Topic #10: Gymnosperms

REQUIREMENTS: Powerpoint Presentations

Objectives

1. Define gymnosperm. What does the name angiosperm imply?
2. Do gymnosperms have flagellated sperm? Some? All? If sperm are flagellated, do they swim externally?
3. Draw the life cycle of pine. How is the male gametophyte delivered to the female cone? What is pollination? Is gymnosperm pollination specifically by certain vectors (e.g., insects; ignore minor exceptions)? Does the female gametophyte form an archegonium? (What is an archegonium?) Does double-fertilization occur? If not, how do the events surrounding fertilization resemble that process?
4. Discuss several advances that are seen in gymnosperms.
5. Do seedless plants typically have a bifacial vascular cambium (i.e., that which gives rise to secondary growth)? Gymnosperms? Typically? Angiosperms? All?
6. Draw a gymnosperm seed. Name three ways it differs from an angiosperm seed. (Hint: endosperm, number of cotyledons, size of female gametophyte.)
7. Describe the general appearance of a cycad. The ginkgo tree. *Welwitschia* (a member of the Gnetophyta).

Lecture

Phylogenetic Orientation

POWERPOINT SLIDES: Phylogenetic orientation with a focus on evolution of traits that distinguish the groups and make the advanced forms more adapted to a terrestrial lifestyle. (This series should be used to complement the phylogenetic orientation given at the beginning of the previous topic.)

Our approach to the gymnosperms (about 700 living species) is going to be similar to that taken with the ferns and fern allies, viz., we will focus on one group, the conifers, and just "survey" three

others. The other three taxa are essentially "miscellaneous"[1] and will be used only sparingly as examples of evolutionary advances. Therefore, no master table follows this topic.

(A) Cycadophyta (cycads).

(B) Ginkgophyta (ginkgo; plural, ginkgoes; variant spelling, also correct,[2] gingko).

(C) Gnetophyta[3] (vessel-containing gymnosperms).

(D) Coniferophyta (conifers).

Evolutionary Advances of Gymnosperms

Gymnosperm is a "catch-all" term for seed plants that do not produce flowers. The first three groups (above) will be covered rather superficially. Then, the course will be concluded with the life cycle of pine.

The following advances are seen in gymnosperms:

(A) Loss of sperm mobility. In the conifers and Gnetales, the sperm are not flagellated; in cycads and ginkgo, sperm are multiflagellated, but

(B) development of pollen grains (partially developed male gametophytes) has freed even these from the need for liquid water for fertilization. Typically the pollen is wind dispersed, and the sperm arrive at the ovule (after the pollen grain arrives at the structure containing it) not by swimming but through an outgrowth of the male gametophyte, the pollen tube.[4] Thus, even in ginkgo and cycads (both of which have flagellated sperm), the presence of external liquid water is not required. In algae generally and in bryophytes, liquid water is required for gamete transfer. In the ferns and their allies,

---

[1]Textbook revision: The gymnosperms have a monophyletic origin. Earlier, the Gnetales, which have some angiosperm-like traits (e.g., vessels), were believed to be allied to the angiosperms, but modern molecular analysis shows them to be related to pines and other conifers. *Ginkgo* is more distantly related, and the cycads are further yet removed. BUT all the gymnosperms have a common ancestor that none of the angiosperms share. See *Trends in Plant Science* 5: 330 (2000).

[2]G. H. M. Lawrence, erstwhile professor at Cornell, tells us (in *Taxonomy of Vascular Plants*, The MacMillan Company, 1951): "Several scholars (. . .) have shown that etymologically the name *Ginkgo* is an orthographic error and that the correct translation of the Chinese characters used to designate the maidenhir tree should be 'Ginkyo'. The error originated . . . in 1712 and was introduced into formal botanical nomenclature by Linnaeus in 1771."

Deni Brown (*Encyclopedia of Herbs and Their Uses*, The Herb Society of America, Dorling Kindersley, 1995) gives us a slightly different version, saying that the name is derived from Japanese (*gin* = silver and *kyo* = apricot).

[3]Gnetophyta is also angiosperm-like in having nectaries (extra-floral, of course, since gymnosperms lack flowers). A bigger surprise is that some ferns also have nectaries. (D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle, *Ecological Communities: Conceptual Issues and the Evidence.* Princeton University Press, Princeton, N.J.)

