PLANT FORM

An Illustrated Guide
to
Flowering Plant Morphology

NEW EDITION

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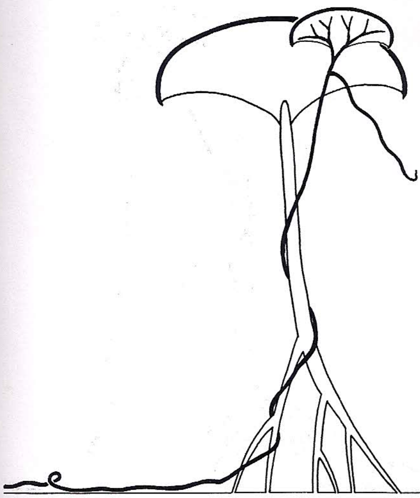
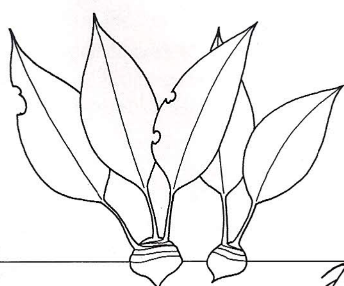
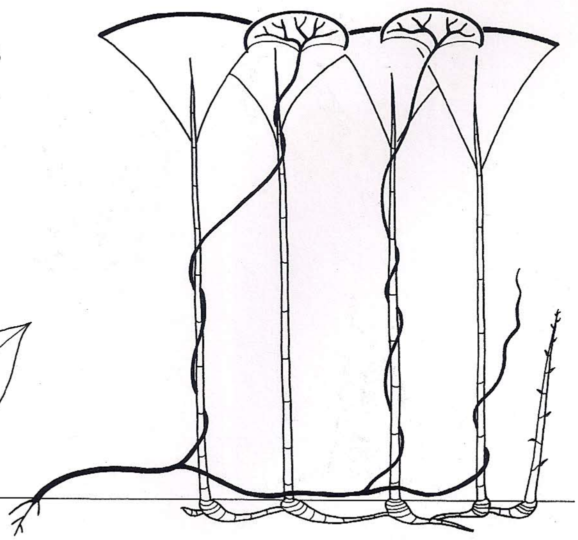
TIMBER PRESS
Portland · London







H I J K

Introduction

Plant morphology is concerned with the study of the external features of plants and is relevant to all aspects of plant biology (Sattler and Rutishauser 1997). Anybody who has an interest in flowering plants must at some time have given a specimen more than a passing glance and found various features that elicit curiosity. Indeed, there is a long history of interest in plant morphology. Perhaps the first scholars to become fascinated by the subject were Greek philosophers, especially Theophrastus (370–285 B.C.), who was bemused by plant form and set about describing it. He was concerned that an animal has a "centre," a heart or a soul, whereas a plant has an apparently unorganized form that is constantly changing shape and has no quiddity ("essence").

As plant morphology became a science, its purely descriptive role gained in importance. Today, description is still the first step in any taxonomic study. The pigeonholing aspect tended to lead to an inflexible facet of morphology (246) only relatively recently shaken off. Nevertheless, morphology has undergone several transformations throughout history (Claßen-Bockhoff 2001; Kaplan 2001a). Goethe (1749–1832) realized that a transition could be seen in the form of a leaf on a plant, perhaps from foliage leaf to scale leaf to sepal and to petal. This is an example of the concept of homology, about which much continues to be written (Sattler 1984; Tomlinson 1984). The foliage leaf on the plant and the petal, having the same developmental sequence and origins, are homologous structures. However, a foliage leaf and a flattened green stem (a cladode, 156) are not homologous. They are merely performing the same activity and thus are analogous. This is the classical view of plant morphology (246). Speculation about homologous relationships formed the basis of phylogenetic studies, that is, the identification of evolutionary sequences in plants. For a long time plant morphology became virtually submerged in this one field, particularly after the advent of Darwin's theory of evolution.

