Laveineopteris polymorpha FROM THE LOWER WESTPHALIAN (LANGSETTIAN) "FERN LEDGES" AT SAINT JOHN, NEW BRUNSWICK, CANADA, AND COMPARISON WITH *Laveineopteris hollandica* FROM EUROPE

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ABSTRACT

A documentation is presented of the pteridosperm (?) foliage species *Laveineopteris polymorpha* (Dawson, 1862) comb. nov. from its type locality at Saint John, New Brunswick. This Canadian species is also present in the United States and in the British Isles. The similar species *Laveineopteris hollandica* (Stockmans, 1933) Cleal & Shute, 1995, of European provenance, is discussed for detailed comparison. Lists of synonymy are provided for both species. These are commented on in detail. The stratigraphic and geographic distribution of these two species is discussed as well.

Keywords: *Laveineopteris*, *Neuropteris*, Langsettian, North America, Europe.

RESUMEN

Se presenta nueva documentación referente a la parte vegetativa de la probable pteridosperma *Laveineopteris polymorpha* (Dawson, 1862) comb. nov. obtenida a partir de material de su localidad tipo en Saint John, Nueva Brunswick. Esta especie canadiense se encuentra también en Estados Unidos y en las Islas Británicas. Es bastante parecida a *Laveineopteris hollandica* (Stockmans, 1933) Cleal & Shute, 1995, descrita en Europa. Se enumeran en extenso las listas de sinonimia de ambas especies y se analizan en detalle. Asimismo, se comentan las distribuciones estratigráficas y geográficas de las dos especies.

Palabras clave: *Laveineopteris*, *Neuropteris*, Langsettiense, Norteamérica, Europa.

INTRODUCTION

A general revision of the lower Westphalian floras of the Maritime Provinces of Canada, undertaken on behalf of the Geological Survey of Canada with the support of local organisations such as the New Brunswick Museum, has confirmed that these floras are closely similar to those present in western Europa, even to a larger extent than the published lists suggest. This refers particularly to the British Isles. It emphasises the close links between these two areas at a time when the Atlantic Ocean had not yet opened up. Whereas in several cases certain species described from Canada proved to be identical with European taxa described earlier, the reverse is also true, as Stopes (1914, 1917) has already pointed out. These involve taxa introduced in the mid 1800s by Dawson. Some of these taxa were poorly documented and superseded, in practice, by better described species based on more adequate material from Europe. Stopes (*op. cit.*) pointed out a few synonymies where Dawson's species enjoyed priority, but should be allowed to lapse in favour of the better known species from Europe.

In other cases, Canadian taxa described by Dawson were either assigned improperly to European species or simply ignored, in view of the poor quality of illustrations and fragmentary nature of the specimens recorded by Daw-

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son. Some of these taxa should be reconsidered, particularly where museum collections allow a better perception of specific characters. A case in point is *Neuropteris polymorpha* Dawson, 1862. This species was introduced on quite fragmentary remains which were illustrated by very diagrammatic drawings. However, a later publication by Dawson (1871) showed a more complete specimen from the type locality at Saint John, New Brunswick. Although the illustration by Dawson (1871) was another diagrammatic drawing, this specimen was refigured photographically by Stopes (1914, 1917). This made it possible to identify the characters of Dawson's species. Unfortunately, Stopes (1914) synonymised *Neuropteris polymorpha* with *Neuropteris heterophylla* Brongniart, 1822, apparently in error. Later authors either ignored *Neuropteris polymorpha*, or swallowed it up in the synonymy of different species (see Bell, 1944: 81).

A revision of the large collection of "Fern Ledges" material in the New Brunswick Museum at Saint John has allowed the range of morphological variation of this fernlike foliage species to be established. This probable pteridosperm species appears quite similar to *Laveineopteris hollandica*, whilst being different to *Neuropteris heterophylla auctorum* (*non* Brongniart). *Laveineopteris hollandica* is a relatively uncommon species in the European area where it has been figured and described most exhaustively by Laveine (1967). *Laveineopteris polymorpha* and *Laveineopteris hollandica* are commented on in the present paper, with the aim to assess the characters of both. Only *Laveineopteris polymorpha* is figured here.

Class CYCADOPSIDA Barnard & Long, 1975
Order TRIGONOCARPALES Seward, 1917, emend. Meyen 1984
Family **Trigonocarpaceae** Seward, 1917, emend. Meyen, 1984
Genus *Laveineopteris* Cleal, Shute & Zodrow, 1990, emend. Laveine, 2005

Laveineopteris polymorpha (Dawson, 1862) comb. nov.

Figs 1-7e

* 1862 *Neuropteris polymorpha* Dawson, p. 320, pl. XV, figs 36a-g.
* 1868 *Neuropteris polymorpha* Dawson – Dawson, p. 548, fig. 192c (copy of Dawson, 1862: pl. XV, fig. 36a), p. 549.
1871 *Neuropteris polymorpha* Dawson – Dawson, p. 49, pl. XVIII, fig. 212 (specimen illustrated photographically by Stopes, 1914).
? 1882 *Cardiopteris Eriana* Dawson, p. 114, Fig. IV.
1888 *Neuropteris polymorpha* Dawson – Dawson, p. 72, fig. 22c (*fide* Stopes, 1914: 58).
? 1893 *Neuropteris Blissii* Lesquereux – Kidston, p. 329-330, pl. I, figs 3, 3a (specimen figured photographically by Crookall, 1959: pl. XXXIX, fig. 4).
1910 *Neuropteris polymorpha* Dawson – Matthew, p. 248 (listed only).
p 1914 *Neuropteris heterophylla* Brongniart – Stopes, p. 58-61, pl. XIV, fig. 35 (photographic reproduction of specimen figured as *Neuropteris polymorpha* by Dawson, 1871: pl. XVIII, fig. 212); pl. XXI, fig. 56 (as *Neuropteris* sp. in plate explanation; attributed to *Neuropteris loshii* Brongniart, 1828a by Laveine, 1967: 145); *non* pl. XV, fig. 36 (specimen from Valenciennes, France, identified as *Neuropteris loshii* by Laveine, 1967); *non* pl. XV, fig. 38 [= *Neuropteris obliqua* (Brongniart, 1834) Göppert, 1846 acc. to Laveine, 1967].
? p 1914 *Neuropteris eriana* (Dawson) Stopes, p. 61-62, textfig. 11 (copy of Dawson, 1882: Fig. IV); *non* pl. XV, fig. 39 (probably a cyclopteroid pinnule of *Paripteris*).
1914 *Neuropteris plicata* Sternberg – Arber, p. 386, 387, 391, pl. 27, figs 10-11 (referred, with doubt, to *Neuropteris* cf. *hollandica* by Laveine, 1967: 161).
1922 *Neuropteris rytoniana* Kidston, p. 134 (*nomen nudum*) (see Crookall, 1959).
1933 *Neuropteris microphylla* Brongniart – Crookall, p. 58, pl. V, fig. 13.
1937 *Neuropteris* sp. (cf. *latenervosa* Jongmans) – Jongmans, p. 408, pl. 28, figs 81-83, pl. 29, figs 84, 84a.
* 1949 *Neuropteris saginawensis* Arnold, p. 192-193, pl. XXI, figs 1-2, 5-6 (referred to *Neuropteris hollandica* by Laveine, 1967).
p 1949 *Neuropteris obliqua* (Brongniart) Zeiller (*sic*) – Arnold, pl. XXIII, fig. 1; *non* p. 196-197, pl. XXIII, figs 2-4 (= *Neuropteris obliqua*).
1959 *Neuropteris rytoniana* Kidston ex Crookall, p. 113-114, text-figs 63A-C, pl. LII, figs 3-4, pl. LIV, fig. 1 (referred to *Neuropteris hollandica* by Laveine, 1967).
? p 1959 *Neuropteris Blissi* Lesquereux – Crookall, p. 127-129, text-fig. 65H, pl. XXXIX, figs 2-4; *non* pl. XLIX, figs 1-2 (aff. *Neuropteris blissii* Lesquereux, 1884); *non* text-fig. 45 (= *Neuropteris blissii* – type); *non* text-fig. 65C (aff. *Neuropteris blissii*).
? 1959 *Neuropteris thymifolia* Sternberg – Crookall, pl. XLVII, figs 1-3.
? 1997 *Neuropteris hollandica* Stockmans – Blake, p. 76 (chart).
? 2007 *Laveineopteris loshii* (Brongniart) – Falcon-Lang & Miller, p. 247.