[4]The pollen tube probably developed as a haustorium ("root") through which the male gametophyte (pollen grain) parasitized the ovule. Thus, the pollen grain received nutrition and then released swimming sperm. In the

the sperm are flagellated, but archegonia and antheridia are at or below ground level and generally very close together. Some gymnosperms retain sperm motility, but swimming is internal. Angiosperms do not have flagellated male gametes.

(C) Usually, ferns and other extant non-seed-bearing plants lack well-developed vascular cambia (which give rise to secondary growth). Therefore, in general, secondary xylem and phloem are found in greater quantities in gymnosperms than in ferns and their allies. Except for cycads (which superficially resemble palms), secondary growth is pronounced in gymnosperms. Even in cycads, secondary growth is present, albeit sluggish.

(D) The gametophyte generation is further reduced. As implied above, gymnosperms are heterosporous. In general, the male gametophyte (pollen grain) is transferred to the vicinity of the ovule. There, the male gametophyte absorbs nutrition. The female gametophyte (developing from a megaspore and containing perhaps 2000 nuclei) is retained on the parent sporophyte. As a result of the reduction of the haploid generation, antheridia, and in some cases archegonia, are absent.

(E) Seed development, as stressed before, was an important evolutionary advance. As mentioned, seeds can be disseminated widely and by various mechanisms (e.g., in water, like coconuts; by animals, like cocklebur; by wind, like maple). Nonseed plants can also be disseminated by spore movement or migration of fragments. Spores are easily and widely distributed, and nonseed plants tend to be "everywhere," whereas seed plants may evolve distinct populations or species in localized areas. Of course, the seed also carries a large nutrition packet, is protected well by the seed coat, and has evolved means to time germination with conditions favorable for growth.

As a matter of redundancy, evolution of the seed is traceable: homospory $\rightarrow$ heterospory; diminution of gametophytic stage of life cycle; isogamy $\rightarrow$ oogamy; retention of megaspore within sporophyte (the megasporangium is the nucellus and participates in seed formation); complete development of female gametophyte within sporophyte, germination and growth of the female gametophyte within the megaspore wall.

POWERPOINT SLIDES: A review of traits required for seed evolution.

POWERPOINT SLIDE: Angiosperm seed types (Figs. 61 and 62 of Porter).

By way of review, the angiosperm seed—at least at some time—contains endosperm. This feature is diagnostic. The embryo has one or two cotyledons. Typically (but not on this diagram), the monocot seed reserve is stored in endosperm, whereas the dicot seed reserve is in the cotyledon.

---

end, the pollen tube has evolved a secondary function—delivery of sperm—and in conifers and some other gymnosperms, the male gametes lost motility.

POWERPOINT SLIDE: Pine seed and seedling (Fig. 15.21 of Ritchie and Carola).

In contrast, the remains of the female gametophyte supply nutrition to the germinating gymnosperm embryo. The cotyledons are numerous. (The presence of more than two cotyledons in the conifers is to be contrasted with the presence of two cotyledons in other gymnosperms.)

Gymnosperm Photogallery

Cycadophyta

POWERPOINT SLIDE: Cycad (Kirstenbosch National Botanical Garden, Republic of South Africa).

POWERPOINT SLIDE: *Zamia*, a native Florida cycad (Florida Governor's mansion).

Numerous imported cycads grow on campus; they are diminutive palm-like trees with dark green foliage.

Cycads are tropical and subtropical; they comprise about 10 genera and 100 species. They are usually large (compared to our native *Zamia*, but still reach only small tree-like proportions, 15–20 feet tall). Secondary growth is present but sluggish (and cycads are therefore smaller than familiar gymnosperms such as pine). The seed-bearing megasporophylls are arranged in a cone. All species are "dioecious" (that is, microspores and megaspores are produced on different plants[5]). The sperm are motile.

Ginkgophyta[6]

Only one species survives, and it may no longer be found in the wild.

POWERPOINT SLIDE: Herbarium sample of *Ginkgo* (National Herbarium, Beijing).

---

[5]Recall, again, that the term "dioecious" is used differently by different authors; some restrict it to flowering plants.

[6]As we have mentioned earlier, some evidence indicates that extracts of *Ginkgo* improve memory, but only to the extent that a candy bar does. (See *Scientific American* 288(4): 89–91 (2003).)

POWERPOINT SLIDE: Dr. Chen points to the single repository of *Gingko* before its horticultural dissemination (National Herbarium, Beijing).

Ginkgo is a dioecious tree. Female trees produce fleshy seeds that superficially resemble pale cherries (they are not, of course, true fruits, which are produced only by angiosperms). It is widely used as an ornamental, but only male trees are propagated (the seeds are messy and abundant and contain butyric acid, a rancid-smelling substance).

