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Article

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Abstract

Hoffmann's species *Neuropteris Scheuchzeri* in Keferstein 1827 is generally – but not exclusively – identified by its 1–4 mm long trichomes or hairs, though he did not mention nor illustrate them in the diagnosis of the species. Basal Cantabrian-age compressions of the species, including "*Odontopteris subcuneata*", from Sydney Coalfield, Canada, are oxidized/macerated by Schulze's process from 3 hours to 12 days to track solubility patterns of the trichomes or hairs, and files. Proposed is also a spectrochemical model for *Macroneuropteris* (ex *Neuropteris*) *scheuchzeri* based on carbon 13 nuclear magnetic resonance (^{13}C NMR) experiments, combined with Fourier transform infrared (FTIR) spectroscopy.

M. scheuchzeri is chemically similar to other medullosaleans in respect to high aliphatic and low aromatic contents, though FTIR analysis signals preservation variability. Hair invariably drops from compressions during HF treatment, it is opaque, pointed and not organically attached to compressions. A secretory origin is hypothesized that requires confirmation, including explanation of physiological function. Files-hair-trichomes, besides dissolving at different rates when oxidized, are physicomorphologically distinguishable from one another; hence hair and trichomes are not synonymous, as assumed by some authors.

Morphological/functional-group changes occur across the basal frond dichotomy (**bfd**). Apart from the "pinnule" differences is that above **bfd** trifoliate foliage shows hair and trichomes, whereas below **bfd** "*O. subcuneata*", for example, shows hair, files, and some trichomes. Most conspicuous in functional-group differences is that aliphatic side-chain branching is lower below than above **bfd**. It is suggested that aspects of Zimmermann's telomic theory may offer an explanation for the phenomenon.

Key words: hair, secretion, trichomes, files, compressions, seed fern, spectrochemical data, Carboniferous.

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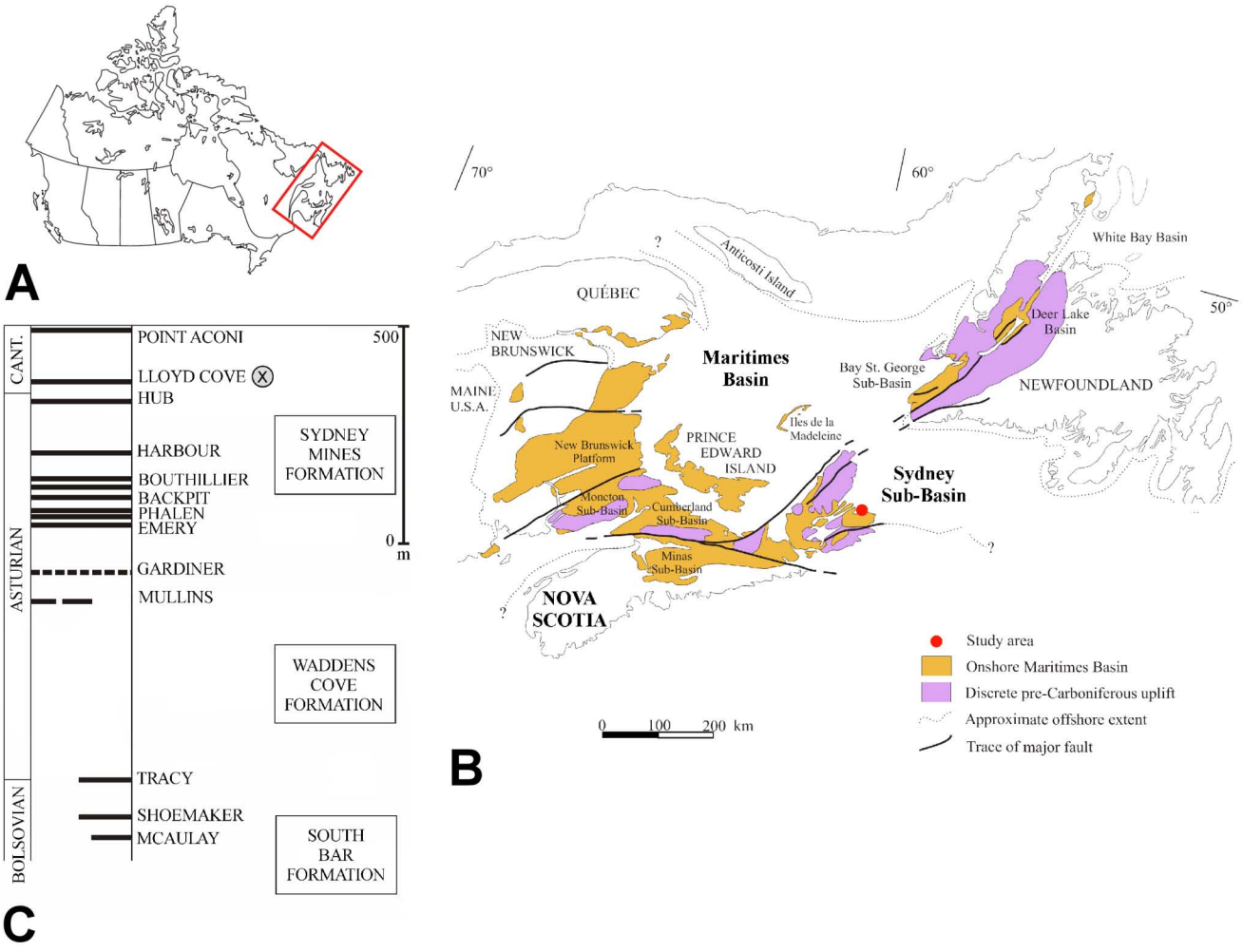
1 Introduction

