We have the receipt of fern-seed, we walk invisible.
Henry IV, Shakespeare

Natural History of Ferns

For many centuries in modern human history, naturalists have puzzled over the reproductive biology of ferns. Even though the fern lineage is among the oldest for vascular land plants, naturalists such as Linneaus tried desperately to find the missing seed of ferns. To Shakespeare and other Elizabethans, the seed of the fern was unknown and to have the recipe for the fern seed was to walk under the cloak of invisibility. The dust-like powder released from fern leaves was equated to pollen of flowering plants. Where pollen is the sperm transportation vehicle of flowering plants, the fern dust was the precursor for an alternate, alien, generation.

My prior employment in the nursery business led to the realization that most modern humans have no insight to fern natural history. We expect homeowners to bring in their fern fronds once those regularly place spots on the leaves appeared. Most believed they were evidence of insect pest and none expected that they were just part of the life cycle.

Ferns preceded dinosaurs in the history of the Earth. The ancestors of ferns began their initial diversification on land some 300 million years ago. While dinosaurs began their domination of the animal world 200 million years ago, it was ferns that reigned for land plants. It is estimated that at least half of the terrestrial forest of dinosaurian times was dominated by tree sized ferns, horsetails, and clubmosses. The sunlight captured by these plants over millions of years was used to generate energy-rich organic molecules as with modern plants. Fortunately, or unfortunately, for modern humans, the trapped organics of these ancient fern forests formed the fossil fuels of today. Unlike dinosaurs, ferns survived the catastrophe asteroid impact of 65 million years. In fact, palynological data in the early tertiary suggest that ferns were initially more abundant and may have recolonized land following the impact.

The diversification of modern fern families occurred between 65 and 100 million years ago. The insect lineage is nearly as old as ferns, but its diversification into modern orders and families occurred as early as 270 million years ago. Flowering plant fossils date to 132 million years, but modern molecular estimates place the origin of the group between 140-180 million years ago. Despite the early arrival of ferns and insects, there are relatively few good examples of insect-fern relationships and interactions as compared to flowering plants and insects. Ferns appear to be largely untouched by herbivorous insects and even mammals.

Fern species have a rich evolutionary history. Molecular and genetic evidence supports the hypothesis that some North American species have evolved in recent, post-glacial, millennia (e.g. log fern, *Dryopteris celsa*). Modern analysis have also shown that some species have multiple, independent origins (e.g., *Asplenium bradleyi* and *Asplenium pinnatifidum*). In addition, hybridization and polyploidy have been hard at work in this group of land plants by reshuffling genes, and providing immediate reproductive isolation creating new species. These evolutionary processes have been at work creating complex relationships that represent a web of life more than a tree of life. These reticulate webs are seen in common fern genera such as wood ferns (*Dryopteris*), spleenworts, (*Asplenium*), and bulblet ferns (*Cystopteris*).
The spleenworts provide an exceptional example of reticulate evolution (Figure ASPLENIUM EVOLUTION). The relationships between the three progenitor diploid species and their hybrid, tetraploid species are well-documented by morphology, karyotypes, and molecular data. *Asplenium bradleyi* is the tetraploid hybrid offspring species between two common species, *A. montanum* and *A. platyneuron*. These parental species have chromosome numbers of 72 and *A. bradleyi* has 144. *Asplenium bradleyi* as a polyploidy is fertile and has intermediate frond morphology between its progenitor species. Sterile diploid hybrids are common where the two progenitors occur. In a molecular examination of the origins of polyploidy *A. bradleyi* in Arkansas, Virginia, North Carolina, and Missouri, Charlie Werth was able to identify at least three independent origins for the polyploid species *A. bradleyi*. While these patterns of reticulate evolution and multiple origins of species may be uncommon in other groups of organisms, they have provided many interesting avenues of evolutionary research in ferns.

Even though fern evolution is contemporary phenomenon, some common fern species are very old. Interrupted fern and sensitive fern are two species that are well-represented in the fossil record. Fossils of interrupted fern indicate it was common on both Antarctica and North America some 200 million years ago and it probably arose while all continents were interconnected as Pangaea (250 million years). Sensitive fern is an Arcto-tertiary relict and is currently found in eastern Asia and eastern North America. Fossil evidence from 55 million years ago indicates this species was once abundant across North America and Asia as well as Greenland.

