

Structure and function of the fig

W. Verkerke

Hugo de Vries Laboratorium, Kruislaan 318, NL-1098 SM Amsterdam (The Netherlands)

Summary. An overview is given of the functional anatomy of the fig. The fig is the site of pollination and oviposition, it produces wasps, seeds and pollen, and it is the unit of dispersal. Therefore the fig acts as both a flower and a fruit. When a flower is both fertilized and receives a wasp egg, it eventually produces a wasp. Fertilization in flowers that do not receive a wasp egg initiates seed production. Wide variation exists in the structural features of figs among different subgenera and sections. Monoecious species and gynodioecious species have different strategies for maintaining the symbiosis with the pollinating fig wasps. Monoecious species produce wasps and seeds in a single fig type and show imperfect heterostyly. Gynodioecious species have specialized figs for wasp and for seed production and are characterized by perfect heterostyly.

Key words. *Ficus*; Moraceae; Agaonidae; dioecy; anatomy; pollination; oviposition; dispersal; ovule.

Introduction

A fig or syconium is an infolded receptacle apically closed off by numerous bracts. These bracts tightly close off the entrance or ostiole, which is externally visible as the 'eye' of the fig. Internally, the fig wall is beset with small unisexual flowers, sometimes called 'florets'. The fig is often called a 'fruit', but as it is both the site of pollination and pollen production and the unit of dispersal, it acts both as a flower and a fruit. The real fruits are the small matured ovaries which, depending on their wall structure, are to be designated as achenes or drupes^{4,6}, but are often called 'seeds'. The true seeds remain enclosed by the tough endocarp layer. In *Ficus*, there are two main groups of species, which each have a different strategy of maintaining the symbiosis with the agaonid wasps: the monoecious and the gynodioecious species. The figs of the monoecious species contain many female flowers with a variable style length and but few male flowers. They produce seeds, wasps, and pollen within a single fig. The gynodioecious species have two fig types, each occurring on separate plants: seed figs which only contain numerous female flowers with long styles, and gall figs containing both many female flowers with short styles and some male flowers. Until maturity, the two fig types are externally indistinguishable, but internally they show characteristic differences. There is a clear division of labour between these two fig types: the gall figs produce wasps and pollen, while the seed figs produce seeds. Hence the seed figs and gall figs are often called 'female figs' and 'male figs', respectively. Functionally speaking this is correct, because the female flowers of the gall figs produce wasps and so contribute to the male function of the fig. The monoecious species are classified in the subgenera *Pharmacosycea*, *Urostigma*, and section *Sycomor*; gynodioecious figs occur in the subgenera *Ficus*, *Sycidium*, and section *Neomorphe*, while section *Sycocarpus* is partly monoecious, partly gynodioecious³. The developmental stages of the sycone are generally subdivided according to the terminology devised by Galil and Eisikowitch²⁰. The stages before the wasp's entry

are called the A or prefloral phase, and this phase may take some 3 weeks. In the receptive or B phase the wasps enter the fig through the ostiole. This phase may last a few (3–6) days; when no wasps enter the fig, it may extend longer. The subsequent phase is the C or interfloreal phase, in which the wasps and the seeds develop in the fig. The C phase can last from 2 to 6 or up to 10 weeks, depending on the species. At the D or emission phase the next generation of wasps emerges, the anthers open, and the female wasps leave the fig, loaded with pollen. This phase may take 3–4 days^{1, 23, 43, 44}. The D phase is lacking in seed figs of the gynodioecious species. After the wasps have left, the fig ripens further and becomes attractive to animal dispersers (E phase). In some species it is reported that gall figs develop and ripen in two-thirds of the time required by seed figs⁸. Most of the time it is C phase figs that are encountered in the field, and hence these are mostly collected. However, during the C phase several developments take place in the fig that may completely change the internal structure, and for a good comparison of different figs, the study of B phase figs is important.

Several anatomical studies on reproductive structures of *Ficus* have been carried out^{6, 7, 22, 30–32, 36–38, 45, 47–51, 53}. This paper summarizes our present knowledge of the reproductive anatomy and morphology, and indicates the main gaps in our understanding of the relationship between structure and function in the fig.

The fig

The inflorescences of the Moraceae are highly variable and may appear as discoid or turbinate discs (*Dorstenia*, *Brosimum*), as globular or clavate inflorescences with the flowers on the external surface (*Artocarpus*, *Treculia*), or as urn-shaped receptacles with the flowers on the inner surface as in *Sparattosyce* and in *Ficus*^{4, 10, 31, 46, 50, 52}. The fig develops from an initially flat disc by incurvation and enlargement. The formation of the fig starts when a series of bracts are initiated; then the receptacle starts to

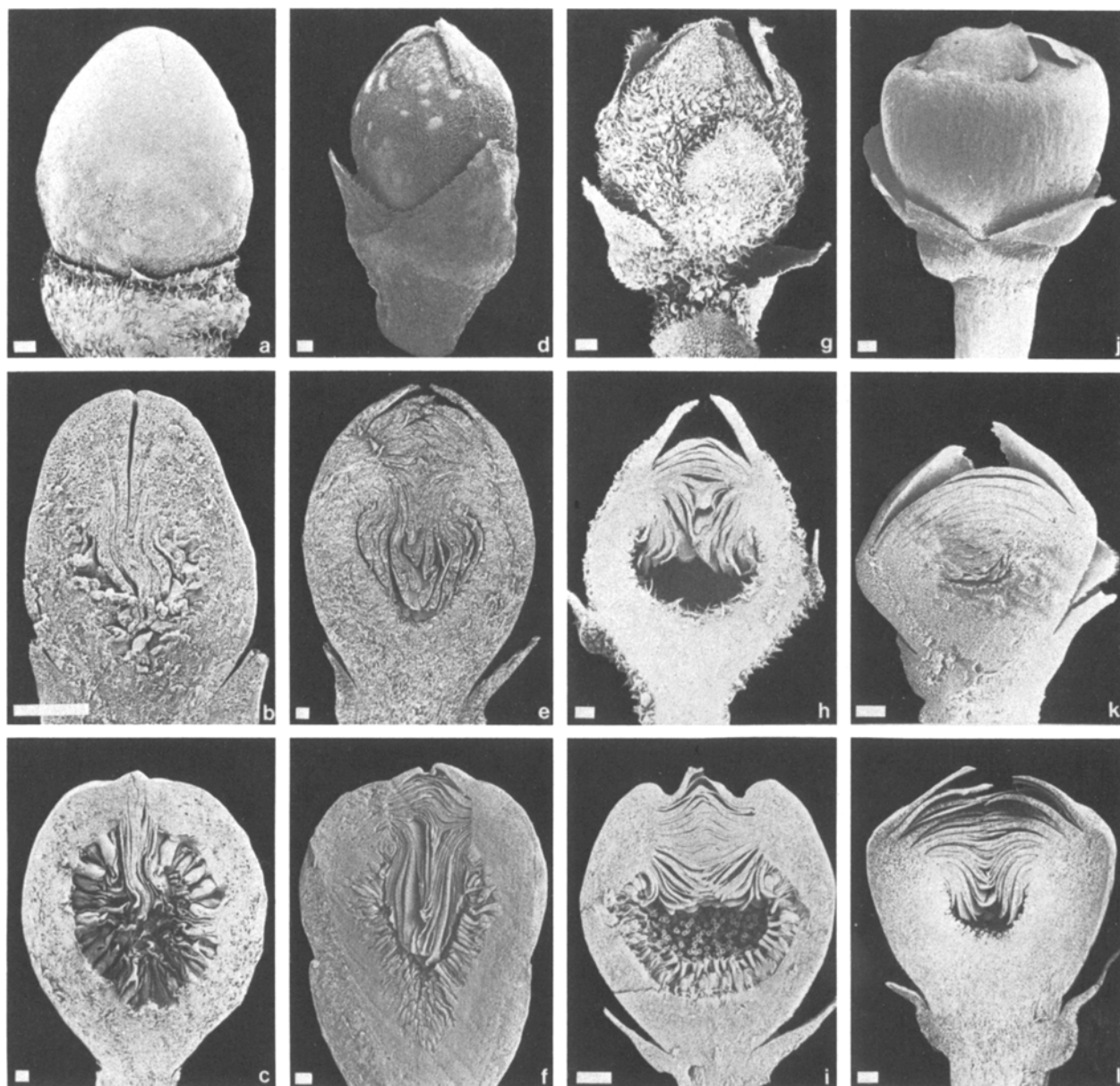


Figure 1. Syconia of different subgenera, early A phase (top row), in longitudinal section, early A phase (middle row), and long section, middle A phase (bottom row), resp.; a–c *Urostigma* section *Galoglychia*;

d–f section *Sycidius*; g–i *Sycidius*; j–l subgenus *Ficus*; bar indicates 200 μ m.

