REPRODUCTIVE BIOLOGY OF THE ARBORESCENT
SEED-FERN LINOPTERIS OBLIQUA: IMPLICATIONS
FOR TAXONOMY (MEDULLOSALES, LATE PENNSYLVANIAN
SYDNEY COALFIELD, CANADA)

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Abstract: A shaley slab (65 x 45 x 7 cm) from the Sydney Coalfield, Canada, Cantabrian age, on splitting apart revealed 2 – 3 layers each entombing thousands of abscised pinnules of Linopteris obliqua and eight dispersed compound-synangial structures. The campanulary-ventral-sporal micromorphology of the best preserved structure of these compares sufficiently well with previously reported structures from the Sydney Coalfield named Potoniea krisiae. Earlier studies involving larger sampling suites furthermore contributed to the observation that Hexagonocarpus sp. (female organ) and P. krisiae (male organ) usually co-occur with abscised L. obliqua pinnules; however, these two organs do not co-occur on isochronous bedding planes. In the absence of confirmatory organic attachments, the presented data provide as yet the strongest support for the hypothesis of the organs’ connectivity, but whether female-male trees existed or not, and the mode of attachment of the organs remain unknown. Hypothesized for the latter is pinnate attachment.

Keywords: Medullosalean, Potoniea krisiae, Hexagonocarpus

INTRODUCTION

The species’ concept of Linopteris (ex Dictyopteris) obliqua (Bunbury 1847) is based on a single pinnule specimen, lectotype “186” (so designated by Zodrow et al. 2007). It is deposited with Cambridge University, Botany School, together with Bunbury’s hand-written “Catalogue of Fossil Plants in my Collection, 1850; Part 1, Ferns and Lycopodiaceae” in which he recorded two additional pinnules of this species “187 and 188” from Cape Breton, Nova Scotia (cf. Zodrow et al. 2007). In fact, Bunbury unknowingly brought to the fore the autecological nature of this species. All three pinnules originated from what is now called the Harbour Seam of the Sydney Mines Formation of the Late Pennsylvanian Sydney Coalfield, Canada (Figure 1C).

However, Bell (1938, fig. 1, pt.1) mapped the stratigraphic occurrences and the lateral extent of L. obliqua in the Sydney Coalfield based on the extensive coal diamond-drill programs, commented on the caducous nature of the pinnules, and established, amongst others, the L. obliqua Zone. It is emended through the collection of L. obliqua specimens from the uppermost strata at Point Aconi, which is part of Bell’s originally defined Ptychocarpus unitus Zone (Zodrow & McCandlish 1978). Bell’s Zonation is used by Zodrow & Cleal (1985, fig. 5, among other plant fossils) for correlating non-marine Asturian (Westphalian D) and Cantabrian strata from Europe and North America. In general, L. obliqua is restricted to tropical Euromerica of Late Pennsylvanian age as is summarized by Tenchov & Popov (1987) and Zodrow & McCandlish (1978), but it also occurs in the Mazon-Creek Flora, U.S.A. (Pfefferkorn 1979).

The present contribution focuses on, and is complementary to earlier studies to strongly support the connectivity of the male organ Potoniea krisiae.
Pšenička et al. 2019 and the female organ Hexagonocarpus sp., compared with H. crassus Renault 1890 by Zodrow et al. (2007), to the seed-fern plant L. obliqua (Zodrow 2002, 2007). Thus, Bell’s original L. Zone is likely characterized by a natural species, not known for any other Carboniferous-zone phytosstratigraphy. In effect, illustrated is the utility of large specimens collected with time-stratigraphic aspects (thickness) in the study of reconstructing seed-fern plants.

**TAXONOMIC EMENDATION OF SPECIMENS FROM SYDNEY COALFIELD**

To avoid perpetuating misinterpreted taxa, we offer the following emendations. Included in the concept of *P. krisiae* are now the previously named: (1) *Dolerotheca* sp. Zodrow (2007, figs 15B-D), and (2) *Bernaultia*-like sp. (ex Dolerotheca Halle), Cleal, Zodrow & Mastalerz (2010, pl. 1, figs 6 and 7).

