Maritimes and the Intrasudetic Basin (Czech Republic) have yielded the first-known cuticles for this species. The cuticles are very similar in these two geographically widely-separated areas, indicating that they represent biologically-meaningful morphospecies. The cuticles are broadly similar to those of other odontopterids except for the poor development of inter-cellular flanges on the abaxial cuticle, and the abundance of forked hairs. These distinctive hairs were perhaps effective as an adaptation to growth as a scrambling plant, enabling adjacent fronds to cling to each other, thus aiding self-support. Some preparations clearly show that the venation for each pinnule is provided by a single vascular strand arising from the basiscopic part of the pinnules, and that there are no subsidiary veins arising directly from the rachis. The rachis appears to have had just a single strand.

KEY WORDS: *Odontopteris*, Medullosales, cuticles, Carboniferous

INTRODUCTION

Odontopteris (Brongniart) Brongniart 1831 (syn. *Filicites* (*Odontopteris*) Brongniart 1822) is a morphogenus of medullosalean foliage found widely in Late Pennsylvanian palaeotropical macrofloras. Unlike most other medullosaleans, *Odontopteris* fronds were relatively small, usually no more then 1.5 metre long (including the petiole) and were probably borne by lianescent or scrambling plants. Because of this small size, knowledge of the frond architecture is well understood for a number of species: the fronds had a bifurcation of the main rachis near the base of the laminate part of the frond, each branch bearing mainly single-pinnate pinnae on the inwards-facing side and bipinnate pinnae on the outwards-facing side, and there were intercalated pinnae/pinnules on the primary rachis branches (e.g. Zeiller 1900, 1906, Langiaux 1984, Šimůnek & Cleal 2004, Krings et al. 2006). There have also been cuticular studies on a number of species (Barthel 1961, 1962, Kerp & Krings 2003, Krings et al. 2000, Šimůnek & Cleal 2004) although for the majority of odontopterids details of epidermal anatomy are unknown.

A species that has proved of great biostratigraphical importance is *Odontopteris cantabrica* Wagner (in Wagner et al. 1969), mainly because of its role as an index to the base of the Stephanian Stage (Cleal et al. 2003). Despite this importance, the species has remained relatively poorly documented, and for many years the only illustrated specimens were the types. Wagner (in Wagner et al. 1983) and Zodrow (1985) have since published additional hand specimens, which have now given a better understanding of the macro morphology of these fronds, but until now the epidermal anatomy has been unknown. In the present paper, we document for the first time well-preserved cuticles obtained from *Odontopteris cantabrica* specimens from the upper Morien Group of the Sydney Coalfield in Cape Breton, Canada, and from the Svatoňovice Member of the Intrasudetic Basin, Czech Republic, both of early Cantabrian (latest Moscovian) age.

MATERIAL AND METHODS

The specimens originated from two localities.

1. From between 0.2 m and 1.0 m above the Lloyd Cove Seam (early Cantabrian age – see Cleal et al. 2003) exposed at Brogan's Pit, 1 km south of Point Aconi, Sydney Coalfield, Cape Breton, Canada (see Zodrow 1982 for further details). The hand specimens were originally figured in Zodrow (1985, pls 1, 2), and the cuticles were subjected to microchemical analysis by methods of Fourier transform infrared spectroscopy (Zodrow & Mastalerz 2001).
2. From the Svatoňovice Member, Odolov Formation (early Cantabrian age, Spudil & Tásler 2001) exposed at the Svatoňovice locality, Ida Gallery, Intrasudetic Basin, Czech Republic. Hand specimens from this locality were figured by Němejc (1949, pl. 3, figs 1–3). The hand specimen was in the Šetlík Collection, Czech Geological Survey.