curve and becomes urn-shaped^{45, 50}. When the outer bracts meet, they close off the receptacle and form the ostiole. The ostiolar bracts may face each other and bend down towards the receptacle or interlock. Depending on the ratio between fig wall growth and the speed of bract initiation in the A phase, other bracts may become scattered on the syconial surface (lateral bracts) or remain at the joint of the fig with the peduncle (basal bracts); bracts may also be present on the peduncle (peduncular bracts, in *Sycidius*). Lateral bracts frequently occur in the gynodioecious sections *Sycidius*, *Sycocarpus*, *Neomorphe*, and subgenus *Ficus*; they are lacking in subgenus *Urostigma* and the monoecious section *Sycomorus*, and are rare in subgenus *Pharmacosycea*^{8, 18}. Some figs ex-

hibit a limited growth above the insertion point of the basal bracts and develop a short neck (stipitate figs). In monoecious species a syconial cavity develops just before the receptive phase, and early A phase figs are completely filled (fig. 1, a–f), but in the gynodioecious species the figs are hollow from the early A phase onwards (fig. 1, g–l). In the interfloral phase the enlarging drupes and galls may fill the syconial cavity completely, but on account of the fig enlargement it opens again at the D phase and allows the wasps to emerge from their galls. The ostiole functions as a barrier against non-pollinating insects. Gland-like structures are present on the ostiolar bracts of *F. ottonifolia*⁴⁷ and anatomically they seem rather similar to the extrafloral nectaries that occur in

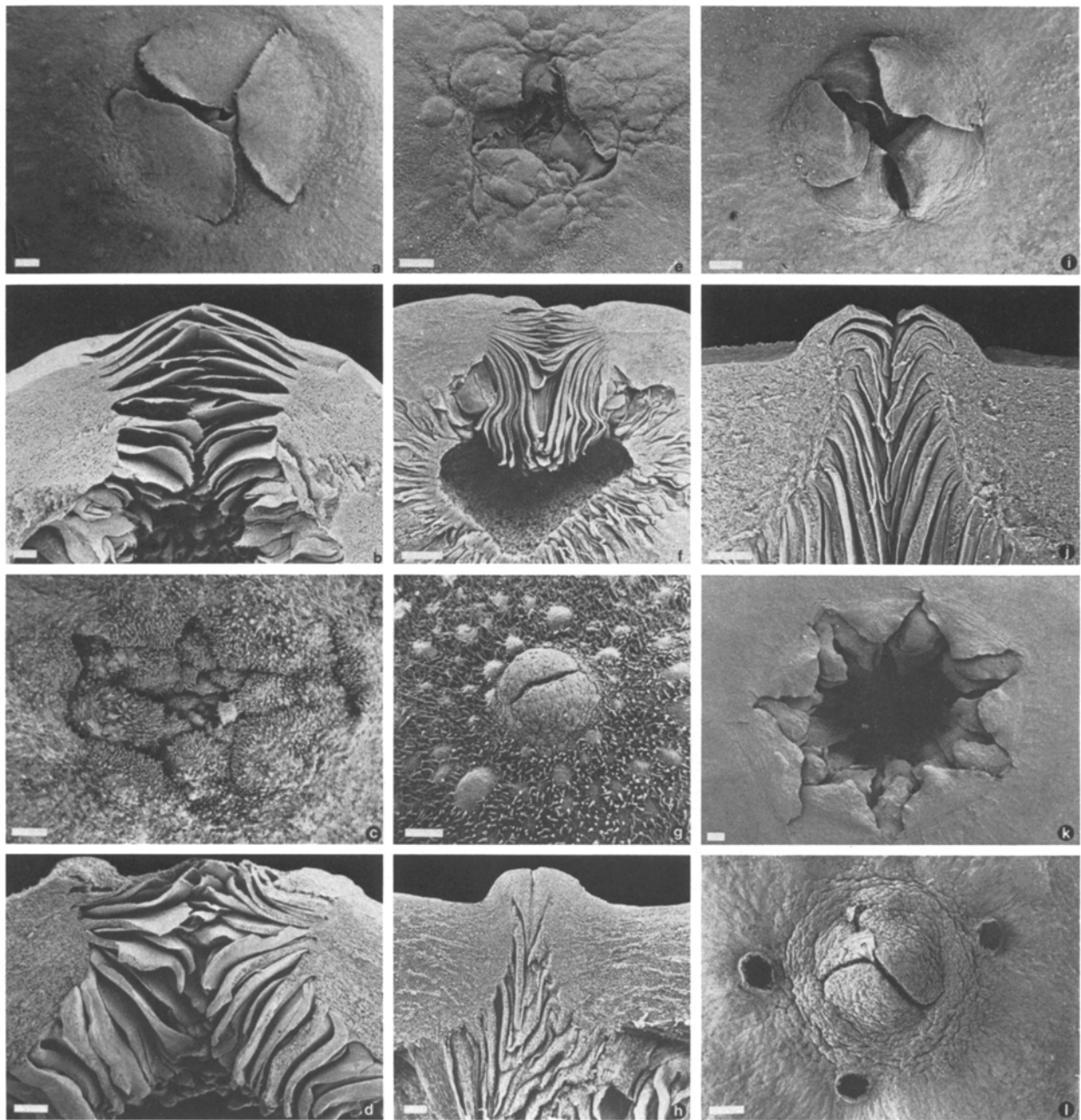


Figure 2. Ostiole in top view (a, c, e, g, i, k, l) and longitudinal section (b, d, f, h, j); a–j: B phase; k, l E phase; a, b subgenus *Ficus*; c, d *Sycidium*; e, f section *Sycomorus*; g, h *Urostigma* section *Galoglychia*;

i, j, k section *Pharmacosycea*; l *Urostigma* section *Americana*; bar indicates 500 μ m.

