Evolution of Flowering Plants - Advanced

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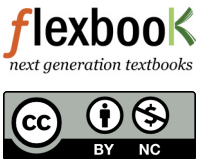

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CHAPTER 1

Evolution of Flowering Plants - Advanced

- Summarize our current understanding of the origin of flowering plants.
- Describe the characteristics of the earliest flowers.
- Analyze the general trends in flowering plant evolution.
- Discuss the co-evolution of flowering plants with insects and other animals.
- Explain the ways in which humans have co-evolved with flowering plants.

What were early flowers like?

They were probably very simple, with just the basic reproductive structures. These flowers from an avocado tree (*Persea americana*) shows the characteristics of ancient flowering-plant lineages. Its petals (which are colorful in most flowers) and sepals (which usually have a green outer layer) are combined into one organ.

Evolution of Angiosperms

Charles Darwin considered the relatively rapid evolution of the flowering plants an "abominable mystery". As you have seen, a flower is complex. It could be considered an **organ system**, analogous to the organ systems in your body. The four concentric rings of organs (**Figure** 1.1) which make up a flower are:

1. Beginning in the center is the "woman's house" or **pistil**.
2. Surrounding the pistil is the "man's house" - a ring of **stamens**.
3. Outside the stamens is the corolla - a whorl of **petals**.
4. Outermost is the calyx - a whorl of **sepals**.

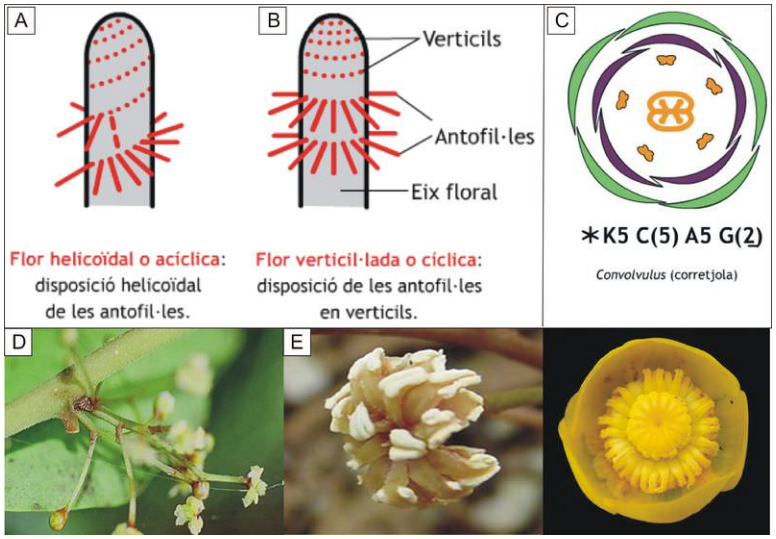

FIGURE 1.1

The evolution of flowers probably involved the change from a spiral of modified leaves (A) to several whorls of reproductive organs (B). In cross section (C), a flower has four concentric rings of organs: innermost female carpel(s), surrounded by a ring of male stamens (yellow-orange), surrounded by sterile petals (brown) and finally, sepals (green). Botanists think that *Amborella* (D) and (E) and waterlilies (F) are similar to the earliest flowers. Shared characteristics include: spiraled (rather than whorled) flower parts, variable number of parts; perfect flowers with dominant ovary, with or without undifferentiated tepals.

How did such a complex system of organs arise?

In previous concepts, you have seen the gradual reduction of the gametophyte stage to pollen and ovule. Their further reduction in angiosperms follows that pattern. You have also seen that these gametophytes are born on modified leaves which form cones. Imagine, then, that flowers began as an elongated stem with series of slightly modified leaves - primordial ovaries, stamens, petals, and sepals - spiraling around just as leaves had always done (**Figure** 1.1). At first, sepals and petals may have been identical (**tepals**), only later differentiating into petals and sepals. Gradually, the space between the **nodes** which bore leaves (the **internodes**) shortened (**Figure** 1.1), until the organs formed whorls, clustered tightly together - the first true flower. This is how biologists hypothesize that flowers evolved.