Cuticles were prepared by initially separating the carbonized phytoleim from the matrix with hydrofluoric acid (HF). The Canadian specimens were preserved as naturally macerated cuticles (Zodrow 1985, Zodrow & Mastalerz 2001), and so only required light maceration (4–5 g potassium chlorate dissolved in 150 ml 70% nitric acid) for about an hour to remove any particulate rock matter; alkali treatment was unnecessary. The Czech specimens were more heavily coalified and so required 24 hours maceration in Schulze's reagent with 20 % $HN0_3$, and then several hours further in Schulze's reagent with 40 % $HN0_3$, followed by washing in diluted ammonium hydroxide (NH_4OH) and finally rinsed in distilled water. The adaxial and abaxial cuticles were then separated and mounted on glass slides with glycerine-jelly (the Canadian specimens with added safranin stain). The cuticles were photographed variously using brightfield illumination, phase contrast or Differential Interference ("Nomarksi") Contrast.

DESCRIPTION

The naturally macerated segments of pinnae (Pl. 1, fig. 1) show squat, round pinnules with a wide venation, characteristic of *Odontopteris cantabrica* Wagner (compare with Wagner et al. 1983, pls 5–6). The ultimate rachis had one or possibly two vascular strands. The venation of each pinnule is formed from a single branch emitted from the rachial vascular strand in the basiscopic area of the pinnule (Fig. 1). This branch then undergoes a series of forks, producing subsidiary branches that arch and extend longitudinally along the pinnule. There are ca 18 veins per 10 mm width of the pinnule lamina. No evidence could be seen of resin ducts as reported in other odontopterids (e.g. Šimůnek & Cleal 2004).

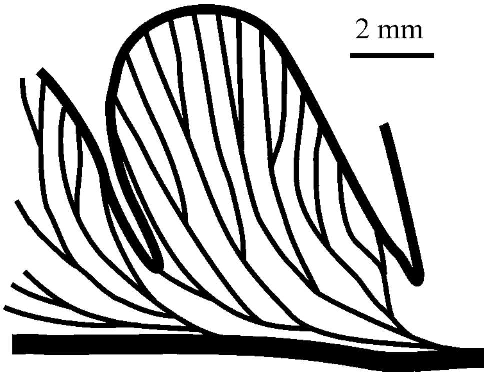

Fig. 1. Tracing of veins as seen in a macerated but not washed cuticle of *Odontopteris cantabrica*. The thick line at the bottom of the diagram represents the vascular strand of the rachis and not the thickness of the rachis itself

The cuticle covering the adaxial epidermis of the pinnules tends mostly to be poorly preserved, but in one Canadian example, evidence of the cell-pattern can be seen. The adaxial epidermis is weakly differentiated into its costal and intercostals fields (Pl. 1, fig. 4). The costal cells are slightly elongate subrectangular to polygonal, up to 100 µm long and 30–40 µm wide; the intercostals cells are more consistently polygonal and isodiametric, 80–100 µm in size.

The abaxial epidermis is often covered by a well-preserved cuticle, but with poorly developed intercellular flanges except surrounding the stomatal guard cells (Pl. 2, figs 1, 2). Little is therefore known about the non-stomatal abaxial epidermal cells.

All of the pieces of rachial cuticle that have been able to orientate appear to be from the abaxial surface, and these show slightly elongate subrectangular to polygonal cells, up to 80 µm long and 20–40 µm wide (Pl. 1, fig. 6). This is similar to the cells along the veins on the adaxial surface of the pinnule lamina. Although we have no unequivocal examples of rachial adaxial cuticle, we assume that there is no significant difference from the abaxial epidermal structure.

Stomata are restricted to the intercostal fields of the abaxial epidermis of the pinnules (Pl. 2, figs 1, 2); no stomata were identified along the rachis. They are apparently randomly orientated and their density is 170–220 per mm^2 (the virtual absence on intercellular flanges made it impossible to determine the Stomatal Index). The stomatal pore is 17–20 µm long. From the outside, the pore is surrounded by a raised rim 3–5 µm wide (Pl. 2, fig. 4). On the inner side of the cuticle, the pores are associated with prominent lateral flaps of cuticle, presumably representing the cutinized inner lips of the stomata (Pl. 2, fig. 3); the flaps are ca 7 µm wide and up to 41 µm long, and have a faint suggestion of radial striae.