Acanthaceae¹⁹, but their possible function in wasp attraction is unknown. In some species the ostiole may open slightly at the receptive stage, but still many prospective pollinating fig wasps do not manage to pass through the ostiole⁴⁰, and the detached wings of a fig wasp often remain visible on the ostiole as a 'bouquet'. Up to 6–10 wasps may be trapped in the tunnel while only two reach the syconial cavity³⁴. The shape of the ostiole has been correlated with the morphology of the wasp, especially in relation to the entering of the fig⁴⁴, but on the other hand ontogenetic studies indicate that in

the monoecious species the bracts also play a major role in flower development and the establishment of heterostyly^{50, 51}. Three main ostiolar types with considerable differences in accessibility of the syconial cavity can be distinguished⁴⁴, as follows. 1) All bracts interlocking to form a helicoidal passage to the syconial cavity (*Urostigma* sections *Americana*, *Urostigma*, *Leucogyne*, *Conosycea*, *Stilpnophyllum*). The gynodioecious species (subgenus *Ficus*, sections *Sycidium*, *Neomorphe*, *Sycocarpus*) have a somewhat similar ostiole, but with the bracts more loosely arranged and often more than one bract

visible from the outside (fig. 2, a–d). In the monoecious section *Sycomorus*, a modified type 1 ostiole is present: the innermost ostiolar bracts are elongated and point towards the receptacle (fig. 2, e and f). 2) The upper ostiolar bracts interlocking, but the lower ones bending down to leave a tunnel-shaped passage to the syconial cavity (section *Pharmacosycea*, fig. 2, i and j). 3) All bracts descending to form a bilabiate (*Urostigma* section *Galoglychia*, fig. 2, g and h) or bilabiate-triradiate (*Urostigma* section *Malvanthera*) slit. During the interfloral phase the ostiole remains firmly closed, but in gall figs of the gynodioecious *Sycidium* the ostiole opens through a lateral enlargement and a simultaneously-occurring relaxation of the bracts at the D phase^{35,49}. Seed figs lack a D phase and their ostioles do not open again. The presence of stomata on the inner ostiolar bracts (*F. fistulosa*, *F. sur*) may play a role in their relaxation. In the subgenus *Urostigma* and the monoecious section *Sycomorus* the ostiole does not open fully at the D phase; the bracts may relax only slightly (*F. sur*) or the ostiole may remain stiffly closed (*F. ottoniifolia*). In section *Pharmacosycea* the opening is variable: in *F. insipida* (fig. 2k) the ostiole swells open whereas in most *F. yoponensis* and some *F. maxima* the male wasps must cut holes through the fig wall (E. A. Herre, pers. comm.). The tunnels can be made either through the ostiolar bracts, or near to the ostiole (fig. 2l), or elsewhere on the fig (*Urostigma* sections *Galoglychia*, *Malvanthera*); apparently this depends on the species of wasp emerging³. Besides this, Corner illustrates gall figs that split completely open at the D phase (*F. lamponga*; subgenus *Ficus* subseries *Dehiscences*)¹³.

The fig wall is generally parenchymatic and contains some 30–40 cell layers. Various sclerified cell layers may occur and their presence or absence has taxonomic significance¹¹. The fig wall contains many laticifers, tannin cells, and a vascularization that supports both the flowers and the ostiolar bracts. The epidermis is densely covered with two types of hairs, i.e., small glandular pluricellular hairs, and larger conical unicellular hairs; the texture of the fig may change upon ripening. Some figs contain typical, white and entirely glabrous epidermal spots which seem to be the only places where stomata occur on the fig surface. The spots lack any vascular supply, and are structurally different from the leaf spots^{39,47}. It is not known whether the pollinators are interested in these spots, and their function is not clear. At the receptive or B phase the fig is often slightly softer, as can be detected by gently squeezing it between two fingers, but C phase figs are usually hard and stuffed with a sticky latex. At the D phase the latex and tanniferous compounds disappear as the fig swells and softens. Many figs are green, yellowish, or red throughout their development, but at the E phase they often enlarge further, become mature and soft, and usually change to a brighter or more intense colour such as a dark red, bright orange or yellow. Some mature figs may also have a sour-sweet

odour^{1,35} while others remain green or brownish and develop a mushroom-like odour⁴⁷, or even smell of rotten fish (*F. calypttrata* (*Urostigma* section *Galoglychia*), C. C. Berg, pers. comm.).

Figs may range from 3–4 mm up to 10 cm in diameter, the largest figs occurring in *Kalosyce*, where gall figs may reach 14×10 cm⁹, but, on the whole, figs of 1 cm and of 2.5–3 cm in diameter seem to be most common. Within a species the gall figs seem to be somewhat larger and, when ripe, more obovoid than seed figs³⁵. Figs can be sessile or be borne on short or long peduncles, and may appear paired (subgenus *Urostigma*) or solitary (subgenus *Pharmacosycea*) in the axis of a leaf. Alternatively, they can be clustered on short spurs which occur on the young branches, on the previous season's growth, or on specialized leafless branches (cauliflorous figs, e.g., sections *Sycidium*, *Sycomorus*, *Neomorphe*, and *Sycocarpus*). Especially in *Sycocarpus* these branches may become subterranean and bear geocarpic figs which often have dull colours, such as blackish green and dark reddish-brown. The subterranean strands may send up aerial shoots that produce fruiting branches; in time they may propagate vegetatively when old connecting strands are separated from their parents^{1,8,18}. Both the size and the position of the fig can be important for the visual presentation of the ripe figs and the attraction of animals that aid in the dispersal of the seeds, but on the other hand could also be related to the rearing of fig wasps³.

The interior of the fig

Flowers, interfloral bracts, and bristles

Although figs of many species may all look rather similar from the outside, internally the figs of the various subgenera differ greatly in the structure and the arrangement of the flowers, interfloral bracts, and bristles. There is ample illustration of this enormous diversity in Corner's excellent drawings^{12–18}. Figs may contain from 50 flowers (*F. mathewsii*) up to 7000 (*F. pumila*), but there is always a strong preponderance of the female flowers. Often there are ten times more female than male flowers; in *Sycidium* the percentage of male flowers may vary between 10 and 30%^{3,35}. In addition there is always strong protogyny, and the onset of anthesis in the female and the male flowers may differ by 2–6 weeks. A comparison of the male and female flowers showed that during the early A phase the flowers are more or less simultaneously initiated^{45,50}, and pollen development initially keeps pace with the embryo sac development, but at the B phase pollen is not released and remains in the anther⁴⁷. Clear differences exist between primordia of female and those of male flowers. The female flowers are always scattered on the inner fig wall. In the gall figs of the gynodioecious species the male flowers are usually grouped in a few rows around the ostiole, but in the monoecious species they may either be ostiolar or they are scattered among the female flowers.