Macroneuropteris (ex *Neuropteris*) *scheuchzeri* (Hoffmann in Keferstein 1827: 157, figs 1–4) Cleal et al. 1990 is an "old" fossil originally named *Phyllitis mineralis* by Lhuyd (1699) that predates Scheuchzer's 1709 publication which is considered the beginning of scientific palaeobotany. Hoffmann did not mention hair, nor illustrated it in his diagnosis of the species, but twenty years later in 1847 Bunbury (pl. XXI) mentioned it for Canadian specimens (Zodrow 2003). Later in 1916, Gothan named hair a diagnostic feature for the species without source documentation. This taxonomic practice prevails to-date. It is exemplified by phrases in the literature, e.g. "villous pinnules" (Bell 1938), "hirsute pinnules" (Arnold 1947, Laveine 1967, Darrah 1969), "3 mm long trichomes" (Remy & Remy 1977), "abaxial, uniseriate trichomes" (Beeler 1983: fig. 33); Schabillion & Reihman (1984), Cleal & Zodrow (1989), Zodrow (2003), Laveine & Belhis (2007), Stull et al. (2012), and many others. Though hairless specimens from Kansas (Cridland et al. 1963: p. 62), and Canatabrian strata in Sydney Coalfield (Bell 1938) were assigned by these authors to *Neuropteris scheuchzeri* (see further Darrah 1969). In addition to preservation by compression in the Sydney locality (Text-fig. 1), intact ad- and abaxial epidermises can occasionally be peeled from the compressions of *M. scheuchzeri*-"*Odontopteris subcuneata*" Bunbury 1847, yielding important morphological information because there is no obliteration of features by intervening chemistry (cf. Text-figs 5D, 7C).

Barthel (1961: Tafel II, Bild 3) recognized that trichomes are not the same as hair, i.e., "...aufgehellte



Text-fig. 1. Location map. **A.** Canada; **B.** Sydney Sub-Basin, Nova Scotia; **C.** Coal lithostratigraphy. X – Lloyd Cove sample location. Cant. – Cantabrian strata.

Fiederfragmente ..." show pointed hair endings and "ansitzende Haare konnten nicht beobachtet werden" which provided the impetus for this experimental study.

We address the nature/relationship/occurrence of hair – trichomes – files by studying only HF-freed compressions, unencumbered from the interfering rock matrix using Schulze's oxidation process for solubility experiments. An ancillary aim is to develop a modern chemical view of *M. scheuchzeri* within the framework of the most common preservation modes (compression and cuticle).

2 Materials and methods

Materials: Detached, 6–8 cm long *M. scheuchzeri* pinnules from two shale slabs, accession numbers 80(=980)-516 and 3-234 (30 cm by 35 cm maximal sizes), two single pinnule specimens named "1/2Pinnule" and "1Pinnule", and one pinnate sample of "*O. subcuneata*" comprise the sample entities. Emphasized is that on the shale slab 80-516 "*O. subcuneata*" and *M. scheuchzeri* co-occur unconnected on the same bedding plane. From selected pinnules, 62 glass-covered slides were prepared (compressions and cuticles). This is in addition to re-examining 120 cuticular slides of *M. scheuchzeri* used for the study by Cleal & Zodrow (1989) and Zodrow (2003: fig. 1).

Sample provenance is a 1-m roof-shale section of the Lloyd Cove Seam (Text-fig. 1C) which is of oil-window maturity (vitrinite reflectance is Ro = 0.65%). The coal is classified as high volatile A bituminous because of its 36% average volatile content (Hacquebard 1993). These are key indicators for well-preserved compressions, particularly as the volatile content exceeds 28% which is mentioned by Barthel (1962) as threshold for successful cuticular maceration.

Methods: Complying with HF-safety protocols, we freed the many compressions from the rock matrix with 48% HF, and routinely scrutinized the used HF solutions for dislodged compression features of all sorts. This is a necessary procedure as the results impact claims relating to inherent presence or lack of hair. Then, the freed compressions were individually oxidized from 3 h to 13 h (one for 12 days) by Schulze's process ("Salpetersäure und chlorsaures Kali": see protocol used by Cleal & Zodrow 1989), and washed for three days. Some oxidized fragments were neutralized with 4.5% v/v ammonium hydroxide to obtain cuticles (= the maceration process). This solution was also checked for dislodged cuticular features.

By methods of FTIR spectrometry, thirty-one IR (infrared) spectra from compressions and one cuticle were obtained. From these, functional-group parameters were computed using the same instrumentation, 4 cm^{-1} wavenumber resolution, 256 co-added scans, and mathematical integration techniques as are detailed by D'Angelo & Zodrow (2011). Basic principles for interpreting organic-matter IR spectra are illustrated, for example, by Walker & Mastalerz (2004: fig. 5) and Zodrow et al. (2010).