POWERPOINT SLIDE: Ginkgo "fruit."

Secondary growth is present and abundant. Sperm are large (about 180 μm) and multiflagellated (>20,000 flagella!).

Gnetophyta

The Gnetophyta consist of three genera, quite different from each other. The sperm are not motile. The Gnetophyta have vessels (as mentioned, an exception to the generality that gymnosperms lack vessels).

POWERPOINT SLIDE: *Welwitschia* (Fig. 21-13c of Curtis and Barnes).

POWERPOINT SLIDE: *Ephedra* (Missouri Botanical Garden).

As was discussed early in this course, double fertilization and the associated formation of the usually triploid endosperm are considered unique and defining features of flowering plants. *Ephedra* is a nonflowering plant that resembles in some ways flowering plants. Multiple fertilization events are not rare in gymnosperms, and indeed, you will observe the formation of up to several embryos, each in a separate archegonium of a single pine female gametophyte. (Usually, only one embryo survives, however.) Formation of an endosperm is thought to have evolved from a "normal" fertilization. Consider the putative ancestor in which two fertilization events occur. In this ancestor, two fertilizations would lead to the formation of two embryos, but some event triggered the failure of the second "embryo" to develop normally. In this hypothesis, the second, abnormal embryo evolved into the genetic dead-end, the endosperm, on which the other embryo is "parasitic."

Coniferophyta

Conifers are the most numerous and widespread of the gymnosperms living today. Extensive forest areas are populated virtually solely by conifers.[7] Among the most common are pine, cypress, cedar, spruce, and fir. This group includes the largest plants[8] and the longest-lived (bristle cone pine, *Pinus aristata*, lives about 5000 years) and includes about 600 species in 50 genera. All are woody, most evergreen. Secondary growth is present. The leaves are often needlelike or scalelike.

POWERPOINT SLIDE: *Metasequoia* (dawn redwood) leaf; until the 20th century, this plant was only known from fossils (gift of S. Q. Zhang).

POWERPOINT SLIDE: *Podocarpus* (with Pretty Girl, north Leon County).

POWERPOINT SLIDE: Sequoia (Yosemite National Park). Note, for perspective, the "portly, rubicund man of middle age." (Thanks to Winston Churchill from whom I lifted the quote.)

POWERPOINT SLIDE: Early logging of redwood trees (National Geographic Magazine, ca. 1907).[9]

POWERPOINT SLIDE: Cypress (Biology Unit I).

POWERPOINT SLIDE: Swollen base of cypress (Alapaha River, Georgia).

POWERPOINT SLIDE: Cypress knees (Suwannee River, Florida).

---

[7]"We next entered a vast forest of the most stately Pine trees that can be imagined, planted by nature, at a moderate distance, on a level, grassy plain . . . . This sublime forest continued five or six miles, when we came to dark groves of Oaks, magnolias, Red bays . . . which proceeding near a mile, we entered open fields, and arrived at the town of Talahasochte, on the banks of the Little St. Juan." . . . from the *Travels* . . . of William Bartram (1791), the first American naturalist, and the first English-speaking person to describe the flora and fauna of the southeastern U.S., particularly of Florida and Georgia. If you are a lover of history, of nature, or of words, this is the book for you. On the other hand, be a little careful about fantasy and fact.

These longleaf pine forests are virtually gone, sad to say—from 80 million acres to about 1000 acres. Robb White (of Thomasville, GA) says: "No other forest in the Americas has changed more radically than the piney woods of the Southeastern coastal plains of the U.S." (*Wooden Boat* 142: 34-41 (1998))

[8]At 365.5 feet, the National Geographic Society Tree, a coastal redwood in Redwood National Park, is the tallest plant. Record heights for other species are 329 feet, Douglas fir; 315 feet, Sitka spruce; 310 feet, giant sequoia (named, incidentally, for Sequoyah); 261 feet, western hemlock; and 158 feet, big-leaf maple.

[9]As you are well aware, the logging of old growth redwood forests is controversial. Big money is involved—a mature redwood on the stump is worth about $50,000, and many jobs depend on processing the lumber. Demand does not seem to have decreased. The price of finger-jointed redwood (that's the cheap stuff) is about $3 per board foot, compared with lodgepole pine (a common framing material) at about $0.22 per board foot. This big

POWERPOINT SLIDE: Cypress Tree, original source on slide. I lifted the photograph from Balfour, III 2002 In Search of the Aucilla. Colson Printing Company, Valdosta, Georgia.