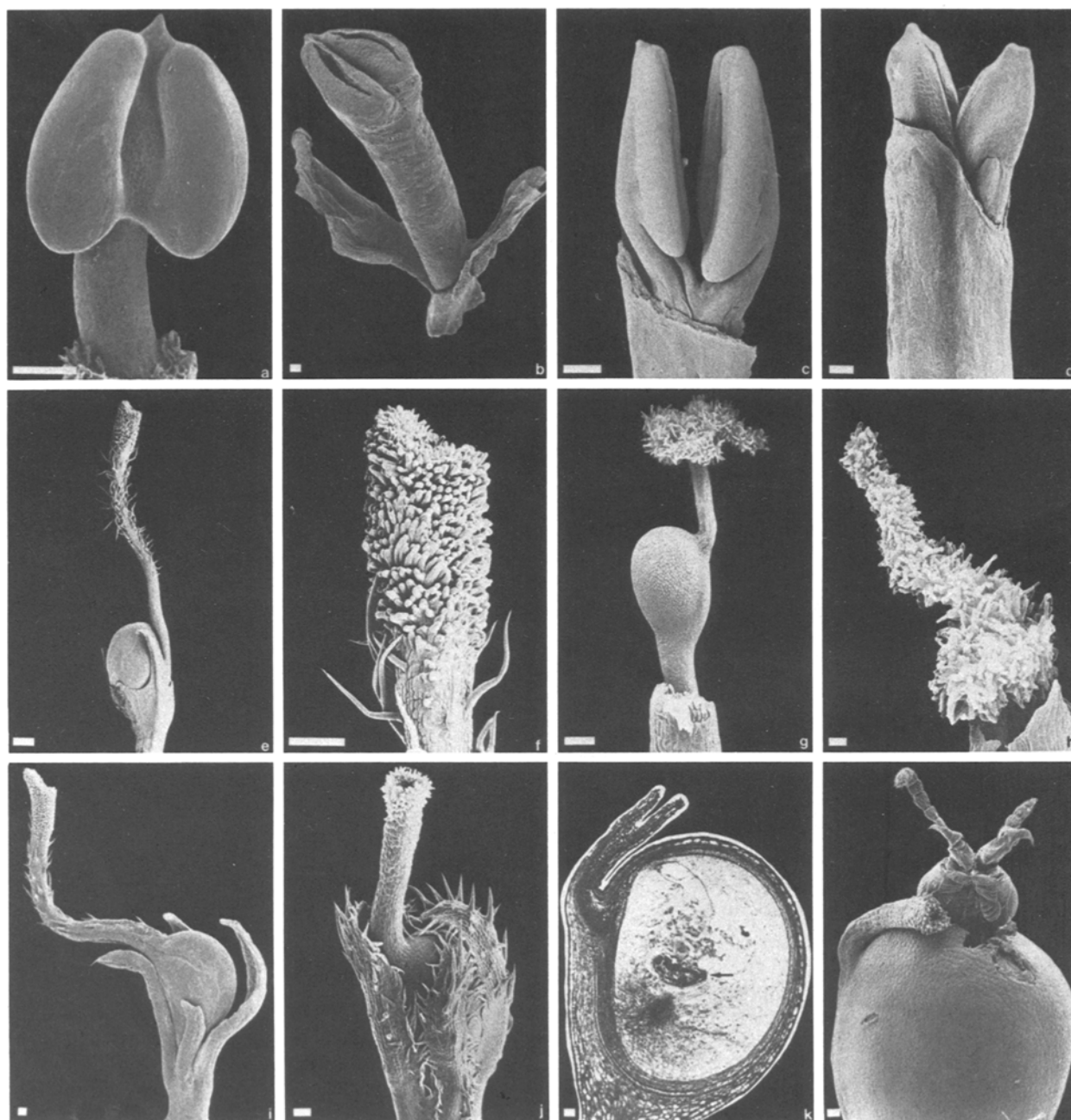


Figure 3. Male (a–d) and female (e–l) flowers; a, b *Urostigma* section *Galoglychia*, B (perianth removed) and D phase resp.; c section *Pharmacosycea*, B phase, perianth removed; d section *Sycomorus*, D phase, showing anthers breaking through the perianth; e, f *Neomorpha*, seed flower, and detail of stigma resp.; g, h *Urostigma* section *Galoglychia*, short-

styled flower (perianth removed), and stigma from a long-styled flower, resp.; i–l *Sydidium*; i seed flower, B phase; j gall flower, B phase; k gall flower, early C phase, arrow indicating wasp larva; l *Kradibia* sp. emerging from gall flower, D phase; bar indicates 200 μ m (a–e) and 100 μ m (f–l), resp.

The staminate or male flower (fig. 3, a–d) generally consists of 1 or 2, sometimes 3 (rarely up to 7) introrse stamens, and is usually surrounded by some simple and free perianth segments¹⁰. The unistaminate (fig. 3 b) or bistaminate (fig. 3 c) condition is an important taxonomic feature. The filament remains short up to the end of the C phase. The anther mostly has four loculi arranged to form two thecae and is dorsally attached; unithecate male flowers occur in *Malvanthera*. The wall formation

follows the monocotyledonous type, and an endothelial layer (1–2 cells thick) and a well-developed stomium may be formed. Dehiscence is usually through the longitudinal slits, but transverse equatorial dehiscence occurs in some *Malvanthera* figs. Within the genus the pollen is rather uniform: is ellipsoidal, measuring $11 \times 6 \mu$ m, with a smooth exine and two apical germ pores; when shed it is two-celled and contains starch grains. The perianth parts usually completely surround the anthers up to

the late C phase; often the outer ones are hooded and fold over around the anthers. In the sections *Sycomorus*, *Neomorpha*, and *Sycocarpus* distinct male flowers occur which have a tubular perianth, consisting of several overlapping and strongly hooded lobes. In addition, the flowers are covered by two bracteoles that originate laterally of the flower primordium.

The presentation of the pollen in the D phase differs in several groups studied, and is directly related to whether pollination is ethodynamic (active pollen collection and unloading by the wasps) or topocentric ('passive' pollen transport)²⁵. In some gynodioecious species with opening ostioles, the elongating filaments expose the anthers, which subsequently dry out and open^{28, 49}. In subgenus *Urostigma* the filament both elongates and swells (fig. 3b), thus tilting and opening the anther within the closed and humid fig⁴⁷. In section *Sycomorus*, at anthesis the elongating filament pushes the anthers upwards and thus tears the perianth and bracteole covering (fig. 3d). The endothecium is reduced, and the pollen sacs do not open but, when tunnelling their way out through the ostiolar region, the male wasps cut the anthers and scatter them through the syconial cavity; subsequently the females actively collect the pollen^{27, 28}.

In some gynodioecious species, and especially in *Sycidium*, the male flowers contain a non-functional pistil or pistillode. Strictly speaking, these have to be regarded as bisexual flowers^{10, 49}. Usually the pistil ceases to develop in the B phase, but Corner pictures male flowers of some *Sycidium* figs showing a pistil with an insect gall¹⁰. In many species of subgenus *Ficus* and section *Sycomorus* the pistil is strongly reduced or absent; it is not uncommon in subgenus *Pharmacosycea*. Neuter flowers, consisting of a well-developed perianth similar to male flowers and a poorly developed gynoecium, may occur in seed figs, but are lacking in section *Sycidium*. They are often ostiolar but alternatively may occur scattered among the female flowers. The features of their perianth covering and the incidental elongation at D phase strongly suggest that they represent the vestigial remains of male flowers. The pistillate or female flowers (fig. 3, e–l) consist of a single unilocular ovary sitting on a short or long pedicel, and are mostly surrounded by a simple perianth. The perianth can be ciliolate or glabrous and it mostly consists of 3–5 segments, which are rarely swollen. A gamophyllous, saccate perianth occurs in *Sycocarpus*; alternatively, the perianth may be strongly reduced or is completely lacking. The colour and form of both the perianth and the ovary have taxonomic importance¹¹. Rarely, the ovary is semi-inferior (*Malvanthera*)¹⁰. The ovary contains a single hemianatropous or anatropous, bitegmic and crassinucellate ovule, which is attached to the ventral side of the carpel. The raphe is short and the raphe bundle is surrounded by elongated cells. In the monoecious species the structure of the ovule seems to be a compromise allowing for the development of either a wasp or a seed, whereas in the gynodioecious species

specialized ovule types occur (ovule dimorphism⁴⁸). In the monoecious species the inner integument is short at the raphe side and does not cover the region where the ovipositor meets the nucellus. Locally in the raphe epidermis an endothelium-like cell layer is formed; these plasm-rich cells probably play a role in the feeding of the wasp egg in the first days after oviposition. In the gynodioecious species the flowers in seed figs have an anatropous ovule, which is the normal forerunner of the seed⁵ and has a normal, circumvallating inner integument. In gall figs the flowers have ovules in which the inner integument is completely lacking at the raphe side, and in these ovules the ovipositor can reach the nucellus without the barrier of an additional cuticular layer covering the integument. A single style is mounted apically or slightly laterally on the ovary, with some variation existing among flowers in its insertion point. In some species the style may even be basally inserted. The hollow stylar canal is compressed and lined with plasm-rich cells. The stigma is dry³³, and can be lobed, with two filiform branches and long stigma papillae (subgenera *Urostigma*, *Pharmacosycea*, *Ficus*), or it is infundibuliform with short stigmatic papillae (sections *Sycidium*, *Sycomorus*, *Neomorpha*, and *Sycocarpus*). In the gynodioecious species there are considerable differences in style morphology between the flowers of seed figs and gall figs (see below). In both ovule types of the gynodioecious species and in that of the monoecious species a normal embryo sac development takes place which follows the Polygonum type. At the B phase the embryo sac is mature, and the stigmatic papillae are fully developed and often of a bright red or pinkish colour.

