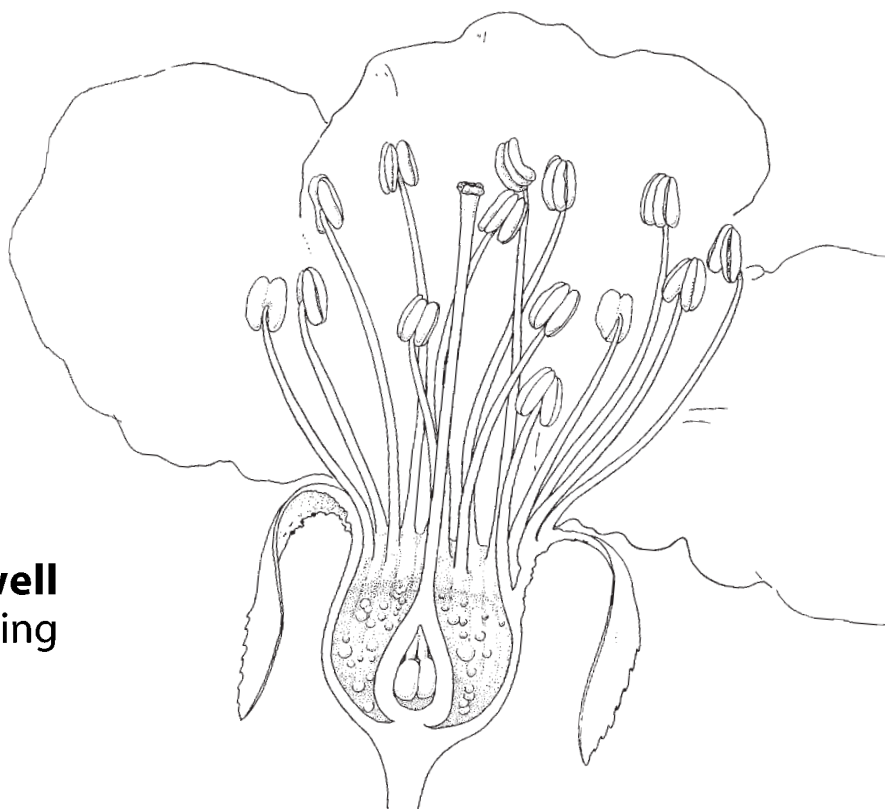


FLOWERING PLANT EMBRYOLOGY

With Emphasis on Economic Species

Nels R. Lersten

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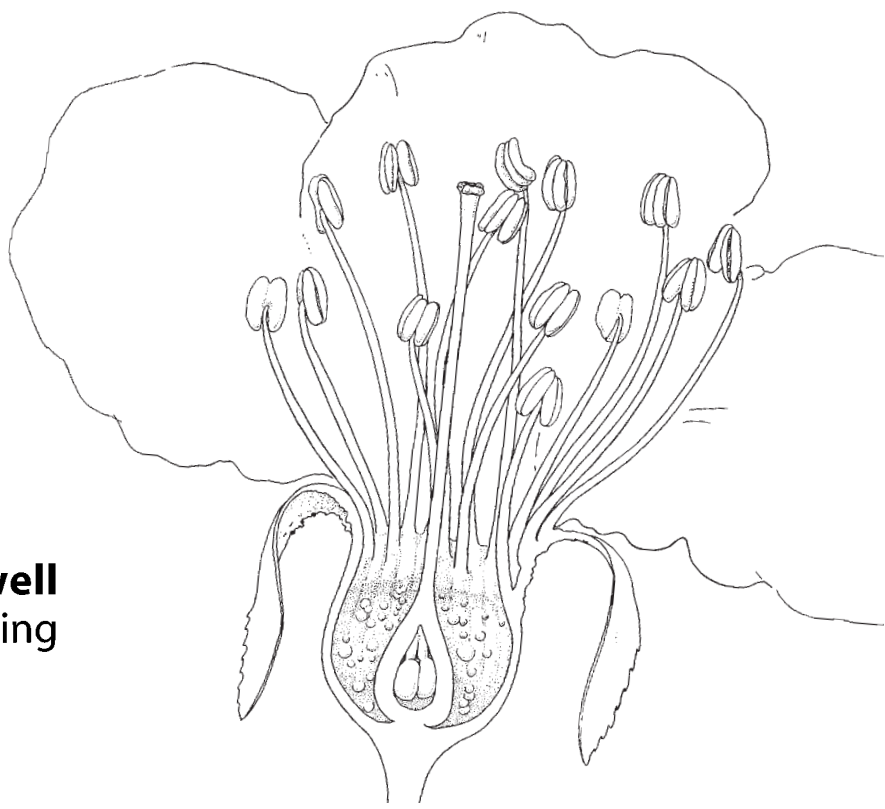
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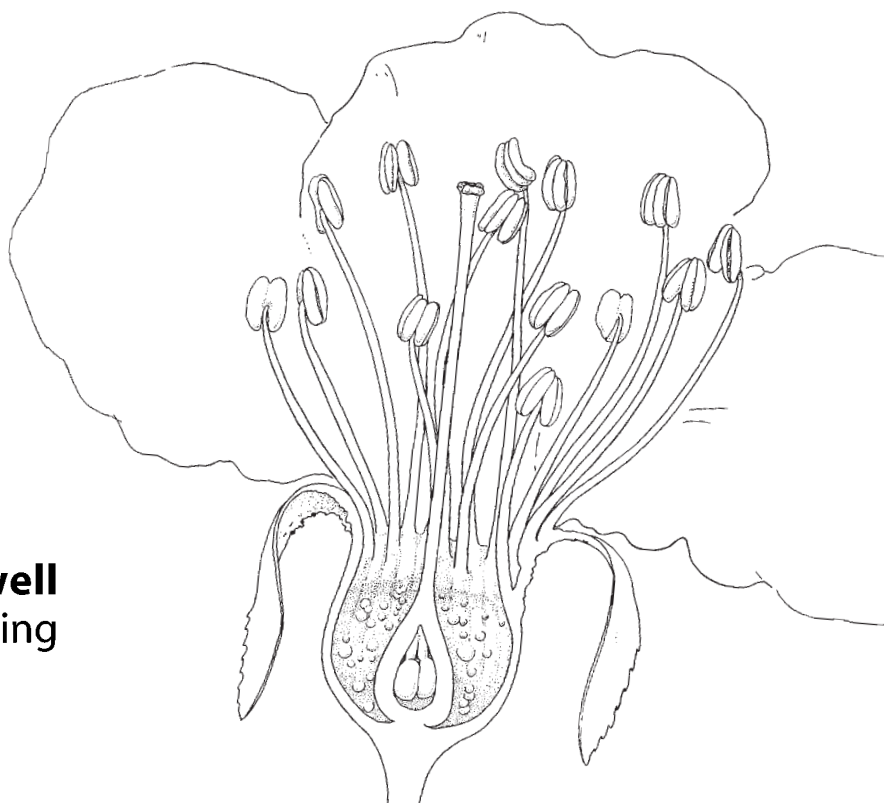


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Nels R. Lersten is Professor Emeritus of Iowa State University and holds a PhD in botany from the University of California, Berkeley and an MS from the University of Chicago. He is a former editor-in-chief of both the *American Journal of Botany* and *Proceedings of the Iowa Academy of Science*.

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Preface

Formal recognition of angiosperm embryology began in 1903 with Coulter and Chamberlain's book. General embryological works since then have not emphasized cultivated or otherwise economically important plants. This book is a general treatment of normal sexual reproduction in angiosperms, but it emphasizes examples from economic plants. Many references from the vast embryological literature are also cited in each chapter, which provides the reader entry into almost any subdiscipline or specialized topic of embryology.

The foreword to a 1984 multi-authored embryology book mentioned that the time for single-authored works in this discipline had passed. This is probably true for advanced treatises, but such works usually have the disadvantages of uneven treatments and styles of contributing authors, and the rich dishes of information they serve up often prove indigestible for nonprofessionals. Single authorship, in contrast, usually provides a uniform style and a reasonably consistent level of treatment. In this book the latter comes from my 20 years of teaching embryology, providing answers and advice to graduate student and faculty researchers, and research and publication (25 papers and book chapters) in embryology. These experiences convinced me of the need for an angiosperm embryology book that emphasizes economic plants.

The many borrowed illustrations that enrich the text are acknowledged in each caption, with sources given in each chapter's literature citations. I thank the many individuals, journals, professional societies, and publishers for their generous permission to reproduce. I thank my illustrator, Anna Gardner, for expertly copying, arranging (sometimes creatively) and labeling the figures, and for turning my original sketches into finished drawings. I also thank the Department of Botany (now Ecology, Evolution and Organismal Biology) for many services rendered over the several years required for this project, and I acknowledge the superb botanical holdings of the Iowa State University Library, without which the book might never have been completed. Dr. H.T. Horner, my longtime friend and colleague, has been a co-investigator in embryology projects, and he and his students and co-workers have contributed numerous illustrations for the book as well as critical insights and ideas—thanks, Jack.