* - type; p – *pars*; ? doubtful.

Lectotype: Specimen figured by Dawson, 1862, pl. XV, fig. 36a (see Fig. 1a of present paper). According to the Catalogue of type and figured fossils in the Redpath Museum, McGill University, Montreal (Alison & Carroll, 1972: 129), the specimen numbered 12,237 would be the holotype. This may be the specimen from which Dawson (1862: pl. XV, figs 36a-g) figured several pinna fragments. Perhaps, the most significant among these fragments is the apical part of a penultimate pinna figured as 36a. This was selected for refiguration by Dawson, 1868, and may be regarded as the lectotype. Similar pinnae appear in the terminal part of a pinna of the penultimate order which was figured by Dawson, 1871, pl. XVIII, fig. 212, refigured here (Figs 1b, 2-3). This specimen is mentioned as a plesiotype by Alison & Carroll (1972).

Material: The New Brunswick Museum collection contains several pinna fragments from the "Fern Ledges" at Saint John, including fragments of pinnae of the penultimate order. All remains are impressions on slaty shale, dark grey in colour (Figs 4-7). Additionally, the specimen figured by Dawson (1871: pl. XVIII, fig. 212) has been examined in the Redpath Museum, Montreal (see Figs 2-3). All the specimens figured by Dawson (1862, 1871) are from the Hartt Collection, and originate from the "Fern Ledges", Carleton Township, Saint John (R.F. Miller, pers. comm., 31-03-2008).

Description: Terminal of penultimate order slender, with well individualised apical pinnule which is bluntly acuminate. Rachis thin. Ultimate pinnae terminals also slender with bluntly acuminate apical pinnules which are variable in size, depending on the location of the pinna; in fully developed pinnae they are not much bigger than the lateral pinnules. Pinna terminals are relatively larger in the small pinnae occurring in the upper part of penultimate pinnae. Pinnules extremely variable in size depending on position in the frond. Pinnae with large, acuminate pinnules and a slightly broader rachis presumably occur in lower part of the frond (Fig. 5e). Other pinnae show ovoid pinnules, twice to three times as long as they are wide, with bluntly acuminate apices, whilst pinnae with shorter, more rounded pinnules also occur. Pinnule bases usually rounded on both sides, but a wider insertion with partial fusion of pinnule base to rachis occurs in near-terminal pinnules. Lamina apparently rather thin, non-vaulted, with thin midrib well marked but not sunken into pinnule limb to a significant degree (however, the slaty condition of the shales carrying the imprints aids in producing a flattened appearance). Midrib thin, extending commonly up to one half the pinnule length and less commonly up

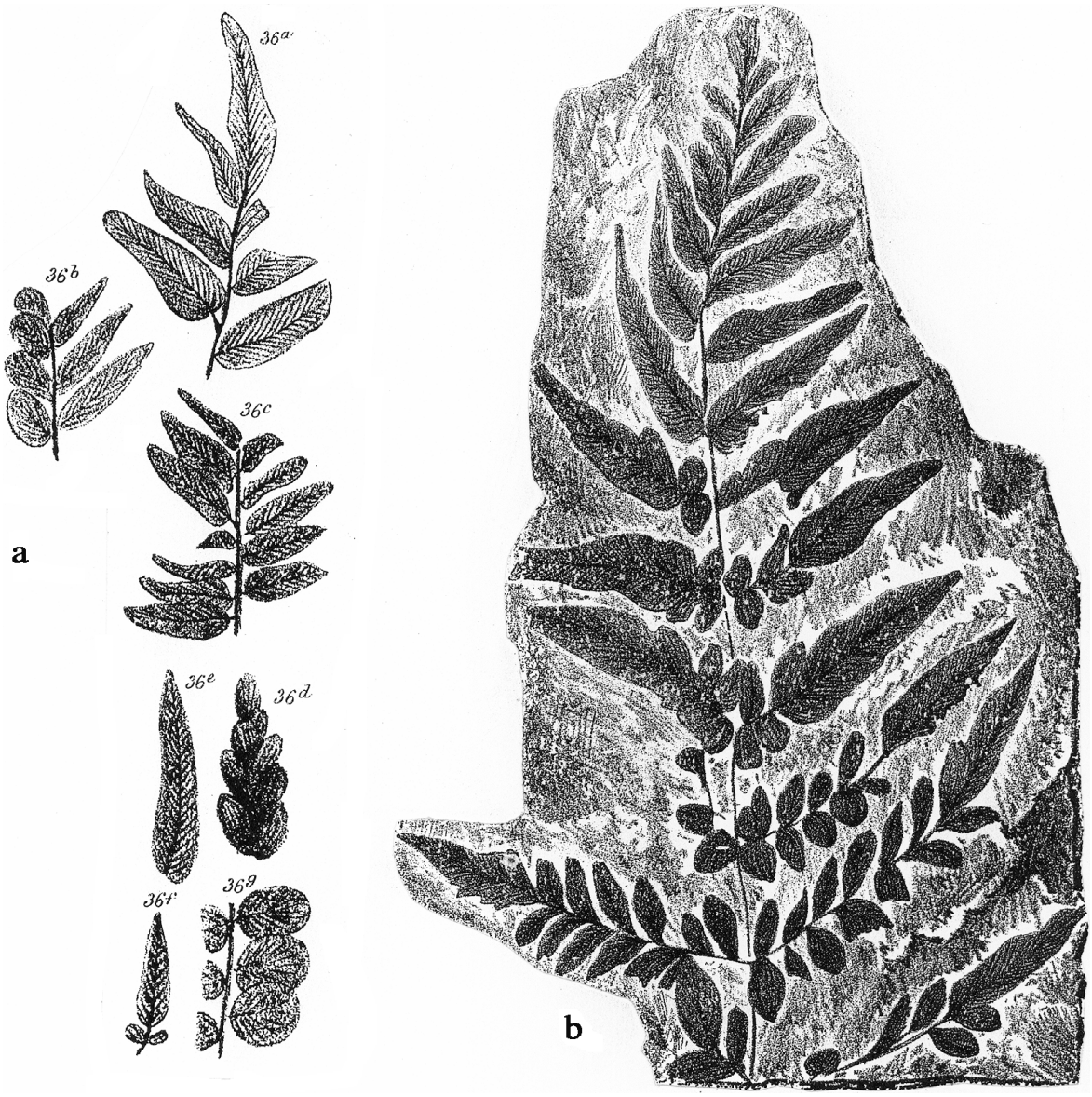


Figure 1. **a**, Copy of the original illustration of *Neuropteris polymorpha* Dawson (lectotype) in 1862, pl. XV, fig. 36c. **b**, Copy of the original drawing of the large pinna of *Neuropteris polymorpha* by Dawson (1871: pl. XVIII, fig. 212), illustrated photographically by Stopes (1914, 1917: pl. XIV).

to two thirds, depending on the size of pinnules. Lateral veins thin, thread-like, ascending steeply and relatively straight, abutting obliquely onto the pinnule margin, generally twice forked. Vein density 16-19 veins/cm.

Dawson's (1862: 320) description was as follows *"Pinnate or bipinnate. Rachis or secondary rachis irregularly striate. Pinnules varying from round to oblong, unequally cordate at base varying from obtuse to acute. Terminal leaflet ovate, acute, angulated or lobed. Midrib delicate, evanescent. Nervures slightly arcuate, at acute angles with the midrib."*

Comparisons: A closely comparable species is *Laveineopteris hollandica* (Stockmans, 1933) Cleal & Shute, 1995, so much so that small fragments of these two species can be confused quite easily. Pinnule shape is similar, although there is a tendency towards a more ovoid shape, with bluntly acuminate apices, in *Laveineopteris polymorpha*. The nervation in both species is characterised by thin, thread-like veins, but *Laveineopteris hollandica* has a more persistent midrib reaching up to two thirds of the pinnule length, and apparently possesses slightly curved, less straight lateral veins. The vein density (measured on the nervation diagram in Laveine, 1967: fig. 25b) is *c*. 28 veins/cm in *Laveineopteris hollandica* and rather less in *Laveineopteris polymorpha* (16-19). Further comments on *Laveineopteris hollandica* are provided later on.

