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Ervin L. Zodrow

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Résumé de l'article

Le *Macroneuropteris scheuchzeri* a été abondamment décrit et a été appelé de nombreux noms différents, en particulier dans la documentation européenne, car l'espèce a été établie en 1699. Il reste encore à documenter une vaste part de la nature de cet arbre arborescent-médullosaléen, c.-à-d. la fructification, le tronc, les racines et l'architecture des frondes, mais on connaît bien son feuillage hétérophylle. Il est possible, en se basant sur les grandes collections de macrofossiles du terrain houiller pennsylvanien de Sydney, Nouvelle-Écosse, Canada, de présenter un aperçu de la nature foliaire diversifiée de ce remarquable arbre médullosaléen. Des hypothèses sont avancées sur la façon dont les nombreuses formes foliaires s'insèrent dans la fronde bipennée de Laveine et Brousmiche (1982).

# Foliar forms of *Macroneuropteris scheuchzeri* (Pennsylvanian, Sydney Coalfield, Nova Scotia, Canada)

ERWIN L. ZODROW

Department of Geology, University College of Cape Breton, Sydney, Nova Scotia, Canada B1P 6L2 <erwin\_zodrow@uccb.ca>

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## ABSTRACT

*Macroneuropteris scheuchzeri* has been extensively figured and called by many different names, particularly in the European literature, since the species was erected in 1699. Much of the nature of this arborescent-medullosalean tree still remains to be documented, i.e., fructification, trunk, root, and frond architecture, but its heterophyllous foliage is well known. Based on the large macrofossil collections from the Pennsylvanian Sydney Coalfield, Nova Scotia, Canada, it is possible to present an overall view of the diverse foliar nature of this remarkable medullosalean tree. Suggestions are offered as to how the many foliar forms fit into the bipinnate frond of Laveine and Brousmiche (1982).

## RÉSUMÉ

Le *Macroneuropteris scheuchzeri* a été abondamment décrit et a été appelé de nombreux noms différents, en particulier dans la documentation européenne, car l'espèce a été établie en 1699. Il reste encore à documenter une vaste part de la nature de cet arbre arborescent-médullosaléen, c.-à-d. la fructification, le tronc, les racines et l'architecture des frondes, mais on connaît bien son feuillage hétérophylle. Il est possible, en se basant sur les grandes collections de macrofossiles du terrain houiller pennsylvanien de Sydney, Nouvelle-Écosse, Canada, de présenter un aperçu de la nature foliaire diversifiée de ce remarquable arbre médullosaléen. Des hypothèses sont avancées sur la façon dont les nombreuses formes foliaires s'insèrent dans la fronde bipennée de Laveine et Brousmiche (1982).

## INTRODUCTION

Presented are different foliar forms of the concept of the morphospecies *Macroneuropteris scheuchzeri* Cleal, Shute and Zodrow, 1990, since the species was erected by Luyd (1669) under the name of *Phyllites mineralis* (see Scheuchzer 1709, 1723, pl. X, p. 48; Laveine 1967; Fischer 1973; Andrews 1980). One hundred years later, after the death of the Swiss naturalist Scheuchzer in 1733, Hoffmann (in Keferstein 1826) renamed *P. mineralis* as *Neuropteris scheuchzeri* to honour the Swiss naturalist.

Bunbury (1847) was the first to recognize *N. scheuchzeri* from North America amongst fossil collections shipped to him by Richard Brown Sr. of Sydney Mines, Cape Breton Island, Nova Scotia, Canada. Bunbury's hand-written records of 1850: Part 1, Ferns and Lycophytes, preserved at Cambridge University, show unequivocally that the fossils originated from the Sydney Coalfield, likely from the Sydney Mines strata that today are considered Westphalian D (Cleal *et al.* 2003). In retroview, Bunbury's recognition of *N. scheuchzeri* was not by direct morphological comparison, but by synonymous equivalency: he compared his new variety that he named *Neuropteris cordata* var. *angustifolia* (1847) with Brongniart's species *Neuropteris angustifolia* (1831, p. 231, pl. 64, figs. 3 and 4). Then with considerable insight Bunbury (1847, p. 424) emphatically stated that Brongniart's species of *N. angustifo-*

*lia* and *N. acutifolia*, and Hoffmann's species of *N. scheuchzeri* were conspecific. This taxonomic claim is still maintained today (Laveine 1967; present paper). Bunbury's new species of *Odontopteris subcuneata* (1847, p. 427, pl. XXIII, figs. 1A,B) was recognized by Bell (1938) as a synonym of *N. scheuchzeri* which is confirmed by taxonomic studies by Laveine (1967), Kotasowa (1973), and the present paper.

The concept of *N. scheuchzeri* was taxonomically refined by Cleal and Zodrow (1989) through epidermal work (see also Barthel 1961). Based on that work, Cleal *et al.* (1990) proposed changing the generic designation of *Neuropteris pro parte* to *Macroneuropteris* Cleal, Shute and Zodrow gen. nov. with *Macroneuropteris macrophylla* (Brongniart) (Cleal *et al.* 1990) as type species while still regarding the new combination *Macroneuropteris scheuchzeri* as a morphogenus.

*M. scheuchzeri* was also one of three medullosalean species whose biochemical make-up was probed, the results of which led to hypothesizing that pteridophylls in general can be separated and determined by their spectral characteristics (functional-carbon groups and certain ratios derived therefrom, and hydrocarbon compounds: see Lyons *et al.* 1995; Zodrow and Mastalerz 2000). In effect, this work introduced chemotaxonomic utility into Carboniferous plant determinations, and it is currently extended to cordaites as well, with encouraging results (Zodrow *et al.* 2003),

