

Alethopteris and Neuralethopteris from the lower Westphalian (Middle Pennsylvanian) of Nova Scotia and New Brunswick, Maritime Provinces, Canada

Carmen Álvarez-Vázquez

Volume 56, 2020

URI : <https://id.erudit.org/iderudit/1069888ar>
DOI : <https://doi.org/10.4138/atlgeol.2020.005>

[Aller au sommaire du numéro](#)

Éditeur(s)

Atlantic Geoscience Society

ISSN

0843-5561 (imprimé)
1718-7885 (numérique)

[Découvrir la revue](#)

Citer cet article

Álvarez-Vázquez, C. (2020). Alethopteris and Neuralethopteris from the lower Westphalian (Middle Pennsylvanian) of Nova Scotia and New Brunswick, Maritime Provinces, Canada. *Atlantic Geology*, 56, 111–145.
<https://doi.org/10.4138/atlgeol.2020.005>

Résumé de l'article

A systematic revision of Alethopteris and Neuralethopteris from upper Namurian and lower Westphalian (Middle Pennsylvanian) strata of Nova Scotia and New Brunswick, eastern Canada, has demonstrated the presence of eight species: Alethopteris bertrandii, Alethopteris decurrents, Alethopteris cf. havlena, Alethopteris urophylla, Alethopteris cf. valida, Neuralethopteris pocahontas, Neuralethopteris schlehanii and Neuralethopteris smithsii. Restudy of the Canadian material has led to new illustrations, observations and refined descriptions of these species. Detailed synonymies focus on records from Canada and the United States. As with other groups reviewed in earlier articles in this series, it is clear that insufficient attention has been paid to material deposited in Canadian institutions in the European literature. The present study emphasizes the similarity of the North American flora with that of western Europe, especially through the synonymies.

Alethopteris and *Neuralethopteris* from the lower Westphalian (Middle Pennsylvanian) of Nova Scotia and New Brunswick, Maritime Provinces, Canada

CARMEN ÁLVAREZ-VÁZQUEZ

Centro Paleobotánico, Real Jardín Botánico de Córdoba, Avenida de Linneo, s/n, 14004 Córdoba, Spain
paleo.calvarez@jardinbotanicodecordoba.com

Date received: 19 January 2020 | Date accepted: 24 March 2020

ABSTRACT

A systematic revision of *Alethopteris* and *Neuralethopteris* from upper Namurian and lower Westphalian (Middle Pennsylvanian) strata of Nova Scotia and New Brunswick, eastern Canada, has demonstrated the presence of eight species: *Alethopteris bertrandii*, *Alethopteris decurrents*, *Alethopteris cf. havlenae*, *Alethopteris urophylla*, *Alethopteris cf. valida*, *Neuralethopteris pocahontas*, *Neuralethopteris schlehanii* and *Neuralethopteris smithsii*. Restudy of the Canadian material has led to new illustrations, observations and refined descriptions of these species. Detailed synonymies focus on records from Canada and the United States. As with other groups reviewed in earlier articles in this series, it is clear that insufficient attention has been paid to material reposed in Canadian institutions in the European literature. The present study emphasizes the similarity of the North American flora with that of western Europe, especially through the synonymies.

RÉSUMÉ

Une révision systématique des *Alethopteris* et *Neuralethopteris* des strates du Namurien supérieur et du Westphalien inférieur (Pennsylvanien moyen) de la Nouvelle-Écosse et du Nouveau-Brunswick, dans l'est du Canada, a démontré la présence de huit espèces : *Alethopteris bertrandii*, *Alethopteris decurrents*, *Alethopteris cf. havlenae*, *Alethopteris urophylla*, *Alethopteris cf. valida*, *Neuralethopteris pocahontas*, *Neuralethopteris schlehanii* et *Neuralethopteris smithsii*. L'étude du matériel canadien a mené à de nouvelles illustrations, observations et descriptions raffinées de ces espèces. Les listes détaillées de synonymes se concentrent sur les documents du Canada et des États-Unis. Comme pour les autres groupes examinés dans les articles précédents de cette série, il est clair qu'une attention insuffisante a été accordée aux documents déposés dans les institutions canadiennes dans la littérature européenne. La présente étude souligne la similitude de la flore nord-américaine avec celle de l'Europe occidentale, notamment à travers les synonymies.

[Traduit par la redaction]

INTRODUCTION

This study is the ninth part of a revision of upper Namurian and lower Westphalian flora of Nova Scotia and New Brunswick, Maritime Provinces, Canada, begun in 2000 by R.H. Wagner at the request of John Utting, then of the Geological Survey of Canada. The reports began with a series of short papers (Wagner 2001, 2005a, b, 2008; Wagner and Álvarez-Vázquez 2008), and continued with more extensive contributions on lycopsids (Álvarez-Vázquez and Wagner 2014), the sphenopsid genera *Annularia* and *Asterophyllites* (Álvarez-Vázquez and Wagner 2017), and ferns (Álvarez-Vázquez 2019). The revision is based on examination of specimens and a critical re-evaluation of illustrations and

descriptions in publications by Dawson (1862, 1863, 1868, 1871), Matthew (1910), Stopes (1914) and Bell (1938, 1944, 1962, 1966).

The specimens involved are mainly preserved as impressions. Most are reposed in the collections of the Geological Survey of Canada (GSC) in Ottawa (catalogue numbers preceded by GSC). They are mostly fragmentary specimens collected in the course of field mapping by Geological Survey of Canada personnel at the end of the Nineteenth Century and the beginning of the Twentieth Century; the collection was initially studied by Walter A. Bell in the mid-Twentieth Century. Bell's (1944) memoir is very comprehensive, but his use of photographs commonly at natural size makes it often difficult to see the details necessary for an accurate

identification — perhaps one of the reasons why Bell's work has not been used extensively. In addition to the collections already mentioned, several specimens from the New Brunswick Museum at Saint John, New Brunswick (14 specimens designated with catalogue numbers with the prefix NBMG), and the Donald Reid Collection, Joggins Fossil Institute, Joggins, Nova Scotia (four specimens designated with catalogue numbers with the prefix DRC), have also been reviewed for the present study.

For more complete information about the localities associated with the GSC material, the reader is referred to the memoirs published by Bell (1938, pp. 108–115; 1944, pp. 111–118).

SYSTEMATIC PALEOBOTANY

As in previous papers in this series (Álvarez-Vázquez and Wagner 2014; Álvarez-Vázquez and Wagner 2017; Álvarez-Vázquez 2019), selective synonymy lists refer mainly to the published records from North America. Only the most significant records from elsewhere and specimens in the collections of the Paleobotanical Centre, Botanical Garden of Córdoba, Spain, are cited where required for a better understanding of the revised taxa. The synonymy lists are thus incomplete, but all old and new synonyms accepted in this study are included. The reader is referred to the *Fossilium Catalogus Plantae* (Jongmans 1957; Jongmans and Dijkstra 1961; Dijkstra and Amerom 1981, 1983) for additional, but uncritical, records.

Annotations in the synonymy lists are as follows: * = protologue; § = first publication of currently accepted combination; T = other illustrations of the holotype; ? = affinity questionable due to poor illustration or preservation; cf. (confer) = compare; p (pars) = only part of the specimens published belong to the species; v (vide) = the author has seen the specimen(s); k = reference includes cuticular evidence; acc. to = according to.

Also provided are: descriptions and/or comparisons and remarks on published specimens; stratigraphic occurrences in accordance with the western European regional chronostratigraphic subdivisions of the Pennsylvanian Subsystem; and geographic distribution of taxa in Canada and the USA.

Names of taxa at generic and lower rank cited herein are listed with full authorship in the Appendix.

Order Medullosales Corsin 1960
Family Alethopteridaceae Corsin 1960
emend. Cleal and Shute 2003

- Genus *Alethopteris* Sternberg 1825
emend. Zodrow and Cleal 1998
- 1825 *Alethopteris* Sternberg, p. 21.
1910 *Johannophyton* Matthew, p. 83–84 (acc. to Stopes 1914).
1912 *Alethopteris* Sternberg; Franke, p. 1–13.
1955 *Alethopteris* Sternberg; Crookall, p. 6–8.

- 1957 *Alethopteris* Sternberg; Jongmans, p. 89–90 (including synonymy).
1961 *Alethopteris* Sternberg; Buisine, p. 65–74 (including synonymy).
1968 *Alethopteris* Sternberg; Wagner, p. 22–30 (including synonymy).
1996 *Alethopteris* Sternberg; Šimůnek, p. 6–7.
1998 *Alethopteris* Sternberg; Zodrow and Cleal, p. 70–71 (emended diagnosis).

Type. *Alethopteris lonchitica* Schlotheim 1820 ex Sternberg 1825.

Diagnosis. Bipartite fronds. Primary pinna tripinnate, with no intercalated pinnules or pinnae on the primary or secondary rachises, which are usually striate. Pinnules asymmetric, fused at the base, decurrent on the basiscopic side, straight or slightly constricted on the acroscopic side. Pinnule lamina thick, giving a vaulted aspect to the pinnules. Venation characterized by a well-marked and strongly decurrent midvein and numerous, non-anastomosed laterals that meet the pinnule margin at about right-angles or somewhat obliquely. Lateral veins fork at irregular intervals, mostly once, sometimes by a tripartite division, and occasionally each fork divides again. (Shortened from the emended diagnosis by Zodrow and Cleal 1998 — cuticular characteristics excluded.).

Remarks. Although also recorded in upper Mississippian strata and extending into the lowermost Permian, *Alethopteris* is essentially a Pennsylvanian genus. The selection of the type as *Alethopteris lonchitica* has given rise to taxonomic problems, as discussed by Wagner and Álvarez-Vázquez (2008). Extensive synonymies can be found in Jongmans (1957), Buisine (1961) and Wagner (1968).

Alethopteris is widespread and fairly closely circumscribed morphologically, forming a natural grouping with *Lonchopteris* (Brongniart 1828) and *Lonchopteridium* (see Gothan 1909, who established *Lonchopteridium* as a “subgroup” of *Lonchopteris*; and Guthörl 1958 who raised *Lonchopteridium* to generic rank). The three genera have pinnules of similar shape and size, with confluent, decurrent bases and are separated by different types of venation: free lateral veins in *Alethopteris*, pseudoanastomosed lateral veins in *Lonchopteridium*, and fully anastomosed veins forming polygonal meshes in *Lonchopteris*. Available evidence on reproductive organs suggests that *Neuralethopteris*, which has pinnules that have stalked to slightly decurrent base and free veins, also belongs to the same natural grouping (Buisine 1961; Goubet *et al.* 2000).

The size of *Alethopteris* fronds seems to have been very substantial, based on the 1.2-m-long fragment recorded by Laveine (1986), who calculated a total frond length of more than 7 m. Laveine *et al.* (1992) figured and described a probably bipartite frond with quadripinnate primary pinnae and without intercalary pinna elements on the rachises. Ovules are of the *Trigonocarpus* type (when preserved as casts or

adpressions) and the *Pachytesta*-type (when anatomically preserved); and pollen producing organs are of the *Whittleseya* type (when adpressions) and the *Bernaultia*-type (when anatomically preserved).

Alethopteris bertrandii Bouroz 1956

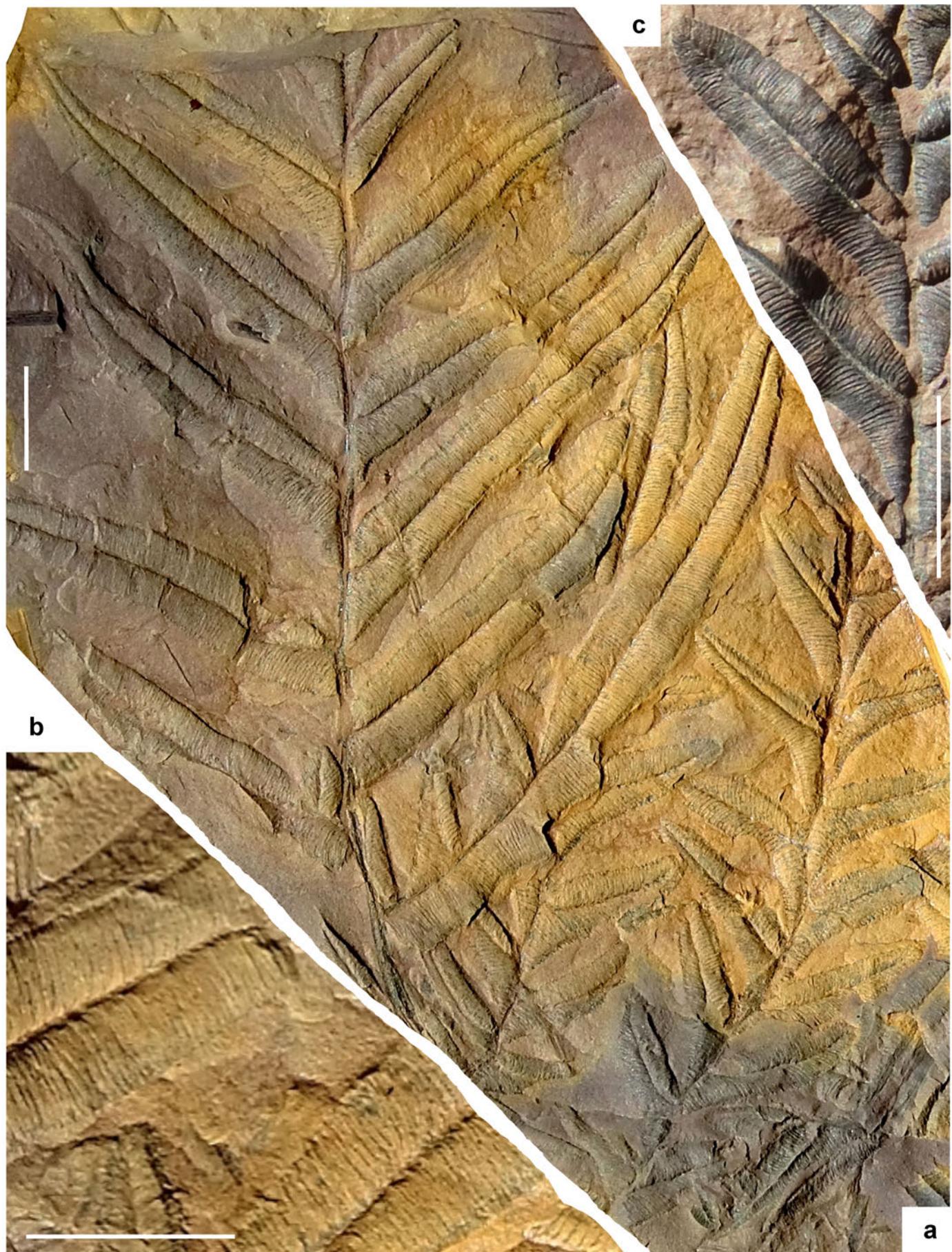
(Figs. 1a–b; 2a–d)

- p 1871 *Alethopteris discrepans* Dawson, p. 54, pl. XVIII, fig. 203; pl. XVIII, figs. 204–204c; non pl. XVIII, fig. 205 (this schematic figure cannot be properly judged, but it is comparable with both *Alethopteris decurrens* and *Alethopteris urophylla*).
- ? 1879–80 *Alethopteris lonchitica* Schlotheim ex Sternberg; Lesquereux, p. 177–179, pl. XXVIII, figs. 7–7a (included in *Alethopteris lancifolia* by Wagner and Álvarez-Vázquez 2008).
- p 1910 *Johannphyton discrepans* Matthew, p. 83–85, pl. II, fig. 7 (included in *Alethopteris lancifolia* by Wagner 2005b); pl. III, fig. 1 (same as Dawson 1871, pl. XVIII, fig. 203); pl. III, figs. 2, 4–6 (same as Dawson 1871, pl. XVIII, figs. 204–204c — *Alethopteris urophylla* acc. to Wagner and Álvarez-Vázquez 2008); non pl. II, figs. 8–9 (sporangia); non pl. III, fig. 3 (resemble *Alethopteris urophylla*); non pl. III, figs. 7, 9 (= *Alethopteris urophylla*); non pl. III, figs. 8, 10 (sporangia).
- v p 1914 *Alethopteris lonchitica* (= *Alethopteris discrepans*) Schlotheim ex Sternberg; Stopes, p. 47–53, pl. XIII, fig. 31 (photographic illustration of Dawson 1871, pl. XVIII, fig. 204 — wrongly cited as fig. 240); pl. XIII, fig. 32 (poorly illustrated); non, pl. XII, fig. 30 (= *Alethopteris urophylla*); non pl. XIII, fig. 33 (fragmentary specimen, here included in *Alethopteris decurrens*); non pl. XVIII, fig. 46 (sporangia and pinnule fragments that may belong either to *Alethopteris* sp. or *Neuralethopteris* sp.); non pl. XXII, fig. 57A (= *Alethopteris* sp. indet. acc. to Wagner and Álvarez-Vázquez 2008); non text-figs. 8A–C (diagrammatic drawings — *Alethopteris urophylla*).
- p 1953 *Alethopteris lonchitica* Schlotheim ex Sternberg; Gothan, Taf. 4, fig. 1 (as *Alethopteris lonchitica* forma *Serli* in the plate); non p. 16–18, Taf. 4, figs. 2, 5 (= *Alethopteris urophylla*), fig. 3 (= *Alethopteris urophylla*?), fig. 4 (= *Alethopteris westphalensis* acc. to Wagner 1968); non Taf. 5, figs. 1, 4, 5 (= *Alethopteris urophylla*), figs. 2–2a (comparable with *Alethopteris westphalensis* acc. to Wagner and Álvarez-Vázquez 2008), fig. 3 (= *Alethopteris pseudograndinoides* acc. to Wagner and Álvarez-Vázquez 2008); non Taf. 6, fig. 1 (comparable with *Alethopteris*

westphalensis acc. to Wagner 1968), figs. 2–4 (= *Alethopteris urophylla*).

- p 1955 *Alethopteris lonchitica* Schlotheim ex Sternberg; Crookall, pl. V, fig. 1; non p. 22–26, pl. V, fig. 2 (= *Alethopteris urophylla*); non pl. X, figs. 1, 3 (= *Alethopteris urophylla*); non text-fig. 7 (reproduction of Schlotheim's original illustration); non text-fig. 14H (venation drawing).
- * 1956 *Alethopteris Bertrandi* Bouroz; p. 137–141, pl. VII, figs. A–C; pl. VIII, figs. D–F; pl. IX, fig. G.
- T 1961 *Alethopteris Bertrandi* Bouroz; Buisine, p. 130–137, pl. XXVIII, fig. 1; pl. XXIX, fig. 1 (same as Bouroz 1956, pl. VII, fig. A), figs. 1a–1c (enlargements); pl. XXX, fig. 1 (same as Bouroz 1956, pl. VIII, fig. D), figs. 1a–1b; pl. XXXI, fig. 1 (same as Bouroz 1956, pl. IX, fig. G), figs. 2–2a; pl. XXXII, figs. 1–1a, figs. 2–2a (same as Bouroz 1956, pl. VII, fig. B); text-fig. 12 (drawing).
- * 1961 *Alethopteris lancifolia* Wagner, p. 6–8, pl. 1, figs. 1–4; pl. 2, figs. 5–8; pl. 3, figs. 9–11; pl. 4, figs. 12–13a.
- 1983 *Alethopteris lonchitica* Schlotheim ex Sternberg; Josten, p. 128–129, Taf. 47, figs. 1–1a; text-fig. 91 (venation drawing).
- 1987 *Alethopteris discrepens latus* Matthew; Miller, p. 20, fig. 19 (photographic illustration of Matthew 1910, pl. II, fig. 7).
- 1988 *Alethopteris discrepens latus* Matthew; Miller and Buhay, p. 223, fig. 5 (same as Miller 1987, fig. 19).
- v 2005b *Alethopteris lancifolia* Wagner; Wagner, p. 16–18, figs. 1a–b (partial counterpart of the specimen figured by Matthew 1910, pl. II, fig. 7).
- 2006 *Alethopteris decurrens* (Artis) Frech; Calder et al., p. 180, 183, fig. 11A (two specimens, part and partial counterpart; the one on the lower part refigured herein as Figs. 1a–b).

Description. Frond at least bipinnate. Penultimate order rachis straight, longitudinally striate, about 1 mm wide. Last order pinnae closely spaced or slightly overlapping laterally, apparently subrectangular, with subparallel margins tapering in the distal part. Dimensions: 80 mm long (incomplete) and 30–100 mm wide. Last order rachis straight, longitudinally striate, ca. 0.5–0.75 mm wide. Pinnules well spaced, inserted at 45–80°, united by a narrow band of lamina; they are large, sturdy, parallel-sided to slightly biconvex, with bluntly acuminate to obtuse apex, constricted acroscopic side and decurrent basiscopic. Dimensions: more than 55 mm length (longest, incomplete, pinnules) and 8–12 mm width; 12–18 mm length and 3–4 mm width the smaller. Lamina thick, vaulted. Venation clearly marked. Midrib straight, well marked and deeply imprinted in the lamina, extending



to the apical part. Lateral veins relatively thin, close, subparallel and nearly perpendicular to both the midrib and pinnule margins, single or once forked near the midrib or at one third of the width. Subsidiary veins simple or, occasionally, once forked. Vein density = 36–40 per centimetre on the pinnule border.

Remarks. I include in *Alethopteris bertrandii* several specimens from Nova Scotia and New Brunswick previously figured as *Alethopteris discrepans*, *Alethopteris lancifolia* and *Alethopteris decurrens*.

Matthew (1910) referred Dawson's (1871) illustration of *Alethopteris discrepans* to the new genus *Johannophyton* on the basis of associated seed capsules (*Sporangites acuminate*) (note that Dawson's "true" *Pecopteris discrepans* is synonymous with *Alethopteris urophylla* — see below). However, a direct connection between pinnae and seeds is nowhere visible, and Stipes (1914) and Bell (1944) rightly synonymized *Johannophyton* with *Alethopteris*. Together with new illustrations of the seeds, Matthew (1910) refigured Dawson's (1871) original illustrations, adding drawings of additional specimens, including a pinna fragment with large pinnules showing a dense venation (Matthew 1910, pl. II, fig. 7). A photograph of this specimen was published by Miller (1987) and Miller and Buhay (1988) as *Alethopteris discrepans* (sic) *latus* Matthew, a manuscript name that appeared on the specimen label. The partial counterpart of this specimen was figured as *Alethopteris lancifolia* by Wagner (2005b).

Alethopteris lancifolia was described by Wagner (1961) from upper Langsettian strata from the Limburg coalfield, Netherlands. Although Wagner (2005b) noted that the Canadian specimens are more ribbon-shaped and the pinnules are somewhat larger, he assumed that this material was at one extreme of a range of variation of *Alethopteris lancifolia*. I herein regard *Alethopteris lancifolia* as a later taxonomic synonym of *Alethopteris bertrandii*, a species that Wagner apparently overlooked.

Comparisons. *Alethopteris bertrandii* is an easily recognizable species due to its large, sturdy, broadly lanceolate pinnae united by a narrow band of lamina. Only *Alethopteris jankii* shows pinnules with similar morphology, but they are even larger, up to 120 mm long, and have a more rounded apex. In addition, vein density is lower, ca. 25–30 veins per centimetre. *Alethopteris jankii* is, like *Alethopteris bertrandii*, a rarely cited species. However, I think that there are some other examples in the literature that should be included in

it: e.g., two of the six specimens figured by Wittry (2006, figs 1, 5) as *Alethopteris serlii* from Mazon Creek. Lastly, *Alethopteris urophylla*, the most abundant and widespread species of *Alethopteris* in the Maritime Provinces (see below), possesses shorter pinnules with a considerably higher vein density, ca. 48–55 veins per centimetre, and it rarely shows unforked lateral veins.

Stratigraphic and geographic distribution. *Alethopteris bertrandii* has not been cited as such outside its type area, the Nord/Pas-de-Calais basin, France. I have tried here to compose a complete synonymy list. The type material is from lower Westphalian C (Bolsovian) strata. The type material of the synonymous *Alethopteris lancifolia* is from upper Westphalian A (Langsettian) strata of the South Limburg Coalfield in the Netherlands. Crookall's (1955) specimen, figured as *Alethopteris lonchitica*, originated from lower Duckmantian strata of the Yorkshire Coalfield, England; the specimen figured by Josten (1983) came from upper Namurian B strata of the Ruhr basin, Germany; and that published by Gothan (1953) came from an indeterminate locality in the Westphalian of the same basin.

Occurrence in the Maritime Provinces, Canada. DONALD REID COLLECTION, JOGGINS, NOVA SCOTIA (1999): DRC-997-72 (here Figs. 1a–b — previously figured by Calder *et al.* 2006 as *Alethopteris decurrens*). FERN LEDGES, NEW BRUNSWICK: locality 135 (two pieces without catalogue number — together with *Psygmorphylum* sp.); locality 351 (one piece without catalogue number). NEW BRUNSWICK MUSEUM COLLECTION: NBMG 3397 (specimen figured by Matthew 1910 as *Johannophyton discrepans*; as *Alethopteris discrepans latus* by Miller 1987 and Miller and Buhay 1988; and as *Alethopteris lancifolia* by Wagner 2005b). FERN LEDGES, NEW BRUNSWICK: Stipes (1914): MCGILL UNIVERSITY COLLECTION 3314 (photographic illustration of Dawson 1871, pl. XVIII, fig. 204).

Occurrence in the United States. PENNSYLVANIA: Lesquerelle (1879–1980).

Alethopteris decurrens (Artis 1825) Frech 1880
(Figs. 3a–f, 4d–e)

- * 1825 *Filicites decurrens* Artis, pl. xxi.
- * 1833 *Pecopteris Mantelli* Brongniart, p. 278–279, pl. 83, figs. 3–4 (acc. to Zeiller 1888).
- * 1876 *Alethopteris gracillima* Boulay, p. 33–34, pl. II, fig. 5 (acc. to Zeiller 1888).

