TALL BEECH FERN

A new beech fern in New England, New York, and Canada

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This document is meant to be an aid to identification of *Phegopteris excelsior*, tall beech fern, which has recently been recognized as a new, but cryptic, species. As outlined below, evidence shows it is of hybrid origin, with half or even three quarters of its genome contributed by long beech fern and the rest by another beech fern species—but what (and where) that species may be, is yet unknown. Its resemblance to the long beech fern in its heritage means tall beech fern can be difficult to identify. My experience over the past 25 years, however, is that it can be field-identified—at least, if plants are relatively well-grown and robust. I have found it in approximately 15–20 locations, more or less evenly divided between central Maine and northern Vermont, where most of my field work has been done.

This guide is primarily visual, showing well-grown plants and giving some pointers on the diagnostic characters. Unfortunately, no completely unequivocal visual characters have emerged and only chromosome number and molecular markers are one hundred percent diagnostic. Nevertheless, avid pteridologists should be able to confidently identify a large majority of plants encountered, based on the images presented here.

I wish to thank Niki Patel and Susan Fawcett, my co-authors on the paper that formalized *P. excelsior*, with special thanks also extended to David Barrington and Heather Driscoll. These botanists accomplished laboratory work and data analysis far beyond my capabilities, which are mainly those of a field botanist. I thank Susan Fawcett again, for the providing the "shadow diagram" of basal pinnae on p. 6, Bertrand Black for the photograph on p. 15, and Michael Sundue for assistance with photographs of spores. The original discoverers of plants that became *P. excelsior*, the Canadian botanists Lionel Cinq-Mars, William Dore, and Gerald Mulligan, have all passed, but their insights provided the basis for this story and they deserve continued recognition for their accomplishment. Finding a new species is, in some ways, a creative process, and they had the imagination to see what *P. excelsior* might be. I also thank Niki, Susan, David, and Heather, as well as Alan Smith and Weston Testo, for helpful reviews, which much improved the ms. I would appreciate receiving information on any new populations of tall beech fern that may come to light, and any insights as to additional characters that may be useful for identification.

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Phegopteris excelsior N. R. Patel & A. V. Gilman, Novon 27(4): 214. 2019.

This is a tetraploid related to long beech fern (*Phegopteris connectilis*), which is triploid; evidence shows it is of hybrid origin with *P. connectilis* as one parent. The other parent is not known but it is not broad beech fern (*P. hexagonoptera*).

Both *Phegopteris connectilis* (in North America) and *P. excelsior* are apomictic species—they do not reproduce sexually. They do, however, produce abundant spores. Upon germination, spores grow into gametophytes, but the gametophytes do not produce eggs (sperm may be produced). So, there is no egg to be fertilized. Instead, a gametophyte simply organizes a shoot tip that grows into a next-generation, mature plant, the sporophyte, which then produces more spores. Thus, new plants are formed without sexual mixing, as they would be in populations of a normal, diploid species. Note, long beech fern does have a sexual, diploid race in the mountains of Japan but, as far as known, tall beech fern is only apomictic.

Long beech fern has a circumboreal distribution, with a gap in central North America and perhaps a gap in central Asia: it is common in northeastern and northwestern North America, Europe, and eastern Asia. As far as known to date, tall beech fern is restricted to northeastern North America—in the US, collections are known from Maine, New Hampshire, Vermont, Massachusetts and New York and, in Canada, it is recorded from Nova Scotia, New Brunswick, and Quebec Many collections are from central Maine, northern Vermont, and the Montregian Hills near Montreal. Broad beech fern is restricted to eastern North America and is a common species southward; it is a diploid.

The first collections of tall beech ferns were made in 1967 at Rougemont, near Montreal, by Cinq-Mars and his field companion, Lawrence Sherk. Specimens were thought to be broad beech fern, but it was shown by Dore and Mulligan at Ottawa that this was not the case—that they were, instead, apomictic tetraploids. Dore and Mulligan hypothesized a hybrid origin, between long beech fern and broad beech fern, but additional data has not supported that hypothesis—broad beech fern is not involved, as more recently and unequivocally shown by analyses of important metabolic enzymes, of chloroplast DNA, and of nuclear DNA. All these analyses show evidence of a hybrid origin, with long beech fern as one parent and an unidentified species as the other. With investigations extending from the 1970s through the 2010s, it was at length decided to name this new species and bring it to public attention.