Another subject with which morphology is intimately associated is that of anatomy. All plant organs are made up of cells, and often the morphologist will want to study the development of an organ (its ontogeny) to understand its construction and affinities (36, 122, 142). Developmental anatomy and details of vascular connections (the veins) within the growing plant are thus an essential feature of many morphological investigations. In some quarters, morphology is indeed taken to cover both the external and internal features of a plant.

Dictionary definitions of *morphology* may exclude any aspect of function in its meaning. However, it is very difficult to ignore the implication of function that is manifest in many plant structures; the function of a leaf tendril (92) in the vertical growth of a climbing plant cannot be disputed. This obvious utility leads to teleological statements ("the plant has evolved tendrils in order to climb"), which should be avoided. Teleology is the philosophy that ascribes a deliberate intention of this nature to an organism. Plant morphology has always had a tendency to drift toward becoming a philosophical subject (Arber 1950), encouraging a contemplation and debate of the inner meaning of the plant (such as plant "intelli-

Tragopogon pratensis. Each fruit (an achene, 193A) borne on the capitulum (173J) has a pappus at its distal end, aiding wind dispersal (cf. 191M).

gence"; Trewavas 2003, 2004; Firn 2004). In contrast, the approach in this book is hopefully more practical. My intention is to provide an account of plant morphology as a working means of describing plant form, to emphasize that knowledge of the development of a plant or plant part is as important as its final shape, and thus to stress that a plant is a growing dynamic structure in light of which the many morphological aspects of the plant should be considered.

PART ONE
Morphological Description

Basic Principles

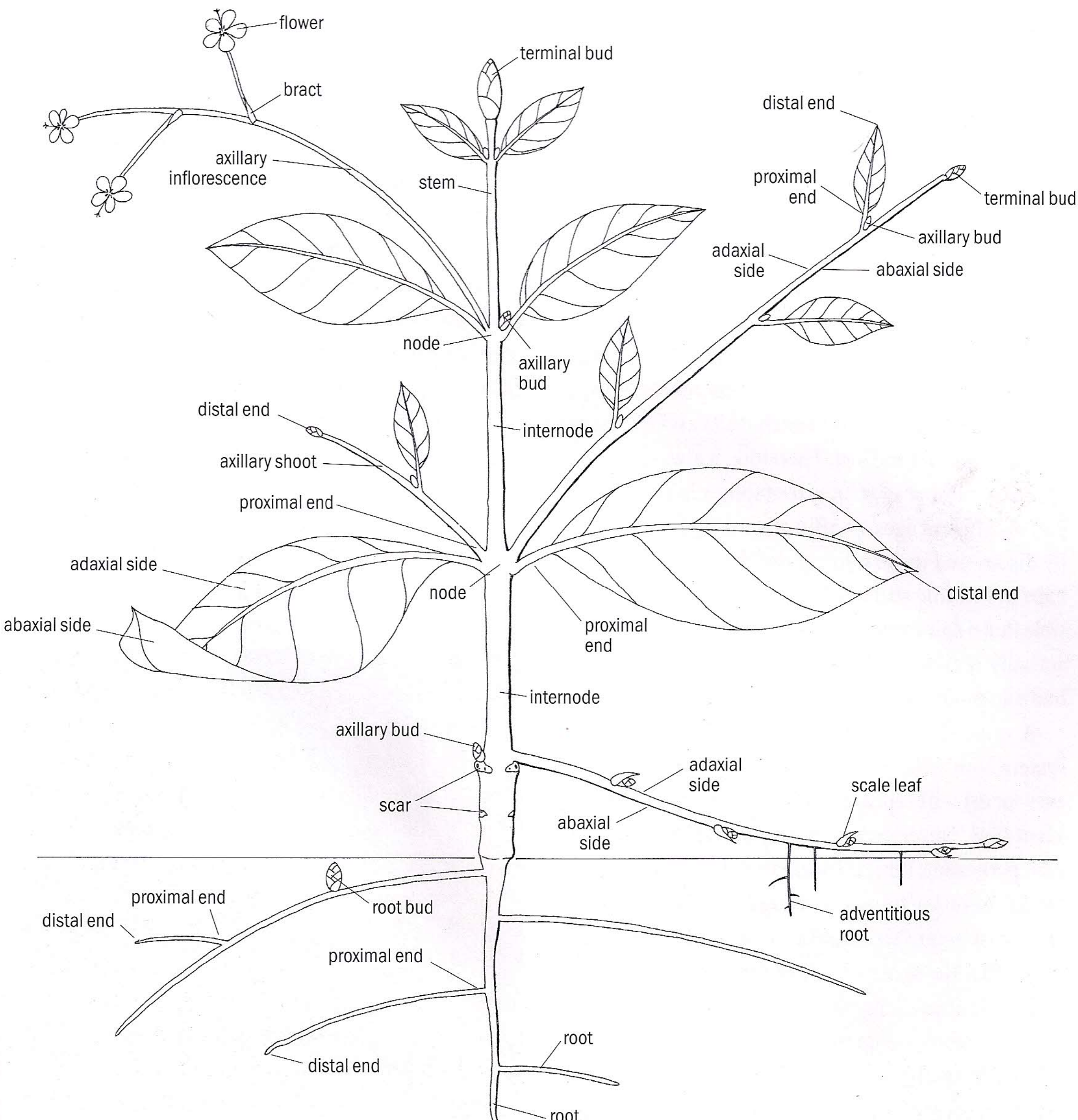
At first sight, many flowering plants have a familiar form. Each has an underground branching root system continuous aboveground with the shoot system (for a critical review of this classical axiom, see Groff and Kaplan 1988). The shoot system consists of stems bearing green (photosynthetic) leaves. The point on the stem at which one or more leaves are inserted (attached) is termed a node, and the interval of stem between two nodes is an internode. In the axil of each leaf (in the angle between the upper side of a leaf and the stem) is a bud or the shoot into which the bud has developed. Such a bud is termed an axillary bud in distinction to one at the end of a shoot, which is known as a terminal bud. A leaf is said to subtend its axillary bud or shoot. Topographical terms are useful. The top of a leaf or axillary shoot is referred to as its adaxial surface, with the underside being the abaxial surface. The part of a leaf, shoot, or root farthest away from its point of attachment is the distal end of that organ. The end nearest the point of attachment is the proximal end.

