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Introduction

1.1 The study of flowers: the evolutionary context

Since the pioneering classical works by J. W. von Goethe (1790) on comparative morphology and by C. K. Sprengel (1793) on comparative flower biology two hundred years ago the study of flowers has diversified into many branches of botany and its interface with zoology. Floral studies now embrace morphology, anatomy, development, pollination biology, breeding systems, genetics, molecular biology, palaeobotany, and diversity and evolution. The past two decades, especially, have been a time of fascinating discoveries with the elaboration of scanning electron microscopy, the advent of new molecular genetic techniques, the detection of well-preserved early fossils, and broader diversity studies. Mainstreams of research have diverged in the course of time into more profound and at the same time more narrow approaches. Thus it becomes difficult to synthesize a picture of our present knowledge about flowers, not only because of the vast literature, but also because the study of complexity and of diversity necessarily have very different approaches, so that a complete picture will never be possible. However, some new views may emerge.

Flowers are devices to allow sexual processes and the subsequent production of propagules. Sexual processes are pervasive in the living world and each organism group has evolved with this phenomenon elaborating successively more complexity around it. The evolution of flowers with their particular functions has to be envisioned starting from the still flowerless early seed plants. This particular historical situation of the angiosperms (or more broadly: the anthophytes) is expressed in that sexual processes take place within the ovules and in that propagules are seeds, which develop from the ovules. The relatively high complexity of flowers involves a number of special functions that finally lead to the sexually derived propagules.

In the course of plant evolution in the higher evolved groups the more complicated sporophytes dominated more and more over the gameto-

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phytes. In the angiosperms this resulted in the highly reduced embryo sacs and pollen tubes as the last remnants of the female and male gametophytes, respectively. The embryo sacs develop within ovules, which are included in carpels. The male gametophytes develop from the microspores, which are produced in the pollen sacs of the stamens. The microspores have to be transported to the carpel surface in order to be able to produce the pollen tubes, which then grow through the carpels to the ovules. Pollen germination takes place on a special site of the carpel surface, the stigma.

In the pathway of the male gametophyte from the pollen sac to the stigma and from the stigma to the ovule there are manifold intricate devices to facilitate or to hinder self or foreign pollen (or gametophytes) in attaining the goal. The very different nature of the two parts of this pathway require (or enable) different means to work. For the first part action of animals or abiotic agents (or sometimes the plant itself) is necessary, resulting in pollination; for the second part physiological and cytological interactions of gametophyte (pollen tube) and sporophyte (carpel and ovule) are required, resulting in fertilization (syngamy) within the embryo sac.

Pollination, especially if effected by animals, requires pollinator attraction by different means. The advent of petals and nectaries early in angiosperm evolution, in addition to many other devices, reflects these needs. And finally, or better, initially, organs for efficient protection of all these parts during the period of their earlier development are required, the more so, the more elaborated (complicated) the flowers become. Sepals have evolved to fulfil these functions. In many cases extrafloral organs, especially bracts, are also involved in flower protection and pollinator attraction.

Owing to their early coevolution with pollinators, flowers were an important factor in the diversification of certain animal groups: bees, butterflies, moths, flies, hummingbirds, bats and others. These animals, in turn, promoted the explosive radiation and diversification of the flowering plants, the flowers being at the centre of this diversity.

Flowers are highly plastic structural systems, so they were able to acquire their overwhelming diversity. On the other hand, there are all kinds of limitations, constraints that prevented the evolution of certain forms.

Therefore, all the flowers of our wildest dreams do not occur in nature. Not only must the forms function in all their respects, but the complicated forms must also arise from an apical meristem by an ordered development. Both these requirements set constraints on the array of conceivable forms.

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Table 1.1. *Aspects of flower structure*

	Emphasis		Example: <i>Thunbergia grandiflora</i>
Organization (Bauplan)	Historical	Macroevolution	Acanthaceous flower
Construction (Gestalt)	Architectural	↕	Lip-flower
Mode	Ecological	Microevolution	<i>Xylocopa</i> bee-flower

Ecology and morphogenesis set outer (ultimate) and inner (proximate) constraints on the forms. By the intervention of the historical dimension, these levels of nature interact in different ways.

Flowers are never completely and ideally adapted to their environment. They are constrained by history: they have a phylogenetic burden. Many levels of their evolutionary history have imprinted their marks on them. They cannot escape them. One can often see traces of earlier phylogenetic (sub)strata in the structure of flowers. One should not forget that each flower, however harmoniously functioning at any time, is a mixture of features that are of different evolutionary ages. Different historical levels are incorporated and work together. The notion of 'evolutionary tinkering' (Jacob 1977) is especially apt for flowers.

