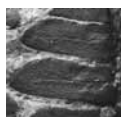


The arborescent *Linopteris obliqua* plant (Medullosales, Pennsylvanian)

ERWIN L. ZODROW, YANAKI G. TENCHOV & CHRISTOPHER J. CLEAL



The foliar morphospecies *Linopteris obliqua* (Bunbury) Zeiller, 1899 was originally based on isolated pinnules from Middle Pennsylvanian (upper Westphalian) strata in the Sydney Coalfield in Nova Scotia, Canada. However, new finds from the type area, including segments of a cauline axis and some fronds, attached juvenile croziers, an attached ovule, and associated pre-pollen organ, allow for a more complete understanding of the whole *Linopteris obliqua* plant. It was arborescent, 9 m to 10 m tall, with fronds *ca* 7 m long. Ovules of the *Hexagonocarpus*-type were attached directly to the petiole near the base of the frond, and pre-pollen was produced by *Potonia*-type structures. The plant produced seeds and pollen at different times to avoid self-pollination. Ovule production was periodic and accompanied by mass pinnule abscission. The venation, especially the areolate-vein geometry, is relatively invariable within the plant species, and thus provides the *typus* (blueprint) for distinguishing other linopterid species, especially when combined with two-dimensional probability surfaces, and traditional pinnule morphology. However, the venation must be viewed on the abaxial surface of the pinnules if it is to be reliably interpreted. The mode of vein reticulation is shown to be quite distinct from the anastomosis-pattern seen in the other medullosalean taxa, and is another character that separates the Potonieaceae from the rest of the order. • Key words: Pennsylvanian potonieacean linopterid tree, monoescious, reconstruction.

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Potonieaceae (also variously known as the Parispermaceae or Rachivistitaceae) is a widespread family of medullosalean pteridosperms that has been reported in tropical and northern temperate fossil floras ranging from late Viséan to Kasimovian in age. Much of our knowledge of these plants was summarized by Laveine *et al.* (1993), who argued that the family originated in China, and progressively migrated westwards towards Euramerica during Serpukhovian and Bashkirian times. Much of the data and the whole-plant reconstruction presented by Laveine *et al.* (1993) were based on an assemblage of exceptionally-preserved fossils from late Viséan deposits in China. However, most other occurrences of fossils of this group of plants are small fragments, with even the fronds usually disaggregating into their component pinnules and the pollen organs into their component pollen-sac clusters (Laveine *et al.* 1991). We therefore have little evidence to corroborate whether the reconstruction proposed by Laveine *et al.* (1993) for the Chinese Viséan representatives of these plants could also be applied to Moscovian Euramerica examples.

In this paper, we document new exceptionally-preserved

finds of a *Linopteris* plant (*i.e.* a representative of the Potonieaceae bearing foliage with anastomosed veins) from late Moscovian (early Cantabrian) deposits of the Sydney Coalfield, Cape Breton, Canada (Fig. 1). These new fossils include well-preserved samples of foliage, ovules, pollen organs, and some of the cauline parts of the plant that have allowed us to reappraise the whole-plant reconstruction and reproductive biology. We also examine the effects of taphonomy on the foliage, and discuss how these influence our interpretation of it. In order to identify the new specimens, we compare them with the types of *Linopteris obliqua* (Bunbury) Zeiller, 1899, which also originated from the Sydney Coalfield. Finally, we address some of the consequences for the nomenclature of the fossils and of the whole-plant concept that arises from our work.

Materials

The new material described in this paper came from six pieces of waste rock in the small open-pit coal mine opera-

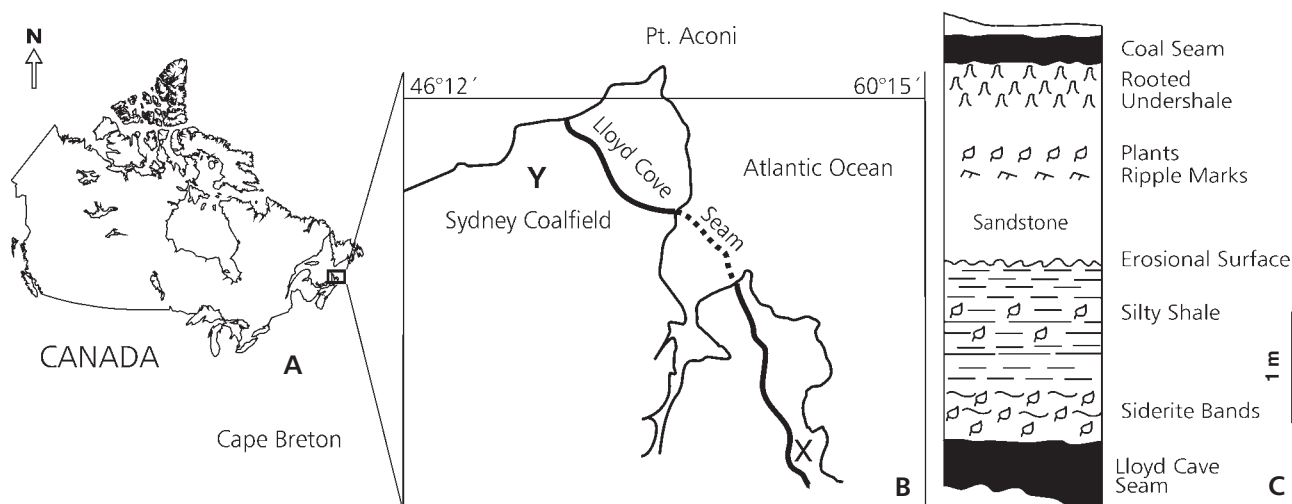


Figure 1. A – Canadian study area. • B – younger part of Sydney Coalfield, Nova Scotia. • C – local stratigraphic column at Brogan's open-pit coal mine at X; Y Prince Mine (Stubbart Seam), both mining operations are closed (2004, 2001, respectively).

ted by Tom Brogan and Sons on Cape Breton Island, Nova Scotia (Fig. 1A, B). These rocks could be tracked back to their origin in the 2-m thick overbank deposit that comprises the fossiliferous roof rocks of the *ca* 1-m thick Lloyd Cove Seam, which is early Cantabrian (late Moscovian) in age (Zodrow & Cleal 1985), Fig. 1C. The rocks are classified as grey, silty shale, moderately fissile, with interspersed thin sideritic bands and smaller nodules (see Zodrow 1983). Associated medium-grained muscovitic sandstone also contained some foliar remains. The largest of these silty-shale slabs is 1.7 m by 1.3 m and 0.46 m thick, accessioned as 05-Lst#0, and it entombed the majority of the data necessary for reconstructing the *Linopteris obliqua* plant.

The fossil plants are mostly preserved as adpressions (*sensu* Shute & Cleal 1986), although a few of the sideritic nodules contained linopterid pinnules preserved by authigenic mineralization (*sensu* Schopf 1975) – the first record for this mode of preservation in Canadian Carboniferous macrofloras. Included in the copious collections are specimens of medullosalean axes of varying sizes and of two differing topographies, and many isolated ovules (see Zodrow 2002 for a preliminary report on this material). Except for fronds of *Alethopteris* (Zodrow 2007), virtually no other pteridospermous species were found in the sample area.

Additional material originated from the Stubbart Seam (Prince Mine: Y Fig. 1B, now closed), *ca* 100 m above the type Harbour Seam (see Zodrow & Cleal 1985).

All of the new specimens (accession numbers 04-Z18 to 04-Z29, 04-GW-1, and slab 05-Lst#0 that yielded specimens 05-Lst#1 to #39), slide-mounted cuticles, and negatives are deposited with the Palaeobotanical Collections at the University College of Cape Breton, Sydney, Nova Scotia, for eventual transfer to the national collections at Ottawa, Ontario. Accession numbers, *e.g.*, 980-540, refer to

the year 1980 and the 540th shale slab collected during that year. Figures are stored on TIFF files, and *camera-lucida* drawings are kept as originals. Authenticated *L. obliqua* samples from the type Harbour Seam are available on request from the senior author (ELZ).

Methods

The specimens were examined and photographed under oblique light, without coating, immersion or any other means of enhancing contrast. In particular, for observing details of the areolate venation, the direction and angle of incident light had to be varied to avoid misinterpreting closed and intricately interconnected areolae as being open-ended (*e.g.*, Zodrow & McCandlish 1978, text-figs 6, 8). Indeed, even under higher magnification ($\times 20$ to $\times 25$), fine details were missed because of improper lighting. Certain pinnules were enlarged to 450-mm length by means of *camera-lucida* equipment to study cross-over areolate venation.

A few *L. obliqua* pinnules were macerated using traditional techniques (*e.g.*, Cleal & Zodrow 1989) but only yielded fragmentary cuticles (see also comments by Barthel 1962). However, by isolating coalified pinnules from the matrix without the use of hydrofluoric acid it was possible to examine both surfaces, and to compare these with the impressions in the matrix.

Basic terms for describing frond/petiole features follow Zodrow & Cleal (1988, text-fig. 2) and Laveine (1997). Venation pattern, one of the most important taxonomic characters in linopterid foliage, is described using the technique employed by Zodrow & McCandlish (1978). Areolae (vein-meshes) are counted on the concave pinnule side along a straight line erected at right angle to the midvein and at the central part of the pinnule (Fig. 2). Maximal

areolate length and width dimensions are consistently measured on areola “1”, and the shortest ones on “9”, respectively. A similar counting technique was used by Bell (1938) for *L. obliqua*, and by Bocheński (1960) and Tenchov (2004) for *Lonchopteris* Brongniart. Our measurements were made at $\times 20$ magnification with a zoom-stereo binocular microscope, using intensified, beam-focused fibre-optic illumination, achieving an accuracy of ± 0.05 mm.

In hexagonal areolae, the triangular termini are referred to as “hats” (h, see Fig. 3A: inset). Areolae at the midvein may show elongate “tails” instead of a hat that point to the pinnule base (Fig. 3A: a).

The line-of-areola is drawn through points in the hats of the successively shorter areolae from the midvein to the margin (Fig. 3A). The obliquity of the line-of-areola relative to the pinnule margin is variable in a pinnule, *i.e.* being orthogonal in the pinnule apex and base. Not realized prior to this study is that the number of areolae along a line at right-angles to the midvein is equal or similar to the number of areolae in the line-of-areolae, although Bocheński (1960) commented on such relationship in his study on lonchopterid venation.

Degaging work, combined with oriented sectioning, was used to probe a continuation of exposed coalified layers of hexagonocarpalean casts (05-Lst#38, 39) into the shale matrix in which they were preserved.

Description

Pinnule morphology

In the specimens from Brogan’s pit (Table 1), the pinnules are stalked with an asymmetric cordate base, longitudinally arched, and margins are invariable curled; length ranges from 4 mm to 20 mm and width from 4.5 mm to 10 mm. Pinnule shapes are round, linguaeform, straight-subtriangular, or slightly falcate-squat falcate, depending on position of attachment along the rachis (see Figs 7, 8, 17); pinnules that are more distal are typically linear, slightly falcate (Fig. 4). Lateral margins are nonparallel in shorter and curvi-parallel in longer pinnules.

The abaxial midvein occupies 80% of the pinnule length, except in the shorter forms where it is relatively shorter. Venation is anastomosed, with the lines-of-areolae changing from being relatively straight in proximal pinnules to being slightly curved in distal pinnules (Fig. 4). Tailed, elongate areolae lie lengthwise (parallel) with the midvein (Fig. 5). Adjacent to these are elongate areolae of variable shape, including hexagonal and septangular meshes (Fig. 6A–F), and then, towards the pinnule-margin, 5, 4, or 3-sided areolae occur that gradually decrease in size. Areolae at the pinnule margin are consistently elongate, open-ended.

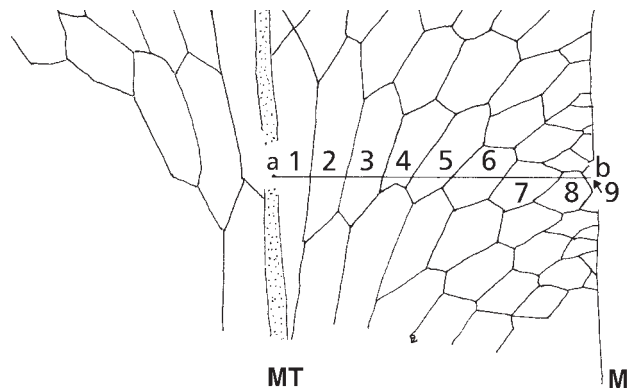


Figure 2. Sampling methodology of areolae in *Linopteris obliqua* (Bunbury) emend. Near the middle part of the midvein (MT) a line “a–b” at right angle to it is erected to subtend at the concave margin (M). Areolae are counted, *e.g.*, “1 to 9”, which intersect with that line. On samples, areolate dimensions for “1” and “9” are recorded in Table 1. The number of areolae intersecting that line on the convex side are also recorded for comparison. Modified after Zodrow & McCandlish (1978, text-fig. 5).

The number of areolae is generally six, excepting in intercalated and proximal pinnules where it is smaller because of limiting laminate space, and areolae (see Fig. 2) range in length from 1.2 mm to 2.7 mm, and in width from 0.35 mm to 0.50 mm (Table 1). Areolae are characterized by densely-distributed punctae.

Morphometric data (Table 1) demonstrate that in 04-Z20b-19-18: (1) the number of areolae is fairly constant over the range of pinnule length-widths, and (2) areola-width is fairly constant over the range of pinnule lengths (Fig. 7), *i.e.* the lateral venation pattern is fairly invariant in the sample population. However, in some specimens the measurements of the lengths, widths, and number of areolae are biased because of arching of the pinnules and their curled margins. A bias estimate of about 1 mm length translates into less than 7% error for the longest pinnules, and 1 areola at the margin. Pinnule shape and size are clearly dependent on position in the ultimate pinna (Fig. 4).

Specimens from the Stubbart Seam (Prince Mine, Fig. 1), although evidently conspecific with the Brogan’s pit material, show some differences in pinnule morphology (see Figs 9, 30). The pinnules attached to the ultimate rachises are 26 mm long and 18 mm wide, parallel-margined, with bluntly pointed asymmetric apex, and 8 to 10 elongate-hexagonal areolae. The areolae, 1.9 to 2.2 mm long and 0.35 to 0.4 mm wide, lie lengthwise strictly parallel to the midvein, without forming a rosette-like structure at the pinnule base. The intercalated pinnules are 11 mm long and 6 mm wide, linguaeform rather than round in outline, and have at the base paired areolae across the midvein, 2.7 mm long and 0.5 mm wide.

In summary, it is clear that there is considerable degree of polymorphism in pinnule form in this species, and the morphological designation “typical pinnule” is meaning-

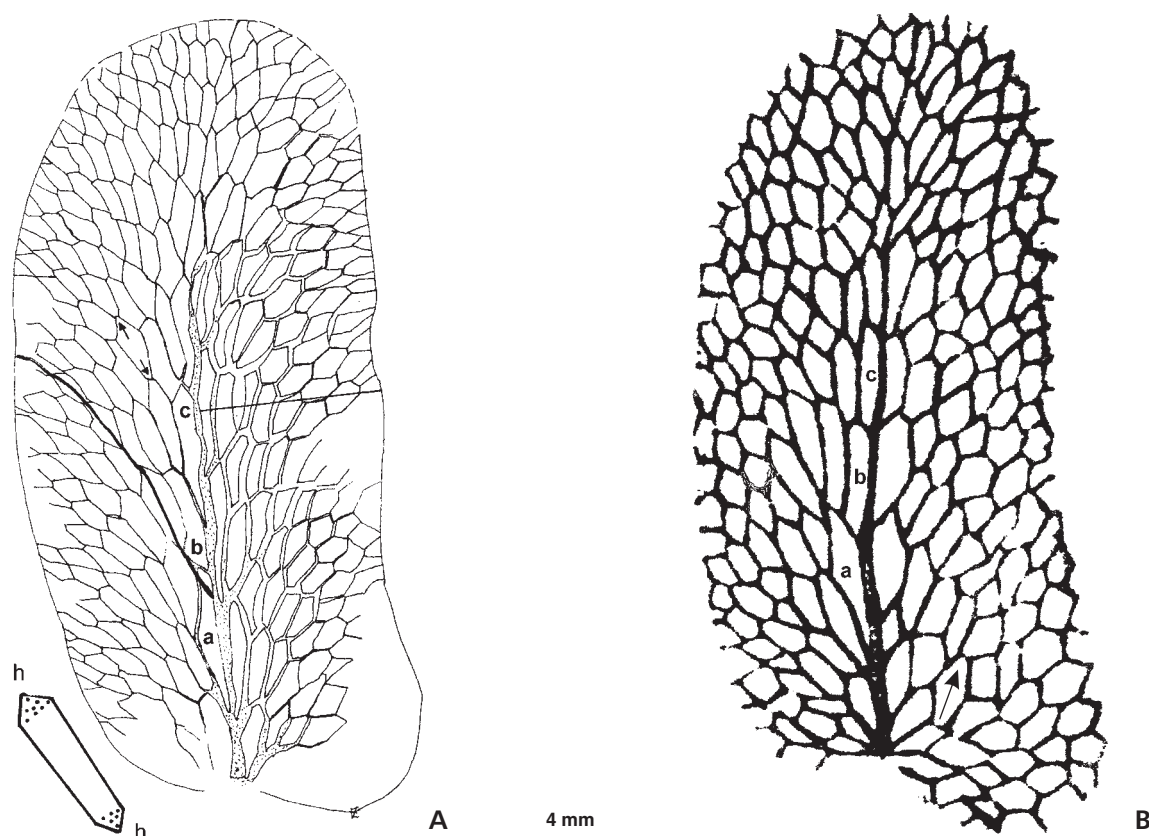


Figure 3. *Linopteris obliqua* (Bunbury) emend. Lectotype 186, adaxial surface; Sydney Coalfield, Cape Breton, Nova Scotia. • A – camera lucida hand-drawing of the lectotype 186. A double-hatted (stippled h-h) areola is shown. The heavy curved line exemplifies a line-of-areola. Areolae are counted along the straight line midvein to margin at “c”, see Fig. 2 “a–b” (Table 1). Small arrows point to crossover connections which cause the formation of “three-sided” hats. • B – lithograph by Bunbury (1847, fig. 2B) of the same specimen. “a– c” corresponding areolate areas.

less. Rather, we prefer to refer to the relative frequency of the different pinnule morphotypes.