**MATERIAL, METHODS, AND STRATIGRAPHIC AGE**

The study material, accession number 08-10/15-9, originated from a 65 x 45 x 7 cm *in situ* argillaceous-shaley slab 1-2 m above the Hub Seam in the now-closed (2002) submarine Prince Mine near Point Aconi (Figure 1C, “X2”, Late Asturian age). The slab is split into two pieces (Plate I, Figs A, B), which are both systematically deconstructed and the fragments are examined under a binocular microscope at variable magnifications of up to × 25. Eight compound-synangial compressions could be collected (Table 1), ignoring fragments smaller than 1 – 2 mm, where the first seven tabulated are of unknown positions. The most complete and best preserved eighth one, however, originated from just below the surface marked “1a, 1b” in Fig. A on Plate I, i.e., part/counterpart Figs. G and H on Plate II, respectively.

Intact sporangia are freed from the compression (Plate II, Fig. H) in 10 – 15 min treatment with

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**Figure 1.** Location map. (A) Canada. (B) The Maritimes Basin. (C) Coal stratigraphy, Sydney Coalfield (Bell 1938, fig. 1), with sample locations of 05-Lst#0 (“X1”) and 08-10/15-9 (“X2”). See also Tables 2 and 1, respectively.
25% v/v hydrofluoric acid, then macerated in Schulze’s solutions maximally for 30 h. Although sporangial cuticles are not observed, the well-preserved microspores mounted on glass slides are examined at × 500 magnification using a binocular (biological) microscope equipped with Nomarski phase-contrast illumination and a digital camera for high-resolution images.

The reference in this paper to *Hexagonocarpus* sp. is based on the many isolated samples retrieved from the systematic destruction of a 1.7 × 1.3 × 0.46 m argillaceous-shaley block, i.e., accession number 05-Lst#0 in Table 2; see Zodrow et al. (2007, fig. 23). It originated from an unknown stratigraphical level in the roof rocks of the Lloyd Cove Seam (Figure 1C, “X1”, Early Cantabrian age).

The slab of Fig. A, B on Plate I with its studied microspore organs is secured by Erwin L. Zodrow (ELZ), and the organ specimens are curated at the West Bohemian Museum, Pilsen, Czech Republic.

Table 1. Compound-synangial specimens cited/studied, Sydney Coalfield, Nova Scotia: n.a. not applicable, n.i. not illustrated.

| Accession no. | Figure   | Analyzed | Compression (comp) | Preserved size (mm) |
|---------------|----------|----------|--------------------|---------------------|
|               |          |          | Impression (imp)   | Width   Height      |
| 08-10/15-9-3  | Plate II, A | n.a.     | comp              | 3       10          |
| 08-10/15-9-5  | Plate II, B | n.a.     | comp              | 20      10         |
| 08-10/15-9-6  | Plate II, C | n.a.     | comp              | 8       10          |
| 08-10/15-9-10 | Plate II, D | n.a.     | comp              | 6       7           |
| 08-10/15-9-9  | Plate II, E | n.a.     | comp              | 3       4           |
| 08-10/15-9-9  | n.i.      | n.a.     | comp              | 2       4           |
| 08-10/15-9-5  | n.i.      | n.a.     | comp              | 2       6           |

Part and counterpart:

| Accession no. | Figure   | Analyzed | Compression (comp) | Preserved size (mm) |
|---------------|----------|----------|--------------------|---------------------|
|               |          |          | Impression (imp)   | Width   Height      |
| 08-10/15-9-1a | Plate II, G | yes      | imp               | 10      17          |
| 08-10/15-9-1b | Plate II, H | yes      | imp               | 9       15          |