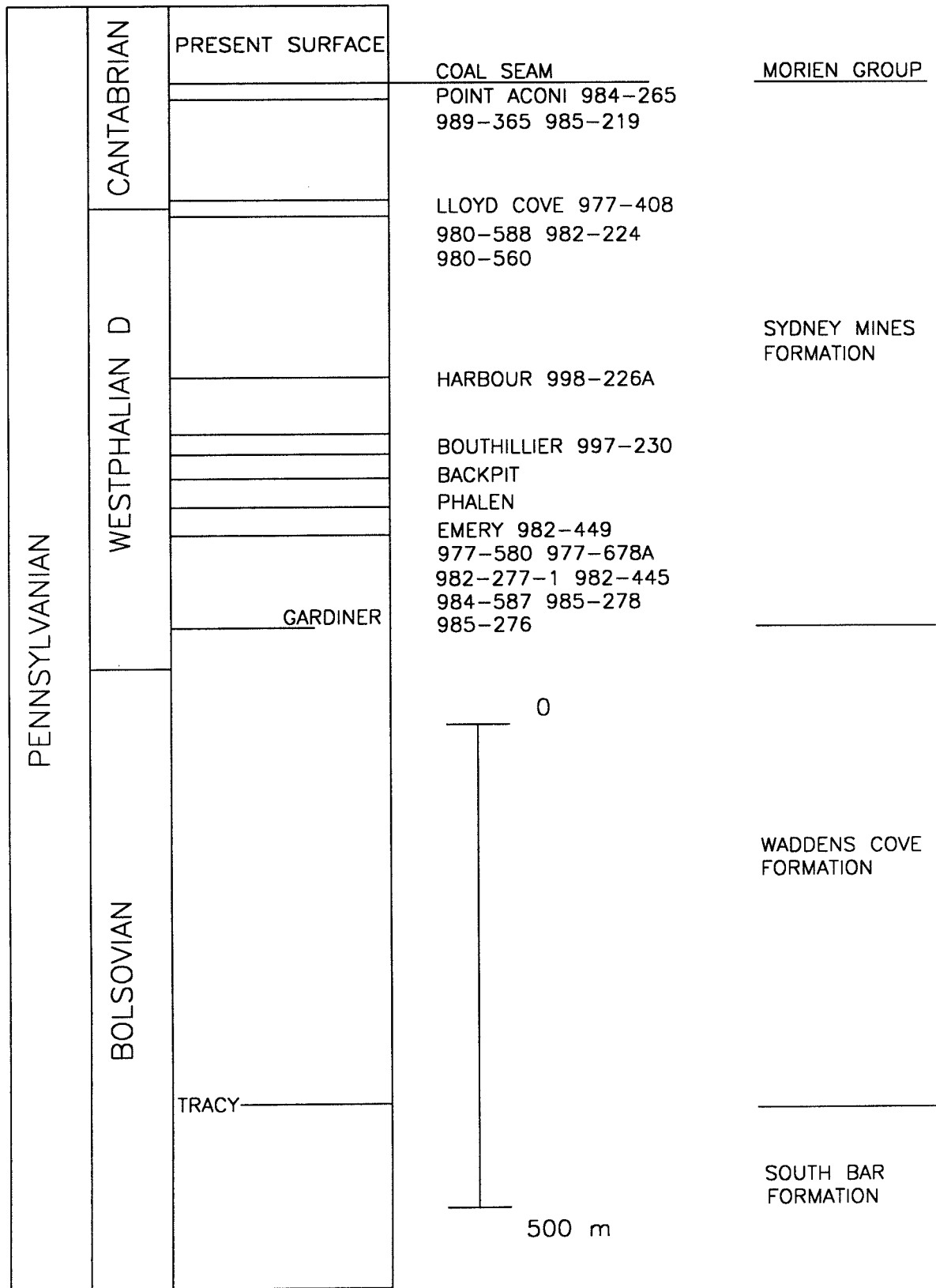


Fig 1 Stratigraphy of Sydney Coalfield, Morien Group, Nova Scotia, Canada, and co-ordinated positions of study specimens identified by accession number (e.g., 984-265) of the Nova Scotia Museum, Halifax.

## GEOLOGICAL SETTING: SYDNEY COALFIELD

The Carboniferous evolution of Nova Scotia was most recently summarized by Calder (1998). Sydney Basin is part of the Maritimes Basin that encompassed nearly all of the Canadian Atlantic Provinces of New Brunswick, Nova Scotia, Prince Edward Island, and southwestern Newfoundland (Calder 1998, fig. 2). Basin-fill sediments were deposited in distinct intervals that can be regionally correlated. During the Westphalian D and early Cantabrian, basin subsidence diminished and widespread coal-forest peats accumulated on near-coastal plains (Ryan *et al.* 1991; Gibling and Bird 1994; Calder 1998).

The ca. 2200 m of the Morien Group (Bell 1938) that com-

prise Sydney Coalfield (on-shore portion of the Sydney Basin) were recently subdivided into three formations (Boehner and Giles 1986): Sydney Mines, Waddens Cove and South Bar formations (Fig. 1), where the first-named formation contains the mineable coal measures of Sydney Coalfield.

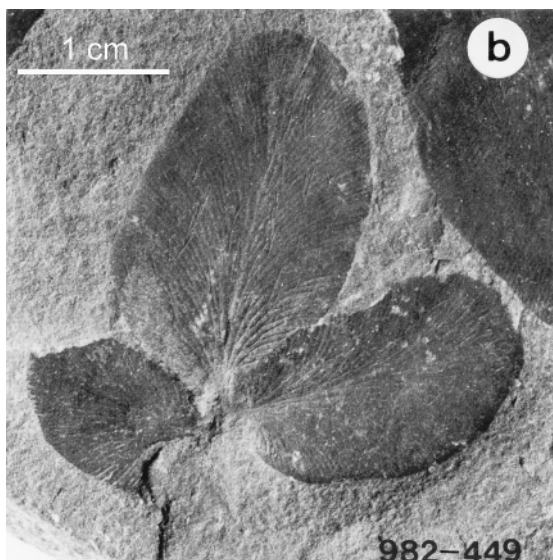
The biostratigraphy of the Morien Group was revised by Zодrow and Cleal (1985), and most recently by Cleal *et al.* (2003). This entailed relocating Bell's (1938) Westphalian D and "C" stage boundaries downwards, and at the same time intercalating the Cantabrian Stage at the Lloyd Cove (Zодrow 1985; see Fig. 1). Carboniferous nomenclature proposed by Menning *et al.* (1991) is followed in this paper.

## SAMPLE DEPOSITORY

The 17 figured specimens from the Sydney Mines Formation, represent critical selections to illustrate diverse forms from a total of ca. 300 *M. scheuchzeri* specimens collected from the entire Morien Group. These are an integral part of the documented ca. 15000 macrofloral specimens retrieved by the author from the Sydney Coalfield since 1973.



**Fig 2** (left & above) Typical *M. scheuchzeri* foliage. a) Upper surface of a broadly-shaped lanceolate pinnule, round apically, with cordate base. 977-408, Lloyd Cove Seam. b) Illustrating copious, epicuticular hair growth on a pinnule; mid section is shown. 997-230; Bouthilier Seam.



These collections are housed at the University College of Cape Breton, Sydney, Nova Scotia, Canada, with the author being the curator.

### SAMPLE MATERIAL AND METHODS

The study material is stratigraphically documented in Fig. 1, bearing accession numbers of the Nova Scotia Museum, e.g., 977(GF)-408. The fossils are preserved by compression in silty-shale and shale rocks, and invariably yielded intact cuticles (Cleal and Zodrow 1989; Lyons *et al.* 1995). A recent survey (unpublished data, January 2003) demonstrated that 45 specimens, representing the entire Morien Group (Fig. 1), all tested positive for intact cuticles. From a 6-cm long “ultimate pinna” of the “*Odontopteris subcuneata*” form of *M. scheuchzeri*, 14 slide-mounted preparations of adaxial and abaxial cuticles (unpublished data, 1991) document the epidermis from different positions along the ultimate rachis.

Chemical methods for extracting the cuticles are detailed in Cleal and Zodrow (1989).