Moreover, strictly elongate-hexagonal areolae are not the most frequently occurring, as compared with pentagonal, tetragonal, or even trigonal areolae. Some, however, are even septangular (see Bunbury’s figs 2B, 3A, B, 6G), which is not referenced in the literature on linopterid taxonomy.

Penultimate pinnae

A number of bipinnate segments were found in the Brogan’s pit assemblage the largest is 230 mm long with a 4-mm wide rachis (Fig. 7). All rachises are densely punctate and striate. Although partly eroded, the penultimate rachis shows sub-oppositely attached ultimate pinnae, between which occur intercalated pinnules. The intercalated pinnules are 4 mm to 5 mm long, and vary from linguaeform to sub-circular shapes. The ultimate pinnae are curved and fan-out, preserved for a maximum length of 150 mm and width of 40 mm, and variably ovate-oblong in outline. The distal parts of adjacent pinnae occur at different levels in the rock matrix, separated from each other by several mm of intervening sediment.

Two other fragments of penultimate pinnae were found, where the rachises are 5 mm to 6 mm wide, and preserved for a length of 30 mm and 70 mm, respectively. Attached ultimate pinnae reach a length of 190 mm (Fig. 8). Rachises are striate and densely interspersed with punctae. The ultimate pinnae are linear in outline, but taper proximally, show areolate geometry (Fig. 5), and morphometrics (Table 1) comparable to the structure in Fig. 7. In all of these three specimens, the pinnules are attached to the upper part of the ultimate rachis, which together with their arched nature, would result in the ultimate pinnae having a “winged” cross section.

Similar penultimate linopterid pinnae were found at the Stubbart Seam (Prince Mine, Fig. 1B: Y), except that the penultimate rachises appear fluted and show no evidence of being punctate (Fig. 9).

Antepenultimate pinnae

Two detached, apparently tripinnate rachises, with parallel, longitudinal striae and densely punctate (Table 2), were found lying on top of each other entombed in the largest

Table 1. Morphometric data of *Linopteris obliqua* (Bunbury) emend. Measurements in mm. Abbreviations: n – number of samples, and number keyed to Figs 4, 7, 8, no – not obtainable because of local erosion, * – for definition see Fig. 2.

Areola: at midvein *			Near concave pinnule margin		No. of areolae		Pinnule		
n	Length	Width	Length	Width	Convex	Concave *	Length	Width	L/W
Lectotype 186; abaxial, Fig. 25									
1	2.5	0.30	0.75	0.40	9	8–9	16	7	2.28
Brogan's open-pit mine									
04-Z20b, abaxial, Fig. 7									
2	1.2	0.40	no	no	6?	7	14	5	2.80
3	2.6	0.50	0.85	0.40	6	6	17	5.5	3.09
4	1.3	0.40	0.65	0.30	6	6	15	5	3.00
5	2.7	0.50	0.60	0.25	5	6	16.5	5.5	3.00
6	2.0	0.35	1.0	0.40	5?	6	15	5	3.00
7	2.2	0.40	0.75	0.25	6	6	16	5	3.20
8	1.8	0.35	0.95	0.35	5	5	10	5	2.00
9	no	no	no	no	no	no	4	5	0.80
10	1.7	0.50	no	no	no	6	11.5	6	1.91
11	2.0	0.35	no	no	no	7	15.5	6	2.58
12	2.4	0.40	no	no	no	7	17.5	6.5	2.46
13	no	no	no	no	no	5?	15	4.5	3.33
14	1.7	0.40	no	no	6?	7	14	6.5	2.15
04-Z19, abaxial									
15	1.7	0.35	no	no	no	6	11	6	1.83
16	no	no	no	no	5?	6?	19	7	2.71
17	no	no	no	no	6?	no	16	7	2.28
04-Z18, abaxial									
18	2.0	0.35	no	no	7	7	16	6	2.66
19	1.5	0.35	no	no	no	6	9	6	1.50
04-Z25a, abaxial, siderite-preserved, Fig. 24									
20	1.5?	0.75?	no	no	no	6?	20	10	2.00
Harbour Seam									
982-201, adaxial, Fig. 31B									
21	2.0	0.50	0.40	0.30	10	10	27	10	2.70
Range (excluding type 186)									
	1.2–2.7	0.35–0.75?	0.40–1.0	0.25–0.40	5(6)–10	5(6)–10	4–27	5–10	0.30–3.33
Average (excluding type lectotype 186)									
	1.9	0.43	–	–	–	–	15	6	2.60

shale slab (Fig. 10). The longer tripinnate rachis is preserved for a length of 1.08 m. It is curved and tapers from a width of 22 mm at the base to 14 mm to 15 mm near the top (Fig. 10A). Alternately attached (secondary) rachises show flared bases which are photographically documented for the trunk in Fig. 19. The secondary rachises occur at intervals decreasing distally from 310 mm to 120 mm; the proximal rachises are 7 mm, and the more distal 5 mm wide. None of the secondary rachises shows evidence for preserved bases of higher-order rachises that could bear lamina. The segment is assumed to have been originally tripinnate, based a comparison with the previously described tripinnate structure. Fig. 10B represents the shorter of the two which is preserved for a length of 0.81 m. The lowest-

order rachis is straight, and 22 mm wide in its most proximal part, tapering to 17 mm distally. Secondary rachises with a flared base are alternately attached at distances that vary from 47 mm to 294 mm, approaching opposition. Two of these secondary rachises each bear the bases of higher-order rachises.

These two specimens are assumed to be parts of antepenultimate frond segments, based on their width compared to the secondary rachises shown in Fig. 19, and the basal width of the highest-order rachises (arrowed in Fig. 10B), compared with those of the ultimate rachises shown in Fig. 7. The wider spacing of the rachises in the curved specimen Fig. 10A suggests that it originated from a more proximal position in the frond compared to the straighter specimen.

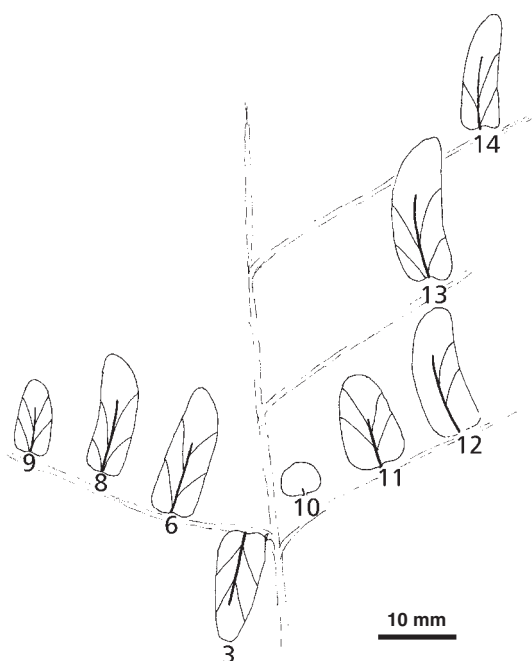


Figure 4. *Linopteris obliqua* (Bunbury) emend., specimen 04-Z20b, Lloyd Cove Seam, Sydney Coalfield, Cape Breton, Nova Scotia; summary of pinnule shapes together with lines-of-areola. Numbers “3 to 14” are keyed to Fig. 7, and to Table 1. Rachial outline is faintly indicated.

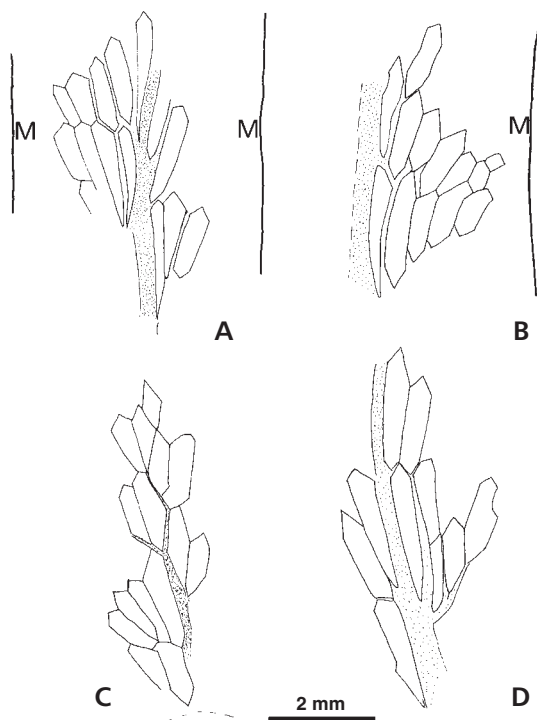


Figure 5. *Linopteris obliqua* (Bunbury) emend., Lloyd Cove Seam, Sydney Coalfield, Cape Breton, Nova Scotia; areolate structure at midveins. • A – more frequent form (specimen 04-Z20b) and pinnule “7” (see Fig. 7). • B – frequent form (specimen 04-Z20b) pinnule “12” (see Fig. 7). • C – linguaeform pinnule (8 mm long), specimen 04-Z18. • D – frequent form, specimen 04-Z18. Stippled areas represent the midvein, and M is the pinnule margin.

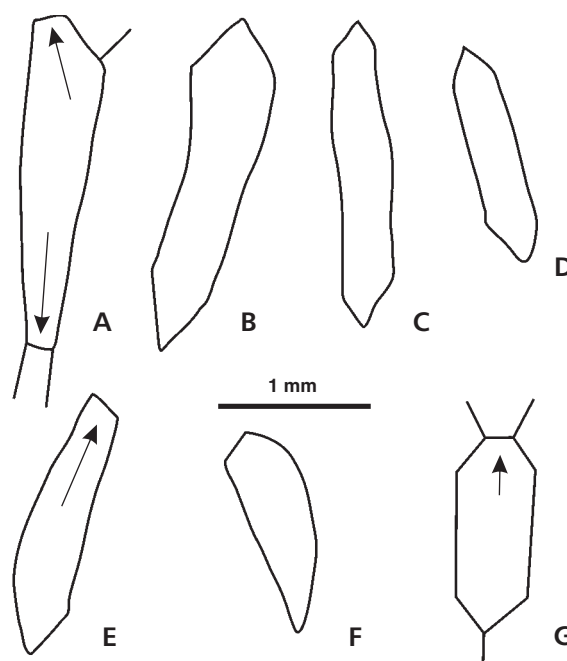


Figure 6. *Linopteris obliqua* (Bunbury) emend., specimen 04-Z20b, Lloyd Cove Seam, Sydney Coalfield, Cape Breton, Nova Scotia. • A–F – illustrating size and shape variation in hexagonal areolae at the midvein (i.e. “1” in Fig. 2). • G – cross-over connection observed near pinnule margin and apex. Arrows point to the cross-over connections.

Trifurcating axes

Associated with the penultimate pinnae at Brogan’s pit are abundant segments of axes up to 100-mm wide. As is the case with the rachises of the penultimate pinnae, they are covered with dense longitudinal ridges, striae, and abundant coarse punctae.

One of these axes, preserved on a large (1 m × 0.6 m × 0.4 m) silty-shale slab, was originally part of a quadri-pinnate frond-segment. The main axis was originally preserved for a length of *ca* 0.8 m, but after preparation this was reduced to only 0.57 m (Figs 11–13). The main axis “I” (petiole) Fig. 12A is trifurcating at “T” (Fig. 11), being inclined to the fracture plane at *ca* 10° that shows rachis “II”. “I” is 45 mm wide, straight, and with slightly concave margins, and the two lateral rachises (“II”) are 19 and 20 mm wide, respectively, straight, and parallel-sided, oppositely placed, and the angle of separation is 100°. These secondary rachises (“II”) bear punctate tertiary rachises (e.g., “III” in Fig. 12) which are 9 mm wide and lie at near to right-angles to the secondary rachises. These tertiary rachises in turn show the bases of what we assume are quaternary rachises (e.g., arrowed at “IV” on Fig. 12A).

A piece, probably split-off from a main axis (embedded in the same block in Fig. 13) shows what may be a laminate structure, 20 mm long and 30 mm wide (Fig. 14).

Another axis 1.7 m long (Fig. 15A and B), with parallel, longitudinal striae and densely distributed punctae

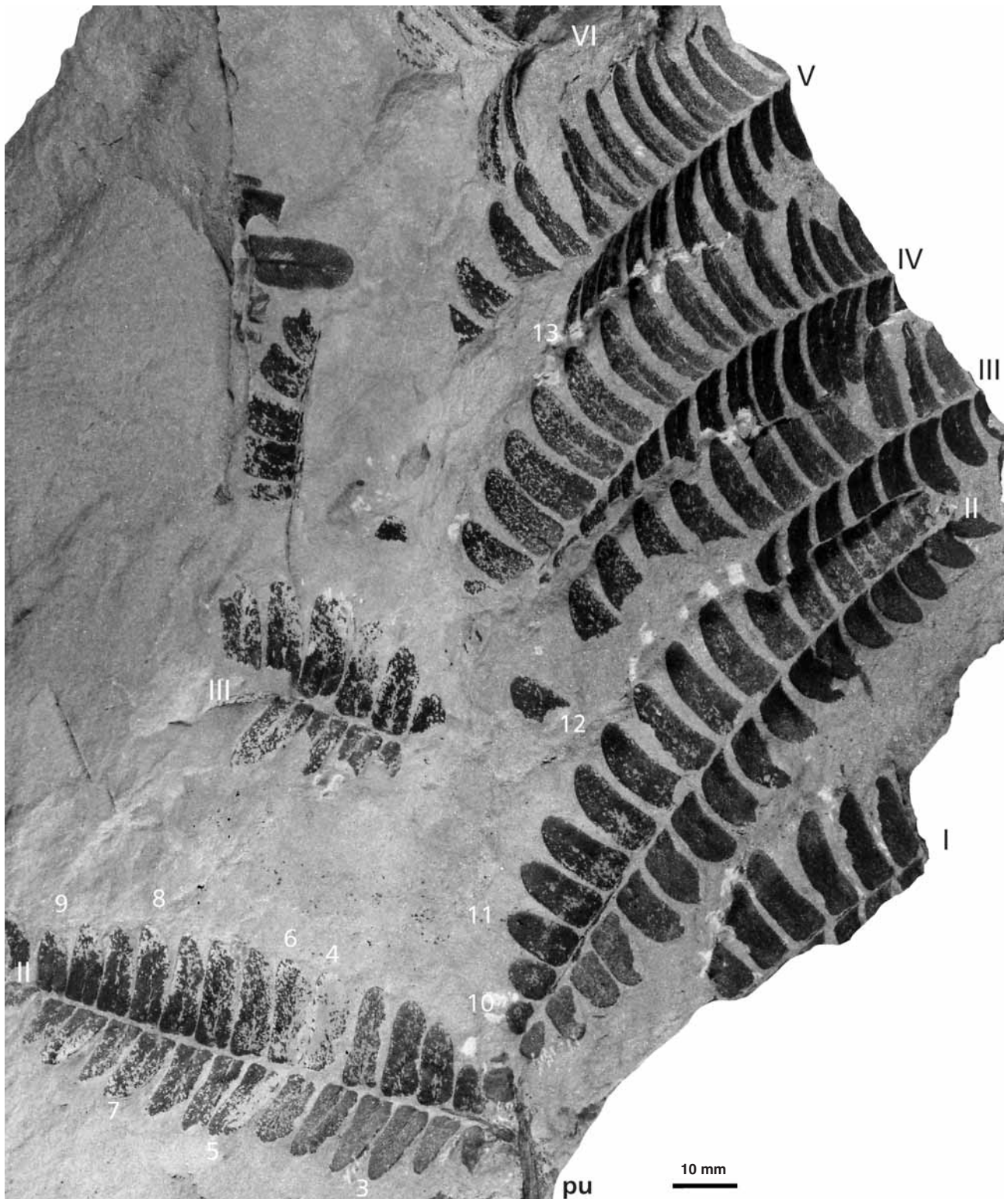
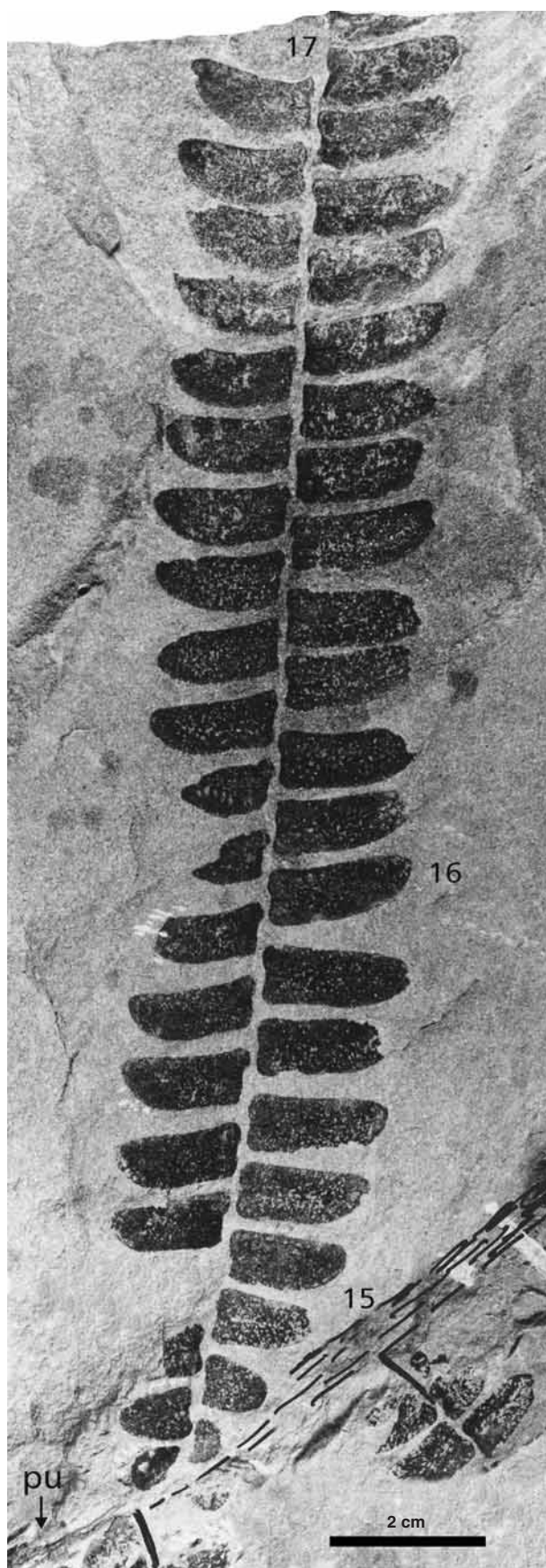


Figure 7. *Linopteris obliqua* (Bunbury) emend., specimen 04-Z20b, Lloyd Cove Seam, Sydney Coalfield, Cape Breton, Nova Scotia; interpreted penultimate rachis “pu” enhanced by hand with India ink. “I to VI” successive superposition of ultimate pinnae, each separated by several mm of sediments; numbers “3 to 14” are keyed to Table 1, and “3, 6, 8, 9, 10 to 14” and to Fig. 4.