Another fairly close comparison is with *Laveineopteris tenuifolia* (Schlotheim, 1820) Cleal, Shute & Zodrow, 1990 which shows a similar variation in pinnule size and shape, although with a lesser degree of polymorphism. It also shows a comparable venation which is, however, a little denser, with around 25-28 veins/cm. *Laveineopteris tenuifolia* is also characterised by a more strongly marked midrib sunken into a somewhat vaulted lamina. Its lateral veins also appear to be less straight, slightly curved. Some of the illustrations in the literature show specimens attributed to *Laveineopteris tenuifolia*, which are suggestive of *Laveineopteris hollandica* and *Laveineopteris polymorpha*, and small fragments may be difficult to tell apart.

Laveineopteris loshii (Brongniart, 1828a) Cleal, Shute & Zodrow, 1990 is also comparable, but its pinnules commonly show more rounded apices, and less thread-like veins. It also appears that *Laveineopteris loshii* is not quite as variable in its pinnule morphology as *Laveineopteris polymorpha*. Bluntly acuminate pinnules as occur in *Neuropteris polymorpha* Dawson, do not seem to be present in *Neuropteris loshii*, which also appears to have a denser venation, around 30 veins/cm. Confusion is possible in small fragments showing the smaller kind of pinnules.

Remarks on published remains from the type locality ("Fern Ledges"): The original illustrations of *Neuropteris polymorpha* in Dawson (1862) are highly diagrammatic renderings of small pinna and pinnule fragments (Fig. 1a of the present paper). These include a pinna terminal (Dawson, 1862: pl. XV, fig. 36a). A later paper by Dawson (1871) shows a larger, more complete specimen (also illustrated as a drawing – Fig. 1b of the present paper) which represents the terminal part of a pinna of the penultimate order. The lower part of this specimen shows several side pinnae with terminals of various sizes depending on the position in the major pinna. A comparison with Dawson, 1862: pl. XV, fig. 36a (lectotype) is quite apparent. A photograph of Dawson's 1871 specimen, which is in the Redpath Museum at McGill University in Montreal (Cat. nº 3311), has been published by Stopes (1914: pl. XIV, fig. 35), at slightly less than natural size (all Stopes's plates were reduced by the Printer). Whereas Dawson's illustrations are too sketchy to allow the proper identification of his *Neuropteris polymorpha*, the photographs published by Stopes remove this problem. All specimens are from the Hartt Collection and originate from the "Fern Ledges" in Carleton County, Saint John (New Brunswick) (Hartt collected exclusively from this locality – pers. comm. from R.F. Miller, 31-03-2008). The more useful 1871 specimen is therefore a topotype. A photograph (x 3) of the upper (terminal) and middle parts of the same specimen is reproduced in the present paper (Figs 2-3). Stopes identified this specimen with *Neuropteris heterophylla* and backed up the identification by figuring a similar specimen from the North of France for comparison (her pl. XV, fig. 36). However, the latter is the form which Laveine (1967) identified with *Neuropteris loshii*, making the point that *Neuropteris heterophylla* had been commonly misidentified in Europe. Indeed, he stated that the specimens illustrated as *Neuropteris heterophylla* in the literature were generally (but not invariably) attributable to *Neuropteris loshii*. Laveine (1967) placed Dawson's (1871) specimen from the "Fern Ledges", as figured by Stopes (1914: pl. XIV, fig. 35), in the synonymy of *Neuropteris loshii*, thus admitting the identification between Canadian and French material. However, this seems questionable. Although it is agreed that *Neuropteris loshii* is closely comparable, and specimens reminiscent of this species have been observed in material from the "Fern Ledges", the generally more bluntly acuminate pinnules of Dawson's specimen are different. Even more different is the fine, thread-like nervation, which is more widely spaced than that of *Neuropteris loshii*. In fact, the nervation is more reminiscent of *Neuropteris hollandica* Stockmans, another European species, which is less commonly recorded. The venation of Dawson's (1871) specimen can only be made out with difficulty on the photograph published by Stopes (1914: pl. XIV), but the enlargements figured in the present paper (Figs 2, 3) show the venation more clearly albeit not quite as sharply as would be desirable. This is due in part to coating with ammonium chloride; the actual preservation is a little better. An additional, more fragmentary specimen from the "Fern Ledges" was figured by Stopes (1914: pl. XXI, fig. 56) as *Neuropteris* foliage. Its venation is not clearly visible on the photograph, but apparently fits that of

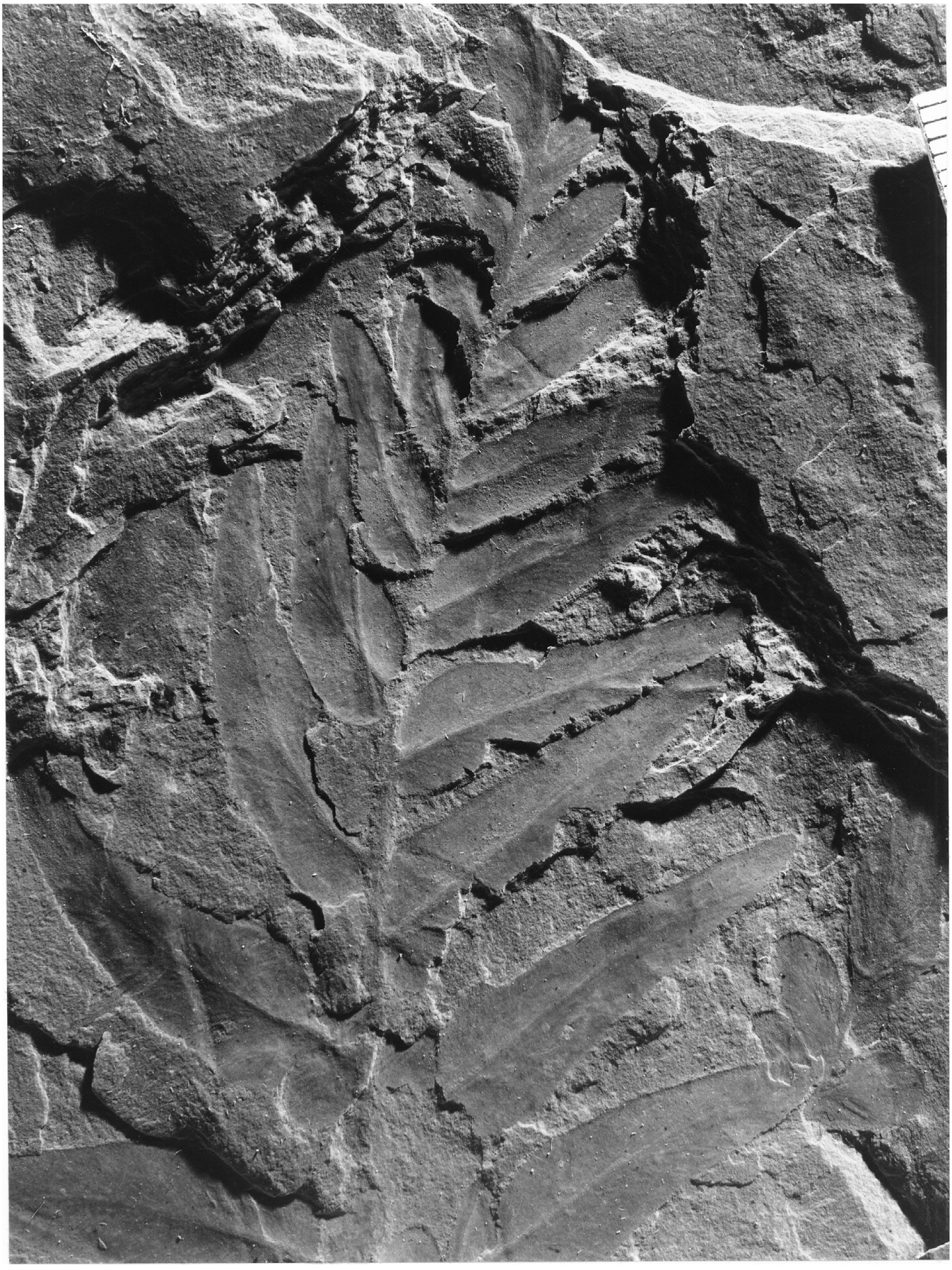


Figure 2. Photographic illustration (x 3) of the upper part of the specimen figured by Dawson (1871: pl. XVIII, fig. 212) and Stopes (1914, 1917: pl. XIV) (Redpath Museum Cat. n° 3311).