The Earliest Flowering Plant

The earliest flowering plant, *Archaefructus ligoningensis*, dates to the early Cretaceous, 125 million years ago. The fossil (**Figure** 1.2) has been interpreted as a "spread-out" primordial flower, with carpels and stamens (but no petals or sepals) spiraling around an elongate stem. However, chemicals used by plants to defend flowers from insect pests (*oleananes*) have been found in 250 million-year-old fossils of late Permian Gigantopterids. No fossils of Gigantopterid flowers have been found, but similarities to angiosperm shoots, vessel elements, and leaves suggest to some that ancestors of today's flowers could have lived much longer ago than the Cretaceous. Gnetophytes also produce vessel elements in their xylem, leading some botanists to suggest that they may be angiosperm ancestors.

Although botanists still do not know which gymnosperms gave rise to the flowering plants, most agree that the living angiosperm species which most closely resemble the first flowering plants are *Amborella trichopoda* and/or the water lilies (**Figure** 1.1). Primitive characteristics include:

- Flower parts: variable number, spiraling about stem, separate but in contact with each other
- Flowers **perfect:** both stamens and carpels within a single flower
- Perianth: undifferentiated tepals - or none - spiraling around the stem
- Flower dominated by the ovary
- Fruit: a red berry containing a single seed

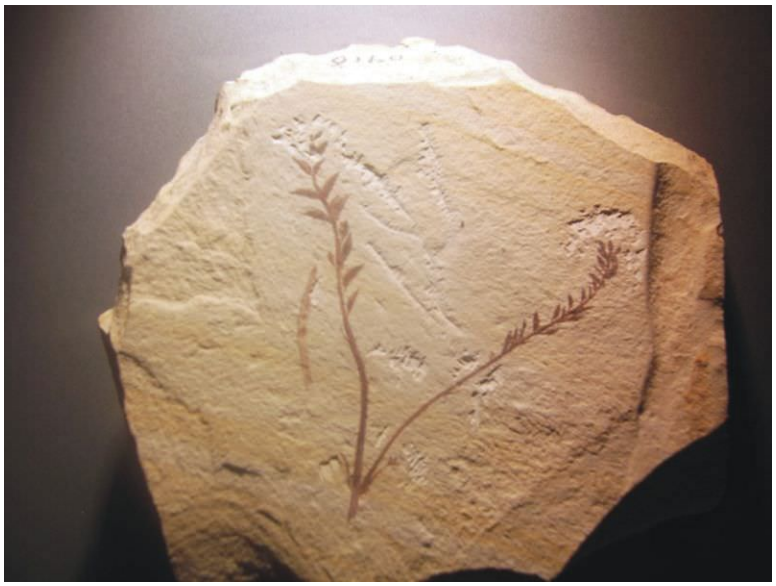

FIGURE 1.2

Archaefructus ("ancient fruit") has been interpreted as the first flowering plant, with carpels and stamens spread out along the stem. The fossil dates back to the early Cretaceous, 125 million years ago.

Advantages of Flowers

What advantages did flowers confer on the plants which expended the energy to produce them? Biologists believe that even the earliest flowers - perhaps appearing on isolated islands - attracted insects. If those insects, dusted with pollen while foraging for nectar, visited several different plants with the same flowers - dropping off and picking up new pollen grains at each stop, they immensely increased the efficiency of fertilization over the random vagaries of wind. Likewise, fruits produced by ovaries or other parts of the flower attracted birds or mammals with their sugars or burrs. Again, flowering plants enlisted the muscle power of animals - this time to do the work of scouting for new habitats. The co-evolutionary relationship between flowers and insects has produced an astounding diversity of forms - elaborate shapes and patterns and scents and nectaries among flowers, and long, curved beaks, proboscis, tongues, and pollen baskets among animals (**Figure** 1.3).