Patricia Brady Lersten ("Pat") has been an exceptionally patient (except when applying needed prodding) and encouraging helpmate during the marathon gestation period required to give birth to this book. She deserves my love and part of any royalties.

Nels R. Lersten, Iowa State University,
January 2004

1

Introduction

Angiosperm embryology is the study of the floral structures and processes directly responsible for seeds. These include stamens (collectively the androecium) and pollen development; pistil or carpels (collectively the gynoecium) and embryo sac development; pollen germination, pollen tube growth and fertilization, and endosperm and embryo development (and sometimes the enclosing seed cover). One could also include seed dormancy, and even onset of seed germination. It is a discipline dominated by all forms of the microscope.

This book sticks closely but not exclusively to embryology as just described. The emphasis is on normal sexual reproduction using economic plants (including garden flowers and weeds) as examples, but what is presented certainly applies to embryology of flowering plants in general. Apomixis and polyembryony, which are forms of asexual reproduction that use some of the sexual apparatus, are also mentioned briefly.

The total number of described angiosperm species is an elusive figure, with estimates ranging from 230,000 to somewhat over 400,000 (Govaerts, 2001). The subset that includes plants of economic significance (including weeds) is also subject to widely varying estimates, but it easily encompasses several thousand species. Although this book concentrates on the subset of economic plants, which has been neglected almost completely by previous embryology texts, it is obviously impossible to cover all such plants. If such

were possible, the result would almost certainly be an unreadable encyclopedic tome.

The goals of this book, in light of the necessary compromises just mentioned, are to:

- Present an outline of angiosperm embryology.
- Put flesh on the life cycle skeleton with supporting facts and enough specific examples to give some appreciation for general embryological features, as well as the diversity among economic plants.
- Present some research results, hypotheses, and speculations to try to explain why some things are as they are.

Every biological discipline is infinitely complex, which sustains the interest of professionals but can intimidate others, and embryology is no exception. Most of the richness of detail about angiosperm embryology reported in its vast literature (easily 30,000 or more publications as an estimate) is therefore necessarily absent from this account, but entry into more specialized secondary and primary sources on most topics is provided by the many citations in the text that are listed at the end of each chapter. My intention is that this book should hover, figuratively speaking, somewhere between a ground-level introductory text and the rarified upper air of a fully detailed research volume—not an easy task since there is no altimeter besides experience to gauge the proper elevation.

Two sections on background that follow describe the standard books on angiosperm

embryology. I mention the number of references in the bibliographies of some of these works to convey an idea of research progress over time, and also to illustrate the huge problem of how to choose a necessarily limited number of publications to support a balanced narrative of reasonable length.

The last three sections of this chapter deal with the nature and evolutionary interpretation of the flower, introduce the components of a flower, and finally present a general diagram of the angiosperm sexual cycle, with a brief accompanying explanation. These last three sections set the stage for the nine more specific chapters that follow.

BACKGROUND: GENERAL WORKS ON EMBRYOLOGY

When the astounding discovery of “double fertilization” (two sperms needed for embryo and seed development—almost a unique characteristic of flowering plants) was made near the end of the 19th century, it suddenly fitted earlier pieces of knowledge into a coherent story. The study of angiosperm sexual reproduction using microscopy suddenly became a very popular endeavor, and the resulting spate of information soon required some organization.

The first synthesis was by Coulter and Chamberlain (1903), in a book that is still useful and readable. They used the term “Special Morphology” for what later came to be called embryology. Their treatment omitted floral morphology, which mostly concerns form and diversity as revealed by the naked eye and the low-power magnification of a hand lens, and pollination biology. These two disciplines had already accumulated a substantial published literature for about 200 years by the end of the 19th century. Surprisingly, Coulter and Chamberlain also remarked in several places that published information about certain embryological topics had already exceeded what could be digested by reasonable effort, thereby acknowledging that use of the microscope for embryological studies had already burgeoned by the early 20th century. Thus the field of

study that would soon be called embryology was already well launched.