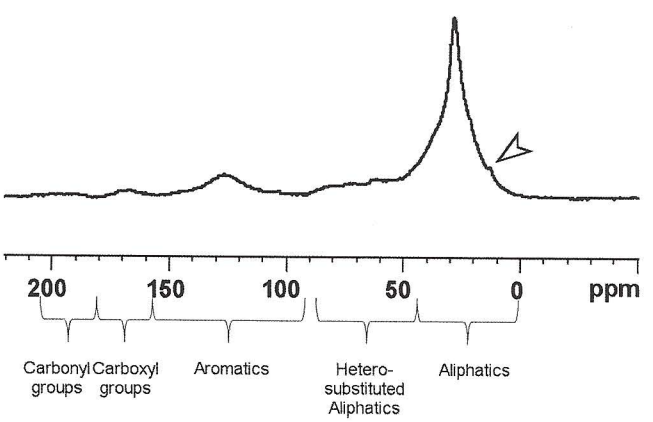
In addition, 24.5 mg of cuticle were analyzed by solid state ^{13}C CP/MAS NMR (cross polarized/ magic angle spinning) on a Bruker Avance NMR spectrometer with a 9.4T magnet (Larmor frequency 400.2 MHz for ^{1}H (proton) and 100.65 MHz for ^{13}C). The material was spun between 7.0 and 12.0 kHz to characterize the signal overlap of the spinning sidebands with the isotropic shift peaks. The spectrum was acquired at 12 kHz spinning speed, causing some weak overlap between the aromatic spinning side bands and the aliphatic isotropic signals on the high-field side (below 3 ppm). Spin-lattice relaxation times for ^{1}H are determined by inversion-recovery sequences. Other parameters for ^{1}H decoupling are optimized on glycine whose carbonyl resonance also served as external, secondary chemical-shift standard at 176.06 ppm. For the final spectrum, 45,056 scans were co-added, with a recycle delay of three seconds.

Principal component analysis (PCA) is used as a statistical strategy to evolve data groupings in terms of chemical structure which are represented by the IR functional groups. Particularly useful in the context are the PCA scores because they focus on the groupings (summary: D'Angelo et al. 2010).

3 Summary of experimental results

3.1 ^{13}C CP/MAS NMR: *scheuchzeri*-cuticle

The annotated NMR spectrum (Text-fig. 2) identifies two separate intensity regions (i) aliphatics and (ii) aromatics. Aliphatic (i) intensities about 2 ppm and 90 ppm correspond to chain sites (chain hydrocarbons, $(CH_2)_n$). The peak at 30 ppm originated from mobile methyl (CH_2) groups which overlap with broader resonances of unsubstituted aliphatic carbons groups (CH_2, CH_3, and branched CH_2). Resonance at 14 ppm originated from the methyl groups that terminate the linear aliphatic hydrocarbon chains $(CH_2)_n$, which were previously not observed for *M.*



Text-fig. 2. ^{13}C CP/MAS NMR spectrum of the cuticle of *Macroneuropteris scheuchzeri*. Location guides for the resonances of some chemical groups are shown. Arrow points to the peak of methyl group terminations of unbranched aliphatic chains.

scheuchzeri by LYONS et al. (1992, 1995). Aromatic (ii) intensities between ca. 110 ppm to 165 ppm resulted from aromatic carbons composed of ring carbons (benzene structure), bridge-head carbons, and oxygen-substituted aromatic carbons with maxima around 120–125 ppm, 140 ppm, and 153 ppm, respectively. Seen also is the long-suspected influence of Schulze's oxidative process at 63, 73, and 83 ppm resonance ranges of primary, secondary, and tertiary alcohols, ether or ester linkages. Band assignments are taken from WERNER-ZWANZIGER et al. (2005) and references there in.

3.2 Functional-group distribution of compressions above the basal frond dichotomy (bfd)

Definitions of area ratios are listed in Table 1, and corresponding semi-quantitative chemical ratios derived from the IR spectra are summarized in Table 2 as mean value and range/sample entity. The compression IR (Text-fig. 3A1) differs from the corresponding cuticle IR spectrum (cf. Text-fig. 3F1). Particularly two spectral zones are useful for differentiating between the two. These are (a) the 1800–1600 cm^{-1} region (aromatic carbon and oxygen containing structures) and (b) the 900–700 cm^{-1} zone (aromatic C–H bending). For example, aromatic carbon peaks (1615 cm^{-1}) in the compression (Text-fig. 3A1) shifted towards higher wavenumbers (1639 cm^{-1}) in the cuticle (Text-fig. 3F1). At the same time, carbonyl groups in the compression are barely detectable, whereas some peaks assigned to the same groups occur in the cuticle at 1702 cm^{-1} (confirmed by present NMR analysis). The semi-quantitave IR data (Table 2) are in agreement with the qualitative information described for the ^{13}C NMR analysis. Compressions show lower C=O/C=C (mean 0.07) and higher C=C cont (mean 0.50) than cuticle. This indicates that compressions have a smaller contribution of carbonyl groups and a comparatively higher content of aromatic carbon structures, respectively. Aromatic peaks at 900–700 cm^{-1} are absent in the cuticle as a result of maceration that probably removed lignin and mesophyllous tissue from the compressed tissue (ZODROW & MASTALERZ 2009: fig. 2). But most important are the differences regarding the aliphatic structures. Thus, the CH_{al}/C=C ratio is higher in the cuticle (4.98) than in any of the compression means, attesting to a higher contribution of aliphatic hydrocarbons in the cuticle. The important increase of the CH_2/CH_3 ratio from 1.9 (mean value, compression: Text-fig. 3A1) to 4.9 (cuticle: Text-fig. 3F1) (cf. D'ANGELO et al. 2013) indicates longer and more branched polymethylenic chains attached to the macromolecular structure of the cuticle. PCA scores of semi-quantitative IR ratios of compressions (Table 2) show unexpected trends for functional groups in a single pinnule (specimen "1Pinnule", Text-fig. 4A). Moreover, the plot of the entire data set (Text-fig. 4B) clearly demonstrates separate groupings: pinnules from the slab 3-234, "1Pinnule" and "*O. subcuneata*" form one group,

Table 1. Definition of semi-quantitative area ratios derived from FTIR spectra.

