A study of the
pollination biology
of the (gyno)dioecious fig,
Ficus capreifolia Del.
(Moraceae)

by

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submitted in partial fulfilment of
the requirements for the degree of

MASTER OF SCIENCE

in the

DEPARTMENT OF BOTANY,
UNIVERSITY OF WESTERN CAPE.

PROMOTER: PROFESSOR H. BAIJNATH
CO-PROMOTER: PROFESSOR C.T. JOHNSON

NOVEMBER 1994

I declare that

A study of the
pollination biology
of the (gyno)dioecious fig,
***Ficus capreifolia* Del. (Moraceae)**

is my own work and that
all the sources I have used or quoted
have been indicated and acknowledged
by means of complete references.

Signed : Naidoo

S. NAIDOO
(CANDIDATE)

I hereby declare that the above statement is true.

Signed: H. Baijnath

PROFESSOR H. BAIJNATH
(PROMOTER)

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Summary

The pollination biology of *Ficus capreifolia* Del. was studied.

Ficus capreifolia is a (gyno)dioecious species with separate male and female plants bearing male and female syconia respectively. Male syconia had staminate flowers near the ostiolar region of their syconia and numerous short-styled pistillate flowers. Female syconia had only long-styled pistillate flowers throughout their syconia. A mature plant produced up to three hundred syconia.

The floral morphology and phenology of *Ficus capreifolia* Del. (Sub-section *Sycidium,* Family: Moraceae) was studied (in the Umdloti area, 29°s and 31°E, Republic of South Africa). Male and female syconia were produced asynchronously on separate plants growing on sandy river banks. Floral characters analysed revealed peduncular bracts, trap-blossom syconia, perfect heterostyly amongst other characteristics in line with other (gyno)dioecious species of figs described. Information is presented about ostiolar bracts, sizes of pedicel, style and ovary in B- and D-phase syconia of gall and seed figs. A developmental cycle of about 120-140 days with an extended prefemale phase was recorded for both gall and seed figs. The marginal southern latitude, cool, dry weather and low population levels of plants and pollinators appeared to limit the spread of this plant.

The developmental anatomy of the male and female syconia was studied at both the LM and SEM levels. The structure and development of gall and seed figs appeared to be similar from initiation to the receptive phase. Only female figs, with long-styled pistillate flowers, developed a synstigma and produce seeds. Hermaphrodite (male) figs, with staminate and short-styled pistillate flowers, did not develop a synstigma but instead showed early embryo and endosperm development, while also providing only for the development of wasps in their ovaries (galls). Anatomical characteristics and development of both the female and male figs are presented in this research. Both LM and SEM micrographs showing the developmental anatomy of the male and female figs are included.

The pollination biology and insects were studied. Female pollinator wasps emerged from the male syconia (gall figs) carrying pollen in their mesothoracic pockets. Coxal combs were also present. Pollination was ethodynamic. Pollen was transferred to short-styled pistillate flowers in male syconia after oviposition occurred and to long-styled pistillate flowers in the female syconia. Wasps only developed in male syconia, and seeds only developed in female syconia (seed figs). Ratios of gall to uninfected and pollinated to unpollinated flowers are given. Levels of infection of gall flowers varied from 25% to 86%. A single species of secondary sycophile also oviposited in the gall flowers of male syconia. Of the total number of wasps in each syconium, there were about 70% females of the pollinator wasp, 19,1% males of the pollinator wasp, 8,1% females of the secondary sycophile and 2% males of the secondary sycophile. The ratio of females to the males of the pollinator was 3,7 : 1 and this was close to the ratio of the females to the males of the secondary sycophile of 4 : 1. Females of the pollinator wasp displayed a positive response to light and a negative response to gravity. Wasp entry; pollination, oviposition and emergence were similar to mechanisms described for other pollinator wasps in (gyno)dioecious figs.

Other insects such as fruit flies and moths laid eggs in certain parts of the syconia. Many smaller and larger animals in riverine ecosystems feed on the ripe figs.

GENERAL INTRODUCTION

Ficus L. is a very large genus with over 750 species widely distributed. The members of this group may be located between approximately 35°N and 35°S latitudes within the tropical and sub-tropical regions. A total of 105 spp. is distributed in Africa and its adjacent islands, including Madagascar (Berg, 1989). Of these, 24 are located in Southern Africa (Van Greuning, 1982).

Ficus is the only genus belonging to the tribe Ficeae, in the Family Moraceae. About half of the 750 spp. are (gyno)dioecious, with only 10 (gyno)dioecious species (*F. palmata* of the section *Ficus* and nine species of the section *sycidium)* being in Africa (Berg, 1989).

Corner (1965) divides this genus into four sub-groups (sub-genera) : *Urostigma* (280 spp.), *Pharmacosycea* (75spp.), *Sycomorus* (13 spp.) and *Ficus* (350 spp.). The sub-genera *Urostigma* and *Pharmacosycea* are monoecious, with *Sycomorus* and *Ficus* being mostly (gyno)dioecious. About 15 spp. only in the latter two sub-genera are monoecious.

Corner (1965) further divides these sub-genera into sections and sub-sections, with *Ficus* having 8 sections including *Ficus* (60 spp.), *Rhizocladus* (55 spp.), *Kalosyce* (20 spp.), *Sinosycidium* (1 sp), *Sycidium* (105 spp

Adenosperma (23 spp.), *Neomorphe* (6 spp.) and *Sycocarpus* (80 spp.). The section *Sycidium* is divided into 3 sub-sections including *Sycidium* (70 spp.), *Varinga* (15 spp.) and *Paleomorphe* (20 spp.).

The members of the genus *Ficus* are characterised by having their flowers borne inside an infolded receptacle, apically closed off at its ostiole by numerous bracts. This infolded receptacle, called a syconium, is not a fruit, although it has frequently been referred to as a fruit. The syconium (closed inflorescence) has numerous small flowers lining its inner wall with the true fruit being the drupes represented by small matured ovaries of the flowers.

Plants belonging to the genus *Ficus* may grow into trees, shrubs or climbers. The ability to form aerial roots has resulted in hemi-epiphytes, root climbers, some holo-epiphytic and (hemi)epilithic species (Berg, 1990a). When mature these plants may produce from a few to numerous syconia (figs) on younger and/or older branches.

Monoecious species produce one type of syconium only with numerous pistillate and some staminate flowers. In these syconia, pistillate flowers may have a range of style lengths varying from short to long. Staminate flowers produce pollen, while short-styled pistillate flowers generally harbour wasps and long-styled pistillate flowers usually produce seeds. As a result both the male and female functions are fulfilled by these syconia. Protogyny ensures that self-pollination within each syconium is not effected.

The (gyno)dioecious species produce "male" and female syconia on separate plants. Male syconia produced on male plants bear numerous short-styled pistillate and some staminate flowers. While these male syconia are hermaphrodite and (gyno)dioecious, they produce pollen in staminate flowers and harbour wasps in short-styled pistillate flowers only. Seeds are not produced in these male syconia, and the species is therefore functionally dioecious, as they enable the species to fulfil the male function only in them.

The members of the genus *Ficus* display a complex mutualistic relationship between pollinating wasps and fig syconia. Research has shown that pollination of flowers in the syconia by wasps has a significant effect on the development of both the syconia and the flowers of the fig.

Females of the pollinator wasp are attracted to receptive syconia and enter the cavity of the fig via the ostiole. Pollen carried on the body or in specialised pockets may be accidently or deliberately transferred onto the stigmatic surfaces of female flowers, thus effecting pollination. These females may also oviposit in the ovaries of short-styled pistillate flowers in the syconia of monoecious figs and in the pistillate flowers of the male syconia of the (gyno)dioecious figs. Males and females of the pollinator wasp then develop within the ovaries (referred to as galls) concurrently with the development and maturing of the syconia. Simultaneously seeds develop in long-styled flowers in the syconia of monoecious figs and in female syconia of (gyno)dioecious figs. When the syconia ripen, males of the pollinator wasp leave their galls first, move around within the syconia, locate galls with females and inseminate the females. Females of the pollinator then leave their galls, make their way to the anthers, collect pollen actively or passively before leaving the syconia through the ostiole or the wall. These females of the pollinator then search for or are attracted to receptive syconia to continue with the cycle of events.

Galil and Eisikowitch (1968c), working on the monoecious fig *F. religiosa,* recognised five phases in the development of the fig:

A. **Prefemale phase** - development of fig from initiation to female phase; ostiole closed

B. **Female phase** - Ovules develop fully; stigmas become receptive; ostiolar scales opened; pollinators penetrate ostiole, pollinate and oviposit

C. **Interfloral phase** - seeds develop to maturity; larvae become adult insects in galls; separates receptivity of pistillate flowers from anthesis of staminate flowers

D. **Male phase** - anthers open; males of pollinator emerge from galls, mate.with females, females leave galls and collect pollen before leaving syconium via ostiole or tunnels made by males

E. **Postfloral phase** - figs ripen; dispersed

Valdeyron and Lloyd (1979), while working on the (gyno)dioecious fig, *F. carica,* modified the phases above for seed figs in which the male phase (donor phase) is absent. In the (gyno)dioecious seed figs, four phases are recognised with the interfloral phase (interim phase) being extended until the seeds ripen. The (gyno)dioecious male figs have five phases:

Phase A - **Pre-receptive** - with two sub-stages (bud and enlarging phases)

Phase B - **Receptive**

Phase C - **Interim**

Phase D - **Donor** (absent in seed figs)

Phase E - **Post Donor**

Much of the reported research on figs has been done on monoecious species. Work on the (gyno)dioecious species include the research on *F. carica* (Condit, 1932 & 1947; Galil & Neeman, 1977; Neeman & Galil, 1978 and Valdeyron & Lloyd, 1979), *F. fistulosa* (Corlett, 1987 and Galil, 1973), *F. erecta* (Okamoto & Tashiro, 1981) and *F. asperifolia* (Verkerke, 1987a & 1987b).