Figure 1 (previous page). (a) *Alethopteris bertrandii*. DRC-997-72. Sideritized specimen. It resembles those figured by Bouroz (1956, pl. VII, fig. A) and Buisine (1961, pl. XXIX, fig. 1). Note the apical parts of the penultimate order pinna with large, elongated pinnules replacing the ultimate order pinnae of the most proximal part. Previously figured as *Alethopteris decurrens* by Calder *et al.* (2006, fig. 11A). Origin: Joggins section (Donald Reid Collection). (b) Enlargement of Fig. 1a showing the vein pattern. (c) DRC-149-99. *Alethopteris urophylla*. Venation details of another sideritized specimen, illustrated for shape and size comparison. Note the small size of pinnules. Origin: Joggins section (Donald Reid Collection). Repository: Joggins Fossil Centre, Joggins, Nova Scotia. Scale bar = 1 cm.

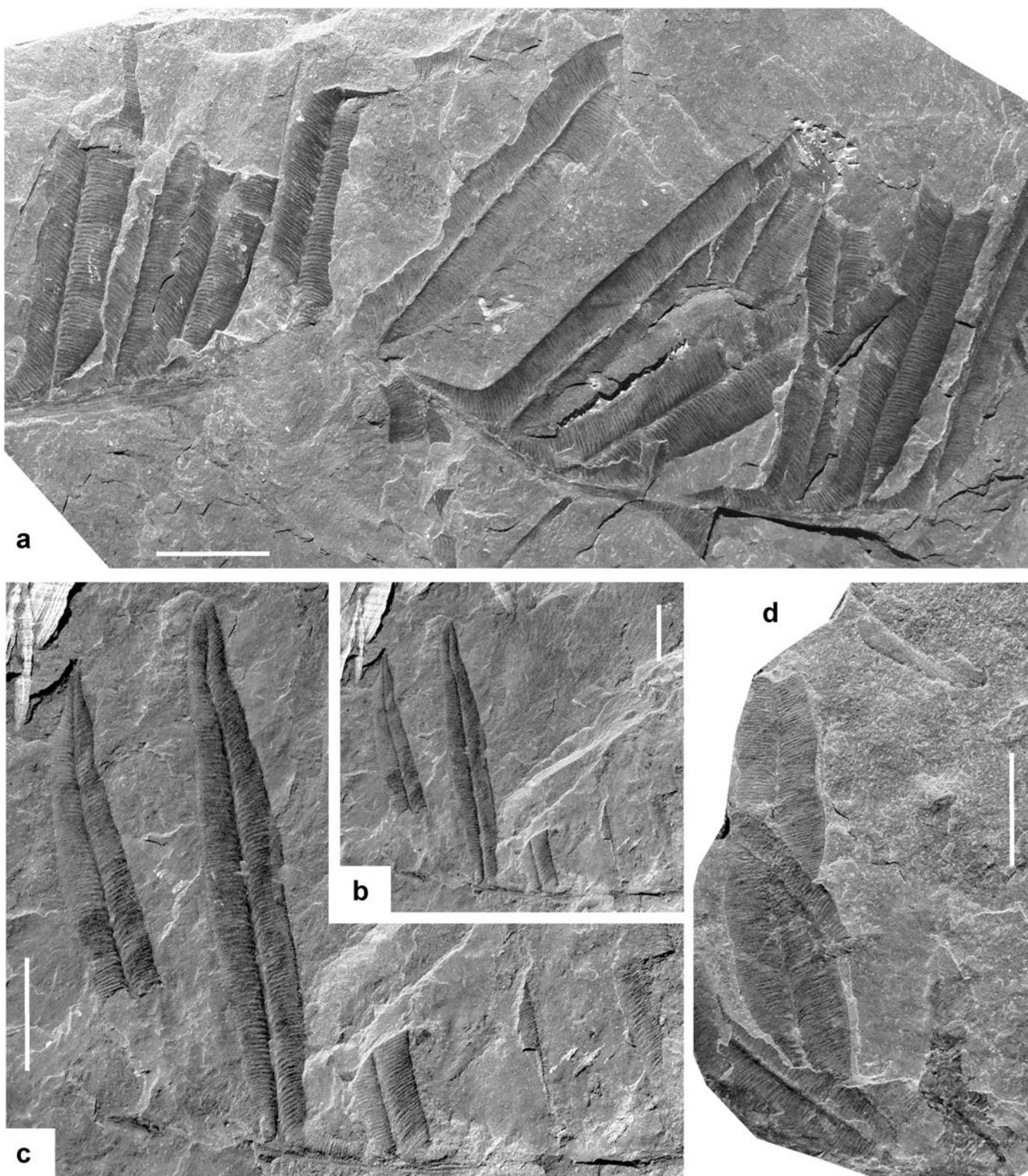
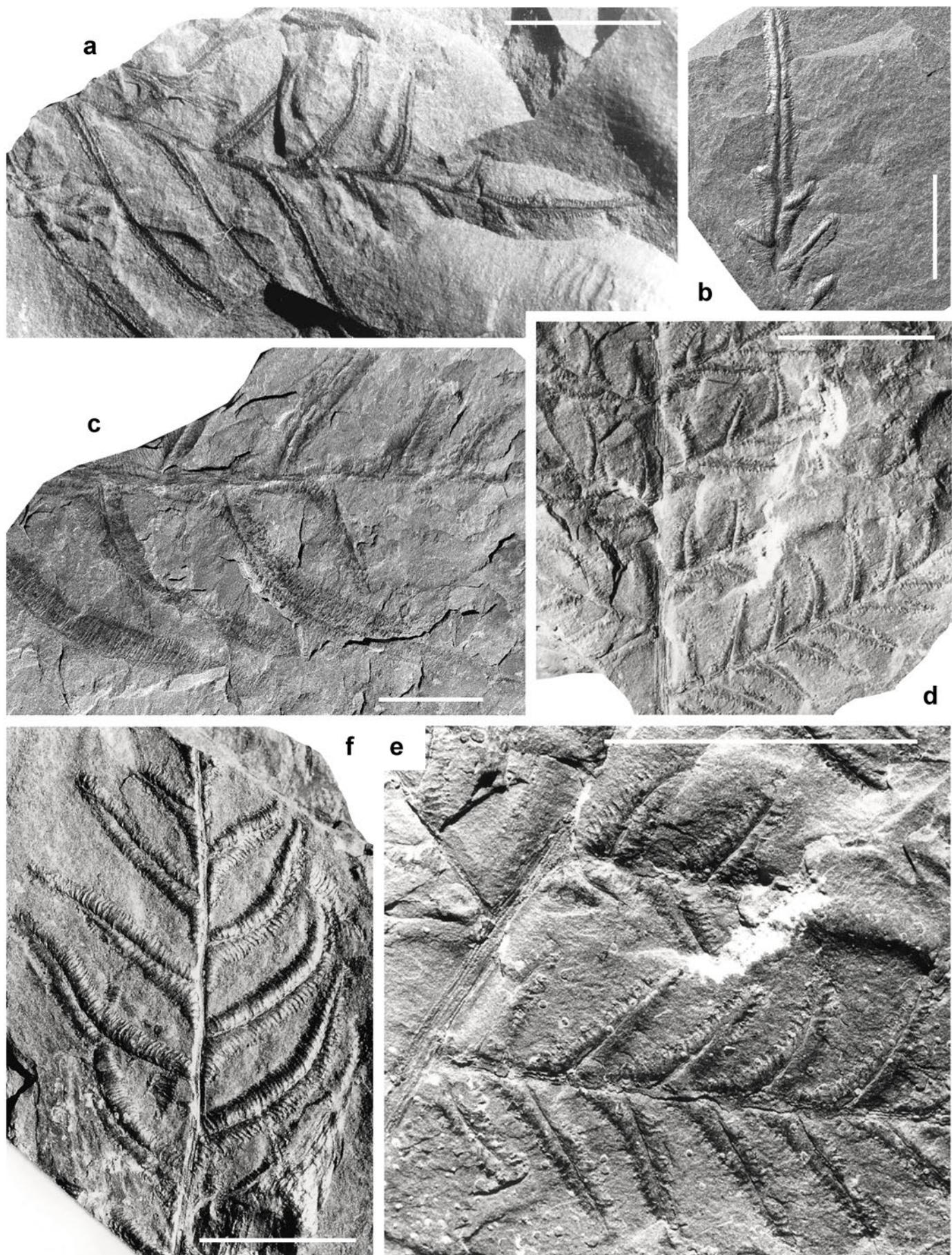


Figure 2. (a) *Alethopteris bertrandii*. Specimen without catalogue number showing the large, sturdy, slightly biconvex pinnules united by a narrow band of lamina and the constricted acroscopic side and decurrent basiscopic. Origin: Fern Ledges, Saint John, New Brunswick (locality 135). (b) *Alethopteris bertrandii*. Specimen without catalogue number. Note the vaulted lamina which makes the pinnules look narrower, and the straight midrib, well-marked and deeply imprinted in the lamina, extending to the apical part. Origin: same as for Fig. 2a (locality 135) (c) Enlargement of Fig. 2b showing the subparallel lateral veins that are nearly perpendicular to both the midrib and pinnule margins. (d) *Alethopteris bertrandii*. Specimen without catalogue number. Origin: Fern Ledges, Saint John, New Brunswick (locality 351). Repository: Geological Survey of Canada, Ottawa. Scale bar = 1 cm.

| | | | | |
|-----|----------|--|--|---|
| § | 1880 | <i>Alethopteris decurrens</i> (Artis) Frech, Taf. 1a, fig. 3. | 1964 | 1–2a; pl. XLIV, figs. 1–5; text-figs. 14a–c. <i>Alethopteris decurrens</i> (Artis) Frech; Read and Mamay, p. 7, pl. 5, fig. 4. |
| | 1886–88 | <i>Alethopteris decurrens</i> (Artis) Frech; Zeiller, p. 221–224, pl. XXXIV, figs. 2–3; pl. XXXV, fig. 1; pl. XXXVI, figs. 3–4. | 1966 | <i>Alethopteris decurrens</i> (Artis) Frech; Bell, p. 10, pl. IV, fig. 4. |
| v p | 1914 | <i>Alethopteris lonchitica</i> (= <i>Alethopteris discraps</i>) Schlotheim ex Sternberg; Stopes, pl. XIII, fig. 33 (fragmentary); non p. 47–53, pl. XII, fig. 30 (= <i>Alethopteris urophylla</i>); non pl. XIII, fig. 31 (= <i>Alethopteris bertrandii</i> — same as Dawson 1871, pl. XVIII, fig. 204); non pl. XIII, fig. 32 (= <i>Alethopteris bertrandii</i>); non pl. XVIII, fig. 46 (sporangia and pinnule fragments that may belong to either <i>Alethopteris</i> sp. or <i>Neuralethopteris</i> sp.); non pl. XXII, fig. 57A (= <i>Alethopteris</i> sp. indet. acc. to Wagner and Álvarez-Vázquez 2008); non text-figs. 8A–C (diagrammatic drawings of <i>Alethopteris urophylla</i>). | 1968 | <i>Alethopteris decurrens</i> (Artis) Frech; Basson, p. 69–70, pl. 12, fig. 1 (figures poor). |
| ? | 1934 | <i>Alethopteris decurrens</i> (Artis) Frech; Arnold, p. 195, pl. II, figs. 1, 3, 7. | ? 1976 | <i>Alethopteris decurrens</i> (Artis) Frech; Gillespie and Pfefferkorn, pl. I, fig. H (also resembles <i>Alethopteris urophylla</i>). |
| * | 1938 | <i>Alethopteris scalariformis</i> Bell, p. 69–70, pl. LXII, fig. 5; pl. LXV, figs. 4–7; pl. LXVI, fig. 3 (acc. to Crookall 1955). | ? 1977 | <i>Alethopteris decurrens</i> (Artis) Frech; Pfefferkorn and Gillespie, pl. 2, fig. Q (same as Gillespie and Pfefferkorn 1976, pl. I, fig. H). |
| v | 1944 | <i>Alethopteris decurrens</i> (Artis) Frech; Bell, p. 87, pl. XL, fig. 1; pl. XLI, figs. 2–3; pl. XLII, fig. 5; pl. XLV, figs. 5–6. | ? 1978 | <i>Alethopteris decurrens</i> (Artis) Frech; Gillespie et al., p. 98, pl. 36, fig. 1 (probably correctly identified, but lacking detail of venation). |
| ? | 1949 | <i>Alethopteris decurrens</i> (Artis) Frech; Arnold, pl. XIX, fig. 4, fig. 7 (same as Arnold 1934, pl. II, fig. 7) (difficult to judge from the illustration — the fragmentary specimens also resemble <i>Alethopteris urophylla</i>). | 1984 | <i>Alethopteris decurrens</i> (Artis) Frech; Jennings, p. 307, pl. 4, fig. 2. |
| * | 1952a–53 | <i>Alethopteris tectensis</i> Stockmans and Willière, p. 241, pl. LVI, figs. 8–8a (the single fragment figured and described by Stockmans and Willière shows the characteristic pinnules of <i>Alethopteris decurrens</i> : flexible, narrow, parallel-sided, decurrent and slightly contracted at the acroscopic side). | 1985 | <i>Alethopteris decurrens</i> (Artis) Frech; Gillespie and Rheams, pl. II, fig. 3 (figures poor). |
| * | 1952a–53 | <i>Alethopteris Edwardsi</i> Stockmans and Willière, p. 240, pl. LVI, figs. 9–9a (the only fragmentary figured specimen came from the same locality as that described as <i>Alethopteris tectensis</i>). | ? 1996 | <i>Alethopteris decurrens</i> (Artis) Frech; Cross et al., p. 412, fig. 23–21.2 (difficult to judge — also resembles <i>Alethopteris urophylla</i>). |
| T | 1955 | <i>Alethopteris decurrens</i> (Artis) Frech; Crookall, p. 26–29 (including synonymy and a reproduction of Artis's illustration), pl. II, figs. 1–3a; pl. VI, figs. 3–3a. | k 1996 | <i>Alethopteris decurrens</i> (Artis) Frech; Šimůnek, p. 7–8, pl. II, figs. 1–7; pl. III, figs. 1–2, figs. 3–9 (cuticles); pl. IV, figs. 1–3 (cuticles); text-figs. 4–7. |
| | 1955 | <i>Alethopteris decurrens</i> var. <i>gracillima</i> Crookall, p. 29–30, pl. II, figs. 4–7; text-fig. 9 (reproduction of Boulay's 1876 holotype of <i>Alethopteris gracillima</i>). | 2014 | <i>Alethopteris decurrens</i> (Artis) Frech; Bashforth et al., p. 247, pl. III, fig. 10. |
| | 1957 | <i>Alethopteris decurrens</i> (Artis) Frech; Janssen, p. 144, fig. 130. | Excludenda: | |
| | 1961 | <i>Alethopteris decurrens</i> (Artis) Frech; Buisine, p. 155–167 (including synonymy), pl. XLI, figs. 1–1c; pl. XLII, figs. 1–3a; pl. XLIII, figs. 1963 | <i>Alethopteris decurrens</i> (Artis) Frech; Wood, p. 48–49, pl. 5, fig. 9 (= <i>Alethopteris urophylla</i>). | |
| | | | 1982 | <i>Alethopteris decurrens</i> (Artis) Frech; Oleksyshyn, p. 94–95, figs. 19B, C (resembles <i>Alethopteris missouriensis</i>). |
| | | | 2002 | <i>Alethopteris decurrens</i> (Artis) Frech; Blake et al., p. 264, 268, 291, pl. XVIII, fig. 2 (= <i>Alethopteris urophylla</i> acc. to Wagner and Álvarez-Vázquez 2008). |
| | | | 2006 | <i>Alethopteris decurrens</i> (Artis) Frech; Calder et al., p. 180, 183, fig. 11A (= <i>Alethopteris bertrandii</i> — see above). |

Description. Frond at least bipinnate. Penultimate order rachis straight, longitudinally striate, ca. 0.5–0.75 mm wide. Last order pinnae closely spaced or slightly touching laterally, elongate, with subparallel margins tapering in the distal part to form an acute angle; apical pinnule well-individualized, elongate, parallel-sided, with a sharply pointed apex, up to 19 mm in length. Dimensions: 60 mm long (incomplete) and 10–40 mm wide. Last order rachis straight, longitudinally striate, ca. 0.25–0.50 mm wide. Pinnules set well apart (3–5 mm), oblique to the rachis (30–60°), decurrent, confluent, slightly contracted at the acroscopic side. Variation in length is considerable, but the approximate width



is consistent. Shorter pinnules straight, subtriangular, with bluntly pointed apex; longer pinnules narrow, parallel-sided and only tapering in the near-apical part, either arched or flexuous. Dimensions: 6–20 mm long and 2.5–3 mm wide; length/breadth ratio = 2.5–6.5. Lamina thick, convex, with a compression border not always visible. Venation characterized by a midrib straight, slightly decurrent, well marked in the vaulted lamina and visible up to the apex. Lateral veins closely spaced, relatively thick, almost perpendicular to both the midrib and pinnule margins, single or once forked at variable distances from the midrib; veins are, on the whole, fairly regularly disposed. Vein density = ca. 30–40 veins per centimetre.

Remarks. Crookall (1955, text-fig. 8) reproduced Artis's original illustration of *Alethopteris decurrens* from Alverthorpe, Yorkshire, England (as reported by Cleal *et al.* 2009, most of Artis's specimens are lost). The holotype is a fragment of pinna of antepenultimate order with relatively strong rachises and widely spaced, confluent, oblique, narrow, almost parallel-sided ("linear") pinnules that tend to become elongate in the terminal part of pinnae. The most extensive documentation of *Alethopteris decurrens* was published by Buisine (1961), who figured material from northern France. Previously, Boulay (1876) had introduced a new species, *Alethopteris gracillima*, also from northern France, which appears identical to *Alethopteris decurrens*. Although some authors consider *Alethopteris gracillima* to be a variety of *Alethopteris decurrens* (e.g., Crookall 1955), I follow Zeiller (1888) and Buisine (1961) in considering *Alethopteris gracillima* a junior synonym of *Alethopteris decurrens*.

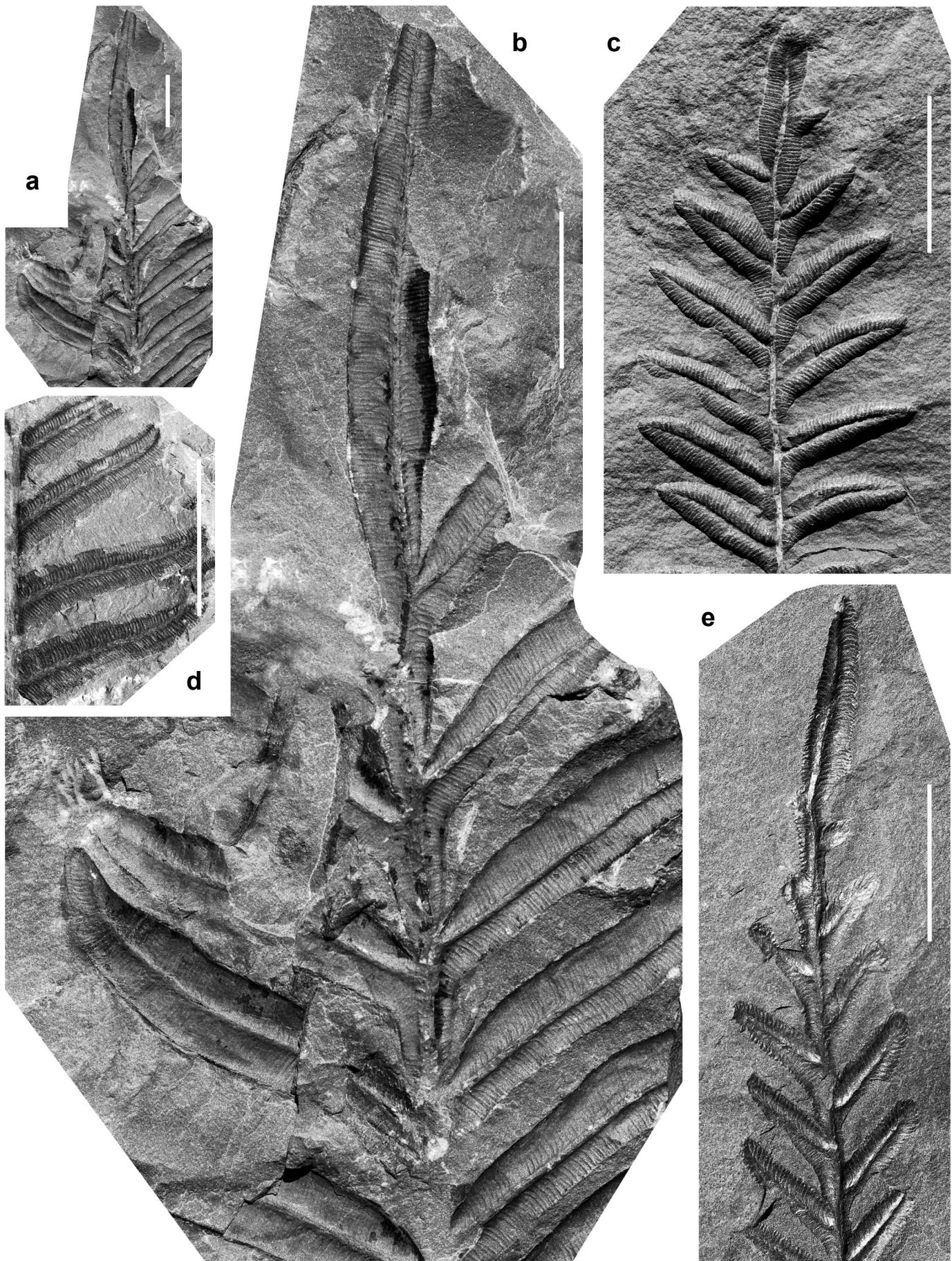
Bell (1944, 1966) illustrated several, very characteristic, specimens of *Alethopteris decurrens* from Nova Scotia showing the widely spaced, elongate and narrow pinnules with strongly marked, fairly regularly disposed lateral veins, most of which are once forked. Previously, Bell (1938) described a new species, *Alethopteris scalariformis*, from the Sydney coalfield, as closely resembling *Alethopteris decurrens*. Bell noted closer and non-decurrent pinnules (except near the apical parts) in *Alethopteris scalariformis*, and more widely

spaced veins that are dichotomized at wider angles. I agree with Crookall (1955) that these superficial differences do not appear to be of specific value and thus consider *Alethopteris scalariformis* to be a taxonomic junior synonym of *Alethopteris decurrens*.

Comparisons. *Alethopteris decurrens* is a distinctive species, identified without much difficulty. Only *Alethopteris davreuxii* could pose problems, but it possesses more rigid pinnules that are subtriangular and tend to become slightly more tapering. Most characteristic of *Alethopteris davreuxii* is its wide venation characterized by once to twice forked veins of flexuous, almost anastomosing aspect. Vein density in *Alethopteris decurrens* is also distinctive, with some 30–45 veins per centimetre according to Buisine (1961). Although *Alethopteris urophylla* shows generally larger and broader pinnules with a tendency to have a biconvex shape and, particularly, a well-marked constriction at the base on the acroscopic side, occasional specimens occur with narrower pinnules that resemble those of *Alethopteris decurrens*. But *Alethopteris urophylla* possesses higher vein density (48–55 veins per centimetre), and it rarely shows unforked lateral veins.

Stratigraphic and geographic distribution. *Alethopteris decurrens* is relatively widespread. The holotype is from lower Westphalian strata of the Yorkshire Coalfield, England. According to Crookall (1955), the species ranges in Great Britain from Westphalian A to C (Langsettian to Bolsovian), being most common in Westphalian B (Duckmantian) and sporadic in Westphalian C (Bolsovian). Šimůnek (1996) recorded it from Namurian C and Westphalian A (Langsettian) strata of the Upper Silesian Basin, and from the Namurian C to the Westphalian B (Duckmantian) of the Intrasudetic Basin. Both *Alethopteris tectensis* and *Alethopteris edwardsii* originated from the same (undetermined) locality in the Assise d'Andenne, upper Namurian (Yeadonian) of Belgium — although Stockmans and Willière (1953) did not rule out the possibility that the specimens came from the Assise de Chokier. In Donbass, *Alethopteris decurrens* ranges

Figure 3. (previous page) (a) *Alethopteris decurrens*. Last order pinna showing the narrow, parallel-sided, flexuous, longer pinnules. Note the elongate, well-individualized apical pinnule. Origin: Chimney Corner area, Inverness County, Cape Breton Island, shore about 2/3 mile north of the old coal mine (locality 1420). (b) *Alethopteris decurrens*. Specimen without catalogue number showing the characteristic, elongate and parallel-sided apical pinnule. Origin: Parrsboro shore between Moose River and Moose Creek (locality 1450). Repository: Geological Survey of Canada, Ottawa. (c) *Alethopteris decurrens*. NBMG 3403. Last order pinna with long, arched pinnules. Origin: Fern Ledges, Saint John, New Brunswick. Repository: New Brunswick Museum, Saint John. (d) *Alethopteris decurrens*. GSC 9313. Penultimate order pinna showing closely spaced last order pinnae with the subtriangular, shorter pinnules. Previously figured by Bell (1944, pl. XLII, fig. 5; pl. XLV, fig. 5). Origin: Chimney Corner area, Inverness County, Cape Breton Island, shore about 1.2 km north of the old coal mine (locality 1420). (e) Enlargement of part of specimen in Fig. 3d to show the straight, slightly decurrent midrib, well-marked in the vaulted lamina and visible up to the apex; also the thick, spaced lateral veins. (f) *Alethopteris decurrens*. GSC 9315. Fragment of last order pinna showing the thick, convex lamina and the well-marked venation, composed by a straight midrib and closely spaced lateral veins almost perpendicular to both the midrib and pinnule margins, single or once forked. Previously figured by Bell (1944, pl. XLV, fig. 6). Origin: Parrsboro shore between Moose River and Moose Creek (locality 1406). Repository: Geological Survey of Canada, Ottawa. Scale bar = 1 cm.



from middle Bashkirian (C_2^1) to lower Moscovian (C_2^6) (Namurian C to Bolsovian) (see Fissunenko in Solovieva *et al.* 1996).