Table 2. Summary of *Linopteris obliqua* pinnules in physical association with *Potoniea krisiae* or *Hexagonocarpus* sp. in Sydney Coalfield. *Bedding planes with pinnules. **Pšenička et al. (2019). ***Zodrow et al. (2007, p. 60; 70-72), Hex. = Hexagonocarpus.*

| Accession No. (Fig.) | Coal Seam       | No. of Layers* | Sediment Separation | Biology of layers |
|----------------------|-----------------|---------------|---------------------|------------------|
|                      |                 |               |                     | *L. obliqua*     |
|                      |                 |               |                     | *P. krisiae*     |
|                      |                 |               |                     | *Hexagonocarpus* |
| Previous data:       |                 |               |                     |                  |
| 003-252              | Roof, 1 m to    | Single        | n.a.                | some             |
| 257 (2) and          | Lloyd Cove      | Specimen      |                     | 6                |
| 004-Z42(2D)**        |                 |               |                     | n.a.             |
| 003-325(3)**         | Roof, 1 m       | Single        | n.a.                | some             |
|                     | Lloyd Cove      | Specimen      |                     | 1                |
|                     |                 |               |                     | n.a.             |
| 05-Lat#0 (3)***      | Roof, 1-2 m     | 4?            | 4 cm                | very dense       |
|                     | Lloyd Cove      |               |                     | accumulation     |
|                     |                 |               |                     | rare              |
|                     |                 |               |                     | none              |
|                     |                 |               |                     | ca. 80            |
| Present data:        | Roof, Hub       | 2-3           | 1.5-2 cm            | very dense       |
| 08-10/15-9 (Plate II, A-H) | |               |                     | accumulation | 8 | none |
| Totals               |                 |               |                     |                  |
|                     |                 |               |                     | 15               |
|                     |                 |               |                     | > 80             |
RESULTS

Linopteris obliqua, state of occurrences and associations

The argillaceous-shaley slab (Plate I, Figs A, B) is fine-grained with dispersed sideritic cementation, millimeter bands of siderite, and scattered nodules (5 – 20 mm) of highly variable shapes (compare with Dolerotheca sp. in a sideritic nodule, Zodrow & Mastalerz 2019, fig. 2). The pristine preservation condition of the L. obliqua pinnules and the compound-synangial structures after 12 years of storage is correlated with the absence of pyrite and its destructive oxidative reaction on the compressions. Of palaeobiological significance are the occurrences of abscised L. obliqua pinnules separated by 1 – 2 mm of sedimentary layers throughout the shale slabs, although apparent also are 2 – 3 layers each composed of six or more stacked pinnules that are not separated by sediments. Casual pinnule counts in areas of about 10 × 10 cm may amount to as many as 100 pinnules from which the occurrence of perhaps thousands of pinnules/layer can be inferred. Although the vast majority of these pinnules settled parallel to the bedding planes, observed are instances where intact pinnules are oriented orthogonally to the bedding planes as if entombed on descent to a resting surface. Noted are rare ultimate sphenopteroid and pecopterid pinnae, and relatively abundant bare axes of unknown affinity to which the isolated rods (Plate II, Fig. E, near center) could be correlated (Zodrow & Mastalerz 2017, and references therein).

The areal extent over which abscised L. obliqua pinnules in the sample area are deposited in Pennsylvanian time in this part of the Cape Breton tropical forest could not be mapped because of rock coverage.

The significant observation from the specimen (Plate I, Figs A, B) is the consistent association of the L. obliqua pinnules with the compound-synangial structures, to the exclusion of any ovules.

The compound-synangial structures and their microspores

These compound-synangial structures are documented in Plate II. Striking are the decidedly different entombment positions: (1) Plate II, Fig. A, dorsal-ventral; (2) Plate II, Figs B – F lateral, showing the longitudinal groves; and (3) Plate II, Figs G – I, ventral. Figure C on Plate II clearly shows an eccentrically positioned, long, narrow (c. 0.3 mm) stalk. All specimens in Plate II are decidedly characterized by synangia that extend over the ventral campanulary margins. Remnants of the cap or shoulder ringing the dorsal portion of, as defined by Pšenička et al. (2019, fig. 3A, “PC”) for P. krisiae, are present in Plate II, Figs B – F, where the thick proximal cap is most clearly preserved in Plate II, Fig. B, arrowed.