Key to *Phegopteris* in Northeastern North America:

1) All pinnae connected by wings of green leaf-tissue along the rachis of the frond: note, especially, the two lowest pinna-pairs, which are connected along the rachis (in all beech ferns, all the other pairs are so connected, but not the basal two); lowermost pinnae wide, only ca. 3× as long as wide; spores 64/sporangium.
Broad beech fern, *P. hexagonoptera*

1) The basal two pinna-pairs not completely connected along the rachis; spores 32/sporangium.
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2) Clones/colonies fairly compact, often dense with overlapping fronds; fronds shorter; lowermost pinnae relatively wide (ca. 4× as long as wide) but not ever as wide as in broad beech fern; often strongly deflexed and projecting forward from the plane of the upper frond; the overall shape ovate with a long-acuminate tip; spores smaller, average <60µm. Long beech fern, *P. connectilis*

2) Clones/colonies often loose, fronds touching but not overlapping; fronds taller; lowermost pinnae relatively narrow (4.5× or 5× as long as wide); somewhat but not strongly deflexed and not projecting as far forward; overall blade shape deltate (triangular, but again with a long tip) and less rounded at bottom; spores larger, average >60µm. Tall beech fern, *P. excelsior*

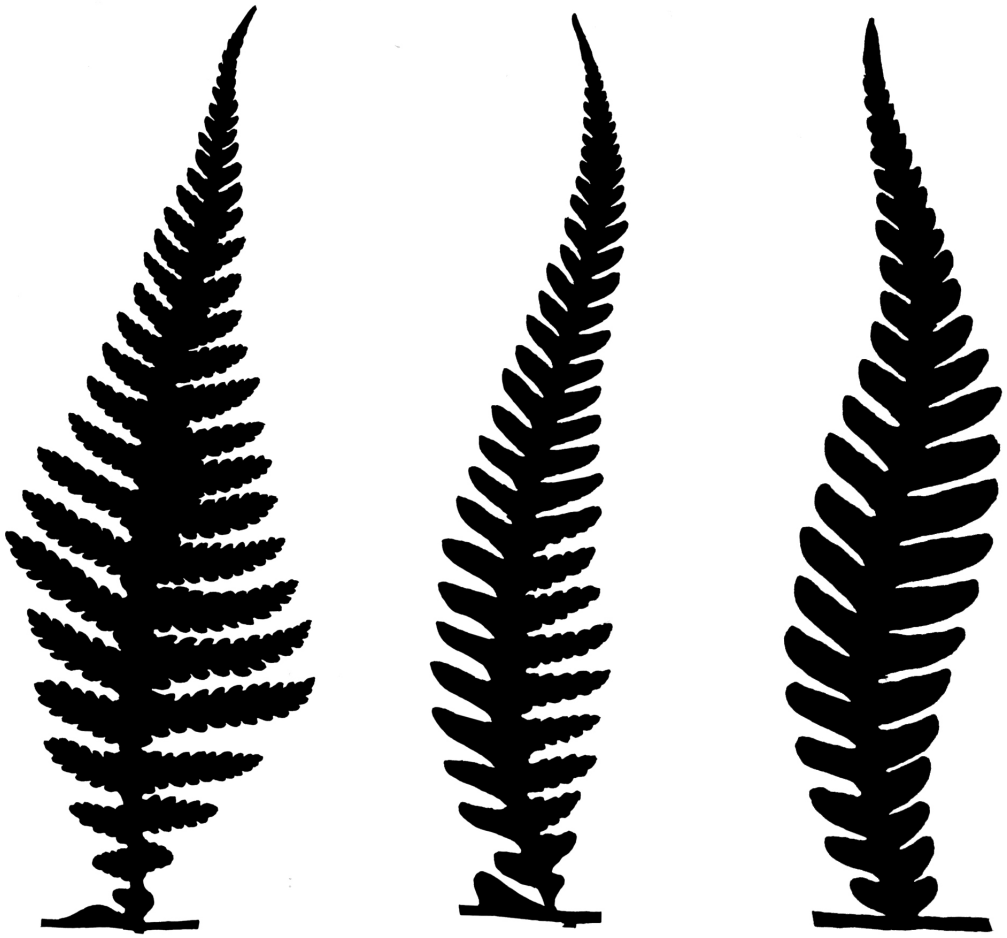
P. connectilis, 3x. Note the ovate (with a long tip) shape of the frond in the middle-right. Fronds often look quite "neat."