A practical approach is to recognize three levels: (1) organization (bauplan, groundplan); (2) construction (architecture, gestalt); and (3) mode (style) (Delpino 1868–74, Vogel 1954) (Table 1.1). These three levels are successively more superficial in terms of their phylogenetic roots. 'Organization' rests on (phylo)genetically deeply rooted patterns that are the least easily changed. 'Construction' relates to proportions that have to do with mechanical properties and architectural features. 'Mode' means relatively superficial adaptations, especially in terms of pollination biology, such as size, colour, scent, indument etc., that are often highly variable at low systematic levels. These three levels do not form closed, mutually exclusive systems, since they are evolutionarily interconnected, and they should not be used in too rigid a manner. They correspond to some extent to the 'historical', 'fabricational' and 'functional' aspects of morphology as used in zoology (Seilacher 1974; see also Reif 1975, Riedl 1978, Gould & Lewontin 1979, Kaplan & Hagemann 1991).

In this book aspects of organization are mainly treated in chapter 2, aspects of construction in chapter 3, and aspects of mode in chapters 4 and 5.

1.2. Tropical flowers

The comparative study of flowers began in temperate regions. Traits of temperate flowers also occur, of course, in tropical ones. In many respects, however, the emphasis is different, and some phenomena are purely tropical. A pioneer of tropical research was F. Müller, whose Brazilian observations brought a wealth of novelties in his time. Although his publications were scattered pieces of information (collected by Möller 1915–21), they were discussed and brought to the attention by his brother H. Müller and by Ch. Darwin. The floral biologist F. Delpino unfortunately had to return early from a travel to South America owing to illness, but he included a number of tropical plants in his classical work (1868–74). Of Darwin's three books on flowers, only the one on orchids (1862) contains information on a fair number of tropical examples, including a balanced treatment from bauplan to pollination biology.

At the end of the last century and in the first half of this century the main activity of tropical botany was in Eastern Asia, centred around the Botanical Gardens in Bogor and Singapore. Most botanists did not devote their work particularly to the study of flowers. They were overwhelmed by the tropical diversity and gave more general accounts including notes on flowers, especially on phenology (e.g. Haberlandt 1893, Massart 1895; for the Neotropics see, for example, Belt 1874, Spruce 1908). Burck's (1890) studies on flowers of Annonaceae are an example of interesting observations with interpretations that did not hold, since they were derived from temperate plants. One of the first authors to give a comparative survey exclusively on some tropical flower phenomena was Beccari (1904) from his observations in Borneo. In Bogor important studies on the anatomy and embryology of tropical flowers were carried out: Treub (1889) and Koorders (1897) investigated the comparative anatomy of water calyces and Treub (1891) detected the chalazogamy in *Casuarina*; Ernst studied tropical parasites and mycotrophic plants, including *Rafflesia* (Ernst & Schmid 1913). Knuth (1898/99) and Knuth *et al.* (1904/05) compiled many observations on tropical pollination biology.

Tropical flower biology also has important roots in Java in the first half of our century with the work of van der Pijl (e.g. 1930), Cammerloher (e.g. 1931), Porsch (e.g. 1936), and Docters van Leeuwen (e.g. 1938). Corner (e.g. 1940), based on the Malayan Peninsula, also included observations on flowers in his general work on tropical plant biology. Other observations on phenology were published, for example, by Coster (1926), Holttum (1940), and van Steenis (1942).

After the second world war, new activities in the study of flowers arose in all parts of the tropics. Corner (e.g. 1946, 1949) and van der Pijl (e.g.

1954) continued their Eastern Asiatic work. Baker (e.g. Baker & Harris 1957) and Vogel (e.g. 1954) studied pollination biology in Africa, Vogel also in South America (e.g. 1957). The general books on tropical plant biology by Richards (1952), Holttum (1954), and Corner (1964) included accounts on flowers.