Coulter and Chamberlain devoted most of their book (about 250 pages) to chapters on pollen and its development, the embryo sac, fertilization, endosperm, and the embryo. They utilized published information about any and all angiosperms without emphasizing economic plants. Their chapter organization has served to define the scope of embryology for later investigators. Their long section on embryology was really a book within a book, followed by about 100 pages dealing with the already well-defined disciplines of taxonomy, anatomy, paleobotany, and evolution.

A quarter of a century later, Schnarf (1929) devoted almost 700 pages to mostly the same embryological topics, but in more detail since he included information from the greatly increased number of published studies since the Coulter and Chamberlain book. Schnarf also added chapters dealing with apomixis and other asexual aberrations of the sexual cycle, of which there are many among angiosperms. Schnarf also ranged over all of the angiosperms, with no emphasis on economic species. His weighty volume was not written for easy reading, even for those who could read German.

Two decades later, P. Maheshwari (1950) published his classic text, mostly organized like Coulter and Chamberlain’s chapters, but with the addition of an introductory historical chapter and some chapters on more specialized topics, including one on the emerging field of experimental embryology. Maheshwari also selected his information from among all angiosperms, with no particular attention to economic species. This treatment, like that of Coulter and Chamberlain, was reasonably readable and suitable for advanced undergraduates and graduate students.

After a lapse of 13 years Maheshwari in 1963 edited a multi-authored book that was really an expanded second edition of his 1950 work, and a tacit admission that knowledge appeared to have swelled beyond one person’s ability to encompass it. Each chapter presented a detailed

treatment of one topic, which elevated the book to advanced text status.

Continued accumulation of published work on all aspects of embryology, as well as the emergence of several specialties based on new technology and experimental work, required another grand overview after 20 more years. This appeared in the form of an 830-page multi-authored volume (Johri, 1984), which the preface described accurately as an “advanced treatise.” This comprehensive work is presently the most current detailed general treatment of angiosperm embryology, that is, a treatment of mostly the same topics in the same order as included in earlier embryology works. A new comprehensive multi-authored work is at hand, however, after another lapse of 20 years, this one in three volumes. Volume 1 is available (Batygina, 2002) as of this writing; it deals with topics up to the female gametophyte (embryo sac).

Another advanced treatise (Raghavan, 1997) is a one-person effort that covers pollen development, pollen and pollen tube interaction with the carpel, embryo sac development, fertilization, embryo, and endosperm, but with a strong emphasis on molecular, genetic, and *in vitro* studies, as reflected in the book’s title, *Molecular Embryology of Flowering Plants*. The almost 700 pages include a 150-page bibliography of over 5000 references, most of which concern research trends of recent decades.

Other recent treatises concentrate on only a specific portion of the embryological cycle, and many of these are cited later in appropriate chapters. Although not a book, the review article of Prakash (1979) deserves mention here because of its general usefulness for those interested in economic plant embryology. He provided a list of 720 economically useful species in 89 families that had been studied embryologically up to that time, citing published studies for each species. Also, a recent multi-authored text deals with the general embryology of temperate zone woody fruit plants (Nyéki and Soltéz, 1996).

BACKGROUND: EMBRYOLOGY AND SYSTEMATICS

Already by the early 20th century enough work had been done to show that embryological structures and behavior vary enormously in detail among and within angiosperm families. It soon became evident that someone needed to organize such information for the benefit of taxonomy and systematics. The first such collation appeared in 1931, when Schnarf reorganized and expanded the information from his 1929 volume and presented it by family categories. He included over 1500 references in this illustrated treatment.

It took another 35 years before Davis (1966) published her exhaustive scholarly work based on information gleaned from a vast 202-page bibliography of more than 4,500 references. The bibliography itself was almost of book length, which forced Davis to squeeze the text to almost telegraphic conciseness and omit illustrations. There is an introductory general description of the kinds of embryological features significant for systematics, followed by descriptions of embryological features listed by families.

More recently an even more ambitious 2-volume illustrated treatise has been published (Johri et al., 1992), also organized mostly by family chapters. There is a general embryological introduction of 112 pages, which amounts to a brief textbook by itself. The family accounts are based collectively on about 5,000 references, not all of them more recent than in Davis’ account, but the new references carry the literature up to 1991.

A quite different and clever visual presentation of embryological information for dicot families and orders (monocots are omitted) is that of Dahlgren (1991). She depicted various embryological features as symbols superimposed on each of 23 repetitions of the same “bubble diagram” of the dicotyledons. Each circular-to-ovate bubble in the diagram represents one order and is of a size relative to the number of species included in it. The bubbles are arranged in their presumed evolutionary

positions and distances from each other; thus the dicot orders are shown in their presumed natural relationships. These diagrams therefore comprise a chart of embryological features.