Occurrence in the Maritime Provinces, Canada. CUMBERLAND BASIN (NOVA SCOTIA): Bell (1944): locality 1070 (one piece without catalogue number — together with *Cordaites* sp.); locality 1338 (GSC 11000); locality 1420 (GSC 9313 — here Figs. 3d–3e); locality 1435 (GSC 9315 + GSC 9320 + GSC 9323 + six pieces without catalogue number — together with *Renaultia* sp., *Bergeria dilatata* and *Annularia ramosa*); locality 1450 (three pieces without catalogue number); locality 1982 (fragmentary — one piece without catalogue number); locality 2982 (one piece without catalogue number). Bell (1966): locality 1450 (GSC 14995). DONALD REID COLLECTION, JOGGINS, NOVA SCOTIA (1999): DRC-997-55. SAINT JOHN (NEW BRUNSWICK): Bell (1944): locality 2573 (one piece without catalogue number). NEW BRUNSWICK MUSEUM: NBMG 3403 (labelled as the type of *Alethopteris discrepans* var. *arctus*, an unpublished name). SYDNEY BASIN (NOVA SCOTIA): Bell (1938): locality 752 (GSC 2640 + GSC 2642 + GSC 2647 — holotype of *Alethopteris scalariformis* + GSC 2668).

Occurrence in the United States. ALABAMA: Gillespie and Rheams (1985). ILLINOIS: Janssen (1957), Read and Mamay (1964), Jennings (1984). MICHIGAN: Arnold (1934), Arnold (1949). MISSOURI: Basson (1968). OHIO: Cross *et al.* (1996). WEST VIRGINIA: Gillespie and Pfefferkorn (1976), Pfefferkorn and Gillespie (1977), Gillespie *et al.* (1978).

Alethopteris cf. havlenae Šimůnek 1996
(Figs. 5a–e)

- 1970 *Alethopteris lonchitica* f. *serlii* Brongniart; Havlena, p. 97, pl. II, fig. 5.
- cf. 1977 *Alethopteris lonchitica* Schlotheim ex Sternberg; Leary and Pfefferkorn, p. 25–27, pl. 9, figs. 1–6 (specimens previously mentioned in Leary 1976, p. 4); text-figs. 9A–D (acc. to Wagner and Álvarez-Vázquez 2008).
- * 1984 *Alethopteris densinervosa* Wagner; Havlena, p. 370–371, pl. I, figs. 2, 3 (designated by Šimůnek 1996 as the holotype of *Alethopteris havlenae*); pl. II, figs. 2, 3 (same as *Alethopteris lonchitica* f.

Figure 4 (previous page). (a) *Alethopteris urophylla*. Apical part of a pinna. Specimen without catalogue number. Previously figured by Wagner and Álvarez-Vázquez (2008, figs 7a, 7b). Origin: Springhill, from unspecified coal mine (locality 205). (b) Enlargement of specimen in Fig. 4a. Note the well-individualized, elongate, apical pinnule, and the narrowly confluent bases, with a constriction on the acroscopic side, of lateral pinnules. Repository: Geological Survey of Canada, Ottawa. (c) *Alethopteris urophylla*. DRC-997-57. Sideritized specimen showing smaller pinnules, subtriangular, with bluntly pointed apex. Origin: Joggins section (Donald Reid Collection). Repository: Joggins Fossil Centre, Joggins, Nova Scotia. (d) *Alethopteris decurrens*. Specimen without catalogue number. Origin: Springhill, mine n° 7 (locality 1070). (e) *Alethopteris decurrens*. Specimen without catalogue number. Terminal part of last order pinna showing the well-individualized, elongate, parallel-sided, and with a sharply pointed apex apical pinnule. Counterpart of Bell (1966, pl. IV, fig. 4). Origin: Parrsboro shore between Moose River and Moose Creek (locality 1450). Repository: Geological Survey of Canada, Ottawa. Scale bar = 1 cm.

- Tk 1996 *Alethopteris havlenae* Šimůnek, p. 10–11, pl. V, figs. 5, 7–8, fig. 6 (cuticle); pl. VI, fig. 1, figs. 2–3 (holotype), figs. 4–5, 7, figs. 6, 8 (cuticles); text-figs. 11–13.
- ? 2014 *Alethopteris urophylla* (Brongniart) Göppert; Bashforth *et al.*, p. 247, pl. III, figs. 3, 4, 6–7, 9 (fragmentary).

Description. Frond at least bipinnate. Last order pinna apparently subrectangular (always incomplete), with parallel margins. Last order rachis straight, ca. 0.5–1 mm wide. Pinnules inserted obliquely (50–60°), closely placed; asymmetrical, tongue-shaped, with convex margins, rounded apex, narrowly confluent on the basiscopic side and with a marked constriction on the acroscopic. Apical pinnule not preserved. Dimensions: 4–12 mm long and 2–5 mm broad; length/breadth ratio = 2–2.5. Lamina relatively thick, vaulted. Venation composed by a midrib straight, relatively wide, extending to near the pinnule apex. Lateral veins thin, leaving the midrib almost at right angle and reaching the pinnule margin at 80–85° on the basiscopic side and at 55–85° on the acroscopic one; generally once forked near the midrib, rarely twice. Subsidiary veins once forked. Vein density = 55–60 veins per centimetre.

Remarks. *Alethopteris havlenae* is characterized by closely spaced, tongue-shaped, asymmetrical pinnules with rounded apex and the narrowly confluent base on the basiscopic side. The species was introduced by Šimůnek (1996) to accommodate specimens from the Upper Silesian Basin previously determined as *Alethopteris serlii* by Šusta (1928) and *Alethopteris densinervosa* by Havlena (1984).

I include in *Alethopteris havlenae* two previously unfigured specimens stored in the New Brunswick Museum, Saint John, and another two from the collections of the Geological Survey of Canada, Ottawa; these specimens came from Fern Ledges. Also included as *Alethopteris havlenae* are five specimens figured as *Alethopteris urophylla* by Bashforth *et al.* (2014) from the Tynemouth Creek Formation, New Brunswick. All these specimens are fragmentary, which is why I include them questionably in *Alethopteris havlenae*.

Comparisons. *Alethopteris serlii* has pinnules of similar

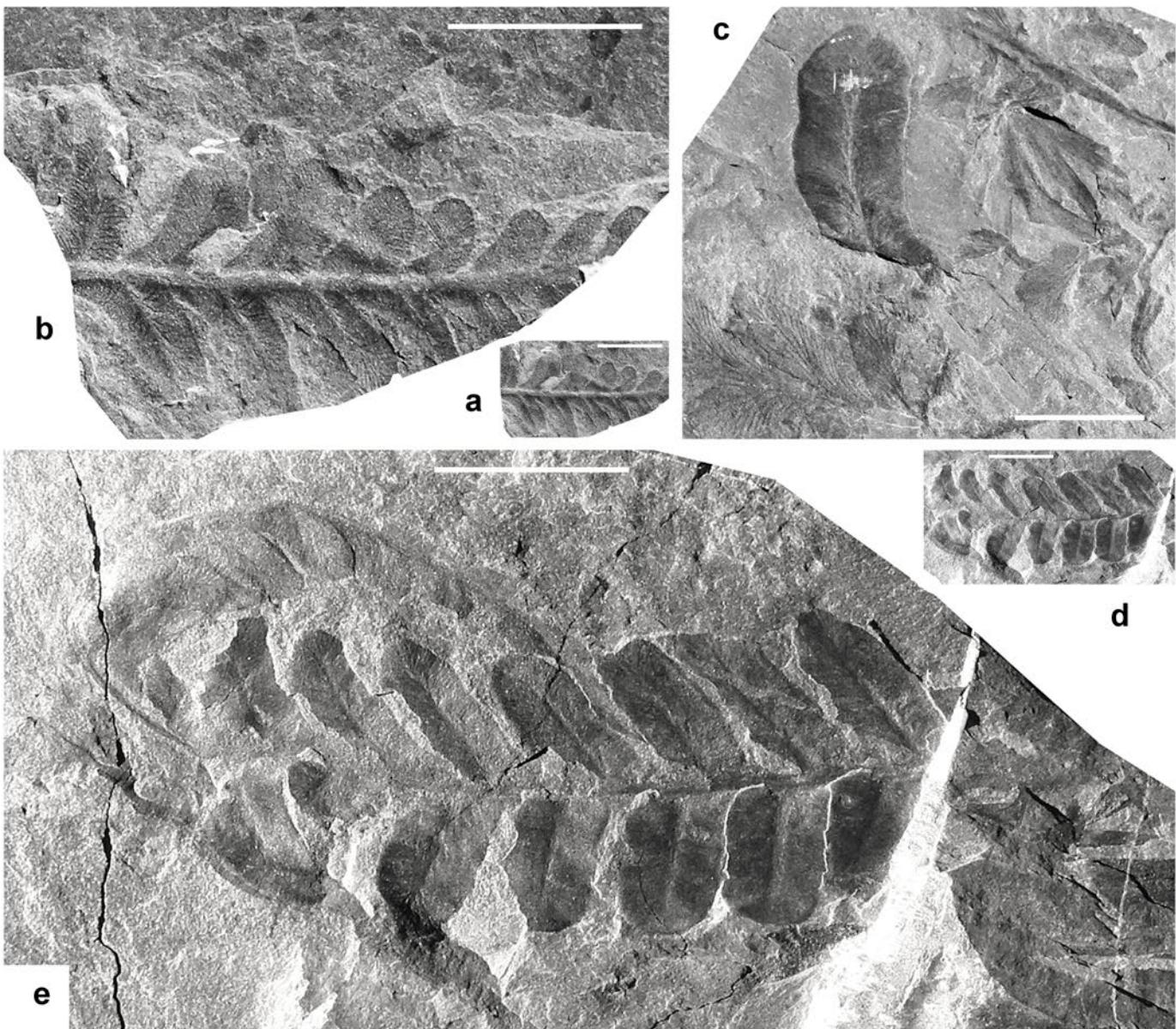


Figure 5. (a) *Alethopteris* cf. *havlenae*. NBMG 7559. Origin: Duck Cove, Saint John, Lancaster, New Brunswick. (b) Enlargement of Fig. 5a to show the obliquely inserted pinnules and thin lateral veins. Repository: New Brunswick Museum, Saint John. (c) *Alethopteris* cf. *havlenae*. Specimen without catalogue number. Isolate pinnule. Origin: Fern Ledges, Saint John, New Brunswick (locality 2254). Repository: Geological Survey of Canada, Ottawa. (d) *Alethopteris* cf. *havlenae*. NBMG 7495. Origin: Duck Cove, Saint John, Lancaster, New Brunswick. Repository: New Brunswick Museum, Saint John. Scale bar = 1 cm. (e) Enlargement of Fig. 5d to show the tongue-shaped pinnules, with convex margins and rounded apex that are narrowly confluent on the basiscopic side and with a marked constriction on the acroscopic.

shape, but with more convex margins and a bluntly acuminate apex; vein density is also different, 30–35 veins per centimetre in *Alethopteris serlii* compared with 55–60 in *Alethopteris havlenae*. *Alethopteris densinervosa* shows clearly biconvex and more closely spaced pinnules that have a slightly higher ratio (2.5–3 times longer than broad); in addition, the midrib is not as thick as in *Alethopteris havlenae*, and lateral veins are fine and less numerous, about 40–45 veins per centimetre according to Wagner (1968). *Alethopteris valida* is characterized by its thick lamina and

large, subtriangular pinnules connected by a broadly confluent lamina, about 2–3 mm wide; moreover, vein density is lower, about 25–30 veins per centimetre in the pinnule margin.

Stratigraphic and geographic distribution. *Alethopteris havlenae* is rarely reported. The holotype is from Namurian C strata of the Karviná Formation in the Upper Silesian Basin. Šimůnek (1996) reported the species in the Namurian C and the Westphalian A (Langsettian) of this basin.

Occurrence in the Maritime Provinces, Canada. SAINT JOHN (NEW BRUNSWICK): Bell (1944): locality 2214 (one piece without catalogue number — together with *Rhacopteris* sp.); locality 2254 (one piece without catalogue number — together with *Neuropteris obliqua*). NEW BRUNSWICK MUSEUM: NBMG 1740 + NBMG 7559. Bashforth *et al.* (2014): NBMG 15440 + NBMG 15441 + NBMG 16210 + NBMG 16729 + NBMG 16730.

Occurrence in the United States. ILLINOIS: Leary (1976); Leary and Pfefferkorn (1977).

- Alethopteris urophylla* (Brongniart 1834) Göppert 1836
(Figs. 1c, 4a–c, 6)
- * v 1834 *Pecopteris urophylla* Brongniart, p. 290–291,
pl. 86.
- § 1836 *Alethopteris urophylla* (Brongniart) Göppert,
p. 300.
- * 1848 *Pecopteris multiformis* Sauveur, pl. XXXVI,
fig. 1 (acc. to Wagner and Álvarez-Vázquez
2008).
- * 1862 *Pecopteris (Alethopteris) decurrens* sp. nov.
Dawson (non Artis), p. 322, pl. XV, figs.
40a–c (diagrammatic drawings of fragmen-
tary specimens).
- * 1862 *Pecopteris (Alethopteris) ingens* sp. nov.
Dawson, p. 322, pl. XV, figs. 41a–b (see com-
ments in Stöples 1914, p. 95–96).
- * 1863 *Pecopteris discrepans* Dawson, p. 468 (name
change on the basis of the homonymy of
Dawson's 1862 *Pecopteris (Alethopteris)*
decurrens with Lesquereux's 1858 *Pecopteris*
decurrens. However, the real homonym
is Artis's *Filicites decurrens* = *Alethopteris*
decurrens).
- 1865 *Alethopteris discrepans* Dawson, p. 136–137.
- 1868 *Alethopteris discrepans* Dawson, p. 552–553,
fig. 192I (same of Dawson 1862, pl. XV, fig.
40a).
- p ? 1871 *Alethopteris discrepans* Dawson, pl. XVIII,
fig. 205 (this schematic figure cannot be
properly judged; it can be also compared
with *Alethopteris decurrens*); non p. 54, pl.
XVIII, fig. 203 (= *Alethopteris bertrandii*);
non pl. XVIII, figs. 204–204c (= *Alethopteris*
bertrandii).
- p 1910 *Johannophyton discrepans* (Dawson) Mat-
thew, pl. III, fig. 3; pl. III, figs. 7, 9; non pl.
II, fig. 7 (= *Alethopteris bertrandii*); non pl.
III, fig. 1 (= *Alethopteris bertrandii* — same
as Dawson 1871, pl. XVIII, fig. 203); non pl.
II, figs. 8–9 (sporangia); non pl. III, figs. 2,
4–6 (same as Dawson 1871, pl. XVIII, figs.
204–204c); non pl. III, figs. 8, 10 (sporangia).
- v p 1914 *Alethopteris lonchitica* (= *Alethopteris dis-
crepans*) Schlotheim ex Sternberg; Stöples,
pl. XII, fig. 30; text-figs. 8A–C (diagram-

- matic drawings); non p. 47–53, pl. XIII, fig.
31 (photographic illustration of Dawson
1871, pl. XVIII, fig. 204 — here *Alethopteris*
bertrandii); non pl. XIII, fig. 32 (fragmen-
tary and poorly illustrated — compared
with *Alethopteris corsinii* by Wagner and
Álvarez-Vázquez 2008 and here included
in *Alethopteris bertrandii*); non pl. XIII, fig.
33 (comparable with *Alethopteris decur-
rens*); non pl. XVIII, fig. 46 (sporangia and
pinnule fragments that, acc. to Wagner and
Álvarez-Vázquez 2008, may belong either to
Alethopteris sp. or *Neuralethopteris* sp.); non
pl. XXII, fig. 57A (= *Alethopteris* sp. indet.
acc. to Wagner and Álvarez-Vázquez 2008).
Alethopteris lonchitica Schlotheim ex Stern-
berg; Corsin, p. 18, pl. VIII, figs. 1–1a; text-
fig. 7.
- 1932 *Alethopteris grandifolia* Newberry; Arnold,
p. 280, fig. 1 (last order pinna with associated
seed), fig. 3 (last order pinna with attached
seed).
- 1935 *Alethopteris grandifolia* Newberry; Arnold,
p. 46, fig. 1 (drawing of the fragment of last
order pinna figured in Arnold 1935, fig. 3).
- 1937 *Alethopteris lonchitica* Schlotheim ex Stern-
berg; Bell, p. 86–87.
- 1944 *Alethopteris Helena* Lesquereux; Arnold,
p. 188–189, pl. XIX, figs. 5–6.
- 1949 *Alethopteris lonchitica* Schlotheim ex Stern-
berg; Buisine, p. 99–115, pl. XIII, fig. 1; pl.
XIII, figs. 2–2b; pls. XIV–XVI; pl. XVII,
fig. 2, 4; pl. XVIII, figs. 1–1b; pls. XIX,
XX; text-figs. 9a–c; non pl. XVII, figs. 1, 3
(= *Alethopteris densinervosa* acc. to Wagner
and Álvarez-Vázquez 2008); non pl. XVIII,
fig. 2 (= *Alethopteris densinervosa* acc. to
Wagner and Álvarez-Vázquez 2008).
- p 1961 *Alethopteris serli* (Brongniart) Göppert;
Buisine, pl. VIII, figs. 2–2a (= *Alethopteris*
urophylla acc. to Wagner 1968); non pls. I–
VII, non pl. VIII, figs. 1–1a (= *Alethopteris*
densinervosa acc. to Wagner 1968); non pl.
IX, figs. 1–1a (= *Alethopteris westphalensis*
acc. to Wagner, 1968); non pl. X, figs. 1–1a,
3–4 (= *Alethopteris densinervosa* acc. to
Wagner 1968); non pl. IX, figs. 1–1a, pl. X,
figs. 2–2a, pl. XI, figs. 1–2, pl. XII, figs. 1a–1c
(= *Alethopteris westphalensis* acc. to Wagner
1968).
- 1963 *Alethopteris decurrens* (Artis) Frech; Wood,
p. 48–49, pl. 5, fig. 9.
- v 1966 *Alethopteris lonchitica* Schlotheim ex Stern-
berg; Bell, p. 16, pl. VII, fig. 4.
- p 1985 *Alethopteris lonchitica* Schlotheim ex Stern-
berg; Gillespie and Rheams, p. 194, 199, pl.
II, fig. 2; non pl. I, fig. 3 (*Alethopteris valida*

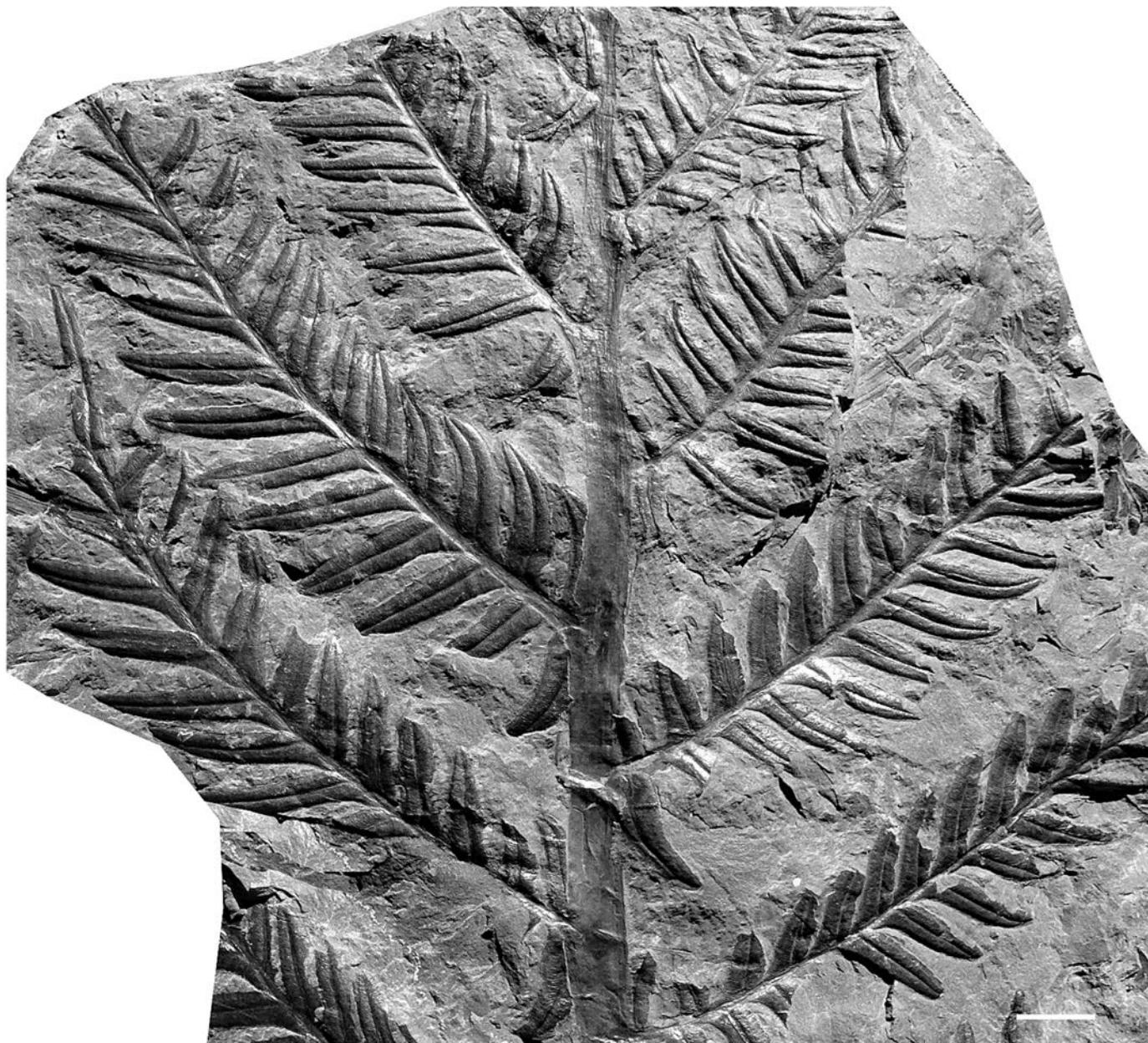


Figure 6. *Alethopteris urophylla*. GSC 14994. Large specimen showing the sturdy, narrowly confluent, asymmetrical pinnules that characterize *Alethopteris urophylla*. Previously figured by Bell (1966, pl. VII, fig. 4). Origin: Springhill mines (locality 205). Repository: Geological Survey of Canada, Ottawa. Scale bar = 1 cm.

