Seeds arose during the Carboniferous (~300 million years ago), a time of wet climate during the Paleozoic; based on that climatic setting, evolution of the seed was probably not an adaptation to drought.

Conifers radiated in the Permian, a drier, cooler time of the Paleozoic, and are the second-most dominant seed plants today, with a strong ecological presence.

Conifers include ~700 species today (<3% the number of angiosperm species), but are more important ecologically as dominants in vegetation than their diversity would suggest.

**Characteristics of conifers:**
1) Simple, single-veined leaves (usually) -- possibly an adaptation to drought during the Permian?
2) Wind-pollinated
3) Seed cones (strobili) are compound, that is, the cone scale is a modified branch; pollen cones are simple, that is, the cone scale is a modified leaf. "Conifer" literally means "cone-bearer" although some members lack seed cones.
4) Worldwide distribution, except Antarctica (but prehistorically there, too), but not in lowland tropics

**Phylogeny of conifers**
- Pinaceae is sister to other families
- Podocarpaceae and Araucariaceae are sister to one another, constituting a mostly Southern Hemisphere clade.
- Cephalotaxaceae (with normal seed cones) and Taxaceae (without seed cones) constitute a clade nested among other conifer clades; therefore, **early ideas about Taxaceae (without seed cones) not being conifers are incorrect** (Taxaceae have lost seed cones)
- Cupressaceae constitute a clade that includes the paraphyletic Taxodiaceae, once treated as a separate family

**Distinguishing features of different conifer families**

Most families can be told apart by number of ovules per cone scale and number off pollen sacs per microsporophyll
<table>
<thead>
<tr>
<th>Family</th>
<th>Mono- or Dioecious?</th>
<th>Leaves</th>
<th>Phyllotaxis</th>
<th>Pollen sacks / scales</th>
<th>ovuliferous structure</th>
<th>female cone scales</th>
<th>ovules / cone scale</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pinaceae</td>
<td>Monoecious</td>
<td>needle / linear</td>
<td>alternate</td>
<td>2</td>
<td>woody</td>
<td>yes</td>
<td>2</td>
</tr>
<tr>
<td>Podocarpaceae</td>
<td>Dioecious (generally)</td>
<td>linear / awl-shaped / scale-like / ovate</td>
<td>alternate (sometimes opposite)</td>
<td>2</td>
<td>fleshy</td>
<td>yes</td>
<td>1</td>
</tr>
<tr>
<td>Araucariaceae</td>
<td>Mono- or Dioecious</td>
<td>awl-shaped / ovate</td>
<td>alternate</td>
<td>many</td>
<td>woody</td>
<td>yes</td>
<td>1</td>
</tr>
<tr>
<td>Taxaceae</td>
<td>Dioecious</td>
<td>linear</td>
<td>alternate</td>
<td>2-8</td>
<td>fleshy</td>
<td>NO</td>
<td>1 terminal seed</td>
</tr>
<tr>
<td>Cephalotaxaceae</td>
<td>Dioecious (generally)</td>
<td>linear</td>
<td>alternate</td>
<td>2+</td>
<td>fleshy</td>
<td>yes</td>
<td>2 (but only 1 develops)</td>
</tr>
<tr>
<td>Cupressaceae</td>
<td>Mono- or Dioecious</td>
<td>opposite (sometimes alternate)</td>
<td>opposite (sometimes alternate)</td>
<td>2-6</td>
<td>mostly woody but fleshy in Juniperus</td>
<td>yes</td>
<td>2-many</td>
</tr>
</tbody>
</table>

**Seed dispersal**

Animal (bird) dispersal of fleshy-coned taxa. Wind-dispersal of woody-coned taxa (generally). Flightless parrot in New Zealand that improves seedling recruitment of members of Podocarpaceae in areas where it occurs.

**Ecology**

Slow seedling establishment (vulnerable to competition with angiosperms?)
Good at survival in stressful habitats (dominate vegetation in some extreme environments)

Cold habitats

- *Larix* (larch) are among northernmost trees, bordering tundra.
- *Pinus* (pines) are often the highest elevation trees.
- *Podocarpus / Prianopitys* are among highest trees in tropical mountains.

Dry habitats

Pinyon pines and junipers form woodlands in much of cool, semi-arid western North America.

Wet (swamp) habitats

*Taxodium* (bald and dwarf cypresses) in southeastern US swamps.
Larix and some Picea (spruce) in northern bogs (low nutrient / low oxygen)

Low fertility habitats
   Pinus (poor or challenging soils, such as sandy situations)
   Cupressus (shallow soils in western North America)

Combination of several of the above habitats
   Pinus longaeva and P. aristata (the bristlecone pines) in high, dry, infertile soils
   (from dolomite); very slow growing, high and dry enough to avoid pathogens and pests --
   the oldest known organisms (>4000 years)

Relicts ("leftover plants") -- remnants of ancient lineages (see handout)
The Coast and Sierra redwoods (Sequoia and Sequoiadendron)
Californian cypresses (e.g., Cupressus goveniana)
Pinus torreyana (Torrey Pine)
Microcachrys, Microstrobus, Neocallitropsis, and Papuacedrus (Southern Hemisphere
Cupressaceae)

Recently diversified conifers
Abies (firs) of Eurasia and N. Africa.