The rachises are densely covered in hairs (Pl. 1, fig. 3) the abaxial surface of the pinnules less so (Pl. 1, fig. 2). The hairs have a basal width of 100–200 µm; those on the rachis are mostly 1–1.75 mm long, those on the pinnules 0.2–1.0 mm long. They are tapered to a narrow, round apex, and are straight (Pl. 2, fig. 7) or gently curved (Pl. 2, fig. 8). They consisted of a single row of cells, now represented by alternating bands of dark and light cuticle along the hair length, 50–100 µm long. The most characteristic feature of the hairs is that many show lateral buds. The smaller buds do not cause the direction of the main hair to be deflected (Pl. 2, fig. 7 right), but larger buds cause a marked lateral deflection of the line of the hair (Pl. 2, fig. 7 left; Pl. 2, fig. 6) and in some cases the bud is proximally-oriented (Pl. 2, fig. 9). In some cases, the distal part of the hair may be bent or hooked (Pl. 2, fig. 5).

Also present on the abaxial cuticle are dark, circular bodies, 50 µm in diameter, surrounded by a slightly larger polygonal structure on the cuticle (Pl. 1, figs 5, 7). They are scattered over much of the pinnule surface, but are more abundant around the edge. In some cases they seem to consist of a tubular length of cuticle extending from the pinnule surface. These may be the remains of abscised hairs, although they are significantly narrower than the complete hairs noted above.

Occasionally present are small circular holes on the abaxial cuticle, about 10 µm in diameter (Pl. 2, fig. 4). They are similar to the unstructured hydathodes described by Cleal and Shute (2003) in other medullosalean foliage, but are far less densely distributed.

COMPARISONS

Odonopteris cantabrica has many epidermal features in common with the other species of odontopterids for which cuticles have been described (*O. brardii* Brongniart, *O. reichiana* Gutbier, *O. nemejcii* Šimůnek & Cleal and *O. subcrenulata* (Rost) Zeiller – see Barthel 1961, 1962, Krings et al. 2000, Kerp & Krings 2003, Šimůnek & Cleal 2004). In all of these species there is a clear differentiation between adaxial and abaxial surfaces of the pinnule, and between the costal and intercostal fields of the abaxial surface. Furthermore, costal and intercostal fields are weakly differentiated on the adaxial surface; abundant trichomes occur along the rachis and sparsely on the abaxial surface of the pinnules; and a clear band of differentiated cells occurs around the pinnule-margin, especially on the abaxial surface. Also like other odontopterids, the stomata of *O. cantabrica* appear to lack morphologically-recognisable subsidiary cells, although the absence of well-developed anticlinal walls on its abaxial cuticle makes this difficult to prove.

Compared with these other *Odontopteris* species, the most obvious point of difference shown by *O. cantabrica* is the virtual absence of intercellular flanges on the abaxial cuticle. This might be considered merely a matter of preservation, but we believe that it is not for three reasons. Firstly, the specimens from neither the Sydney nor the Intra-Sudetic basins have intercellular flanges on the abaxial cuticle. Secondly, a similar consistent lack of intercellular flanges also occurs in the cuticles of another type of medullosalean frond, *Laveineopteris* Cleal et al. And finally, if it was due to poor preservation, why are intercellular flanges preserved on the adaxial cuticle and not the abaxial? In our view, the absence of intercellular flanges reflects a combination of flat topography of the abaxial epidermis, and the absence of cuticular penetration of the epidermal cell anticlinal walls. The significance of such relatively featureless cuticles is not clear, although it occurs in several groups of Late Carboniferous palaeotropical plants (Barthel 1961, 1962, Cleal & Zodrow 1989, Cleal & Shute 2003).