Condit (1932) studied *F. carica,* pollinated by *Blastophaga psenes.* He reported that, in this dioecious fig, syconia of the female tree produce long-styled (1,5 to 2,0mm long) pistillate flowers only and syconia of the male tree produce male flowers as well as short-styled (o,55 to 0,90mm long) pistillate flowers. Pistillate flowers are reported as being pedicellate with 5 perianth lobes, a spherical ovary and a cleft stigma while staminate flowers are pedicellate with 5 perianth lobes and 5 stamens. He reported the presence of fertile drupelets from gall flowers and also suggested that the nucellus and embryo sac are used as nourishment for the developing embryo. Condit (1947) described topocentric pollination of *F. carica* by *B. psenes* and indicated that the pollen is carried on the body of the female wasp.

Hill (1967) and Verkerke (1987b) noted that staminate flowers form between 10% to 25% of the total floral count in the *Sycidium* group. They noted that considerable differences exist between the numbers in the various groups of *Ficus.* Galil (1973) attributed these differences to the ethodynamic and topocentric modes of pollination.

Galil (1973) described pollination in *F. fistulosa* by *Ceratosolen hewittii,* with males cutting off and scattering anthers inside the syconial cavity. He noted that mesothoracic pockets are present and covered by flaps. Coxal corbiculae are absent although coxal combs are present, and he suggested that the combs aid in pocket filling.

Considerable variation exists in the ratios of male to female wasps amongst the different (gyno)dioecious groups of *Ficus.* Abdurahiman and Joseph (1976) reported a ratio of 0,3 to 0,4 males per female in *F. hispida.* Nair and Abdurahiman (1984) reported a ratio of 0,25 to 0,4 males per female in *F. exasperata.* Ibrahim (1985) noted a ratio of 0,1 to 0,25 males per female in *F. carica.*

Gali! and Neeman (1977) discussed the conditions in the syconial cavity and speculated on their roles in polleniferous and receptive figs during pollination in *F. carica.*

Neeman and Galil (1978) showed that short-styled female flowers of *F. carica* are capable of producing normal seeds.

Okamoto and Tashiro (1981) reported the storage of pollen along the median line of the 7th sternite in *Blastophaga nipponica*, pollinator of *F. erecta*, aided by the actions of the three pairs of legs.

Berg (1990b) analysed the the dimensions of syconia in relation to the numbers of flowers in the male and female syconia of (gyno)dioecious figs, and in monoecious figs, and concluded that the number of flowers with the size of the fig tends to be proportionately less in (gyno)dioecious than in monoecious species. He also suggested that seed figs tend to be smaller (less inflated) than gall figs.

The members of the' section *Sycidium* are exclusively (gyno)dioecious with an absence of neuter flowers in "gall figs", interfloral bracts are replaced by hairs (bristles) amongst the flowers, hairs may also be present on the tepals and styles. The stigma is clavate and funnel-shaped, staminate flowers are found near a wide ostiole covered by several ostiolar bracts and syconia are trap-blossoms, since they release pollinators by loosening of ostiolar scales (Berg, 1989). Other characteristics of the section lis_ted by Berg (1989) include: staminate flowers with pistils similar to those of short-styled flowers, others with pistillodes, basal bracts found on the peduncle and lacking on the syconium, figs often borne on older wood, topocentric pollination, scabrous unequal-sided leaves, waxy glandular spots on leaves can be nodal and members of this group are trees or shrubs.

The *Sycidium* group is mainly located in Asia and Australia, extending to Madagascar and the Mascarene Islands with five species. Four species are located in continental Africa (Berg, 1989). These four species include *F. asperifolia, F. exasperata, F. pygmaea* and *F. capreifolia.* Of these both *F. pygmaea* and *F. capreifolia* are located in Southern Africa.

Verkerke (1987a & 1987b) reported extensively on the developmental anatomy of *F. asperifolia.* He discussed and speculated on aspects of the shape and structure of the style, features of the stigma, differential growth of the pedicel, dimorphism, heterostyly, proportion of staminate flowers and the occurrence of double fertilisation in the embryo sac which initiates the development of the endosperm and the embryo.

Verkerke (1987) presented a detailed account of the functional anatomy and morphology *F. asperifolia* , which is very closely related to *F. capreifolia.* Some of his findings are listed below:

1. After pollination and fertilisation, the development of the 'endosperm and embryo is initiated in both gall and seed figs. However, in gall figs, the embryo soon aborts but the endosperm continues

to proliferate as long as the ovule is occupied by a wasp egg/larva. He suggested that if wasps are not present in gall fig ovules then they would produce seeds.

2. He suggested that pollen pockets are finely adjusted tools for pollination in oviposited gall flowers, and for the prevention (through non-pollination) of seed formation in non-oviposited gall flowers, to avoid competition for space within syconia.

3. He showed that there is ovule dimorphism, with the gall flower ovule differing from the normal hemianatropous seed flower ovule. The gall flower ovule, with its short inner integument at the raphal side, elongated cells bordering the raphal strand and plasm-rich endothelium-like raphal epidermal cells bordering the nucellus, is adapted for wasp oviposition. He pointed out that the lack of an inner integument at the raphal side allows the ovipositor to deposit the egg directly adjacent to the nucellus.

4. The male far outnumber the female plants in the area studied. Wasp population is apparently kept stable by producing gall figs throughout the year. Seeds are produced in female figs at intervals.

Two phenological patterns occur in fig species, as summarized by Berg (1990b):

1. Individual fig plants within a population are synchronous and aseasonal, producing from one to a few crops of syconia per year. Syconial production at the population level is asynchronous thus ensuring continuous year round availability of syconia to pollinator wasps. This type of phenology is the predominant one in monoecious fig species.

2. Individual fig plants within a population are asynchronous and aseasonal, producing from one to many crops of syconia per year. Syconial production differs for gall and seed fig plants, with seed fig plants producing one or two distinct crops per year and gall fig plants producing syconia continuously throughout the year. This type of phenology is common in the (gyno)dioecious species.

Nair and Abdurahiman (1984) reported that, in *F. exasperata,* seed fig plants have one or two distinct crops per year while gall fig plants flower almost continuously. In *F. carica,* gall fig trees have two or three distinct crops per year while seed fig trees have one main crop per year (Condit, 1932; Kjellberg and Valdeyron, 1984; Valdeyron and Lloyd, 1979).

Berg (1990b) suggested that in both phenological patterns seasonal influences may become stronger due to climatic differences. Further, not all stages may be present together, the duration of phases may vary according to climatic influences and the numbers of figs in a crop may also vary according to seasonal and climatic influences. These conditions may influence the number and availability of pollinators (Galil and Eisikowitch, 1971).

The sandpaper fig, *Ficus capreifolia* Del. is distributed in Africa from Senegal to most parts of Ethiopia, along the major rivers in S. Somalia, through Zaire and south to South Africa (Friis, 1990). Van Greuning (1982) includes Otjinungwa, Skukuza, Blyde River bridge and Jozini in South Africa, as well as Guinea in the West and Lower Sudan in the East as other African locations of *F. capreifolia.*

F. capreifolia has been described as a small, much-branched shrub up to 3m high, prominent in riparian scrub in drier areas at altitudes between 50m to 2600m, with plants in Somalia only located at altitudes below 1000m (Friis, 1990). Van Greuning (1982) described these plants as being 5m tall, with their syconia borne singly or in pairs, having 1 to 2 stamens per flower and 4 to 5 petals per flower.

Verkerke (1989) stated that the study of relations between fig size, the number of flowers per fig, and the size of the syconial cavity in B phase related to the wasp size and the number of wasps entering each fig may be important factors influencing wasp oviposition and pollination. He also suggested that, for a fuller understanding of figs, we need more detailed studies of flower development in a number of different species, both monoecious and (gyno)dioecious.

The present research on *F. capreifolia* was undertaken to examine its morphology, phenology, developmental anatomy and relationship with insects. Except for references to *F. capreifolia* and its characteristics in taxonomic treatments, no detailed work has been done on this (gyno)dioecious species. Field work on this plant was combined with anatomical work with both scanning and light microscope examinations of the plant. Behavioural studies of insects in the field together with observations under the dissecting microscope were undertaken.

It is hoped that this research study will provide other fig researchers with some relevant reference material to enhance biologists' knowledge of figs.

This research on *F. capreifolia* Del. (Moraceae) will be presented mainly in the form of three articles for publication in the South African Journal of Botany and are indicated below:

PAPER 1: Floral morphology and phenology in the (gyno)dioecious fig *Ficus capreifolia* Del. (Moraceae).