The impression (Plate II, Fig. G) and the compression (Plate II, Fig. H), document the heretofore unknown part-counterpart preservation states of this compound-synangial structure from the Sydney Coalfield, and probably worldwide. The ventral preservation most likely delineates the campanulary margin most reliably in Plate II, Fig. G which would mean a near-rectangular ventral dimension of 17 × 10 mm. The synangia extending over the margins are most prominently visible (measurable in situ) in the top part of Plate II, Fig. I. Striking are the lateral preservation positions of the seven near-straight rows of synangia as if carefully “combed” into one direction, i.e., to the right in Plate II, Fig. G (or to the left in Plate II, Fig. H). Each of these rows is composed of approximately 26 – 30 synangial positions, where under microscopic examination each appears composed of three “stacked” synangia. This would amount to an estimated 600 sporangia.

Sporangia are approximately 1 – 1.4 mm long, slightly curved with a round tip (Plate III, Fig. F), and characterized by grooves running down the sporangial walls. In situ microspores are macerated from sporangia in Plate II, Fig. H. Microspores are circular, if not distorted, 60 – 83 μm in diameter, n = 11, with remnants of trilete marks, and an outer ring particularly well visible in Plate III, Fig. D. Ubisch bodies are presumably presented by the small protuberances on the microspores.

Comparison with Potoniea krisiae

Pšenička et al. (2019) detailed the taxonomic reasons for the erection of the species P. krisiae as a new taxon of the genus Potoniea Zeiller 1899 from the Canadian Sydney Coalfield. These authors also describe the process of deposition, the macromorphological attributes, and based on scanning electron microscopy, the micromorphological features.
Plate I *Linopteris obliqua* pinnules. Slab 08-10/15-9 (Fig. 1C, “X2”). A and B - Separated parts, where “1a and 1b” locate part/counterpart in Plate II, Figs G - I. A) scale bar = 50 mm, B) scale bar = 20 mm.
Plate II
Overall, the lateral macromorphology, even when disregarding the fragmentary states and consequently the inaccurate size measurements, the present specimens conform remarkably well to the specimens published by Pšenička et al. (2019). Comparable are also the quasi-rectangular ventral shapes (Plate II, Figs. G and H vs Pšenička et al. 2019, figs. 2A – 2C), dimensions of 17 × 10 mm for the present specimen in Plate II, Fig. G compared with 16 x 10 mm for P. krisiae (Pšenička et al. 2019, e.g. fig. 2C). Also, comparison of the lateral-preserved specimen between the present material and specimens published by Pšenička et al. (2019) are identical, where these structures are 5 mm high (Plate II, Fig. D vs Pšenička et al. 2019, fig. 3A). Even the sporangial dimensions are of similar size (2 – 5 mm long and c. 0.5 mm wide from Pšenička et al. 2019 vs 1.5 – 5 mm long and c. 0.5 mm wide from the present material). The slightly curved shape in the present ones, differing from the straight P. krisiae sporangia, is likely the result of differing preservation factors, alternative-

Plate II Potoniea krisiae specimens, Hub Seam, Fig. 1C. A - specimens 08-10/15-9-3; Scale bar = 2.5 mm. B - Arrow points to the campanulary cap. Specimen 08-10/15-9-5. Scale bar = 1 mm. C - Partially hidden stalk, arrowed. Specimen 08-10/15-9-6. Scale bar = 1 mm. D - Specimen 08-10/15-9-10; Scale bar = 2.5 mm. E - Arrow points to fragmentary specimen 08-10/15-9-9. Scale bar = 5 mm. F - Detail of (E). Scale bar = 2 mm. G - Impression (“1a”). Specimen 08-10/15-9-1a-3. Scale bar = 5 mm. H - Compression (“1b”). Specimen 08-10/15-9-1b-5. Scale bar = 5 mm. I - Detail of the top part of the compression (H). Scale bar = 2.5 mm.