POWERPOINT SLIDE: *Araucaria angustifolia* (Rio Grande do Sul, Brazil).

POWERPOINT SLIDE: Longleaf pine forest.

POWERPOINT SLIDE: Rayonier Pulp Mill (Jesup, GA).[10] When it was revamped in 1992, this became the largest pulp processing plant in the world.

POWERPOINT SLIDE: (from White, R. (1998) Rise Again? The demise of the longleaf yellow pine. *Wooden Boat* May/June 1998 (no. 142) 34-41. Series of three slides relating to timber harvest in the local area.

POWERPOINT SLIDE: Catface (left, from Lanier County, Georgia) + tin tar cups (originally from Mount Pleasant, Florida (Gadsden County), and now in North Leon County) + clay tar cups (retrieved from a swamp on my farm in Berrien County, Georgia) + tar barrel .((originally from near Havana, Florida (Gadsden County), and now in North Leon County). The photograph of the historical sequence of tar receptacles was taken at General Coffee State Park (Nicholls, Georgia).

POWERPOINT SLIDE: Turpentine Still (Thomas County, Georgia). These local stills used steam distillation to recover the turpentine from the other components (resin or, as it is also called, rosin). Turpentine had and continues to have many uses.[11]

---

price difference is, of course, an incentive to lie—some of the products, e.g. picnic tables, passed off as redwood are only red wood because they are stained.

[10]Gymnosperms are big business!!! For example, Rayonier employees 2700 people and has sales of over $1 billion per year. They sell to over 70 foreign countries, and foreign sales make up 55% of their sales (good for trade balance). Of course, you are familiar with "obvious" uses of wood, such as in building materials. You may not be as aware, however, of specialty pulp products (depending on the grade, 90–99% cellulose): (1) chemical cellulose; dissolving pulps designed for diverse chemical processes such as acetylation, viscose, etherification, nitration . . . . These include acetate pulps (for textile fibers, cigarette filters, impact-resistant plastics, photographic film, rigid packaging), viscose pulps (for high-tenacity rayon cord (used in tires, industrial belts, and hoses, textile fibers, sausage casing, cellophane), ethers and microcrystalline cellulose pulps (for chemical intermediates used in pharmaceuticals, cosmetics, food products, textile sizing, paints, cement), nitration pulps (for explosives, lacquers, printing inks, rocket propellants), and Lyocell pulps (for premium textile fibers); (2) fluff pulps (for disposable products, such as diapers, personal hygiene products, and incontinence pads and for non-woven fabrics); (3) specialty paper pulps (for use as primary material for filter-paper applications, decorative laminate papers; also special printing and writing papers); and (4) naval stores (crude tall oil (CTO) and crude sulfate turpentine (CST) derived from processing pine chips into pulp). This information is from http://www.rayonier.com, but if you consult their pamphlet ("The art of creating a forest tapestry in the Southeast."), you see that that is not the end—enter pulp products into grated cheese, shampoo . . . . The problem, of course, is the lignin—how to get rid of it at an environmentally acceptable cost.

[11] Taken verbatim from http://www.hchsonline.org/places/turpentine.html : "One method of extracting the product involved old fallen trees which had high concentrations of gum—what an Horry Countian would call "lightard" (lightwood). These logs were cut up and piled in a shallow pit and covered with earth. A slow burning fire lighted in the top of the pile caused the gum to liquefy and the tar to run down into catch basins outside the mound. These tar kilns were a common sight in the area from the earliest settlement. (new para) "In the early 19th century industrialization was accelerating in the United States. Those who found themselves amidst forests of pine were sitting in the middle of a resource for which there was an enormous demand in the outside world--a demand comparable to that for petroleum in our time. Like petroleum, it became almost a universal ingredient in

Pine Life Cycle

General overview of pine life cycle:

The following points will be emphasized in the detailed presentation later.

(A) The familiar tree is the sporophyte.

(B) Gametophytes are small and cannot lead an independent existence.

(C) In haploid stages, the sexes are separate.

POWERPOINT SLIDE: Male pine cones (north Leon County, Florida).

POWERPOINT SLIDE: Female pine cones (north Leon County, Florida).

POWERPOINT SLIDE: Pine life cycle (custom).

(A) The mature sporophyte produces microspores and megaspores, borne in separate, morphologically distinct cones. (As is true of all gymnosperms, conifers are heterosporous.)