PAPER 2: Developmental fig anatomy and related reproductive biology in the (gyno)dioecious fig *Ficus capreifolia* Del. (Moraceae)

PAPER 3: Pollination biology and insects in the (gyno)dioecious fig *Ficus capreifolia* Del. (Moraceae)

These papers will form the three chapters listed below:

Chapter 1: Floral morphology and phenology

Chapter 2: Developmental fig anatomy and related reproductive biology

Chapter 3: Pollination biology and insects

Chapter 1

Morphology and phenology

Abstract

The floral morphology and phenology of *Ficus capreifolia* Del. (Sub-section *Sycidium*, Family: Moraceae) were studied (in the Umdloti area, Natal, South Africa). Male and female syconia were produced asynchronously on separate plants growing on sandy river banks. Floral characters analysed revealed peduncular bracts, trap-blossom syconia, perfect heterostyly amongst other characteristics in line with other (gyno)dioecious species of figs described. A developmental cycle of about 120-140 days with an extended prefemale phase was recorded for both gall and seed figs. The marginal southern latitude, cool, dry weather and low population levels of plants and pollinators appeared to limit the spread of this plant.

Key Words: *Ficus*, *Sycidium*, Moraceae, phenology, (gyno)dioecious, developmental cycle, floral morphology, fruit set, floral ratios.

INTRODUCTION

Ficus capreifolia Del., is one of four African members of the section *Sycidium*, sub-genus *Ficus* (Berg, 1989). The other members are *F. asperifolia* Miq., *F. pygmaea* Welw. ex Hiern and *F. exasperata* Vahl.

The sandpaper fig, *Ficus capreifolia* Del. is distributed in Africa from Senegal to most parts of Ethiopia, along the major rivers in S. Somalia, through Zaire and south to South Africa (Friis, 1990). The plant has been described as a small, much-branched shrub up to 3m high, prominent in riparian scrub in drier areas at altitudes between 50m to 2600m, with only plants in Somalia recorded at altitudes below 1000m (Friis, 1990).

The members of the genus *Ficus* display a complex mutualistic relationship between pollinating wasps and fig syconia. Much of the reported research on figs has been done in monoecious species. Work on the (gyno)dioecious figs include work on *F. carica* (Condit, 1932; Galil & Neeman, 1977; Neeman & Galil, 1978 and Valdeyron & Lloyd, 1979), *F.tistulosa* (Corlett, 1987; Galil, 1973) and *F. asperifolia* (Verkerke, 1987a & 1987b).

The (gyno) dioecious species produce "male" and female syconia on separate plants. Male syconia produced on male plants bear numerous short-styled pistillate and some staminate flowers. While these male syconia are hermaphrodite and (gyno)dioecious, they produce pollen in staminate flowers and harbour pollinator wasps in short-styled pistillate flowers only. Seeds are not produced in these male syconia, and they are therefore functionally dioecious, as they enable the species to fulfil the male function only in them.

Condit (1932) studied *F. carica,* pollinated by *Blastophaga psenes.* He reported that, in this (gyno)dioecious fig, syconia of the female tree produce long-styled (1,5 to 2,0mm long) pistillate flowers only and syconia of the male tree produce male flowers as well as short-styled (0,55 to 0,90mm long) pistillate flowers. Pistillate flowers are reported as being pedicellate with 5 perianth lobes, a spherical ovary and a cleft stigma while staminate flowers are pedicellate with 5 perianth lobes and 5 stamens. He reported the presence of fertile drupelets from gall flowers.

Hill (1967) and Verkerke (1987) noted that staminate flowers form between 10% to 25% in the species of the *Sycidium* group studied. They noted that considerable differences exist between the numbers in the various subgenera of *Ficus.* Galil (1973) attributed these differences to the ethodynamic and topocentric modes of pollination.

The section *Sycidium* is divided into 3 sub-sections including *Sycidium* (70 spp.), *Varinga* (15 spp.} and

Paleomorphe (20 spp.). The members of the section *Sycidium* are exclusively (gyno)dioecious with an absence of neuter flowers in "gall figs". Interfloral bracts are replaced by hairs (bristles) and such hairs may also be present on the tepals and styles. The stigma is clavate and funnel-shaped. Staminate flowers are found near a wide ostiole covered by several ostiolar bracts. Syconia are "trap-blossoms" since they release pollinators by loosening of ostiolar scales (Berg, 1989). Other characteristics of the section listed by Berg (1989) include: staminate flowers with pistils similar to those of short-styled flowers, others with pistillodes, basal bracts found on the peduncle and lacking on the syconium, figs borne on older wood, topocentric pollination, scabrous unequal-sided leaves, waxy glandular spots on leaves may be at the nodes and members of this group are trees or shrubs.

Corlett (1987) recorded a 11,5 to 12,5 week cycle for the seed figs and a 7,5 to 9 week cycle for gall figs of the (gyno)dioecious fig, *F. fistulosa.* Information about developmental cycles in other (gyno) dioecious figs is lacking.

Verkerke (1987) discussed and speculated on aspects of the shape and structure of the style, features of the stigma, differential growth of the pedicel, dimorphism, heterostyly and proportion of staminate flowers. He also recorded that hermaphroditic plants far outnumber the female plants in the area studied. Wasp population is apparently kept stable by producing gall figs throughout the year. Seeds are also produced in female figs at intervals.

Berg (1990) summarized the phenological patterns in fig species. He noted that, in the (gyno)dioecious species, individual fig plants within a population are asynchronous and aseasonal producing from one to many crops of syconia per year. Syconial production differs for gall and seed fig plants, with seed fig plants producing one or two distinct crops per year and gall fig plants producing syconia continuously throughout the year.

Nair and Abdurahiman (1984) reported that, in *F. exasperata,* seed fig plants have one or two distinct crops per year while gall fig plants flower almost continuously. In ***F.*** *carica,* gall fig trees have two or three distinct crops per year while seed fig trees have one main crop per year (Condit, 1932; Kjellberg and Valdeyron, 1984; Valdeyron and Lloyd, 1979).

Berg (1990) suggested that, in both phenological patterns, seasonal influences may become stronger due to climatic differences. Further not all stages may be present together, the duration of phases may vary according to climatic influences and the numbers of figs in a crop may also vary according to seasonal and climatic influences. These conditions may influence the number and availability of pollinators (Galil and Eisikowitch, 1971).

Some work has been done on a few monoecious fig pecies only in South Africa. This research was undertaken to investigate the floral morphology and phenology of the male (gall) and female (seed) figs of *F. capreifolia.* No detailed work about *F. capreifolia* has been done, except for some taxonomic work by some researchers and this investigation was a part of a research project to understand the pollination biology of this species. Further investigations in this project will focus on the developmental anatomy and pollination biology of this fig species.

The work done in this study on *F. capreifolia* provides information on new locations, growth forms of this plant and its possible ecological role as a pioneer, asynchronous fruiting patterns and comparison of morphological characteristics with other (gyno)dioecious species studied. Data on ostiolar bracts, dimensions of flowers (overall, pedicel, style and ovary lengths), ratios of pistillate and staminate flowers, numbers of pollinated and unpollinated flowers, fruiting patterns of the population and the developmental cycles of male and female trees are provided. It is hoped that this investigation will provide other fig researchers with valuable data and information.

MATERIALS AND METHODS

Fifteen shrubs of *Ficus capreifolia* were located along the banks of the Umdloti river, between 29° 38'S and 31° 06'E, Verulam, in a 4,5 km stretch between Canelands and Mt. Moreland with an annual rainfall of 1000mm at an altitude of less than 50m (Figs la & b). Most of these plants grew on the sandy river banks away from the waters edge. A few were located on built up silt beds, and others on raised banks (from 3m to 50m away).

Of these 10 accessible shrubs were selected for monthly censuses of leaves and fruit over a period of 24 months. Figs were collected and examined to determine the sexes of the plants. Mature syconia were split and examined under a dissecting microscope, and their floral morphology was analysed.

Selected syconia on "male" and female plants were labelled at initiation and biweekly diameter measurements were made using vernier calipers. Monthly observations of the flowering phenology at different phases were made.

Some scanning electron microscope (SEM) work was done using late A phase figs and isolated C phase gall flowers, which were fixed in 70% ethanol after collection. These were first washed in water after fixation, then dehydrated in an alcohol series (70%, 90% and 2X 100% for 10 min. each), critical point dried in a Bio-Rad CPD 750 unit, mounted on stubs and coated in a Polaron SEM E5000 unit before observation in a SEM.

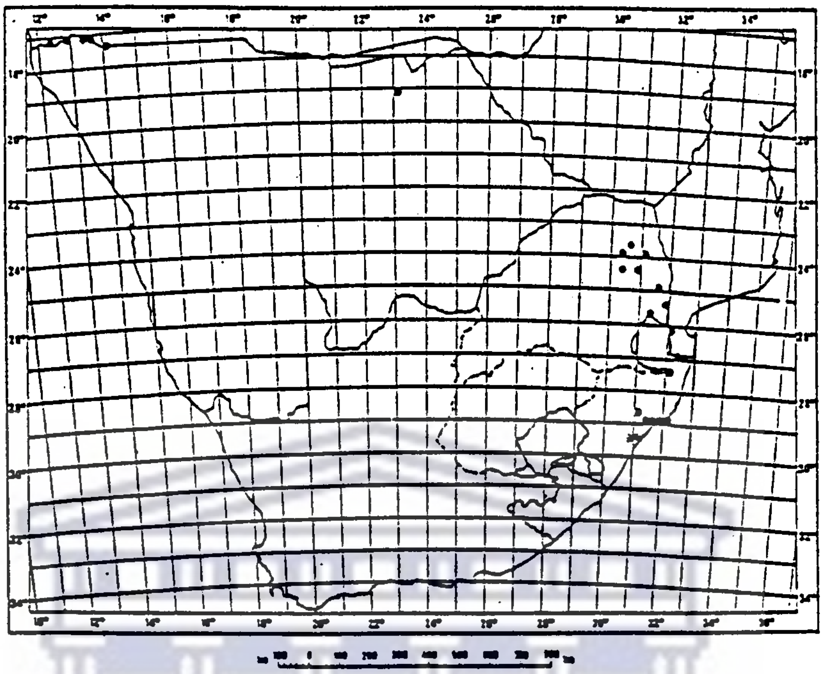


Fig 1(a): Distribution of *F. capreifolia* in Southern Africa, with plants in this study indicated by * (after Greuning, 1982)