P. excelsior, 4x. A slightly more disheveled look to the overall colony.

P. excelsior, top row, and *P. connectilis*, bottom row. In the photos on this page, which compare typical fronds from colonies in the same habitat, note that *excelsior* fronds are typically 10%-20% larger than *connectilis* fronds.

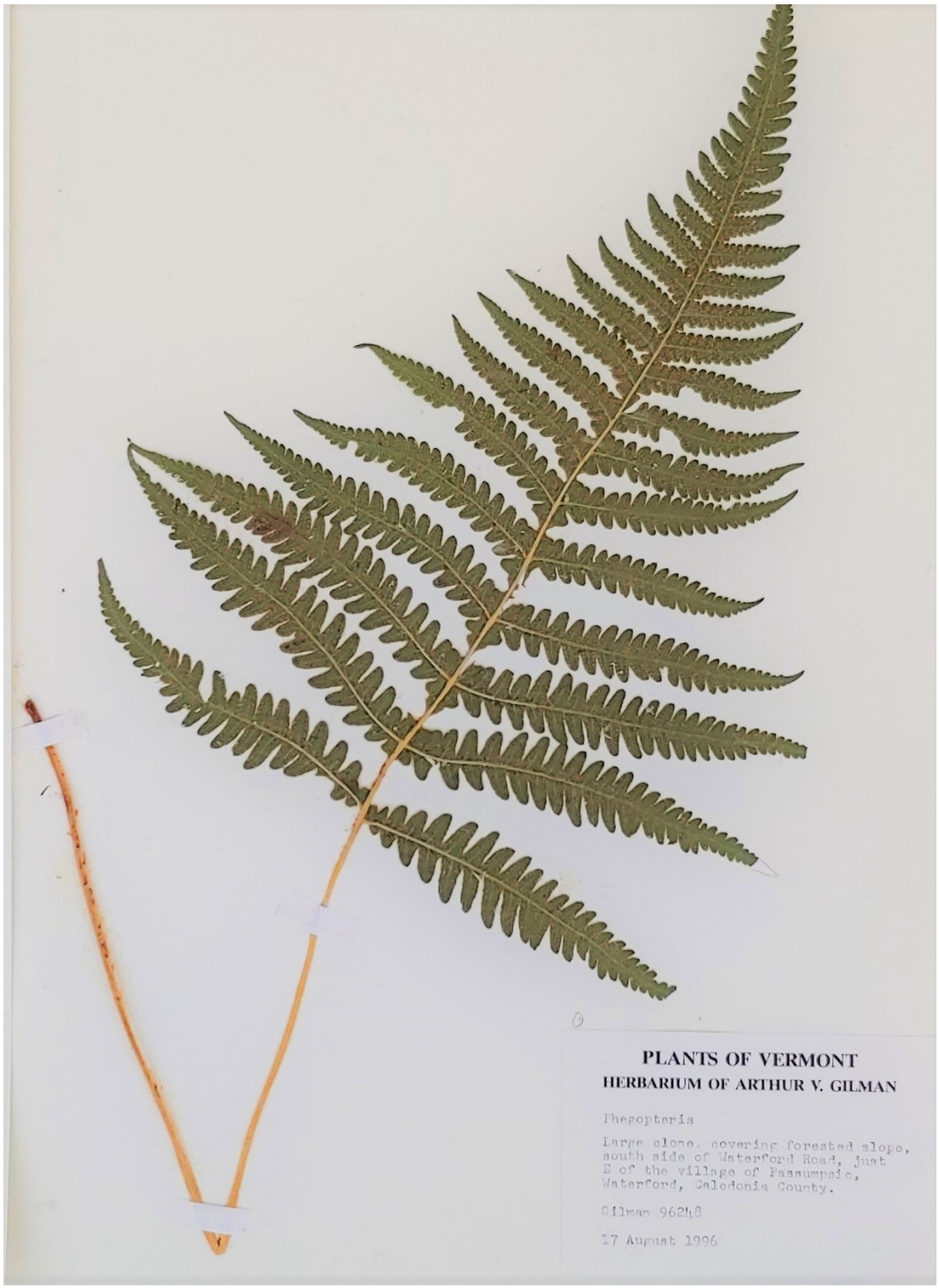
P. excelsior, left, and *P. connectilis*, right.