The other notable difference between *Odontopteris cantabrica* and the other odontopterid species is the forked hairs. All odontopterids for which cuticles are known are densely haired along the rachises and sparsely on the abaxial surface of the pinnule. However, in none of these other species have hairs been reported with lateral buds or other modifications.

In addition to these characters, *Odonto-*

pteris subcrenulata can also be differentiated from *O. cantabrica* by the presence of numerous papillae on the abaxial epidermis, and the presence of stomata along the rachises.

DISCUSSION

Most odontopterids, with the possible exception of *Odontopteris subcrenulata* (Rost) Zeiller, represent a reasonably homogeneous group in terms of their epidermal features. The lack of intercellular flanges on the abaxial cuticle of *O. cantabrica* is an obvious difference from the others, but this may have little systematic significance. The absence of intercellular flanges on the abaxial cuticle was one of the features used by Cleal et al. (1990) to separate *Laveineopteris* from *Neuropteris*, but it was only one of the characters. There were other, morphological features (e.g. the presence of *Cyclopteris* leaves in *Laveineopteris* – see also Shute & Cleal 2002, Cleal & Shute 2003) and Cleal et al. (1990) emphasised that it was the combination of cuticular and morphological characters that was the justification for separating these genera. There are no comparable morphological differences justifying the generic separation of *O. cantabrica* from these other odontopterids, except perhaps for the very wide venation, but again we remain to be convinced of the taxonomic significance of this feature.

The evidence in this paper may ultimately help with resolving the on-going problem of the taxonomic separation of *Odontopteris cantabrica* from *O. schlotheimii* Brongniart (*O. osmundaeformis* (Schlotheim) Zeiller, nom. illeg.). Wagner (in Wagner et al. 1969) suggested that the pinnules of *O. cantabrica* tend to be smaller and the pinnae more slender, but that the taxonomic significance of these differences might be trivial. The main justification given by Wagner for the separation of the species was the marked stratigraphical gap between the material that he had found in Spain (lower Cantabrian Substage) and the strata in which *O. schlotheimii* normally occurs (Stephanian B Substage to lower Autunian Series). Such an argument would nowadays be regarded as invalid, as the diagnosis of a plant species must be based solely on features of the plants and not on where it was found (ICBN Art. 32.1 – Greuter et al. 2000). Clearly, if *O. schlotheimii* could be shown to have essentially similar cuticles to *O. cantabrica*, the justification for maintaining them as separate species would have to be reviewed, and perhaps the latter name would have to be suppressed as superfluous. To date, however, no cuticles have been reported for *O. schlotheimii* and so the issue must remain unresolved. Other apparently similar species to *Odontopteris cantabrica* are *O. aequalis* Lesquereux and *O. robusta* Zalessky, but the latter are both based on small fragments and their systematic position cannot be presently resolved.

The naturally macerated cuticles (Pl. 1, fig. 1, Fig. 1) clearly show that the venation for each pinnule is supplied from a single vascular strand emitted from the rachial vascular strand near the basiscopic edge of the pinnule. There is no evidence of subsidiary veins arising directly from the rachis. This has also been shown by Šimůnek and Cleal (2004) in *Odontopteris reichiana* Gutbier and *O. nemejcii* Šimůnek & Cleal, although it may be seen to be a little less surprising in these species as their pinnules mostly are partly constricted at the base. *O. cantabrica* pinnules, in contrast, are mostly fully fused to the rachis without evidence of any subsidiary veins. This confirms similar observations made in other medullosalean fronds with pinnules that are fully or partly fused to the rachis *Alethopteris* Sternberg and *Lonchopteris* Brongniart (Bocheński 1960), *Callipteridium* Weiss (Teixeira 1951), *Neuropteris* (Brongniart) Brongniart (Saltzwedel 1969), and the absence of subsidiary veins appears to be a characteristic feature of the order.