Neuropteris polymorpha. This specimen was attributed to *Neuropteris tenuifolia* (Schlotheim, 1820) Sternberg, 1825 by Bell (1944: 80). Although this may be regarded as a better approximation than *Neuropteris loshii*, the present writer prefers to include it with *Laveineopteris polymorpha*. It is noted that Bell (1944: 81) referred *Neuropteris polymorpha* Dawson, including the specimens figured as *Neuropteris heterophylla* by Stopes (1914: pl. XIV, fig. 35; pl. XV, fig. 38) and *Neuropteris* sp. (Stopes, 1914: pl. XV, fig. 40) to *Neuropteris obliqua*. The latter is another species of variable pinnule morphology, although characterised by decurrent pinnule bases in the terminal parts of pinnae. This character is less apparent in *Laveineopteris polymorpha*, which only shows partly adherent pinnule bases in some near-terminal pinna fragments (e.g. Fig. 4d-e). *Neuropteris obliqua* shows pinnae with large triangular pinnules (forma *impar*) in the lower part of the frond. Although the variation in pinnule size and shape is also quite large in *Laveineopteris polymorpha* (probably more so than in other species of *Laveineopteris*), the forma *impar* is more extreme in its size variation. This being said, it is true that *Neuropteris obliqua* has been interpreted quite widely in the literature (not always correctly).

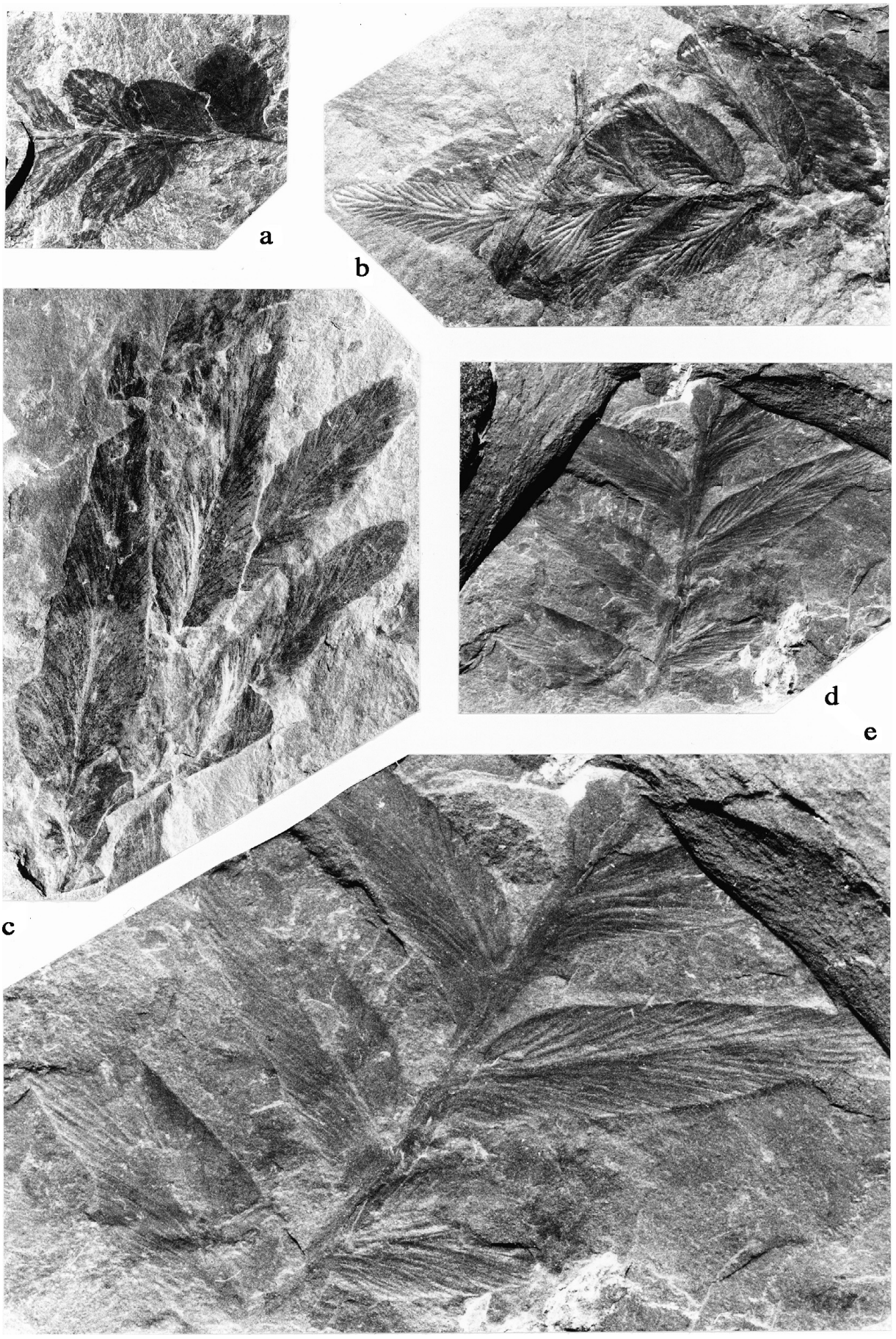
Laveine (1967) accepted that the specimens figured from the "Fern Ledges" by Stopes (1914) on her pl. XV, figs 38, 40 [as *Neuropteris heterophylla* and *Neuropteris* sp. (= *Nephropteris varia* Dawson, 1871), respectively], would belong to *Neuropteris obliqua*. The present writer concurs. Finally, a single cyclopteroid pinnule figured as *Neuropteris eriana* (Dawson, 1881) Stopes, 1914 by Stopes (1914: pl. XV, fig. 39) and which she incorporated tentatively with *Neuropteris polymorpha* (see Stopes, 1914: 62), was also attributed to *Neuropteris tenuifolia* by Bell (1944: 80). This attribution cannot be accepted. It is likely that this single pinnule should be assigned to *Paripteris*. The type of the species originally described as *Cardiopteris eriana* by Dawson (1881: pl. XIII, fig. 18), is too fragmentary for this species to be retained as a viable taxon. Stopes (1914: p. 61-62) did retain this species, as *Neuropteris eriana*, albeit provisionally.

It is noted that Falcon-Lang & Miller (2007) mentioned *Laveineopteris loshii* from the "Fern Ledges", recording it as abundant on some horizons. Judging from the New Brunswick Museum collection (as examined by the present writer), it is likely that their records refer, in the main, to *Laveineopteris polymorpha*, which is common in the "Fern Ledges". However, the "Fern Ledges" also contain (rarer) remains of *Laveineopteris loshii* and *Neuropteris obliqua* (a species which is not recorded as present by Falcon-Lang and Miller). This leaves an element of doubt which can only be resolved by a recount of the specimens studied by these authors, who did not illustrate examples of the different species recorded.