Phegopteris connectilis, left; *P. excelsior*, center; and *P. hexagonoptera*, right. This comparative photo shows pressed fronds. Again, note the ovate shape of *connectilis*, left, compared to the nearly deltate blade of *excelsior*, center. Although *excelsior* can be much larger than *connectilis*, and sometimes nearly as large as *hexagonoptera*, note how much narrower the basal pinnae are, especially in comparison to *hexagonoptera*. The individual images are given below.



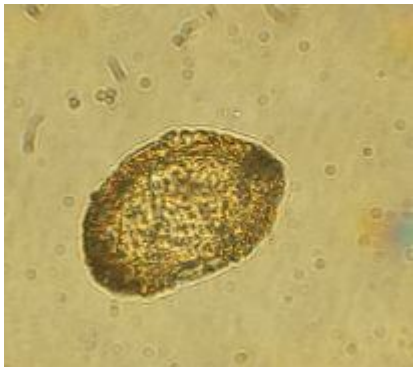
This shadow diagram shows a single proximal pinna (left to right) for *P. hexagonoptera*, *P. excelsior* and *P. connectilis*, scaled to emphasize the difference in shape. Illustration by Susan Fawcett.

Phegopteris connectilis.

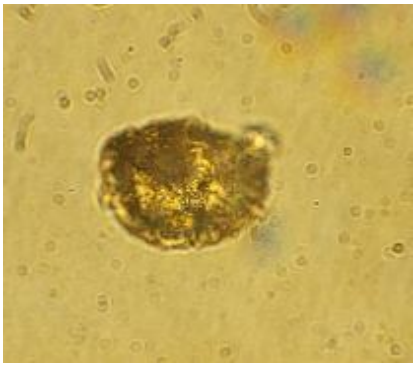


Phegopteris excelsior. In this photo, the gap between the two lowest two pinna-pairs is evident. In some individuals, it is partially filled by "wings" from the second pinnae pair coming down along the rachis, but this gap is always present—compare with the photo of *P. hexagonoptera*. Overall, large fronds of *P. excelsior* seem not to "fill the plane" as fully as *P. connectilis*, i.e., there is more space between the pinnae.

Phegopteris hexagonoptera. Note that a "wing" of green tissue extends along the rachis between the lowest two pinna-pairs. This may be narrow, perhaps only a few cells wide at the narrowest point, but it is always present. (What appears as a gap between the 2nd and 3rd pinna-pairs is a strip of white linen tape used in mounting this specimen.) The overall frond shape is deltate, or, if the basal pinnae are extra wide, as they occasionally may be, almost pentagonal.



P. excelsior spore (from an isotype). Length averages > 60µm.



P. connectilis spore. Length averages <60 µm. These two photos were taken at the same scale.

The spores of *P. excelsior* were measured by Mulligan et al. (1972, see additional reading), and also by Patel et al. (2019). Both found that they are significantly larger than those of *P. connectilis*, while those of *P. hexagonoptera* are significantly smaller than either. Spore size in many ferns (but not all, e.g. some *Asplenium*) is generally related to ploidy, with larger spores found in species that have higher ploidies. This pattern is found in this group, with tetraploid *P. excelsior* having larger spores than triploid *P. connectilis*. Diploid *P. connectilis* (from Japan) has spores that are smaller still—approximately the same size as those of the diploid *P. hexagonoptera* (e.g.,Honshu: *Boufford 23464 & Shimizu*, A!, length ca. 42 µm). The range of sizes can be quite wide within a species, so it is important to sample at least ten spores to get an average.