The presence of one or two vascular strands in the ultimate rachis of *O. cantabrica* is similar to what was reported by Hamer and Rothwell (1988) in *Medullosa endocentrica* Baxter, which probably represents an anatomically preserved *Odontopteris*-bearing plant. It is also similar to that reported in anatomically-preserved pinnae of *Laveineopteris rarinervis* (Bunbury) Cleal et al. (Oestry-Stidd 1979). In contrast, the ultimate rachises of *Neuropteris* and *Alethopteris* fronds have significantly more vascular strands (Beeler 1983, Pryor 1990), although this may just reflect the much larger size of these fronds.

One of the most remarkable features of the *O. cantabrica* cuticles are the forked hairs.

The only other published record of similar forked hairs on probable medullosalean foliage is in the protologue of *Cyclopteris hirta* Florin. Florin (1926) made no comments as to what the function of these forked hairs might be, although he noted that no other Palaeozoic or Mesozoic gymnosperm was then known to have such hairs. The systematic position of *C. hirta* is unknown (Cleal & Shute 2003). *Blanzyopteris praedentata* (Gothan) Krings & Kerp has branching hairs, mainly on the abaxial surface of the climbing-tendrils (Krings & Kerp 1999, Krings et al. 2004). *Alethopteris zeilleri* (Ragot) Zeiller has also been reported with similarly-forked hairs (Zodrow 2007) although they were not reported in previous published descriptions of cuticles of this species (Doubinger & Grauvogel-Stamm 1970, Šimůnek 1989, Kerp & Barthel 1993).

The adaptive significance of such branched hairs is not fully clear. Krings et al. (2004) suggested that the barbed hairs in *Blanzyopteris praedentata* were to help in the initial support of the climbing plant, before adhesive discs had developed on the climbing tendrils (see also Krings et al. 2003). As pointed out by Krings et al. (2004), however, *B. praedentata* mainly supported itself on the host plant by the adhesive discs. No such climbing tendrils have been reported for *Odontopteris cantabrica* and it is unlikely that the barbed hairs on the frond alone would have been long or strong enough to have supported it as a climbing plant. Rather than clinging to other objects, a better explanation might be that the branched hairs were helping the fronds cling to each other, in a manner similar to hook and loop ("Velcro") fabric fasteners. This could have aided a lianescent plant, or more likely a scrambling plant similar to modern-day *Galium* but on a somewhat larger scale; a similar scrambling habit has been suggested for Carboniferous *Sphenophyllum* (Batenburg 1981). If *Odontopteris cantabrica* was a scrambling plant, this suggests that it was probably adapted to growing in more open parts of the forests, where the fern and pteridosperms trees would not have shaded it significantly. In such open conditions, there would have been more air-movement, and so the plants would have suffered less from the transpiration problems that more shaded plants were subjected to, such as juvenile *Laveineopteris* (Shute & Cleal 2002). This in turn may explain the absence of limited development of hydathodes in *O. cantabrica* compared to many other medullosalean fronds.

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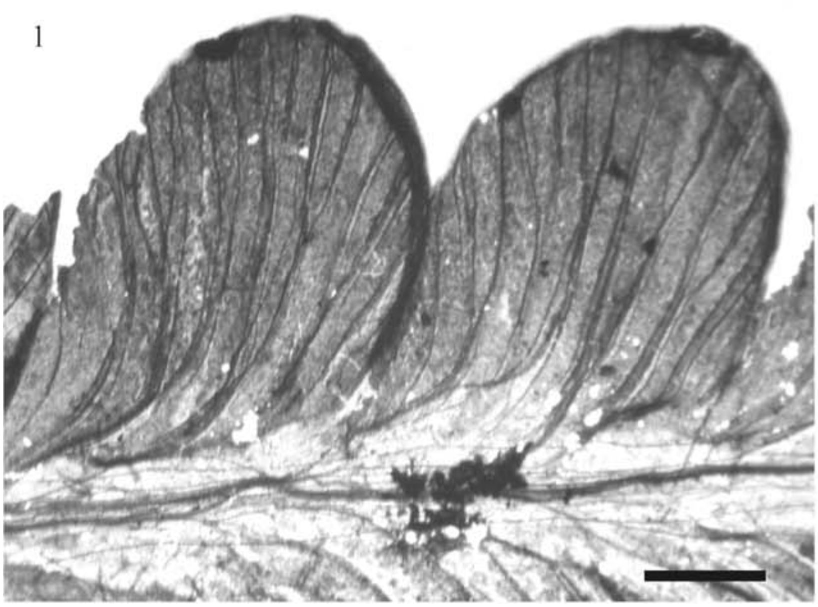
PLATES