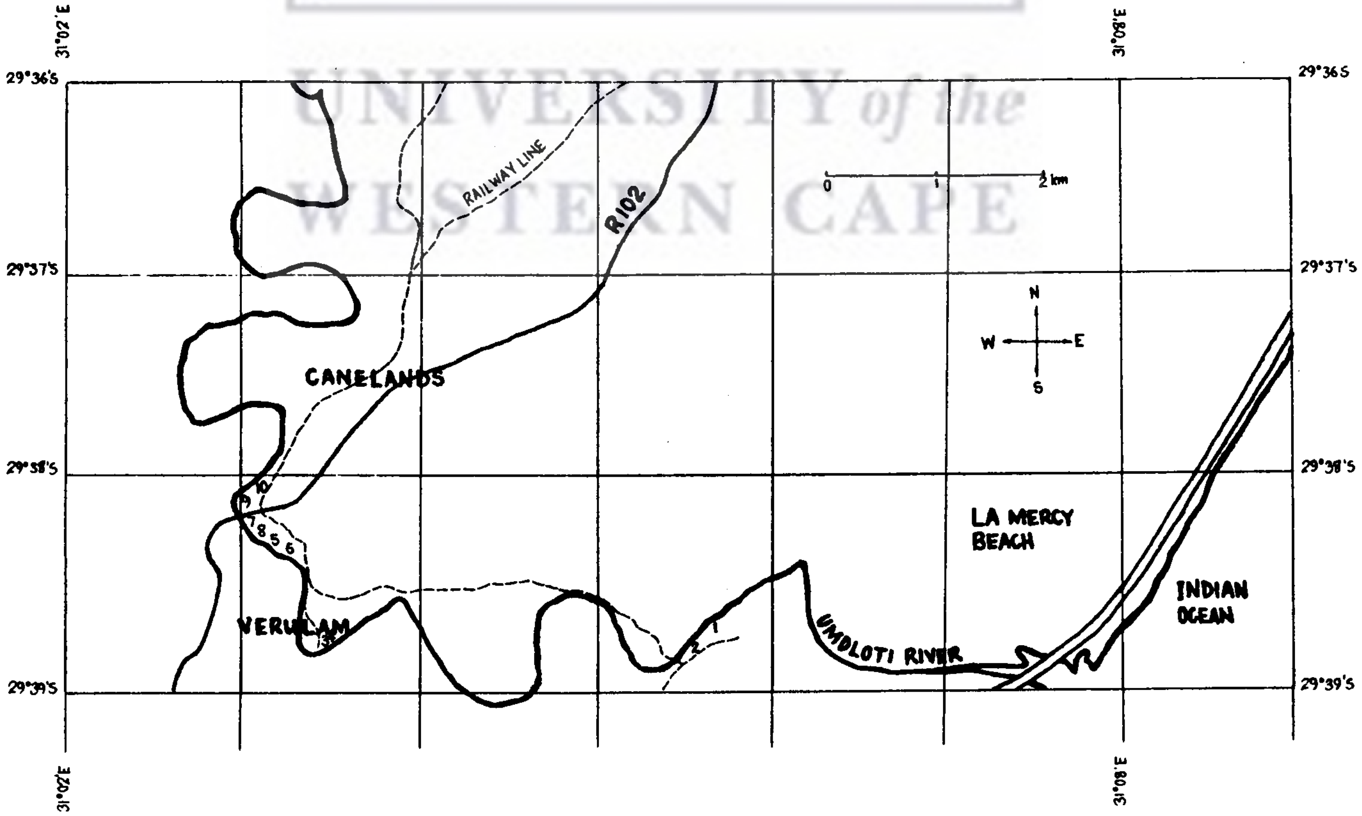


Fig 1(b): Location of shrubs of *F. capreifolia*

RESULTS/OBSERVATIONS

Ficus capreifolia is a riverine, evergreen shrub up to 3m tall and sometimes spreading with a diameter of up to 10m on the sandy soil (Figs 2 & 3). Stems displayed stoloniferous growth producing shoots and adventitious roots at various nodes. Prostrate branches occasionally gave rise to upright villous branches and branchlets (fig 4). The stem was greenish-grey bearing exstipulate leaves on horizontal and vertical branches. In favourable conditions rapid leaf growth occurred with leaves present throughout (evergreen). Leaves were oblong-ovate, unequal-sided with a slightly rounded base (fig 5). The apex of a leaf was acute or trifid, with the margin varying from entire to somewhat crenate. Both leaf surfaces were scabrous giving the plant its sandpaper quality.

Syconia arose singly in an axillary position (fig 5). Mature syconia were between 15mm to 26mm in diameter and yellow to purple when ripe. Syconia in female plants reached a maximum diameter of around 15mm to 16mm, while "male" syconia reached a maximum diameter of 16mm to 26mm. Basal bracts were scattered over a short peduncle (about 10mm to 15mm). Towards the base all the syconia had 5 longitudinal ridges.

F. capreifolia is (gyno)dioecious with "male" plants (fig 2) bearing hermaphrodite syconia and female plants (fig 3) bearing female syconia. The plant is functionally

Fig 2: Male plant of
of *F. capreifolia*
(Bar = 40mm)

Fig 3: Female plant
F.capreifolia
(Bar = 50mm)

Fig 4: Male plant of *F. capreifolia*
on sandy river bank
(Bar = 100mm)

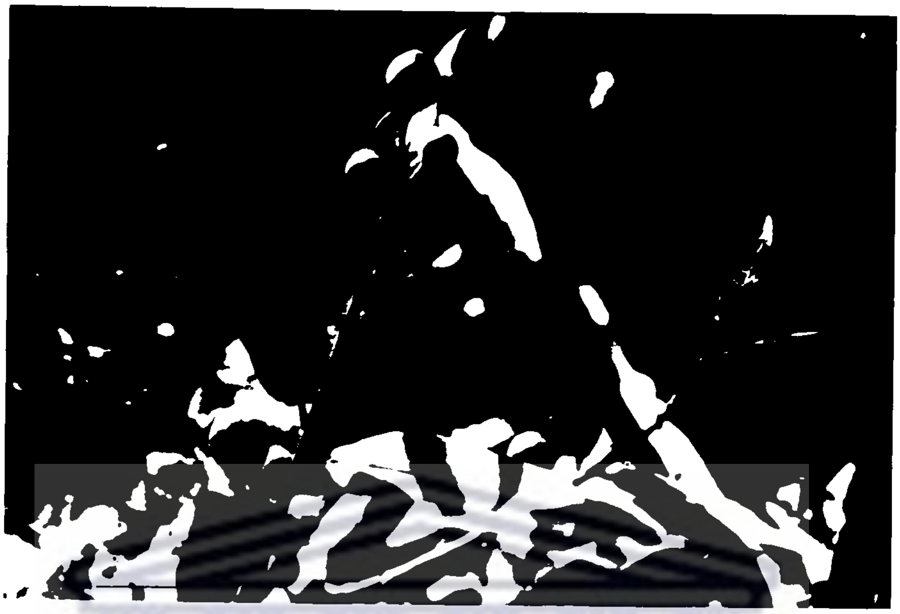


Fig 5(a): Branch of male plant of *F. capreifolia* showing leaves and syconia Bar = 20mm)

Fig 5(b): Upright branch of male plant of *F.capreifolia* showing C-phase syconia (Bar = 20mm) dioecious and structurally (gyno)dioecious. Both types of syconia were similar externally and no distinction could be made from an observation of their vegetative parts. Externally both types of syconia had a smooth to slightly warty texture.

Male and female syconia had similar ostioles covered by imbricate horizontal and vertical bracts (scales). Horizontal ostiolar bracts were arranged transversely towards the outside of the ostiole and the vertical bracts descended into the ostiole (figs 6a & b). Outer horizontal bracts were thick, wide and green (like the syconium wall), while the inner horizontal bracts were thin, narrow and colourless. Outer bracts had fine pinkish hairs on their margins (figs 6a). One or more bracts on the outside had slightly longer brown hairs with glandular tips (swollen). The outer horizontal bracts were initially in rows of five (for 4 to 5 rows) and thereafter arranged spirally as there was a transition to the vertical bracts which descended into the syconial cavity. The apices only of the outer vertical bracts were turned downwards. The greater part of the inner vertical bracts hung downwards. The innermost bracts lay flat against the staminate flowers, displaying considerable variation in shape and size, with most of the bracts appearing tepaline. The size and arrangement of the bracts made the ostiolar passage and opening continuous with the syconial cavity. As the ostiolar bracts were removed for counts the thicker outer bracts emitted a milky sap while the inner bracts emitted

Fig 6(a): SEM view of L/S of A-phase male fig (5,1mm diameter) of *F. capreifolia* showing horizontal& vertical bracts, syconial wall & cavity and pistillate & staminate flowers
(Bar = 100um)

Fig 6(b): SEM view of L/S of ostiolar region of A-phase female fig (6,2mm diameter) of *F. capreifolia* showing bracts
(Bar = 0,175mm)

a watery fluid. Both the horizontal and vertical bracts of mature male (19,7mm diameter) and female (16,0mm diameter) syconia were removed and analysed (Table 1). The mean number of bracts in the male syconia was 186,8 (range 153 to 222) and 139,4 (range 117 to 160) in the female syconia. The mean ratio of vertical:horizontal bracts was 3,34:1 (range 2,67:1 to 5,00:1) in the male syconia and 4,62:1 (range 3,31:1 to 6,60:1) in the female syconia. The female syconia had a smaller number of horizontal bracts (mean 24,8) than the male syconia (mean 43,0).