### HETEROPHYLLOUS NATURE OF *M. SCHEUCHZERI*

#### Specific definition

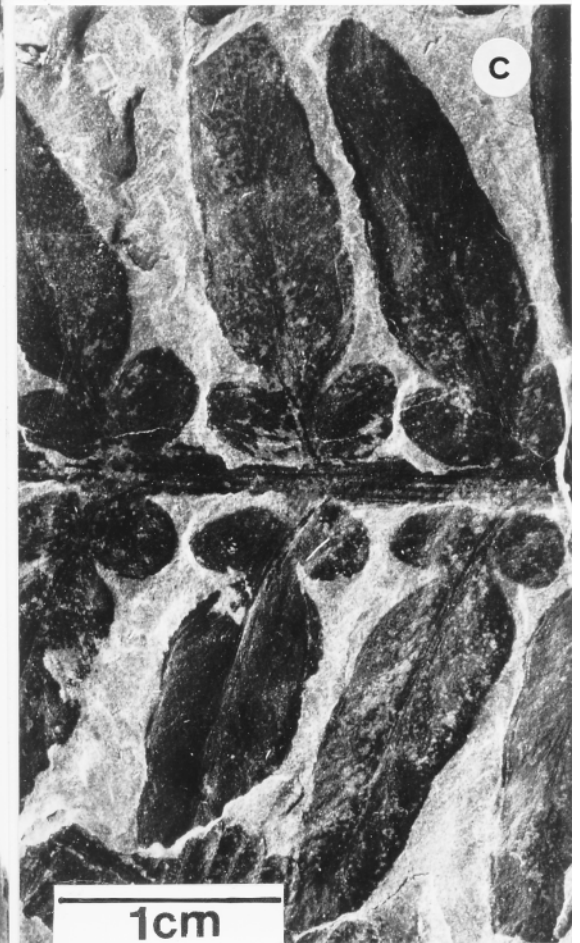
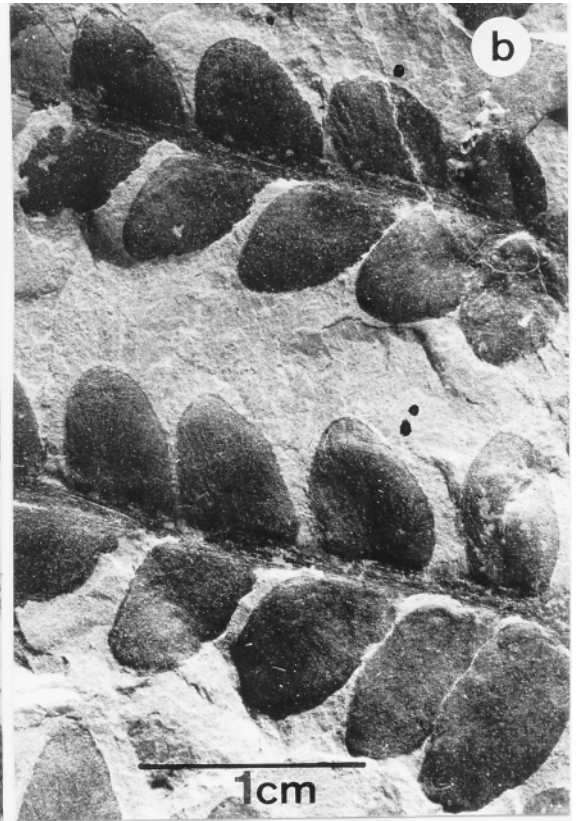
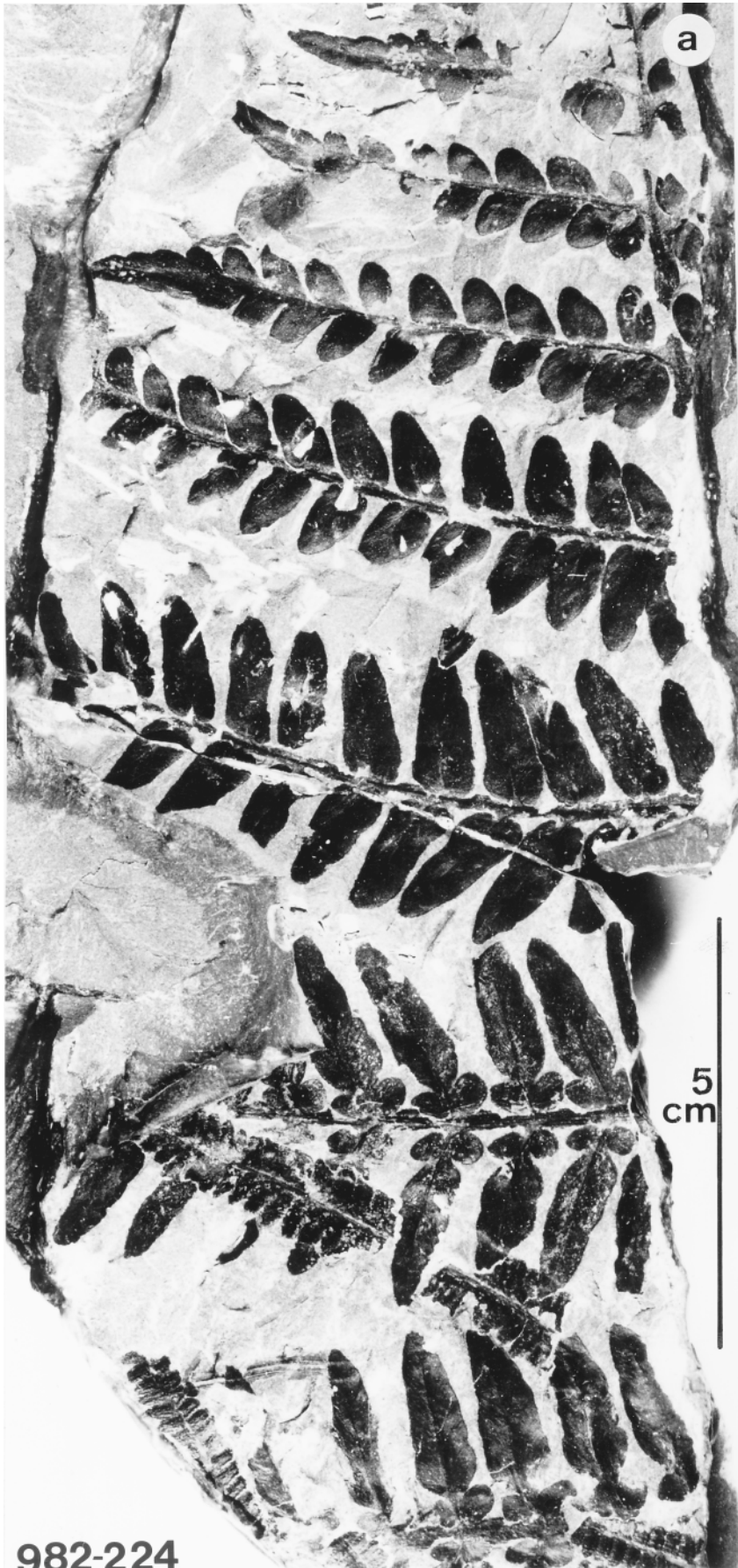
*M. scheuchzeri* (Order Trigonocarpales Meyen, Satellite morphogenus *Macroneuropteris*) is defined by gross morphology and epidermal characteristics (Cleal *et al.* 1990). The latter include large, irregularly shaped polygonal cells, 220  $\mu\text{m}$  long and 60  $\mu\text{m}$  wide on the adaxial surface, and somewhat smaller cells on the abaxial surface that also shows brachyparacytic stomata (two subsidiary cells); trichomes bases are present on both surfaces (Cleal and Zodrow 1989, text-fig. 3; Cleal *et al.* 1990).

The frond is bipinnate and has a basal dichotomy (Laveine 1967; Laveine *et al.* 1977; Laveine and Brousseau 1982; Laveine *et al.* 1998). A comprehensive proposal for the recon-

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**Fig 3** (left) *M. scheuchzeri*, terminal pinnules. a) Elongate oval terminal, probably of the primary pinna (P1, see Fig. 7). 980-588, unnamed seam (ca. 8 m above the Lloyd Cove Seam). b) Broadly oval termini of an ultimate pinna (p2, see Fig. 7) on which epicuticular hair is plainly visible. 982-449, Emery Seam.

**Fig 4** (right) *M. scheuchzeri*, 982-224, unnamed Seam (ca. 8 m above the Lloyd Cove Seam). a) An exceptional specimen that shows great foliar heterophylly in one short, fragmentary frond section. b) Detail of the frond section that shows odontopteroid pinnule morphology. c) Detail of a trifoliate-pinnule morphology (two orbicular pinnules basal to a larger pinnule).