Ratio	Band-region (cm^{-1}) or Band-region ratios	Interpretation and remarks
CH_2/CH_3	3000–2800	Methylene/methyl ratio. It relates to aliphatic chain length and degree of branching of aliphatic side groups (side chains attached to macromolecular structure; LIN & RITZ 1993a, LIN & RITZ 1993b). Higher value implies comparatively longer and straight chains, a lower value shorter and more branched chains. Caution is advised using the ratio, as it may be misleading due to the contribution from CH_2 and CH_3 groups attached directly to aromatic rings (PETERSEN & NYTOFT 2006).
CH_{al}/C=C	(3000–2800) / (1600–1500)	Aliphatic/aromatic carbon groups ratio. Relative contribution of aliphatic C-H stretching bands to aromatic carbon groups (C=C). Higher values indicate increasing aliphatic groups to aromatic carbon groups. This ratio is equivalent to the I1 index of GUO & BUSTIN (1998).
C=O/C=C	(1700–1600) / (1600–1500)	Carbonyl/aromatic carbon groups ratio. Relative contribution of C=O to aromatic carbon groups. Higher values indicate increasing carbonyl/carboxyl groups to aromatic carbon groups.
C=C cont	(~1600) / (1800–1600)	Aromatic carbon contribution. Relative contribution of aromatic carbon groups (C=C; peak in 1650 to 1520 cm^{-1} region, centered near 1600 cm^{-1}) to combined contribution of oxygen-containing groups and aromatic carbon (C=C) structures.

Table 2. Semi-quantitative chemistry (IR-derived data) of compressions and one cuticle of *Macroneuropteris scheuchzeri* above and **below** the basal frond dichotomy (**bfd**).

Specimen (no. of samples)	CH_2/CH_3 Mean (range)	C=O/C=C Mean (range)	C=C cont Mean (range)	CH_{al}/C=C Mean (range)
	Above bfd			
"1Pinnule", base (1)	2.2	0.03	0.51	0.99
center (4)	2.0–2.5	0.02–0.3	0.5–0.55	0.87–1.09
tip (3)	2.1	0.02	0.49–0.53	1.01
80-516 (8)	1.9 (1.8–2.0)	0.2	0.26 (0.24–0.3)	1.98 (1.61–2.44)
3-234, 3-234-1, "1Pinnule" (21)	2.3 (2.0–2.7)	0.07	0.50 (0.44–0.53)	1.09 (0.87–1.31)
Cuticle 80-516 (1)	4.9	0.37	0.18	4.98
	Below bfd			
"*O. subcuneata*"(2) 80-516-1	2.7	0.02	0.39	1.26
Lloyd Cove, vitrain	0.9	0.003	0.77	0.69

whereas pinnules from the slab 80-516 another. The chemical separation of the compressions "*O. subcuneata*" from *M. scheuchzeri* (both entombed on the slab 80-516) attests to localized diagenetic influence on *M. scheuchzeri*, or what BARTHEL (2006) would call "naturmazerierte Pflanzenfossilien". We observe that it is not uncommon in Carboniferous compression flora to find adjacent pinnules on one bedding plane that are differently affected by diagenesis (cf. D'ANGELO et al. 2012a).

3.3 Comparison of functional-group distribution above and below the basal frond dichotomy (bfd)

"*O. subcuneata*" is one of the structures that is certainly borne below the basal frond dichotomy of the heterophyllous *M. scheuchzeri* frond (BELL 1938, LAVEINE & BELHIS 2007).

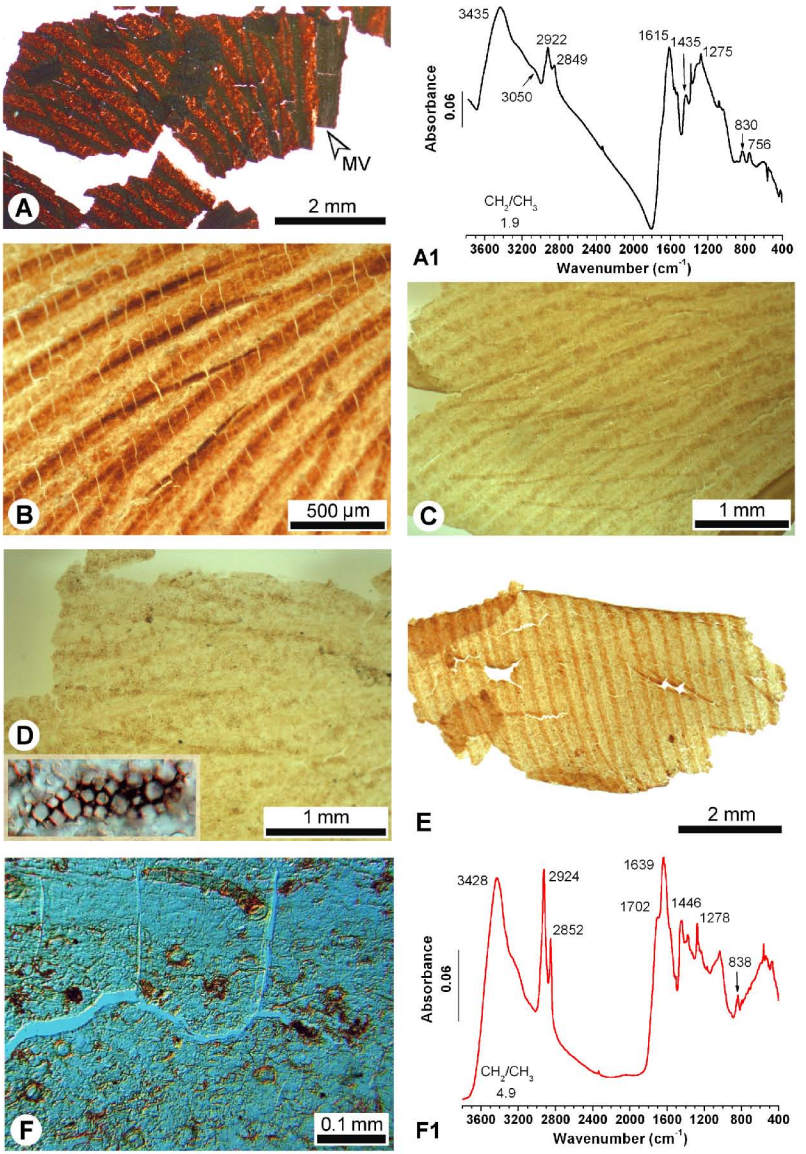
IR-derived ratios of pinnules from below and above **bfd** differ from each other (Table 2) in small but subtle ways. Pinnules from above **bfd** exhibit higher C=O/C=C (mean 0.07) and C=C cont (mean 0.5) than those below **bfd** (0.02 and 0.39, respectively) (Table 2). This indicates that "*O. subcuneata*" compressions have smaller contributions of both carbonyl/ carboxyl groups and aromatic carbon structures. In general, compressions above **bfd** have shorter and less branched polymethylenic chains attached to the macromolecular structure as well as a slightly lower aliphatic contribution than pinnules below **bfd**. Support for these differences is inferred from PCA scores that show the separation of "*O. subcuneata*" from the *M. scheuchzeri* samples (Text-fig. 4B).