| | | | |
|--------|--|------|---|
| 1989 | acc. to Wagner and Álvarez-Vázquez 2008). | | |
| | <i>Alethopteris lonchitica</i> Schlotheim ex Sternberg; Gillespie et al., p. 5, pl. 2, fig. 7. | | |
| p 1996 | <i>Alethopteris urophylla</i> (Brongniart) Göppert; Šimůnek, p. 13–16, pl. X, figs. 1, 4 (after Šusta 1928, Taf. XXXIV, fig. 3), fig. 6 (trichome); pl. XI, fig. 1 (after Purkyňová 1990, Tab. II, fig. 4), figs. 2–7 (cuticles); pl. XII, fig. 1 (fragmentary; difficult to judge), figs. 2–4, fig. 5 (?), figs. 6–10 (cuticles); pl. XIII, figs. 1–8 (cuticles); pl. XIV, fig. 1; text-figs. 18–23; non pl. X, figs. 2–3 (resemble <i>Alethopteris</i> | 1997 | <i>decurrens</i>); non pl. X, fig. 5 (difficult to judge, but resembles <i>Alethopteris havlena</i> e); non text-fig. 17 (possibly <i>Alethopteris havlena</i> e). |
| | | 2002 | <i>Alethopteris lonchitica</i> Schlotheim ex Sternberg; Blake, p. 84, 85, pl. 2, figs. 1–3. |
| | | ? | <i>Alethopteris decurrens</i> (Artis) Frech; Blake et al., p. 264, 268, 291, pl. XVIII, fig. 2. |
| | | 2002 | <i>Alethopteris urophylla</i> (Brongniart) Göppert; Blake et al., p. 264, 269, 291, 292, pl. XVIII, figs. 3, 5. |
| | | ? | <i>Alethopteris discrepans</i> (cf. <i>A. lonchitica</i>) Dawson; Calder et al., fig. 11B (difficult to |

| | | | |
|---|--|------|--|
| | judge from the illustration at less than natural size). | | berg; Olekyshyn, p. 98–99, figs. 19F–H (acc. to Wagner and Álvarez-Vázquez 2008 resembles <i>Alethopteris missouriensis</i>). |
| 2006 | <i>Alethopteris</i> Sternberg; Falcon-Lang, p. 44, fig. 10C (only an isolated pinnule but showing the slightly biconvex margins, bluntly acuminate apex and the constriction on the acroscopic side characteristic of the species). <i>Alethopteris urophylla</i> (Brongniart) Göppert; Wagner and Álvarez-Vázquez, p. 166–177 (including synonymy), fig. 1 (copy of Brongniart 1834, pl. 86), figs. 2–4 (photograph of the holotype), figs. 5–7d, figs. 8a–10 (same specimen as in Buisine 1961, pl. XIII, fig. 1), figs. 11a–12. | 1985 | <i>Alethopteris</i> cf. <i>lonchitica</i> Schlotheim ex Sternberg; Lyons <i>et al.</i> , pl. XI, fig. b (fragmentary and difficult to judge — either <i>Neuralethopteris</i> sp. indet. or <i>Alethopteris</i> sp. indet. acc. to Wagner and Álvarez-Vázquez 2008). |
| v T 2008 | <i>Alethopteris urophylla</i> (Brongniart) Göppert; Wagner and Álvarez-Vázquez, p. 166–177 (including synonymy), fig. 1 (copy of Brongniart 1834, pl. 86), figs. 2–4 (photograph of the holotype), figs. 5–7d, figs. 8a–10 (same specimen as in Buisine 1961, pl. XIII, fig. 1), figs. 11a–12. | 2014 | <i>Alethopteris lonchitica</i> Schlotheim ex Sternberg; Moore <i>et al.</i> , p. 38, 39, pl. VII, figs. 7–8 (fragmentary; comparable with <i>Alethopteris lesquereuxii</i>). |
| v 2010 | <i>Alethopteris urophylla</i> (Brongniart) Göppert; Wagner and Álvarez-Vázquez, p. 257, 258, 261–262, 266, 307, pl. IX, fig. 1 (together with <i>Paripteris gigantea</i> — same as Wagner and Álvarez-Vázquez 2008, fig. 11a). | 2014 | <i>Alethopteris urophylla</i> (Brongniart) Göppert; Bashforth <i>et al.</i> , p. 247, pl. III, figs. 3, 4, 6–7, 9 (although fragmentary, comparable with <i>Alethopteris havlenae</i>). |
| Excludenda (including <i>Alethopteris lonchitica autorum</i>): | | | |
| 1879–80 | <i>Alethopteris lonchitica</i> Schlotheim ex Sternberg; Lesquereux, p. 177–179, pl. XXVIII, figs. 7–7a (= <i>Alethopteris lancifolia</i> acc. to Wagner and Álvarez-Vázquez 2008). | | |
| 1938 | <i>Alethopteris lonchitica</i> Schlotheim ex Sternberg; Bell, p. 67, pl. LXI, fig. 5 (refigured by Zodrow and Cleal 1998, pl. 2, fig. 3 — acc. to Wagner and Álvarez-Vázquez 2008, it may be attributed to the <i>Alethopteris lonchitifolia-westphalensis</i> complex). | | |
| 1939 | <i>Alethopteris lonchitica</i> Schlotheim ex Sternberg; Janssen, p. 143, fig. 129 (mentioned in Leary 1976) (difficult to judge from the illustration; Wagner and Álvarez-Vázquez 2008 compared with <i>Alethopteris lonchitifolia</i>). | | |
| 1958 | <i>Alethopteris lonchitica</i> Schlotheim ex Sternberg; Langford, p. 241, figs. 438–439 (mentioned in Leary 1976) (Wagner and Álvarez-Vázquez 2008 compared with <i>Alethopteris lesquereuxii</i>). | | |
| 1962 | <i>Alethopteris lonchitica</i> Schlotheim ex Sternberg; Bell, pl. XLII, fig. 4. (= <i>Alethopteris</i> cf. <i>davreuxii</i> ? acc. to Wagner and Álvarez-Vázquez 2008). | | |
| 1977 | <i>Alethopteris lonchitica</i> Schlotheim ex Sternberg; Leary and Pfefferkorn, p. 25–27, pl. 9, figs. 1–6 (previously mentioned in Leary 1976, p. 4); text-fig. 9A–D (comparable with <i>Alethopteris havlenae</i> acc. Wagner and Álvarez-Vázquez 2008). | | |
| 1978 | <i>Alethopteris lonchitica</i> Schlotheim ex Sternberg; Gillespie <i>et al.</i> , p. 100, pl. 35, fig. 3 (venation diagram); pl. 36, fig. 7 (acc. to Wagner and Alvarez-Vázquez 2008, pointed pinnules tending to a lanceolate shape not suggestive of <i>Alethopteris urophylla</i>). | | |
| 1982 | <i>Alethopteris lonchitica</i> Schlotheim ex Stern- | | |
| | | | Description. Frond at least tripinnate. Penultimate order rachis strong, flat, straight, longitudinally striate, up to 10 mm wide. Last order pinnae alternate, close or slightly touching laterally; subrectangular, parallel-sided, tapering only in the distal part; lateral pinnules in the terminals only slightly shorter than the other laterals; apical pinnule well-individualized, elongate, parallel-sided, with a sharply pointed apex, up to 35 mm long. Dimensions: up to 130 mm long (incomplete) and 20–60 mm broad. Last order rachis inserted at 45–80°, straight, longitudinally striate, ca. 0.5–1.5 mm wide. Lateral pinnules spaced (3–5 mm), oblique to the rachis (at 45–80°), decurrent, with narrowly confluent bases and a constriction on the acroscopic side. Pinnule length variable depending on the position in the frond, whilst retaining the approximate width. Shorter pinnules straight, subtriangular, with bluntly pointed apex; longer pinnules parallel-sided to slightly biconvex, tapering in the near-apical part to a bluntly acuminate to rounded apex, either arched or flexuous. Dimensions: 9–27 mm long and 2.5–5 mm wide; length/breadth ratio = 3.6–5.4. Lamina thick, convex, with a compression border not always clearly visible. Venation well marked, characterized by a midrib straight, very slightly decurrent, deeply imprinted in the lamina and extending up to near pinnule apex. Lateral veins thin, regularly disposed and closely spaced, slightly curved near the midrib and reaching the pinnule margin at right angles; generally once forked at variable distances from the midrib, rarely simple or with a second bifurcation. Subsidiary veins simple or once forked. Vein density = 48–55 veins per centimetre. |
| | | | Remarks. <i>Alethopteris urophylla</i> was discussed by Wagner and Álvarez-Vázquez (2008), who refigured and described the holotype (Brongniart 1834, pl. 86) and provided a full synonymy list. Comments on the synonymy are repeated herein if relevant to the Canadian and American material. |
| | | | Originally described from Merthyr Tydfil in South Wales (Brongniart 1834), <i>Alethopteris urophylla</i> has been recorded widely from the Pennsylvanian paleoequatorial belt as represented in North America and Europe. Records have been mostly under the name of <i>Alethopteris lonchitica</i> , a |

Stephanian species that Zodrow and Cleal (1998) showed to be different from *Alethopteris urophylla* (see also Wagner and Álvarez-Vázquez 2008).

Buisine (1961) discussed *Alethopteris discrepans*, a substitute name provided by Dawson (1863) for *Pecopteris* (*Alethopteris*) *decurrans*, which was introduced by Dawson (1862) (see comment in the synonymy list); this species is based on diagrammatic drawings of very fragmentary specimens. In agreement with Stoops (1914), Buisine, included *Alethopteris discrepans* as a taxonomic junior synonym of *Alethopteris lonchitica* (meaning *Alethopteris lonchitica auctorum* = *Alethopteris urophylla*). This synonymy is supported by the illustration of material from Dawson's original locality, the Fern Ledges at Saint John, New Brunswick, as well as other fragmentary remains from the Joggins section, Nova Scotia (see Stoops 1914).

Although Bell (1944, p. 87) mentioned *Alethopteris lonchitica* as the most abundant and widespread species in the Cumberland Group (he recorded it from 57 localities), he gave only a short description and no illustrations. Only at a later date did he figure a large and well-preserved specimen from Springhill (Bell 1966, pl. VII, fig. 4 — herein Fig. 6). The present restudy of the collections of the Geological Survey of Canada and the Joggins Fossil Institute confirms the abundance of *Alethopteris urophylla* in the Maritime Provinces.

Comparisons. *Alethopteris lonchitica* also shows parallel-sided pinnules of similar size, but they are slender and have a more broadly rounded apex. In addition, pinnules in *Alethopteris lonchitica* tend to be more pecopteroid and perpendicular to the rachis, and the midrib is wider and lateral veins more widely spaced. *Alethopteris decurrents* has narrower and more-parallel-sided pinnules that are much more spaced out; additionally, longer pinnules are arched or flexuous, vein density is lower, ca. 30–40 veins per centimetre, and lateral veins seem to be more irregular. *Alethopteris corsinii* has pinnules of similar shape and size, but they are broader and more broadly confluent, with less marked constriction on the acroscopic side; venation is wider, only 30–35 veins per centimetre on the pinnule margin, and lateral veins are simple or fork once close to the midrib. *Alethopteris bertrandii* possesses larger, stiff, lanceolate pinnules. In addition, venation is wider, with about 40–45 veins per centimetre on the pinnule margin (Buisine 1961), and the elongate last order pinna terminals are very characteristic. *Alethopteris solutifolia* also possess decurrent, parallel-sided pinnules with rounded apex, narrowly confluent bases and a constriction on the acroscopic side; but the pinnules in that species are longer and narrower. Additionally, lateral veins are forked up to three times and are more widely spaced, with about 35 veins per centimetre in the pinnule margin.

Stratigraphic and geographic distribution. *Alethopteris urophylla* is widespread in the paleoequatorial belt, from Michigan in the west to the Donbass in the east. The holotype is from lower Westphalian horizons at Merthyr

Tydfil in South Wales. According to Wagner and Álvarez-Vázquez (2008), the species ranges from middle Namurian (Kinderscoutian) to lower Bolsovian, with most records from Langsettian and Duckmantian strata. *Pecopteris multiformis* was described originally from an unknown horizon in the lower Westphalian of Belgium.

Occurrence in the Maritime Provinces, Canada.

CUMBER-LAND BASIN (NOVA SCOTIA): Bell (1944): locality 999 (GSC 7562 — together with *Calamites carinatus* + GSC 8586 — together with *Diaphorodendron decurtatum* + GSC 9556 + GSC 9575 + eight pieces without catalogue number — together with *Zeilleria avoldensis*); locality 1031 (GSC 10084 + five pieces without catalogue number — with *Cordaites* sp. and seeds); locality 1052 (GSC 9879 — fragmentary but characteristic; together with *Sphenophyllum cuneifolium*, *Cordaites* sp. and *Trigonocarpus* sp.); locality 1070 (GSC 10192); locality 1081 (one piece without catalogue number); locality 1085 (two pieces without catalogue number — together with cf. *Zeilleria hymenophylloides*); locality 1089 (GSC 10164 + one piece without catalogue number — fragmentary); locality 1339 (one piece without catalogue number); locality 1363 (one piece without catalogue number — fragmentary); locality 1491 (one piece without catalogue number — fragmentary and poorly preserved; with cf.); locality 1495 (one piece without catalogue number from a borehole — fragmentary and poorly preserved); locality 1498 (two pieces without catalogue number from a borehole — fragmentary); locality 2986 (three pieces without catalogue number); locality 2991 (one piece without catalogue number — poorly preserved). Bell (1966): locality 205 (GSC 14994 — Fig. 6 herein + six pieces without catalogue number, three of them figured in Wagner and Álvarez-Vázquez 2008, figs. 7a–d — together with *Calamites cistii* and *Sphenophyllum cuneifolium*). DONALD REID COLLECTION, JOGGINS, NOVA SCOTIA (1999): DRC-149-99 + DRC-153-99 — together with *Sigillaria scutellata* and *Lepidostrobophyllum lanceolatum*. FERN LEDGES, NEW BRUNSWICK: Stoops (1914); MCGILL UNIVERSITY COLLECTION 3312. NEW BRUNSWICK MUSEUM: NBMG 1805 (figured by Falcon-Lang 2006) + NBMG 12056. PRINCE EDWARD ISLAND: locality 4454 (two pieces without catalogue number).

Occurrence in the United States. ALABAMA: Gillespie and Rheams (1985). GEORGIA: Gillespie *et al.* (1989). INDIANA: Wood (1963). MICHIGAN: Arnold (1949). OHIO: Arnold (1935, 1937). WEST VIRGINIA: Blake *et al.* (2002).

Alethopteris cf. valida Boulay 1876

(Fig. 7)

- * 1876 *Alethopteris valida* Boulay, p. 35, pl. I, fig. 8.
- * 1884 *Alethopteris Evansii* Lesquereux, p. 834–835 (name and description only — acc. to Blake 1997, p. 82).
- 1886–88 *Alethopteris valida* Boulay; Zeiller, p. 231–233, pl. XXXIII, figs. 1–2A; pl. XXXIV, figs. 1–1A.

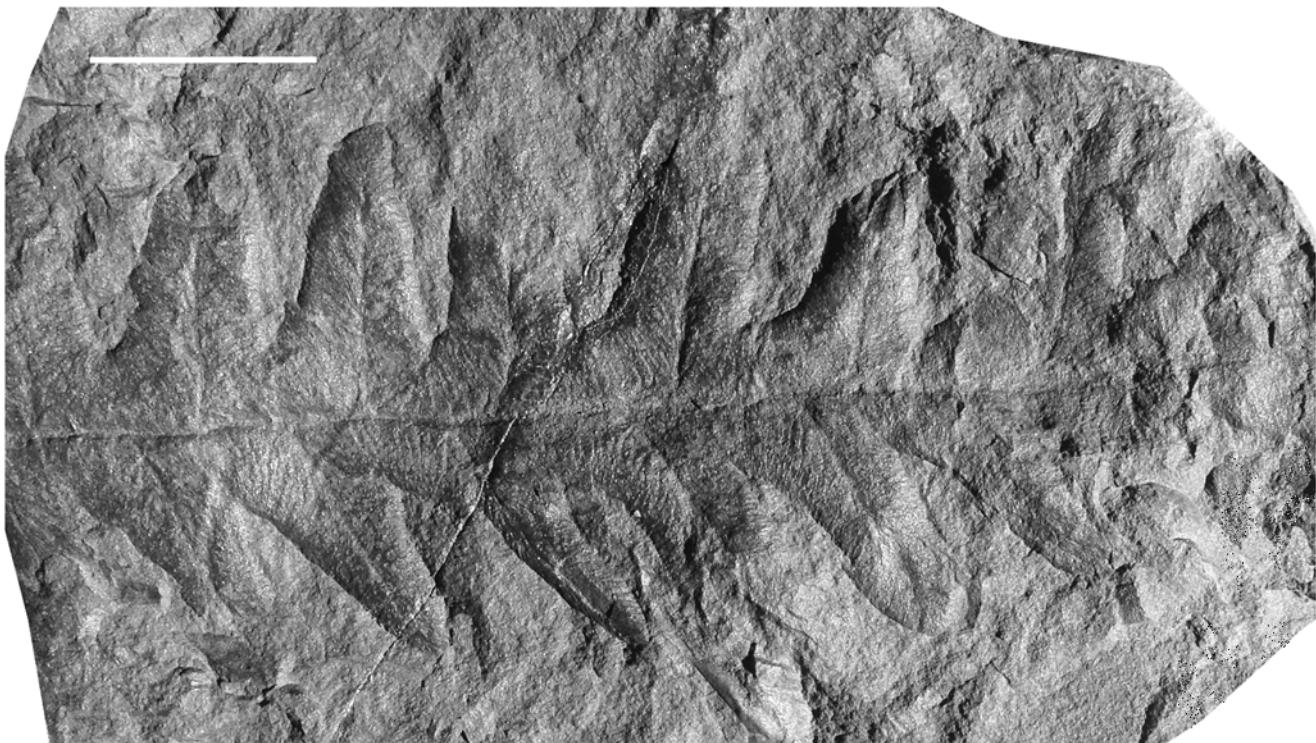


Figure 7. *Alethopteris* cf. *valida*. GSC 10852. Note the characteristic subtriangular pinnules and the broadly confluent lamina. Origin: Black river; Springhill area (locality 1178). Repository: Geological Survey of Canada, Ottawa. Scale bar = 1 cm.

| | | | | |
|--------|--|---|-------------|---|
| 1900 | <i>Alethopteris Evansii</i> Lesquereux; White, p. 887, pl. CXCII, figs. 7–8a. | | | <i>al.</i> , pl. 36, fig. 5; non pl. 36, fig. 3 (= <i>Alethopteris davreuxii</i>). |
| 1932 | <i>Alethopteris valida</i> Boulay; Corsin, p. 19–20, pl. XI, figs. 1–1a; text-fig. 8 (same as Zeiller 1886, pl. XXXIII, figs. 1A–2A). | p | 1985 | <i>Alethopteris lonchitica</i> Schlotheim ex Sternberg; Gillespie and Rheams, p. 196, pl. I, fig. 3; non p. 194, 199, pl. II, fig. 2 (= <i>Alethopteris urophylla</i>). |
| 1951 | <i>Alethopteris</i> nov. sp.?: Stockmans and Willière, pl. D, figs. 3–3a. | | 1985 | <i>Alethopteris serli forma lonchitifolia</i> Bertrand; Lyons <i>et al.</i> , p. 228, 238, pl. XIII, figs. c–d. |
| T 1955 | <i>Alethopteris valida</i> Boulay; Crookall, p. 13–17, pl. I, figs. 3–4, figs. 5–5a (same as Crookall 1932, pl. VI, fig. 3); text-figs. 5A–B (drawings); text-fig. 5C (reproduction of Boulay's illustration). | ? | 1985 | <i>Alethopteris</i> cf. <i>integra</i> (Gothan) Kidston; Gillespie and Crawford, p. 255, pl. III, fig. 4 (fragmentary). |
| ? 1957 | <i>Alethopteris davreuxii</i> (Brongniart) Göppert; Janssen, p. 145, fig. 132 (difficult to judge from the illustration). | k | 1996 | <i>Alethopteris valida</i> Boulay; Šimůnek, p. 18–20, pl. XV, figs. 7–8; pl. XVI, figs. 1–6; pl. XVII, figs. 1–3, figs. 4–7 (cuticles); pl. XVIII, fig. 1, figs. 2–8 (cuticles); text-figs 27–31. |
| 1959 | <i>Alethopteris (Callipteridium) sullivantii</i> (Lesquereux) Fontaine and White; Canright, pl. 4, fig. 11. | | 1997 | <i>Alethopteris valida</i> Boulay; Blake, p. 82, pl. 2, figs. 4–5. |
| T 1961 | <i>Alethopteris valida</i> Boulay; Buisine, p. 168–179 (including synonymy), pl. XLV, figs. 1–1b (reillustration of the holotype), figs. 2–2a; pl. XLVI, fig. 1; pl. XLVII, figs. 1a–2b; pl. XLVIII, figs. 1–1b (same as Corsin 1932, pl. XI, fig. 1), fig. 2; text-figs. 15a–c. | | 1997 | <i>Alethopteris davreuxii</i> (Brongniart) Göppert; Blake, p. 82, pl. 7, fig. 4; pl. 11, fig. 5. |
| 1963 | <i>Alethopteris grandini</i> Brongniart; Wood, p. 49, pl. 6, fig. 3. | | 2002 | <i>Alethopteris valida</i> Boulay; Blake <i>et al.</i> , p. 268, 290, pl. XVI, fig. 3. |
| 1963 | <i>Callipteridium sullivantii</i> (Lesquereux) Weiss; Wood, p. 50, pl. 6, fig. 6. | | 2005 | <i>Alethopteris valida</i> Boulay; Dilcher <i>et al.</i> , p. 161, fig. 4.3. |
| p 1978 | <i>Alethopteris evansi</i> Lesquereux; Gillespie <i>et</i> | | Excludenda: | <i>Alethopteris valida</i> Boulay; Dilcher and Lott, pl. 131, fig. 1 (same as Dilcher <i>et al.</i> 2005, fig. 4.3), figs. 2–3. |
| | | | 1938 | <i>Alethopteris valida</i> Boulay; Bell, p. 68–69, |

- pl. LXIV; pl. LXV, figs. 1–3; pl. LXVII, fig. 1 (Zodrow and Cleal 1998, p. 103 included all these specimens in *Praecallipteridium* cf. *jongmansii*).
- 1968 *Alethopteris valida* Boulay; Basson, pp. 72–73, pl. 11, fig. 2 (comparable with *Alethopteris grandinii*).
- 1982 *Alethopteris valida* Boulay; Oleksyshyn, pp. 104–105, figs 20G–H (the fragmentary specimens resemble *Alethopteris lesquereuxii*).

Description. Frond at least bipinnate. Last order rachis relatively straight, longitudinally striate, ca. 0.5 mm. Pinnules spaced, slightly obliquely inserted, decurrent, with a broadly confluent lamina (3 mm); these are subtriangular, with a bluntly pointed apex. Dimensions: 10–12 mm long and 5 mm broad; length/breadth ratio = 2–2.4. Lamina thick, vaulted. Midrib thin, clearly marked, visible in two third or more of the pinnule; lateral veins well spaced, one to twice forked, reaching the pinnule margin with a oblique angle. Vein density = ca. 30 veins per centimetre.

Remarks. *Alethopteris valida* is a very distinctive species that has been regularly recorded from upper Namurian to middle Westphalian strata, although generally as fragmentary specimens and single records. The species was originally described by Boulay (1876) from northern France, from where it was documented extensively by Buisine (1961). Although specimens of this species have been figured from several basins in the United States, Bell (1944, 1966) did not record *Alethopteris valida* from the Maritimes. Figured and described here is a fragment of last order pinna; although fragmentary and not well preserved, it is sufficiently characteristic to be assigned tentatively to the species as *Alethopteris* cf. *valida*.

Comparisons. *Alethopteris valida* is a distinctive species, easily separated from members of the genus by its thick lamina and large, subtriangular pinnules united by a broadly confluent lamina. It resembles *Lonchopteridium eschweilerianum*, but the subreticulate venation of the latter are distinctive.

Stratigraphic and geographic distribution. *Alethopteris valida* ranges from (Marsdenian?) Yeadonian to lower Bolsovian. In the Nord de la France, Buisine (1961) recorded it from upper Namurian (Yeadonian) to upper Westphalian B (Duckmantian), being most abundant in Westphalian A (Langsettian) strata. In Great Britain it is mostly confined to Westphalian A and B (Langsettian and Duckmantian; see Crookall 1955). In the Intrasudetic Basin, Šimůnek (1996) recorded this species from Namurian C to Westphalian B.

Occurrence in the Maritime Provinces, Canada.
CUMBER-LAND BASIN (NOVA SCOTIA): locality 1178 (GSC 10852).

Occurrence in the United States. ALABAMA: Gillespie and

Rheams (1985), Lyons *et al.* (1985), Dilcher and Lott (2005), Dilcher *et al.* (2005). GEORGIA: Lesquereux (1884), Gillespie and Crawford (1985). ILLINOIS: Janssen (1957). INDIANA: Canright (1959); Wood (1963). TENNESSEE: Lesquereux (1884). WEST VIRGINIA: Gillespie *et al.* (1978), Blake (1997), Blake *et al.* (2002).

Genus *Neuralethopteris* Cremer 1893
emend. Laveine 1967

- 1893 *Neuralethopteris* Cremer, p. 32–33.
1965 *Neuralethopteris* Cremer; Wagner, p. 38, 39, 40.
1967 *Neuralethopteris* Cremer; Laveine, p. 97–102.
1995 *Neuralethopteris* Cremer; Cleal and Shute, p. 10, 12.
2000 *Neuralethopteris* Cremer; Goubet *et al.*, p. 14–15.
2010 *Neuralethopteris* Cremer; Tenchov and Cleal, p. 300–301.

Type. *Neuralethopteris schlehanii* (Stur 1877) Cremer 1893.

Diagnosis. Pinnules tongue-shaped, with a cordate base, occasionally stalked in the proximal part, and more or less attached by the entire base in the distal part of the pinnae; apex more or less rounded. Terminal pinnule strongly varying in shape and size depending on the species: ovate, lanceolate or linear. Venation of alethopteroid type with a midvein strong, reaching nearly to the apex of the pinnule. Lateral veins departing at an acute angle, reaching the margin perpendicularly, forking two or three times, with first bifurcation close to the midvein, and the second about half way between the midvein and the margin, often directly following the major curvature of the veins; the third, if present, near the margin. (Shortened from Goubet *et al.* 2000, p. 14.)

Remarks. *Neuralethopteris* is a widely distributed and biostratigraphically important genus that has been recorded from middle Namurian to lower Westphalian strata. The presence of pinnules with alethopterid venation in combination with basally constricted bases caused most species to be initially assigned to *Neuropteris*.

Laveine (1967) and Tenchov and Cleal (2010) summarized the historical development of the concept of *Neuralethopteris*; and Goubet *et al.* (2000) documented the genus for the first time in North America, including five species not found in Europe. Furthermore, Laveine *et al.* (1992) recorded the presence of a bipartite frond without intercalary pinna elements on the rachises, as in *Alethopteris*, and indicated that the frond would be about 5 m long. Associated ovules are of the *Trigonocarpus*-type and pollen organs are of the *Aulacotheca/Boulayatheca/Whittleseya*-types.

According to Wagner (1984), *Neuralethopteris* is common and characteristic in both the *Neuralethopteris larischii-Pecopteris aspera* (Chokierian to Yeadonian) and *Lyginopteris hoeninghausii-Neuralethopteris schlehanii* (Langsettian) macrofloral zones. Although some records occur in the basal Duckmantian (e.g., Tenchov and Cleal 2010), the extinction of *Neuralethopteris* is usually placed at the end of the Langsettian Substage.