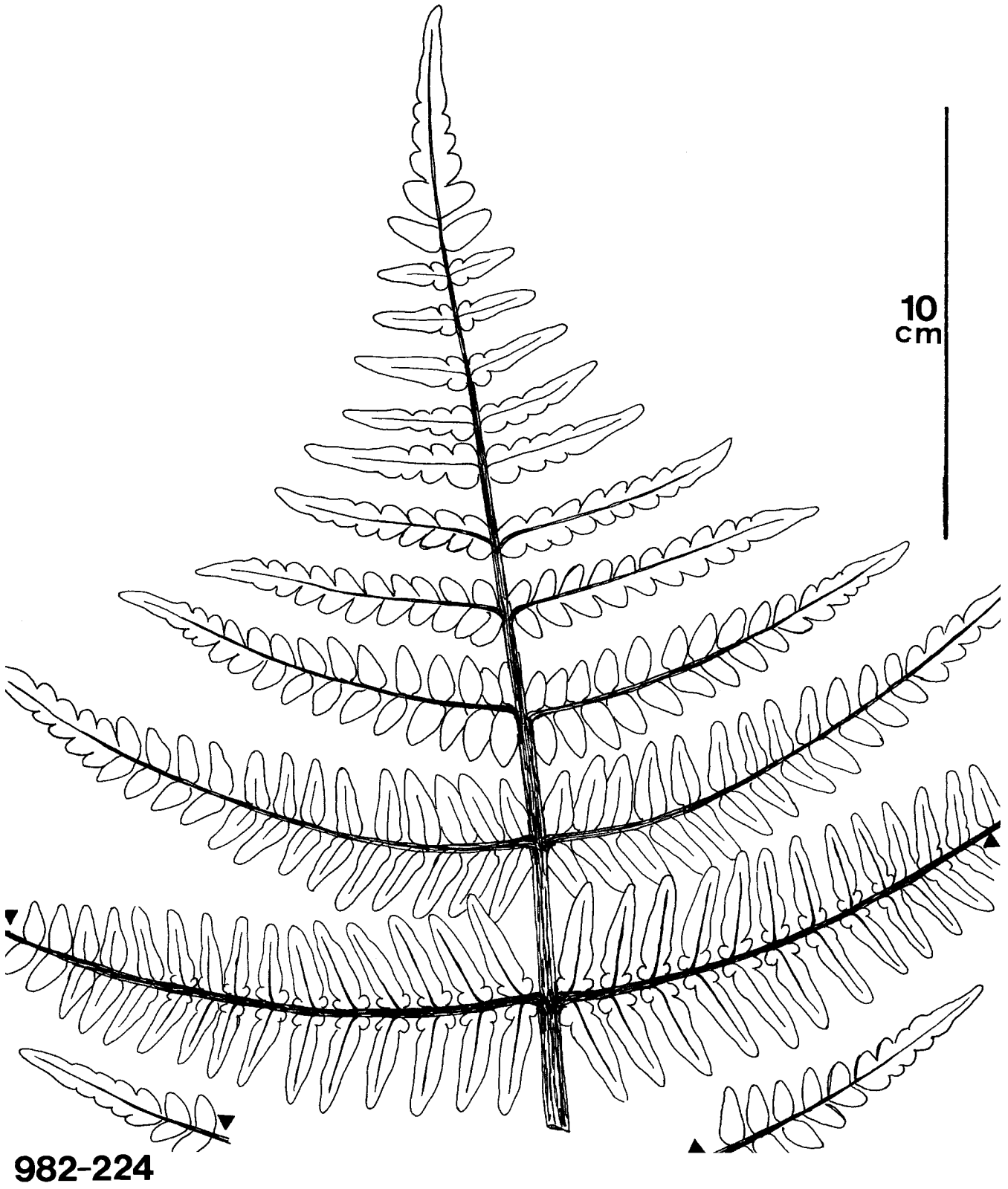


Fig 5 Reconstructed frond segment of Figure 4, as tip, based on self similarity for that part.

struction of the plant *M. scheuchzeri* is forthcoming (pers. comm. J.-P. Laveine, February, 2003).

### Distribution

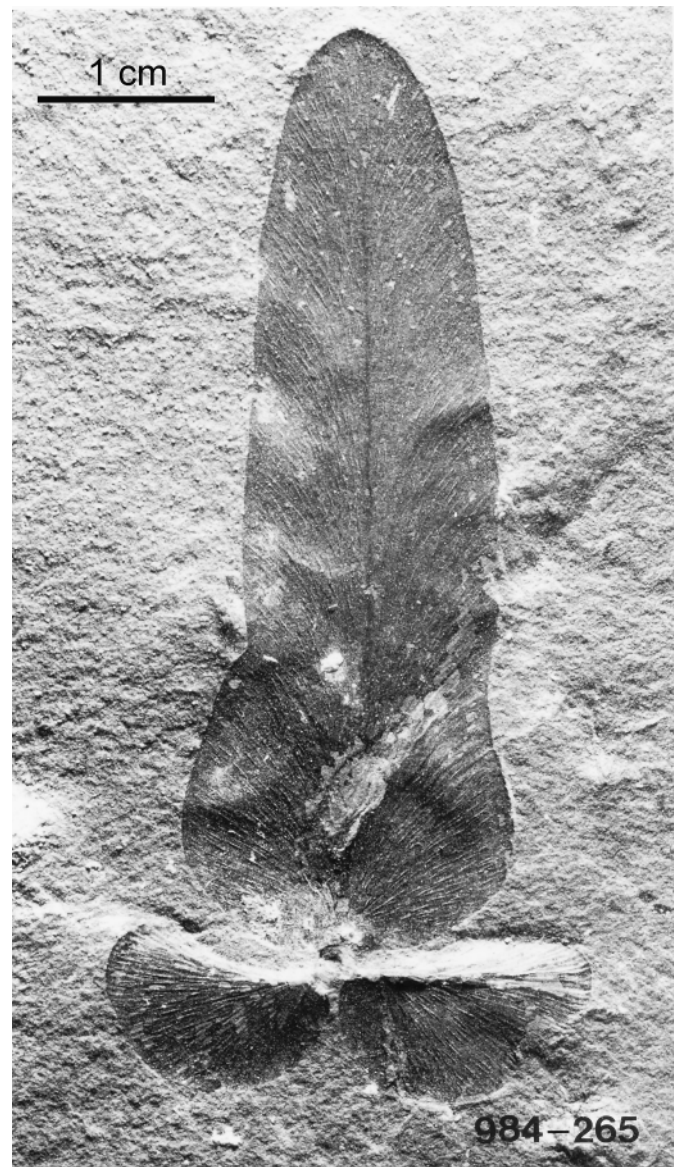
*M. scheuchzeri* is one of the very few azonal macrofossil plants in the Morien Group, as it ranges from the lowest strata at the Shoemaker Seam (Bolsovian) to the highest strata at the Point Aconi Seam (lower Cantabrian), see Bell (1938, Fig. 1). This is similar to the range in the Cantabrian in NW Spain (Wagner 1983, fig. 4). This contrasts with the distribution of the species in the Late Carboniferous Period of West and Central Europe, where it ranges from the Duckmantian to the top of the Westphalian D as an index for the Stephanian (summary: Josten 1991). In general, the species has a global distribution over palaeoequatorial tropical, Late Carboniferous, coal forests, and spans a time interval conservatively estimated to be at least 15 Ma, or three Westphalian Stages.