Comments on the general taxonomy: Apart from the fragmentary specimens which may or may not be correctly ascribed to *Neuropteris obliqua*, a species that does occur in the "Fern Ledges" locality (albeit less commonly), most of the remains identified as *Neuropteris polymorpha* belong to the general group of *Neuropteris tenuifolia* and *Neuropteris loshii* which Cleal *et al*. (1990) described as *Laveineopteris*. They defined this genus on the basis of a dichotomous frond structure with the presence of large, orbicular to reniform cyclopterid pinnules attached below the frond dichotomy, imparipinnate pinnae, and anomocytic stomata. Laveine (1997, 2005) pointed out that *Neuropteris sensu stricto* and *Laveineopteris* were closely similar, particularly with regard to frond structure and the shape of cyclopterid pinnules in the basal part of the fronds. However, in the final analysis, he accepted the genus *Laveineopteris* on the basis of a marked foliar polymorphism in the basal part of the frond (Laveine, 1997: 178). Laveine (2005) emended the generic description, from which he excluded the cuticular characters. These were regarded as broadly similar for different genera. Although the *Neuropteris polymorpha* remains, as known from the "Fern Ledges" in New Brunswick, are too fragmentary to show the frond structure as mentioned for *Laveineopteris*, and cuticular characters cannot be ascertained, the apparent similarity with *Laveineopteris tenuifolia* suggests that *Laveineopteris* is involved. Also, only isolated, poorly preserved remains of *Cyclopteris* are known from the "Fern Ledges". Although possibly attributable to *Neuropteris polymorpha*, this is by no means certain.

Considerations with regard to the list of synonymy: Apart from the records from the type locality in New Brunswick, Canada, *Laveineopteris polymorpha* remains have turned up in at least two different places in North America. Arnold (1949) described a *Neuropteris saginawensis* which is clearly identical to *Laveineopteris polymorpha*. It is noted that Laveine (1967) placed Arnold's species in synonymy with *Neuropteris hollandica*, which is closely similar to *Laveineopteris polymorpha*. One of the specimens figured by Arnold (1949: pl. XXIII, fig. 1) as *Neuropteris obliqua* from the same locality in the Michigan Basin, also seems referable to *Laveineopteris polymorpha*. This is the terminal part of a last order pinna, which shows partly adherent pinnule bases in the highest part of the pinna. The ovoid shape of the lateral pinnules in this specimen is characteristic of *Laveineopteris polymorpha*. Unfortunately, its nervation can only be guessed

Figure 3. Photograph (x 3) of the middle part of the specimen figured by Dawson (1871: pl. XVIII, fig. 212) and Stopes (1914, 1917: pl. XIV). Note partial overlap with Fig. 2.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at. Other specimens from North America, which seem referable to *Laveineopteris polymorpha*, are those figured from West Virginia (Appalachian region) by Jongmans (1937). These specimens (Jongmans, 1937: 407-408; his locality 33) came from the upper Kanawha, i.e. upper Duckmantian/lower Bolsovian, according to Blake *et al*. (2002). Jongmans (*op*. *cit*.) identified these remains with a manuscript species from the upper Duckmantian (ex Westphalian B) of South Limburg, the Netherlands, which he had named *Neuropteris latenervosa* Jongmans, 1937 (see also Jongmans & Gothan, 1934). His description of the American specimens fits that of *Laveineopteris polymorpha*. It is noted that Jongmans (1952: 18) later referred to his species as *Neuropteris heterophylla* forma *latenervosa*. Although not exactly a *nomen nudum*, Jongmans's species or forma fell short of being introduced formally. It is noted that the forma *latenervosa* as figured by Jongmans (1952) from Djerada, Morocco, probably conforms to *Laveineopteris loshii*.

Laveineopteris polymorpha also seems to be present in the British Isles where *Neuropteris rytoniana* Kidston, 1922, as figured and described by Crookall (1959), is an apparent synonym. It is noted that this species was referred to *Neuropteris hollandica* by Laveine (1967). Crookall (1959) described *Neuropteris rytoniana* together with *Neuropteris formosa* Kidston, 1922, both from the same locality, i.e. the Crow Coal, of Duckmantian age, at Ryton in Durham County, England. It is worth noting that both *Neuropteris rytoniana* and *Neuropteris formosa* were assigned to *Laveineopteris hollandica* by Cleal & Shute (1995). This may well be the correct identification for *Neuropteris formosa*. It is recalled that *Laveineopteris polymorpha* and *Laveineopteris hollandica* are closely comparable.

Crookall (1959) also figured some fragmentary remains of pinnae from the Langsettian (ex Westphalian A) of Lanarkshire, Scotland, under the name of *Neuropteris thymifolia* Sternberg 1933. This refers to a species originally figured by Lindley & Hutton (1832) as *Neuropteris soretii* Brongniart, 1828a, an apparent misidentification as Sternberg (1833) observed. Crookall figured a nervation diagram of the type specimen (*op*. *cit*.: text-fig 64B), as drawn by R. Kidston, and noted that the type was too poorly preserved for photographic reproduction. Although Crookall (1959: 105) expressed his doubts about the possibility of distinguishing *Neuropteris thymifolia* as a viable taxon, he respected Kidston's opinion (in manuscript) and maintained Sternberg's species. Crookall's figures suggest the presence of *Laveineopteris polymorpha*. Whether or not he identified these fragments correctly as *Neuropteris thymifolia* is an open question.

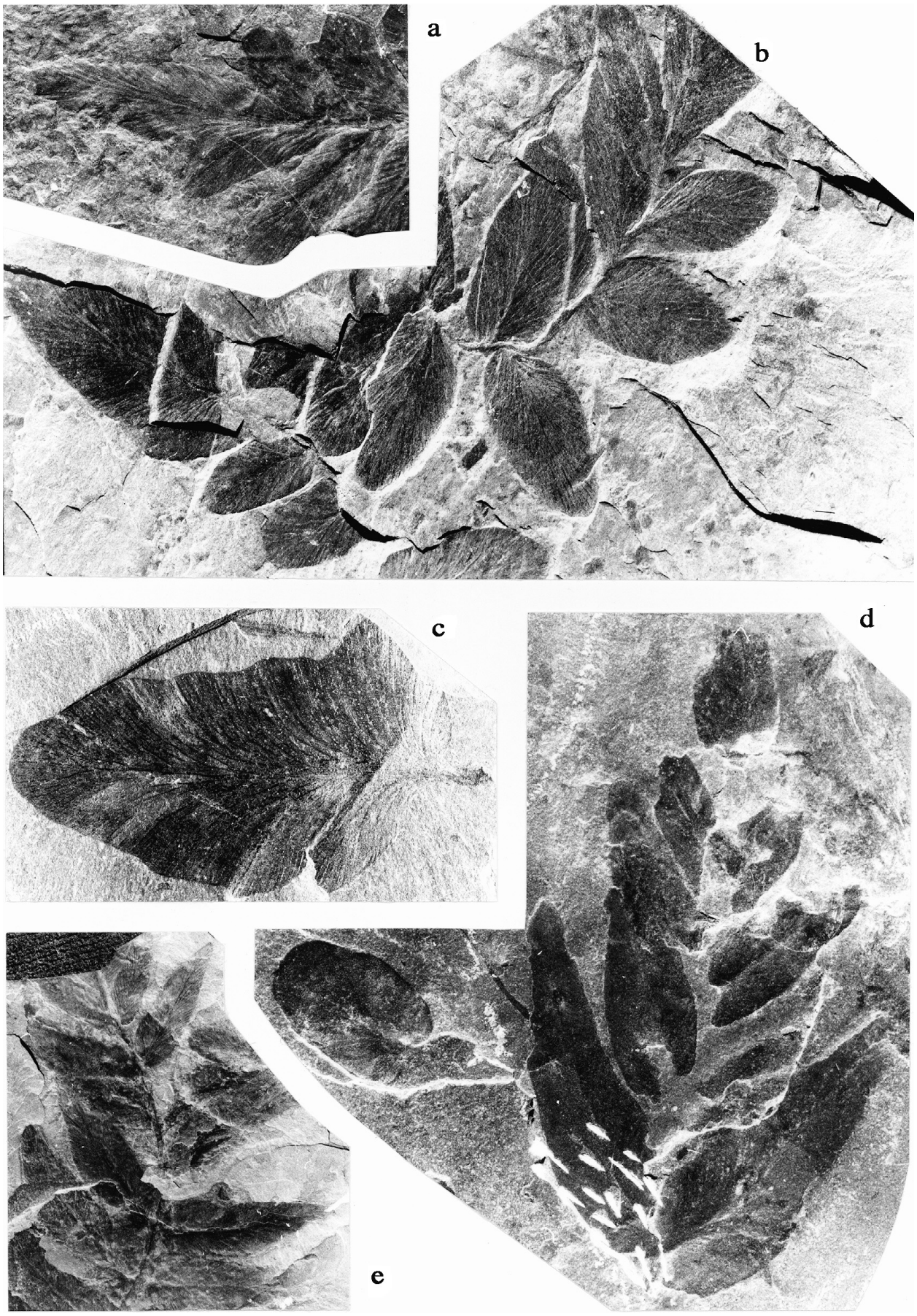
Two pinna fragments with relatively large pinnules were figured from the Duckmantian of Derbyshire, England by Crookall (1959: pl. XXXIX, figs 2, 3, 3a) as *Neuropteris blissii* Lesquereux, 1884. The ovoid pinnule shape with a bluntly acuminate apex suggests *Laveineopteris polymorpha* and so does the vein pattern. Crookall's identification with *Neuropteris blissii* is almost certainly incorrect. It seems likely that an additional specimen from the Duckmantian of Ayrshire (Crookall, 1959: pl. XXXIX, fig. 4) also belongs to *Laveineopteris polymorpha*, but this is less certain. This latter specimen is most comparable to the form recorded as *Neuropteris* cf. *hollandica* by Laveine (1967: 161, pl. XXVIII, figs 1-3).