In the 1960s, studies on floral biology expanded rapidly in all regions of the tropics but with a prominent concentration in the Neotropics. These studies yielded many exciting new insights, which will be discussed in this book. A number of surveys, textbooks, and research programmes of tropical biology, including aspects of flowers, have also been published since that time (e.g. Baker 1964, Baker *et al.* 1982, van der Pijl 1969, Janzen 1975, 1977, 1983a, Ashton 1977, Tomlinson 1977, 1980, 1986, 1990, Croat 1978, Hallé *et al.* 1978, Raven 1980a, Longman & Jenik 1987, Bawa *et al.* 1990, Benzing 1990, Whitmore 1990, Mabberley 1992). Other general works, even if centred in temperate regions, contributed to the advance in our understanding of flowers (e.g. Knoll 1956, Werth 1956a, Jaeger 1959, Meeuse 1961, Percival 1965, Free 1970, Kugler 1970, Proctor & Yeo 1973, Sattler 1973, Frankel & Galun 1977, Faegri & van der Pijl 1979, Guédès 1979, Bernier *et al.* 1981/85, Barth 1982, Rohweder & Endress 1983, Vogel 1983, Willson 1983, Willson & Burley 1983, Meeuse & Morris 1984, Richards 1986, Moncur 1988, Sedgley & Griffin 1989, Weberling 1989, Fahn 1990, Hess 1990, Dafni 1992). In addition, a large number of edited books containing articles on flowers have appeared in this period, which cannot all be mentioned here.

Today, facing the threats to biodiversity, especially in the tropics, better knowledge of the biology of flowers in the widest sense is urgent. The understanding of flowers is a central theme for the phylogenetic reconstruction of the angiosperms at all levels. Better knowledge of phylogenetic history and of interactions between animals and plants is vital for evaluation of conservation actions (e.g. Bobisud & Neuhaus 1975, Janzen 1977, 1986a,b, Tomlinson 1977, Prance 1990, 1991, Soulé 1990, Bawa & Ashton 1991).

1.3 *Delonix regia*, the flamboyant (Caesalpinaceae): an introductory example

‘This tree is a joy of creation, beyond the invention of man’
 (Corner 1988: *Wayside trees of Malaya* 1, p. 435).

The flamboyant (*Delonix regia*), with its exceedingly attractive flowers, is one of the most familiar ornamental trees in the tropics (Fig. 1.1). The trees flower best in regions of the wet tropics with a longer dry period.



Figure 1.1. *Delonix regia* (Caesalpinaceae). 1. Inflorescence ($\times 0.3$).
 2. First-day flower with expanded flag ($\times 0.7$).
 3. Second-day flower with folded flag ($\times 0.7$). 4. Two differently folded flags of older flowers ($\times 0.7$).

Flowering is at the end of the dry season, when the trees may be in flower for a month or so (Ghouse & Hashmi 1981).

But where is the origin of this widely cultivated tree? What is its reproductive biology, and especially the biology of its fulminant flower display? In 1828 the Austrian botanist Wenzel Bojer discovered the species at Foul Point on the east coast of Madagascar (Blatter & Millard 1977). In 1829 the original description (as *Poinciana regia*) accompanied by a coloured plate was published in Curtis's Botanical Magazine (tab. 2884). In 1837 Rafinesque used the name *Delonix regia* for the first time. Bojer introduced the tree in Mauritius, and from here it was distributed to several other tropical regions. In Singapore it is recorded from 1840 (Corner 1988). Later the species seemed to be extinct in the wild and its origin was uncertain. Only after a century, in October 1932, was the plant refound, apparently indigenous, in the forest reserve of Antsingy (West Madagascar) by Léandri (1933, 1936).

Although the tree regularly produces fruits and seeds in cultivation, almost nothing is known about its floral biology. The fruits are conspicuous, large, woody pods and contain numerous seeds. There are only vague indications about pollinators. They have never been observed in the putative natural environment of the species in Madagascar. Only scattered observations from cultivated specimens outside Madagascar mention birds (Winkler 1906, Werth 1915, Arroyo 1981) and butterflies, mainly Papilionidae (Vogel 1954, Owen 1971, DeVries 1983a,b) as flower visitors. Arroyo (1981) rates *Delonix regia* as a 'classic ornithophilous species of the Old World' that acquired ornithophily through butterfly-pollinated intermediaries. Winkler (1906) interprets the adaptational situation of the species as transitional from butterfly to bird pollination but more on the ornithophilous side.

Not even the floral behaviour during anthesis has been studied in detail so far, except for a short note by Corner (1988): 'Though the flowers are not fully open until 9 a.m. or later, the petals begin to emerge from the calyx-bud shortly after midnight. The flowers last only two days, and the standard curls up and fades on the evening of the first day'. One also knows of the peculiar asymmetric nectar gate at the flower base (Lindman 1902, Troll 1951), the amount of nectar production per day of the flowers (Fahn 1949), some features of floral anatomy (Rao & Sirdesmukh 1956), details on pollen structure with its peculiar viscin threads (Cruden & Jensen 1979, Hesse 1984a,b), and the occurrence of a crateriform wet stigma (Owens 1990).