Table 1: Mean number of vertical (V) and horizontal (H) ostiolar bracts in mature male and female syconia of *F. capreifolia* (N=10)

CATEGORY		MALE	FEMALE
MEAN **DIAMETER** (mm)		19,7	16,0
TOTAL (H + V)	:**MEAN**	**186,8**	**139,4**
	:RANGE	152 - 222	117 - 160
HORIZONTAL	:**MEAN**	**43,0**	**24,8**
	:RANGE	34 - 48	20 - 38
	: %	23	17,8
VERTICAL	:**MEAN**	**143,8**	**114,6**
	:RANGE	113 - 178	93 - 136
	: %	77,0	82,2
RATIO V : H		3,3 : 1	4,6 : 1

Wasp wings and other appendages were found between the bracts. The vertical bracts in the female figs were much shorter than those in the gall figs.

Male syconia had staminate flowers in two to three rows near the ostiolar region with one stamen (sometimes two or rarely three). A pistil containing a stigma, style and ,

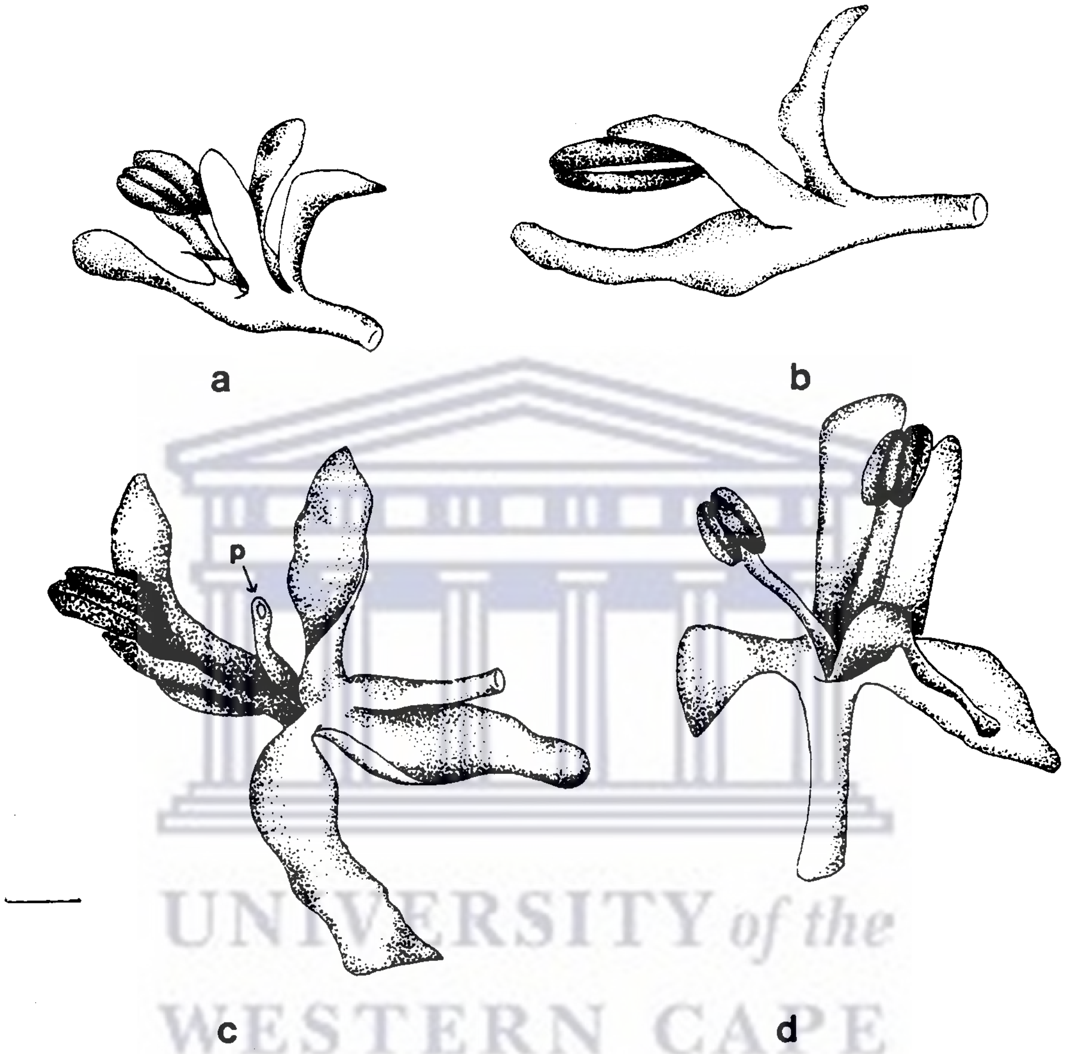


Fig 7(a) -(d): Staminate flowers of *F. capreifolia* showing (a) anther supported by filament (b) side view (c) top view with pistillode and (d) flower with two stamens and a pistil
(Bar = 1mm)
p - pistillode

Fig 8(a) & (b): Pistillate flowers of *F. capreifolia* showing (a) long-pedicelled flower and (b) short-pedicelled flower (Bar = 0,5mm) ovary was present in a few male flowers in the transition zone towards the female flowers. Mostly four or rarely five perianth segments arose from a basally fused perianth tube. Flowers were about 4mm long with large bilobed anthers, 0,8mm to 1,5mm long, dehiscing by longitudinal slits. Filaments were attached to the back of the anthers and enlarged at the point of attachment (Figs 7a to d). Anthers with pollen were yellow, and on drying turned dark brown.

Table 2: Mean lengths (mm) of B-phase and D-phase pistillate flowers in male syconia of *F. capreifolia*

CATEGORY	SHORT-PEDICELLED		LONG-PEDICELLED	
PHASE	**B**	D	**B**	D
OVERALL LENGTH				
-MEAN	**1,54**	**3,26**	**1,75**	**6,33**
-RANGE	1,3-1,7	2,5-3,9	1,6-2,0	5,2-7,3
PEDICEL				
-MEAN	**0,33**	**1,61**	**0,69**	**4,40**
-RANGE	0,2-0,4	1,1-2,1	0,6-0,8	3,7-5,0
STYLE				
-MEAN	**0,55**	**0,67**	**0,55**	**0,66**
-RANGE	0,4-0,7	0,6-0,7	0,4-0,6	0,6-0,7
GALL OVARY				
-MEAN	**0,64**	**1,71**	**0,61**	**1,76**
-RANGE	0,5-0,8	1,6-1,9	0,5-0,8	1,6-1,9

NB: MEAN **OVIPOSITOR LENGTHS** OF FEMALES OF POLLINATOR WASP RANGE FROM **0,4mm - 0,7mm.**

Pistillate flowers were found occupying the rest of the space in the male syconium. They were attached to a thick syconial wall, of up to 1,7mm wide, by a pedicel of 0,2mm to 5,0mm long. No sessile pistillate flowers were present in male syconia. Each flower had an oval-shaped, superior ovary (0,5mm to 1,9mm long), a tubular style (0,4mm to 0,7mm long) and a large clavate, funnelled stigma (Figs 8a & b). Four long perianth segments (*ca.* 2,0mm long) formed a short perianth tube near the base. One perianth lobe was twice as long as the other three and curved inwards at the apex to form a hood. Near the transition zone, one or two pistillate flowers had anthers. The style generally arose from a lateral position near the apex of a laterally-flattened ovary. Ovaries (galls) carrying wasp larvae increased in length, from 0,5mm in B-phase to 1,9mm in D-phase. Each floret was pale green with the style and stigma being purple to pink due to the presence of hairs.

While there was a range of pedicel lengths from 0,2mm to over 5,0mm, there were two categories of B-phase pistillate flowers (Figs 9a & b), with short-pedicelled flowers having a mean pedicel length of 0,33mm (range 0,2mm to 0,4mm), and long-pedicelled flowers with a mean pedicel length of 0,69mm, having a range 0,6mm to 0,8mm (Table 2). In D-phase these pedicel lengths increased markedly to a mean of 1,61mm (range 1,1mm to 2,1mm) in short-pedicelled flowers, and to a mean of 4,4mm (range 3,7mm to 5,0mm) in long-pedicelled flowers. Short-pedicelled flowers lay closer to the syconium wall and the pedicels of many long-pedicelled flowers, especially in D-phase, were twisted to draw the galls into available space. All these pistillate flowers had relatively short styles compared to those in seed flowers (Tables 3 & 4). Many uninfected flowers were located in areas which

Fig 9(a): Short-pedicelled pistillate flower in male fig (13,4mm diameter) of *F. capreifolia* also showing gall ovary (Bar = 100um)

Fig 9(b): Long-pedicelled pistillate flower in male fig (14,0mm diameter) of *F. capreifolia* (Bar = 100um) appeared to be inaccessible (in the lower V-shaped part of the syconium). These flowers still had their stigmas covered by the perianth lobes also.