(B) Microsporangia (male cones) are usually borne on the same tree but tend to be on lower limbs than megasporangia.

(C) Each scale bears two microsporangia, each of which becomes a pollen sac. Each microsporangium contains numerous microspore mother cells, which in spring undergo meiosis.

(D) Each haploid microspore develops into a four-celled pollen grain.

(E) The female cones bear two ovules on each scale. (For technical reasons, we will not refer to this sporangium-bearing structure as a "sporophyll"; each scale is interpreted to be a branch; however, the scales on the male cones are sporophylls.)

(F) Each ovule contains a multicellular nucellus (= megasporangium), which is surrounded by an integument with an opening, the micropyle.

---

manufacturing. That is, many products were made from it and it was used in the production of many others. (new para) "Early in this century a government publication listed the use of turpentine in thinners for paints and varnishes, solvents for waxes in polishes, waterproof cements, cleaners to remove paints and oils from fabrics, disinfectants, liniments, medicated soaps, internal medicines, ointments, synthetic camphor, celluloid, explosives, fire works, synthetic rubber, glazing putty, printing inks, lubricants for grinding and drilling glass, moth repellents, insecticides, crayons, patent leather, in petroleum refinement, textile manufacturing, and ore refinement. And this is just the turpentine. (new para) "Rosin was used in soaps, sizing for paper products, paint dryers, axle grease, waterproofing products, emulsified oils, leather dressings, enamels used in ceramic manufacture, fire kindling, artificial wood, papier-mâché, roofing materials and roofing cement, grafting wax used for trees, linoleum, oil cloth, lutes and violin bows (!), ointments, plasters, veterinary medicines, disinfecting compounds, dry batteries and electrical insulation, setting bristles in hair brushes, insect powders, fly papers, printing inks, cements for glass—and the list goes on."

(G) Each ovule contains a single megaspore mother cell. Three of the haploid cells that are formed from meiosis disintegrate.

(H) Pollination occurs in spring.[12] Pollen sticks to a drop of sticky fluid. As the fluid evaporates, the pollen grain is pulled down through the micropyle.

(I) Shortly after pollination, the scales close up and thus offer a high degree of protection to the developing ovule. The pollen grain germinates, forming a pollen tube.

(J) About a month after pollination, the megaspore mother cell undergoes meiosis; three of the four megaspores disintegrate. Over the next 12 months, the megaspore produces a female gametophyte of about 2000 cells, which are at first free nuclei.

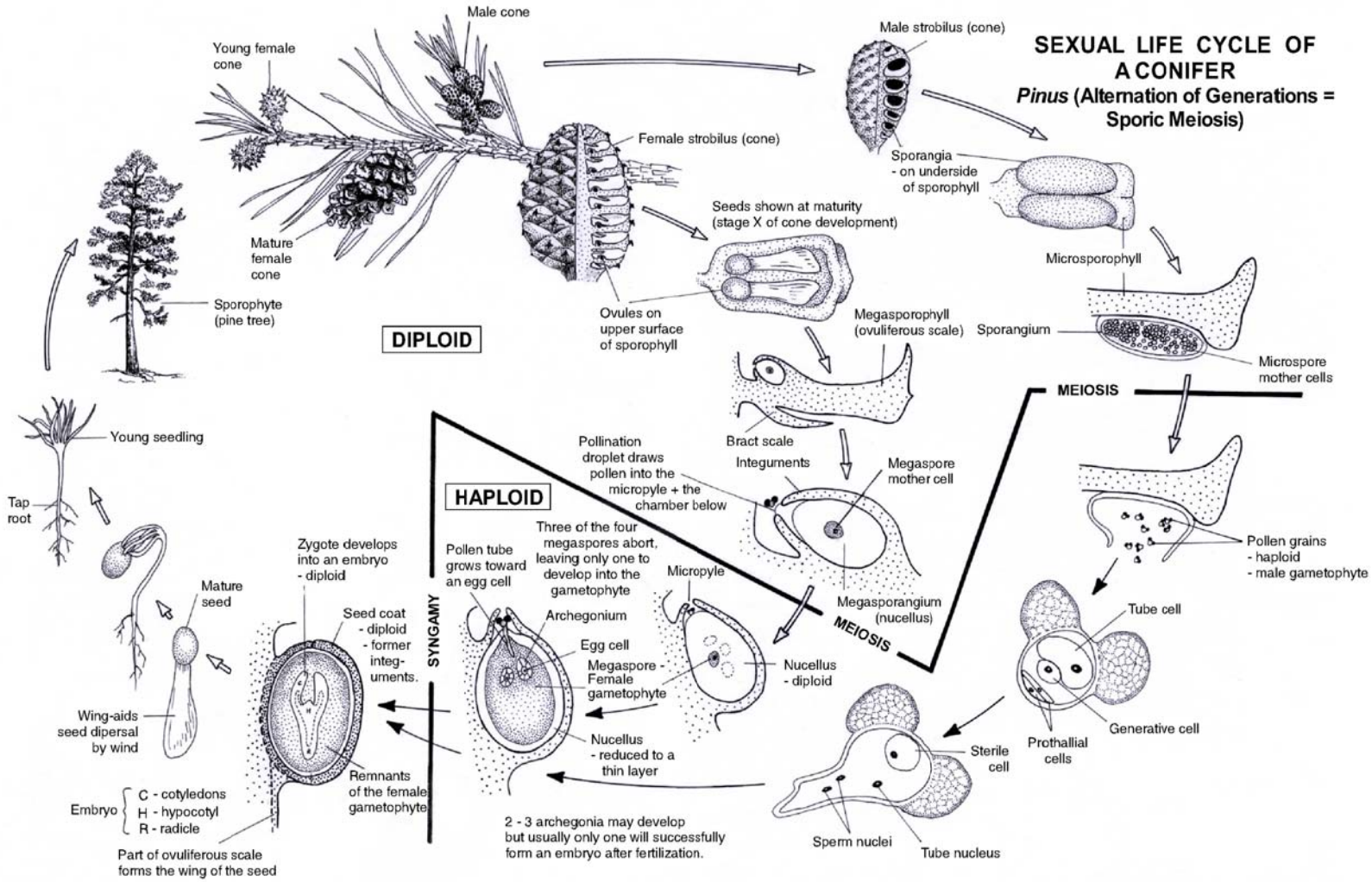
(K) In the next two months (i.e., 15 months after pollination) two or three archegonia differentiate.