- Neuralethopteris pocahontas* (White 1900)
Goubet *et al.* 2000
(Figs. 8a–d)
- * 1900 *Neuropteris Pocahontas* White, p. 888–890, pl. CLXXXIX, figs. 4–4a; pl. CXCI, figs. 5–5a (holotype).
- 1900 *Neuropteris Pocahontas* var. *inæqualis* White, p. 890–892, pl. CLXXXVIII, figs. 5–5a; pl. CXC, fig. 7; pl. CXCI, figs. 1–4 (acc. to Goubet *et al.* 2000).
- 1937 *Neuropteris Pocahontas* White; Jongmans, p. 396, 397, 398, 400, 412; pl. 13, figs. 15–15a; pl. 14, figs. 16–20a; pl. 16, fig. 27; pl. 17, fig. 30.
- v 1944 *Neuropteris smithsi* Lesquereux; Bell, p. 79–80, pl. XXIX, fig. 2; pl. XXX, fig. 2 (reproduced partially herein as Fig. 8d); pl. XXXI, fig. 1 (Figs 8b–c herein), fig. 4; pl. XXXIII, fig. 3 (Fig. 8a herein), fig. 4; pl. LXVII, fig. 4.
- 1964 *Neuropteris pocahontas* White; Read and May, p. 6, pl. 4, fig. 2.
- v 1966 *Crossotheca pinnatifida* (Gutbier) Potonié; Bell, p. 16, pl. IV, fig. 1.
- p 1966 *Neuropteris pocahontas* White; Gillespie *et al.*, p. 90, 91, pl. 25, fig. 4; non pl. 25, figs. 2–3 (comparable with *Neuralethopteris sergiorum*).
- ? 1967 *Neuropteris cf. pocahontas* White; Tidwell, p. 43, pl. 5, figs. 4, 6.
- 1976 *Neuropteris pocahontas* White; Gillespie and Pfefferkorn, pl. I, figs. A, B.
- 1977 *Neuropteris pocahontas* White; Pfefferkorn and Gillespie, p. 23, pl. 2, fig. J (same as Gillespie and Pfefferkorn 1976, pl. I, fig. A), pl. 2, figs. K–L.
- 1978 *Neuropteris pocahontas* White; Gillespie *et al.*, p. 6, 7, 102–103, 115, 128, pl. 2, fig. 1 (same as Pfefferkorn and Gillespie 1977, pl. 2, fig. L); pl. 47, fig. 1 (same as Gillespie *et al.* 1966, pl. 25, fig. 4), fig. 2 (same as Pfefferkorn and Gillespie 1977, pl. 2, fig. K), fig. 3 (same as Gillespie and Pfefferkorn 1976, pl. I, fig. A, and Pfefferkorn and Gillespie 1977, pl. 2, fig. J), fig. 5 (same as Pfefferkorn and Gillespie 1977, pl. 2, fig. L), figs. 7–8.
- 1979 *Neuropteris pocahontas* White; Gillespie and Pfefferkorn, pl. 1, fig. 1.
- 1981 “*Neuropteris pocahontas*” White; Pfefferkorn and Gillespie, p. 160, 162, pl. 2, figs. 1–4.
- ? 1985 *Neuropteris (Neuralethopteris) pocahontas* White; Gastaldo, p. 292, pl. 3, fig. C (poorly figured).
- 1986 *Neuropteris pocahontas* White; Gillespie and Pfefferkorn, p. 127, 128, pl. 3, fig. 1 (same as Pfefferkorn and Gillespie 1981, pl. 2, fig. 3), pl. 3, fig. 2 (same as Gillespie and Pfefferkorn 1979, pl. 1, fig. 1).
- 1989 *Neuropteris pocahontas* White; Gillespie *et al.*, p. 5, 6, pl. 1, fig. 3 (same as Gillespie and Pfefferkorn 1976, pl. I, fig. A, and Gillespie *et al.* 1978, pl. 47, fig. 3).
- 1997 *Neuropteris (Neuralethopteris) pocahontas* White; Blake, p. 81, 83, 84, pl. 4, figs. 1–2; pl. 6, fig. 5; pl. 7, fig. 1.
- § T 2000 *Neuralethopteris pocahontas* (White) Goubet *et al.*, p. 18–19 (including synonymy), figs. 5.3–5.6; fig. 6 (drawing); fig. 7.3 (photograph of White's holotype); figs. 7.4–7.5 (same as White 1900, pl. CLXXXVIII, figs. 5–5a); figs. 7.6–7.7; fig. 17.10 (associated with seeds).
- 2002 *Neuralethopteris pocahontas* (White) Goubet *et al.*; Blake *et al.*, p. 268, pl. XIV, figs. 3–4; pl. XV, fig. 9 (same as Pfefferkorn and Gillespie 1977, pl. 2, fig. L, and Gillespie *et al.* 1978, pl. 47, fig. 5).
- 2005 *Neuralethopteris pocahontas* (White) Goubet *et al.*; Dilcher *et al.*, p. 163, fig. 4.5.
- 2005 *Neuralethopteris pocahontas* (White) Goubet *et al.*; Dilcher and Lott, pl. 134, fig. 2 (same as Dilcher *et al.* 2005, fig. 4.5); pl. 135, fig. 3; pl. 136, fig. 3 (difficult to judge from the illustration).

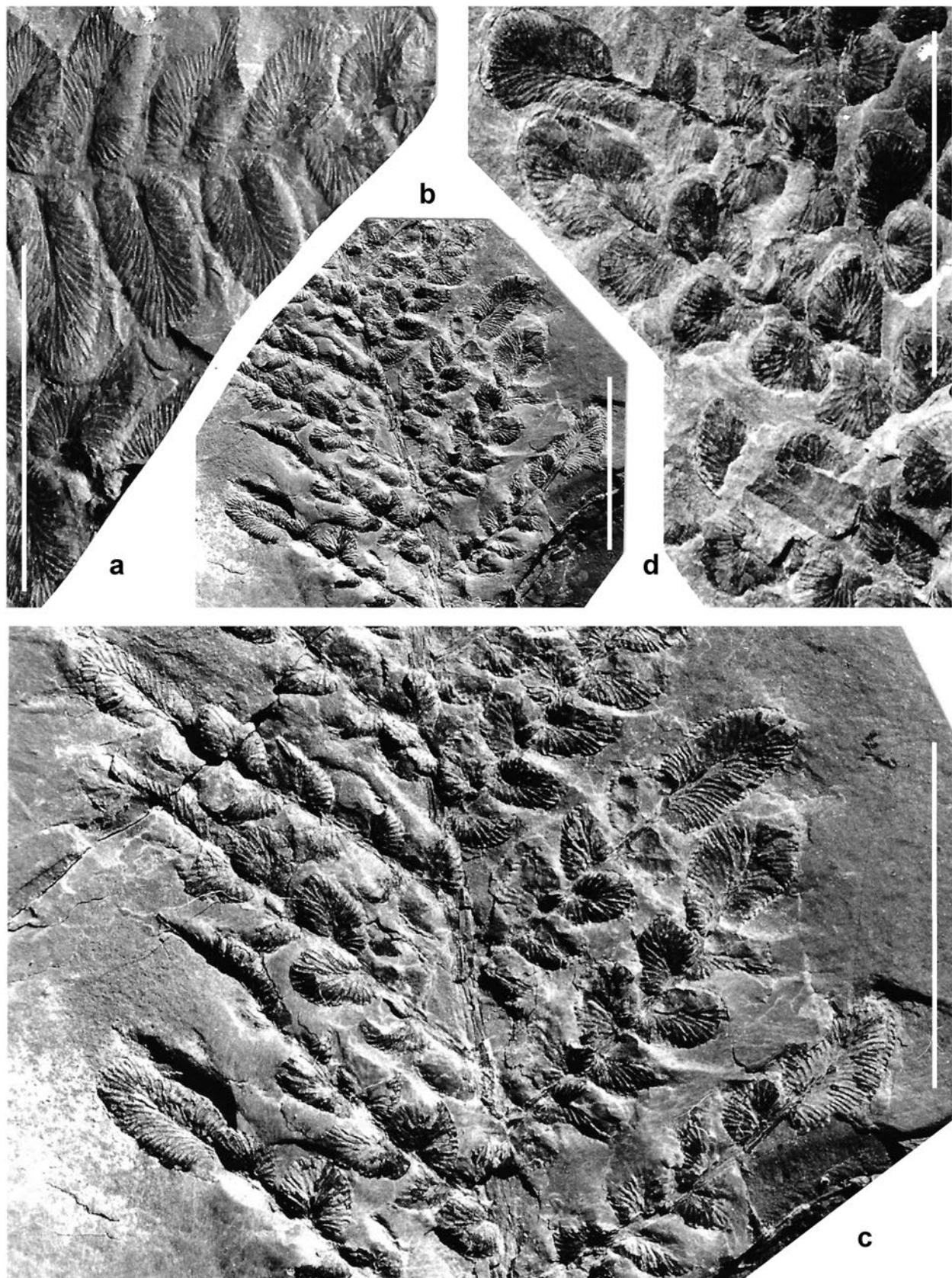
Description. Frond at least bipinnate. Penultimate order rachis straight, longitudinally striate, ca. 0.75 mm wide. Last order pinnae subrectangular, inserted at 60–80°. Last order rachis straight, rounded, longitudinally striate, ca. 0.25 mm wide. Pinnules alternate, closely spaced, either oblong, with cordate base, or rounded and broadly attached to the rachis. Dimensions: up to 30 mm long and 6–8 mm broad. Lamina thick, vaulted. Venation well-marked; in the smaller pinnules the midrib is not clearly differentiated and lateral veins, up to two times forked, depart directly from the rachis; in larger, more elongate pinnules the straight midrib extends in the lower two thirds of the pinnule and lateral veins are two (rarely three) times forked. Vein density = ca. 55 veins per centimetre.

Remarks. *Neuralethopteris pocahontas* is a very variable species that, according to Gillespie *et al.* (1978), grades morphologically into *Neuralethopteris smithsii*. Although Goubet *et al.* (2000) also noted that it is difficult to distinguish these two species in eastern North America, they did not follow Williams's (1937) proposal to synonymize the two taxa (along with *Neuralethopteris schlehanii*), citing stratigraphic and geographic differences.

I include in *Neuralethopteris pocahontas* all the specimens from Nova Scotia previously figured and described by Bell (1944) as *Neuropteris smithsii* and that figured by Bell (1966) as *Crossotheca pinnatifida* (= *Remia pinnatifida* — an upper Stephanian species). Bell (1944) records *Neuralethopteris smithsii* from 18 localities, but all his figured specimens are from locality 1392, Inverness County, Cape Breton Island. This focus is possibly due to poor and/or fragmentary preservation in all other localities, an explanation supported by the fact that most of the material that I have reviewed is very fragmentary.

Neuralethopteris pocahontas is usually recorded from fragmentary ultimate or penultimate order pinnae, thus preventing an understanding of its frond architecture.

Comparisons. Larger, more elongate pinnules of both *Neuralethopteris pocahontas* and *Neuralethopteris smithsii* have similar size and shape; but lateral veins in the latter reach the



pinnule margin at approximate right angles, in contrast to an obtuse angle in *Neuralethopteris pocahontas*. In addition, the smallest pinnules of *Neuralethopteris pocahontas* do not show a clearly differentiated midrib, and veins emanate directly from the rachis. *Neuralethopteris pocahontas* has superficial similarities with some specimens of the recently described *Wagneropteris minima*. The latter also has ovoid to subrectangular pinnules, commonly attached by a short, broad stalk; but the first anadromous and catadromous pinnules of last order pinnae are shorter than the standard laterals, allowing space for intercalary pinnules on the penultimate rachis.

Stratigraphic and geographic distribution. Goubet *et al.* (2000) recorded *Neuralethopteris pocahontas* as very common in lower Langsettian strata of the Pocahontas Formation in West Virginia, occurring in nearly all known plant fossil localities. The type material is from Pottsville, Southern Anthracite Field, Appalachian Basin, where Blake *et al.* (2002) reported the species as endemic. Prior to the present work, *Neuralethopteris pocahontas* has been reported only from the United States.

Occurrence in the Maritime Provinces, Canada. CUMBERLAND BASIN (NOVA SCOTIA): Bell (1944): locality 1392 (GSC 3089 + GSC 9361 + GSC 9362 + GSC 9363 + GSC 9365); NEW BRUNSWICK: Bell (1966): locality 887 (GSC 6627 + GSC 6632 + GSC 6638 + GSC 6639 + GSC 6643 + GSC 6644 + GSC 15040).

Occurrence in the United States. ALABAMA: White (1900), Gastaldo (1985), Gillespie and Rheams (1985), Dilcher and Lott (2005), Dilcher *et al.* (2005). GEORGIA: Gillespie and Pfefferkorn (1976), Pfefferkorn and Gillespie (1977), Gillespie *et al.* (1978), Gillespie *et al.* (1989). PENNSYLVANIA: White (1900), Goubet *et al.* (2000). UTAH: Tidwell (1967). VIRGINIA: Pfefferkorn and Gillespie (1977), Gillespie *et al.* (1978), Gillespie and Pfefferkorn (1979), Pfefferkorn and Gillespie (1981), Gillespie and Pfefferkorn (1986), Blake *et al.* (2002). WEST VIRGINIA: White (1900), Read and Maymay (1964), Gillespie *et al.* (1966), Pfefferkorn and Gillespie (1977), Gillespie *et al.* (1978), Pfefferkorn and Gillespie (1981), Gillespie and Pfefferkorn (1986), Blake (1997), Goubet *et al.* (2000).

Neuralethopteris schlehani (Stur 1877) Cremer 1893
(Figs. 9a–d)
* ? 1871 *Neuropteris Selwyni* Dawson, p. 50, pl. XVII,

- fig. 198 (schematic drawing — synonymy first proposed by Stöpes 1914).
- | | |
|-------------|--|
| * 1877 | <i>Neuropteris Schlehani</i> Stur, p. 289 [183], Taf. XI [XXVIII], figs. 7–8c. |
| * 1877 | <i>Neuropteris Dluhoschi</i> Stur, p. 289 [183]–290 [184], Taf. XI [XXVIII], fig. 9 (acc. to Zeiller 1888). |
| 1877 | <i>Neuropteris microphylla</i> Brongniart; Heer, p. 24, Taf. V, fig. 6a; Taf. VI, figs. 1–9. |
| * p 1879–84 | <i>Neuropteris Elrodi</i> Lesquereux, p. 107–108, pl. XIII, fig. 4 (acc. to Zeiller 1888); non p. 735–736, pl. XCVI, figs. 1–2 (= <i>Neuralethopteris biformis</i> acc. to Goubet <i>et al.</i> 2000). |
| § 1893 | <i>Neuralethopteris Schlehani</i> (Stur) Cremer, p. 33. |
| ? 1914 | <i>Neuropteris Selwyni</i> Dawson (? <i>Neuropteris Schlehani</i> Stur); Stöpes, p. 64–66, pl. XV, fig. 37 (photograph of Dawson's holotype — fragmentary and poorly preserved); text-fig. 12 (drawing). |
| 1934 | <i>Neuropteris dluhoschi</i> Stur; Read, p. 81, 83–84, pl. 17, fig. 5. |
| 1937 | <i>Neuropteris Schlehani</i> Stur; Jongmans, p. 402, 403, 412, pl. 21, fig. 44; pl. 22, figs. 48–49 (together with <i>Aulacotheca</i>). |
| 1941 | <i>Neuropteris Dluhoschi</i> Stur; Arnold, p. 59, pl. I, figs. 3–4. |
| v 1944 | <i>Neuropteris schlehani</i> Stur; Bell, p. 79, pl. XXX, fig. 3; pl. XXXII; pl. XXXIII, figs. 5–6. |
| 1947 | <i>Neuropteris Schlehani</i> Stur; Arnold, p. 220, fig. 105B. |
| 1949 | <i>Neuropteris Schlehani</i> Stur; Arnold, p. 199–201, pl. XXIV, fig. 7 (same as Arnold 1947, fig. 105B), figs. 8, 9; pl. XXIV, fig. 10. |
| * 1952a–53 | <i>Neuropteris schlehanoides</i> Stockmans and Willière, p. 233, pl. XXXI, figs. 3–3a, 7y; pl. XXXVI, fig. 2 (acc. to Cleal and Shute 1995). |
| 1957 | <i>Neuropteris schlehani</i> Stur; Leggewie and Schonefeld, p. 13–15, Taf. 4, Abb. 1–5; Taf. 5, Abb. 1–4; Taf. 6, Abb. 1–4; Taf. 7, Abb. 1. |
| 1960 | <i>Neuropteris parvifolia</i> Stockmans; Jongmans, p. 61, Taf. 23, figs. 127–127a (photograph of Heer's 1877, Taf. VI, fig. 3), figs. 128–128a (same as Heer, 1877, Taf. VI, fig. 4), figs. 129–130a. |
| v 1966 | <i>Neuropteris schlehani</i> Stur; Bell, pl. IV, fig. 7 (counterpart of Bell 1944, pl. XXXIII, fig. 5), fig. 12; pl. V, fig. 9; pl. VI, fig. 5 (same as Bell |

Figure 8 (previous page). (a) *Neuralethopteris pocahontas*. GSC 3089. Detail of the specimen figured as *Neuropteris smithsii* by Bell (1944, pl. XXXIII, fig. 3). Origin: Whale Cove, Inverness County, about 0.4 km south of Grey Point (locality 1392). (b) *Neuralethopteris pocahontas*. GSC 9361. Penultimate order pinna closely similar, although with smaller pinnules, to White's holotype. As *Neuropteris smithsii* in Bell (1944, pl. XXXI, fig. 1; pl. LXVII, fig. 4). Origin: same as Fig. 8a (locality 1392). (c) *Neuralethopteris pocahontas*. Enlargement of Fig. 8b. Note the thick, vaulted lamina and lateral veins departing directly from the rachis. (d) *Neuralethopteris pocahontas*. GSC 9362. As *Neuropteris smithsii* in Bell (1944, pl. XXX, fig. 2). Origin: same as for Figs. 8a–8c (locality 1392). Repository: Geological Survey of Canada, Ottawa. Scale bar = 1 cm.

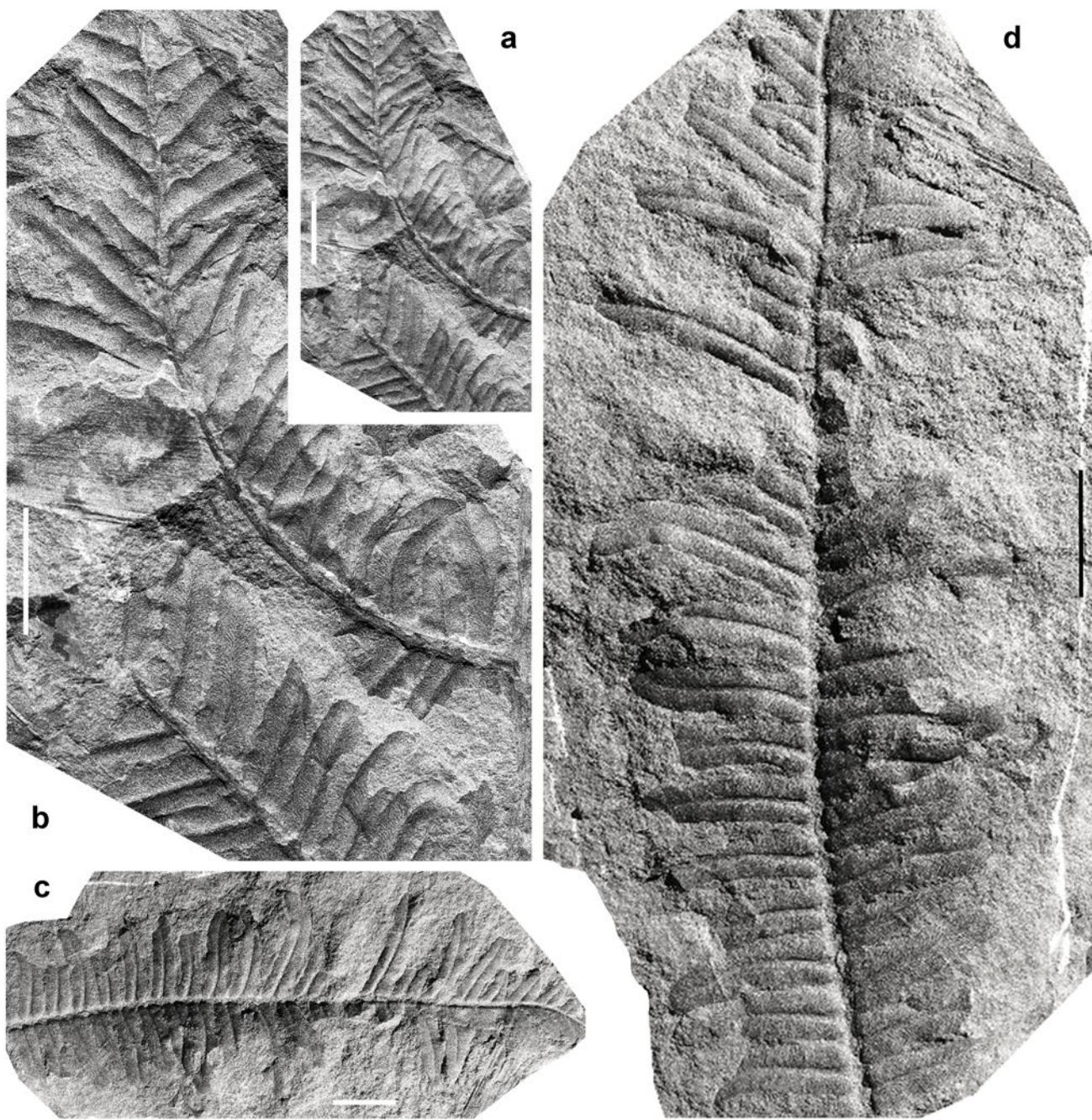


Figure 9. (a) *Neuralethopteris schlehanii*. GSC 10959. Previously figured by Bell (1944, pl. XXXIII, fig. 5). Origin: Cape Maringouin, south of Hard Ledge, New Brunswick (loc. 1357). (b) Enlargement of Fig. 9a. (c) *Neuralethopteris schlehanii*. GSC 10958. Last order pinna showing the larger, most characteristic pinnules: subrectangular, with subparallel margins, obtuse apex and cordate base. Figitured by Bell (1944, pl. XXXIII, fig. 6). Origin: same as Figs. 9a–9b. (d) Enlargement of Fig. 9c. Repository: Geological Survey of Canada, Ottawa. Scale bar = 1 cm.

- | | |
|---|--|
| 1944, pl. XXXII). 1967 <i>Neuralethopteris schlehani</i> (Stur) Cremer; Laveine, p. 113–120 (including synonymy), pl. V, figs. 1–3b; pl. VI, figs. 1–4; pl. VII, figs. 1–3a; pl. VIII, figs. 1–4a; text-fig. 18. * 1977 <i>Neuropteris rectinervis</i> f. <i>obtusa</i> Tenchov, p. 59–60, Taf. XX, figs. 3–4 (acc. to Cleal and Shute 1995). | * 1977 <i>Neuropteris lata</i> Tenchov, p. 60, Taf. XXI, figs. 2–3 (acc. to Cleal and Shute 1995). * 1977 <i>Neuropteris longifolia</i> Tenchov, p. 61, Taf. XXI, figs. 4–7, 9 (acc. to Cleal and Shute 1995) (all specimens figured and described by Tenchov as <i>Neuropteris rectinervis</i> f. <i>obtusa</i> , <i>Neuropteris lata</i> and <i>Neuropteris longifolia</i> originated from localities where that author |
|---|--|

- 1984 also records *Neuralethopteris schlehanii*).
Neuropteris schlehanii Stur; Jennings, p. 307, pl. 4, fig. 1.
- p 1985 *Neuralethopteris schlehanii* (Stur) Cremer; Lyons et al., p. 232, pl. VI, figs. c-d; pl. XI, fig. d; non pl. XIV, fig. c (= *Neuralethopteris biformis* acc. to Goubet et al. 2000).
- 1985 *Neuralethopteris schlehanii* (?) (Stur) Cremer; Lyons et al., p. 232–233, pl. X, fig. c.
- 1985 *Neuropteris pocahontas* cf. var. *inaequalis* White; Lyons et al., p. 219, pl. VI, fig. g (acc. to Goubet et al. 2000).
- 1985 *Neuropteris* cf. *schlehanii* Stur; Gillespie and Crawford, p. 252, 255, pl. III, fig. 7.
- 1985 *Neuropteris pocahontas* White; Gillespie and Rheams, p. 194, 196, 199, pl. II, fig. 7 (acc. to Goubet et al. 2000).
- 1995 *Neuralethopteris schlehanii* (Stur) Cremer; Cleal and Shute, p. 24 (including synonymy), fig. 8 (p. 13).
- 1996 *Neuralethopteris schlehanii* (Stur) Cremer; Brousmiche Delcambre et al., p. 83, pl. 3, figs. 3–6a; pl. 7, figs. 1–8; pl. 8, figs. 1–3; pl. 10, fig. 11.
- 1997 *Neuralethopteris schlehanii* (Stur) Cremer; Blake, p. 84, 85, 90, pl. 3, fig. 8; pl. 8, figs. 1–2; pl. 9, fig. 5; pl. 10, fig. 2.
- 1998 *Neuralethopteris schlehanii* (Stur) Cremer; Brousmiche Delcambre et al., p. 106–107, pl. 12, figs. 1–12; pl. 13, figs. 1–4.
- 2000 *Neuralethopteris schlehanii* (Stur) Cremer; Goubet et al., p. 15–18 (including synonymy), figs. 4.1–4.2; figs. 5.1–5.2, 5.7–5.8.
- 2002 *Neuralethopteris schlehanii* (Stur) Cremer; Blake et al., p. 264, 268, 269, pl. XV, figs. 7–8.
- p 2002 *Neuropteris bulupalganensis* Zalessky; Blake et al., p. 263, 289, pl. XIII, fig. 9; non p. 288, pl. XIII, fig. 3 (= *Senftenbergia aspera*).
- 2010 *Neuralethopteris schlehanii* (Stur) Cremer; Tenchov and Cleal, p. 301, 303, pl. I, figs. 1–2.
- v 2010 *Neuralethopteris schlehanii* (Stur) Cremer; Wagner and Álvarez-Vázquez, p. 254, 257, 258, pl. VI, fig. 1.
- 2014 *Neuralethopteris schlehanii* (Stur) Cremer; Bashforth et al., p. 247, pl. III, figs. 2, 5, 8.
- 2018 *Neuralethopteris schlehanii* (Stur) Cremer; Lyons and Sproule, p. 319, figs. 3a–b.
- Excludenda:
- 1985 *Neuropteris schlehanii* Stur; Gillespie and Rheams, p. 194, 196, 199, pl. II, figs. 9–10 (= *Neuralethopteris biformis* acc. to Goubet et al. 2000).

Description. Frond at least bipinnate. Penultimate order pinnae apparently lanceolate, with an approximately constant width in the lower three quarters, then quickly taper-

ing to form an acute apex. Dimensions: up to 160 mm long and 150 mm wide. Penultimate order rachis straight, longitudinally striate, ca. 1.25–1.50 mm wide. Last order pinnae alternate, closely spaced or slightly touching each other by their margins; subrectangular, elongate, with subparallel margins; apical pinnule lanceolate to oval, small but longer than the adjacent laterals. Dimensions: 30–110 mm long and 6–15 mm wide; length/breadth ratio = 5–6.5. Last order rachis inserted at 50–75°, longitudinally striate, rounded, ca. 0.5–0.75 mm. Pinnules alternate, close, subperpendicular or obliquely inserted (45–60°), of fairly constant size along the pinna; the larger ones are subrectangular, elongate, with subparallel margins, obtuse apex and cordate base, attached to the rachis through a short stalk; smaller pinnules are subtriangular to ovoid, with cordate base, except in the apical parts of pinnae where they are more broadly united to the rachis. Dimensions: 4–14 mm long and 1.5–3.5 mm broad; length/breadth ratio = 2.5–4. Lamina thick, vaulted. Venation clearly marked. Midrib thick, straight, distinct in the lower three quarters of the pinnule length. Lateral veins thin, usually twice forked, the first fork occurring near the midrib, the second about half-way between the midrib and the margin; lateral veins reaching the pinnule margin with 75–85°. Vein density = 40–50 veins per centimetre.