### Palaeobiology

To date, organically attached male and female fructifications of *M. scheuchzeri* have not been documented. From Sydney Coalfield, one pteridosperm seed attached to foliage of *Neuropteris flexuosa* is known (Zodrow and McCandlish 1980) which emphasizes the rarity of attached female organs to determinable foliage. However, Bell (1938) thought that the large, detached seeds of *Trigonocarpus* (*Schizospermum*) *noeggerati* Sternberg could represent ovules of the species. Ovules of this type are ubiquitous and are found throughout the strata of the Sydney Coalfield (see Zodrow 2002, Fig. 16c), and commonly in physical association with *M. scheuchzeri* foliage. Laveine (1967, fig 1d) suggested that *Codonothecca caduca* Sellard is the male organ.

### Descriptions of foliar forms from Sydney Coalfield

In its most typical form in Sydney Coalfield, *M. scheuchzeri* (Fig. 2a) has large, lanceolate pinnules that reach a length of 12 cm or more and a width of 2.5 to 3.0 cm, rarely 5 cm, with a slightly round or acuminate apex. These measurements are larger than West and Central European measurements of 2 to 9 cm length and 0.6 to 2.5 cm width (summary: Josten 1991, p. 331). The pinnule base is cordate, or stalked, and the margin entire. The midvein is prominent and extends for most of the pinnule length. Venation is dense; lateral veins fork 3 to 5 times, and broadly arch to reach the lateral margin at an oblique angle, 70 to 80 degrees. Over most of the pinnule, abundant epicuticular hair (Fig. 2b) is present that can reach a maximum length of 2 mm. Hair is cross-aligned to the venation pattern, imparting a prominent pseudo-hexagonal pattern, and presents an important taxonomic feature (e.g., Bunbury 1847, pl. XXI; Laveine 1967; Kotasowa 1973; Cleal and Zodrow 1989; Josten 1991; present paper) for differentiating *M. scheuchzeri*



**Fig 6** *M. scheuchzeri*. A hairy trifoliate pinnule. 984-265; Point Aconi Seam.

from all of the other macroneuropterid species (Cleal *et al.* 1990; Josten 1991).

*M. scheuchzeri* bears large terminal pinnules that reach a length of over 6 cm, a width of 2.5 cm, are elongate (Fig. 3a), or broadly oval (Fig. 3b), and are typically profusely covered with long, epicuticular hair.

Based on the aforementioned gross morphological features, typical *M. scheuchzeri* is a most-easily recognizable species in the Late Carboniferous, worldwide.

Figures 4 and 5 illustrate a specimen of great interest in this discussion because it shows considerable morphological changes over its axial length of 30 cm. Its near-tip section is odontopteroid in form (Fig. 4a, detail 4b). These pinnules are attached to a rachis by their entire base, lateral veins are parallel to each other (no midvein is present), and they originate directly from the rachis. Neuropteroid morphology follows



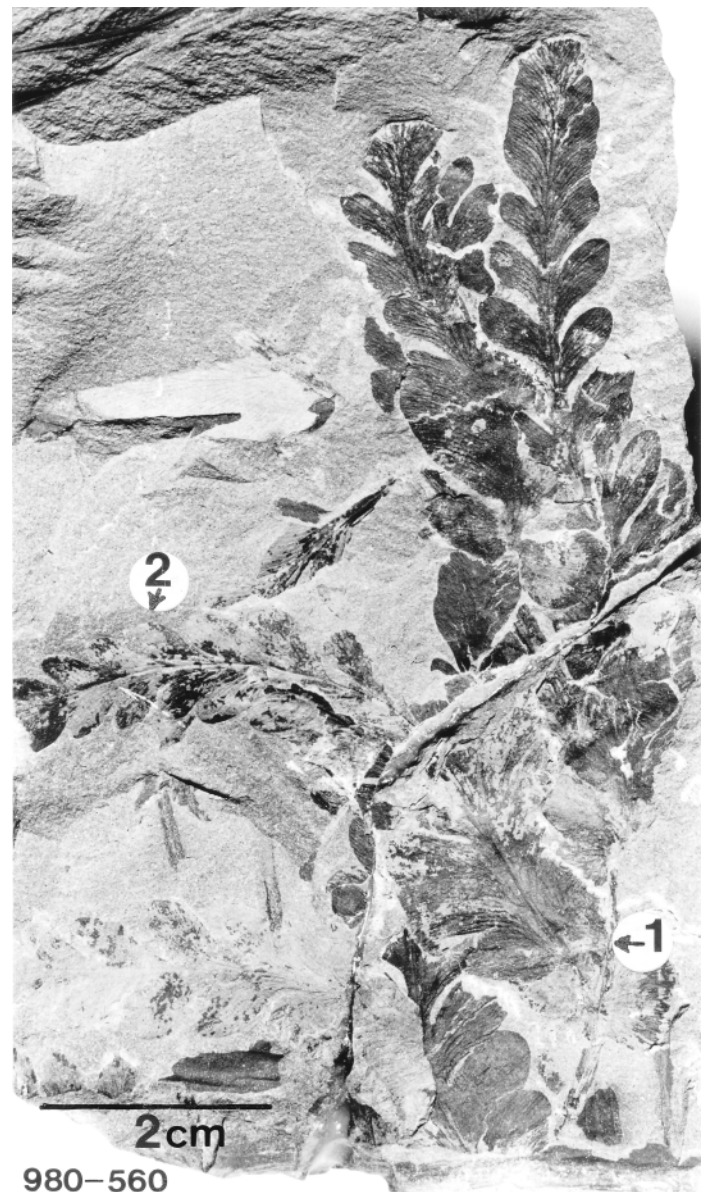


Fig 7 *M. scheuchzeri*. Part of the frond with only trifoliate pinnules. The specimen shows intercalated pinnules (arrowed), but they are difficult to see on the photograph. 998-226A; Quarry Seam, just below the Harbour Seam.

and pinnules have a cordate base, and are stalked-attached to a rachis. This morphology changes to the trifoliate form (Fig. 4c), with some transitional elements. In general, trifoliate pinnules are composed of a main pinnule of various lengths to which are basally attached two symmetrically-placed, smaller, orbicular pinnules, maximally 3 cm in length. Hair is absent in these pinnules, as confirmed in part by cuticular analysis. However, cuticular analysis of material illustrated in Fig. 4 reveals a stomatal structure, distribution of stomata, and shape of epidermal cells that are similar to those of *M. scheuchzeri* (see Cleal and Zodrow 1989, pl. 106). It is observed that trifoliate pinnules that reach a minimum length of 4 cm grew abundant hair, including on the orbiculars (Fig. 6; see also Bunbury 1847). Unless it can be demonstrated that the morphologies in Fig. 5 are reproducible over the distal parts of the frond, the usual assumption of self similarity (Heggie and Zodrow 1994) is called into question for *M. scheuchzeri*.