(L) In the meantime, the pollen tube has continued growing. The pollen tube grows into the egg cell and discharges cytoplasm and two sperm nuclei—one unites with the egg nucleus; the other disintegrates. (In a similar way, the eggs in all archegonia may be fertilized, but only one embryo/ovule usually develops fully.)

(M) Over the next few months, embryology is completed, and in autumn of the second year, seeds are shed.

---

[12]Interestingly, in angiosperms, the *general* rule is that plastids and mitochondria are inherited only through the female gametophyte. I.e., with exceptions (e.g., geranium), these organelles in the male gametophyte do not survive and become part of the zygote. Thus, some traits are not transmitted in a Mendelian fashion. In contrast, the general rule is that these organelles are inherited paternally in gymnosperms. It is not clear why only one plastid type survives in a cell, but if cells are artificially fused, the same thing happens (i.e., the plastids of one of the fusing partners are eliminated).


SEXUAL LIFE CYCLE OF A CONIFER
Pinus (Alternation of Generations = Sporic Meiosis)
Male cone
Young female cone
Male strobilus (cone)
Female strobilus (cone)
Sporangia - on underside of sporophyll
Seeds shown at maturity (stage X of cone development)
Mature female cone
Microsporophyll
Sporophyte (pine tree)
Ovules on upper surface of sporophyll
Megasporophyll (ovuliferous scale)
Sporangium
Microspore mother cells
DIPLOID
MEIOSIS
Bract scale
Young seedling
Pollination droplet draws pollen into the micropyle + the chamber below
Integuments
Megaspore mother cell
Tap root
HAPLOID
Pollen grains - haploid - male gametophyte
Three of the four megaspores abort, leaving only one to develop into the gametophyte
Zygote develops into an embryo - diploid
Pollen tube grows toward an egg cell
Micropyle
Megasporangium (nucellus)
Tube cell
Mature seed
Archegonium
Seed coat - diploid - former integ-uments.
SYNGAMY
Egg cell
MEIOSIS
Megaspore - Female gametophyte
Nucellus - diploid
Wing-aids seed dipersal by wind
Nucellus - reduced to a thin layer
Generative cell
Prothallial cells
Sterile cell
Remnants of the female gametophyte
Embryo C - cotyledons H - hypocotyl R - radicle
2 - 3 archegonia may develop but usually only one will successfully form an embryo after fertilization.
Sperm nuclei
Tube nucleus
Part of ovuliferous scale forms the wing of the seed