WHAT IS A FLOWER?

Embryology as described earlier in this chapter deals with floral structures and reproductive processes occurring within them. But step back and ask a broader question: what is a flower? Forests of paper and lakes of ink have been consumed by theorists who have proposed numerous hypotheses and speculations and by those who have defended or criticized them. Speculating on what is a flower and how it has evolved is fascinating for many people, but in this book only a venerable and widely accepted theory will be presented, one that most people find easy to understand, and which may even be proven correct some day.

The “foliar theory,” which is over 200 years old, interprets the flower to be a specialized stem tip or side branch with compressed internodes and nodes with attached appendages that represent leaves that have evolved into modified appendages to serve reproductive purposes. These leaf-derived appendages are sepals, petals, stamens, and carpels, produced in ascending order from floral base to tip. Because these floral appendages have evolved in innumerable and often radically different ways among the more than 300 flowering plant families recognized today, the attractively simple idea of the flower as a greatly shortened branch with specialized leaves is often difficult, if not impossible, to discern. This has stimulated formulation of many alternate hypotheses about how the flower originated and evolved. Some of these concepts of the flower are presented, along with a defense of the foliar theory, in a very readable article by Eyde (1975). In this book the foliar theory will be assumed, and accordingly the floral appendages considered to be modified leaflike appendages.

THE FLORAL APPENDAGES

There are four types of floral appendages. Most economic species have all four in one flower,

but one or more types of appendage may be absent from flowers of some species. A representative angiosperm flower that illustrates the four appendage types is the cherry blossom shown at the beginning of Chapter 2 (Fig. 2.1). The most leaflike appendage in most flowers is the sepal (collective noun is calyx). The typically green sepals serve primarily as floral bud scales, developing early and enclosing and protecting the other appendages as they arise and develop. In some groups, however, sepals have also become adapted to entice pollinators by exhibiting colors other than green or by bearing nectaries. Nectaries are, however, not restricted to sepals; among different families they are known to occur on any of the other floral appendages, and in some groups even between appendages on the floral axis.

The next appendages in most flowers are the petals (collective noun is corolla), also usually recognizably leaflike, but adapted to entice pollinators by color and to act as “landing fields” for pollinators (they often have patches of roughened epidermal cells that make landing easy for insects). Some groups of plants lack petals, especially those in which wind pollination or self pollination occurs. Sepals and petals (collective noun is perianth) are not directly involved in embryological processes, and they will be almost entirely ignored elsewhere in this book.

Stamens, the third set of appendages (collective noun is androecium), are specialized for pollen manufacture and usually do not appear to be leaflike, but they can be linked via intermediate forms in some groups to truly leaflike stamens in certain tropical families thought to be at the base of the angiosperm lineage.

Carpels (or pistils) are the ovule- and seed-bearing appendages (collective noun is gynoecium), and they are the least leaflike and the most difficult to link to leafy precursors, although they can also be linked by intermediates to carpels that look like folded leaves in some tropical families. Flowers that have both an androecium and a gynoecium are bisexual or perfect, the most common condition, and species with only one or the other are unisexu-

al or imperfect, as in kiwi fruit, hemp, and mulberry, for example.

THE SEXUAL LIFE CYCLE

Figure 1.1 outlines the angiosperm life cycle, but shows only idealized stamens and carpels, and the structures and processes that occur within them. Starting with the mature seed at the left side of Figure 1.1, the progression from vegetative to floral structures and events can be

followed clockwise, finally returning to the seed. This life cycle diagram includes some details above an introductory text level but avoids almost all of the many variations that would obscure the fundamental features of the life cycle. It is the skeleton that will be fleshed out gradually in Chapters 2–10, which describe and discuss in detail successive clockwise portions of Figure 1.1. It will become evident in these later chapters that each part of this gener-