(Table 2) shows a sub-trifurcation similar to that seen in Figs 11–13. The axis tapers distally from a width of 65 mm to 45 mm, and the trifurcation occurs towards the distal end (*ca* 1.22 m from the base). Careful field degaging along the axis revealed no attached rachises or laminate structures.

Juvenile foliage

Fig. 16 documents a *ca* 0.2 m long axial-branching system that is associated with the other specimens from Brogan's pit. All axes are coarsely punctate and densely striate (Table 2). The main axis is approximately 25 mm wide in its most proximal part, and on its left-hand side there is attached an 11 mm wide subsidiary axis. Above this branch, the main axis continues at a reduced width (15 to 16 mm). About 50 mm further along the main axis, another subsidiary axis, 8 to 9 mm wide, occurs on the left-hand side, and this overlies the more-proximal subsidiary axis. Judging from the displacement of the line of the main axis at the arrowed-point shown on Fig. 16, the possibility of a subsidiary axis exists on the right-hand side.

The more distal of the two preserved subsidiary axes is twisted, and shows two attached unfurling juvenile pinnae, with one (the more proximal) being adpressed upon the other. The completely exposed juvenile pinna is *ca* 80 mm long with an intact, curved terminal part. The rachises bear a profusion of short, stocky spines, *ca* 600 μ m to 1,000 μ m in length (Fig. 16). The juvenile pinna has between eight and ten unfurling subsidiary pinnae (the exact number is difficult to ascertain as they are closely packed in the distal part of the structure). Each of these is 10 mm to 12 mm long and on its concave side bears the basal parts of striate pinnules, with midveins attached to the rachis (*e.g.*, Fig. 18); punctae could not be observed. Completely individualized pinnules are not evident, but it appears that at this developmental stage they were slender, 3 mm to 4 mm long and already longitudinally arched. A few fully-developed areolae are preserved, complete with hats, 350 μ m long and 55 μ m wide (Fig. 18). Less developed areolae are *ca* 100 μ m long and 60 μ m to 66 μ m wide, slender-elongate and without the hexagonal habit. Generally, the areolae decrease in size distally from the midvein, and also change shape away from elongate-hexagonal to more isodiametric. Whether the areolae are open-ended at the margin or not could not be ascertained.

Figure 8. *Linopteris obliqua* (Bunbury) emend., specimen 04-Z19, Lloyd Cove Seam, Sydney Coalfield, Cape Breton, Nova Scotia; an attached 190 mm long, near-complete elongate-ovate shaped ultimate pinna. Penultimate-pinna rachis "pu" is emphasized by hand India inking. See Fig. 17 for details of intercalated pinnules on the penultimate-pinna rachis. Numbers "15 to 17" are keyed to Table 1.

Punctate axes

Table 2 presents a general overview of data on the punctae seen on axes of different widths, but it is not a statistical analyses with probability-circumscribed inferences. We can only say that these three structures (Figs 10, 15, 16, 19), and indeed all axes uncovered in the largest shale slab 05-Lst#0, and some from elsewhere in the sample area, have a surface characterized by longitudinal ridges or striations that are mutually parallel, and invariably interspersed with punctae shown in negative relief that may interrupt the striae. Punctae are of variable dimension and shape. In any particular axis, they may vary in diameter from <0.1 mm to 2.5 mm, with the smallest being invariable round and the larger ones variably round to oval. It appears that a correlation exists between the variability of the largest punctae per axis and the diameter of the axes, where the trunk shows the largest punctae.

In summary, it is reasonable to assume that (1) the shared topographical features point to a common linopterid origin for these structures listed in Table 2, and (2) the larger punctae (>1 mm) represent bases of spines.

Cauline axis

A fragmentary trunk (stem) is preserved for a length of 1.16 m and width of 0.21 m in the largest shale slab (Figs 19, 20). As an adpression, it consists of a sequence of layers:

(1) an outer coalified layer showing heavy covering of bases of punctae; (2) an impression of longitudinal striations interspersed with coarse punctae; (3) wavy longitudinally-arranged impressions of cortical sclerentymatous fibrous bundles; and (4) an innermost coalified layer. This sequence is then repeated in reverse order towards the rock matrix, probably representing a compressed cross section of the trunk. The coalified layers are impregnated with sulfide minerals, mostly pyrite.

The trunk shows two organically-connected petioles, all of which are striate and coarsely punctate (Table 2). The upper petiole (#1, Fig. 20) is preserved for a length of 0.54 m, and a width of 80 mm. On removing an overlying, detached 72-mm wide petiole (#9, Fig. 20) that is traceable for 1.19 m across the largest silty-shale slab, the lowermost attached petiole (#10, Fig. 20) was exposed. It is 73 mm wide and is seen clearly broken off at 0.20 m from its point of attachment, as shown by the steep angle at which it lies to the bedding plane. The base of each petiole flares out considerably to a width of 100 mm to 120 mm, with fibrous strands extending from the trunk into each petiole. There is no evidence for branching rachises nor for laminate structure attached to the petioles.



Figure 9. *Linopteris obliqua* (Bunbury) emend., specimen 985-212, Stubbart Seam (Prince Mine), Sydney Coalfield, Cape Breton, Nova Scotia; a fragmentary-bipinnate structure with longer pinnules, linguaeform-intercalated pinnules, and fluted ultimate rachises. “pu” indicates the eroded penultimate-pinna rachis.

Ovules

On the lowermost attached petiole #10 in Fig. 20, a thickly coalified ovule is seen in an axillary position (Fig. 21A, B). It is 24 mm long and 14 mm wide, ovate in shape, and slightly eroded on the right-hand side. Visible are three? longitudinal ribs, slightly curved upwards, which makes it possible to observe much of its flattened distal (micropylar) end which has circular structures that express the curvature in each rib (Fig. 22A). Removal of the thicker outer coalified layer exposed densely distributed punctae at its flattened end. Preserved is also a flange-like structure about the ovule. Undisputable organic attachment could not be demonstrated because of some fragmentation.

Both at the Brogan’s pit (Lloyd Cove Seam), and the Harbour Seam (type seam for *L. obliqua*), single, detached ovules are associated with linopterid foliage, but not exclusively so (Zodrow 2002, fig. 16d). They occur either as incomplete casts (hemispheric-like, round: Figs 22B, 23A), or as incomplete molds, compressed to show 1 mm to 2-mm wide flanges. The outline is ovoid-acuminate, length ranges from 17 mm to 24 mm and total width from 12 mm

Table 2. Survey data of punctae on linopterid axes per 1 cm square unit area. Sydney Coalfield, Nova Scotia, Canada.

Point of sampling and specimens	Axial width mm	Axial designation	Punctae (trichomes/spines)			
			Unit area	Size range mm	n	Shape(s)
Rachis (Fig. 17)						
04-Z19	5	isolated pen ultimate rachis	22+	0.1 to < 0.1	22	round
Juvenile frond (Fig. 16)						
04-GW-1	20	frond rachis	7 to 10	0.4 to 1.0	27	elongate
Trifurcating frond (Fig. 12)						
04-Z22b	29	main axis, distal	7 to 9	0.1 to 0.8	16	round
	40	proximal	7 to 12	0.1 to 1.2	19	round to oval
	20	left branch	15 to 23	0.1 to 0.7	38	round
	20	right branch	21 to 23	0.1 to 0.5	44	round
Trunk and petioles (Figs 10, 19)						
05-Lst#2	200	trunk	4 to 9	0.8 to 2.5	35	uniformly round
n0 05-Lst#1	80	upper petiole	9 to 40	0.1 to 2.5	79	round to oval
05-Lst#10	65	lower petiole	6 to 13	0.3 to 2.0?	19	rounds to oval
05-Lst#11	50	isolated petiole	6 to 18	0.1 to 2.0	73	round to oval-elongate, respectively
Rachis (Fig. 10A, B)						
05-Lst#25	19	isolated antepen-ultimate rachis	22–35	0.2 to 1.0	57	round to oval
05-Lst#27	7	isolated antepen-ultimate rachis	18	0.1 to 0.9	8	round to oval

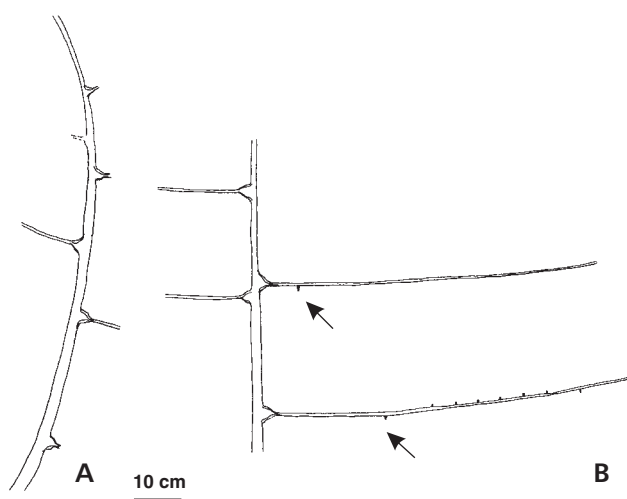


Figure 10. Detached antepenultimate rachises, on slab 05-Lst#0. Lloyd Cove Seam, Sydney Coalfield, Nova Scotia. • A – naturally curved rachis with alternately attached penultimate rachises. 05-Lst#25. • B – straight rachis with alternately and sub-oppositely attached penultimate rachises. Arrows point to bases of ultimate rachises. 05-Lst#27. Note swelling of rachial bases, slightly exaggerated. Based on field mapping, aided by photographs.

to 15 mm. Surfaces are micro-reticulate. At most three major, longitudinal ribs, each 4 to 5 mm wide are present, and one or two faintly outlined ribs are seen confined, however, to one-half or so of the ovular length. At most two of what appears to be commissures are exposed (see Taylor 1965), summary Table 3.

Of the *ca* 80 ovules collected at Brogan's pit, most of them from the largest shale slab 05-Lst#0, one is a partial

mold that unambiguously shows six-fold symmetry, which apparently has not been previously identified in compressions (Laveine *et al.* 1993, p. 108). The hexagonal symmetry exists both in respect to ribs and commissures, where the latter bisect the major ribs (Figs 22C, 23B). Several overprinted or juxtaposed ovules were also found (see Zodrow 2004).

Of biological significance (see later) is that in the largest shale slab (05-Lst#0), these hexagonal-symmetric ovules co-occur in bedding planes with dense accumulation of only *L. obliqua* pinnules (Fig. 23C). Four of these successive "biodepositional" bedding planes were observed, each separated by a 40 to 45 mm thick afossiliferous silty shale band.

Pollen organs

In contrast to the abundant ovules, pollen organs are exceedingly scarce, but a few small fragments were found in the largest shale slab (05-Lst#0). These show the pollen-sac structure characteristic of the morphogenus *Potonia* Zeiller. Significantly, the pollen organs were preserved in a separate layer within the largest shale slab from the biodepositional foliage-ovules layers.

Taphonomy

Two main taphonomic influences have been identified that acted on the linopterid foliage to alter its appearance from how it looked in life. For adpressions, it is to do with the

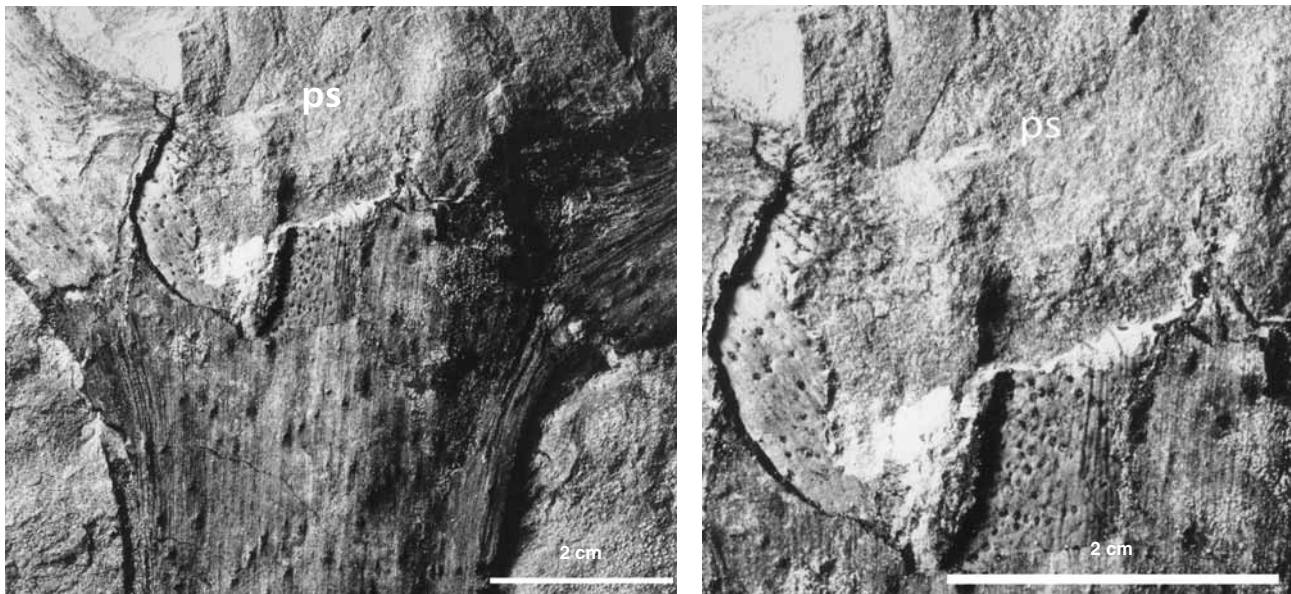


Figure 11. Field photograph, Lloyd Cove Seam, Sydney Coalfield, Cape Breton, Nova Scotia; detail of pseudocounter part of Fig. 13. Note the buried prolongation at “ps”, and strong punctate, and longitudinal striate topography. The right fork appears preserved (now exposed) below the bedding plane that contains the left fork. Illumination is from the left.

texture and composition (especially clay mineralogy and its varied diagenesis) of the clastic rocks. For the authigenic mineralization, it was the crystallization pressure of precipitating siderite during diagenesis in a reducing environment.

Effect on adpressions

Taphonomic loss/gain information (see summary: Wilson 1988) was determined by studying adaxial and abaxial topographies of compressions, and the impressions that they leave in the rock when the coalified tissue is removed. Two sets of specimens were studied. The first was from the Lloyd Cove Seam, preserved in the silty shale mainly composed of mica/illite/kaolinite, with 22 weight-percent detrital quartz that is maximally 80 μm in diameter (Zodrow *et al.* 2000). The compressed pinnules, 15 mm long and 5 mm wide, are 20 μm to 25 μm thick, and could physically be lifted intact from the rock matrix. This allowed both compression surfaces to be observed, as well as the impression left by the abaxial surface of the coalified tissue. The second set of specimens was found associated with the Stubbart Seam (Fig. 1B-Y) in shale composed of mica/illite/ and 16 weight-percent quartz that is maximally 8 μm in diameter (Zodrow & Mastalerz 2001). These specimens showed the abaxial surface of the compression. It was physically impossible to detach the coalified tissue in this second set of specimens, and so it was removed by maceration with Schulze’s solution. This procedure invariably fragmented the compressions beyond recognition, but re-

vealed the underlying impression caused by the adaxial surface of the compression.

On the adaxial surface of the coalified tissue, the venation was represented by indistinct positive relief, but was much more clearly defined on the impression of that surface. A midvein was traceable to at most the lower half on the compression, but was shorter on the impression. Punctae were not recognizable on the compression, but the impressions showed intercostal punctae, and very faint punctae on the midvein that appeared smaller than those visible on the corresponding compressions.

Abaxial coalified surfaces showed the venation in strong positive relief, including a flexuous stout midvein that is traceable to *ca* 80% of the pinnule length. Thereafter, the midvein branched into subsidiary veins. In the Stubbart Seam specimens, the abaxial surface of the compression showed (in positive relief) individual strands of the lateral veins connecting adjacent areolae, and pseudo-anastomotic connections (see Zodrow & Vasey 1986, figs 9A and 9D, respectively). The impressions of the abaxial coalified surface, as expected, only showed faint negative-reticulate relief that included the midvein. Punctae are recognizable on the abaxial coalified surface.

In general, topographies on the sample compressions from the Stubbart Seam (8 μm quartz) are much more clearly defined in higher negative relief, compared with the adaxial sample impressions from the Lloyd Cove Seam (80 μm quartz). This is in part a function of grain size of the entombing sediments (the finer the sediments, the better the topographical detail). It also is probably a consequence of the adaxial surface of the pinnule in life

Table 3. Comparison of ovules associated with *Linopteris* Presl. Measurements in mm.

	Width	Width flange	Total width	Length	Shape	In between ribs	Surface texture
Sydney, Nova Scotia, Canada							
<i>Hexagonocarpus</i> Renault associated with <i>Linopteris obliqua</i>							
	10–13	2	12–15	17–20	ovoid ecuminate	1–2, only ½ ovular length	Micro-reticulation
05-Lst#10	14	1?	15?	24	ovoid	Maybe?	Not known
France							
<i>Hexagonocarpus inaequalis</i>							
	13	?	13?	21–22	almond	Yes, not pronounced	Reticulate
<i>Hexapterospermum boulayi</i> associated with <i>Linopteris sub-brongniartii</i>							
	8–10	?	8–10?	14–17	elongate acuminate	1, not pronounced	Reticulate

showing the venation less clearly than the abaxial surface, and this is reflected in what is preserved in the corresponding impressions. From this we conclude that the venation is most unbiasedly preserved on the abaxial surface of the pinnule.