Female trees bore female syconia only. These syconia were lined with pistillate flowers. Each flower was sessile or pedicellate. Pedicel length varied (range 0,3mm to 1,0mm) to accommodate the ovary in the syconial cavity. Perianth segments similar to those in the gall flower, with four lobes joined at the base to form a perianth tube of *ca*. 1,6mm long, were 2,3mm to 3,1mm long with curved edges enclosing the ovary. One perianth segment was very large and spathe-like, one opposite was smaller and also spathe-like and two laterals were flattened. The laterally compressed, superior ovary was 0,7mm to 1,0mm long when the flower was receptive and thereafter increased to 1,0mm to 2,0mm long during development (Table 3). A style arose laterally near the apex and was 0,9mm to 2,0mm long. The tubular style (longer than in gall flowers) supported a large clavate stigma at its end. The stigma, style and ovary turned purplish to pink as the syconium reached the receptive stage. Hairs were visible on the style and stigma. At the receptive stage the stigmatic surfaces were linked to form a synstigma. Each ovary had a single parietal ovule and these became brown as they matured in the ripening syconium. Seeds (in the ovary) became covered in a slimy, succulent substance as they ripened for dispersal.

Table 3: Mean dimensions (mm) in B- and E-phase pistillate flowers in female syconia of *F. capreifolia*

CATEGORY	PHASE	**OVERALL LENGTH**		**PEDICEL LENGTH**	
		MEAN	RANGE	**MEAN**	RANGE
SESSILE	**B**	**2,67**	2,3-3,0	-	-
	E	2,97	2,4-3,3	-	-
SHORT-PEDICELLED	**B**	**2,71**	2,4-3,0	**0,34**	0,3-0,4
	E	3,43	3,0-4,0	1,11	0,8-1,3
LONG-PEDICELLED	**B**	**2,89**	2,6-3,1	**0,74**	0,6-1,0
	E	4,06	3,2-4,8	2,17	1,6-3,0

CATEGORY	PHASE	**STYLE LENGTH**		**PEDICEL LENGTH**	
		MEAN	RANGE	**MEAN**	RANGE
SESSILE	**B**	**1,71**	1,5-2,0	**0,86**	0,7-1,0
	E	1,69	1,3-2,0	1,34	1,0-1,7
SHORT-PEDICELLED	**B**	**1,34**	1,0-1,6	**0,85**	0,7-0,9
	E	1,34	1,0-1,8	1,57	1,2-2,0
LONG-PEDICELLED	**B**	**1,18**	0,9-1,4	**0,86**	0,8-0,9
	E	1,19	0,9-1,6	1,52	1,3-1,8

Three categories of pistillate flowers were present in female syconia:- sessile, short-pedicelled and long-pedicelled. In the sessile flowers of the B-phase, the styles, with a mean length of 1,69mm (range of 1,3mm to 2,0mm), were slightly longer than in the pedicelled pistillate flowers. In E-phase these sessile flowers usually had enlarged ovaries with seeds only (from 0,86mm to 1,34mm). In the short-pedicelled flowers of B-phase, the pedicels had a mean length of 0,34mm (range 0,3mm to 0,4mm) and a mean style length of 1,34mm (range 1,0mm to 1,6mm). In the E-phase these pedicels had increased their mean length to 1,11mm (range 0,8mm to 1,3mm) with the enlarged ovaries containing seeds increasing from 0,85mm to 1,57mm in length. In the long-pedicelled flowers of B-phase, the pedicels had a mean length of 0,74mm (range 0,6mm to 1,0mm) and a mean style length of 1,18mm (range 0,9mm to 1,4mm). In the E-phase these pedicels had increased their mean length to 2,17mm (range 1,6mm to 3,0mm), and the ovaries containing seeds had increased from 0,86mm to 1,52mm in length.

The styles of the sessile and short-pedicelled flowers were straight while the long-pedicelled flowers had variously-shaped styles (clearly noticeable in the B-phase). Styles were hooked, curved, wavy or folded. Synstigmas were formed in pistillate seed flowers when the stigmatic surfaces were aligned to form a platform. The ovaries were in layers (or series) in the syconial space.

Glandular hairs were pink (to red) in the stigmas, styles and margins of the ostiolar bracts. The colour extended into the open stigma for up to 0,5mm.

An analysis of mature male syconia (Table 4) revealed that the mean diameter was 20,6mm (range 16,1mm to 25,5mm) with each having a mean number of 1439,1 flowers (range 1142 to 1692). Of these there was a mean of 91,7% or 1320,4 (range 1026 to 1584) pistillate flowers and 8,3% or 118,7 (range 101 to 150) staminate flowers, giving a ratio of 11,1 pistillate flowers to 1 staminate flower per syconium. Of the 1320,4 pistillate, 60,9% or 803,6 (range 328 to 1360) produced galls and 39,1% or 516,8 (range 136 to 996) were not pollinated or infected.

Table 4: Mean numbers of pistillate and staminate flowers per male syconium in *F. capreifolia* (N = 10)

CATEGORY	**PISTILLATE FLOWERS (P)**		**STAMINATE FLOWERS (S)**		**RATIO**
	NUMBER	%	**NUMBER**	%	P : S
TOTAL	**1320,4**	91,7	**118,7**	8,3	**11,1 : 1**
GALL FLOWERS	**803,6**	55,8	-	-	-
UNINFECTED/ UNPOLLINATED	**516,8**	35,9	-	-	-

NB: 1. MEAN DIAMETER OF MALE SYCONIA - **20,6mm**
2. MEAN NUMBER OF FLOWERS PER MALE SYCONIUM - **1439,1**

An analysis of mature female syconia (table 5) revealed that the mean diameter was 15,1mm (range 13,1mm to 15,8mm), with each having an average of 1080,8 (range 988 to 1186) pistillate flowers. Of these there was an average of 85,2% or 921,2 (range 762 to 1062) pollinated and 14,8% or 159,6 (range 96 to 226) unpollinated flowers, representing an average ratio of 5,8 pollinated to 1 unpollinated flower. Most of the unpollinated flowers were found in the pedunculate and ostiolar ends of the syconium.

Table 5: Mean numbers of pollinated and unpollinated flowers per female syconium in *F. capreifolia*

TOTAL	**POLLINATED FLOWERS (P)**		UNPOLLINATED FLOWERS (U)		**RATIO**
P + U	**NUMBER**	%	NUMBER	%	P : U
1080,8	**921,2**	85,2	159,6	14,8	**5,8 : 1**

NB: MEAN DIAMETERS OF FEMALE SYCONIA: **15,1**

Table 6: Number of female syconia in different diameter ranges and phases on a single shrub of *F. capreifolia*

PHASE	DIAMETER RANGES	NUMBER	CUMULATIVE	
			PHASE	TOTAL
PRE-FEMALE A	1,1-2,0	1		
	2,1-3,0	3		
	3,1-4,0	0		
	4,1-5,0	4		
	5,1-6,0	6		
	6,1-7,0	7	21	21
FEMALE B	7,1-8,0	4		
	8,1-9,0	4		
	9,1-10,0	2		
	10,1-11,0	1	11	32
INTER-FLORAL C	11,1-12,0	1		
	12,1-13,0	1		
	13,1-14,0	4	6	38
RIPE E	14,1-15,0	4		
	15,1-16,0	2		
	16,1-17,0	1	7	45

Production of syconia on a plant was asynchronous. At any one time it was possible to observe or collect syconia of all the different developmental stages on/from a shrub (as seen in Table 6).

It was also interesting to note that only certain branches produced syconia and that a few branches had syconia in the young stages only, and some had old syconia whilst others had a range from very young to old stages. Young syconia appeared to be closer to the apical region in many branches, indicating that syconia were first initiated in the older sections of branches and developed to the apex.

Although ten plants were monitored, only six (three female and three male) plants produced syconia. The other four did not produce any syconia during the study period. Plants 2, 5 and 6 (female) that produced syconia were separated, with plants 5 and 6 being closer together and plant 2 being about 1,5km. away. One "fruiting" male plant (plant 3) was located between the two groups of female plants, and the other two male plants (plants 9 and 10) were located about 0,5km west of plants 5 and 6.

Table 7: Fruiting patterns of female plants (P) of *F. capreifolia* showing young, mature and ripe syconia during a two-year period (1991/1992)

YEAR	MONTH	**FEMALE PLANTS**								
		YOUNG (A & B)			MATURE (C)			RIPE (D)		
		P2	P5	P6	P2	P5	P6	P2	P5	P6
1991	**JAN**			**X**	**X**		**X**	**X**		
	FEB			X	X		X	X		X
	MAR	**X**	**X**	**X**			**X**			**X**
	APR	X	X	X	X	X	X			X
	MAY	**X**		**X**	**X**	**X**	**X**	**X**	**X**	**X**
	JUN				X		X	X	X	X
	JUL							**X**		**X**
	AUG									
	SEPT			**X**						
	OCT	X		X			X			
	NOV	**X**		**X**	**X**		**X**			**X**
	DEC	X			X		X	X		X
1992	**JAN**	**X**		**X**	**X**		**X**	**X**		**X**
	FEB	X		X	X		X	X		X
	MAR			**X**			**X**	**X**		**X**
	APR			X			X			X
	MAY			**X**			**X**			
	JUN			X			X			X
	JUL			**X**			**X**			**X**
	AUG									
	SEP	**X**								
	OCT	X		X						
	NOV				**X**			**X**		
	DEC				X			X		

Of the three female plants only one (plant 6) produced syconia on a fairly regular basis (Table 7). However, the number of syconia was limited and this made collections for study difficult. Furthermore, a fire, in July 1992, burnt the leaves and syconia (marked in a developmental study) of this plant. It took this plant about 6 months to recover with new syconia only re-appearing another 3 months later.