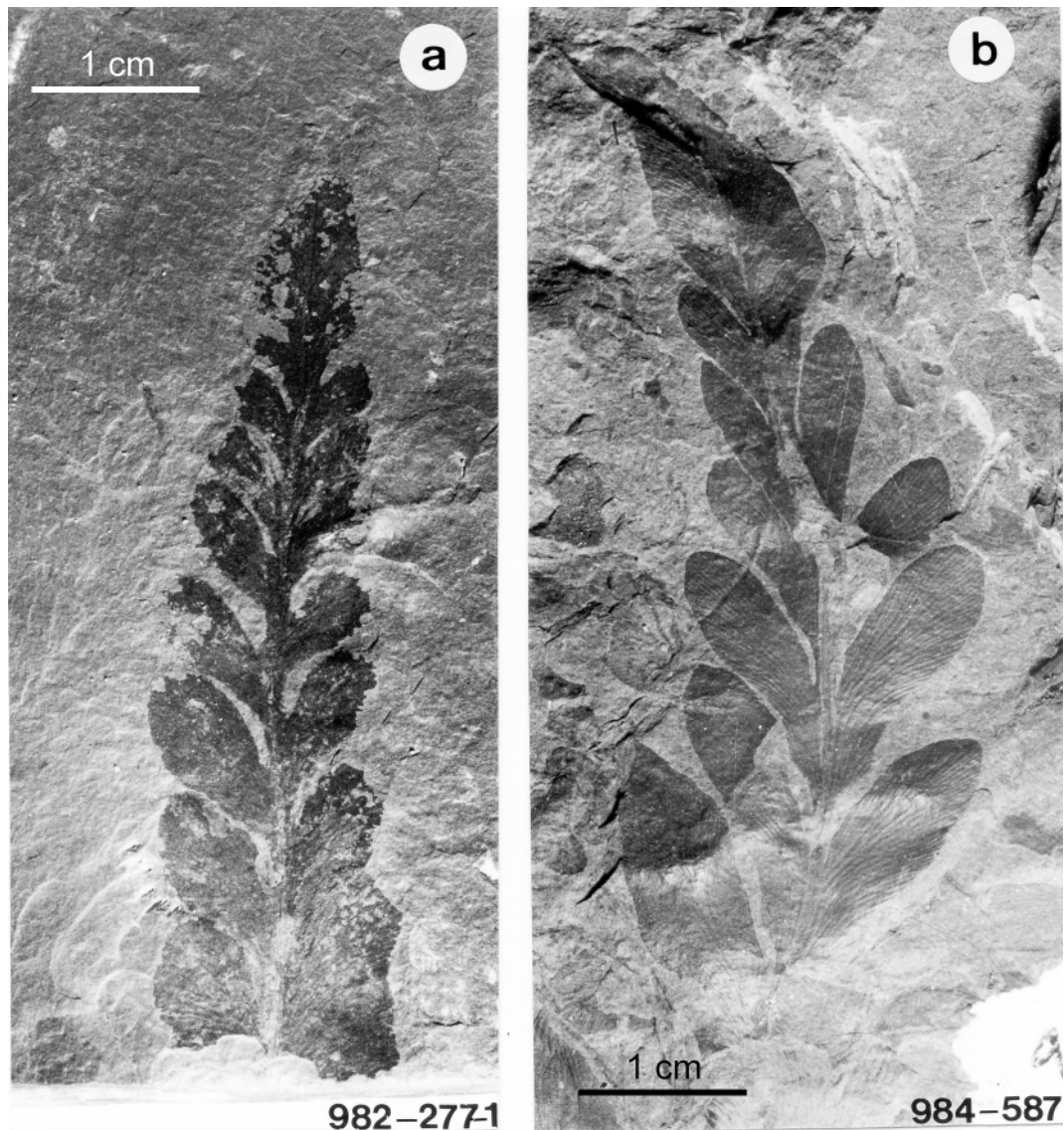
The largest specimen of *M. scheuchzeri* (Fig. 7) from the Canadian Pennsylvanian originated from the historical coal-mining town of Sydney Mines, Sydney Coalfield. The primary rachis is preserved for a length of 22 cm, and is 1 cm wide with longitudinal striations that represent medullolean sclerenchymatous fibres (imparting strength to the frond structure). The rachis also shows intercalated pinnules, as is typical for *M. scheuchzeri* (Bertrand 1930, pl. IX). Oppositely-placed ultimate rachides, 0.5 cm wide and striated, are preserved for a length of 17 cm, and are spaced ca. 11 cm apart; terminal pinnules are eroded. The fragmentary frond only bears trifoliate pinnules that are up to 6.5 cm long and 1.5 cm wide, and axially spaced at ca. 2 cm intervals. Abundant hair is present on all of the pinnules and orbiculars. This specimen fits Bunbury's (1847, pl. XXI, figs. 1A and 1B) concept of *N. cordata* var. *angustifolia*. The largest *M. scheuchzeri* specimen known with such morphology is 1 meter long, 50 cm wide, and is figured by Bertrand (1930, pl. IX).

Apart from these forms, foliage of the *M. scheuchzeri* frond is furthermore characterized by laciniate, or deeply cut leaves that additionally show odontopteroid morphology (but it is not true odontopterid!). Bunbury (1847, pl. XXIII, fig. 1A, 1B) figured "*Odontopteris subcuneata*" from Sydney Mines, but he did not mention the presence of epicuticular hair on the holotype [that Bell in 1938 had recognized as being a synonym of *M. scheuchzeri*]. However, epidermal features of the 6-cm specimen of Bunbury's laciniate species include irregular, cluster-distributed trichomal bases on adaxial and abaxial surfaces, and on intercostal and costal fields. Epidermal cells are also similar in shape and size to those described by Cleal and Zodrow (1989) for *M. scheuchzeri*. Fig. 8 is one example of laciniate "*O. subcuneata*" that at the same time is the contiguous apical part of an otherwise typical *M. scheuchzeri* complete with epicuticular hair. This direct evidence confirms conspecificity between Bunbury's "*O. subcuneata*" and Hoffmann's species *M. scheuchzeri*, a proposition which Bell (1938) assumed all along.



**Fig 8** "*Odontopteris subcuneata*", *M. scheuchzeri*. Basal part (arrowed "1") is typical *M. scheuchzeri* with epicuticular hair, whereas the laciniate apex arrowed "2") is typical "*O. subcuneata*" without hair. 980-560; Lloyd Cove Seam.

Detached "*O. subcuneata*" forms are shown in Fig. 9a, b. A deeply cut laciniate form, different from Bunbury's "*O. subcuneata*", is shown in Fig. 10a, whereas Fig. 10b compares with pl. XII of Bertrand (1930). Fig. 11a illustrates yet another atypical foliar form, haired, by its comparatively narrow, long and linear pinnule, without basal orbicular pinnules, and with a conspicuous acuminate tip. Smaller foliar versions of this form are shown in Figure 11b. This form is figured as *Neuropteris angustifolia* by Brongniart (1831, pl. 64, figs. 3 and 4), or as *N. cordata* var. *angustifolia* by Bunbury (1847). Fig. 12 docu-



**Fig 9** “*Odontopteris subcuneata*”. Emery Seam. a) Typical apical segment. 982-277-1. b) This specimen shows larger subcuneate pinnules. 984-587.

ments a rather broad and short pinnule (compare with typical *M. scheuchzeri*, Fig. 2a). Transitional forms between being lacinate and typical pinnules are documented in Fig. 13 a,b; the lower parts of these leaflets are haired, whereas the apical parts are not.