Effect on iron-carbonate nodules

Laveine (1989) reported what was then the only known occurrence of *L. obliqua* pinnules preserved together on the same slab in both siderite and in shale. The pinnules preserved in siderite were found to be *ca* 30% larger than the juxtaposed shale-preserved pinnules. Laveine suggested that this might be due to a differential rate of lithification (diagenesis) in the shale and siderite specimens. Because the pinnule preserved in shale had been subjected to a relatively slow process of compaction and dehydration during diagenesis, it would have shrunk. Siderite, on the other hand, precipitated much more quickly and thus preserved the pinnule before any significant shrinkage had occurred. Laveine also tentatively suggested that the siderite may have expanded slightly after precipitation, but he clearly favoured the hypothesis that the bulk of the difference in pinnule-sizes was due to shrinkage in the specimens preserved in shale.

A second occurrence of siderite-preserved *L. obliqua* is reported here (Fig. 24). The pinnule is “ballooned” out in size and resembles squat *L. obliqua* pinnules illustrated by Zeiller (1886, pl. 1, figs 1, 2). The reticulation pattern is distorted, but the midvein is not and shows striae and punctae that in the shale-preserved pinnules are only faintly visible and open to misinterpretation as being sedimentological in origin. This suggests that the pinnule had been caused to swell, particularly affecting the more delicate tissue where the reticulate veining occurs, but less so the more robust midvein. This swelling must have occurred after the precipitation of the siderite had occurred, but prior to the organic tissue of the pinnule becoming completely coalified.

Recent experimental work by Cleal & Shute (paper in

review) has shown that dehydration can cause shrinkage by up to 10% in Palaeozoic cuticles. Combined with the observation reported in the present paper, we can concur with the general conclusions of Laveine (1989): the difference in sizes of the pinnules preserved in shale and in siderite is partly due to shrinkage in shale and partly due to expansion in siderite (crystallization pressure). However, the evidence suggests that the bulk of the difference is due to the expansion of the siderite, and not due to the shrinkage in shale as suggested by Laveine, although this needs to be verified by a better understanding of the paragenetic relationships in the system of siderite genesis (see Krauskopf 1979, pp. 68, 69).

The types of *Linopteris obliqua*

Following Zodrow & McCandlish (1978), we assume that our new foliar specimens belong to *L. obliqua*, the types of which originated from the Sydney Coalfield (Bunbury 1847). To try to verify this assumption, we have examined these types, which have not been described in detail before, nor have they been photographically documented.

When the senior author (ELZ) originally examined the three syntypes of this species, they were kept at the School of Botany, University of Cambridge, but they have subsequently been transferred to the Sedgwick Museum at the same University. The specimens are numbered 186, 187 and 188. Associated manuscript records show that they were collected by Richard Brown, Sr. (see also Brown 1850, p. 115), who in the 1850s was General Manager of the General Mining Association of London (GMAL). During that time, GMAL mined coal near Sydney Mines in Cape Breton, Nova Scotia (Zodrow *et al.* 2001, p. 68). Brown (1850, p. 126) reported that the most exploited seam then was the “Main Seam”, which Bell (1938) correlated with the Harbour Seam. If so, then the syntypes are middle Asturian (‘Westphalian D’) in age (Zodrow & Cleal 1985).

Specimens 186 and 187 are compressions of single pinnules, whereas 188 has impressions of several

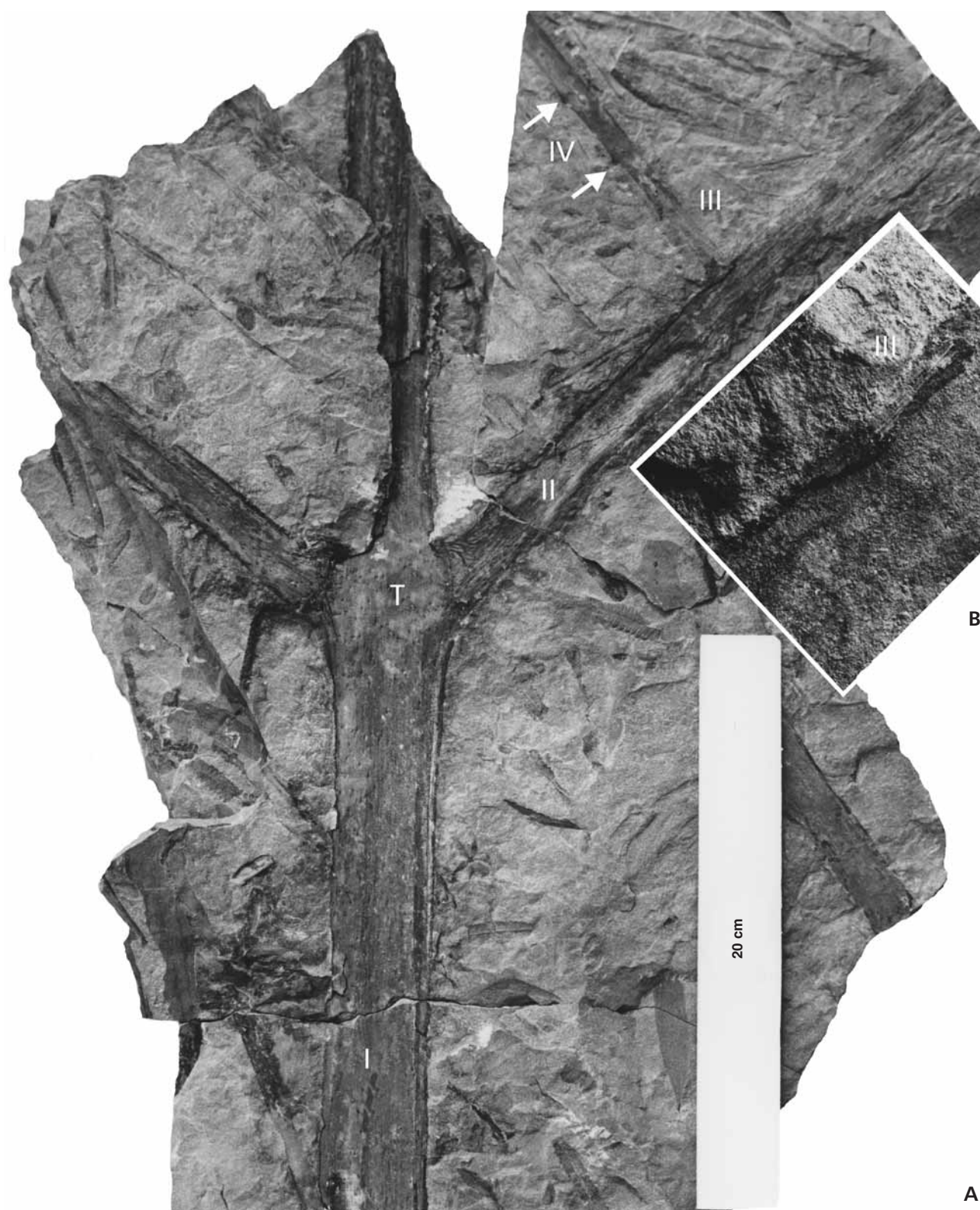


Figure 12. A – detail of axis (from Fig. 11), specimen 04-Z22b, properly prepared to expose the trifurcation at “T”. Roman numerals “I to IV” correspond with the rachial order, where “T” is the referenced petiole. Arrows at “IV” point to bases, presumably pinnule-bearing. • Inset B (× 3) shows the area of organic attachment of axis “III” to axis “II”, based on the thin coal band representing compressed axis “II”.



Figure 13. Field photograph, specimen 04-Z22a, Lloyd Cove Seam, Sydney Coalfield, Cape Breton, Nova Scotia; part of the pseudodichotomous axis preserved on a ca 1 m by 0.60 m × 0.40 m thick silty shale slab. See detail of pseudocounter part Fig. 11 and the carefully prepared trifurcate axis in Fig. 12.



Figure 14. Petiole with possible attached laciniate structure (L), specimen 04-Z29, Lloyd Cove Seam, Sydney Coalfield, Cape Breton, Nova Scotia. From the same block as Fig. 13.

pinnules. The specimens are still in good condition because of the absence of destructive pyritic oxidation (Zodrow 2005). However, the coalified layer of 186 has deteriorated slightly because of localized clayey or sideritic oxidation (Zodrow 1983) in the rock matrix (the obverse is pristine). The specimens also include associated *Macroneuropteris scheuchzeri* (Hoffmann) Cleal *et al.*, *Lobatopteris vestita* auct. non Lesquereux, lycophyte foliage, and orbicular pinnules reminiscent of odontopterids of a type often found in the Sydney Coalfield (Zodrow 1985, text-fig. 16a).

Bunbury (1847) did not designate a holotype among the specimens of this species that he had available for study. However, he figured only one of the specimens (assigned number 186) and, as this shows all the key features for identifying the species, it is designated the lectotype.

Lectotype 186

Fig. 25A shows the first published photograph of the lectotype, and Fig. 3A the first *camera-lucida* close-up of it, juxtaposed with a copy of the drawing published by Bunbury (1847, fig. 2B); Fig. 26 shows the pinnule outlines of all the syntypes. Lectotype 186 consists of a single pinnule that appears to be punctate, ca 16 mm long and 7 mm wide, and slightly eroded at the apex. The pinnule is laterally asymmetric, reflected both in the venation and the presence of an auricle only on the right-hand side.

The right-hand (concave) side of the pinnule has been slightly distorted. Consequently, the venation on this side looks different from that on the left-hand side: areolae on the right-hand side tend to be curved and somewhat twisted (including the hats), the midvein is locally curved (Fig. 3B at 'a'), the lateral veins appear thicker and diffused, and the micron-sized connecting-veins are

Figure 15. Basal sub-trifurcation of a linopterid petiole, specimen 05-Lst-#11, Lloyd Cove Seam, Sydney Coalfield, Cape Breton, Nova Scotia. • A – 1.7 m long, naked petiole. Field photograph at oblique angle. Chisel is 302 mm long. • B – shows a detail of the basal sub-trifurcation, X. Association with cauline structure is shown in Fig. 20.



very difficult to observe. This, together with the curled margin of the pinnule, and the fact that the fossil shows the adaxial surface of the compression, probably accounts for some of the inaccuracies drawn in Bunbury's fig. 2B. This includes the erroneous number and size of the areolae in areas between the midvein and the pinnule-margin that have been drawn too isodiametrically, and the pinnule shown too wide, particularly on the lower right-hand side. However, the length of the midvein is accurately represented, as are the batteries of areolae adjacent to the left side of the midvein (compare Fig. 3A, B: a–c). Bunbury correctly showed no open-ended ('neuropteroid') areolae, except at the pinnule margin, but failed to note the distinctly elongate open ends of the marginal areolae.

Correctly observed by Bunbury were double-hatted areolae, where those adjacent to the midvein are aligned parallel with the midvein, and branching at the midvein that started in the lower part of the pinnule. He recognized the very short vein connectives between certain areolae (Fig. 3B, arrowed).

The *camera lucida* drawing, Fig. 3A, shows the flexuous midvein, probably caused by micro-distortion, defined for 80% of the pinnule length. Four to five oppositely arranged branches emerge from the midvein and proceed somewhat parallel to it, arching to reach the margin very obliquely. Areolae proximal to the midvein in the lower two-thirds of the pinnule show slender, thinning basal tails. In more distal positions, the areolae change to being six-sided, having mostly curvilinear-parallel sides, and are terminated on top and bottom by hats. Occasionally, septangular areolae are present (Fig. 3A arrows). When undistorted, the angle of the hat is 30° to 45°, seldom much below the lower value. The more proximal areolae on the left-hand pinnule side form the most regularly-elongate hexagonal outline, with sides that are comparatively straight and near-parallel. Then, approaching the margin, the areolae become pentagonal, tetragonal or even trigonal, the frequency of micron-sized crossover vein connections increases as a result of shorter bifurcations (see Fig. 27B), and at the margin areolae are consistently, elongate open-ended. Vein density per 10 mm/pinnule margin is *ca* 45. The number of areolae on the concave side, 8 or 9 (see Fig. 3A: line c to the margin), is approximately equal to the number of successive areolae along the veins (line-of areolae). Areola "1" (as in Fig. 2) is 2.5 mm long and areola "9" is 0.3 mm wide (Table 1). Thereafter areolae decrease in size towards the margin (as factually depicted in Bunbury's fig. 2B).

The pinnule is laterally asymmetric: the size, geometry and often the number of areolae are different on either side of the midvein (usually fewer on the convex-side); and there is an auricle on the right-hand side, not mirrored on the left-hand side. The lines-of-areolae (Fig. 26A) cannot

be used for the asymmetry-argument because of bias due to micro-distortion.

Paratypes 187 and 188

These specimens are also illustrated here for the first time. Specimen 187 (Figs 25B, 26B) shows the abaxial surface of a compression, 22 mm long and 5 mm wide, with possible punctae within the areolae. The number of areolae is 7 or 8, and areolate dimensions are 1.6 mm length and 0.3 mm width, decreasing in size towards the margin. The obliquity of the line-of-areole is slight.

The small slab 188 preserves several pinnules as adaxial impressions. The longest three pinnules (incomplete length 23 mm, width 6 mm) were originally part of a fragmentary ultimate pinna, but the pinnule-bases and the ultimate rachis have been removed by erosion. The number of areolae is 8 or 9, and areolate dimensions are 1.9 mm length and 0.3 mm width. An intact pinnule on the 188 slab, preserved as an adaxial impression (Figs 25C, 26C), is 13 mm long and 6 mm wide. Because of its smaller size, it is only slightly falcate, and the lines-of-areola are nearly straight, as normally occurs in the smaller pinnules. The number of areolae does not exceed five, and areolate dimensions are 1.2 mm length and 0.2 mm width. Fig. 28 shows the areolate architecture at the midvein of Bunbury's three Cape Breton specimens.

Comparison with new specimens

The overall form and venation of the pinnules in the specimen figured in Fig. 7, as well as in the other specimens discussed, are very similar to those seen in the lectotype 186 (although not as it was originally illustrated in Bunbury 1847, fig. 2B) (Table 1). This includes pinnule size, average dimensions of the areolae, similar curvature of the lines-of-areolae, identical architecture of the areolae at the midvein, and within limits of counting bias due to curved pinnule margins identical number of areolae. Bunbury's single-pinnule lectotype could have originated from a position proximal to an antepenultimate rachis in this larger specimen. Of the total number of pinnules therein (*ca* $n = 130$: Fig. 7), 7 to 10 pinnules (*ca* 5% to 7%) compare morphologically with the lectotype. In contrast, in larger accumulation of *L. obliqua* pinnules, forms larger than 17 mm are not abundant. For example, in a 100 mm² area on a *ca* 600 mm² silty shale slab from the Lloyd Cove Seam, of the 100 detached *L. obliqua* pinnules counted over 90% were of the lectotype form, and did not exceed 17 mm in length. It is clear that in the Sydney Coalfield sample bias exists in collections.



Figure 16. Juvenile frond segment of *Linopteris obliqua* (Bunbury) emend., specimen 04-GW-1; two attached unfurling linopterid pinnae (“J”). Lloyd Cove Seam, Sydney Coalfield, Sydney Coalfield, Cape Breton, Nova Scotia. Arrow points to a possible branching rachis.

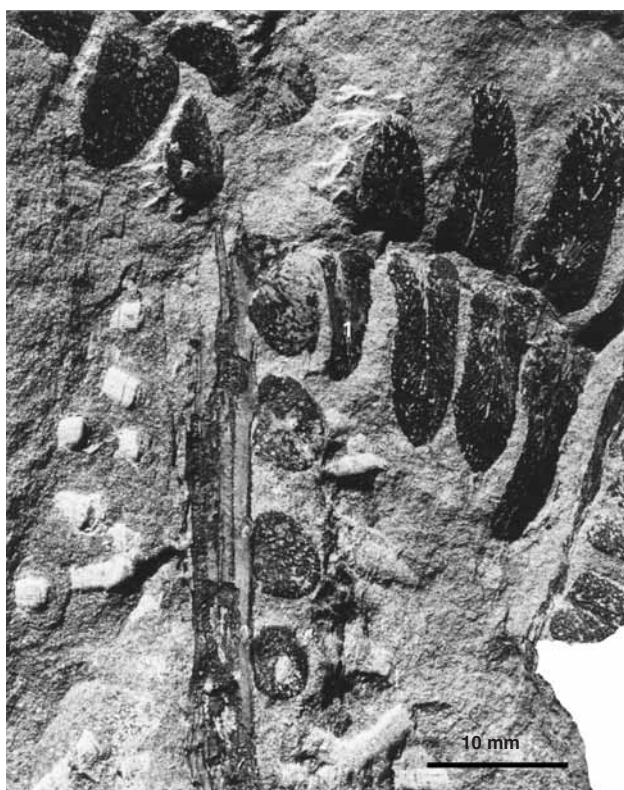


Figure 17. *Linopteris obliqua* (Bunbury) emend., specimen 04-Z19, Lloyd Cove Seam, Sydney Coalfield, Cape Breton, Nova Scotia; detail of a series of four intercalated pinnules exhibiting transitional morphology from linguaeform opposite ("1") to following round pinnules in decreasing size. Expected intercalated pinnules on the left-hand side of the penultimate rachis are not preserved.