Plate 1

Cuticles from *Odontopteris cantabrica* Wagner pinnae from Sydney Coalfield

1. Part of pinna macerated in Schulze solution only, showing details of venation and vascular strands in rachis. UCCB (University Collage of Cape Breton) slide 980-281(1). Scale bar 2 mm
2. Macerated short pinna showing terminal pinnule and a pair of small lateral pinnules. Note concentration of hairs around main vein of terminal pinnules. UCCB Slide 981-302a(7). Scale bar 2 mm
3. Macerated pinnule attached to rachis densely covered in hairs. UCCB Slide 981-302a(11). Scale bar 2 mm
4. Adaxial cuticle, showing costal and intercostals fields. UCCB Slide 981-458-0. Scale bar 50 µm
5. Cuticular boss on abaxial cuticle. UCCB Slide 981-302a(1). Scale bar 50 µm
6. Rachial cuticle showing numerous hair bases. UCCB Slide 980-281. Scale bar 50 µm
7. Cuticular boss on abaxial cuticle. UCCB Slide 981-302a(2). Scale bar 50 µm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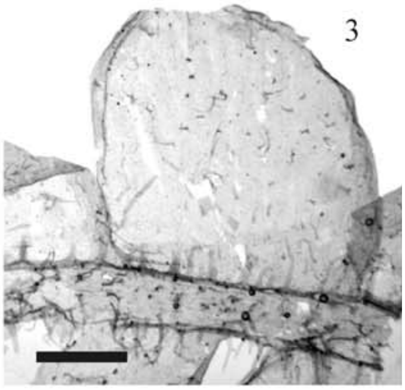
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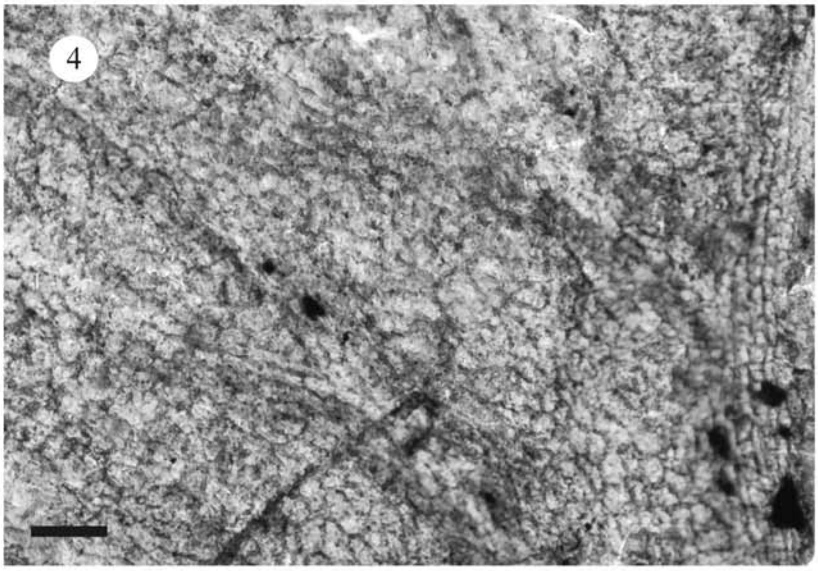