Table 8: Fruiting patterns of male plants (P) of *F. capreifolia* showing young, mature and ripe syconia during a two-year period (1991/1992)

YEAR	MONTH	MALE PLANTS								
		YOUNG (A&B)			MATURE (C)			RIPE (D&E)		
		P3	P9	P10	P3	P9	P10	P3	P9	P10
1991	**JAN**	**X**					**X**	**X**		**X**
	FEB	X			X					
	MAR	**X**	**X**	**X**	**X**		**X**			
	APR	X	X	X	X	X	X	X		X
	MAY	**X**		**X**	**X**	**X**	**X**	**X**	**X**	**X**
	JUN				X	X	X	X	X	X
	JUL	**X**		**X**	**X**			**X**	**X**	
	AUG	X	X	X			X	X		
	SEP		**X**	**X**	**X**	**X**	**X**			
	OCT				X	X	X	X		X
	NOV		**X**		**X**	**X**	**X**	**X**	**X**	**X**
	DEC		X	X	X	X		X	X	X
1992	**JAN**	**X**	**X**	**X**		**X**	**X**		**X**	**X**
	FEB	X	X	X		X	X		X	X
	MAR	**X**	**X**	**X**	**X**	**X**	**X**			**X**
	APR	X	X	X	X	X	X	X	X	X
	MAY	**X**		**X**	**X**	**X**	**X**	**X**	**X**	**X**
	JUN	X	X	X	X	X	X	X	X	X
	JUL	**X**	**X**	**X**	**X**		**X**	**X**	**X**	**X**
	AUG	X	X	X	X		X	X	X	X
	SEP	**X**		**X**	**X**	**X**	**X**			**X**
	OCT	X		X	X		X			X
	NOV	**X**	**X**		**X**	**X**	**X**	**X**		**X**
	DEC	X	X		X	X	X	X	X	X

The three male plants produced syconia regularly (Table 8). While there were numerous syconia that aborted fairly regularly after the female stages (on both male and female plants), there were syconia present at most times on at least one of the three male plants.

The developmental cycle of the male syconia of *F. capreifolia* lasted about 130 to 140 days (see Table 9 & Graph 1). The developmental stages were analysed in relation to the 5 stages as first recognised by Galil & Eisikowitch (1968a), in *F. sycomorus,* for monoecious figs and later modified by Valdeyron and Lloyd (1979) for *F. carica,* a (gyno)dioecious fig.

<u>Phase A</u>: The prefemale phase lasted between 45 to 55 days until a diameter of over 7,0mm to 8,0mm was reached. Syconia were collected and split open at different times of the year to record variations. Shorter cycles were noted in the warmer, wetter months (October to December) of the year, with earlier maturation times for each stage and shorter phases.

<u>Phase B</u>: The female phase started at about the 45th to 50th day and lasted generally for 5 to 8 days. The ostiolar bracts loosened and a small opening was visible. This ostiolar area ranged from pink to red in colour with numerous fine hairs. Syconia of about 7,0mm to 10,0mm were receptive at this phase and, only if fertilisation occurred, rapid development followed thereafter, as the syconium passed into the next phase. In the absence of fertilisation this phase was extended by about a week or

two before the unfertilised figs dried and aborted. Many of these were split open and revealed an absence of insects.

Phase C: The interfloral phase started at about the 50th to the 60th day and lasted to the 100th to 125th day (a period of 40 to 75 days, or even longer in adverse conditions). This was a fairly long period and showed a constant increase in size, from about 8-16mm in diameter. The syconia enlarged and hardened, with the ostiolar bracts becoming compact and closing off the ostiole. The syconial space disappeared as the ovaries containing galls enlarged and filled up all the available space within. Only towards the end of this phase was it possible to see the outlines of the developing wasps in the ovaries.

Phase D: The male phase started between the 120th to 125th days and lasted for about 3 to 5 days. During this phase wasps hatched out of ovaries, became fertilised and collected pollen from the mature anthers before leaving the syconia via the ostiole. The ostiolar bracts loosened at this stage.

Phase E: The postfloral phase started about the 130th to 135th day (or later in adverse conditions). Very rapid increase in the syconial diameter from about 17,0mm to 20,0mm occurred in a few days as it ripened. The wall became softer, succulent and yellow to brown. These figs were eaten by birds, mice, monkeys or they fell off.

In favourable weather (summer/spring), a developmental cycle of under 100 days was observed, with shorter periods for each phase (A -up to 35 days, B - 35 to 42 days, C - 42 to 84 days, D - 84 to 91 days and E - 91 to 98 days) in a male plant.

The developmental cycle of the female syconia of *F. capreifolia* lasted about 120 to 130 days (see Table 9 and Graph 2). These stages were also analysed in relation to the modified stages as recognised by Valdeyron and Lloyd (1979) for *F. carica*. There was no male phase in female syconia.

<u>Phase A</u>: The prefemale phase was similar to that in the gall fig. It lasted about 50 days.

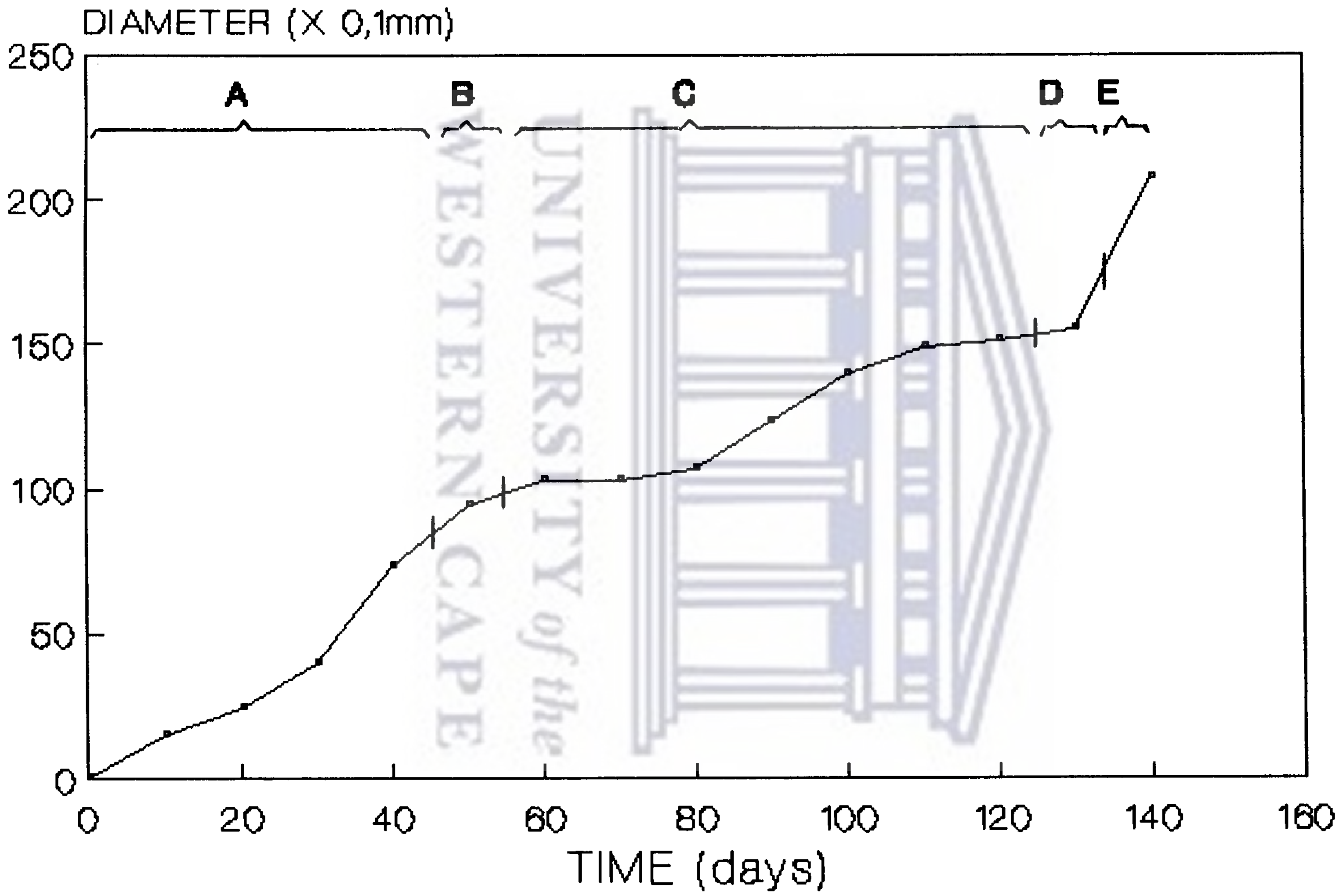
<u>Phase B</u>: The female (receptive) phase which was similar to that in the gall fig, started between the 50th to the 60th days and lasted for about 5 to 10 days (or longer in adverse conditions - up to 2 to 3 weeks).

<u>Phase C</u>: The interfloral phase started at about the 60th day and lasted up to the 100th day (for 40 days). There was an increase in size of about 2mm to 3mm during this time, as the fertilised ovules became transformed into seeds in their ovaries. The syconia enlarged and hardened, with the ostiolar bracts sealing off the ostiole. Internally the syconial space disappeared as the developing seeds (in ovaries) filled up all the available space.