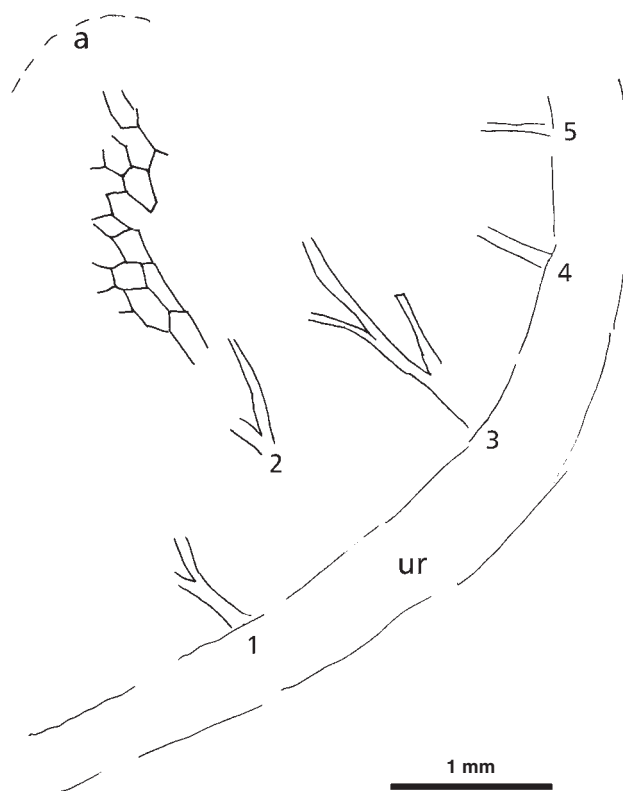


Figure 18. *Linopteris obliqua* (Bunbury) emend., specimen 04GW-1, Lloyd Cove Seam, Sydney Coalfield, Cape Breton, Nova Scotia; detail of the juvenile pinnules (midvein base "1 to 5") attached to the rachis "ur", except that at "2" the base connection is eroded; "a" the approximate pinnule apex. Areolae are partly preserved in pinnule with midvein "2". Camera-lucida hand drawing.

Morphological interpretation

Pinnule-growth pattern

A scattergram of pinnule length/width measurements (Fig. 29) suggests an empirical growth curve with length somewhat dependent on width. This is in marked contrast to other medullosalean neuropteroids, where lateral and apical growths are correlated (Zodrow & Cleal 1998, text-fig. 21B). This is further justification, therefore, for Gothan's (1941) separation of the paripterid/linopterid complex from the other, imparipinnate neuropteroids.

Pinnule abscission

Bell (1938) and Zodrow & McCandlish (1978) have noted previously that massive accumulations of isolated *L. obliqua* pinnules occur repeatedly in the Sydney Coalfield, in the range of *L. obliqua* from the Harbour to Lloyd Cove Seams (Zodrow & McCandlish 1978). Such a pattern may be interpreted as a type of event stratigraphy *sensu* Seilacher (1982), which almost certainly reflects periodic mass-pinnule abscission.

Various factors can cause leaf abscission in tropical plants, including leaf-senescence, fruiting, and ecological stress (e.g., Addicott 1982). In the case of the abscised linopterid pinnules, it is possible that it was a response to external ecological stress. Linopterid (and paripterid) pinnules had relatively thin cuticles (e.g., Barthel 1962) which may have made them more vulnerable to environmental stress. It has been suggested that these coastal Variscan Foreland plains were subjected to monsoonal climatic changes (Gibling & Bird 1994), and in modern-day tropical plants relatively small-scale ecological changes can result in sudden leaf fall (Richards 1952).

However, in this case we are not dealing with the shedding of entire leaves, which is rarely seen in any of the known Pennsylvanian-aged tropical plants (the only well-documented example is *Eremopteris* – Delevoryas & Taylor 1969). Rather, we are dealing with the mass shedding of the photosynthetic pinnules, presumably leaving the rachial "skeleton" of the leaf intact. Pinnules could presumably grow back later, suggesting that the defoliation process was a temporary and possibly a periodic process. An explanation may lie in the co-association of the pinnules with the larger numbers of ovules. In several mod-



Figure 19. Linopterid trunk, branching, specimen 05-Lst#2. Lloyd Cove Seam, Sydney Coalfield, Nova Scotia; field photograph prior to any preparatory work. Minimum width of the trunk is 21 cm. Arrow points to connected ovulate-like structure (see Fig. 21). The chisel is 302 mm long and lies on one of the four biodepositional bedding planes comprised of pinnules of *L. obliqua* which is a few cm below the bedding plane that contains the trunk.

ern-day tropical plants, it has been shown that leaf fall is correlated with fruit production, as the trees temporarily divert resources away from vegetative growth to reproduction (e.g., Singh & Kushwara 2006). The seeds of the linopterid plant were of substantial size and to produce them in the numbers that we have seen at Brogan's pit would have represented a significant resource-investment for the plant. It would seem reasonable, therefore, for the linopterid plant briefly to shed its photosynthetic pinnules to concentrate on seed-production.

Frond architecture

The present data suggest a frond at least 7 m long. We arrived at our estimate by interpreting the 1.7-m long axis in Fig. 15 as being petiolate because of the tapering width that compares with that of the axes found attached to the cauline specimen (Fig. 19), and lack of attached rachises or laminate structures along its entire length. If correct, this would indicate a minimal length for a petiole. Moreover,

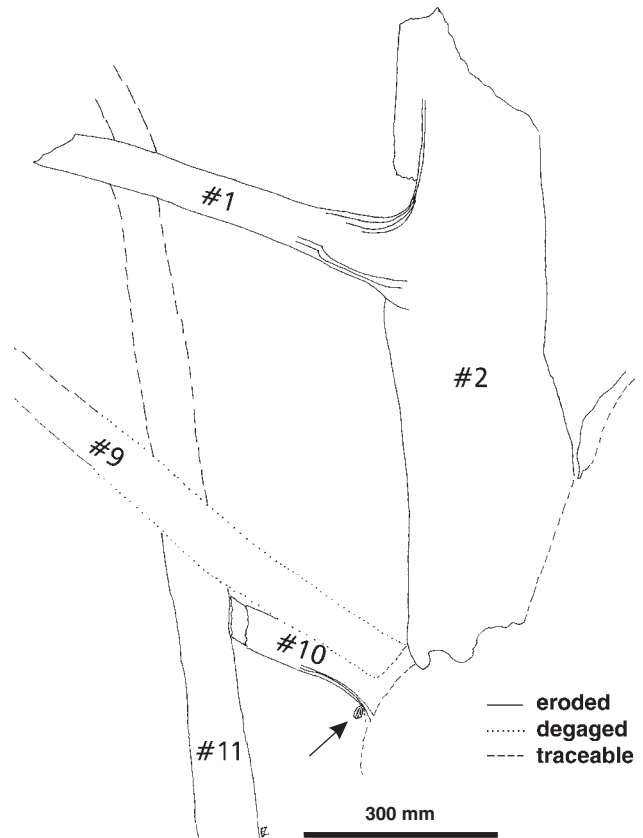


Figure 20. Cauline and rachial structures on slab 05-Lst#0, Lloyd Cove Seam, Sydney Coalfield, Cape Breton, Nova Scotia; see Fig. 19. Succession of fossil structures uncovered (top to bottom): trunk #2 (05-Lst#2) with petioles #1, #9, #10, and #11, although separation is measured only in several mm of sediments. Documented and hand drawn in the field, assisted by photographs.

the axis in Fig. 12 only shows one trifurcation that occurs along an 0.80-m length of a primary rachis. Wnuk & Pfefferkorn (1984, fig. 14) indicated that the fully-developed linopterid frond produced four to five pairs of secondary pinnules along the primary rachis, and estimated the full length of the frond at ca 3.5 m (in agreement with Stidd *et al.* 1975). We regard this as too conservative, and our estimate of 7-m is more compatible with the frond as reconstructed by Laveine *et al.* (1993, text-fig. 11) which is 6 m long and 3 m wide.

Our evidence appears to corroborate the 'pseudo-pinnate' model for the *Linopteris* frond as developed by Laveine *et al.* (1993; see also Laveine 1997). In this model, the frond is not produced through the progressive differentiation of pinnules into pinnae, as occurs in many ferns, but is the result of a series of rachial bifurcations. As a consequence, all rachises within the frond are essentially homologous and bear pinnules. Also as a consequence, there are no pinnatifid pinnules within the frond, representing the transition from ultimate pinnules to pinna. Both points can be seen in our material.

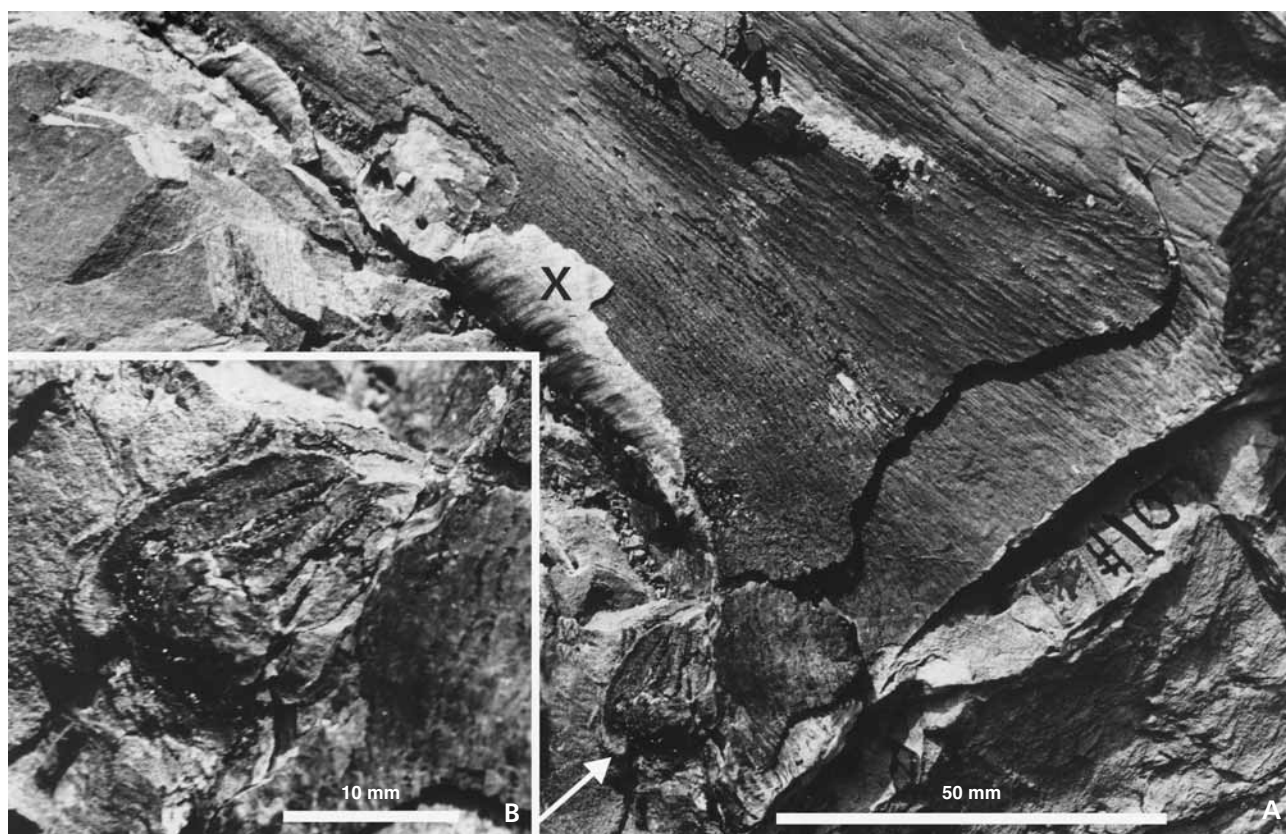


Figure 21. *Hexagonocarpus* Renault. Lloyd Cove Seam, Sydney Coalfield, Cape Breton, Nova Scotia. • A – arrow points to the ovule at the lower petiole-trunk juncture (05-Lst #10-05-Lst#2, respectively). Field photograph. X, crater splash in muddy sediment, is regarded stratigraphically the bottom of the shale slab. • B – enlargement of the ovular structure, noting that the distal part appears the broadest.

We also have evidence to support the view of Laveine *et al.* (1993) that secondary rachises are alternately arranged in the distal part of the frond, but may converge to being apparently oppositely arranged in the proximal part of the frond (Figs 10B, 11–13). However, where this apparently opposite arrangement is found, the resulting trifurcation is often not in a single plane, giving this part of the frond a certain degree of three-dimensionality. Other evidence of three-dimensionality within the frond is shown in Fig. 7, where ultimate pinnae are fanned-out, and the laterally overlapping ultimate pinnae are significantly separated from each other by a layer of sediments.

In our view, therefore, the *Linopteris* frond is not a strictly planar structure as suggested by Laveine *et al.* (1993) and Wnuk & Pfefferkorn (1984), but shows some evidence of three-dimensionality within its architecture. This is not surprising if we accept the pseudo-pinnate model for the *Linopteris* frond architecture. Although the repeating bifurcations by which the *Linopteris* frond was built-up occurred primarily in one plane to produce a mainly dorsi-ventral photosynthetic structure, they were presumably derived from three-dimensional branching systems, such as suggested in Zimmermann's Telome Theory (Zimmermann 1952). What we are seeing in *Linopteris* is the retention of

some of this primitive three-dimensionality within the frond, notably in those parts where the repeated bifurcations have become telescoped to produce 'pseudo-opposite' branches and thus have imposed some constraints of space for the branching.

Juvenile foliage

We interpret the specimen shown on Fig. 16: J as representing part of a young quadripinnate foliar segment. The only alternative explanation would be that the main axis was part of a stem, and that this bore tripinnate fronds. We find this untenable for three reasons. Firstly, our evidence suggests that the fully-developed fronds of this plant were quadripinnate which is borne out by previous reconstructions of the fronds of Potoniaceae (*e.g.*, Laveine *et al.* 1993). Secondly, the subsidiary axes appear to be laterally attached to the main axis, rather than helically attached as would be expected if the latter were a stem. Thirdly, the main axis is substantially narrower than the example of the 0.21-m thick stem that we document in Fig. 19.

The general architecture and ontogeny of this juvenile frond appears to be similar to that documented for *Pari-*

pteris Gothan by Cleal & Laveine (1988). However, in the absence of attached secondary rachises on the right-hand side of the linopterid specimen, the exact rachial architecture cannot unequivocally be determined. The two preserved secondary pinnae on the left-hand side of the main pinna appear to be very closely spaced, which may indicate an incompletely developed frond. Alternatively, it is possible that the more distal of the two secondary rachises was originally attached to the right-hand side of the main rachis, and that it had been twisted around during burial; it should be noted that the more distal secondary rachis shows clear evidence of twisting along its length. In this case, however, it would suggest that the secondary pinnae were alternately attached, whereas most other evidence suggests that they were oppositely attached, producing the apparently trifurcating branches discussed previously.

Epidermal hairs

The punctae that occur on the pinnules and all orders of rachises in *L. obliqua* have traditionally been interpreted as hair bases. Although hair-covered abaxial, and sometimes adaxial pinnule surfaces, are well-documented in the Medullosales (e.g., Barthel 1962, Cleal & Zodrow 1989, Zodrow & Cleal 1998), if the *L. obliqua* punctae are correctly interpreted as hair bases their density would be exceptional among the Medullosales; in life, the foliar surface would have resembled a clothes brush. Such a densely hairy surface would have been an ideal defence against attacks by insects, or even foraging tetrapods. It has to be noted, though, that no actual hairs were recovered from macerations of *L. obliqua* pinnules in this or other studies, and it could be argued that the holes observed in its cuticles (e.g., Fig. 30B) represent hydathode pores. As discussed by Shute & Cleal (2002), hydathodes can have a multitude of forms and structures, and some can be difficult to distinguish from hair bases. However, in this case, the holes are surrounded by a far more prominent collar of cuticle than normally occurs in hydathodes and, on balance, we suspect that they represent hair bases.

Reproductive structures

Ovules preserved as adpressions similar to those found at Brogan's pit have traditionally been known as *Hexagonocarpus* Renault. Carpentier (1911) reported similar ovules associated with *Linopteris subbrongniartii* Grand'Eury (see also Laveine 1967a). However, for the first time we report an ovule in probable direct attachment to a linopterid plant. Documented examples of organically-attached medullosalean ovules are extremely rare (summarized by Zodrow 2007), the present discovery being only the second known case from the Sydney Coalfield (see Zodrow & McCandlish 1980).

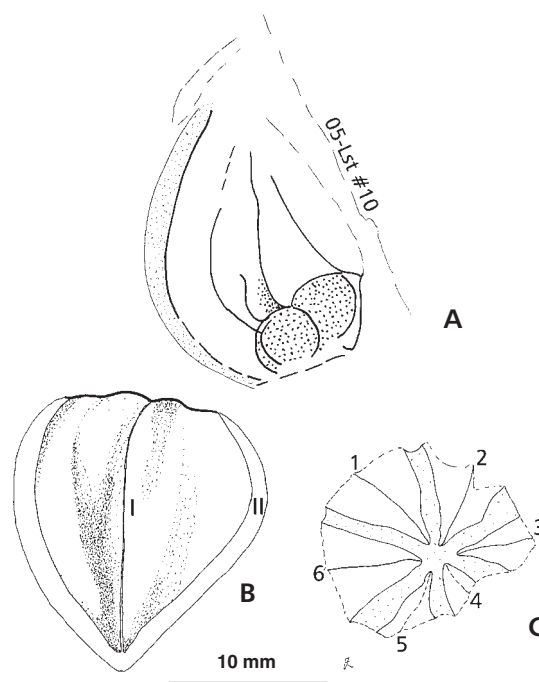


Figure 22. *Hexagonocarpus* Renault, Lloyd Cove Seam, Sydney Coalfield, Cape Breton, Nova Scotia. • A – axillary-associated ovule (see Fig. 21), specimen 05-Lst#10. Peripheral flange-like structure (stippled). Camera-lucida hand drawing. • B – detached ovule 980-540 showing ribs (shaded), commissure (I), and flange-like structure (II). • C – partial mold showing hexagonal symmetry (stippled ribs) intersected by what is interpreted as commissures, numbered “1 to 6”, where dashed lines indicate some erosion. Based on the specimen figured in Fig. 23B.

In comparison with Carpentier's (1911) material (Table 3), the Sydney ovules tend to be a little longer and more pyriform in shape, but Carpentier's material appears differently preserved by consistently showing three narrow longitudinal ribs (sclerotesta?). The distal end of the attached Sydney ovule (Fig. 22A) has a similar configuration and shape to Carpentier's (1911, Pl. VI, fig. 1) “face inférieure”, although the latter author did not mention the positive relief. Also noticeable on some of Carpentier's material is a flange-like structure surrounding the ovules, similar to that observed in the present material (see Figs 22A, B, 23A).

The position of attachment of the Sydney ovule to the proximal part of a frond-petiole (Fig. 21) is unique among the medullosaleans; the few other known examples of attached medullosalean ovules have them connected to the distal parts of the fronds (e.g., Buisine 1961), or to branching axes whose position relative to the rest of the plant is unknown (Drinnan & Crane 1994).