During the early Tertiary period between 38-55 million years ago, a warm and humid planet encouraged the expansion of temperate and tropical forests. The temperate forests moved northward into Greenland and subpolar regions. The forests were continuous across the Bering land bridge into Europe and Asia and persisted for millions of years. As the planet cooled and dried, deciduous forests retreated below 45ºN latitude but the fragmented forests retained similarities between Eastern Asia, Europe, Western North America, and Eastern North America. When one travels from eastern North America to eastern Asia it is easy to see and feel the similarities in the forest. Asian forests have retained the same or similar species of Magnolia and Tulip poplar as well as many forest herbs such as *Trillium* and *Aquilegia*, and several groups of fern such as sensitive, interrupted, and maidenhair fern. These similarities in diversity support the hypotheses from geological data that North American and Eurasian continents were once interconnected and that the planet has undergone other bouts of global climate change.

We find and expect ferns in moist, humid forests of temperate and tropical zones. Ferns do have roots, stems, and leaves (i.e., fronds) with vascular tissue, and are very capable of transporting water throughout the plant. The fronds have pores and cuticle to protect from desiccation. So, why don’t ferns grow in open areas. Ferns transplanted to open areas can survive, although their fronds may be sun bleached. Royal fern leaves the forest and proliferates along streams and rivers with rich organic sediment and moist shorelines. Ferns are among the first to colonize volcanic slopes in the Hawaiian archipelago. Bracken fern is often found growing across fields throughout North America. Bracken fern escapes forests by way of
underground rhizomes. In addition, bracken does have a higher degree of toughness than many other ferns and withstands drought and heat.

Most ferns are relegated to forest by way of moisture requirements for sexual reproduction. The alternate generation of the fern is produced by the dust-like spores that puzzled Linnaeus. Spores germinate and produce a thin, heart-shaped plant that is, for most species, no bigger than a typewritten “o” on this page. In nature, these gametophyte plants are difficult to find and really require diligence of those who search for them. The gametophyte is the gamete producing generation (Figure Fern Development). It is short-lived, but responsible for producing sperm and eggs in separate structure. Fertilization is accomplished by motile sperm tracking chemical trail to the egg-producing structure. The resulting zygote and embryo grows and develops into the large, robust spore-producing plant, (i.e., sporophyte) that we quickly recognize as a fern. For many ferns, it is the delicate situation of relying on a thin, flimsy gametophyte and free swimming sperm in need of a thin water film for reproduction that restrict them to the moist shade of forests.

The biology of ferns is alien to nearly all, and terminology used to describe the morphology and anatomy is not very user friendly. Instead of leaves ferns have megaphylls called fronds. There are dimorphic and monomorphic fern species. Fronds may be divided once, twice, thrice or more into pinnules of different size and shape that may be described as pinnate, pinnatifid, pinnate-pinnatifid, bipinnatifid, bipinnate, or tripinnate. Ferns may be leptosporiate or eusporiate. For a pteridologist, these terms describe conditions that enable proper description and identification of fern species. For an amateur naturalist, these descriptions are a high hurdle to enjoying ferns.

Nevertheless, some basic nomenclature is necessary to identify and at least discuss ferns. Contrary to popular belief, all ferns do have stems. In the temperate zone, most fern stems or rhizomes lie horizontally along the surface of the ground others are short and vertical. The rhizome may appear bristly and course with scales and former attachment sites of fronds and roots. The tip of the rhizome produces new fronds that develop as coiled fronds called fiddleheads that unroll and expand in three dimensions to form the frond (Figure FERN FIDDLEHEAD). The growth of the fiddlehead into a frond is due to unequal cell growth on lower and upper frond surfaces. Cells on the upper surface increase in length faster and allow the frond to unroll in a highly controlled and predictable manner.

Fronds are attached to the rhizome by a stipe which is the equivalent to a leaf stalk or petiole. The stipe becomes the rachis at the blade. The plumbing tissue of fern fronds is packaged into veins and vascular bundles in the blade and stipe/rachis respectively. The number and shape of vascular bundles on a stipe cross section is a useful trait for describing and identifying many of the common north temperate ferns.