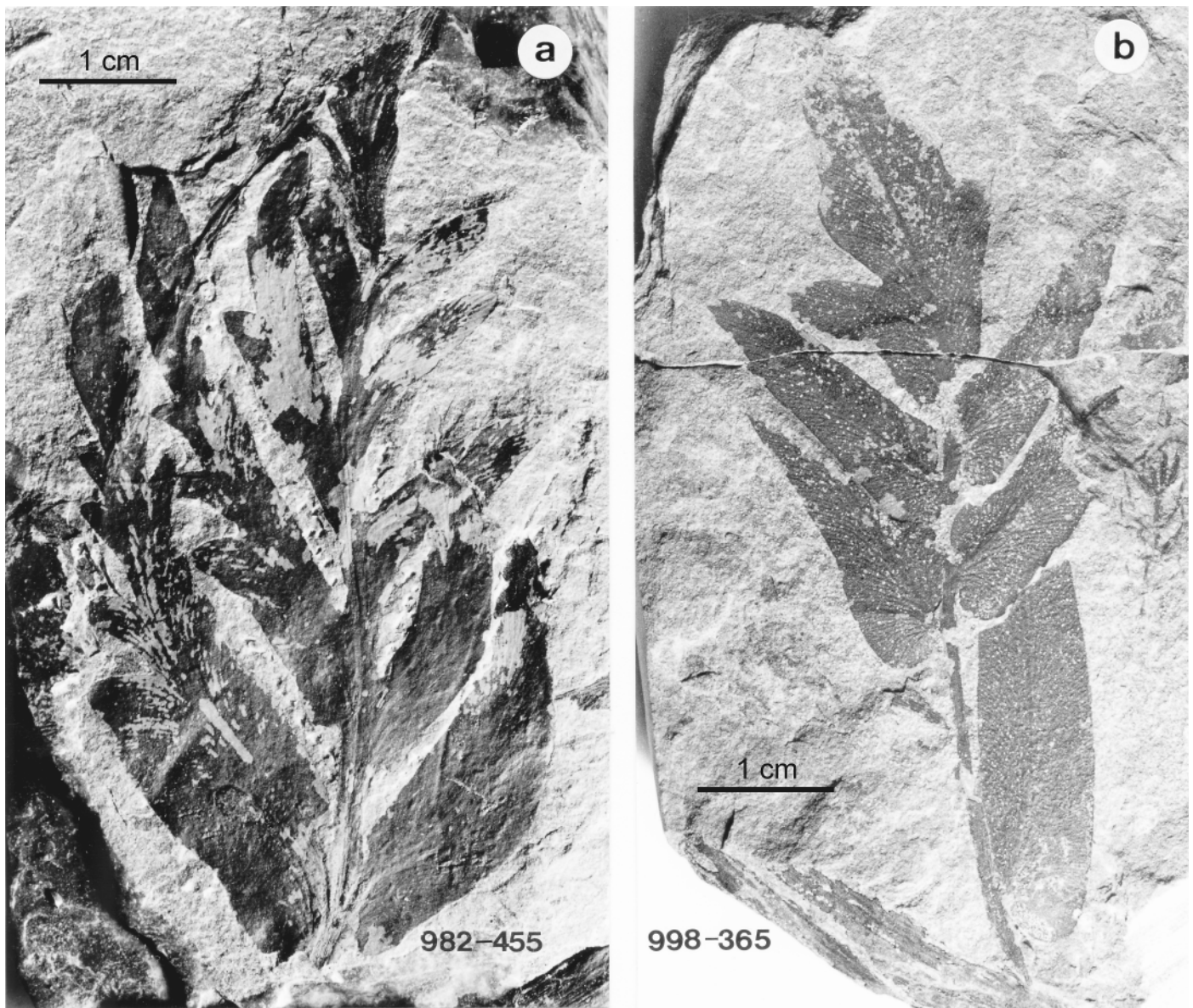
#### Palaeoecological aspects

*M. scheuchzeri* has all of the characteristics of a water-retaining, drought-adapted, arborescent pteridospermous plant which includes having a very thick cuticle, densely distributed trichomes and sunken stomata (observed on the cuticle; Cleal and Zodrow 1989), and epicuticular hair. Its larger leaf size presumably dissipated heat at a slower rate (summary: Wing and DiMichele 1992).

#### Foliar forms in the frond structure of *M. scheuchzeri*

The rachial architecture of the *M. scheuchzeri* frond is demonstrably bipinnate (Laveine and Brousmiche 1982), with intercalated pinnate structures (Bertrand 1930; this paper). The frond furthermore possesses the basal dichotomy of the neuropteroid-frond structure, and an apical bifurcation (Laveine and Brousmiche 1982, pl. 1, fig. 3; Laveine et al. 1998). Laveine (1967, 1989, p. 44) interpreted the frond as being retarded structurally, i.e., the typical or trifoliate pinnule is actually homologous to an imparipterid ultimate pinna that normally is composed of a number of lateral pinnules with one definite terminal pinnule.

Bertrand’s largest specimen (1930, pl. IX) shows remark-

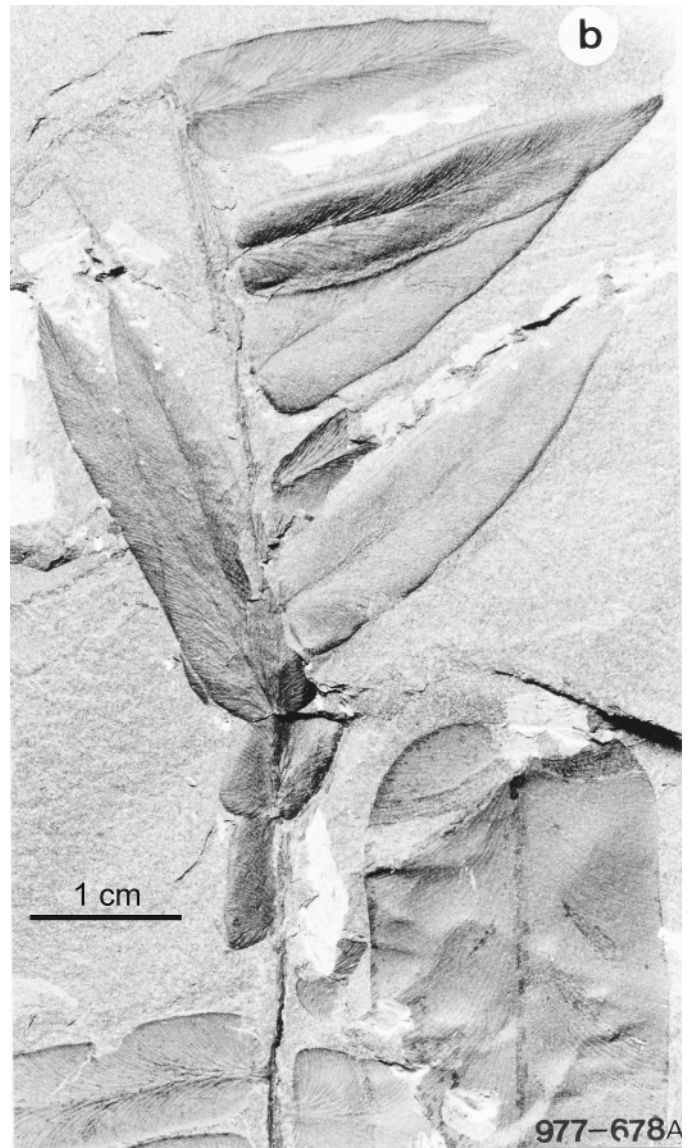


**Fig 10** *M. scheuchzeri*. a) Pinnate heterophylly, where the left side of the rachis shows lacinate pinnules. 982-455. Emery Seam. b) Acuminate pinnules near the terminal of a pinnate structure. 998-365, Pt Aconi Seam.

able invariant-pinnule morphology in the proximal part of the one-meter long primary rachis. By contrast, Figs. 4 and 5 show remarkable variability in proximal-pinnule morphology in a 30-cm long specimen to suggest that it originated from the distal part of the bipinnate frond where morphology changes very rapidly. It is material schematized in Fig. 5 that would fit into a position above an apical bifurcation of a neuropteroid frond (see also Zодrow and Cleal 1988) which does not bear intercalated pinnate structures and whose terminal pinnules are comparatively smaller (compare Fig. 3a). Figure 7 would fit into the more central part of the bipinnate frond.