Phegopteris excelsior in Caledonia County, VT. Associated plants are *Thuja occidentalis*, *Aralia nudicaulis*, and *Carex pedunculata.* Habitat is mesic.

Phegopteris excelsior, a colony in Androscoggin County, Maine. Note the large size of the calf-high fronds.

P. excelsior, a colony in Chittenden County, VT. This colony covered a steep ravine slope on sandy soil, in a hemlock forest above a seasonal stream.

P. excelsior, from the colony in Chittenden County, VT. Again, note the large size—the fronds a hand-span wide and long.

This photograph shows the large size that fronds can achieve, and the often “loose” nature of the clones. Photograph of the author by Bertrand Black.

Additional Reading:

1972: **Mulligan**, **G. A., L. Cinq-Mars & W. J. Cody.** Natural interspecific hybridization between sexual and apogamous species of *Phegopteris* Fée. Canad. J. Bot. 50: 1295–1300.

Discovery of the tetraploid at Rougement, QC, and chromosome investigations at Ottawa. It is demonstrated that the tetraploid is apomictic (reproducing asexually), as is P. connectilis. The hypothesis is made that it is a hybrid derived from a cross of a triploid egg from P. connectilis and a haploid sperm from P. hexagonoptera, a diploid sexual species that is rare in Canada but present in the Rougement area.

1979: **Mulligan, G. A. & W. J. Cody.** Chromosome numbers in Canadian *Phegopteris*. Canad. J. Bot. 57: 1815–1819.

Additional populations found, extending the range from Quebec to Nova Scotia, even though P. hexagonoptera is not known from that region. The recommendation is made that, although of hybrid origin, it should be treated within P. connectilis because it is cryptic and hard to detect.

2003: **Driscoll, H. E., D. S. Barrington & A. V. Gilman.** A reexamination of the apogamous tetraploid *Phegopteris* (Thelypteridaceae) from northeastern North America. Rhodora 105: 309–321.

Following discovery of large-frond plants in Vermont, investigations of metabolic enzymes (isozymes) are conducted and a morphometric analysis is undertaken. This re-examination concludes that it is a hybrid, but that P. hexagonoptera is likely not involved.

2016: **Grusz, A.** A current perspective on apomixis in ferns. J. Syst. Evol. 54(6): 656–665.

Review of the mechanisms and consequences of apomixis in ferns.

2018: **Patel, N. R.** Apomixis, Hybridization, and Biodiversity in Ferns: Insights from Genera *Phegopteris* and *Polystichum*. Ph.D. Thesis, University of Vermont, Burlington.

Using molecular data—nuclear and chloroplast DNA—it is again demonstrated that the tetraploid is of hybrid origin, and that P. connectilis is probably one parent. However, the other parent could not be identified.

2018: **Hörandl, E.** The classification of asexual organisms: old myths, new facts, and a novel pluralistic approach. Taxon 67(6): 1066–1081.

Taxonomic treatment of asexual, apomictic species receives much discussion through the 2010s by Hörandl and others who work with "difficult" taxa. This article advocates for treatment of entities as species, not as varieties, and not in informal categories such as "microspecies."

2019: **Patel N. R., S. Fawcett & A. V. Gilman.** *Phegopteris excelsior* (Thelypteridaceae): A new species of North American tetraploid beech fern. Novon 27(4): 211–218.

Phegopteris excelsior is formally described, named, and illustrated. Specimens in regional herbaria are listed, and a range map is given showing distribution in NS, NB, QC, ME, NH, VT, MA, CT, and NY. A Principal Components Analysis (PCA) is given, which shows that excelsior is generally intermediate between P. connectilis and P. hexagonoptera, but authors suggest that this results mostly from gross characters such as size, number of pinnae, etc., which might also indicate that the unknown parent is a large-frond plant, like P. hexagonoptera.