Jongmans (1937: pl. 28, fig. 81) illustrated an associated small *Cyclopteris* leaflet which he noted as probably belonging to his *Neuropteris latenervosa* from West Virginia. A similar small *Cyclopteris* occurs with the material from the "Fern Ledges" in the museum at Saint John (NBMG 7440). There is no guarantee that this isolated specimen actually belongs to *Laveineopteris polymorpha*, although this is the most common *Laveineopteris* at this locality. It has not been regarded as worth figuring.

Comments on the specimens illustrated: The most complete specimen known is the terminal part of a pinna of the penultimate order as figured by Dawson (1871: pl. XVIII, fig. 212), and refigured photographically by Stopes (1914, 1917: pl. XIV). Enlargements (x 3) of this specimen are illustrated as Figs 2 and 3 of the present paper. It shows a good deal of variation in pinnule sizes and shapes, ranging from large triangular pinnules through more ovoid ones to smaller, more isodiametric pinnules with rounded apices (as occur in small, hardly individualised side pinnae). These pinnule shapes are quite similar to those occurring in *Laveineopteris hollandica*, but the venation is different. The midribs of the smaller pinnules are barely visible, occupying only one third to one half of the pinnule length. Lateral veins are steeply inclined, more or less straight and not arched as in *Laveineopteris hollandica*. Dawson's drawing of this specimen gives a reasonable impression of the vein pattern, although it is only a diagrammatic representation. The photograph published by Stopes does it less justice with regard to the nervation. The enlargements figured in the present paper show the nervation only faintly; however, where the venation is visible it is compatible with that of the more neatly imprinted, smaller fragments illustrated from the same locality (Figs 4-7).

Dawson (1871: 49) gives the locality of his *Neuropteris polymorpha* as "shales of Carlton near St. John" (New Brunswick). He mentions that the original description

Figure 4. **a** (NBMG 12053/2), x 3; **b** (NBMG 10447), x 3; **c** (NBMG 7387/1), x 3; **d** (NBMG 12052/2), x 3; **e** (same as d, x 6). Pinna fragments showing variations in size and shape of pinnules with tendency to tapering sides with lengthening. Note relatively small terminal in (**b**). Straight, thread-like veins are characteristic.


a
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e

(Dawson, 1862) was based on fragments, but that "A few perfect specimens occur in the collection of Prof. Hartt". It seems that Hartt collected exclusively from the "Fern Ledges" locality at the DeMill property, at about a mile west of Carleton (the old name of a community on the west side of Saint John) (R.F. Miller, pers. comm., 31-03-2008). All the specimens collected by Hartt were entrusted to Dawson. The later, more complete specimen refigured here at Figs 2-3, thus originated from the same locality as the more fragmentary remains figured by Dawson in 1862.

Smaller fragments from the "Fern Ledges" at Saint John (New Brunswick), as figured in Figs 4-7, show a wide range of pinnule sizes linked to different shapes. They fully justify the specific epithet of "*polymorpha*". Pinnule shapes range from elongate, almost subtriangular, to ovoid, but approximating, in some cases, a subcircular shape in the transition between massive, elongate pinnules and side pinnae (compare Fig. 3 and Fig. 7e). Although the pinnules are generally similar to those of *Laveineopteris hollandica*, the latter is not quite as polymorph, and does not show the bluntly acuminate pinnule apices which are characteristic of *Laveineopteris polymorpha*. Both species share the thin, thread-like venation, but *Laveineopteris polymorpha* is characterised by more widely spaced, generally straighter lateral veins.

Occurrence in New Brunswick, Canada: "Fern Ledges" at Saint John, NBMG Catalogue n^{os} 1684/1, 1684/2, 1684/3, 1730, 2306, 2318, 2319, 7261, 7298, 7387/1, 7525, 7736, 10441, 10447, 10448/1, 10448/2, 10455, 12044, 12045, 12050/1, 12050/2, 12052/2.
"Fern Ledges", GSC locs. 133 (with *Cyclopteris* fragment), 134, 146, 351 (6 specimens), 352, 804, 810 (2 specimens), 2254 (11 specimens), 3415.
Rugged Head: GSC loc. 645 (Lepreau Basin).
Gardner's Creek: GSC loc. 701 (3 specimens with cf.), 712 (3 specimens), 794, 799 (near Russell's farm - 1 specimen).
McCoy Head: GSC loc. 793 (1 specimen).
Tynemouth Creek: GSC loc. 802.
NBMG refers to New Brunswick Museum Geology collection at Saint John.
GSC refers to Geological Survey of Canada, Ottawa.

Occurrence in Nova Scotia, Canada: East of Pudsey Point: GSC loc. 3111.

Laveineopteris hollandica (Stockmans, 1933) Cleal & Shute, 1995

1915 *Neuropteris* cf. *callosa* Lesquereux – Jongmans & Gothan, p. 165-167, Taf. II, figs 3-6, Taf. III, figs 1-2a.

1928 *Neuropteris callosa* Lesquereux – Jongmans, p. 21, 49, pl. 14, fig. 1.

? 1932 *Neuropteris* cf. *callosa* Lesquereux – Corsin, p. 20, pl. XI, figs 2-5.

* 1933 *Neuropteris hollandica* Stockmans, p. 31-34, pl. X, figs 1, 1a (holotype).

? 1933 *Neuropteris callosa* Jongmans & Gothan (*sic*) – Crookall, p. 58, pl. VI, fig. 7 (cannot be judged very well from the illustration).

1938 *Neuropteris hollandica* Stockmans – Renier & Stockmans *in* Renier *et al*., p. 78, p. 15 (plate explanation), pl. 68.

1939 *Neuropteris callosa* Jongmans & Kidston (*sic*) (= *Neuropteris hollandica*) – Jongmans, p. 46, 48, 66, 67, pl. XXVII, figs 73, 73a? (could also be *Laveineopteris tenuifolia*), pl. XXIX, figs 79, 79a, 79bis.

? 1944 *Neuropteris hollandica* Stockmans – Zalessky, p. 285-295, Abb. 1-2 (nervation diagrams).

p 1953 *Imparipteris (Neuropteris) hollandica* Stockmans – Gothan , p. 52-53, Taf. 23, figs 1a, 2b, Taf. 26, fig. 2, Taf. 27, fig. 1, ? fig. 2 (comparable to *Laveineopteris loshii*), Taf. 28, figs 1, 3-4.

p 1959 *Neuropteris hollandica* Stockmans – Crookall, p. 108-110, text-fig. 37 (copy of Jongmans & Gothan, 1915: Taf. II, fig. 5a, Taf. III, fig. 2a), ? pl. XXXI, figs 4-5 (very fragmentary specimens which have been assigned tentatively to *Neuropteris tenuifolia* by Laveine, 1967: 159).

1959 *Neuropteris formosa* Kidston ex Crookall, p. 139-140, text-fig. 63D, pl. LII, figs 1-2 (also according to Cleal & Shute, 1995: p. 20).

1962 *Neuropteris hollandica* Stockmans – Stockmans & Willière, p. 59, 60, 62, 65, 76, 77, 87, pl. D, figs 9-10.