Interfloral bracts occur dispersed between the female flowers in most monoecious species, with the exception of section *Urostigma* and section *Sycomorus*. They are elongate sterile structures which are a few cell layers thick and of various shapes, originating on the inner fig wall long before the flowers appear. During the early A phase they fill the fig centre and completely obscure the incipient flower primordia. Only at the B phase are the interfloral bracts surpassed by the elongated flowers, and in subsequent developmental stages they may be difficult to trace. The slender bristles that may occur between the flowers in many gynodioecious species may be homologous with interfloral bracts.

The synstigma – the wasp's working platform

At the B phase the syconial cavity is lined by the stigmata of the female flowers, which all end up in roughly one plane; this structure is called a synstigma^{20, 21}. The build-up of the synstigma is not always the same. In the figs of section *Sycomorus* the unbranched stigmata are mutually attached over their complete outer receptive area. The short stigmatic papillae firmly glue the styles together, and provide a coherent and solid synstigmatic surface to ovipositing wasps (fig. 4a). In the subgenera *Urostigma* and *Pharmacosycea*, the branched stigma

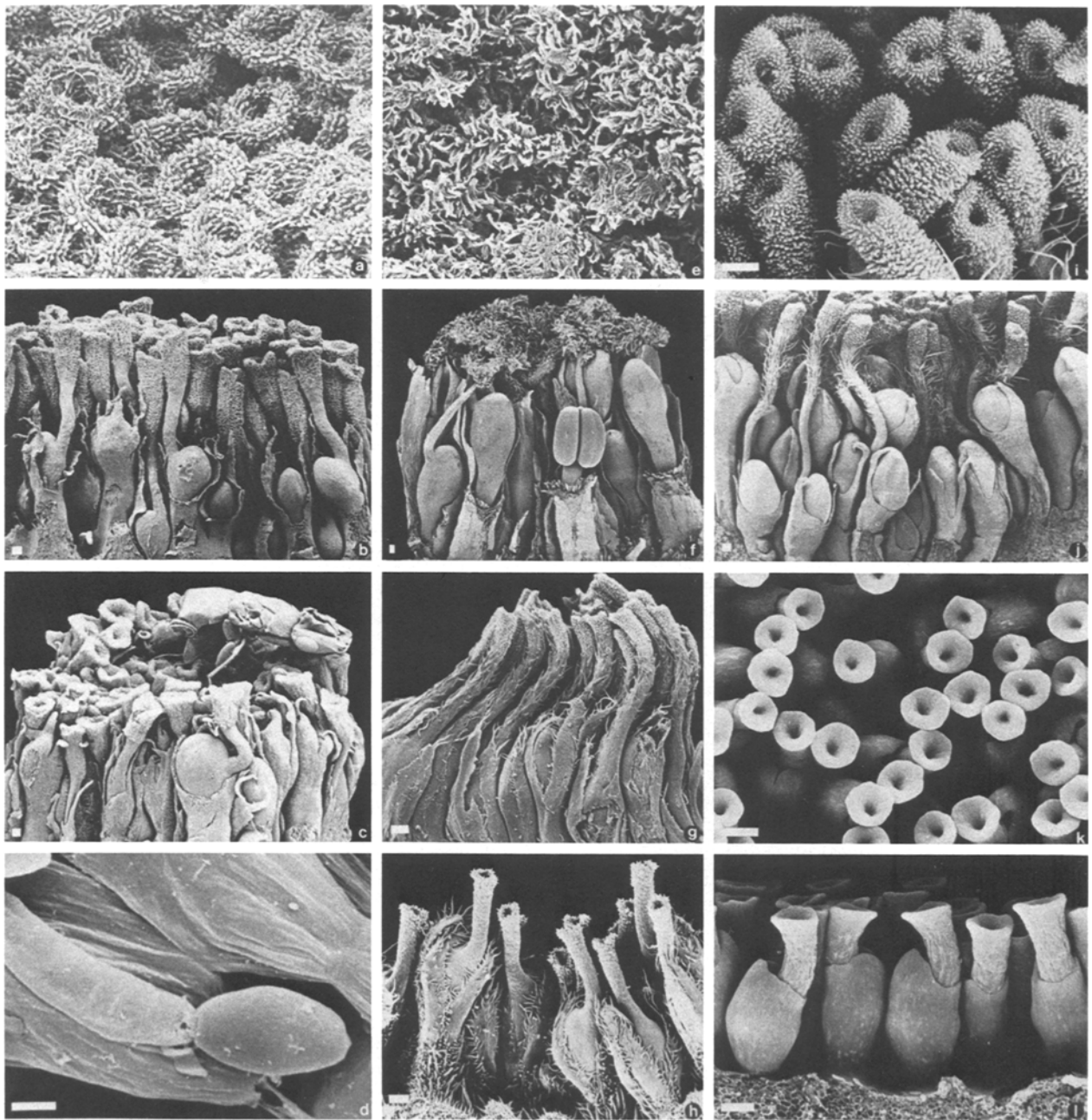


Figure 4. Surface view (a, d, e, i, k) and lateral view (b, c, f, g, h, j, l) of female flowers; a–f monoecious figs; g–l gynodioecious figs; a–d section *Sycomorus*; c ovipositing *Ceratosolen* spp.; d germinating pollen grain;

e, f *Urostigma* section *Galoglychia*; g, h *Sycidium*, seed flowers and gall flowers, resp.; i, j *Neomorphe*, seed flowers; k, l *Sycocarpus*, gall flowers; bar indicates 100 μ m (a–c, j–l), 5 μ m (d), and 200 μ m (e–h), resp.

lobes have elongated stigmatic papillae. The stigmatic papillae are gently coherent, and as a result the synstigma is cobwebby and somewhat loosely organized (fig. 4e). Ovipositing wasps frequently stumble and fall between different attempts to oviposit⁴⁷. In the *Sycidium*⁴⁹ and *Neomorphe* (pers. obs.) seed figs, the unbranched stigmata gently cohere through interlocking hairs on the style (fig. 4, g, i, j) and are easily separable by a needle⁴⁹. In *F. exasperata* (section *Sycidium*) the interfloral clavate bristles might contribute to the firmness of the synstigma. On account of the differences in style morphology and

flower organization, a synstigma is lacking in gall figs (fig. 4, h, k, l). Corner's extensive illustration of the floral morphology in various Malaysian figs suggests that such a synstigma organization through interlocking style hairs as well as the lack of a synstigma in gall figs is frequent in many gynodioecious species^{8, 12, 13, 16, 18}.

Various functions of the synstigma have been proposed. It exposes all flowers to the wasps in the syconial cavity and thus acts as the wasp's working platform. The pollen germinates on the stigmatic papillae. Potentially, the synstigma could conduct growing pollen tubes to all female

flowers, and thus would serve as a device for equalizing the chances of a successful pollination for all flowers. Pollen tubes can grow over the synstigma and enter neighbouring flowers⁵¹, but the fate of the pollen deposited on the synstigma is largely unknown. The structural differences between different synstigma types might influence the pollination behaviour of wasps in different figs. The great diversity in stigma organization among sections suggests that within *Ficus* the synstigma may have developed along different evolutionary pathways.

Style length differentiation in monoecious and gynodioecious figs

The differences in floral organization between the monoecious and gynodioecious species encountered are directly related with their different strategies of maintaining the symbiosis with the pollinating wasps: the gynodioecious species have specialized figs for wasp and for seed production, whereas the monoecious species produce wasps and seeds in a single fig type.

The great and continuous variation in style length of the female flowers is a typical characteristic of monoecious figs (fig. 4, a–f). Style lengths may range from 250 to 910 μm in *F. vogelii*, from 600 to 1800 μm in *F. ottoniifolia*, from 650 to 2300 in *F. religiosa*, and from 650 to 1650 in *F. sur* and *F. sycomorus*^{20, 36, 43, 47, 51}. On account of their expected function in the fig-fig wasp symbiosis, the extremely long-styled and extremely short-styled flowers were traditionally called 'seed flowers' and 'gall flowers'. However, the extremes are linked by numerous flowers with an intermediate style length (imperfect heterostyly). Moreover, both seeds and wasps may alternatively develop in any flower, and in the monoecious species an a priori distinction in seed and gall flowers is untenable; for a full discussion see Verkerke⁵⁰. In *F. ottoniifolia* and *F. sur*, the longer styles are comparatively thinner and contain more elongated cells; the shorter styles are slightly thicker and contain fewer elongated cells.