Remarks. Specimens figured as *Neuropteris schlehanii* by Bell (1944, 1966) confirm the presence of this species in the Maritime Provinces. This is particularly the case for the well-preserved terminal of antepenultimate order pinna figured from the roof shales of coal n° 1 at Springhill, Nova Scotia (Bell 1944, pl. XXXII; Bell 1966, pl. VI, fig. 5), which shows the characteristic medium-sized pinnules with cordate base, broadly rounded apex and subparallel margins. *Neuralethopteris schlehanii* is found also in association with White's *Whittleseya brevifolia* (male synangium) in several localities.

Dawson's (1871) fragmentary type of *Neuropteris selwynii*, a poorly preserved fragment of last order pinna showing only four pinnules, was photographically illustrated by Stopes (1914, pl. XV, fig. 37), who suggested its synonymy with *Neuropteris schlehanii*. This synonymy was accepted by Bell (1944) who stated that Dawson's *Neuropteris selwynii* is merely an "aberrant" form of *Neuropteris schlehanii*. Bell (1944) also included Kidston's *Neuropteris rectinervis* (= *Neuralethopteris rectinervis*) in synonymy with *Neuropteris schlehanii*. In contrast, Laveine (1967) includes Stopes's illustration of *Neuropteris selwynii* in the synonymy of *Neuralethopteris rectinervis*; and Tenchov and Cleal (2010) compare the venation pattern of *Neuropteris selwynii* with that of *Neuralethopteris jongmansii*.

I have not been able to review Dawson's holotype of *Neuropteris selwynii*, so it is only questionably included in the synonymy of *Neuralethopteris schlehanii*. If it were proved that *Neuropteris selwynii* and *Neuralethopteris schlehanii* are conspecific, Dawson's name would take priority. Although Stur's type material of *Neuropteris schlehanii* is also fragmentary, consisting three fragments

of last order pinnae without apical pinnules, the use of the name *Neuralethopteris schlehanii* should justify the proposal for conservation of the latter name should the synonymy be confirmed (see also Tenchov and Cleal 2010).

Comparisons. The larger pinnules of both *Neuralethopteris pocahontas* and *Neuralethopteris schlehanii* are similar. However, the smaller pinnules — rounded, broadly attached to the rachis and without clearly differentiated midvein — are common and characteristics in *Neuralethopteris pocahontas* but absent in *Neuralethopteris schlehanii*. *Neuralethopteris jongmansii* has longer and broader pinnules and more regular venation, both in terms of curvature and density. Pinnules of *Neuralethopteris biformis* are more subtriangular, with margins gradually tapering in the distal two thirds. In addition, the venation *Neuralethopteris biformis* is coarse, with lateral veins twice or occasionally three-times forked, reaching the margin at an angle of about 60°.

Stratigraphic and geographic distribution. *Neuralethopteris schlehanii* is the most abundant and widely distributed species of *Neuralethopteris* over the paleoequatorial belt. It ranges in age from upper Namurian A to basal Duckmantian. The type material is from Vítkovice, Upper Silesian Basin, Czech Republic (Stur 1877). The species is common in Langsettian strata of Great Britain (Crookall, 1955). In France, Laveine (1967) recorded it from Westphalian A (Langsettian) strata of Nord/Pas-de-Calais, and Brousmiche Delcambre *et al.* (1996, 1998) from the Namurian B and C of Briançon. The species was recorded in Belgium from the upper part of the Namurian A up to the top of Westphalian A (Langsettian; Stockmans and Willière 1952a–53, 1952b). In the Iberian Peninsula, Wagner and Álvarez-Vázquez (2010) recorded *Neuralethopteris schlehanii* from middle Namurian strata of the central Pyrenees, from the upper Namurian of La Camocha Coalfield of northwestern Spain, from the Langsettian of different localities in the Cantabrian Mountains of northwestern Spain, and from upper Langsettian strata of the Peñarroya-Belmez-Espiel Coalfield of southwestern Spain. Tenchov and Cleal (2010) reported the species in Langsettian and basal Duckmantian strata of the Dobrudzha Coalfield of Bulgaria.

Occurrence in the Maritime Provinces, Canada. CUMBERLAND BASIN (NOVA SCOTIA): Bell (1944): locality 187 (four pieces without catalogue number — cf; fragmentary); locality 876 (GSC 5929 — together with one seed); locality 1337 (GSC 10957); locality 1354 (GSC 10960); locality 1357 (GSC 10958 + GSC 10959). Bell (1966): locality 1337 (GSC 10957 — same as 1944); locality 1357 (GSC 14955 + GSC 14946). NEW BRUNSWICK: Bell (1944): locality 793 (one piece without catalogue number—fragmentary); locality 3557 (one piece without catalogue number). Bell (1966): locality 1429 (GSC 14954). Dawson (1871): as *Neuropteris selwyni* — included questionably in the synonymy. Stopes (1914): same as Dawson (1871). NEW BRUNSWICK MUSEUM COLLECTION: NBMG 12052/1

(together with *Sphenopteris valida*). Bashforth *et al.* (2014): NBMG 15438 + NBMG 16196 + NBMG 16218a).

Occurrence in the United States. ALABAMA: Lesquereux (1879–80), Gillespie and Rheams (1985), Lyons *et al.* (1985), Goubet *et al.* (2000). COLORADO: Read (1934), Arnold (1941). GEORGIA: Lesquereux (1884), Gillespie and Crawford (1985). ILLINOIS: Jennings (1984). INDIANA: Lesquereux (1879–80). MASSACHUSETTS: Lyons and Sproule (2018); MICHIGAN: Arnold (1947, 1949). WEST VIRGINIA: Jongmans (1937), Goubet *et al.* (2000), Blake (1997), Blake *et al.* (2002).

Neuralethopteris smithsii (Lesquereux 1879)

- Goubet *et al.* 2000
(Figs. 10a–d)
- | | | |
|-----|---------|---|
| * ? | 1831 | <i>Neuropteris microphylla</i> Brongniart, p. 245, pl. 74, figs. 6–6a (reproduction of Brongniart illustration, as <i>Neuropteris heterophylla</i> , by Crookall 1959, text-fig. 35). |
| * | 1879–84 | <i>Neuropteris Smithsii</i> Lesquereux, p. 106–107, 734–735, pl. XIII, fig. 1, fig. 2 (lectotype designated by Goubet <i>et al.</i> 2000), figs. 3–3a; pl. XCVI, figs. 3–3a. |
| | 1905 | <i>Neuropteris cf. Smithii</i> Lesquereux; White, p. 380, pl. LV (magnificent specimen — antepenultimate order pinna, more than 50 cm long). |
| | 1926 | <i>Neuropteris smithii</i> Lesquereux; Butts, p. 224, pl. 70C, figs. 1–3. |
| | 1937 | <i>Neuropteris Smithsii</i> Lesquereux; Jongmans, p. 400, 401, 404, 412, pl. 20, figs. 42–43. |
| * v | 1944 | <i>Sphenopteris minuscula</i> n. sp. Bell, p. 63–64, pl. VI, figs. 1, 3–5; pl. X, fig. 5; pl. XI; pl. LXVI, figs. 4–5. |
| ? p | 1967 | <i>Neuropteris rarinervis</i> Bunbury; Laveine, pl. G, figs. 2–2a (photograph of the holotype of <i>Neuropteris microphylla</i>); text-fig. 31d; non p. 181–190, pls. XL–XLVII (= <i>Laveineopteris rarinervis</i>); text-figs. 31a–c, e–i (drawings of <i>Laveineopteris rarinervis</i>). |
| | 1979 | <i>Neuropteris smithsii</i> Lesquereux; Gillespie and Pfefferkorn, pl. 1, figs. 5–6. |
| ? | 1985 | <i>Neuropteris (?Neuralethopteris) smithsii</i> Lesquereux; Gastaldo, p. 292, pl. 3, fig. B (poorly figured). |
| | 1985 | <i>Neuropteris smithi</i> (sic) Lesquereux; Gillespie and Rheams, p. 196, pl. I, fig. 1. |
| | 1985 | <i>Neuropteris smithsii</i> Lesquereux; Lyons <i>et al.</i> , p. 234, pl. II, figs. A–C, fig. E (? — fragmentary, isolated pinnule); pl. VI, figs. a–b; pl. X, figs. a–b. |
| | 1985 | <i>Neuropteris smithi</i> (sic) Lesquereux; Gillespie and Crawford, p. 252, pl. II, fig. 6. |
| § | 2000 | <i>Neuralethopteris smithsii</i> (Lesquereux) Goubet <i>et al.</i> , p. 19–23 (including synonymy), figs. 7.1–7.2; figs. 8.1–8.2 (drawings); |

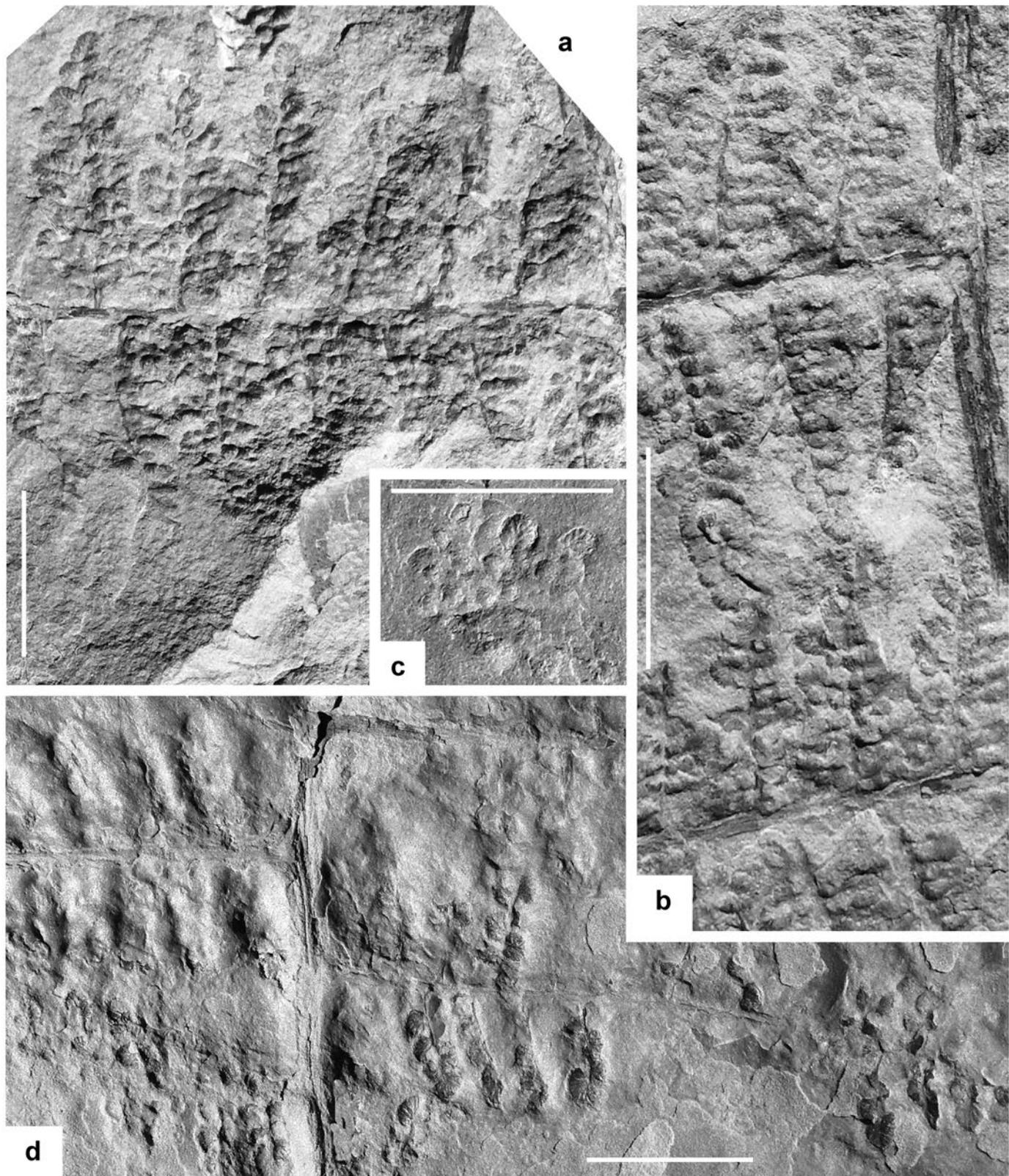


Figure 10. (a) *Neuralethopteris smithsii*. GSC 5857. Lower part of the holotype of *Sphenopteris minuscula* (Bell 1944, pl. XI). Origin: East Branch River Philip, Oxford area, Nova Scotia (locality 860). (b) Detail of the holotype. Note the close similarity to the specimen figured by Goubet *et al.* (2000, figs. 7.1 and 7.2). Origin: same as Fig. 11a. (c) GSC 5853. Paratype of *Sphenopteris minuscula*. Previously figured by Bell (1944, pl. VI, figs 1, 5). Origin: same as Figs. 11a–11b. (d) GSC 5593. Another paratype of *Sphenopteris minuscula*. Figured by Bell (1944, pl. X, fig. 5). Origin: same as Figs. 11a–11c. Repository: Geological Survey of Canada, Ottawa. Scale bar = 1 cm.

- 2002 figs. 9.1–9.4; figs. 15.5–15.7 (together with *Aulacotheca* prepollen organs).
- Neuralethopteris smithsii* (Lesquereux)
Goubet *et al.*; Blake *et al.*, p. 264, 267, 268, pl. XIV, fig. 7; pl. XV, fig. 1; pl. XVIII, fig. 4.

Description. Frond at least tripinnate. Antepenultimate order rachis straight, longitudinally striate, ca. 4 mm wide. Penultimate order pinnae alternate, apparently subtriangular (always incomplete), with at least 85 mm long and up to 55 mm wide. Penultimate order rachis inserted at 85–90°, straight, longitudinally striate, ca. 1.5–2 mm wide. Last order pinnae alternate, subtriangular, elongated, inserted at 80–90°. Pinna terminal relatively large, massive-looking in pinnae with smaller (shorter) pinnules, more elongate in those with larger (longer) pinnules. Dimensions: up to 16 mm long and 6–7 mm wide. Last order rachis inserted at 80–90°, straight, ca. 0.4–0.5 mm. Pinnules alternate, subperpendicularly inserted, ovate or rounded, with cordate base even in distal parts. Dimensions: 2–6 mm long and 1.5–2.5 mm wide; length/breadth ratio = 1.3–2.4. Lamina thick, vaulted. Venation well marked, widely spaced. Midrib thin, deeply imprinted in the convex lamina. Lateral veins thin, oblique, twice forked, the first time near the midrib; lateral veins reaching the margin at approximately right angle. Vein density = 30–32 veins per centimetre.

Remarks. Both Bell (1944) and Laveine (1967) suggested the inclusion of *Neuropteris smithsii* with *Neuralethopteris* on the basis of its fairly constant association with the prepollen-bearing synangium *Whittleseya desiderata*, a species figured and described from Nova Scotia by White (1901, pl. VII, figs. 1–2). In the same paper, White figured and described another two species, *Whittleseya brevifolia* (pl. VII, figs 3–3a) and *Whittleseya dawsoniana* (pl. VII, figs. 4–4a), based on specimens from Nova Scotia and New Brunswick, respectively. To confirm or discard the possible synonymy of part or of all these taxa, the palynological content of these species should be studied, along with that of *Whittleseya concinna* (and its varieties, *Whittleseya concinna* var. *lata* and *Whittleseya concinna* var. *arcta*), which was described by Matthew (1910) from the Fern Ledges.

Goubet *et al.* (2000) formally transferred *Neuropteris smithsii* to *Neuralethopteris*. *Neuralethopteris smithsii* was analyzed extensively by Goubet *et al.* (2000), who reviewed the occurrence of *Neuralethopteris* in eastern North America. These authors designated as lectotype the specimen figured by Lesquereux (1880, pl. XIII, fig. 2). Goubet *et al.* (2000) did not compare *Neuralethopteris smithsii* with *Neuropteris microphylla*, a species described by Brongniart in 1831 from a single specimen from Wilkesbarre, Pennsylvania, in the same general area (the Appalachian Basin) as the type material of *Neuralethopteris smithsii*. I think that Brongniart's specimen, photographed by Laveine (1967, pl. G, figs. 2–2a), who included it in *Neuropteris rarineris* (now *Laveineopteris rarineris*), fits the shape and dimensions of *Neuralethopteris smithsii*. Even though Laveine's photograph

does not show the venation — Stockmans 1933 examined the type of *Neuropteris microphylla* and noted that its venation is not well preserved — I consider the resemblance so close that I include *Neuropteris microphylla* questionably in synonymy with *Neuralethopteris smithsii*. Should this synonymy be confirmed, the widespread use of the name *Neuralethopteris smithsii* should justify the proposal for its conservation. *Neuropteris microphylla* was consistently misidentified in Europe until Stockmans (1933) described the European form as a new species, *Neuropteris parvifolia*.

Bell (1944) described and illustrated *Sphenopteris minuscula* from several poorly preserved specimens and compared it with *Sphenopteris nummularia* and *Sphenopteris hollandica* (both now in *Eusphenopteris*) and *Neuropteris smithsii*. He thus appeared in no doubt that the attribution of *Sphenopteris minuscula* was to the pteridosperms. Although Bell mentioned three different localities for this new species, all figured specimens, including the holotype, came from locality 860 in Nova Scotia. (In the plate caption, the holotype was wrongly indicated as having come from locality 1392, although this site was not mentioned in the description of *Sphenopteris minuscula*.) Bell's specimens are impressions on siltstone to fine grained sandstones. Because of the combination of the coarseness of the sediment grain and the vaulted lamina, the exact outline of pinnules and venation is rarely discernible, making detailed observation and photography difficult. No subsequent records of *Sphenopteris minuscula* are known. I regard *Neuralethopteris smithsii* as the senior synonym of *Sphenopteris minuscula*.

At first sight, *Sphenopteris minuscula* could be also compared with several species of *Margaritopteris*. Gothan (1913) based that genus on *Margaritopteris pseudocoemansii*, a species that Laveine *et al.* (1977, p. 783) regarded as synonymous with *Margaritopteris conwayi*. In the latter extensive paper, *Margaritopteris* is placed in a series leading from the lower Namurian *Neuropteris multivenosa* (a species later referred to *Margaritopteris* by Cleal and Shute 1995) through *Margaritopteris* of Westphalian age to *Praecallipteridium* and *Callipteridium* of upper Asturian to Stephanian age. In this view, progressive reduction of elements of a large frond and fusion of pinnular elements lead from intercalated pinnae to intercalated pinnules on ante-penultimate and penultimate rachises and to larger, fused pinnules in *Praecallipteridium* and *Callipteridium*. The most complete documentation of *Margaritopteris conwayi* is by Crookall (1976), who figured a large antepenultimate pinna fragment more than 24 cm long from Duckmantian strata of South Wales. Crookall's illustration shows that *Margaritopteris* pinnules are united to each other and attached to the rachis by the whole base. In addition, veins are undivided and the faintly longitudinally striate rachis usually bears close transverse bars. None of these characteristics are present in *Sphenopteris minuscula*.

Although European authors have shown an awareness of *Neuropteris smithsii*, this species has not been recorded as such from Europe.

Comparisons. Larger pinnules of *Neuralethopteris pocahon-*

tas possess similar size and shape to those of *Neuropteris smithsii*. However, the smallest pinnules of the former species do not show a clear differentiated midrib: several parallel veins originate directly from the rachis, forking twice. Although the midrib is more clearly marked in elongated pinnules, some veins enter directly from the pinna axis, and lateral veins reach the margins at obtuse angles, not at right angles as in *Neuralethopteris smithsii*. Some similarity exists between *Neuropteris smithsii* and *Neuralethopteris weilii* (Josten and Amerom 2003), a species from middle Namurian strata of Westphalia, western Germany. Pinnules of the latter species are small, oval to subrectangular, have slightly convex margins, slightly constricted bases and rounded apices. Additionally, apical pinnules in *Neuralethopteris weilii* are wide, fused, and have loose venation, with lateral veins forked up to three times. *Neuralethopteris smithsii* shows also some similarity with the lower Bolsovian species *Wagneropteris minima* (see Álvarez-Vázquez and Cleal 2016). Both species have small, broadly oval to rounded pinnules with cordate bases and ovoid, well-individualized terminals. In addition, in the two species the lamina is thick, convex, and with similar vein density. However, the first anadromous and catadromous pinnules of *Wagneropteris minima* are smaller than the other laterals, thus allowing space for the characteristic intercalary pinnules that characterize *Wagneropteris*.

Stratigraphic and geographic distribution. Gillespie and Pfefferkorn (1979) recorded *Neuralethopteris smithsii* from upper Namurian (Yeadonian) to lower Westphalian A (= Langsettian) strata (middle Pocahontas to New River formations) in the Appalachian Basin. From the same area, Goubet *et al.* (2000) regarded *Neuralethopteris smithsii* as particularly abundant in the lower and middle part of the New River Formation (up to the Sewell coal interval), which is of middle Langsettian age.

Occurrence in the Maritime Provinces, Canada. CUMBERLAND BASIN (NOVA SCOTIA): Bell (1944): locality 860 (GSC 5593 + GSC 5840 + GSC 5849 + GSC 5850 + GSC 5853 + GSC 5859 + GS 5860 + GSC 5955 + GSC 5986 — paratypes of *Sphenopteris minuscula* + GSC 5857 — holotype of *Sphenopteris minuscula*); locality 1356 (four fragmentary specimens without catalogue number — cf.; it could be compared also with *Neuralethopteris pocahontas*); locality 1462 (two pieces without catalogue number — together with *Pseudadiantites rhomboideus*, *Neuropteris* sp. and *Zeilleria frenzlii*, which comprise six other pieces of the same locality); locality 1685 (three pieces without catalogue number). NEW BRUNSWICK: Bell (1944): locality 791 (poorly preserved specimen without catalogue number); locality 828 (three pieces, with fragmentary and poorly preserved specimens, without catalogue number — cf.; together with *Calamites* sp.); locality 831 (two pieces without catalogue number — cf.; poorly preserved); locality 1359 (four pieces without catalogue number — fragmentary); locality 1369 (two pieces without catalogue number).

Occurrence in the United States. ALABAMA: Lesquereux (1879–84), White (1905), Butts (1926), Gastaldo (1985), Gillespie and Rheams (1985), Lyons *et al.* (1985), Goubet *et al.* (2000). GEORGIA: Lesquereux (1884), Gillespie and Crawford (1985). TENNESSEE: Lesquereux (1884). VIRGINIA: Blake *et al.* (2002). WEST VIRGINIA: Lesquereux (1879–84), Jongmans (1937), Gillespie and Pfefferkorn (1979), Goubet *et al.* (2000), Blake *et al.* (2002).

SUMMARY AND CONCLUSIONS

The revision of *Alethopteris* and *Neuralethopteris* from lower Westphalian strata of Nova Scotia and New Brunswick, eastern Canada, has yielded eight species; three of these — *Alethopteris bertrandii*, *Alethopteris* cf. *haylenae* and *Neuralethopteris pocahontas*, — are cited for the first time in Canada. This revision was based on material deposited in the collections of the Geological Survey of Canada, Ottawa, recorded by Bell (1944, 1966), plus additional specimens stored in the collections of the New Brunswick Museum, Saint John, and in the Donald Reid Collection at the Joggins Fossil Institute.

Three species described by Dawson (1862, 1863, 1871), *Pecopteris discrepans* (= *Pecopteris decurrens* Dawson non Artis), *Pecopteris ingens* and *Neuropteris selwynii*, and one described by Bell (1944), *Sphenopteris minuscula*, are regarded as synonyms of European taxa. Although *Neuropteris selwynii* was described from Canadian material before its probable synonym *Neuralethopteris schlehanii*, the widespread use that has been made in the literature of the last name, combined with the fragmentary nature of Dawson's *Neuropteris selwynii* and its poor illustration and description, justify retaining *Neuralethopteris schlehanii* provisionally; and eventually, if the synonymy is confirmed, making a proposal to conserve the name *Neuralethopteris schlehanii*.

As with the other recently revised taxa (Lycopida, Filicopsida, *Annularia* and *Asterophyllites*), Canadian taxa are basically the same as those recorded from strata of the same age in Europe. This newest revision enhances the striking resemblance of the Westphalian flora of the Canadian Maritime Provinces with that known from western Europe, as well as its paleogeographic proximity.

ACKNOWLEDGEMENTS

The late John Utting and the late Robert H. Wagner are both gratefully acknowledged for the initiative to promote the revision of lower Westphalian floras in the Maritime Provinces of Canada. Jean Dougherty, formerly of Geological Survey of Canada, Ottawa, and Randall Miller, formerly of the New Brunswick Museum, Saint John, provided essential access and data regarding the fossil collections in their institutions. The late Donald Reid and the Joggins Fossil Centre kindly lent several specimens. The paper benefited from constructive comments and suggestions by the reviewers,

Chris Cleal and Zbyněk Šimůnek. The helpful, well-focused suggestions and meticulous editing by Rob Fensome are gratefully acknowledged.