3.4 Hair and trichomes on foliage above (bfd)

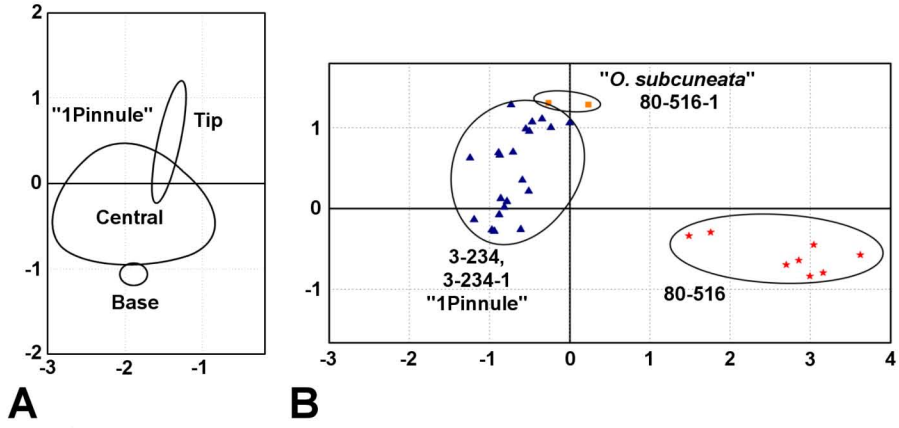
On *M. scheuchzeri* compressions/impressions, Mazon-Creek type of concretions (DARRAH 1969), and on coal-ball petrification (BEELER 1983), hair, if abundant, is a conspicuous surfacial feature. In contrast, compressions of the orbicular pinnules show sparse hair possibly as a result of drop-offs, as noted.

The compression (Text-fig. 5A, B) shows hair impressions (molds), and hair crossing abaxial veins, respectively. Hair is opaque (Text-fig. 5C and E) unless diagenetically altered (Text-fig. 5D), acellular, hollow? biterminally acuminate, 1–4 mm long, mostly straight, broadest in the center (38–60 μm) (e.g. Text-fig. 5D), gradually tapering to 1–2 μm terminals (e.g., Text-fig. 5E). The resulting shape is elongate, spindle-like. Microscopic examination at ×250 magnification confirmed BARTHEL's (1961) observation that hair is not organically attached to the compression.

Hair is generally most abundant in the lower part of the abaxial pinnule, where it is obliquely oriented to the venation pattern. Towards the apical regions, the distribution thins out and hair may be near-parallel or superimposed on lateral venation (Text-fig. 3B). Overall, though, the distribution of hair over a compression shows a definite trend alignment. Text-fig. 3 docu-



Text-fig. 3. Hair solubility: see text. Slide A. 80-516/1. A1. IR spectrum of A; B. 80-516 Oxi 6 h 0 min; C. 80-516 Oxi 10 h/1; D. 80-516 Oxi 13 h 30 min; E. 80-516 Oxi 40-60-80; F. Cuticle of B., temporary slide; F1. IR spectrum of F. B. to E. photographed submersed in water (transmitted light). F. Nomarski phase contrast. MV – midvein.