1967 *Neuropteris hollandica* Stockmans – Laveine, p. 156-161, pls XXVI-XXVII.

1967 *Neuropteris* cf. *hollandica* Stockmans – Laveine, p. 161-162, pl. XXVIII, figs 1-3.

p ? 1969 *Neuropteris hollandica* Stockmans – Daber, p. 258, Taf. II, Bild 7 (doubtful, poorly preserved specimen).

1991 *Neuropteris hollandica* Stockmans – Josten, p. 320-321, Taf. 185, figs 1-3.

1995 *Laveineopteris hollandica* (Stockmans) Cleal & Shute, p. 20.

Excludenda

1963 *Neuropteris hollandica* Stockmans – Josten, p. 96, Taf. 1, figs 1, 1a [= *Pseudadiantites sessilis* (Roehl, 1868) Gothan, 1929 – also excluded by Laveine, 1967: 159].

p 1969 *Neuropteris hollandica* Stockmans – Daber, p. 258; Taf. X, Bild 8 (poorly preserved, possibly *Neuropteris attenuata* Lindley & Hutton, 1835).

1985 *Neuropteris hollandica* Stockmans – Gillespie & Rheams, pl. II, fig. 4 (= *Laveineopteris loshii*?).

Figure 5. **a** (NBMG 12045), x 3; **b** (NBMG 2306), x 3; **c** (NBMG 12044), x 3; **d** (NBMG 12050/1), x 3; **e** (NBMG 7525), x 3. Pinna fragments showing tapering pinnule shapes and relatively small terminals (apical pinnules). (**c**) is attributed with doubt (mainly on the kind of venation).

Remarks on the synonymy: Records from the British Isles are reduced to the two specimens figured as *Neuropteris formosa* by Crookall (1959: pl. LII, figs 1-2). These are from the Duckmantian of County Durham in NE England. It is worth mentioning that Cleal & Shute (1995) included these specimens in *Laveineopteris hollandica*, thus verifying the presence of this species in Britain, whilst, on the other hand, it is not included in the distribution charts published by Cleal (2005, 2007) for the Pennine Basin in England, and for South Wales, respectively. This seems to indicate its extreme rarity in the British Isles.

Indeed, most records from western Europe are concentrated in the area extending from northern France (Laveine, 1967) through Belgium (Stockmans, 1933; Renier *et al*., 1938) into South Limburg, Netherlands (Jongmans & Gothan, 1915; Jongmans, 1928) and western Germany (Josten, 1991).

Records from northeastern Germany are doubtful. Daber (1969) recorded two specimens of *Neuropteris hollandica* from a deep borehole in NE Germany. One of his specimens is accepted with doubt; the other must be rejected.

Jongmans (1939) figured two specimens from the Donbass under the name of *Neuropteris callosa* (= *Neuropteris hollandica*). One of the specimens figured (Jongmans, 1939: Taf. XXIX, figs 79, 79a) does indeed suggest *Laveineopteris hollandica*. This specimen came from the Lotikova Mine, and the horizon is given as C_2^6. This upper Westphalian record is stratigraphically anomalous. The other specimen (*op. cit*.: pl. XXVII, figs 73, 73a) is too fragmentary to be identified reliably.

Two additional records of *Neuropteris hollandica* from the upper Westphalian of the Donbass (Zalessky, 1944) can only be regarded as doubtful in view of the illustrations which are drawings. Although Zalessky discussed his finds in detail, he was not in a position to publish photographs (he worked from W. Gothan's laboratory in Berlin, and did not have access to his collections which were destroyed in a fire during the Second World War). Zalessky (1944) did publish two well executed drawings, but these fail to convince. Zalessky referred to the records of *Neuropteris hollandica* from the Donbass by Jongmans (1939), and expressed his disagreement with Jongmans's stratigraphic attribution.

Neuropteris hollandica is listed (but not illustrated) by Fissunenko (*in* Einor *et al*., 1996: 97) from the Donbass. Only a single horizon (coal seam k5) is given for what is obviously regarded as a rare species. This locality, which is referred to Lower Moscovian on the chart, is presumably the same as that recorded as K1 by Fissunenko in the Field Guidebook (p. 222) issued for the Donets Basin excursion on the occasion of the VIII International Congress on Carboniferous Stratigraphy and Geology, held in Moscow, 1973. A Westphalian B (= Duckmantian) age is suggested in the Guidebook.

Figure 6. Pinna fragment (NBMG 1730), x 3, showing a rhombic terminal with odontopteroid, subterminal pinnules and, lower down the pinna, relatively large elongate ovoid pinnules which are strikingly similar to *Neuropteris saginawensis*.

Discussion: This species is the most closely similar to *Laveineopteris polymorpha*, and it is possible that a broader interpretation of the intraspecific variation might allow uniting these two taxa described from Canada and western Europe, respectively.

Neuropteris hollandica was introduced by Stockmans (1933) for specimens which Jongmans & Gothan (1915) had compared with *Neuropteris callosa* Lesquereux, 1879. At least one of Lesquereux's type specimens (Lesquereux, 1879: pl. XVI, fig. 1) is suggestive of *Laveineopteris polymorpha*, but the illustrations (drawings) published by Lesquereux are too diagrammatic to allow an identification. A photograph of the same specimen as published by Darrah (1969: pl. 72, fig. 1) does not allow the characters of this species to become apparent. Lesquereux's (1880: 115) description mentions a "thick subcoriaceous texture" which seems to exclude *Laveineopteris polymorpha* and *Laveineopteris hollandica*, and the stratigraphic level (Upper Coal strata of Pennsylvania and Ohio) is also quite different.

Stockmans (1933: pl. X, figs 2-5) figured several of Lesquereux's types of *Neuropteris callosa* photographically (although not his pl. XVI, fig. 1, refigured later by Darrah), and showed that these were inadequate to typify a species, and were certainly different to the remains recorded by Jongmans & Gothan (1915) from South Limburg. Darrah (1969: 24, 97) provided a brief description of *Neuropteris callosa*, which he regarded as a usable species, and figured a "paratype" (*op. cit.*: pl. 72, fig. 1). This was the specimen figured by Lesquereux (1879: pl. XVI, fig. 1). Unfortunately, as Darrah himself admitted, this photograph is too indistinct for a proper identification of *Neuropteris callosa*. This species should probably be regarded as *species dubia*. It has been generally ignored.

After proving that *Neuropteris callosa* had been identified incorrectly from South Limburg, Stockmans (1933) proceeded to describe the European taxon as *Neuropteris hollandica*. This was typified by a single specimen (holotype) from the Duckmantian (ex Westphalian B) of South Belgium, near Charleroi. This single specimen (terminal part of a last order pinna) could well be mistaken for *Laveineopteris polymorpha,* although slight differences may be observed in the vein pattern. Stockmans (1933: 32) mentioned a thin midrib reaching up to close the pinnule apex, and lateral veins which are slightly curved. The holotype of *Neuropteris hollandica* seems quite insufficient to characterise a frond species with intraspecific variability.

A fuller description was provided by Laveine (1967), who dealt with material from the North of France, in the continuation of southern Belgium. If the documentation in Laveine (1967: 156-161, pls XXVI-XXVII) is taken as properly representing the species introduced by Stockmans (which is likely but not entirely certain in view of the fragmentary nature of the holotype), there are differences with regard to *Laveineopteris polymorpha*. These differences, which are possibly minor, have been noted already under "Comparisons".

It may be useful to transcribe Laveine's description in English translation: "Elongate, oval to triangular pinnules which are slightly arched, alternate, with a cordate base. Pinnules close to pinna terminals adherent to the rachis by a small part of the base. Apical pinnules larger than adjacent pinnules, and very elongate deltoid. Thin nervation. Midrib distinct in three fourths of the pinnule length. Lateral veins well spaced out, issuing at a narrow angle and slightly arched, often a little flexuous, dichotomising twice to four times and arriving quite obliquely to the pinnule border. The lateral veins are well marked. Last order pinnae imparipinnate, of elongate oval shape. Rachis longitudinally striate and generally rather wide."