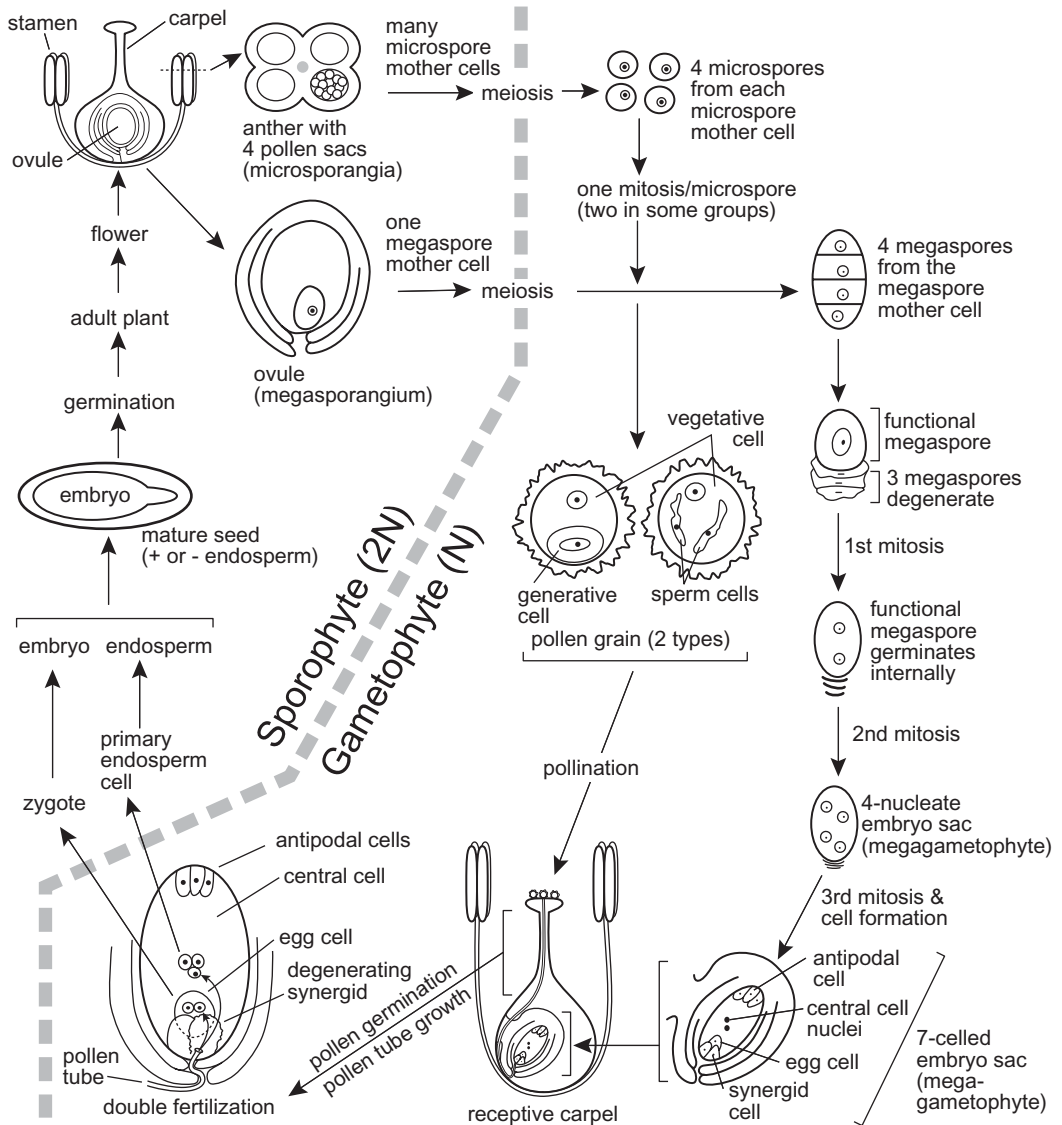


Figure 1.1. Representative sexual life cycle of an angiosperm. The parts of the cycle are described more fully in Chapters 2–10.

alized sexual life cycle can be expanded almost endlessly in complexity.

The major division of the life cycle into Sporophyte (2N—double set of chromosomes) and Gametophyte (N—single set of chromosomes) generations is usually described as the “alternation of generations,” a characteristic of all sexually reproducing organisms. In angiosperms the sporophyte (Greek, “spore-bearing plant”) generation is the visible plant, which greatly exceeds the two microscopic gametophytes (pollen grain and embryo sac) in size and longevity; in other groups of plants, such as ferns, mosses, and many algae, the gametophyte (Greek, “marriage-partner plant”) generation may approach, equal, or even surpass the sporophyte in size and longevity. Reproduction in these non-flowering plant groups depends on at least a film of external water so that the ciliated or flagellated sperm can swim to the egg cell. Sexual reproduction in flowering plants is independent of the need for external water, and many unique structural and physiochemical features have evolved as a consequence, of which the most conspicuous is the release from ground-hugging so that the sexual cycle can occur at considerable distances in the air (gymnosperms had already developed this adaptation much earlier).