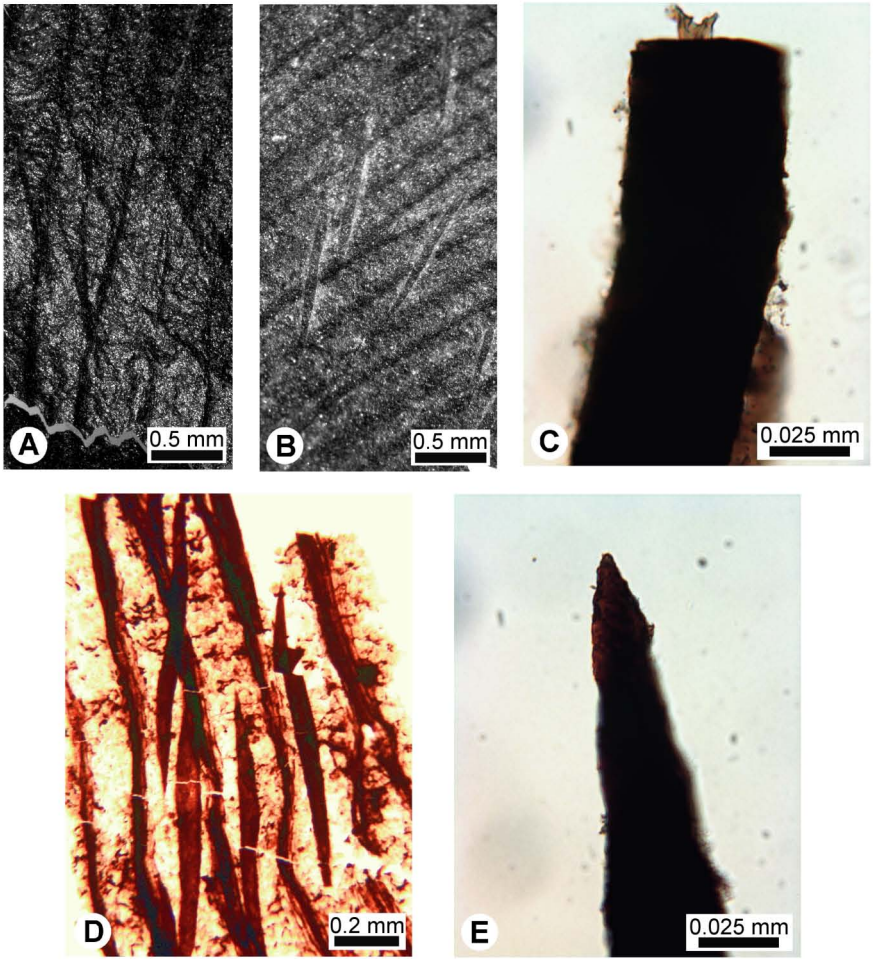
Text-fig. 4. Principal component analysis. Scores' plot of the two-principal component model (97.12% explained variance). **A.** Functional-group trend of "1Pinnule". **B.** Separation of "*O. subcuneata*"-*M. scheuchzeri* from the *M. scheuchzeri* pinnules that occur on slab 80-516. Input data for the plots are the four variables from Table 2.

ments one of the many serial solubility experiments we conducted in the course of this study involving hair, and necessarily trichomes and files. Text-fig. 3A shows a compression fragment with abundant hair crossing the lateral veins, noting that preservation resembles an incomplete fossilized-cuticle. After 6 h oxidation, hair had turned darker in color than the lateral veins (Text-fig. 3B), and after an additional 4 h hair is faintly visible (Text-fig. 3C). Three more hours and 30 min of oxidation leaves linear tracks of former hair marked by framboid-pyrite deposition (Text-fig. 3D, inset). A fragment different from the above has been oxidized more slowly for 11 d and 40 min (3 h 40%; 4 d 60%, and 7 d 80%), leaving hair still faintly visible (Text-fig. 3E). Ammonium hydroxide treatment of Text-fig. 3B resulted in the cuticle (Text-fig. 3F) on which occasional, incomplete trichomes remained, though hair has vanished by dissolution. Epicuticular, multicellular appendages (transparent after maceration) are referred to as trichomes (cf. SCHABILION & REIHMAN 1985: fig. 1; KRINGS et al. 2003). Text-fig. 6A exemplifies an in situ trichome (285 µm long) that survived maceration intact. Unmistakably aligned along the pinnule margin are round bases (27–38 µm) (Text-fig. 6B: cf. "*O. subcuneata*", Text-fig. 7B), probably mistaken as papillate pinnule margin by BARTHEL (1961: pl. III, fig. 1)?

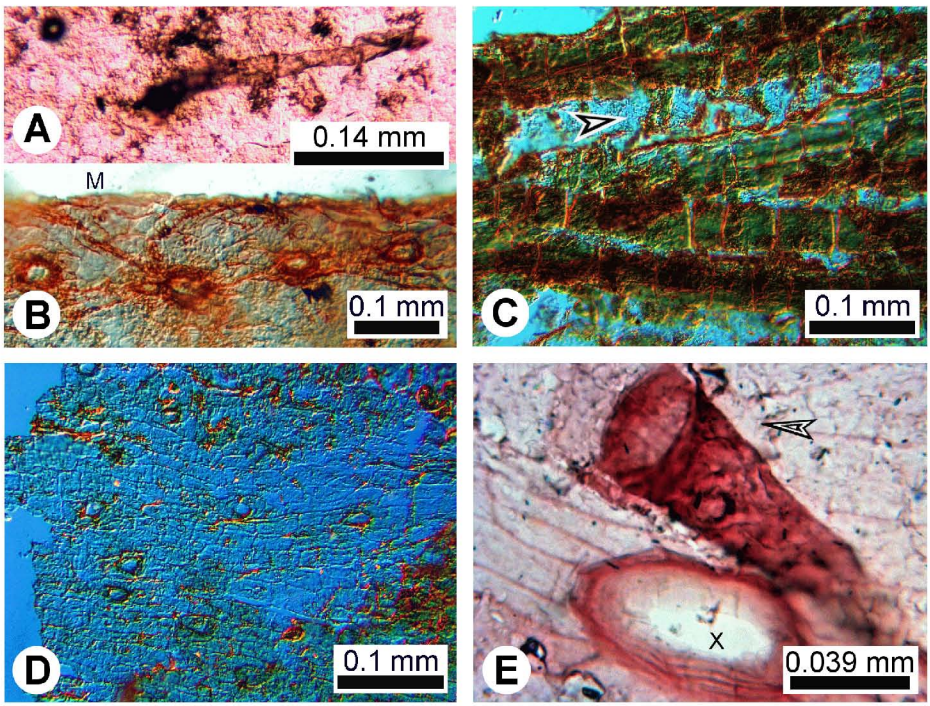
Abaxial epidermises "as preserved" (not chemically treated) abound with in situ trichomes truncated after what appears to be the first constituent cell (cf. SCHABILION & REIHMAN 1985: fig. 1). After 8 h 30 min oxidation, the truncated trichomes are still intact (Text-fig. 6C), but solubilized on subsequent ammonium-hydroxide treatment, leaving a field of multitudinous bases as is typical for the abaxial *scheuchzeri*-cuticle (Text-fig. 6D). Hair had solubilized. Text-fig. 6E shows a toppled-over trichome with a round 39-µm diameter base, hollow and not deformed juxtaposed to an oval base 38 µm by 78 µm. The latter is assumed a trichomatous size-variant by some authors (i.e, Gothan 1916: pl. 32, fig. 6; CLEAL & ZODROW 1989, and others). We find that claim difficult to accept, but cannot offer an alternative explanation at this juncture, except to note our inability to match basal dimensions of any epicuticular appendages to these oval bases.