REFERENCES

- Álvarez-Vázquez, C. 2019. Filicopsida from the lower Westphalian (Middle Pennsylvanian) of Nova Scotia and New Brunswick, Maritime Provinces, Canada. *Atlantic Geology*, 55, pp. 1–55. <https://doi.org/10.4138/atgeol.2019.001>
- Álvarez-Vázquez, C. and Cleal, C.J. 2016. *Wagneropteris minima*, a new medullosalean pteridosperm from the middle Westphalian (Middle Pennsylvanian) of the Peñarroya-Belmez-Espiel Coalfield (Córdoba province, SW Spain). *Spanish Journal of Palaeontology*, 31 (1), pp. 5–24. <https://doi.org/10.7203/sjp.31.1.17119>
- Álvarez-Vázquez, C. and Wagner, R.H. 2014. Lycopsida from the lower Westphalian (Middle Pennsylvanian) of the Maritime Provinces, Canada. *Atlantic Geology*, 50, pp. 167–232. <https://doi.org/10.4138/atgeol.2014.011>
- Álvarez-Vázquez, C. and Wagner, R.H. 2017. A revision of *Annularia* and *Asterophyllites* species from the lower Westphalian (Middle Pennsylvanian) of the Maritime Provinces, Canada. *Atlantic Geology*, 53, pp. 17–62. <https://doi.org/10.1088/1475-7516/2017/10/002>
- Arnold, C.A. 1934. A preliminary study of the fossil flora of the Michigan Coal Basin. Contributions from the Museum of Paleontology, University of Michigan, 4 (11), pp. 77–203.
- Arnold, C.A. 1935. Observations on *Alethopteris grandifolia* Newberry and its seeds. Contributions from the Museum of Paleontology, University of Michigan, 4 (15), pp. 279–282.
- Arnold, C.A. 1937. The seeds of *Alethopteris*, and other pteridosperms from North America. *Compte Rendu 2^e Congrès Congrès International de Stratigraphie et de Géologie du Carbonifère*, Heerlen 1935, 1, pp. 41–45.
- Arnold, C.A. 1941. Some Paleozoic plants from central Colorado and their stratigraphic significance. Contributions from the Museum of Paleontology, University of Michigan, 6 (4), pp. 59–70.
- Arnold, C.A. 1947. An introduction to paleobotany. McGraw-Hill Book Company, New York, 433 p.
- Arnold, C.A. 1949. Fossil flora of the Michigan Coal Basin. Contributions from the Museum of Paleontology, University of Michigan, 7 (9), pp. 131–269.
- Artis, E.T. 1825. Antediluvian phytology, as illustrated by a collection of the fossil remains of plants peculiar to the coal formation of Great Britain. London, xiii + 24 p. <https://doi.org/10.5962/bhl.title.119718>
- Bailey, L.W. 1865. Observations on the geology of southern New Brunswick, made principally during the summer of 1864 by Prof. L.W. Bailey, Messrs. Geo. F. Matthew, and C.F. Hartt, prepared and arranged, with a geological map. G.E. Fenety, Fredericton, 185 p.
- Bashforth, A., Cleal, C.J., Gibling, M.R., Falcon-Lang, H.J., and Miller, R.F. 2014. Paleoecology of Early Pennsylvanian vegetation on a seasonally dry tropical landscape (Tynemouth Creek Formation, New Brunswick, Canada). *Review of Palaeobotany and Palynology*, 200, pp. 229–263. <https://doi.org/10.1016/j.revpalbo.2013.09.006>
- Basson, P.W. 1968. The fossil flora of the Drywood Formation of southwestern Missouri. *University of Missouri Studies*, 44, pp. 1–170.
- Bell, W.A. 1938. Fossil flora of Sydney Coalfield, Nova Scotia. Canada Department of Mines and Resources, Mines and Geology Branch, Geological Survey, Memoir 215, pp. 1–334. <https://doi.org/10.4095/101646>
- Bell, W.A. 1944. Carboniferous rocks and fossil floras of northern Nova Scotia. Canada Department of Mines and Resources, Mines and Geology Branch, Geological Survey, Memoir 238, pp. 1–119. <https://doi.org/10.4095/119859>
- Bell, W.A. 1962. Flora of Pennsylvanian Pictou Group of New Brunswick. Geological Survey of Canada, Department of Mines and Technical Surveys, Bulletin 87, pp. 1–71. <https://doi.org/10.4095/100605>
- Bell, W.A. 1966. Illustrations of Canadian fossils. Carboniferous plants of eastern Canada. Geological Survey of Canada, Department of Mines and Technical Surveys, Paper 66–11, pl. I–XXXVI. <https://doi.org/10.4095/100977>
- Bertrand, P. 1932. Bassin houiller de la Sarre et de la Lorraine. I. Flore fossile. 2^{me} fascicule. Aléthoptéridées. Études des Gîtes Minéraux de la France, Service de Topographies Souterraines. Text: pp. 65–107; Atlas: pl. XXXI–LX.
- Blake, B.M. 1997. Revised lithostratigraphy and megafunal biostratigraphy of the New River and Kanawha formations (Pottsville Group: Lower and Middle Pennsylvanian) in southern West Virginia. Unpublished M.Sc. Thesis, West Virginia University, Morgantown, pp. 1–149.
- Blake, B.M., Cross, A.T., Eble, C.F., Gillespie, W.H., and Pfefkerkorn, H.W. 2002. Selected plant megafossils from the Carboniferous of the Appalachian region, eastern United States: geographic and stratigraphic distribution. In Carboniferous and Permian of the World. Proceedings XIV International Congress Carboniferous and Permian Stratigraphy, Calgary, Alberta 1999. Edited by L.V. Hills, C.M. Henderson, and E.W. Bamber. Canadian Society of Petroleum Geologists, Memoir 19, pp. 259–335.
- Boulay, N. 1876. Le terrain houiller du Nord de la France et ses végétaux fossiles. Thèse de Géologie, Faculté des Sciences de Caen, Imprimerie Lefebvre-Ducrocq, Lille, 74 p.
- Bouroz, A. 1956. *Alethopteris Bertrandi* nov. sp. du Westphalien C du Pas-de-Calais. Annales de la Société géologique du Nord, 75 (1955), pp. 137–143.
- Brongniart, A. 1822. Sur la classification et la distribution des végétaux fossiles en général, et sur ceux des terrains de sédiment supérieur en particulier. Mémoires Muséum d'Histoire naturelle de Paris, 8, pp. 203–348.
- Brongniart, A. 1828. Prodrome d'une histoire des végétaux fossiles. Paris and Strasbourg, F.G. Levrault, 225 p. <https://doi.org/10.5962/bhl.title.62840>
- Brongniart, A. 1831. Histoire des végétaux fossiles, ou recherches botaniques et géologiques sur les végétaux

- renfermés dans les diverses couches du globe. Texte, n° 5: pp. 209–248; 6; Atlas: I — pl. 1–166. Facsimile Edition W. Junk, Berlin (1915).
- Brongniart, A. 1833. Histoire des végétaux fossiles, ou recherches botaniques et géologiques sur les végétaux renfermés dans les diverses couches du globe. Texte, n° 7: pp. 265–288; Atlas: I — pl. 1–166. Facsimile Edition W. Junk, Berlin (1915).
- Brongniart, A. 1834. Histoire des végétaux fossiles, ou recherches botaniques et géologiques sur les végétaux renfermés dans les diverses couches du globe. Texte, n° 8: pp. 289–312; Atlas: I — pl. 1–166. Facsimile Edition W. Junk, Berlin (1915).
- Brongniart, A. 1874. Étude sur les graines fossiles trouvées à l'état silicifié dans le terrain houiller de Saint-Étienne. Annales Sciences naturelles, Botanique, série 5, pp. 234–265.
- Brousmiche Delcambre, C., Mercier, D., and Coquel, R. 1996. Révision de la flore carbonifère du Briançonnais. Implications stratigraphiques. Ière partie: vallée de la Durance au sud de Briançon. Palaeontographica, Abteilung B, 239 (4–6), pp. 77–107.
- Brousmiche Delcambre, C., Mercier, D., and Coquel, R. 1998. Révision de la flore carbonifère du Briançonnais. Implications stratigraphiques. Partie II: Le Nord de Briançon, de la vallée de la Guisane à celle de la Clarée. Palaeontographica, Abteilung B, 248 (4–6), pp. 87–125.
- Buisine, M. 1961. Contribution à l'étude de la flore du terrain houiller. Les Aléthoptéridées du Nord de la France. I. Flore fossile, 4^e fascicule. Études Géologiques pour l'Atlas de Topographie Souterraine, Service Géologique des H.B.N.P.C. Texte: pp. 1–317. Atlas: pl. I–LXXIV.
- Bunbury, C.J.F. 1847. On fossil plants from the Coal Formation of Cape Breton. Quarterly Journal of the Geological Society, London, 3, pp. 423–438. <https://doi.org/10.1144/GSL.JGS.1847.003.01-02.44>
- Butts, C. 1926. The Paleozoic rocks. In Geology of Alabama. Edited by G.I. Adams, C. Butts, L.W. Stephenson, and W. Cooke. Geological Survey of Alabama, Special Report 14, pp. 206–229.
- Calder, J.H., Gibling, M.R., Scott, A.C., Davies, S.J., and Hebert, B.L. 2006. A fossil lycopsid forest succession in the classic Joggins section of Nova Scotia: paleoecology of a disturbance-prone Pennsylvanian wetland. Geological Society of America, Special Paper 399, pp. 169–195. [https://doi.org/10.1130/2006.2399\(09\)](https://doi.org/10.1130/2006.2399(09))
- Canright, J.E. 1959. Fossil plants of Indiana. Indiana Department of Conservation, Geological Survey, Report of Progress, 14, pp. 1–45.
- Cleal, C.J. and Shute, C.H. 1995. A synopsis of neuropteroid foliage from the Carboniferous and Lower Permian of Europe. Bulletin of the Natural History Museum London, Geology Series, 51 (1), pp. 1–52.
- Cleal, C.J. and Shute, C.H. 2003. Systematics of the Late Carboniferous medullosalean pteridosperm *Laveineopteris* and its associated *Cyclopteris* leaves. Palaeontology, 46 (2), pp. 353–411. <https://doi.org/10.1111/1475-4983.00303>
- Cleal, C.J., Shute, C.H., and Zodrow, E.L. 1990. A revised taxonomy for Palaeozoic neuropterid foliage. Taxon, 39 (3), pp. 486–492. <https://doi.org/10.2307/1223109>
- Cleal, C.J., Fraser, H.E., Lazarus, M., and Dannell, G. 2009. The forests before the flood: the palaeobotanical contributions of Edmund Tyrell Artis (1789–1847). Earth Sciences History, 28 (2), 245–275. <https://doi.org/10.17704/eshi.28.2.31w8363563403478>
- Coquel, R. and Laveine, J.P. 1979. *Alethopteris jankii* nov. sp., du Westphalien C–D du Nord de la France. Annales de la Société géologique du Nord, 98, 123–126.
- Corsin, P. 1932. Guide paléontologique dans le terrain houiller du Nord de la France. Travaux et Mémoires de l'Université de Lille, 5, pp. 1–44.
- Corsin, P. 1960. Classification des ptéridophytes et des ptéridospermophytes du Carbonifère. Bulletin de la Société géologique de France, Série 7, 2, pp. 566–572.
- Cremer, L. 1893. Über die Fossilen Farne des Westfälischen Carbons und ihre Bedeutung für eine Gliederung des letzteren. Mitteilungen aus dem geologischen Museum der Westfälischen Berggewerkschaftskasse, 1, pp. 1–49.
- Crookall, R. 1929. Coal Measure plants. Edward and Co Publishers, London, 80 p.
- Crookall, R. 1932. The relative value of fossil plants in the stratigraphy of the Coal Measures. Memoirs and Proceedings of the Manchester Literary and Philosophical Society, 76 (1931–32), pp. 91–122.
- Crookall, R. 1955. Fossil plants of the Carboniferous rocks of Great Britain. (Second section.) Memoirs of the Geological Survey of Great Britain, Palaeontology, 4 (1), pp. 1–84, pl. I–XXIV.
- Crookall, R. 1959. Fossil plants of the Carboniferous rocks of Great Britain. (Second Section.) Memoirs of the Geological Survey of Great Britain, Palaeontology, 4 (2), pp. 85–216, pl. XXV–LVIII.
- Crookall, R. 1976. Fossil plants of the Carboniferous rocks of Great Britain. (Second section.) Memoirs of the Geological Survey of Great Britain, Palaeontology, 4 (7), pp. 841–956, pl. CLX–CLXXIII.
- Cross, A.T., Gillespie, W.H., and Taggart, R.E. 1996. Upper Paleozoic vascular plants. Chapter 23. In Fossils of Ohio. Department of Natural Resources, Division of Geological Survey, Bulletin 70, pp. 396–479.
- Dawson, J.W. 1862. On the flora of the Devonian Period in north-eastern America. Quarterly Journal of the Geological Society of London, 18, pp. 296–330. <https://doi.org/10.1144/GSL.JGS.1862.018.01-02.42>
- Dawson, J.W. 1863. Further observations on the Devonian plants of Maine, Gaspé, and New York. Quarterly Journal of the Geological Society of London, 19, pp. 458–469. <https://doi.org/10.1144/GSL.JGS.1863.019.01-02.41>
- Dawson, J.W. 1868. Acadian geology. The geological structure, organic remains, and mineral resources of Nova Scotia, New Brunswick, and Prince Edward Island. London, 694 p. <https://doi.org/10.5962/bhl.title.38560>
- Dawson, J.W. 1871. The fossil plants of the Devonian and Upper Silurian formations. Geological Survey of Canada, Report, 92 p. <https://doi.org/10.4095/216073>

- Dijkstra, S.J. and Amerom, H.W.J. van 1981. Fossilium Catalogus. II: Plantae. Pars 88 (43). Filicales, Pteridospermae, Cycadales. 2. Supplement, A–C. Kluger Publications, Amsterdam, pp. 1–143.
- Dijkstra, S.J. and Amerom, H.W.J. van 1983. Fossilium Catalogus. II: Plantae. Pars 90 (45). Filicales, Pteridospermae, Cycadales. 2. Supplement, L–O. Kluger Publications, Amsterdam, pp. 293–460.
- Dilcher, D.L. and Lott, T.A. 2005. Atlas of Union Chapel mine fossil plants. In Pennsylvanian footprints in the Black Warrior Basin of Alabama. Edited by R.J. Buta, A.K. Rindsberg, and D.C. Kopaska-Merkel. Alabama Paleontological Society, Monograph, 1, pp. 339–365.
- Dilcher, D.L., Lott, T.A., and Axsmith, B.J. 2005. Fossil plants from the Union Chapel mine, Alabama. In Pennsylvanian footprints in the Black Warrior Basin of Alabama. Edited by R.J. Buta, A.K. Rindsberg, and D.C. Kopaska-Merkel. Alabama Paleontological Society, Monograph, 1, pp. 153–168.
- Ettingshausen, C. von 1852. Die Steinkohlenflora von Stradonitz in Böhmen. Abhandlungen Kaiserlich-Königlichen Geologischen Reichsanstalt, 2 (3), pp. 1–13.
- Falcon-Lang, H.J. 2006. Vegetation ecology of Early Pennsylvanian alluvial fan and piedmont environments in southern New Brunswick, Canada. Palaeogeography, Palaeoclimatology, Palaeoecology, 233, pp. 34–50. <https://doi.org/10.1016/j.palaeo.2005.09.005>
- Fontaine, M. and White, I.C. 1880. The fossil flora of the Upper Carboniferous or Permian in West Virginia and south-west Pennsylvania. Second Geological Survey of Pennsylvania: Report of Progress PP, pp. 1–143. <https://doi.org/10.5962/bhl.title.100048>
- Franke, F. 1912. *Alethopteris*. In H. Potonié (coord.). Abbildungen und Beschreibungen fossiler Pflanzen-Reste, Lieferun VIII, 158, pp. 1–13.
- Frech, F. 1880. *Lethaea Geognostica*. Handbuch der Erdgeschichte mit Abbildungen der für die Formationen bezeichnendsten Versteinerungen. Heraugegeben von Geologen unter Redaktion von Fritsch Frech. Stuttgart, Schweizerbartsche Verlag, Textband I, Lieferung 1, 324 p.
- Gastaldo, R.A. 1985. Upper Carboniferous paleoecological reconstructions: observations and reconsiderations. Compte Rendu 10^e Congrès International de Stratigraphie et de Géologie du Carbonifère, Madrid 1983, 2, pp. 281–296.
- Gillespie, W.H. and Crawford, T.J. 1985. Plant megafossils from the Carboniferous of Georgia, U.S.A. Compte Rendu 10^e Congrès International de Stratigraphie et de Géologie du Carbonifère, Madrid 1983, 2, pp. 247–256.
- Gillespie, W.H. and Pfefferkorn, H.W. 1976. Plant fossils in early and middle parts of the proposed Pennsylvanian System stratotype in West Virginia. Carboniferous stratigraphy of southwestern Virginia and southern West Virginia, Geological Society of America Field Trip Guidebook No. 3, pp. 1–6.
- Gillespie, W.H. and Pfefferkorn, H.W. 1979. Distribution of commonly occurring plant megafossils in the proposed Pennsylvanian System stratotype. Ninth International Congress of Carboniferous Stratigraphy and Geology. Field Trip No. 1, AGI Selected Guidebook Series, No. 1, pp. 87–97.
- Gillespie, W.H. and Pfefferkorn, H.W. 1986. Plant fossils of the New River Gorge, West Virginia. Proceedings of the West Virginia Academy of Science, Papers of the Fifty-Ninth Annual Session, 56 (2, 3, 4), pp. 124–135.
- Gillespie, W.H. and Rheams, L.J. 1985. Plant megafossils from the Carboniferous of Alabama, U.S.A. Compte Rendu 10^e Congrès International de Stratigraphie et de Géologie du Carbonifère, Madrid 1983, 2, pp. 191–202.
- Gillespie, W.H., Latimer, L.S., and Clendening, J.A. 1966. Plant fossils of West Virginia. West Virginia Geological and Economic Survey, Educational Series, pp. 1–131.
- Gillespie, W.H., Clendening, J.A., and Pfefferkorn, H.W. 1978. Plant fossils of West Virginia and adjacent areas. West Virginia Geological and Economic Survey, Educational Series ED-3A, pp. 1–172.
- Gillespie, W.H., Crawford, T.J., and Waters, J.A. 1989. Plant fossils of the Pennsylvanian System of Georgia. 38th Annual Meeting, Southeastern Section, The Geological Society of America, Guidebook Addendum, pp. 1–13.
- Göppert, H.R. 1836. Die Fossilen Farrnkräuter. Verhandlungen der Kaiserlichen Leopoldinisch-Carolinischen Akademie der Naturforscher, XVII Suppl., 486 p.
- Gothan, W. 1906. *Desmopteris integra*. In Abbildungen und Beschreibungen fossiler Pflanzen-Reste. Edited by H. Potonié. Königlich Preussischen Geologischen Landesanstalt, IV–64, pp. 1–3.
- Gothan, W. 1909. *Lonchopteris*. In Abbildungen und Beschreibungen fossiler Pflanzen-Reste. Edited by H. Potonié. Königlich Preussischen Geologischen Landesanstalt, VI–117, pp. 1–7.
- Gothan, W. 1913. Die Oberschlesische Steinkohlenflora. I. Farne und farnähnliche Gewächse (Cycadofilices bzw. Pteridospermen). Abhandlungen der Königlichen Preussischen Geologischen Landesanstalt, (Neue Folge), 75, pp. 1–278. <https://doi.org/10.5962/bhl.title.150544>
- Gothan, W. 1953. Die Steinkohlenflora der westlichen paralischen Steinkohlenreviere Deutschlands. Beihefte zum Geologischen Jahrbuch, 10, pp. 1–83.
- Goubet, P., Pfefferkorn, H.W., and Gillespie, W.H. 2000. Neuralethopterids (trigonocarpalean pteridosperms) from the Early Pennsylvanian of eastern North America. PaleoBios, 20 (3), pp. 11–37.
- Grand'Eury, C. 1877. Mémoire sur la flore Carbonifère du Département de la Loire et du centre de la France. Étudiée aux trois points de vue botanique, stratigraphique et géognostique. Mémoires Académie des Sciences de l'Institut National de France, 24 (1), pp. 1–624.
- Gropp, W. 1932. Über das Vorkommen von *Lyginopteris* (*Sphenopteris*) *porubensis* (Trapl) Gothan. Arbeiten Institut Paläobotanik Petrographie Brennsteine, 2 (2), 233–239.
- Gutbier, A. von 1835. Abdrücke und Versteinerungen des

- Zwickauer Schwarzkohlengebirges und seiner Umgebungen. Zwickau, Verlag G. Richter'schen Buchhandlung, 80 p. <https://doi.org/10.5962/bhl.title.152878>
- Guthörl, P. 1958. Neue Funde von *Lonchopteridium* Gothan aus dem Saarkarbon. Journal of the Palaeontological Society of India, Lucknow. Birbal Sahni Memorial No, 2, pp. 35–42.
- Halle, T.G. 1933. The structure of certain fossil spore-bearing organs believed to belong to pteridosperms. Kungliga Svenska Vetenskaps Akademiens Handlingar, 12 (6), pp. 1–101.
- Havlena, V. 1970. Representatives of the genus *Mariopteris* Zeiller in the strata between the seams 40 and 34 of the Ostrava-Karviná coal district in the Upper Silesian Basin. Věstník Ústředního ústavu geologického, 45, pp. 45–48.
- Havlena, V. 1984. Alethopterids of the middle and upper Namurian, Ostrava-Karviná coalfield. Časopis pro mineralogii a geologii, 29 (4), pp. 369–377.
- Heer, O. 1877. Flora fossilis Helvetiae. Die vorweltliche Flora der Schweiz. Verlag von J. Wurster and Comp., Zürich, 182 p.
- Janssen, R.E. 1939. Leaves and stems from fossil forests. A handbook of the paleobotanical collections in the Illinois State Museum. Illinois State Museum, Popular Science Series, 1, 190 p.
- Janssen, R.E. 1957. Leaves and stems from fossil forests. A handbook of the paleobotanical collections in the Illinois State Museum. Illinois State Museum, Popular Science Series, 1, 190 p. (Second printing).
- Jennings, J.R. 1984. Distribution of fossil plant taxa in the Upper Mississippian and Lower Pennsylvanian of the Illinois Basin. Compte Rendu 9^e Congrès International de Stratigraphie et Géologie du Carbonifère, Washington and Champaign-Urbana 1979, 2, pp. 301–312.
- Jongmans, W.J. 1928. Stratigraphie van het Karboon in het algemeen en van Limburg in het bijzonder. Algemeen overzicht over het Zuid-Limburgsche Karboon. Mededeeling, 6, 1926–1928, pp. 525–590.
- Jongmans, W.J. 1937. Comparison of the floral sucession in the Carboniferous of West Virginia with Europe. Compte Rendu 2^e Congrès Congrès International de Stratigraphie et de Géologie du Carbonifère, Heerlen 1935, 1, pp. 393–415.
- Jongmans, W.J. 1957. Fossilium Catalogus. II: Plantae. Pars 30 (3). Filicales, Pteridospermae, Cycadales. Ed. W. Junk, The Hague, pp. 89–178.
- Jongmans, W.J. 1960. Die Karbonflora der Schweiz. Beiträge zur Geologischen Karte der Schweiz, Schweizerischen Geologischen Kommission, Neue Folge, 108, pp. 1–97.
- Jongmans, W.J. and Dijkstra, S.J. 1961. Fossilium Catalogus. II: Plantae. Pars 45 (18). Filicales, Pteridospermae, Cycadales. Ed. W. Junk, The Hague, pp. 1597–1686.
- Josten, K.-H. 1983. Die fossilen Floren im Namur des Ruhrkarbons. Fortschritte in der Geologie von Rheinland und Westfalen, Geologisches Landesamt Nordrhein-Westfalen, Krefeld, 31, pp. 1–327.
- Josten, K.-H. and Amerom, H.W.J. van 2003. Die Flora des Namur B aus Hagen-Vorhalle. Geologie und Paläontologie in Westfalen, 61, pp. 1–303.
- Kidston, R. 1884. On the fructification of *Zeilleria (Sphenopteris) delicatula*, Sternb., sp.; with remarks on *Urnatopterus (Sphenopteris) tenella*, Brongt., and *Hymenophylites (Sphenopteris) quadridactylites*, Gutbier, sp. Quarterly Journal of the Geological Society, London, 40, pp. 590–598. <https://doi.org/10.1144/GSL.JGS.1884.40.01-04.49>
- Kidston, R. 1888. On the fructification of two coal-measure ferns. Annals and Magazine of Natural History, Series B, 2, pp. 22–27. <https://doi.org/10.1080/00222938809460871>
- Kidston, R. 1914. On the fossil flora of the Staffordshire coal fields. Part III. — The fossil flora of the Westphalian Series of the South Staffordshire Coal Field. Transactions of the Royal Society of Edinburgh, 50, part I (5), pp. 73–199. <https://doi.org/10.1017/S0080456800017282>
- Kidston, R. 1924. Fossil plants of the Carboniferous rocks of Great Britain. Memoirs Geological Survey of Great Britain, Palaeontology, 2 (5) (1924), pp. 377–522.
- Knight, J. 1985. The stratigraphy of the Stephanian rocks of the Sabero Coalfield, León (NW. Spain) and an investigation of the fossil flora. Part III. Systematic Palaeobotany; Pecopterids. Palaeontographica, Abteilung B, 197 (1–3), pp. 1–80.
- Langford, G. 1958. The Wilmington Coal Flora from a Pennsylvanian deposit in Will County, Illinois. Earth Science Club of Northern Illinois, Esconi Associates, Illinois, 360 p.
- Laveine, J.-P. 1967. Contribution à l'étude de la flore du terrain houiller. Les neuroptéridées du bassin houiller du Nord de la France. Études géologiques pour l'atlas de topographie souterraine publiées par le Service Géologique des Houillères du Bassin du Nord et du Pas-de-Calais. I. Flore fossile, 5^e fascicule. Texte: pp. 1–338; Atlas: pl. A–P; I–LXXXIV.
- Laveine, J.-P. 1986. The size of the frond in the genus *Alethopteris* Sternberg (Pteridospermopsida, Carboniferous). Geobios, 19 (1), pp. 49–56; [https://doi.org/10.1016/S0016-6995\(86\)80035-3](https://doi.org/10.1016/S0016-6995(86)80035-3)
- Laveine, J.-P., Coquel, R., and Loboziak, S. 1977. Phylogénie générale des calliptéridacées (Pteridospermopsida). Géobios, 10 (6), pp. 757–847. [https://doi.org/10.1016/S0016-6995\(77\)80080-6](https://doi.org/10.1016/S0016-6995(77)80080-6)
- Laveine, J.-P., Belhis, A., Lemoigne, Y., and Zhang, S. 1992. Frond architecture in the genera *Neuralethopteris* Cremer, *Alethopteris* Sternberg and *Lonchopteris* Brongniart (Carboniferous pteridosperms). Revue de Paléobiologie, volume spécial, 6, pp. 149–166.
- Leary, R.L. 1976. Inventory of the type and figured paleobotanical specimens in the Illinois State Museum. Illinois State Museum, Inventory of Geological Collections, 2 (2), pp. 1–64.
- Leary, R.L. and Pfefferkorn, H.W. 1977. An Early Pennsylvanian flora with *Megalopteris* and *Noeggerathiales* from west-central Illinois. Illinois State Geological Survey, Circular 500, pp. 1–77. <https://doi.org/10.5962/bhl.title.61520>