As flowers have evolved and diversity has increased, some general trends include a number of changes in flowers which attract specific pollinators:

- Reduction of the number of flower parts
- Fusion of flower parts
- Precision in design and number of flower parts
- Special attractants: scents, heat, nectar glands
- Timing mechanisms, both seasonal and diurnal
- Specific sexes in a single flower or plant (dioecious or monoecious species)

Polyploidy (multiplying chromosome sets) and gene duplication are common means of evolution among flowering plants: strawberries, for example, are octaploid. And as climates changed, flowering plants continued to coevolve with animals. Specific examples of each of these trends will be discussed in the *Flowering Plants: Diversity (Advanced)* concept.

According to molecular clock analyses, one more powerful selective force began to influence the evolution of flowering plants some 10,000 years ago. First in the Fertile Crescent with wheat, then in the New World with teosinte, and finally about 6,500 years ago wth rice, human agriculture increasingly chooses which characteristics will survive. The result has been dramatic change in amount of endosperm, or size of tubers, or sweetness of fruits - as we cultivate our food (**Figure** 1.4). Or did the rice, the wheat, the corn, and so many more species choose us - by appealing to our desires - to handle their soil preparation, planting, fertilizing, irrigation, and even pollination? As

FIGURE 1.3

Coevolution between flowers and animals result corresponding adaptations in each. Nectaries within flowers (A) are deeply hidden. Bees are among the mostly closely co-adapted; pollen baskets on the "bees knees" (C) collect food to carry back to larvae in the hive. B: SEM of butterfly proboscis; D and G: hummingbird moth; E: Gold Dust Day Gecko and Bird-of-paradise flower; F: Hawaiian honeycreeper and Alpine Blue-sow-thistle.

Michael Pollan reminds us in the *The Botany of Desire*, the process of cultivation is a two-way street more akin to coevolution than to human dominion over nature. We depend almost entirely on angiosperms for our food - as well as for timber, wood, paper, fibers, medicines, drugs, landscaping, gardening, and the beauty of flowers.

As we harness fossil fuels to increase industrialization and technology, we have become even more of a force in the evolution - often unwittingly. Our increasing mobility results in the introduction of exotic animals and plants which alter the ecology of habitats, rendering some species invasive and others extinct. As we increase our population and thus our demands on agriculture and land, we are destroying habitats for many species of plants and losing genetic diversity among the survivors. As we fight species we consider to be "weeds" and insect "pests" with chemicals, we destroy pollinators and the species which depend on them.

Summary

- As flowers diversified, general trends included:
- Among today's flowers, *Amborella* and water lilies most closely resemble the first flowers.
- The identity of the gymnosperm ancestor to angiosperms is unknown.
- The oldest fossil is 125 million years old, but other evidence suggests flowers have lived 250 million years.
- Flowers probably began as a series of modified leaves spiraled around the stem.
- Flowering plants further reduced the gametophyte stage - to 3-celled pollen and 8-nucleated ovule.
  - co-evolution with pollinators, especially insects
  - reduced number of flower parts; fusion to create specific designs

FIGURE 1.4

Beginning some 10,000 years ago, humans have been a major force in the evolution of flowering plants - and plants have been a major force in the evolution of humans. Domestic corn (right), for example, has much more endosperm and greatly reduced carpels, compared to wild forms, which are known as teosinte.

  - attractants: scents, heat, nectar glands
  - timing mechanisms, both seasonal and diurnal, and
  - specific sexes in a single flower or plant

- Polyploidy and gene duplication have been important forces in flowering plant evolution.
- Humans, too, have co-evolved with flowering plants - as through agriculture and habitat destruction.

Review

1. Summarize our current understanding of the origin of flowering plants, including a description of the first flowers.

References

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