The shift from 2N sporophyte to N gametophyte occurs when meiosis is completed. In both anther and ovule this process of reducing chromosome number by half, which is really the removal of one whole set of chromosomes, results in four offspring cells. In the anther these cells are called microspores, and all four will develop into pollen grains (microgametophytes). In the ovule, the four meiotic products are called megaspores, and three of them will usually degenerate, leaving only one functional megaspore to enlarge and develop into the embryo sac (megagametophyte). Furthermore, there are many more microspore mother cells in an anther compared to a single megaspore mother cell in an ovule. The result of this great numerical difference is that a typical flower sends out an army of pollen grains to pursue

one embryo sac; this needs emphasis here because the simplified Figure 1.1 cannot show this great disparity in numbers.

Figure 1.1 also shows two versions of the pollen grain. They both eventually produce a pollen tube containing two sperm cells, but in one type (tri-cellular pollen) the sperm cells form before the pollen grain is shed from the anther, whereas in the other type (bi-cellular pollen) the generative cell does not divide by mitosis to produce the two sperm cells until after the pollen germinates and produces a pollen tube of a certain length. Other differences are also associated with these two pollen types.

An almost unique feature of angiosperm reproduction is the requirement for two sperm cells for successful fertilization instead of just one. One sperm has the expected task of combining with an egg cell, but a second sperm is needed to initiate endosperm, a tissue unique to angiosperms. Despite a few exceptions elsewhere (a similar if not identical double fertilization occurs in two gymnosperm groups—see discussion by Magallon and Sanderson, 2002), the two-sperm requirement is one of the defining characteristics of angiosperms.

Variations in the number and form of floral appendages are the basis for classification of angiosperms into taxonomic units from order down to species. These variations are relatively easy to see, but hidden within the flowers are endless variations in microscopic embryological features and processes. These are of great intrinsic interest for the embryologist, but some knowledge and appreciation of them is also needed by more practical-minded investigators whose purpose is to manipulate aspects of the life cycle for increased production or other agronomic or horticultural purposes.

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2

Stamen and Androecium

The Latin word stamen means approximately “standing thread,” a good descriptive term coined in the 17th century for the common type of stamen with a terminal swelling (the anther) supported on a slender, threadlike stalk (the filament), as in a cherry blossom (Fig. 2.1). Stamens seem to be simple entities, but they are not, as this chapter demonstrates. Stamens are neglected as objects of study in embryology texts except for pollen development within the anther. There is one book, however (D’Arcy and Keating, 1994), that describes various aspects of stamens. This chapter examines the stamen without involving pollen development, which is the topic for the next two chapters.

The collective name for all stamens in a flower is androecium (Greek, meaning “male household”). In a typically organized flower the stamens are initiated just after the petals have appeared; they appear at first as small featureless primordia (bumps) spaced evenly around the flank of the dome-like floral apex. Slightly later in development, each stamen resembles a leaf primordium, not surprising since according to the foliar theory of the flower (see Chapter 1) the stamen is a specialized leaf, an interpretation implicit in its technical name of microsporophyll (Latin for “leaf that produces microspores”—the cells that will become pollen—see Chapter 3). But beyond this early stage a typical stamen quickly acquires features that make it quite unleaflike.

The stamens of a flower may all be entirely separate from each other, variously attached to each other (connate), or attached to other floral parts (adnate). Some stamens may even become sterile “staminodes” that produce no pollen and in some plants even develop into nectaries. The many possible arrangements will not be considered further here because they are well described in any book on plant taxonomy. McGregor (1976) includes many fine drawings of flowers of cultivated species (some reproduced in this book), which depict most of the range of stamen number, arrangement, and form.

The number of stamens in a flower differs among and within families, although 4, 5, 10, or even more than 20 are found most commonly among cultivated dicots, and 3 or 6 among cultivated monocots. But there are exceptions, as in the extreme example of the reduced flower of the poinsettia, *Euphorbia pulcherrima* (dicot: Euphorbiaceae), which has only one stamen. The variation in numbers of stamens usually has no obvious explanation, but constraints of floral architecture and type of pollination mechanism are certainly involved.