3.5 Files vs. trichomes vs. hair on "*O. subcuneata*" below (bfd)

"*O. subcuneata*" compressions (e.g. Text-fig. 7A) show false fimbriate-pinnule margins due to lamina erosion that exposed the more resistant lateral veins as fimbriate; when intact the margins have trichomatous appendages (e.g. Text-fig. 7B; cf. Text-fig. 6B). A larger fragment of an abaxial surface that peeled-off the compression (not chemically treated) exposes between lateral veins a mat-like epidermis (e.g. Text-fig. 7C) dense with in situ files that are overlain by hair (e.g. Text-fig. 7D), demonstrating indisputably lack of organic connection of hair with the epidermis. Files (e.g. Text-fig. 7E) and hair were also found detached in the diluted HF solutions, whereas trichomes were not. Files are non-segmented (uniseriate?) and naturally



Text-fig. 5. Hair. **A.** Adaxial, and **B.** Abaxial surfaces of one and the same *M. scheuchzeri* compression. Photographed immersed in water. Reflected light. Slab 80-516; **C.** Middle part of a hair. ×500. Slide 980-516-1/3; **D.** Diagenetically altered hair. Chemically untreated abaxial epidermis. Transmitted light. Slide "1/2Pinnule"/1; **E.** Hair tip of C. ×500. C. and E. Nomarski phase contrast.

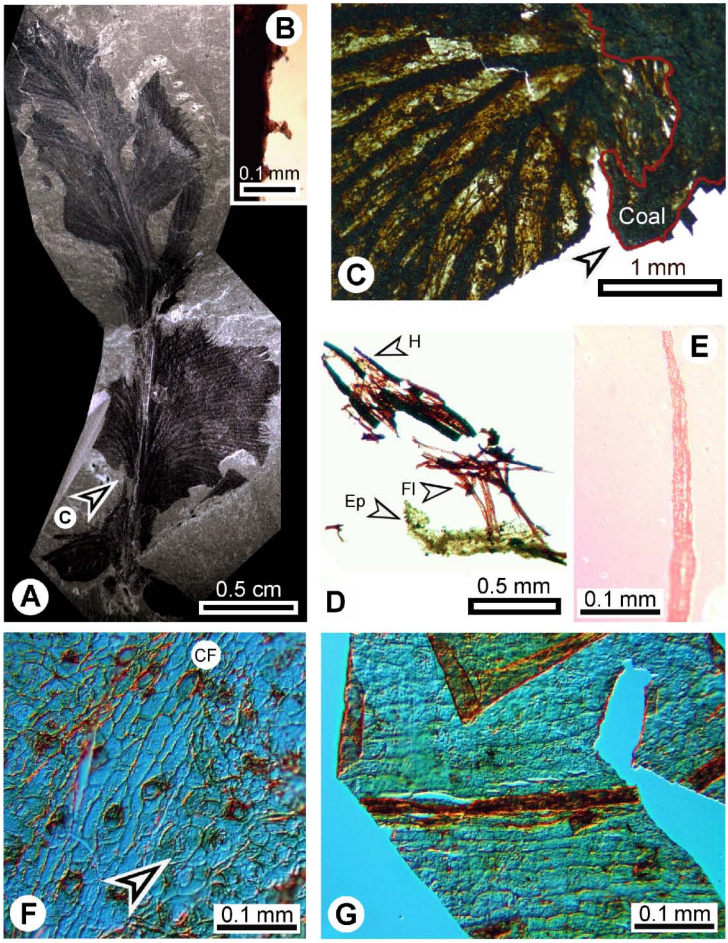


Text-fig. 6. *M. scheuchzeri*. A. Intact attached, recumbent trichome; B. Pinnule margin (M) with round bases; A. and B. slide 80-516/2; C. Lower epidermis with truncated trichomes in situ (arrowed). Slide "1/2Pinnule"/2; D. Cuticle of C. with trichomatous bases. Slide "1/2Pinnule"/4; E. Toppled trichome (arrowed) adjacent to an oval structure marked X. ×500. Slide 77-427a/2. All Nomarski phase contrast.

transparent. They are proximally pointed but tapered to a diameter of ca. 12 μm at the base from the widest width of 15–23 μm at the mid section. Multiple files (strands) may emerge through one single base. Complete file lengths could not be determined because files are fragmented in situ or when detached.