Through a reciprocal staggering of the pedicel length, the stigmata of all flowers ultimately lie at approximately the same level. The numerous flowers are densely crowded, and the ovaries are located at different heights (multiseriate ovary organization), thus allowing for a denser packing of the flowers. Comparative ontogenetical studies suggest a mechanism leading to this multiseriate ovary organization. In the monoecious species studied up to now, the early stages of flower development take place in a space-stressed environment⁵¹. In subgenus *Urostigma*, and probably in subgenus *Pharmacosycea* (pers. obs.), the inwardly running bracts and the interfloral bracts completely fill the young syconium. This leaves limited room for flower development, and strongly suggests that the early differentiation of styles is hampered by competition for space. In the monoecious section *Sycomorus* the differential elongation of the flowers is even more influenced through the presence of a plug of ostiolar

bracts^{50, 51}. During the A phase, the stigmata become strongly mutually adherent. Eventually, when the ovule develops and the ovary increases in diameter, the ovaries come to be located at different heights, and differential style and pedicel lengths develop in order to pack the flowers closely inside the fig. The two different ontogenetical processes that lead to a large variation in style length suggest that the imperfect heterostyly of subgenus *Urostigma* and *Pharmacosycea* on the one hand, and that of section *Sycomorus* on the other, have been reached along different evolutionary pathways.

In the gynodioecious species the floral organization is fundamentally different and here the terms 'gall flower' and 'seed flower' are certainly useful, although both may cause semantic difficulties. The ovaries are less densely packed, and are mostly well lined up along the fig wall (uniseriate ovary organization), although this may be less pronounced in seed figs. The styles of the gall and the seed flowers are entirely different in shape (fig. 4, g–l). In seed flowers the styles are rather long; they may range from 1600 to 2400 μm in *F. asperifolia*⁴⁹. Extremely long styles (up to 10 mm) occur in some *Sycocarpus* seed figs¹⁰. The styles of gall figs are short (600–620 μm long in *F. asperifolia*) and may be funnel-shaped. In each of the two fig types, flowers with an intermediate style morphology are completely lacking (i.e., there is perfect heterostyly).

Gynodioecious figs generally show a free flower development in a syconial cavity which develops early. Characteristically, the interfloral bracts are lacking. The ontogeny of the differential style length has not yet been investigated, but at least in *Sycidium* gall figs the style lengths are fairly similar and narrowly distributed; in the seed figs more variation seems to occur.

It has been considered that the relation between the style length and the length of the wasp's ovipositor roughly determines whether a flower will receive a wasp egg or not²⁰, and in the gynodioecious species this no doubt holds true²⁴. In the monoecious species the situation seems somewhat more complicated, and recent investigations have further refined the original concept of Jacob Galil and Dan Eisikowitch. Several students have wondered why the ovipositor of the wasp has not elongated over evolutionary time, so as to increase the chances of leaving offspring. Several hypotheses have been proposed⁴¹, but it is questionable whether a longer ovipositor would be a functionally better ovipositor, since oviposition is also influenced by the shape of the stigma, the thickness of the style, the insertion point on the ovary, and the ovular structure^{47, 51}. Several investigations show that in monoecious species the ovipositor is already long enough to deposit eggs in the flowers with the longest styles^{1, 20, 36, 43, 47, 51}. Morphological studies indicate that the great variation in style length might cause a variation in accessibility of the ovaries, and that apparently long-styled flowers stand a lower chance of receiving a wasp egg⁵¹.

Wasp and seed development after oviposition and fertilization

Wasp oviposition and pollination cause major changes in the fig. For oviposition, the ovipositor is inserted in the stylar canal, and when its tip reaches the bend in that canal, it forces its way in between the elongate cells that border the raphal strand and punctures the ovule. The elongate cells split along their middle lamellae and guide the ovipositor to the insertion point of the nucellus. The egg is deposited within the ovule between the nucellus and the raphe, and thus leaves the embryo sac undisturbed^{32,47}. Egg deposition is followed by the secretion of a drop of fluid which probably causes the subsequent swelling of the ovary. Within 8 days the ovary may reach its final shape. There is evidence that the initiation of the metamorphosis of the ovary into a gall is independent of fertilization^{23,49}. The empty 'bladders', which often occur in C phase figs, might be ovaries that received a wasp egg but were not successfully fertilized, or could be the result of multiple ovipositions (S. G. Compton, pers. comm.). Both in the ovules of monoecious species and in the two ovule types of the gynodioecious ones, there is evidence for the occurrence of a normal double fertilization^{6,36,42,47,49,51}. The occurrence of parthenocarpy, as reported from *F. carica*^{38,53} has not been confirmed from undomesticated species and cannot be the rule. In flowers that received a wasp egg, the double fertilization produces incipient plant embryos that may reach the octant stage surrounded by nuclear endosperm. The ovipositing wasps carefully leave the embryo sac intact and do not interfere with the normal fertilization process. After the embryo and endosperm have been formed, the egg turns into a larva and enters the now enlarged nucellus in search of the embryo sac (fig. 3k). The embryo disappears and the endosperm now serves the same function for the wasp as it would have done for the plant embryo; that is, nourishing the developing larvae. Therefore, the wasp's proximate aim in pollinating is to nourish its progeny better, and pollination leading to seed production is only a by-product. All cases studied up to now are similar in showing that pollinating wasps lay eggs outside the nucellus, and that a normal double fertilization takes place that forms endosperm as nourishing tissue for the wasp. This is different from the oviposition of *Sycophaga sycomori*, which has a long ovipositor and lays its eggs directly into the embryo sac and thus causes a proliferation of nucellar cells which serves as nourishing tissue²².

For seed development, pollen must germinate on the stigmata, and pollen tubes must enter the embryo sacs of flowers that do not receive a wasp egg⁵¹. Usually, seeds develop through a normal fertilization^{6,36,47}. Usually 10% of the flowers apparently do not become fertilized; they do not show any further development and gradually wilt³.

After oviposition and fertilization, in the monoecious species, the multiseriate arrangement of the ovaries de-

velops further on account of a competition for space. In the gynodioecious species a uniseriate organization may be replaced by a multiseriate ovary placement. In a situation similar to that in the A phase of monoecious species, the ovaries compete for space and adjust their pedicel lengths to allow the closest packing. Drupes and galls each attain a very different shape and wall structure. Galled ovaries enlarge explosively; usually they become stipitate and free from the perianth while their pedicels may elongate. The pericarp cells become stretched and develop thickened walls. Usually the apex of the gall has a much thinner wall where later the adult wasp emerges (fig. 3l). In fertilized flowers that did not receive a wasp egg, the ovaries merely enlarge. The drupes develop a solid endocarp, of which the inner layer consists of thick-walled, radially elongated, sclerotic cells that form the main mechanical layer in the fruit. Next to it lies the characteristic middle layer of small isodiametric cells with typical crystals⁴⁷. The outer layers can be mucilaginous, and the epidermis is often strongly tanniferous. In the D phase the mucilaginous and sticky layer may swell to expose the endocarp body in the syconial cavity⁴⁷. The endocarp body is mostly 1–2 mm, in *F. deltoidea* (subgenus *Ficus*) up to 3–5 mm long, and may be keeled, auriculate, or reniform. Shape, colour, and structure of the achenes or drupes ('seeds') have taxonomic significance for the distinction of the subordinate units^{2,11}. The endospermous seed contains a small, spatulate embryo which has two flattened cotyledons and is often slightly curved. The seed coat is poorly developed and does not contribute to the mechanical protection of the embryo. Upon germination, which requires a permanent humidity, the endocarp splits in two halves along the vascular bundles^{29,47,51}.