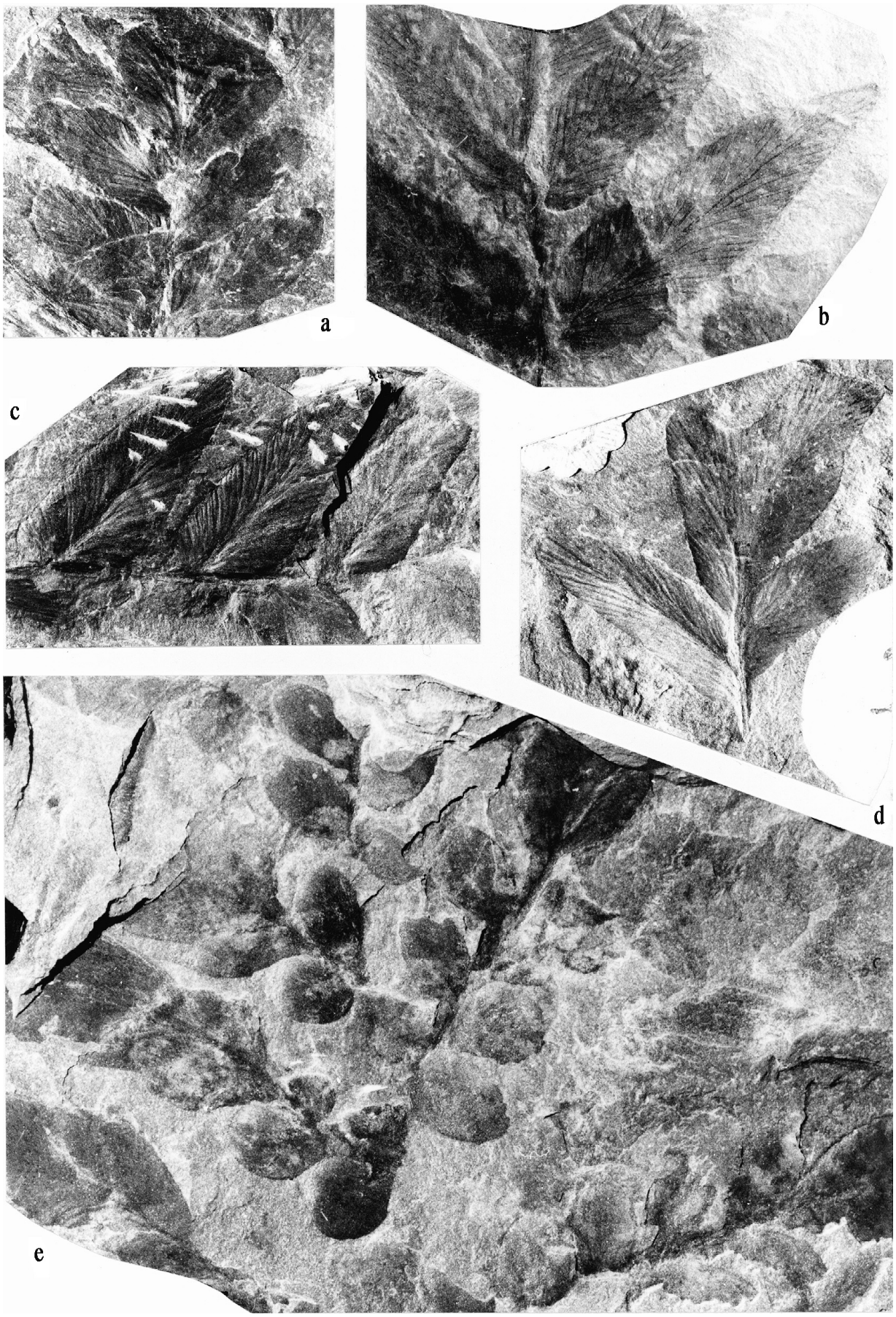
One might add that the nervation density as measured on the nervation diagram provided by Laveine (1967: 157, fig. 25b) comes to c. 28 veins/cm on the pinnule border.

Similar remains of *Neuropteris hollandica* were recorded from NW Germany by Josten (1991: 320-321, Taf. 185, figs 1-3). His nervation diagram (*op. cit.*: Abb. 206) shows several times forked nervules with a nervation density of c. 23 veins/cm. The ovoid shape of the pinnules is characteristic, as is the distinctly marked venation consisting of a thin midrib and thread-like lateral veins.

The documentation provided by Laveine (1967) and Josten (1991) from a single sedimentary basin in western Europe (to which the coalfield at Charleroi, Belgium, belongs as well) allows the rare species, *Laveineopteris hollandica*, to be identified without difficulty. This species is subtly different from *Laveineopteris polymorpha* from North America, which shows generally more acuminate pinnules, with a less persistent midrib and straighter lateral veins which are less repeatedly dichotomous and a little more widely spaced.

Still, the list of synonymy published by Laveine (1967) contains a couple of references to species recorded from North America and the British Isles (i.e. *Neuropteris saginawensis* and *Neuropteris rytoniana*) which the present writer prefers to assign to *Laveineopteris polymorpha*. It thus appears that *Laveineopteris hollandica* and *Laveineopteris polymorpha* are sufficiently close to be confused in such cases where only fragmentary remains are available. An effort has been made to compose a list of synonymy for *Laveineopteris hollandica*. This may allow drawing certain conclusions with regard to the stratigraphic ranges and the geographical distribution of the two species involved. An updated list of synonymy is provided.

Stratigraphic and geographic distribution: The two similar (but not quite identical) species, *Laveineopteris polymorpha* and *Laveineopteris hollandica*, share the same stratigraphic distribution. This refers to the lower Westphalian, i.e. Langsettian and Duckmantian substages. The records of *Laveineopteris polymorpha* are too sparse for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further precision. Laveine (1967: range chart on p. 299) shows *Laveineopteris hollandica* as occurring mainly in the Duckmantian (ex Westphalian B) but with occasional finds in the highest Langsettian. Josten (1991, 2005: range chart) also shows the first occurrence of *Laveineopteris hollandica* in the highest Langsettian, but extends its range into the upper Bolsovian, where its records are sparser however (*op. cit.*). The figured specimens from western Germany are both from the Duckmantian of the Ruhr District.

It may be that the records of *Laveineopteris polymorpha* (including its synonyms *Neuropteris saginawensis* and *Neuropteris rytoniana*) are too sparse to allow a proper appreciation of the geographical distribution of this species. However, all the known records pertain to North America and the British Isles. On the other hand, there are no reliable records of *Laveineopteris hollandica* from North America, and almost none from the British Isles (where it has been ignored in the distribution charts published by Cleal, 2005, 2007). Indeed, most of the well documented records are from the belt of coal-bearing strata extending from the North of France, through Belgium and Netherlands Limburg into western Germany. Its geographic distribution possibly extends eastwards into NE Germany (Daber, 1969) and the Donbass, South of the Russian Platform. Although sparsely illustrated (Jongmans, 1939), *Laveineopteris hollandica* does seem to occur in the Donbass. One would have expected this species to have been found also in the well sampled strata of the Upper Silesian Basin (including the Ostrava-Karviná area of Moravia in the Czech Republic), which lies in the intermediate area, but it seems that no published records of *Laveineopteris hollandica* exist for this area.

It is noted that no records exist of either *Laveineopteris polymorpha* or *Laveineopteris hollandica* from the well sampled lower Westphalian strata in different parts of the Iberian Peninsula. *Laveineopteris* does occur in both NW Spain (Cantabrian Mountains) and SW Spain (Peñarroya Coalfield), but the species recorded, *Laveineopteris resobae* (Cleal, 1981) Cleal & Shute, 1995 and *Laveineopteris guadiatensis* (Wagner, 1983) Cleal & Shute, 1995 are close to *Laveineopteris tenuifolia*.

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Figure 7. **a** (NBMG 10455), x 3; **b** (NBMG 7525, same as Fig. 5e, x 6); **c** (NBMG 7736), x 3; **d** (NBMG 7261), x 3; **e** (NBMG 12050/2), x 3. Pinna fragments showing variations in size and shape, (**e**) being least characteristic (with rounded pinnules reminiscent of *Laveineopteris loshii*).

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