Medullosalean seeds are generally uncommon in the compression fossil record, and we know of no other published record of abundant ovules being associated with abundant vegetative remains of mainly one species. We speculate, therefore, that we are seeing here a reproductive biology characterized by brief periods of seed production.

In contrast to the abundance of the ovules, the extreme

Table 4. Summary of morphological characteristics of selected linopterid types. Measurements in mm. Data from Tenchov *et al.* (2005), except that for *L. obliqua* (Bunbury) emend.

Form species and synonyms	Pinnule morphology				Areolae		
	Length	Width	Margin	Shape	Number	Length/width	Shape
(1) <i>L. obliqua</i> (Bunbury) Zeiller	16	7	curviparallel	falcate	6–7	2.0/0.5	hexagonal
(1A) <i>L. bunburi</i> Bell	10–11	3–5	curviparallel	elongateovate	4–5	??	open hexagonal
(2) <i>L. neuropteroides</i> (Gutbier) Potonie	30–35	12–13	curviparallel	falcate	8–12	10.0/0.3	sharp elongate
(2A) <i>L. palentina</i> Wagner	subjective synonym of <i>L. neuropteroides</i>						
(2B) <i>L. gangamopteroides</i> de Stefani	part of the <i>L. neuropteroides</i> group						
(3) <i>L. neuropteroides</i> var. <i>minor</i> (Potonie) Bertrand	22	6	parallel	linear/falcate	6–7	5.0/0.25	hexagonal
(3A) <i>L. neuropteroides</i> var. <i>latenervosa</i> Teixeira	synonym of <i>L. neuropteroides</i> var. <i>minor</i>						
(3B) <i>L. minor</i> var. <i>linearis</i> Wagner	subjective synonym of <i>L. neuropteroides</i> var. <i>minor</i>						
(3C) <i>L. duplex</i> Němejc	synonym of <i>L. neuropteroides</i> var. <i>minor</i>						
(4) <i>L. brongniartii</i> (Gutbier) Zeiller	15–25	12	parallel	linear/falcate	8?	3.5/0.5	hexagonal
(5) <i>L. subbrongniartii</i> (Grand'Eury) <i>sensu</i> Zeiller	25	9–12	parallel slightly convex	falcate	10–14	6.0/0.4	subrhomboidal
(6) ? <i>L. semianastomosa</i> Tenchov	27	8	semiparallel	linguaeform	4–5	2.0/0.3	rhombic
(7) <i>L. elongata</i> Zeiller	30–35	7–8	parallel	elongate	5–6	6–7.0/0.8	hexagonal
(8) <i>L. regniezii</i> Laveine	15–20	5–7	parallel	linguaeform	6–7	3.1/0.5	rhomboid
(9) <i>L. florinii</i> Teixeira	dubious as species and based on strongly deformed pinnules						
(10) <i>L. weigeli</i> (Sterzel) Daber	70	25	parallel	linguaeform	> 10	9.0/1.0	elongate hexagonal
(11) <i>L. havlenae</i> Tenchov & Popov	30	7–13	parallel	slightly falcate	> 10	8.0/0.3	elongate

scarcity of the *Potoniea* pollen-organs in Brogan's pit is noteworthy. It is the reverse situation from China, where Laveine *et al.* (1993) reported a great abundance of *Potoniea* Zeiller associated with Potonieaceae foliage, in the absence of ovules. Poor preservation is unlikely to be an explanation for the Canadian situation, as preservation is extremely fine here. It could be that the linopterid plants were dioecious, and that the specimens found at Brogan's pit were female and those reported from China by Laveine *et al.* (1993) were male. However, there has been no evidence to suggest that other medullosaleans were dioecious so this explanation is also probably unlikely. A more likely explanation is that what we are seeing are plants that produced their ovulate and pollinate structures at different times in order to avoid self-pollination, an idea which is supported by the observation that the male and female organs were preserved in different layers within the rock [compare with similar observations made by Jongmans (1952) and Retallack & Dilcher (1988) on the reproductive biology of other Carboniferous pteridosperms].

Reconstruction of the plant

Laveine *et al.* (1993, text-fig. 12) reconstructed their Viséan paripterid from China as being a self-supporting plant some 12 m high, with a trunk just under 0.2 m in diameter and fronds estimated to be up to 6 m long. The Brogan's pit

material appears to represent a plant of very similar habit, with a trunk just over 0.2 m in diameter in its distal part and fronds 7 m long. The petioles of both the Chinese and Canadian fronds have a somewhat swollen base, of a form often interpreted as indicating a climbing habit for the plant, but we agree with Laveine *et al.* (1993) that this is unlikely in view of the width of the trunk.

Laveine *et al.* (1993) suggested that the apparently slender trunk of the *Linopteris*-bearing tree may have been partly supported by adventitious roots, as found in other arborescent medullosaleans, but little evidence of this was found in either their study or ours. Since most examples of trunks that could be linked with *Linopteris* were from near the top of the tree, it is possible that the trunk may have been rather wider at ground-level, which would have given it more support. On the other hand, the trunks of a number of modern-day tree-ferns of the Cyatheaceae are of similar height and girth, and can support frond many meters long.

Vein reticulation in *Linopteris*

Reticulation pattern as a taxonomic parameter in *Linopteris* Presl

Venation is most clearly observed on the abaxial surface of linopterid pinnules, as the veins protrude from the lamina.

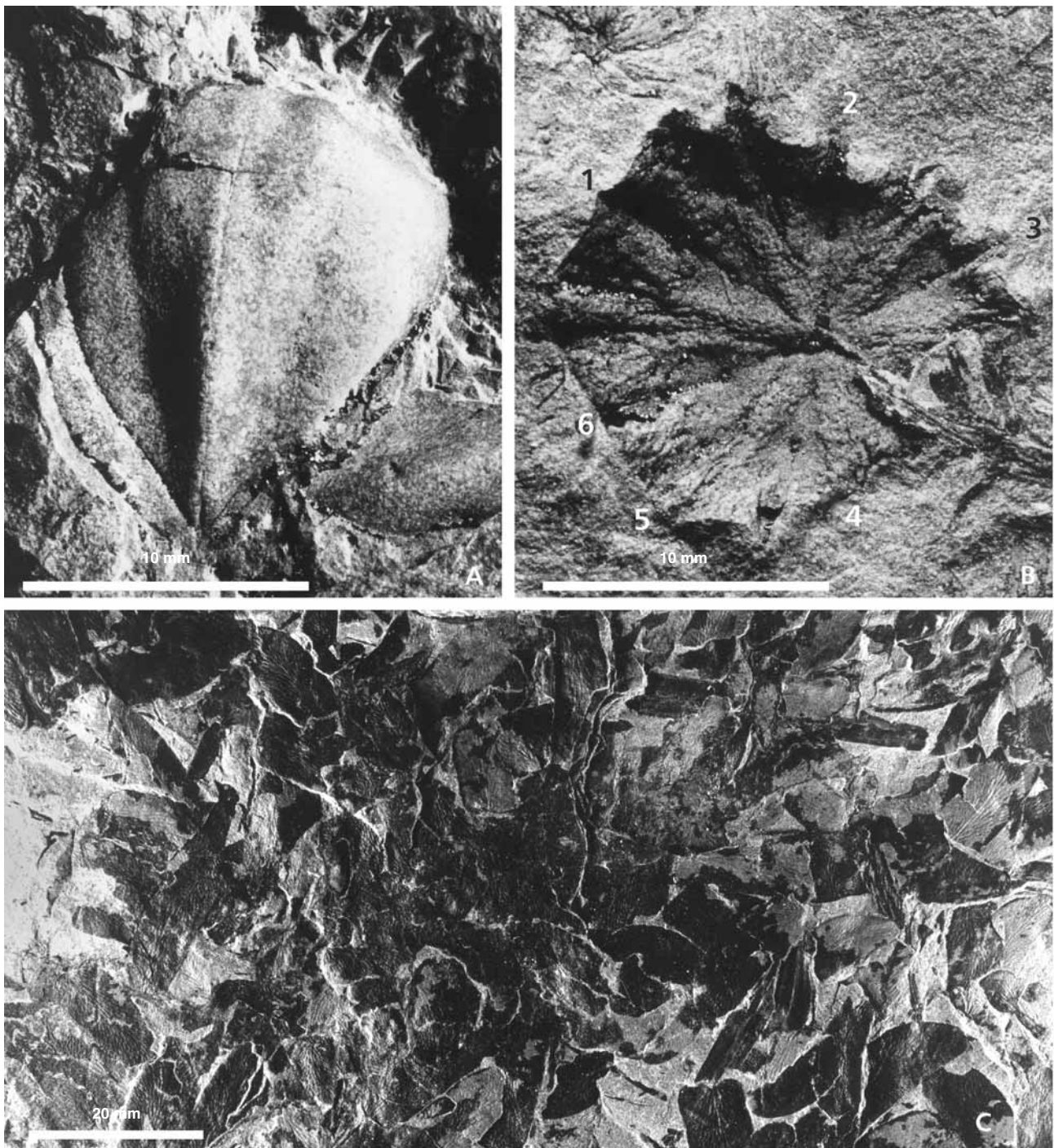


Figure 23. Lloyd Cove Seam, Sydney Coalfield, Cape Breton, Nova Scotia. • A – *Hexagonocarpus* Renault showing flange-like structure at the left, and broad ribs. • B – partial mold showing commissures numbered “1 to 6”, and attendant 6-fold symmetry structure emanating from the center. • C – detail of one of the four bedding planes defined by a plethora of abscised pinnules of *L. obliqua* (Bunbury) emend. 1.7 m × 1.3 m by 0.46 slabs (05-Lst#0).

In particular, the midvein length always appears longer on the abaxial surface compared with the adaxial surface (see Figs 3A, 31 compare A to B). Any taxonomic arguments based on midvein parameters without reference to which side of the pinnule is being studied [*e.g.*, Crookall 1959, p. 211, on the separation of *L. obliqua* from *Linopteris neu-*

ropteroides (Gutbier) Potonié] can be highly misleading. Also, the tailed areolae discussed earlier can only be considered taxonomically significant if it can be shown they are not due to differential merging with a thicker lamina.

Based on a literature survey of seventeen published linopterid types and suggested synonymies (summarized in

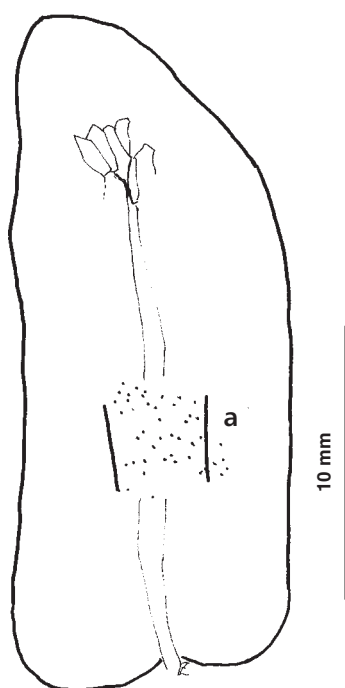


Figure 24. *Linopteris obliqua* (Bunbury) emend., specimen 04-Z25a, Lloyd Cove Seam, Sydney Coalfield, Cape Breton, Nova Scotia; figured is an abaxial-pinnule impression ballooned in width by siderite crystallization (concretionary genesis). Inset “a” represents a factual portion of the magnified midvein with accurately positioned punctae. Dense punctae also occur on the entire lamina.

Table 4), it is clear that there has been a tendency to rely on qualitative taxonomic parameters (*e.g.*, pinnule and areolate shapes) that have been subjectively interpreted, and which can differ on the abaxial and adaxial surfaces of the lamina, as demonstrated in this paper. The solution clearly hinges on the ability to analyze the lateral-venation pattern that shows complex and variable reticulate patterns generally based on elongate, polygonal areolae.

We suggest that linopterid foliage can be separated based on an areolate ground plan (or *typus* *sensu* Schindewolf’s 1980, p. 240) similar to Bocheński’s (1960) concept of peri-rachial characters for distinguishing species of *Alethopteris* Sternberg and *Lonchopteris* Brongniart. For linopterids, the *typus* is extensively manifest in the areolate architecture at the midvein, and is assumed to be independent of frond position for any given *Linopteris* species. To illustrate this, we have chosen the *typus* of seven linopterid specimens, emphasized by blotting out the remaining pinnule venation for each (Fig. 32). We propose the following battery of test variables, designed to capture the geometric-dimensional attributes of the areolae near the midvein.

- (1) Proportion of the long-axis of the areolae that is parallel to the midvein.
- (2) Length-width dimensions.
- (3) Geometry of the hat.
- (4) Curvature.

(5) Dimension (5a), geometric shape (5b) and curvature (5c) of areolae in the proximal part of pinnule but still in contact with the midvein.

Of these, variable (5) was already implicitly emphasized by Potonié (1904) in his description of lateral-vein development in *L. neuropteroides* (Gutbier) var. *minor* Potonié (see Fig. 27C).

A focused summary of *typus* attributes of seven linopterid specimens (including six types) is given in Table 5 (based on data in Fig. 32). Three form groups (A) to (C) are recognizable (A) *L. obliqua*–*L. cf. obliqua*–*L. neuropteroides* var. *minor*, (B) *L. regnietzii*, and (C) *L. neuropteroides* var. *major*. *L. brongniartii* fits somewhere in between because the vein areolae are less parallel and form a rosette in the proximal part of the pinnule. *L. neuropteroides* (Gutbier) var. *minor* shown in Fig. 32F is similar to that of the larger linopterid pinnules in the Sydney Coalfield (*e.g.*, Fig. 9). This would seem to lend some support to the general thesis of Zhang *et al.* (1992) and Laveine *et al.* (2003) that many of the presently-recognized linopterid morphospecies merely represent intraspecific variation within highly polymorphic fronds. In our view, however, their assertion that *L. neuropteroides*, *L. subbrongniartii*, *L. obliqua* and *L. brongniartii* should be interpreted as one species is taking the argument too far, at this juncture. To develop the analysis further, the type specimens themselves clearly need to be re-studied and compared directly to allow a full generic circumscription to be established, and a “a generic similarity matrix” be developed *sensu* Pšenička (2005); see also Darrah (1969, p. 83) for an analysis of the pitfalls of iconography.

Bocheński (1960, figs 1, 4) used the characteristics of vein meshes adjoining the midvein (his first-row meshes), and the vein branching-pattern in the peri-rachial (proximal) part of the pinnule, to distinguish lonchopterid species. A cursory analysis showed that, on this basis, the netted genera of *Lonchopteris* Brongniart, *Lonchopteridium* (Gothan) Guthörl emend. Zörow & Cleal, *Linopteris* Presl, and *Reticulopteris* Gothan are objectively separable, although they may share a common phylogeny. On the other hand, using these same criteria, it is difficult to distinguish isolated pinnules of the imparipinnate medullosalean *Barthelopteris germari* (Giebel) Zörow & Cleal (*e.g.*, Krings & Kerp 1998, figs 3–5) from detached pinnules of the paripinnate medullosalean *L. obliqua*. This emphasizes the necessity of integrating frond architectural and cuticular data, coupled with statistical models (see below) to confirm form-specific linopterid determinations in a taxonomically consistent manner.

Modeling vein reticulation in *Linopteris*

Modeling venation pattern in *Linopteris* Presl may help identify more objective taxonomic parameters. Unlike other

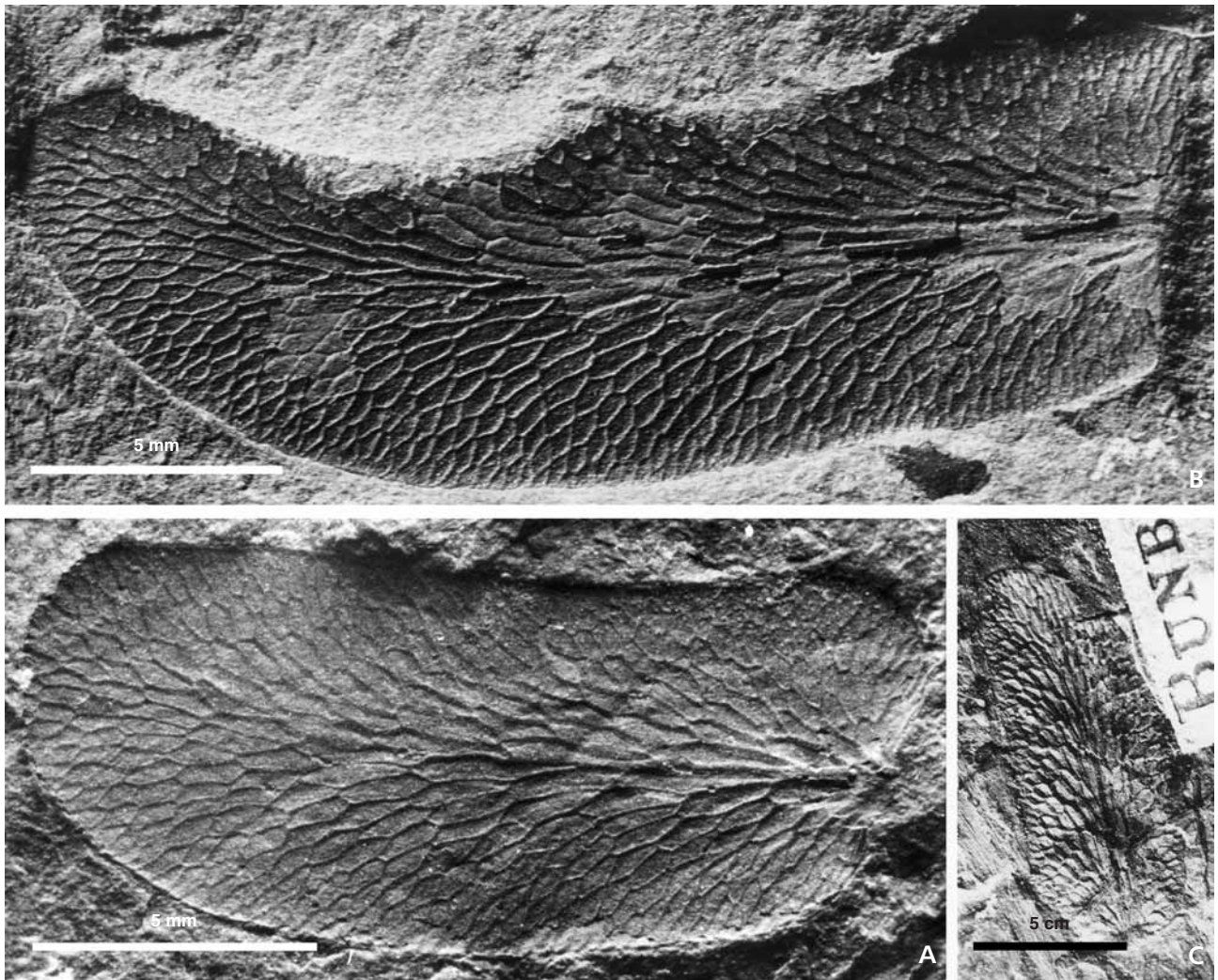


Figure 25. Bunbury's specimens, Bunbury Collection, Cambridge University. • A – *Dictyopteris obliqua* Bunbury; 186, Bunbury (1847, fig. 2B). Catalogued by Bunbury (1850) as *Dictyopteris* Gutbier, *D. Brongniarti* var. *minor*. Sydney, Cape Breton. Richard Brown, Esq. • B–C – paratypes, 187 and 188, are not figured in Bunbury (1847), but catalogued by him in 1850 as *Dictyopteris* Gutbier, *D. Brongniarti* var. *minor* respectively. Sydney, Cape Breton. Richard Brown, Esq. "Open-ended" areolae seen in the photographs are due to incident-light beam. In fact, they are interconnected to form closed networks.

pteridospermous groups with a one-dimensional (linear) venation pattern, *Linopteris* Presl venation is of two-dimensional geometry and thus ready-made for mathematical treatment. Two mathematical models merit consideration (Krumbein & Graybill 1965). One is a deterministic model to account for the observation that areolae are most elongate near the midvein, becoming shorter thereafter in the direction of the pinnule margin. We have followed Bocheński's (1960) notation in naming rows, choosing one of the main branching systems in the lower (proximal) part of the pinnule as a starting point (Fig. 33). Let the midvein be designated the zero (0) areola, the adjacent areola 1, and continuing outward along a lateral branching system (e.g., Fig. 27B), a series is realized 0, 1, 2, 3, 5, 8, 9 (Fig. 33) which on first approximation resembles the Fibonacci Series 0, 1, 1, 2, 3, 5, 8, 13 (see Smith 1958). The differences

between our observed sequence and the classic Fibonacci Series can be explained by the limited laminate width and the variable pattern of bifurcations. Alternatively, the observed pattern of areolae in Fig. 33 could mathematically be simulated to reproduce the venation *typus*, for instance using fractal geometry (see Heggie & Zodrow 1994 for the use of fractal geometry for modeling a Carboniferous lobatopterid-fern frond).