What is still poorly understood is the position of the many illustrated lacinate pinnule forms within the frond structure of *M. scheuchzeri*. In the first instance, Sydney Coalfield is characterized by an abundance of atypical, lacinate forms,

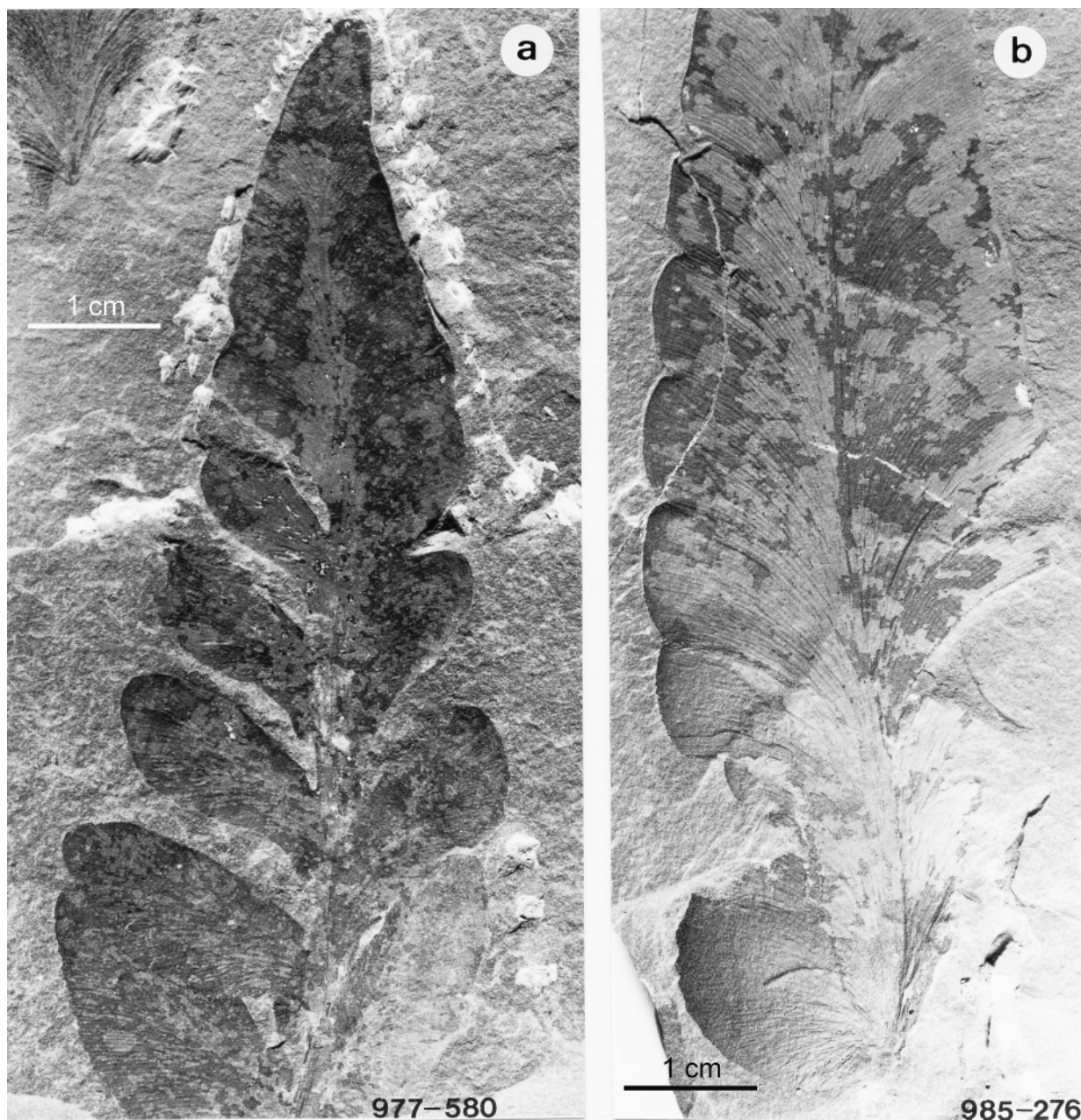
originating particularly from the stratigraphical level of the Emery Seam (Fig.1), mid-Westphalian D. At an equivalent stratigraphical horizon in the Saarland, Germany (Cleal and Zодrow 1989; Josten 1991), these forms are absent, nor do they occur to such a level of abundance in the French Late Carboniferous (Laveine 1967; 1989). Either the significance of the differences has never been properly understood, or it could simply be sample bias! Laveine (1967) explained that these lacinate pinnule forms were attached near the base of the frond, below the frond dichotomy (such attachments are normal for medullosalean fronds). However, if such is the case, the evidence presented in this paper points to highly variable forms occupying the segment below the main dichotomy of the frond. An alternative explanation would be that some of these forms are actually intercalated on a primary pinna rachis.



**Fig 11** (above) *M. scheuchzeri*, narrow, linear, apically pointed pinnules. a) Haired pinnule with linear lateral margins (angustiformis type). 985-219, Pt. Aconi Seam. b) Attached linear pinnules. A typical *M. scheuchzeri* pinnule is seen in the lower right-hand corner. 977-678A, Emery Seam.



**Fig 12** (left) *M. scheuchzeri*. A broad foliar form. 985-278, Emery Seam.



**Fig 13** *M. scheuchzeri*, Emery Seam, transitional foliar forms. a) Atypically large lacinate pinnules, basal part is richly haired. 977-580. b) Pinnule with lobate lateral margins, basal part is haired. 985-276.

### CONCLUSION

*Macroneuropteris scheuchzeri*, taken as a whole-plant species of a pteridospermous tree, is a remarkable species from several perspectives:

- (1) the frond is bipinnate which differs from all other dichotomizing medullosalean fronds that are, by contrast, tripinnate
- (2) foliar diversity is considerable, as recognized already by Bunbury when in 1847 he stated that the *N.*

*scheuchzeri* plant well deserves to be called heterophylla. Subsequently, about 25 synonyms (see Laveine 1967) underpin Bunbury's insight

- (3) hair grew on lacinate forms such as "*Odontopteris subcuneata*", although much more sparingly than on typical leaves, i.e., it's a developmental feature
- (4) hair that is so abundantly present on the compressions of typical *M. scheuchzeri* is commonly obliterated by the maceration process, leaving bases as evidence

- (5) apparently the usual assumption of self similarity is called into question for *M. scheuchzeri* which would be a remarkable exception
- (6) only *Macroneuropteris macrophylla* (Brongniart) approaches the size of *M. scheuchzeri* that undoubtedly has one of the largest “pinnule” structure of arborescent medullosalean plants of the Late Carboniferous Period
- (7) future collections will be required to identify the as yet unknown reproductive organs, trunk and root structures of *M. scheuchzeri*, and
- (8) *M. scheuchzeri* has a disparate vertical distribution in the Canadian Pennsylvanian, compared with the Spanish and Central and West European Late Carboniferous Period.

#### ACKNOWLEDGEMENTS

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*Editorial responsibility: Ron K. Pickerill*