Abaxial and adaxial cuticles of "*O. subcuneata*" required different maceration times, i.e. for the former (Text-fig. 7F) 5 h, and the latter 2 h 14 min (Text-fig. 7G). The abaxial cuticle is stomatiferous in intercostal fields, and the stomatal apparatus appears similar to that in foliage above **bfd**. Costal fields are differentiated from the intercostal fields. Cells of the former are 38–76 μm long and 11.4–19 μm wide, variably elongate in shape with slightly wavy anticlinal walls; cells for the latter are 12 μm × 27 μm equally variable in shape, appearing blocky (cf. Cleal & Zodrow 1989: pl. 106, fig. 5). All files are solubilized. The densely distributed round bases measure 19–38 μm (cf. 12–53 μm on pinnules above the **bfd**). Oval bases measure 38–65 μm by 27–46 μm and are rare in comparison with the larger ones occurring above **bfd** that measure 35–106 μm by 19–68 μm. Appendages whose basal dimensions are similar to, or matching the oval bases, and papillae, were not found.

Adaxial cuticular surfaces of "*O. subcuneata*" are astomatiferous, without trichomes, files, or papillae (e.g. Text-fig. 7G). Costal fields appear weakly to moderately differentiated from intercostal fields, where cells of the former are 26–195 μm long and 26–32 μm wide, and those of the latter are 26 μm × 65 μm. Anticlinal walls appear to be comparatively wavy.



Text-fig. 7. "*Odontopteris subcuneata*" 80-516-1, below **bfd**. **A.** Entire structure, HF-freed; arrow identifies detail in C.; **B.** Marginal trichomes (truncated). Slide 980-516-1/3; **C.** Abaxial epidermis peeled-off A. with files and sparse hair. Temporary slide; **D.** Abaxial epidermis (Ep) peeled-off C. with attached files (Fl) overlain by hair (H). Slide 980-516-1/2; **E.** Transparent file, double strands without noticeable segmentation. No chemical treatment. Slide 980-516-13; **F.** Abaxial cuticle of C., stomata, arrowed. CF – costal field. Slide 980-516-1/5; **G.** Adaxial cuticle. Slide 980-516-1/18a. E., F., and G. Nomarski phase contrast.

4 Concluding summary

The spectrochemical model of the *M. scheuchzeri* cuticle/compression involves a relatively high aliphatic content which explains the high resistance to the brutal oxidation treatment that after 12 d left in place an intact cuticle (see also GUPTA et al. 2007). In contrast, the aromatic content is comparatively low. In general, the aliphatic/aromatic signature is similar, but not the same, for other medullosalean cuticles we have investigated since 1995, which has implications for chemotaxonomy, as noted by LYONS et al. (1995) and D'ANGELO et al. (2012b).

Trichomes-files-hair have differing reaction rates in controlled *in vitro* oxidizing-neutralization chemistry. Applying our maceration protocol (CLEAL & ZODROW 1989), we observe that trichomes are the relatively most resistant, followed by hair and files. This is raising the following questions: What are the chemical differences buttressing these observations? And can the round bases, particularly the smallest, found on pinnules above **bfd**, exclusively be ascribed to trichomes?

Seen across the **bfd** there are differences in putative pinnate morphology, and in addition functional-group distributions. The question that arises is how to integrate these phenomena within the precincts of pteridophytic evolution? In this context, we quote WILSON (2005) that "The anatomy of some species of Medullosaceae supports certain aspects of ZIMMERMANN's telome theory." In particular, WILSON mentioned "... early stage foliar and cauline differentiation." We speculate at this juncture that our data point to a cauline-related *scheuchzeri*-petiole, differentiating it from the megaphyll, which if confirmed, opens new vistas for the study of pteridosperm-frond evolution. Arguments leading up to, and the comments relating to the telomic theory itself, hinge on the assumption that "*O. subcuneata*" was organically attached to the petiole. Present observations, i.e., common elements which include distribution of trichomes, round and oval bases (though smaller), hair, similar stomatal apparatuses, similar cellular topography (though less undulate and smaller measurements), and marginal pinnule bases, support the prevailing assumption for such an attachment.

Not finding hair on *M. scheuchzeri* compressions **still attached to the rock matrix** ought not to be equated with intrinsic lack of it (cf. BELL 1938, and CRIDLAND et al. 1963). However, hair impressions found on counterparts, irrespective of non-observation on compression, is authoritative evidence for its presence. Hence, the various neuropterid species from the Appalachian coalfields that are synonymized with *Neuropteris scheuchzeri* (DARRAH 1969), for example, require reinvestigation.

We hypothesize a secretory origin for hair which is supported by its distribution trend. Ultimately, however we believe, an organic connection with the pinnules must be demonstrated for hair to be considered a diagnostic parameter for *M. scheuchzeri*. KRINGS (2000) pointed out that individual secretory bodies on cuticles of certain Stephanian pteridosperms show up as round "black" features, which makes an interesting case checking for structure by optical cross-polarization analysis (crossed nicols) to account for the blackness on the cuticle. We have not found any round black features on our *M. scheuchzeri* slides, but wonder if secretory cells are necessary to explain the orientation and abundance of pinnule hair (see SCHABILION & REIHMAN 1985: "club cells"?).

So, specifically unresolved is the question if "hairy" *M. scheuchzeri* is conspecific with HOFFMANN's non-hairy *N. scheuchzeri* types, recalling that KIDSTON (1888) had emphasized hair as major taxonomic character for the species. Alternatively, do hairy and non-hairy *M. scheuchzeri* represent two taxa? Two ecotypes? And in general, can taxonomic parameters observed on compressions still adpressed on the rock matrix be trusted for providing efficient and unbiased morphological sampling attributes?

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