The second modelling approach is through probability theory: the stochastic model that assumes independent variables and random data, *i.e.* introduction of an uncertainty factor into the deterministic model. A highly complex model that could explain vein reticulation as a purely abstracted physical phenomenon can be represented by Markov Chains of conditional [transition] probability (Kolmogorov 1956, and references therein).

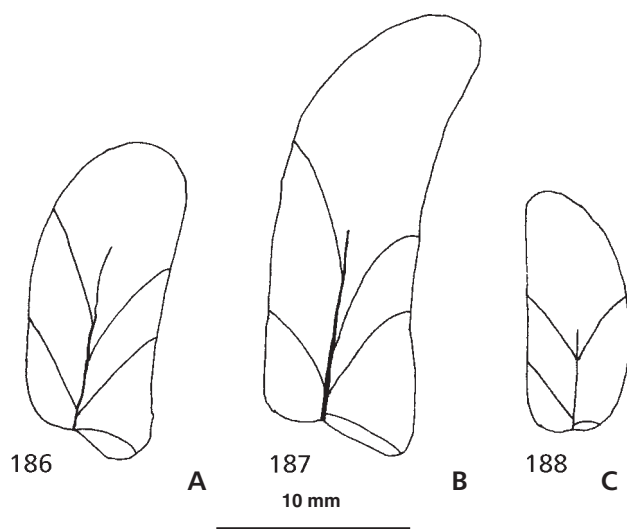


Figure 26. *Linopteris obliqua* (Bunbury) emend. Sydney Coalfield, Cape Breton, Nova Scotia; pinnule outlines with lines-of-areola in the syntypes. • A – lectotype 186. • B–C – paratypes, 187 and 188, respectively.

If explanatory interests centre on the probability-distribution phenomenon of “vein endings” (positive integers = events), *i.e.* premodeled by linopterid branching as in Fig. 27B, then Zodrow & Banerjee’s (1993) approach merits consideration which models the generalization of the binomial probability law to the n th degree of vein endings.

Simultaneous areolate length-width variation in the form of a two-dimensional probability surfaces (the continuous bivariate model) would *à priori* exclude the normal LaPlace-Gauss law because of the natural trend in areolate-length-width reduction that appears to be uniform (monotonic decreasing function) in the direction of margins. Such data derived from inherent trends have the frequency characteristic of the mode not being equal to the mean, resulting in a tailed distribution best represented by a skewed model, such as the well-understood family of exponential (lognormal) curves which on appropriate logarithmic-base transformation of variables approximates characteristics of the normal curve (Zodrow 1973).

Clearly much potential exists for statistical modelling to improve our understanding of the mathematical nature of the linopterid venation. Specifically, appealing are the concepts of the 3rd and 4th mathematical moments in continuous-distribution theory for being population discriminators in biometrics (Cramér 1945, p. 175). The bivariate length-width areolate model is recommended. However, a rigorous mathematical development, evaluation, and application of such techniques are beyond the scope of the present paper.

Development of Potonieaceae vein-reticulation

Reticulate venation patterns of linopterid taxa have been presented and described in the literature as depicted in

Fig. 27A, *i.e.* generally without reference to (1) ontogenetic development, (2) adaxial/abaxial orientation, and (3) branching pattern at the midvein (however, see Bocheński 1960 and Tenchov & Popov 1987). In addition, the underlying assumption that reticulation is by anastomosis is based on venation characteristics determined from coalified compressions (see Bocheński 1960), and could be subject to thermal bias (organic metamorphism). Anastomosis has never been confirmed by observation in *Linopteris* Presl, either through cuticular analysis or coal-ball sectioning, to shed light on the nature of the lateral-vein fusion and cross-over veins, as being anastomosed.

Reticulate venation can develop in different ways [*e.g.*, see examples found in extant ferns discussed by Wagner (1979); see also Tryon *et al.* (1990, p. 253, fig. 129)]. The best documented in the Medullosales is where the veins become progressively more flexuous, and adjacent veins ultimately merge by tangential anastomosis. This has been most clearly demonstrated in the Neurodopteridaceae, with a progressive change through the Westphalian Stage of the Variscan Foreland from of the open-veined *Neuropteris obliqua* (Brongniart) Zeiller to the reticulate-veined *Reticulopteris muensteri* (Eichwald) Gothan (Josten 1962, Tenchov & Popov 1991). Details of the tangential anastomosis of the veins have also been demonstrated in naturally macerated cuticles (Zodrow & Vasey 1986). Bocheński (1960) argued that a similar transition could be identified in the Alethopteridaceae, but this has not been documented in such detail.

However, vein reticulation appears to have developed in a different fashion in the Potonieaceae (Tenchov & Popov 1987). In this family, adjacent lateral veins become connected by cross-over veins (for an analogy, see Zodrow & Vasey 1986, fig. 16A). These cross-over veins are very short, and manifest in three-sided hats that resulted also in septangular areolae (Fig. 3A, arrow, Fig. 6G), or connections between the midvein and the branches (Fig. 27B). If the cross-over veins are erased from the veining pattern in this figure, and using the main-lateral veins emitted from the midvein (recognizable by their sturdy appearance) as a guide for locating ensuing bifurcations, a zigzag lateral-branching pattern is revealed (Fig. 27B). These main-lateral veins are sub-oppositely arranged on either side of the flexuous midvein, mostly originating in the proximal part of the pinnule, and are initially relatively straight and quasi-parallel to the midvein. They extend into the apical regions of the pinnule, with only three to four of these main veins on either side of the midvein to food-supply the entire pinnule lamina (see analogous situation in Fig. 27C). The main-lateral veins bifurcate at most five times and zigzag, reaching the margin open-ended and obliquely, producing a marginal vein density of 40–45 veins per 10 mm.

The pattern of vein reticulation in the Potonieaceae, where there is no evidence of tangential anastomosis, is

clearly quite different from that seen in the Neurodopteridaceae and probably the Alethopteridaceae, and is another feature that serves to separate the former from the other families within the Medullosales. Nevertheless, there is no sharp demarcation between *Paripteris* Gothan & *Linopteris* Presl, as the former can sometimes show rare cross-over veins, the generic distinction between the open-veined and reticulate-veined forms clearly being artificial (e.g., see comments by Zodrow & Cleal 1998). For species definition, however, areolate geometry (i.e. the *typus*) remains an important discriminating taxonomic character.

Linear measurements suggest an estimated 10% to 20% increase in vein length is realized by reticulation, as compared with the curvilinear open venation. The observed change from *Neuropteris* to *Reticulopteris* in the Neurodopteridaceae appears to correlate with a change to less-wet climatic conditions (Zodrow & Cleal 1993, Cleal & Shute 1995). The equivalent change from *Paripteris* Gothan to *Linopteris* Presl cannot so readily be interpreted, however, and reticulate veining in extant plants has been shown to result from various selection pressures that can include mechanical strength of the leaf and its response to herbivory, as well as hydraulic factors (Uhl & Mosbrugger 1999, Roth-Nebelsick et al. 2001). At present, we have insufficient evidence to interpret these changes in the Potoniaceae.

Systematics

Although *Linopteris* Presl has traditionally been used as a morphogenus for foliar fossil material (e.g., Laveine 1967a), Barthel (1962) suggested that it could be re-interpreted as a natural genus for a whole plant, a view with which Laveine et al. (1993) later agreed. The evidence for interpreting *Linopteris* Presl as such (following the methodology of Retallack & Dilcher 1988) appears compelling. Details of the architecture of the fronds have been worked out in some detail (Laveine 1967a, 1997; Wnuk & Pfefferkorn 1984; Pfefferkorn et al. 1984; Laveine et al. 1993; and this study), and epidermal characteristics are known, including the type of monocyclic stomata (Barthel 1962). We now have provided evidence for an attached ovule of the type of *Hexagonocarpus* Renault, and there is a consistent physical association of linopterid foliage with pre-pollen organs *Potonia* Zeiller (Carpentier 1911; Laveine 1967a, 1971; for summary see Laveine et al. 1993, and this study). There is even evidence that the plant was arborescent, and it is widely assumed that the stems, when anatomically-preserved, are of the *Sutcliffia* Scott type which bears affinity with *Medullosa* Cotta (see summary Laveine et al. 1989, Stidd et al. 1975), although the biological connection between them has as yet not been fully demonstrated.

Tempting therefore is a revision of the formal taxonomy of these fossil fragments as whole organisms. How-

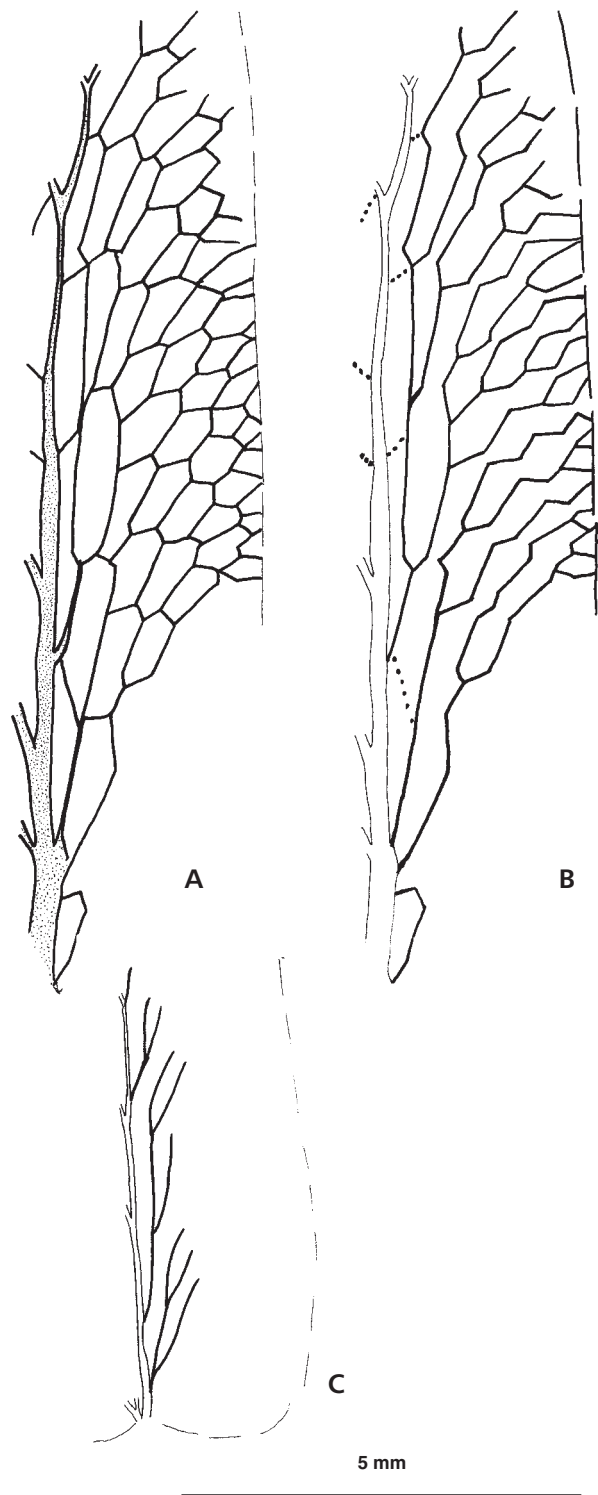


Figure 27. Modelling areolate-venation pattern in *Linopteris* Presl. • A–B – *Linopteris obliqua* (Bunbury) emend., Lloyd Cove Seam, Sydney Coalfield, Cape Breton, Nova Scotia. • A – following literature to depict reticulation pattern, specimen 04-Z27. • B – after removal of crossover connections at the midvein (...) and elsewhere of A to diagnose the branching pattern. • C – branching architecture at the midvein in *Linopteris neuropteroides* var. *minor* (Potonié 1904, Lief. II, 28) homologous to B.

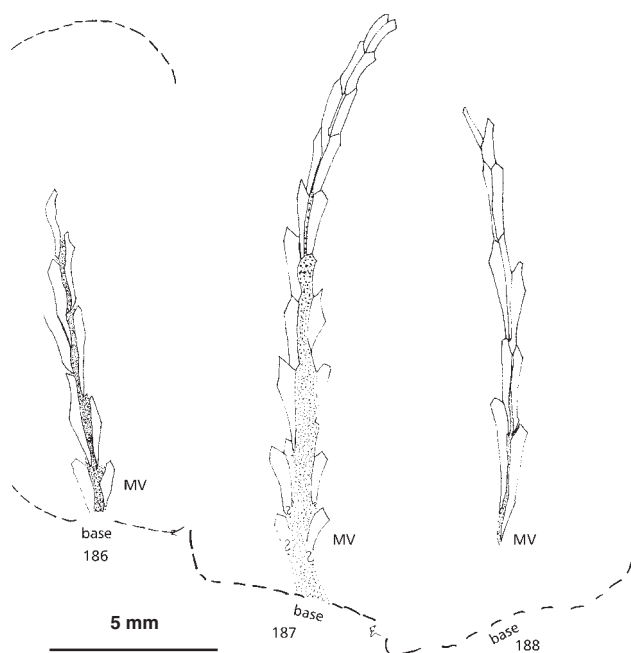


Figure 28. *Linopteris obliqua* (Bunbury) emend. Sydney Coalfield, Nova Scotia; areolate architecture at the midvein of the syntypes. Lectotype 186, paratypes 187 and 188. Length for 188 is incomplete. “Base” = pinnule base; MV – midvein.

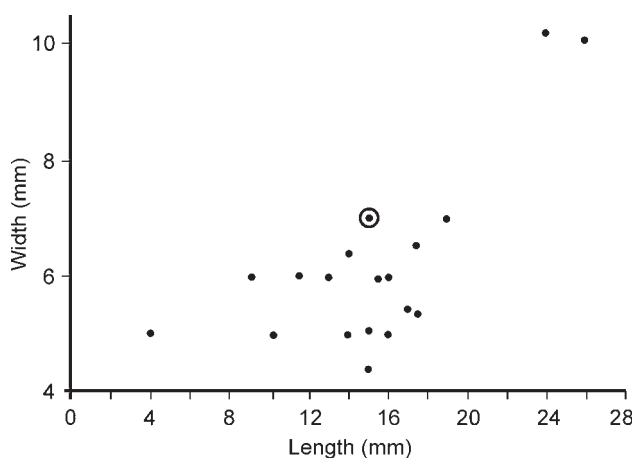


Figure 29. Scattergram, pinnule length/width of *Linopteris obliqua* (Bunbury) emend. (Table 1, n = 19). The encircled point represents the lectotype 186. Note a trend shift to the right.

ever, as soon as we look at the practicalities of doing this, nomenclatural problems arise immediately (see Chaloner 1986, for a discussion of the problems of naming whole fossil plants). We can undoubtedly have a coherent whole-plant concept to which the specific epithet *obliqua* can be linked. The problem arises when we consider the genus to which it should be assigned. One option might be to propose formally an emendation of the morphogenus *Linopteris* Presl so that its diagnosis and circumscription encompass the entire plant. However, this assumes that the

type of *Linopteris* Presl (*L. gutbieriana* Presl ?*L. brongniartii* (Gutbier) Potonié), which is currently based purely on foliar features, can confidently be accommodated within the radius of this whole-plant concept. Also, where would this leave all of the other morphospecies currently included within *Linopteris* Presl but for which we have less complete evidence of the rest of the plant? Some would undoubtedly belong to the same whole-plant genus, but possibly not all. So, we would end up with the unsatisfactory situation where another morphogenus would have to be erected to accommodate morphospecies of linopterid-like foliage but which, for lack of information, cannot be included within the whole-plant genus.