Conclusion

Our knowledge of the biology of the fig has improved through comparative studies of its functional anatomy. In many parts of the fig, a strong relationship between structure and function is found. Often, structural compromises are encountered that adapt the fig to its various functions such as pollination, oviposition, and dispersal. Certain structural aspects of the fig have already been correlated with wasp behaviour, but some of those (e.g., the structure of the ostiole) seem to have their largest impact on ontogenetical processes of the plant in the early A phase. Ontogenetical study of the different flower types has revealed that among gynodioecious and monoecious species, many differences exist in the number of flower primordia per fig. The synchronization of the growth in young flowers is influenced by the growth of the fig, and by the timing of the opening of the ostiolar cavity. This process is very different among gynodioecious and monoecious species, but for its full understanding we need more detailed studies of flower development in a number of different species, both gynodioecious and

monoecious. We now have detailed information on the process of fertilization and oviposition in the ovule, and their role in the development of wasps and seeds in the fig. The wasps do not eat the seeds: they use them as well-protected breeding places. The double fertilization allows the plants' resources to reach the developing wasp larvae. This explains the wasps' efforts to transport pollen from donor figs to receptive figs as a way of better nourishing their larvae. From the wasps' viewpoint, seed production in neighbouring flowers of receptive figs is only a by-product.

The different strategies that monoecious and gynodioecious species have for maintaining the symbiosis with the pollinating wasp are beginning to become clear. The absolute differences between the female flowers of gynodioecious figs means that seed figs are adapted as wasp-trapping, seed-producing containers that make the seed dispersal of the plant possible, while the gall figs produce pollen and maintain the population of wasps.

The structural differences between synstigma types of different sections of the genus suggest that the behaviour of wasps towards them might be different. Detailed study of the style anatomy indicates that among ovaries, differences in accessibility on account of style length and style firmness exist. Such differences in accessibility of flowers and differences in wasp behaviour remain to be studied. Anatomical studies indicate that the study of relations between fig size, the number of flowers per fig, and the size of the syconial cavity at B phase on the one hand, and wasp size and the number of wasps entering per fig on the other, seem to be very important factors with regard to wasp oviposition and pollination. The structure of figs is still incompletely known in several sections of *Ficus* (*Pharmacosycea*, *Oreosycea*, *Sycocarpus*, *Neomorphe*, most sections of *Urostigma*); in particular, comparison of the structure of B phase seed and gall figs is lacking. This hampers any serious investigation of the evolutionary history of the genus. We still know very little about the dispersion of pollen in the syconial cavity. Only from one species (*F. sur*) is there evidence that pollen tubes can grow over the synstigma and enter neighbouring flowers, but does this also occur in other figs with different synstigma types? Moreover, if fertilization also generally occurs in gall flowers, how can we explain for the absence of even accidental seed production in gall figs? Has it anything to do with the lack of a synstigma in such figs? Observation of wasp oviposition and pollination directly – or at least as directly as possible – could elucidate whether ovipositing wasps actually can choose between different flowers, and whether such behaviour is different among figs with different types of synstigma.

Acknowledgments. I thank Kees Berg, Ferry Bouman, Steve Compton, Alan Herre, and Prof. Dr A. D. J. Meeuse for the critical reading of the manuscript.

1 Baijnath, H., and Ramcharun, S., Aspects of pollination and floral development in *Ficus capensis* Thunb. (Moraceae). *Bothalia* 14 (1983) 883–888.

- 2 Berg, C. C., Subdivision of *Ficus* subg. *Urostigma* sect. *Galoglychia* (Moraceae). *Proc. K. ned. Akad. Wet. C* 89 (1986) 121–127.
- 3 Berg, C. C., Reproduction and evolution in *Ficus* (Moraceae): traits connected with the adequate rearing of pollinators. (1989) in press.
- 4 Bernbeck, F., Vergleichende Morphologie der Urticaceen- und Moraceen-Infloreszenzen. *Bot. Abh.* 19 (1932) 1–100.
- 5 Bouman, F., The ovule, in: *Embryology of Angiosperms*, pp. 123–157. Ed. B. M. Johri. Springer, Berlin 1984.
- 6 Chopra, R. N., and Kaur, H., Pollination and fertilization in some *Ficus* species. *Beitr. Biol. Pfl.* 45 (1969) 441–446.
- 7 Condit, I. J., The structure and development of flowers in *Ficus carica* L. *Hilgardia* 6 (1932) 443–481.
- 8 Corner, E. J. H., A revision of the Malayan species of *Ficus*: *Covellia* and *Neomorphe*. *J. Malay. Brch R. Asiat. Soc.* 9 (1933) 1–65.
- 9 Corner, E. J. H., A revision of *Ficus*, subgenus *Synoechia*. *Gdns' Bull. Straits Settl.* 10 (1938) 82–161.
- 10 Corner, E. J. H., The classification of the Moraceae. *Gdns' Bull., Singapore* 19 (1962) 325–355.
- 11 Corner, E. J. H., Check-list of *Ficus* in Asia and Australasia. *Gdns' Bull., Singapore* 21 (1965) 1–186.
- 12 Corner, E. J. H., *Ficus* in the Solomon Islands and its bearing on the post-Jurassic history of Melanesia. *Phil. Trans. R. Soc., Lond. Ser. B* 253 (1967) 23–159.
- 13 Corner, E. J. H., *Ficus* subgen. *Ficus*. Two rare and primitive pachycaul species. *Phil. Trans. R. Soc., Lond. Ser. B* 259 (1970) 353–381.
- 14 Corner, E. J. H., *Ficus* subgen. *Pharmacosycea* with reference to the species of New Caledonia. *Phil. Trans. R. Soc., Lond. Ser. B* 259 (1970) 383–433.
- 15 Corner, E. J. H., *Ficus* in the New Hebrides. *Phil. Trans. R. Soc., Lond. Ser. B* 272 (1975) 343–367.
- 16 Corner, E. J. H., The climbing species of *Ficus*. *Phil. Trans. R. Soc., Lond. Ser. B* 273 (1976) 359–386.
- 17 Corner, E. J. H., *Ficus glaberrima* and the pedunculate species of *Ficus* sect. *Sycocarpus*. *Phil. Trans. R. Soc., Lond. Ser. B* 281 (1978) 347–371.
- 18 Corner, E. J. H., *Ficus dammaropsis* and the multibracteate species of *Ficus* sect. *Sycocarpus*. *Phil. Trans. R. Soc., Lond. Ser. B* 281 (1978) 373–406.
- 19 Durkee, L. T., Ultrastructure of extrafloral nectaries in *Aphelandra* spp. (Acanthaceae). *Proc. Iowa Acad. Sci.* 94 (1987) 78–83.
- 20 Galil, J., and Eisikowitch, D., On the pollination of *Ficus sycomorus* in East Africa. *Ecology* 49 (1968) 259–269.
- 21 Galil, J., and Eisikowitch, D., On the pollination ecology of *Ficus religiosa* in Israel. *Phytomorphology* 18 (1968) 356–363.
- 22 Galil, J., Dulberger, R., and Rosen, D., The effects of *Sycophaga sycomori* L. on the structure and development of the syconia in *Ficus sycomorus* L. *New Phytol.* 69 (1970) 103–111.
- 23 Galil, J., and Eisikowitch, D., Studies on mutualistic symbiosis between syconia and sycophilous wasps in monoecious figs. *New Phytol.* 70 (1971) 773–787.
- 24 Galil, J., Pollination in dioecious figs. Pollination of *Ficus fistulosa* by *Ceratosolen hewitti*. *Gdns' Bull., Singapore* 26 (1973) 303–311.
- 25 Galil, J., Topocentric and ethodynamic pollination, in: *Pollination and Dispersal*, pp. 85–100. Eds N. B. M. Brantjes and H. F. Linskens. Dept. Botany, Univ. Nijmegen 1973.
- 26 Galil, J., Ramirez B., W., and Eisikowitch, D., Pollination of *Ficus costaricana* and *F. hemsleyana* by *Blastophaga estherae* and *B. tonduzi* in Costa Rica (Hymenoptera: Chalcidoidea, Agaonidae). *Tijdschr. Ent.* 116 (1973) 175–183.
- 27 Galil, J., and Eisikowitch, D., Further studies on pollination ecology in *Ficus sycomorus*. II. Pocket filling and emptying by *Ceratosolen arabicus* Mayr. *New Phytol.* 73 (1974) 515–528.
- 28 Galil, J., and Meiri, L., Number and structure of anthers in fig syconia in relation to behaviour of pollen vectors. *New Phytol.* 88 (1981) 83–87.
- 29 Galil, J., and Meiri, L., Drupelet germination in *Ficus religiosa* L. *Israel J. Bot.* 30 (1981) 41–47.
- 30 Goebel, K., Über die Verzweigung dorsiventraler Sprosse. *Arb. bot. Inst. Würzburg* 2 (1880) 353–436.
- 31 Goebel, K., Blütenbildung und Sprossgestaltung (Anthokladien und Infloreszenzen) Zweiter Ergänzungsband zur Organographie der Pflanzen. Fischer, Jena 1931.
- 32 Grover, H., and Chopra, R. N., Observations on oviposition, nutrition and emergence of some fig insects. *J. Indian Bot. Soc.* 50A (1971) 107–115.
- 33 Heslop-Harrison, Y., Stigma characteristics and angiosperm taxonomy. *Nord. J. Bot.* 1 (1981) 401–420.
- 34 Hill, D. S., Figs (*Ficus* spp.) and fig-wasps (Chalcidoidea). *J. nat. Hist.* 1 (1967) 413–434.