- Leggewie, W. and Schonefeld, W. 1957. Pteridophyten und Pteridospermen der Sprockhöveler (= Magerkohlen-) Schichten (Namur C). *Palaeontographica*, Abteilung B, 101, pp. 1–29.
- Lesquereux, L. 1854. New species of fossil plants, from the anthracite and bituminous coal-fields of Pennsylvania; collected and described by Leo Lesquereux. With introductory observations by Henry Darwin Rogers. *Boston Journal of Natural History*, 6 (4), pp. 409–431.
- Lesquereux, L. 1858. Fossil plants of the coal strata of Pennsylvania. In H.D. Rogers, *The geology of Pennsylvania*, 2 (2), pp. 835–884.
- Lesquereux, L. 1879–1884. Description of the coal flora of the Carboniferous formation in Pennsylvania and throughout the United States. Second Geological Survey of Pennsylvania, Report of Progress. Text — I (1880): pp. 1–354; II (1880): pp. 355–694, i–lxiii, pl. LXXXVI, LXXXVII; III (1884): pp. 695–977, pl. LXXXVIII–CXI. Atlas (1879): pl. A, B; pl. I–LXXXV.
- Lindley, J. and Hutton, W. 1831. The fossil flora of Great Britain; or, figures and descriptions of the vegetable remains found in a fossil state in this country. I, pp. 1–47, pl. 1–14. James Ridgway and Sons, London. <https://doi.org/10.5962/bhl.title.149330>
- Lindley, J. and Hutton, W. 1835. The fossil flora of Great Britain; or, figures and descriptions of the vegetable remains found in a fossil state in this country. II, pp. 1–72, pl. 157–176. James Ridgway and Sons, London.
- Lyons, P.C. and Sproule, R.G. 2018. The fossil flora and age of the Wamsutta Formation red beds (Middle Pennsylvanian), Narragansett Basin, southeastern Massachusetts, USA and correlation with the Cumberland Group of the Maritime Provinces of Canada. *Atlantic Geology*, 54, pp. 315–334. <https://doi.org/10.4138/atgeol.2018.011>
- Lyons, P.C., Zeissner, C.R., Barwood, H.L., and Adinolfi, F.G. 1985. North American and European megafloral correlations with the upper part of the Pottsville Formation of the Warrior Coal Field; Alabama, U.S.A. Compte Rendu 10^e Congrès International de Stratigraphie et Géologie du Carbonifère, Madrid 1983, 2, pp. 203–245.
- Matthew, G.F. 1910. Revision of the flora of the Little River Group No. II. Transactions of the Royal Society of Canada, Third Series, 3 (4), pp. 77–113.
- Miller, R.F. 1987. George Frederic Matthew (1837–1923). Victorian Science in Saint John. *New Brunswick Museum News*, August–September 1987, pp. 3–26.
- Miller, R.F. and Buhay, D.N. 1988. The Steinhammer Club: geology and a foundation for a natural history society in New Brunswick. *Geoscience Canada*, 15 (3), pp. 221–226.
- Moore, L.C., Wittry, J., and DiMichele, W.A. 2014. The Okmulgee, Oklahoma fossil flora, a Mazon Creek equivalent: spatial conservatism in the composition of Middle Pennsylvanian wetland vegetation over 1100 km. Review of *Palaeobotany and Palynology*, 200, pp. 24–52. <https://doi.org/10.1016/j.revpalbo.2013.08.002>
- Newberry, J.S. 1853. Fossil plants from the Ohio coal basin. *Annals of Science*, Cleveland, 5 (8), pp. 95–97.
- Newberry, J.S. 1873. Descriptions of fossil plants from the coal measures of Ohio. *Geological Survey of Ohio, Paleontology*, I, pp. 359–385.
- Novik, K. 1947. Classification of Carboniferous Pteridospermae. *Doklady Akademii Nauk S.S.S.R.*, 58 (2), pp. 277–279 (in Russian).
- Oleksyshyn, J. 1982. Fossil plants from the anthracite coal fields of eastern Pennsylvania. *Pennsylvania Geological Survey, General Geology Report* 72, pp. 1–157.
- Pfefferkorn, H.W. and Gillespie, W.H. 1977. Plant fossils in the proposed Pennsylvanian System stratotype. In *A field guide to proposed Pennsylvanian System stratotype, West Virginia*. Edited by K.J. Englund, H.H. Arndt, W.H. Gillespie, T.W. Henry, and H.W. Pfefferkorn. Annual AAPG/SEPM Convention, Washington, Pre-Meeting Field Trip, June 1977, pp. 21–26.
- Pfefferkorn, H.W. and Gillespie, W.H. 1981. Biostratigraphic significance of plant megafossils near the Mississippian–Pennsylvanian boundary in southern West Virginia and southwestern Virginia. In *GSA Cincinnati '81 field trip guidebooks. volume I: stratigraphy, sedimentology*. Edited by T.G. Roberts. American Geological Institute, pp. 159–164.
- Potonié, H. 1893. Ueber das Rothliegende des Thüringer Waldes. Theil II: Die Flora des Rothliegenden von Thüringen. *Abhandlungen der Königlich Preussischen geologischen Landesanstalt*. Neue Folge 9, pp. 1–298.
- Purkyňová, E. 1970. Die Unternamurflora des Beckens von Horní Slezsko (ČSSR). *Paläontologische Abhandlungen*, Abteilung B, Paläobotanik, III (2), pp. 129–268.
- Purkyňová, E. 1990. K biostratigrafii karbonu v doubravských vrstvách hornoslezské černouhelné pánve. *Časopis Slezského Muzea Opava* (A), 39, 213–224.
- Read, C.B. 1934. A flora of Pottsville age from the Mosquito Range, Colorado. *Geological Survey, Professional Paper* 185–D, pp. 79–96. <https://doi.org/10.3133/pp185D>
- Read, C.B. and Mamay, S.H. 1964. Upper Paleozoic floral zones and floral provinces of the United States. Shorter contributions to general geology. *Geological Survey Professional Paper* 454–K, pp. K1–K35. <https://doi.org/10.3133/pp454K>
- Rothwell, G.W. and Eggert, D.A. 1986. A monograph of *Dolerotheca* Halle, and related complex permineralised medullosan pollen organs. *Transactions Royal Society of Edinburgh*, 77, pp. 47–79. <https://doi.org/10.1017/S0263593300099995>
- Sauveur, M. 1848. Végétaux fossiles des terrains houillers de la Belgique. *Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique*, pl. I–XXXVI.
- Schimper, W.P. 1869. *Traité de paléontologie végétale ou la flore du monde primitif dans ses rapports avec les formations géologiques et la flore du monde actuel*. Texte — I: pp. 1–738. J.B. Baillièvre et Fils, Paris. <https://doi.org/10.5962/bhl.title.60570>
- Schlotheim, E.F. von 1820. *Die Petrefactenkunde auf ihrem jetzigen Standpunkte, durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier-*

- und Pflanzenreichs der Vorwelt erläutert. Gotha, i-lxii (Einleitung), pp. 1–437, pl. I–XXXVI.
- Šimůnek, Z. 1996. Carboniferous alethopterids of the Karviná and Žacléř formations (Czech Republic). *Sborník geologických věd, Paleontologie*, 33, pp. 5–37.
- Solovieva, M.N., Gubareva, V.S., Ivanova, E.A., Fissunenko, O.P., Shcherbakov, O.A., and Einor, O.L. 1996. Moscovian Stage. In *The Carboniferous of the World. III. The former USSR, Mongolia, Middle Eastern Platform, Afghanistan, and Iran*. Edited by R.H. Wagner, C.F. Winkler Prins, and L.F. Granados. International Union of Geological Sciences Publication 33, pp. 69–98. Instituto Geológico y Minero de España, Madrid.
- Sternberg, K. von 1821. Versuch einer geognostisch-botanischer Darstellung der Flora der Vorwelt. I — 1: pp. 1–24, Tafn I–XIII.
- Sternberg, K. von 1823. Versuch einer geognostisch-botanischer Darstellung der Flora der Vorwelt. I — 2: pp. 1–33, Tafn XIV–XXVI.
- Sternberg, K. von 1824. Versuch einer geognostisch-botanischer Darstellung der Flora der Vorwelt. I — 3: pp. 1–40, Tafn XXVII–XXXIX.
- Sternberg, K. von 1825. Versuch einer geognostisch-botanischer Darstellung der Flora der Vorwelt. I — 4: pp. 1–48, Tafn XL–LIX, Tafn A–E.
- Stockmans, F. 1933. Les neuroptéridées des bassins houillers belges (première partie). *Mémoires du Musée Royal d'Histoire Naturelle de Belgique*, 57, pp. 1–61.
- Stockmans, F. and Willière, Y. 1951. Quelques végétaux namuriens et westphaliens du Charbonnage d'Aiseau-Presle. In *Étude géologique du Bassin Houiller de Charleroi. La concession Tergnée-Aiseau-Presle* (première partie). Edited by W. van Leckwyck. Association pour l'étude de la Paléontologie et de la Stratigraphie houillères, 9, pl. A–D.
- Stockmans, F. and Willière, Y. 1952a–1953. Végétaux namuriens de la Belgique. Association pour l'Étude de la Paléontologie et de la Stratigraphie houillères, 13. Texte (1953): pp. 1–382. Atlas (1952): pl. I–LVII.
- Stockmans, F. and Willière, Y. 1952b. Quelques végétaux namuriens de la Galerie de Ben. In *Étude géologique du Gisement Houiller d'Andenne-Huy*. Edited by W. van Leckwyck, F. Demanet, Y. Willière and H. Chaudoir. Publications Association pour l'Étude de la Paléontologie et de la Stratigraphie Houillères, Bruxelles, 11, pl. A–F.
- Stopes, M.C. 1914. The “Fern Ledges” Carboniferous flora of St. John, New Brunswick. Geological Survey of Canada, Memoir 41 (38 of Geological Series), pp. 1–142, pl. I–XXV. <https://doi.org/10.5962/bhl.title.64206>
- Stur, D. 1877. Die Culm-Flora der Ostrauer und Waldenburger Schichten. Abhandlungen der Kaiserlichen-Königlichen Geologischen Reichsanstalt, 8, pp. 1–366, pl. I–XXVII (XVIII–XLIV).
- Stur, D. 1883. Zur Morphologie und Systematik der Culm- und Carbonfarne. Sitzberichte Königlichen Akademie der Wissenschaften, I Abtheilung, LXXXVIII, pp. 633–846 (1–214).
- Suckow, G.A. 1784. Beschreibung einiger merkwürdiger Abdrücke von der Art der sogenannten Calamiten. *Acta Academiae Theodoro-Palatinae*, 5, Pars Physica, pp. 166–200.
- Šusta, V. 1928. Stratigraphie des Ostrau-Karviner Steinkohlenreviers im Lichte der Paläontologie. In: Der Kohlenbergbau des Ostrau-Karviner Steinkohlenreviers (Direktoren-Konferenz des Ostrau-Karviner Steinkohlenreviers in Mährisch Ostrau im Zehnten Jahre der Čechoslovakischen Republik), pp. 381–484.
- Šusta, V. 1930. *Neuropteris Larischii*, n. sp. *Sborník Přírodnědecké společnosti v Moravské Ostravě*, pp. 3–6.
- Taylor, T.N. and Kurmann, M. H. 1985. *Boulayatheca*, the new name for the seed fern pollen organ *Boulaya* Carpenter. *Taxon*, 34 (4), pp. 666–667. <https://doi.org/10.2307/1222209>
- Tenčov, Y.G. 1977. Flora und Biostratigraphie des Oberkarbons im Svoge-Becken (VR Bulgarien). *Schriftenreihe für Geologische Wissenschaften*, Berlin, 7, pp. 1–163.
- Tenčov, Y.G. and Cleal, C.J. 2010. *Neuralethopteris* foliage (Medulloiales) in the Carboniferous of the Dobrudzha Coalfield, Bulgaria. Review of Palaeobotany and Palynology, 158, pp. 298–307. <https://doi.org/10.1016/j.revpalbo.2009.10.001>
- Tidwell, W.D. 1967. Flora of Manning Canyon Shale. Part I: A lowermost Pennsylvanian flora from the Manning Canyon Shale, Utah, and its stratigraphic significance. *Brigham Young University Geology Studies*, 14, pp. 1–66.
- Unger, F. 1850. Genera et species plantarum fossilium. Sumptibus Academiae Caesareae Scientiarum. W. Braumüller, Vindobonae, 628 p. <https://doi.org/10.5962/bhl.title.26645>
- Wagner, R.H. 1961. Some Alethopterideae from the South Limburg Coalfield. Mededelingen Geologische Stichting, Nieuwe Serie, 14, pp. 5–13.
- Wagner, R.H. 1963. Sur les *Callipteridium* du Westphalien supérieur et du Stéphanien. Comptes rendus de l'Académie des Sciences, 257, pp. 719–721.
- Wagner, R.H. 1965. Stephanian B flora from the Ciñera-Mataliana Coalfield (León) and neighbouring outliers. III. *Callipteridium* and *Alethopteris*. Notas y Comunicaciones del Instituto Geológico y Minero de España, 78, pp. 5–69.
- Wagner, R.H. 1968. Upper Westphalian and Stephanian species of *Alethopteris* from Europe, Asia Minor and North America. Mededelingen Rijks Geologische Dienst, Serie C, III–1 (6), pp. 1–188.
- Wagner, R.H. 1984. Megafloral Zones of the Carboniferous. Compte Rendu 9^e Congrès Carbonifère, Washington-Urbana 1979, 2, pp. 109–134.
- Wagner, R.H. 2001. The extrabasinal elements in lower Pennsylvanian floras of the Maritime Provinces, Canada: description of *Adiantites*, *Pseudadiantites* and *Rhacopteridium*. *Revista Española de Paleontología*, 16 (2), pp. 187–207.
- Wagner, R.H. 2005a. *Dicranophyllum glabrum* (Dawson) Stopes, an unusual element of lower Westphalian floras in Atlantic Canada. *Revista Española de Paleontología*, 20

- (1), pp. 7–13.
- Wagner, R.H. 2005b. *Alethopteris lancifolia* Wagner, a rare element of lower Westphalian “Fern Ledges” of Atlantic Canada. *Revista Española de Paleontología*, 20 (1), pp. 15–19.
- Wagner, R.H. 2008. *Laveineopteris polymorpha* from the lower Westphalian (Langsettian) “Fern Ledges” at Saint John, New Brunswick, Canada, and comparison with *Laveineopteris hollandica* from Europe. *Revista Española de Paleontología*, 23 (2), pp. 139–156.
- Wagner, R.H. and Álvarez-Vázquez, C. 2008. A revision of the lower Pennsylvanian *Alethopteris lonchitica* (*auctorum*) and its identity with *Alethopteris urophylla*. *Revista Española de Paleontología*, 23 (2), pp. 157–192.
- Wagner, R.H. and Álvarez-Vázquez, C. 2010. The Carboniferous floras of the Iberian Peninsula: a synthesis with geological connotations. *Review of Palaeobotany and Palynology*, 162 (3), pp. 238–324. <https://doi.org/10.1016/j.repalbo.2010.06.005>
- Weiss, C.E. 1884. Beiträge zur fossilen Flora. III. Steinkohlen-Calamarien. II. Königlich Preussischen geologischen Landesanstalt, 5 (2), Text: pp. 87–290; Atlas: pl. I–XXVIII.
- Weiss, E. 1870. Studien über Odontopteridem. *Zeitschrift der Deutschen Geologischen Gesellschaft*, 22 (4), pp. 853–888.
- White, D. 1899. Fossil flora of the Lower Coal Measures of Missouri. United States Geological Survey, Monographs, 37, pp. 1–467. <https://doi.org/10.5962/bhl.title.38916>
- White, D. 1900. The stratigraphic succession of the fossil floras of the Pottsville Formation in the Southern Anthracite coal field, Pennsylvania. Twentieth Annual Report United States Geological Survey, 1898–1899, Part 2 — General Geology and Paleontology, pp. 749–918. <https://doi.org/10.5962/bhl.title.7601>
- White, D. 1901. The Canadian species of the genus *Whittleseya* and their systematic relations. *The Ottawa Naturalist*, 15 (4), pp. 98–110.
- White, D. 1905. Fossil plants of the group Cycadofilices. *Smithsonian Miscellaneous Collection*, 47, pp. 377–390.
- Williams, L. 1937. A study of *Neuropteris schlehani* Stur. *Journal of Paleontology*, 11 (5), pp. 462–465.
- Wittry, J. 2006. The Mazon Creek fossil flora. Earth Science Club of Northern Illinois, Esconi Associates, Illinois, pp. 1–154.
- Wood, J.M. 1963. The Stanley Cemetery flora (early Pennsylvanian) of Greene County, Indiana. Indiana Department of Conservation, Geological Survey, Bulletin 29, pp. 1–73.
- Zalessky, M.D. 1937. Sur quelques végétaux fossiles nouveaux des terrains Carbonifère et Permien du Bassin du Donetz. In *Problems of Paleontology*, II–III. Edited by A. Hartmann-Weinberg. Laboratory of Paleontology, Moscow University, pp. 155–193.
- Zeiller, R. 1879. Végétaux fossiles du terrain houiller de la France. Explication de la Carte Géologique détaillée de la France, Tome Quatrième, Seconde Partie, pp. 1–185.
- Zeiller, R. 1883. Fructifications de fougères du terrain houiller. *Annales Sciences naturelles*, Paris, Botanique, 6^e série, 17, pp. 130–143.
- Zeiller, R. 1886–1888. Bassin houiller de Valenciennes. Description de la flore fossile. Études des Gîtes Minéraux de la France. Texte (1888): 1–729. Atlas (1886): pl. I–XCIV.
- Zodrow, E.L. and Cleal, C.J. 1998. Revision of the pteridosperm foliage *Alethopteris* and *Lonchopteridium* (Upper Carboniferous), Sydney Coalfield, Nova Scotia, Canada. *Palaearctographica*, Abteilung B, 247 (3–6), pp. 65–122.

APPENDIX

List of names of genera, species and infraspecific taxa cited herein, with authorships

- Alethopteris* Sternberg 1825
Alethopteris bertrandii Bouroz 1956
Alethopteris corsinii Buisine 1961
Alethopteris davreuxii (Brongniart 1828) Göppert 1836
Alethopteris decurrens (Artis 1825) Frech 1880
Alethopteris decurrens var. *gracillima* Crookall 1955
Alethopteris densinervosa Wagner 1968
Alethopteris discrepans (Dawson 1863) Dawson in Bailey 1865
Alethopteris edwardsii Stockmans and Willière 1952a
Alethopteris evansii Lesquereux 1884
Alethopteris gracillima Boulay 1876
Alethopteris grandifolia Newberry 1873
Alethopteris grandinii (Brongniart 1828) Göppert 1836
Alethopteris havlena Šimůnek 1996
Alethopteris helenae Lesquereux 1879
Alethopteris integra (Gothan 1906) Kidston 1914
Alethopteris jankii Coquel and Laveine 1979
Alethopteris lancifolia Wagner 1961
Alethopteris lesquereuxii Wagner 1968
Alethopteris lonchitica Schlotheim 1820 ex Sternberg 1825
Alethopteris lonchitica forma *serlii* Brongniart 1828
Alethopteris lonchitifolia Bertrand 1932
Alethopteris missouriensis White 1899
Alethopteris pseudograndinoides Zodrow and Cleal 1998
Alethopteris scalariformis Bell 1938
Alethopteris serlii (Brongniart 1828) Göppert 1836
Alethopteris serlii forma *lonchitifolia* Bertrand 1932
Alethopteris solutifolia Josten and Amerom 2003
Alethopteris sullivantii (Lesquereux 1858) Fontaine and White 1880
Alethopteris tectensis Stockmans and Willière 1952a
Alethopteris urophylla (Brongniart 1834) Göppert 1836
Alethopteris valida Boulay 1876
Alethopteris westphalensis Wagner 1968
Annularia Sternberg 1821
Annularia ramosa Weiss 1884
Asterophyllites Brongniart 1822
Aulacotheca Halle 1933
Bergeria dilatata (Lindley and Hutton 1831) Álvarez-

- Vázquez and Wagner 2014
Bernaultia Rothwell and Eggert 1986
Boulayatheca Taylor and Kurmann 1985
Calamites Suckow 1784
Calamites carinatus Sternberg 1824
Calamites cistii Brongniart 1828
Callipteridium Weiss 1870
Callipteridium sullivanti (Lesquereux 1854) Weiss 1870
Cordaianthus Grand'Eury 1877
Cordaites Unger 1850
Crossotheca pinnatifida (Gutbier 1835) Potonié 1893
Diaphorodendron decurtatum (Dawson 1868) Álvarez-Vázquez and Wagner 2014
Eusphenopteris Gothan 1913 ex Novik 1947
Filicites decurrens Artis 1825
Johannophyton Matthew 1910
Johannophyton discrepans (Dawson in Bailey 1865) Matthew 1910
Laveineopteris rarinervis (Bunbury 1847) Cleal *et al.* 1990
Lepidostrobophyllum lanceolatum (Lindley and Hutton 1831) Bell 1938
Lonchopteridium (Gothan 1909) Guthörl 1958
Lonchopteris Brongniart 1828
Lyginopteris hoeninghausii (Brongniart 1828) Groppe 1932
Margaritopteris Gothan 1913
Margaritopteris conwayi (Lindley and Hutton 1835) Crookall 1929
Margaritopteris pseudocoemansii Gothan 1913
Neuralethopteris Cremer 1893
Neuralethopteris biformis (Lesquereux 1880) Goubet *et al.* 2000
Neuralethopteris jongmansii Laveine 1967
Neuralethopteris larischii (Šusta 1930) Laveine 1967
Neuralethopteris pocahontas (White 1900) Goubet *et al.* 2000
Neuralethopteris rectinervis (Kidston 1888) Laveine 1967
Neuralethopteris schlehanii (Stur 1877) Cremer 1893
Neuralethopteris sergiorum Goubet *et al.* 2000
Neuralethopteris smithsii (Lesquereux 1879) Goubet *et al.* 2000
Neuralethopteris weilii Josten and Amerom 2003
Neuropteris (Brongniart 1822) Sternberg 1825
Neuropteris bulupalganensis Zalessky 1937
Neuropteris dluhoschii Stur 1877
Neuropteris elrodii Lesquereux 1880
Neuropteris heterophylla (Brongniart 1822) Sternberg 1825
Neuropteris lata Tenchov 1977
Neuropteris longifolia Tenchov 1977
Neuropteris microphylla Brongniart 1831
Neuropteris multivenosa Purkyňová 1970
Neuropteris parvifolia Stockmans 1933
Neuropteris pocahontas White 1900
Neuropteris pocahontas var. *inaequalis* White 1900
Neuropteris rarinervis Bunbury 1847
Neuropteris rectinervis Kidston 1888
Neuropteris rectinervis forma *obtusa* Tenchov 1977
Neuropteris schlehanii Stur 1877
Neuropteris schlehanoides Stockmans and Willière 1952a
Neuropteris selwynii Dawson 1871
Neuropteris smithsii Lesquereux 1879
Pachytesta Brongniart 1874
Paripteris gigantea (Sternberg 1823) Gothan 1953
Pecopteris aspera Brongniart 1828
Pecopteris decurrens Dawson 1862
Pecopteris discrepans Dawson 1863
Pecopteris ingens Dawson 1862
Pecopteris mantellii Brongniart 1833
Pecopteris multiformis Sauveur 1848
Pecopteris urophylla Brongniart 1834
Pseudadianites rhomboideus (Ettingshausen 1852) Wagner 2001
Praecallipteridium Wagner 1963
Praecallipteridium jongmansii (Bertrand 1932) Wagner 1963
Remia pinnatifida (Gutbier 1835) Knight 1985
Renaultia Zeiller 1883
Rhacopteris Schimper 1869
Senftenbergia aspera (Brongniart 1828) Stur 1877
Sigillaria scutellata Brongniart 1822
Sphenophyllum Brongniart 1828
Sphenophyllum cuneifolium (Sternberg 1823) Zeiller 1879
Sphenopteris hollandica Gothan and Jongmans in Jongmans 1928
Sphenopteris minuscula Bell 1944
Sphenopteris nummularia Gutbier 1835
Sporangites acuminatus (Dawson 1862) Dawson 1871
Trigonocarpus Brongniart 1828
Wagneropteris minima Álvarez-Vázquez and Cleal 2016
Whittleseya Newberry 1853
Whittleseya brevifolia White 1901
Whittleseya concinna Matthew 1910
Whittleseya concinna var. *arcta* Matthew 1910
Whittleseya concinna var. *lata* Matthew 1910
Whittleseya dawsoniana White 1901
Whittleseya desiderata White 1901
Zeilleria avoldensis (Stur 1883) Kidston 1884
Zeilleria frenzlii (Stur 1883) Kidston 1884
Zeilleria hymenophylloides Kidston 1924

Editorial responsibility: Robert A. Fensome