Fern dissection is one of the more difficult concepts to grasp and master for naturalists. Frond dissection refers to the complexity or laciness of the leaf. Although we tend to describe
the degree of laciness as though there were discrete differences between categories, in reality the degree of dissection represents a continuum. The simplest frond form would be a simple, undissected frond. This frond type is common to a difficult to find and identify group of ferns called Ophioglossum (Figure FERN DISSECTION).

Assume that we can different frond styles simply by making similar cuts into the blade. If a simple blade was cut along the surface from the edge toward the rachis with little sections of green removed, then a “once-cut” frond is formed. In our flora, maidenhair spleenwort, rock and Christmas ferns are the best examples of a once-cut frond. A “twice-cut” frond is made by taking each remaining green section on a once-cut frond and once again making similar cuts along the length of edge towards the vein in each leaflet. Silvery glade, New York, cinnamon, and interrupted ferns are excellent examples of ferns with twice-cut fronds. Similarly, a thrice-cut frond is constructed by further cutting the smallest unit of twice-cut frond. Royal, bracken, lady, hay-scented, and evergreen wood ferns are solid examples of thrice-cut leaves.

Ferns vary in their habit or growth form. Rhizomes are capable of substantial growth and branching to produce large three dimensional plants. Several ferns appear to run along the ground and, indeed, they do have vigorous rhizomes. Hay-scented, interrupted, New York, sensitive and bracken fern tend toward this weedy attribute. All of these species have the capability of form large beds of uniform sized ferns along the forest floor. For simplicity sake, I refer to these ferns as runners. The wood ferns, cinnamon fern, and lady fern form nice, discrete clumps. Although I like to refer to this as a “vase-habit”, clump forming ferns work just as well.

The number and shape of vascular bundles in the cut stipe provide another trait that helps greatly with identification (Figure FERN VASCULAR BUNDLES). When the stipe is cut near the rhizome, the vascular bundles are easily seen in the cut cross-section. There are four common vascular bundle forms seen in our ferns. Lady fern and its relatives have two, strap-like, vascular bundles oriented at an angle from each other. Hay-scented, cinnamon, and interrupted ferns have horseshoe-shaped vascular bundles. The ends of the horseshoe form a little curl on these species. The two preceding vascular bundle conditions are most common in our ferns. The wood ferns have a ring of a few (five or so) small, circular vascular bundles. Bracken fern has numerous, round vascular bundles scattered across the cut surface of the stipe.

Spores are produced in small, stalked structures (i.e., sporangia) on fertile fronds (Figure FROND FORM). Species with strongly dimorphic fronds will have photosynthetic, sterile fronds, and brownish, non-photosynthetic fronds. Ostrich, cinnamon, and sensitive fern exemplify this concept. In ferns with monomorphic
fronds, both sterile and fertile fronds are identical with the exception of the presence or absence of spore producing structures. New York, and hay-scented fern are monomorphic. Many ferns are intermediate between these two extremes. For example, the sterile and fertile fronds of Christmas fern are photosynthetic and similar in structure, although the fertile fronds are more elongate and have smaller terminal pinnae that bear the sporangia.

Sporangia are clustered into discrete populations called sori (sing. sorus) (Figure FERN SORI). In most ferns the sorus has a thin protective cap called an indusium. Together the sorus and indusium have a shape that is characteristic of the fern. In lady fern and other members of the genus Athyrium the sorus is crescent shaped. Wood ferns often have rounded to kidney shaped sori, and hay-scented fern has unusual cup-shaped sori surrounding the sporangia. Bracken and maidenhair ferns lack discrete sori and instead have sporangia lining the margin on the lower frond surface. The polypody ferns have nice rounded sori, but lack the indusium altogether.

Each sporangium has a single layered line of cells that stretches around two-thirds of its circumference called an annulus. The lateral and interior cell walls of the annulus are thickened. As water evaporates through the thin outer cell wall, the annulus folds back upon itself exposing the spores. The cell walls are pulled together because water had strong adhesive affinities for organic molecules such as cellulose and lignin. Water molecules are also strongly cohesive. As the annular cells dry, water stretches like an elastic band and pulls the lateral walls of the cell toward one another. The annulus folds back upon itself until the thin band of water cavitates or snaps. The sporangium acts like a trebuchet when the annulus snaps back into place catapulting spores away and into the air (See Fern Development). The process is easy to observe using dissecting microscopes by drying sporangia with lights. As spores jump from the microscope stage, one can see dust-like particles flying through the light. This mechanism is very effective as fern spores are carried great distances from the plant and may even drift to great heights in the atmosphere.