Thus, there are a number of very scattered bits of information, which do not give a coherent understanding of the flowering in this species. It

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may stand as an example for the paradoxical situation of how poorly known even ‘familiar’, conspicuous and widely used plants in the tropics are and how they are threatened by extinction in their natural habitat. Some new observations on *Delonix* will be presented in section 8.6.1.

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Floral organization (bauplan, groundplan)

2.1. Structural units and floral symmetry

Flowers are complicated plant parts. They are differentiated into regions with different structures and functions. Each region contains a number of structural units. Flowers have a closed organization, since the floral apex is no longer active after initiation of the innermost floral organs. Different kinds of organs have different functions in the flower. Repetitive patterns abound in that each kind of organ mostly occurs in sets of variable or fixed numbers (structural units). A flower or floral axis is usually situated in the angle between a subtending leaf (a bract or a foliage leaf) and an axis. This subtending leaf is the perophyll of the flower. Often the floral axis contains one (adaxial) or two (lateral) bracteoles (prophylls) below the flower.

Many flowers are so attractive to us because of their often high symmetry, be it the bizarre mirror-symmetrical form of an orchid or the 5-parted windwheel of a periwinkle. The two most common symmetry patterns are polysymmetric (actinomorphic, radially symmetric, regular) flowers having several symmetry planes, and monosymmetric (zygomorphic, dorsiventral) flowers having only one symmetry plane. Dissymmetric flowers (with two symmetry planes) and asymmetric flowers are more rare.

Symmetry is primarily determined by the number and arrangement pattern of the structural units. Monosymmetry is often superimposed on a primary polysymmetric configuration of the structural units (and asymmetry often on a monosymmetric configuration) by unequal differentiation of floral sectors (see also sections 3.5 and 9.2.1).

The floral organs arise on the floral apex in ordered patterns, basically in a centripetal sequence, as do the organs of the vegetative shoots. At transition from the vegetative into the floral state the apical meristem becomes more massive (deep) and may develop into a 'meristem plug' (Rauh & Reznik 1951). At its upper edges the outermost floral organs are

initiated, followed rapidly by the inner ones. The formation of a massive apical meristem is a precondition for the rapid initiation of the floral organs. The floral organs appear as fully meristematic hemispherical or somewhat laterally (tangentially) extended mounds. These first stages are similar for all organ types. Organ initiation often manifests itself as a locally more intensely staining field in the floral meristem. The first periclinal cell divisions that follow organ initiation and are associated with the beginning of bulging up of the organ primordium occur in the second and/or deeper layers of the floral meristem, apparently merely depending on the later thickness of the organ (Rohweder 1963, Guédès 1979). The formation of an organ primordium induces a procambial strand that later becomes the main (middle or dorsal) vascular bundle of the organ. The procambial strand connects with one or more older vascular bundles deeper in the floral base. As the organ grows, more procambial strands may be formed. Procambial strands are initiated where they are needed, i.e. in the direction of main photosynthate attraction by a morphogenetic centre, whereby certain taxon-specific patterns may be superimposed (e.g. Carlquist 1970, Kaplan 1971, Rohweder 1972, Schmid 1972).

During floral development, centres of activity of growth and differentiation arise and are replaced by other ones at other sites. Each centre influences its neighbourhood in that the adjacent regions have to adjust to the newly arisen changes. During the entire development process, regions in the floral base are influenced at different times from different directions, involving differential thickening, tissue differentiation and vascular bundle formation. The structural interpretation of mature organs has to take this into consideration.

With the process of floral elaboration in the course of evolution, floral organs of one kind may fuse postgenitally (in that free parts fuse during ontogeny) or congenitally (in that a common base of several organs develops as a ring wall, which may eventually form a tube). In the most elaborate flowers, organs of different kinds may also fuse (postgenitally or congenitally) to form complicated structures (organ complexes). Other terms for congenital fusion are phylogenetic fusion (Cusick 1966), meristem fusion (Hagemann 1970) and interprimordial growth (Sattler 1978). The growth process of the congenitally united base of organs is also referred to as zonal growth. Mechanisms of postgenital fusion have been reviewed by Verbeke (1992). The terms 'fusion' and 'union' are often used in the same sense, but one tends to use 'fusion' if organs of different kinds are involved, and 'union' if organs of the same kind are involved.

Plants, in contrast to animals, have rigid cell walls, and there is no cell migration during development. Therefore, the surfaces of mature floral