STAMEN VARIATION IN REPRESENTATIVE FAMILIES

It would take many pages to describe the different forms and arrangements of stamens, even among families with cultivated members. The following brief list of 11 families with economically important species includes represen-

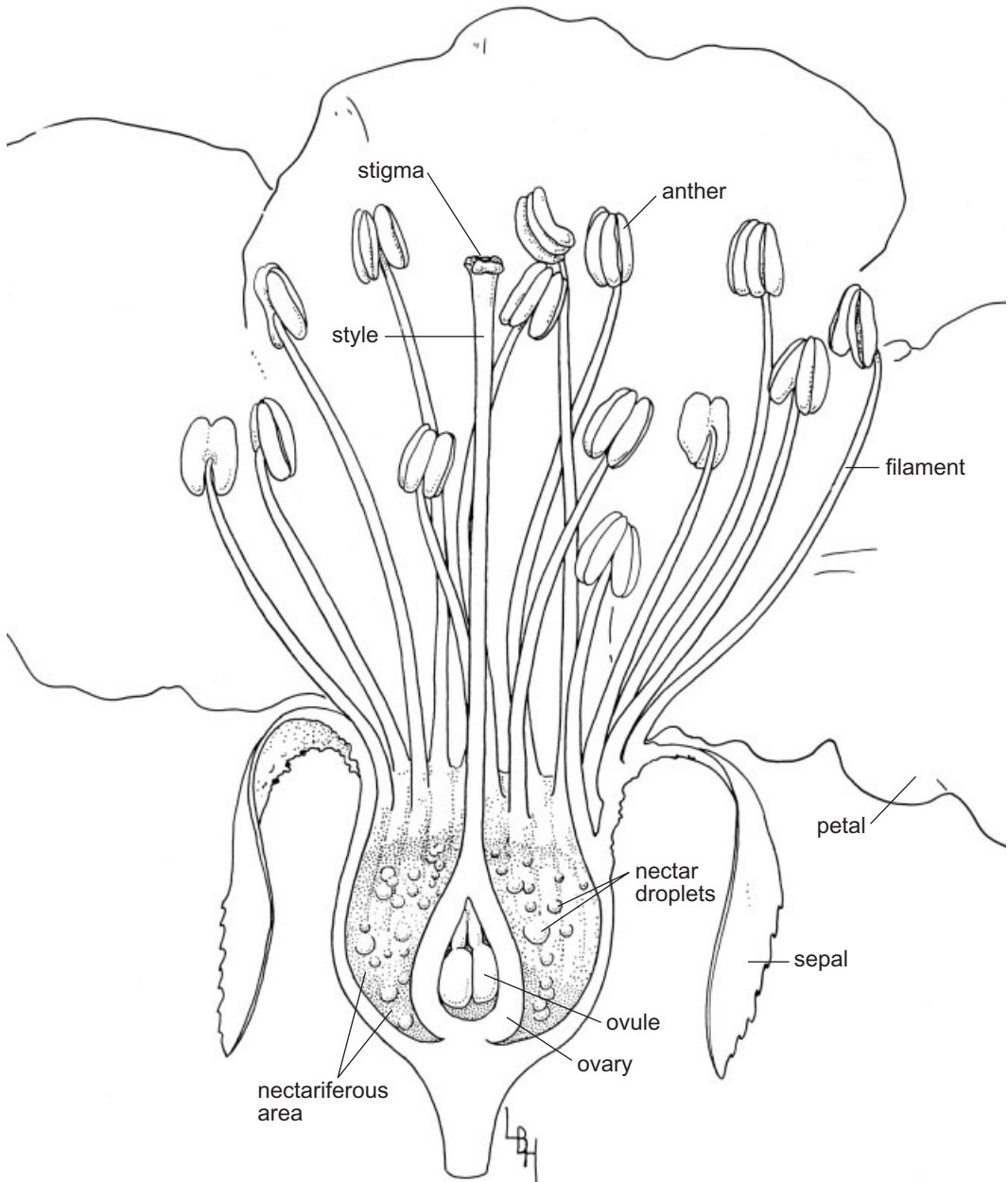


Figure 2.1. Longitudinal cutaway view of cherry flower showing typical stamens and simple carpel with two ovules in ovary. *From McGregor (1976).*

tative examples from the spectrum of stamen variation. A few technical descriptive terms are also introduced and explained. An important feature is how the filament is attached to the anther. The filament apex usually merges with

the base of the anther (basifixed) but in some plants—for example, lilies and the wind-pollinated cereal grasses—it connects instead about halfway up the outer side of the anther (dorsifixed), where it forms a flexible swivel joint