Ostrich and bracken ferns are common ferns worthy of additional discussion. Both species have historically been used as food in the Northeast. However, bracken fern should be totally avoided as a natural food and ostrich fern has been identified as a probably suspect in some food poisonings.

Bracken fern has several natural toxins and at least one known carcinogen. The fern is widespread over all continents with the exception of Antarctica. Short term ingestion, two to four weeks, of bracken can lead to potentially lethal vitamin B deficiency. The fern produces the enzyme thiaminase and the enzyme readily degrades vitamin B following ingestion of the fern. Lethal bracken poisoning has been well-documented in domesticated cows, horses, and sheep. Bracken also produces ptquiloside (PTQ) which has been attributed to esophageal and gastric cancers in farm animals and humans. Asians have historically eaten bracken fern fiddleheads and the fern is believed to contribute to elevated cancers in this region. PTQ is water soluble and can contaminate water wells in sandy soils where bracken fern is abundant. Bracken fern is an unmistakable common in fields and forests. It has a large broadly triangular blade that bends to become parallel to the ground. Bracken sporangia are found along the blade edges and are protected under a thin stretch of marginal tissue.
Ostrich fern is common along rivers, streams and in wet fields throughout northern United States and southern Canada. Ostrich fern sterile fronds are tall with broad rounded ends except for an abrupt nipple-like tip. Fertile fronds are dark brown with beads along shortened stalks near the rachis. Ostrich fern fiddleheads have a long history of safe use as a cooked vegetable in these regions. It is easy to collect in the spring and can be found in natural food groceries as a canned or fresh frozen vegetable. In 1994, the Centers for Disease Control documented a series of food poisonings in western Canada and New York State where ostrich fern was the suspect. The poisonings occurred at restaurants and the ferns could not be attributed to a single source or distributor. The CDC investigation suspected that the poisonings occurred following ingestion of raw or undercooked fiddleheads. Although the secondary chemistry of ostrich fern has not been investigated, it may possess heat labile toxins that breakdown when cooked properly. I, and many students, have safely eaten freshly collected and cooked ostrich fern fiddleheads. The vegetable is a bit stringy and has a strong taste reminiscent of green beans or asparagus.

http://www.cdc.gov/mmwr/preview/mmwrhtml/00032588.htm
http://www.ars.usda.gov/Services/docs.htm?docid=9859


Common Ferns
Ostrich Fern (Matteuccia struthiopteris)
Christmas (Polystichum acrostichoides)
Sensitive (Onoclea sensibilis)
Marginal Wood (Dryopteris marginalis)
Evergreen Wood (Dryopteris intermedia)
Maidenhair (Adiantum pedatum)
Cinnamon (Osmunda cinnamomea)
Interrupted (Osmunda claytoniana)
Royal (Osmunda regalis)
Silvery Glade (Deparia acrostichoides)
Hay-scented (Dennstaedtia punctiloba)
New York (Thelypteris novaboracensis). Common woodland fern with nearly identical sterile and fertile fronds. Pinnae taper towards the base and tip along a smooth rachis. Twice dissected Lady (Athyrium felix-femina)
Bulblet (Cystopteris bulbifera)
Bracken (Pteridium aquilinum var. )
Oak (Gymnocarpium dryopteris)
Ebony Spleenwort (Asplenium platyneuron)
Walking Spleenwort (Asplenium rhizophyllum)
Maidenhair Spleenwort (Asplenium trichomanes)
Brittle Bladderfern
Upland Brittle Bladderfern
Purple Cliff Brake (Pellea atropurpurea)
Recurring Origins of Allopolyploid Species in Asplenium
Author(s): Charles R. Werth, Sheldon I. Guttman, W. Hardy Eshbaugh

Electrophoretic Evidence of Reticulate Evolution in the Appalachian Asplenium Complex
Author(s): Charles R. Werth, Sheldon I. Guttman, W. Hardy Eshbaugh

**Fig. 1.** Relationships in the Appalachian *Asplenium* complex (adapted from Wagner 1954).