Plate III Microspores from “1a and 1b”. A - Portion of a 1-mm macerated sporangium with in situ microspores and faintly preserved trilet markings. Inset (F) shows a 1.4 mm synangium. Scale bar = 0.5 mm. B to E - The sample-size range of microspores, where (D) with the trilet mark is the smallest, and (E) the largest sample spore with presumably Ubisch bodies. Scale bar for (B) to (E) = 50 μm. F - Photograph shows a 1.4 mm synangium. Scale bar 0.5 mm; Microslide documentation: 08-10/15-9-1b/2; 08-10/15-1b/1, and /2, respectively.
ly the result of compression orientation. Other nearly identical characters of the present material and of *P. krisiae* are as follows: Narrow stalks ec-

centrically inserted on the compound synangial

group (Plate II, Fig. C), presence of a significantly

thick proximal cap (e.g., Plate II, Fig. B), and free

sporangial tips extending from the distal organ

surface (Plate II, Fig. C).

In terms of microsporal comparison, the present

measurements of 60 – 83 μm diameter differ little

in size from the 40 – 83 μm diameter of the *Verru-
cosisporites* type of microspores of *P. krisiae*

(Pšenička et al. 2019, p. 5). The perceived differen-
ces in surficial ornamental structures on the *P. kri-
siae* and on the present microspores are likely

related to methods of scanning electron microscopy,

and to the white-light transmission microscopy,

respectively.

The presently described compound-synangial

structures are therefore deemed to conform suffi-
ciently well to *P. krisiae* Pšenička et al. (2019, fig. 6) to propose conspecifity, rather than erecting

a new taxon for *Potoniea* Zeiller.

**CONCLUDING REMARKS**

Documented are outstanding specimens with a large abundance of drop-off *Linopteris obliqua* foliage that exemplify what Bell (1938, p. 64) might have called “readily cadu-
cous”. The only other example of this phenomenon in the Sydney Coalfield are abscised pinnules of the seed-fern *Macroneuropteris scheuchzeri* (Hoff-
mann) that are found at times greatly concentrated

locally; see also the discussion by Laveine & Belhis

(2007, p. 33).

Emphasized is that all reproductive organs

(Table 2) are dispersed and are only observed

physically associated with abscised *L. obliqua*

pinnules. In particular, however, and as recorded in that table, the secured specimens of *Hexagono-
carpus* sp. (Zodrow 2002, fig. 16) vastly outnum-
ber those of *P. krisiae*. This is likely sampling bias, considering that the grooved fragmentary *P. krisiae*

resembles a fragmentary pinnule. Although strati-
graphically separated by 70 m of shaley lithology, 05-5-Lst#0 and 08-10/15-9 from the Lloyd Cove and the Hub Seams, respectively, are the only pub-
lished sources known to the authors that furnish
certain data for the far-reaching inferences arrived

at herein. First and foremost is that both *P. krisiae*

and *Hexagonocarpus* sp. are indubitably connected

with the *obliqua* plant, and secondly the brief

period of producing of male and females organs.

A hypothetical trigger for the latter is likely

ecological stress as discussed by Zodrow et al.

(2007), but an evolutionary development cannot be

ruled out, although hardly anything is known

about this aspect for pteridosperms. However, the

sampling evidence that male and female organs do

not occur together on the same bedding planes, are

not isochronous, leaves open the question as yet

dioecy or monoecy. Also unsettled is the ques-
tion of the attachment modes to the plant(s),

although a pinnate attachment is not ruled out

given the small dimensions of the organs (ca.

20-mm for the ovules); compare with the 12-mm

trigonocarpalean ovule pinnately attached (Zodrow

& McCandlish 1980).

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