- 35 Hill, D. S., Figs (*Ficus* spp.) of Hong Kong. Hong Kong University Press, Hong Kong 1967.
- 36 Johri, B. M., and Konar, R. N., The floral morphology and embryology of *Ficus religiosa* Linn. *Phytomorphology* 6 (1956) 97–111.
- 37 Leclerc du Sablon, M., Sur la symbiose du Figuier et du Blastophage. *C. r. hebd. Séanc. Acad. Sci.* 144 (1907) 146–148.
- 38 Leclerc du Sablon, M., Structure et développement de l'albumen du caprifuier. *Revue gén. Bot.* 20 (1908) 14–24.
- 39 Lersten, N. R., and Peterson, W. H., Anatomy of hydathodes and pigment discs in leaves of *Ficus diversifolia* (Moraceae). *Bot. J. Linn. Soc.* 68 (1974) 109–113.
- 40 Michaloud, G., Figueiers tropicaux et pollinisation. Film, réalisation: A. R. Devez, production: Service du Film de Recherche Scientifique, Paris 1982.
- 41 Murray, M. G., Figs (*Ficus* spp.) and fig wasps (Chalcidoidea, Agaonidae): hypotheses for an ancient symbiosis. *Bot. J. Linn. Soc.* 26 (1985) 69–81.
- 42 Neeman, G., and Galil, J., Seed set in the male syconia of the common fig, *Ficus carica* L. (Caprificus). *New Phytol.* 81 (1978) 375–380.
- 43 Newton, L. E., and Lomo, A., The pollination of *Ficus vogelii* in Ghana. *Bot. J. Linn. Soc.* 78 (1979) 21–30.
- 44 Ramirez B., W., Coevolution of *Ficus* and Agaonidae. *Ann. Mo. bot. Gdn* 61 (1974) 770–780.
- 45 Rauh, W., and Reznik, H., Histogenetische Untersuchungen an Blüten- und Infloreszenzachsen. *Sitzungsber. Heidelberger Akad. Wiss., Math.-Naturwiss. Kl.* 1951 3 (1951) 139–207.
- 46 Roth, I., Fruits of the angiosperms. *Handb. Pfl. Anat.* (1977).
- 47 Verkerke, W., Anatomy of *Ficus ottoniifolia* (Moraceae) syconia and its role in the fig-fig wasp symbiosis. *Proc. K. ned. Akad. Wet. C* 89 (1986) 443–469.
- 48 Verkerke, W., Ovule dimorphism in *Ficus asperifolia* Miquel. *Acta bot. neerl.* 36 (1987) 121–124.
- 49 Verkerke, W., Syconial anatomy of *Ficus asperifolia* (Moraceae), a gynodioecious tropical fig. *Proc. K. ned. Akad. Wet. C* 90 (1987) 461–492.
- 50 Verkerke, W., Flower development in *Ficus sur* Forsskål (Moraceae). *Proc. K. ned. Akad. Wet. C* 91 (1988) 175–195.
- 51 Verkerke, W., Sycone morphology and its influence on the flower structure of *Ficus sur* (Moraceae). *Proc. K. ned. Akad. Wet. C* 91 (1988) 319–344.
- 52 Weberling, F., *Morphologie der Blüten und der Blütenstände*. Ulmer, Stuttgart 1981.
- 53 Zamotaylov, S. S., Embriologiya inzhira pri raznikh variantakh opyleniya (Embryology of the fig with different types of pollination). *Izv. Akad. Nauk SSSR, Ser. Biol.* 1955 2 (1955) 103–121.

0014-4754/89/070612-11\$1.50 + 0.20/0
© Birkhäuser Verlag Basel, 1989

A mutualism at the edge of its range

J. L. Bronstein

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson (Arizona 85721, USA)

Summary. Comparing populations that differ in access to mutualists can suggest how traits associated with these interactions have evolved. I discuss geographical and seasonal variation in the success of a primarily tropical mutualism (the fig/pollinator interaction), and evaluate some possible adaptations allowing it to persist at the edge of its range. Pollinators probably have difficulty in seasonal sites because 1) fig trees flower rarely in winter and 2) trees that do flower are less detectable and more difficult to reach. Fig biologists believe that seasonality must have selected for adaptations allowing pollinators to survive winter. However, geographical comparisons do not support two current ideas, the synchrony-breakdown hypothesis and the specificity-breakdown hypothesis. I pose two alternatives: plasticity of fruit and wasp developmental time, and adaptations of free-living fig wasps. I also distinguish between the impact of seasonality on monoecious versus dioecious figs; the latter group appear better adapted to reproduce in cool climates. A combination of comparative, observational, and experimental approaches has great potential for advancing our understanding of mutualisms.

Key words. Agaonidae; coevolution; *Ficus*; fig; mutualism; phenology; pollination; seasonality.

Introduction

Coevolved mutualisms can only persist in places that both partners can reach, and can survive and reproduce in once there. This simple constraint has profound consequences for the ecology and evolution of species dependent upon mutualists. Mutualisms (particularly obligate ones) commonly involve organisms of distant taxa¹⁴, and their ecological requirements must often be widely divergent. A species whose mutualist is excluded from a given location may be unable to invade^{35, 71}, may interact with an alternative partner^{10, 34}, or may stop relying upon mutualists altogether^{73, 101}, either on an ecological or evolutionary time scale. However, even if both partners are present, environmental conditions are likely to

be more harsh for one of them. The success of the mutualism itself will therefore vary in space, as will selection pressures on it. Environment-specific selection pressures lead to the possibility of environment-specific adaptations over the range of a single mutualistic interaction. Few data are available on geographic variation within mutualisms, because these interactions have nearly always been studied at a single site^{7, 39, 66, 84, 99}. Even basic information about the components of a particular mutualistic interaction that are most sensitive to environmental variation is rare. My intention here is to review information on geographic and seasonal variation in the success of a primarily tropical mutualism, the fig/pollina-