The various parts of such a conventional flowering plant are usually readily identified. A root bears other roots and in some cases will also bear buds (root buds, 214) but never leaves. A shoot bears leaves with buds in their axils and may also bear roots (adventitious roots, 126). Leaves can drop off, leaving scars (148), but there will still be a bud, or the shoot into which it has developed, in the axil of the leaf scar. Leaves may not be leaf-like in appearance: they may be represented by insignificant scale leaves (cataphylls, 88) or may develop in various ways, for example, as spines (20, 94) or tendrils (92). An underground structure lacking leaves is probably a root (122), but many plants have roots developing aboveground, and in some cases they are green (136B, 136C, 236). Conversely, a great many plants (particularly monocotyledons, 28) have underground stems (rhizomes, 160) that mostly bear scale leaves and adventitious roots (126). Thus, a plant should be searched for clues as to the nature of its parts: roots bearing usually only roots and stems bearing leaves of whatever morphology, each with its axillary bud. Leaves are usually relatively regular in their location (260). If the shoot is viewed with the youngest (distal) end uppermost (not necessarily the way it was growing), then a leaf will appear *beneath* each bud or shoot.

Many plants show variations of these basic formats. The most common variation is a shoot system that is sympodial rather than monopodial (294) with an apparent departure from the leaf–axillary bud arrangement along the axis. A relatively complicated example of sympodial growth is explained on pages 24 and 26. Other variations are leaves that lack associated axillary buds (288), leaves that subtend or apparently subtend more than one bud (280, 282), and buds that are not in the axils of leaves but are located on roots (214), in a displaced position on stems (274), in a normal position but with leaves absent, as occurs in many inflorescences (170), or buds actually *on* leaves (98). Many plants do not have a resting stage and thus have no buds as such, only apical meristems (34, 306). A careful study of the plant will normally reveal such morphological features; a dissection of the youngest growing parts will help to identify the relationship of the parts and an understanding of development is useful (leaf, 36; root, 122; stem, 142). It may be necessary to conduct a microscopic investigation of very early stages in some instances. Another factor that can

Photo page 17: *Hugonia* sp. The leaves are simple (42), and each has a pair of stipules (74) at the base of its petiole (60); the stipules are unusually compound (42). The stem is covered with scale insects.

mask the situation is that different organs can develop in unison and thus be joined together in the final form. This may be responsible both for the apparent displacement of buds (274) and the location of buds on leaves (98) as well as the fusion of parts (278). Some structures on stems and leaves do not represent leaves, buds, or roots: they are termed emergences (102, 146) and develop from epidermal and subepidermal tissue. The morphology of a plant can be recorded in many ways (22).



Interpretation Example, Spine

A spine is usually identified as a tough, probably woody structure with a sharp point. In morphological terms it may develop from almost any part of the plant or represent a modification of any organ, depending upon the species (102). In interpreting its nature, the basic rules of plant morphology outlined on page 18 should be borne in mind. A hand lens of 10× magnification is indispensable. Is the spine subtended by a leaf, that is, is it in the axil of an existing leaf or scar where a leaf has dropped off? If so, then the spine represents a modified stem (152). In many cases this will be confirmed by the presence of leaves (or leaf scars) on the spine itself (155C). However, a stem spine might be completely devoid of structures upon it. Also, it may be encroached upon by the expanding stem on which it sits and all traces of its subtending leaf lost. Therefore, it always pays to look at a number of structures (spines in this example) of different ages, as affinities are often more easily discovered in very young developing stages, perhaps even while still in a bud. For example, it is possible that a spine that is apparently in the axil of a leaf actually represents one of the leaves of the axillary bud and not the shoot axis itself (241B).

A spine that itself subtends a bud (or the shoot system into which the bud has developed of whatever form) will represent a modified leaf or part of a leaf (94). Nevertheless, it may be very woody and very persistent, remaining on the plant indefinitely. Again, in order to discover exact origins, a developmental sequence should be studied. This may reveal that the spine or spines represents the whole leaf (95D) or perhaps just its petiole (60B), and then either the whole petiole or just a predictable part of it (62A). Frequently, spines are found in pairs and then usually represent the stipules of a leaf (see photo this page, 79A, G). If the spine does not appear to fit into the leaf–axillary bud format, then there are still several possible explanations. For example, the spines of the Cactaceae (240) in fact represent modified leaves, but this is not at all apparent from casual observation; some plants have morphologies that are only decipherable with detailed, usually microscopic, study. A spine may be formed from a root (137E). It will therefore not be associated with a leaf, and its root origins will have to be identified by section cutting to show that it is endogenous (having its origin deep in existing tissue) in development and that it has a root anatomy and probably a root cap in its early stages (122). Leaf and stem spines are exogenous, arising at the surface of their parent organ (36, 142). Leaf, stem, and root spines will contain veins (vascular bundles). A fourth category of spine may be found on a leaf (102) or stem (146). This type of spine, a prickle, is not in the axil of a leaf, does not subtend a bud, is not endogenous in origin, and lacks vascular tissue. It is termed an emergence because it develops from epidermal and just subepidermal

Acacia sphaerocephala, with persistent stipular spines (78).

tissues. Emergences are usually much more easily detachable than stem, leaf, or root spines. This general account of spine could equally well have taken tendril (92, 152) as its theme. The same rules apply, bearing in mind that some plants are nonconformists (246) and that displacement and merging of different organs can take place (bud displacement, 274; adventitious buds, 276; adnation, 278; teratology, 316).

The range of structures forming spines (see also stipular spine, 78; bract spine, 85C; leaf spine, 94; leaf emergence, 102; adventitious root spine, 136D; root spine, 136; stem emergence, 146; stem spine, 152; inflorescence (peduncle) spine, 177F).