Alternatively, we could opt to erect a new genus for the whole plant that bore *L. obliqua* foliage. There is the drawback here of introducing an additional name into the taxonomic literature, the scientific benefits of which are debatable. There is also the problem of designating the type. Although the type of a genus is often quoted as a species, in fact the *International Code of Botanical Nomenclature* (Greuter *et al.* 2000) stated that it is a specimen. Since our knowledge of these plants is based exclusively on fragments, there can be no specimen of the whole plant that could act as type. We would therefore have to choose as type a fossil that would only represent part of the plant. Although there is nothing in the *Code* that would invalidate such a choice, there are clearly potential difficulties in this approach.

One of them is the philosophical issue of whether formal taxonomic nomenclature should be used for something that is not real. Although the evidence for the reconstruction might be strong, in almost all circumstances the reconstructed plant will be a construct in the mind of the beholding palaeobotanist. Only if we find the fossilized remains of a complete plant will the reconstruction become a reality, and even then an incomplete one due to the loss of most soft tissues and cellular detail.

At the end of the day, we have to ask if the taxonomic benefits that would be accrued through developing such a whole plant genus outweigh the nomenclatural and philosophical problems that would result. Since we are for the most part using this nomenclature for naming the fossilized fragments of the plants, then the answer must probably be “no”. Only in generalized discussions on plant ecology would a name be needed for the whole plant. To surmount, for example, a comparable problem, Crane (1984) used the informal name ‘*Nyssidium* plant’ to describe the whole angiosperm plant bearing *Nyssidium* fruit and *Trochodendroides* leaves, and we believe that a similar approach is best in the case dealt with in the present paper. So, we will continue to regard the formal taxon *Linopteris obliqua* (Bunbury) as a foliar morphospecies (including details of frond architecture and epidermal structure: see Diagnosis), and refer to the whole plant informally as the *Linopteris obliqua* plant.

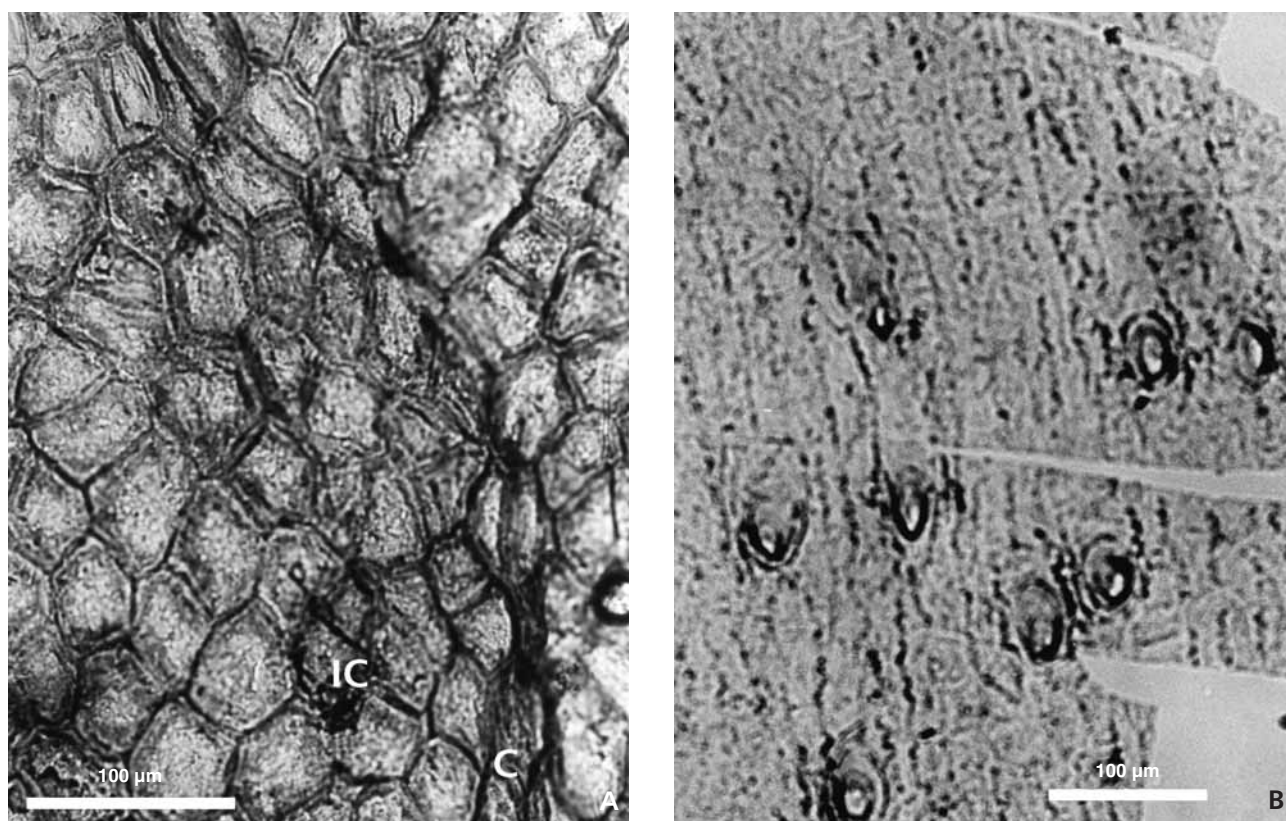


Figure 30. *Linopteris obliqua* (Bunbury) emend., epidermis; Sydney Coalfield, Cape Breton, Nova Scotia. • A – upper epidermal intercostal (IC) and costal (C) cell structures. 985-212b/6, Stubbart Seam (Prince Mine) (see Fig. 9). • B – lower epidermis with densely-spaced hair bases, (?)hydathodes. Stomatal details are not preserved. 982-201, Harbour Seam (Fig. 31B).

The systematic position of *L. obliqua* given below is based on the classification given in Anderson *et al.* (in press).

Class Cycadopsida Brongniart, 1843
Order Medullosales Corsin, 1960
Family Potonieaceae Halle, 1933

Genus *Linopteris* Presl, 1838

Linopteris obliqua (Bunbury) Zeiller, 1899 emend. nov.

Types. – Bunbury (1847) based his description of the species on three syntypes, identified in his hand-written “Catalogue of Fossil Plants in My Collection, 1850” as specimens 186, 187 and 188. These specimens are photographically illustrated for the first time in the present paper (Fig. 25), and we designated specimen 186 as the lectotype, probably as intended by him. All three syntypes originated from strata associated with the middle Asturian (*ex* Westphalian D) Harbour Seam in the Sydney Coalfield, Cape Breton, Canada.

Diagnosis. – Frond up to 7 m long, axis 40 mm wide, at least quadripinnate, trifurcating, hairy and spiny (all axes), non-

planar, winged, (?)lacinate lamina below main trifurcation. Penultimate pinna at least 200 mm long, with small (4 mm long) linguaeform to round intercalated pinnules that lack a midvein. Ultimate pinna, length variable, at least 200 mm long, 36 mm wide, shape linear, oblong, ovate-oblong, variable. Pinnules, densely hairy, polymorphic, asymmetric, round, linguaeform-subtriangular, slightly falcate-frequent form- narrow-elongate falcate, 4 mm to 27 mm long and 4 to mm to 19 mm wide. Margin curvilinear, parallel, non-parallel. Midvein, with 2 to 4 branches nearly reaching apex, flexuous, longitudinally finely striae and punctae, abaxially 80% length of pinnule, then replaced by areolae. Venation reticulate; areolate geometry variably elongate-hexagonal at midvein, changing occasionally to being septangular, 5-, 4-, or 3-sided towards margin with increased frequency of cross-over connections, generally showing acute-angled hats, straight-curvilinear sides; areolae 1.2 mm to 2.7 mm long, and 0.2 mm to 0.5 mm wide at midvein, decreasing at margin to 0.4 to 0.9 mm in length and 0.4 mm width; 5 to 10 areolae midvein to concave margin, where at margin elongate open-ended; line-of-areolae straight to slightly curved meeting margin acutely. Vein density *ca* 45 veins/10 mm pinnule margin. Pinnule hypostomatic, stomatal type monocyclic, stomata randomly oriented, lower epidermis with hair bases.

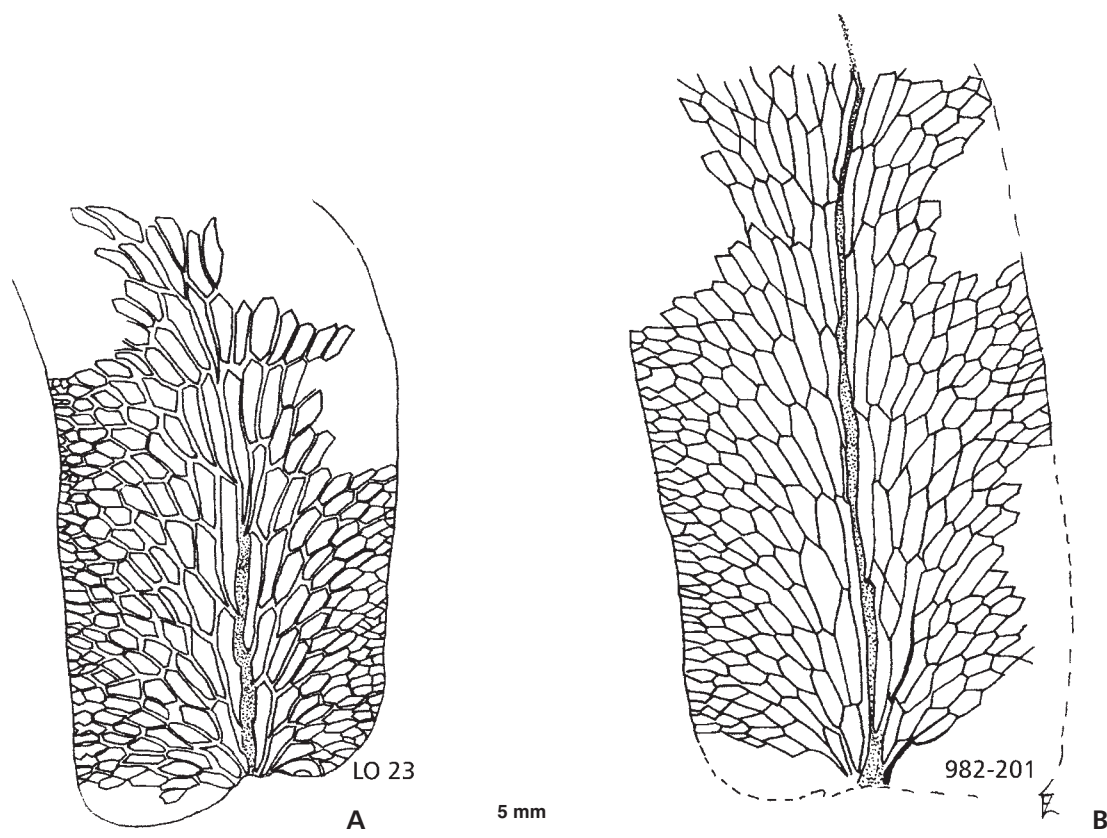


Figure 31. *Linopteris obliqua* (Bunbury) emend. Adaxial and abaxial midvein representations, type Harbour Seam, Sydney Coalfield, Cape Breton, Nova Scotia. • A – adaxial impression (not macerated), precision hand drawing showing the flexuous midvein (stippled) biased to less than $\frac{1}{2}$ the pinnule length, and the highly variable areolate geometry, particularly near the margin. Lo. 23. • B – abaxial compression, precision hand drawing showing the flexuous midvein to about $\frac{5}{10}$ of the pinnule length, but it continues to $\frac{8}{10}$ on the specimen 982-201.

Table 5. *Typus* characteristics of seven linopterid specimens: areolate geometry at the midvein.

Criterion, see text (1)	(2)	(3)	(4)	(5)		
Fig. 32 A–G	Proportion of parallelism to the midvein	Length mm	Width	Hat geometry	Curvature	Pinnule base
A – <i>L. obliqua</i>	100%	2.5	0.3	triangular	slight	no rosette
B – <i>L. cf. obliqua</i>	40–100%	2.6	0.3	triangular	slight	small rosette
C – <i>L. regniezii</i>	50–80%	4.1	0.5	curvi acuminate	slight	incipient rosette
D – <i>L. neuropteroides</i> var. <i>minor</i>	nearly 100%	2.8	0.3	triangular	slight	small rosette
E – <i>L. neuropteroides</i> var. <i>major</i>	10–40%	8.3	0.7	acute	slight	fully developed rosette
F – <i>L. neuropteroides</i> var. <i>minor</i>	nearly 100%	2.8	0.2	triangular	none	no rosette
G – <i>L. brongniartii</i>	10–100%	2.5	0.3	triangular	slight	somewhat developed rosette

Remarks. – Cuticular data incorporated in the emendation is mostly from Barthel (1962), but also from our Fig. 30.

Bell (1938, p. 64) stated emphatically that *Linopteris obliqua* var. *bunburi* Bell has a rather “loose network of veins” (with some open form, neuropteroid areolae). Open-ended areolae (other than marginal ones), or neuropteroid-like areolate venation of any kind, however, have not been observed in the present samples, including the juvenile areolae. More generally, linopterid foliage with the “loose network of veins” mentioned by Bell (1938) has not

been observed in the large sample size from Sydney Coalfield that was studied preparatory for this paper. Moreover, re-examination of the material published by Zodrow & McCandlish (1978) equally showed no such vein characteristics. In a future paper on linopterid typification, the position of Bell’s species will be clarified.

The most important distinguishing characteristics of *L. obliqua* foliage are that the first row of areolae are strictly lengthwise parallel to the midvein, and do not form a rosette-like pattern at the base of the midvein. Areolae at



Figure 32. Selected linopterid types and their *typus* architecture at the midvein. • A – lectotype 186. • B–G – unaltered original figured by the authors. • B – *L. cf. obliqua* (Bunbury), Laveine's interpretation (1967a, fig. 47). • C – *L. regnietzii* Laveine (1967a, fig. 48; 1967b). • D – *L. neuropteroides* (Gutbier) var. *minor*, Zeiller's interpretation (1899, fig. 10). • E – *L. neuropteroides* (Gutbier) Zeiller var. *major* (Remy & Remy 1977, Bild 147). • F – *L. neuropteroides* (Gutbier) var. *minor*, Potonié's interpretation (1904, Lief. II, 28, 1). • G – *L. brongniartii* (Zeiller 1878, Pl. CLXV, fig. 2).

the midvein are elongate-hexagonal with triangular hats, or basal tail, less than 3 mm long and *ca* 0.4 mm wide. Thereafter, they are variable in size and shape, strictly closed over the lamina, but consistently elongate-open at the margin. Pinnate characteristics include paripinnate terminals, spiny rachis, small to medium-sized spiny? pinnules, and 4 mm to 11 mm long intercalated pinnules.

The biostratigraphic range of *L. obliqua* (Bunbury) emend. is stable in the Sydney Coalfield, Nova Scotia, as outlined by Zodrow & McCandlish (1978, Table 5).

Conclusion

For the first time, we provide empirical evidence for reconstructing the *L. obliqua* plant, including our initial understanding of the complex frond (Fig. 34). It appears to have been a medium-tall arborescent plant with a trunk *ca* 0.2 m wide. Fronds *ca* 7 m long probably had ovules attached singly to the base of the petiole, although this still requires confirmation. All orders of rachis were covered in punctae of variable sizes, although further cuticular and phytochemical work will be needed to determine the function of these trichomes. We found no new evidence of attached pollen-organs, although based on previously published evidence they were probably borne in complex clusters, attached either directly to the cauline axis or to the pri-

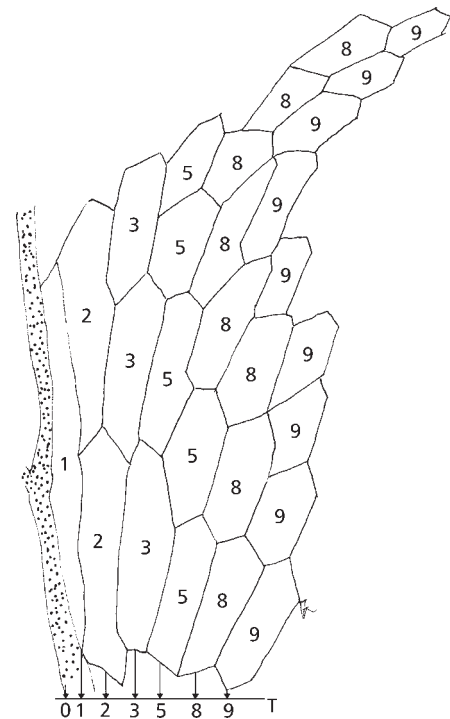


Figure 33. Empirical derivation of the terms for Fibonacci's Series. 982-201, abaxial surface, Harbour Seam, Sydney Coalfield, Cape Breton, Nova Scotia; T, derived from summing the number of vertical areolae, represents the terms (see text).

mary rachis/petiole of the frond (e.g., Laveine *et al.* 1991). Current evidence suggests that the plants belonged to a family that arose in China in Early Carboniferous times and migrated westwards along southern Laurasia during Late Carboniferous times. The Sydney Coalfield in Nova Scotia seems to have been close to the western limit of this migration of the genus.

The specimens described are small relative to the 7-m probable size of the whole frond. Nevertheless, they provide the first concrete evidence for highly polymorphic ultimate foliar segments, with rapid changes in pinnule shapes being observable even in relatively small specimens. *L. obliqua* foliage generally cannot be objectively distinguished from other linopterid morphospecies by only one parameter. However, the probability of successful distinction increases when the *typus*-parameters are combined with morphological parameters of the pinnae. To this end, we propose new parametric variables, which are rooted in geometrical concepts that best mimic the variable geometry of the two-dimensional vein-reticulation. We believe that objective recognition of the linopterid *typus*, coupled with a geometrical-statistical analysis of the morphological data, would be sufficient for the specific determination even of single pinnules. However, because of the current absence of such data for most other *Linopteris* species, we have not been able to make detailed comparisons with those species.



Figure 34. Reconstructed *Linopteris* plant showing salient features mentioned in the text.

We suggest from indirect evidence that the reproductive biology of the *L. obliqua* plant was characterized by periodic short-lived intervals of seed production, maybe triggered by ecological stress. These times of seed-production coincided with the mass shedding of the photosynthetic pinnules so as to redirect resources to reproduction.

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