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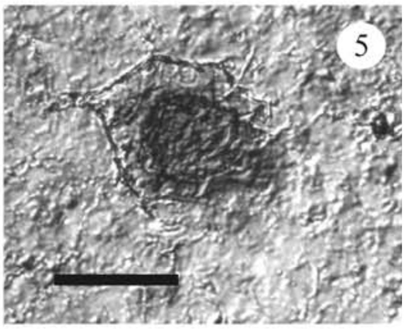
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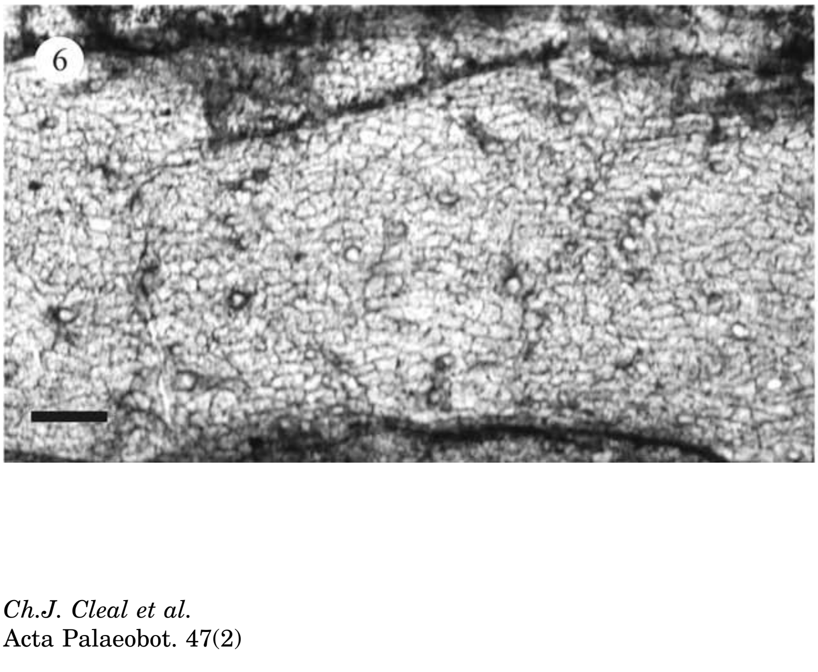
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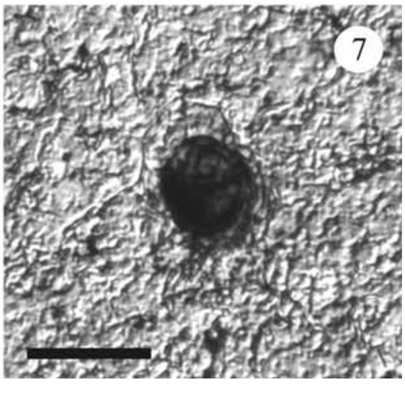
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Plate 2

Cuticles from *Odontopteris cantabrica* Wagner pinnae from Intrasudetic Basin (figs 1, 3, 5) and Sydney Coalfield (figs 2, 4, 6–9)

1. Abaxial cuticle with many stomata. CGS (Czech Geological Survey) slide 373/5. Scale bar 100 µm
2. Abaxial surface with stomata. UCCB Slide 981-458(0). Scale bar 50 µm
3. Close-up of stoma viewed from inner surface of cuticle shown in fig. 1. Scale bar 10 µm
4. Close-up of stoma viewed from outer surface of cuticle. UCCB Slide 981-302a(11). Scale bar 10 µm
5. Forked and hooked hairs from a rachis. CGS Slide 373/5. Scale bar 50 µm

6–9. Forked and hooked hairs from a rachis. UCCB Slide 981-302a-(4). Scale bars 50 µm

Plate 2