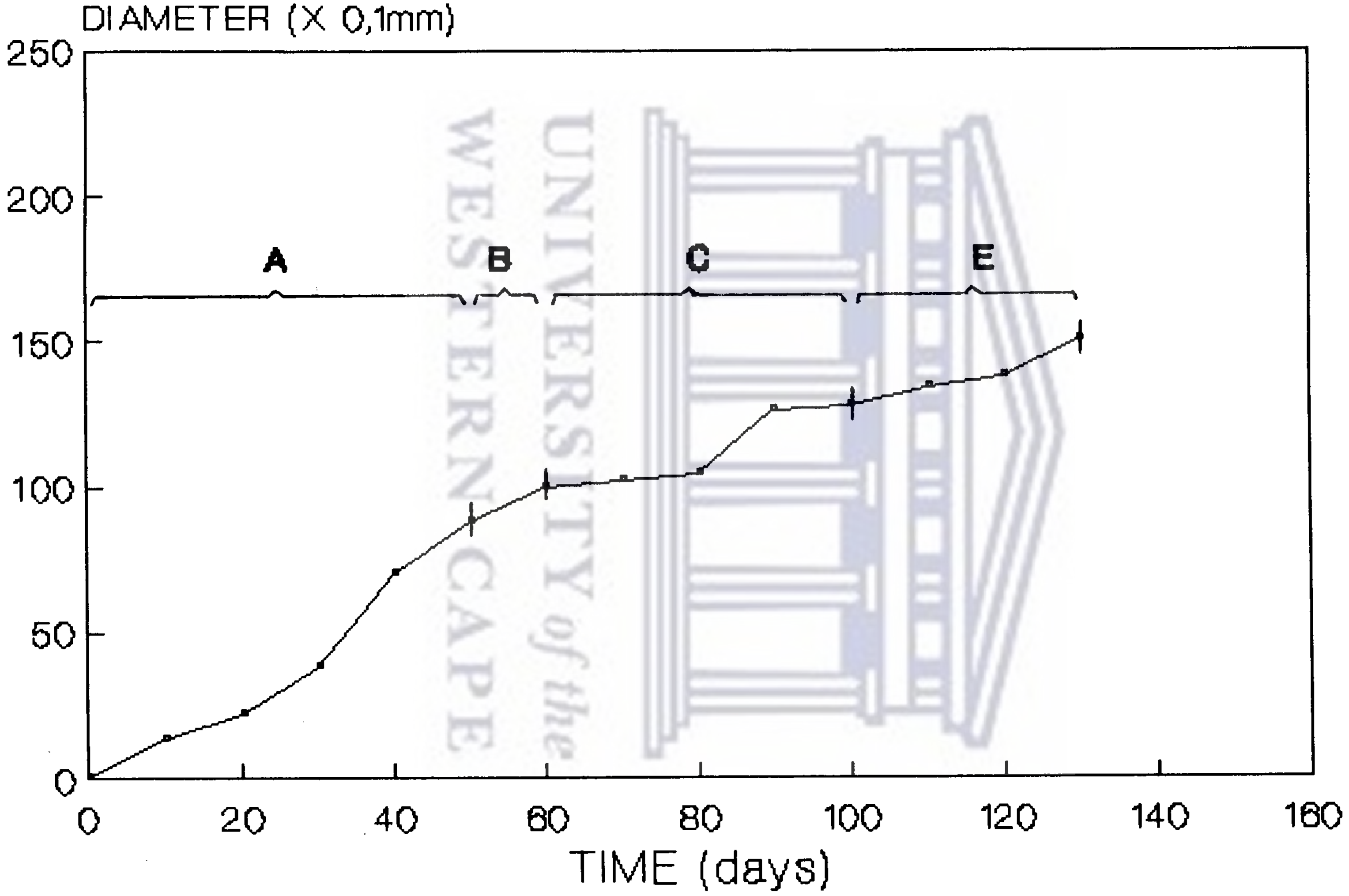
Phase E: There was no equivalent male phase (as in gall figs) in a seed fig. The postfloral (ripe phase) was the last phase in the development and began at about the 90th or 95th day. There was a gradual increase in size from about 12,8mm to 15,8mm in 20 to 30 days as the fruit ripened. A few syconia of about 17,0mm to 18,0mm were also observed. The fruit took on a brown colour as they ripened and a sticky substance accumulated around the seed. Finally the wall softened and the syconia became brown to purple as they ripened. Similar dispersal agents were found here as noted in the male syconia.

Table 9: Mean diameters of male and female syconia of *F. capreifolia* during developmental stages

NUMBER OF DAYS	MALE SYCONIUM	FEMALE SYCONIUM
	DIAMETER (mm)	DIAMETER (mm)
10	1,5	1,3
20	2,4	2,2
30	4,0	3,8
40	7,3	7,0
50	9,4	8,8
60	10,3	10,0
70	10,3	10,2
80	10,7	10,4
90	12,3	12,6
100	13,9	12,8
110	14,9	13,4
120	15,1	13,8
130	15,5	15,0
140	20,7	-



Graph 1: Mean growth rates of male syconia of *F. capreifolia*



Graph 2: Mean growth rates of female syconia of *F. capreifolia*

DISCUSSION

In Southern Africa, *Ficus capreifolia* and *F. pygmaea* occur in relatively dry areas and are found in habitats such as the banks of streams and marshes (Berg, 1990). Friis (1990) indicated that *F. capreifolia* is widely distributed in most parts of Ethiopia and along the major rivers in S. Somalia at altitudes between 50m to 2600m. In the present study area, these plants were growing at an altitude below 50 metres, and the Umdloti/Verulam area represented its southernmost limit (35^0S). The migration of these plants to this southern location needs further investigation because a few rivers surveyed further north did not reveal this species. These plants could have been transported during one of the more recent floods (1977, 1984 or 1987). It is possible that seed dispersal by birds may have been responsible for the migration of these plants to this location.

Van Greuning (1990) includes Otjinungwa, Skukuza, Blyde River bridge and Jozini in South Africa, and Guinea in the West and lower Sudan in the East as other African locations of *F. capreifolia*. Van Greuning described these plants as being 5 metres tall (Friis, 1990, described these as being 3m tall), with their syconia borne singly or in pairs, having 1 to 2 stamens per flower and with 4 to 5 petals per flower. This study showed these plants to be about 3m tall, syconia arising singly, with single stamens mostly (less than 5% have 2 or more) and with 4 tepals per flower (less than 2% have 5).

Vertical growth was limited in sandy soil, while lateral growth by stoloniferous branches enabled the plant to spread rapidly to cover the bare sandy soil. Other plants, including grasses and herbs quickly invaded the stable habitat provided by *F. capreifolia,* which acted as a pioneer on the sandy river banks. In the two year study period these plants had increased by up to 30% (from about 4m and 6m to 7m and 9m) in spreading diameter. It would appear that this population, barring any climatic or other accident would become an established species in the area. Plants in this population appear relatively young and may have arrived through one or more of the recent floods.

New leaves were produced at various times of the year with the plant being evergreen. Growth improved in warmer, wetter weather. There was no relationship between leafing and fruiting.

Syconia arose from all branches, including the upright branches, and the stoloniferous branches. Syconia grew on the older and younger branches, although the younger syconia appeared to be, at times, closer to the apical regions of branches. Generally syconia were produced asynchronously on a plant. However it had been observed that when a branch initiated syconia, then this pattern occurred throughout the branch with the syconia being produced over a few weeks, such that after the initial flush, up to 2 or 3 phases occurred together on a branch. There was very little or no size differentiation between the male and female syconia in A, B and C phases. In later C phase, D and E phases the male figs grew more rapidly and larger than the female figs. This was in keeping with the size of the wasps which were larger than the seeds produced.

Janzen (1979) carried out a review of pollination and embryological systems in which he suggested that ostiolar tightness is important for the sterility of the syconial cavity. He also suggested that the ostiole served as the barrier since the size, scale tightness and scale surface, sculpture and thickness of the scale pile varied greatly. Male syconia, in *F. capreifolia*, had a higher number (186,8) of ostiolar bracts (scales) than female syconia (139,4), and this applied to both the vertical (143,8 : 114,6) as well as the horizontal bracts (43,0 : 24,8). The vertical bracts hung downwards into the syconial cavity and in this way formed a passageway which made it easy for the entering wasp(s) to reach the syconial cavity and facilitate pollination and/or oviposition into the female flowers. The smoothness of the bracts probably facilitated the wasp entry into the cavity. The thicker horizontal bracts surrounded and sealed the ostiole and were thick enough to form an effective barrier against unwanted visitors.

The shape of the ostiolar bracts changed from being broad, triangular on the outside to becoming narrower, longer (or shorter), thinner and more tepaloid on the inside. The innermost tepaloid ostiolar bracts in gall figs were shorter and lay flat (horizontally) against the staminate flowers. It is possible that the shorter bracts in this region made it easier for pollen from the anthers to be accessed by the wasps, and this could have made it easier also for the wasps to find the ostiole during their exit journey.

Ostiolar bracts loosened at B-phase possibly to facilitate entry of wasps, and closed up/tightened immediately after to exclude other wasps or insects. Not much is known about how this happens. Researchers, such as Verkerke (1986), have suggested changes in turgidity. The bracts may be sensitive to touch, which could have triggered off changes in turgor and therefore closed off rapidly after the first wasps had entered. These bracts again loosened during D-phase in gall figs only to facilitate the exit of the wasps' progeny. However an examination of many syconia in this phase showed that the ostiole opened slightly even before the male wasps emerged from their galls. It is probable that the presence of this opening may have been related to increased growth or enlargening of the syconium. The syconium remains closed at first and the higher CO_2 levels may favour the activity of the male wasps (Galil et al, 1973). They propose that once the males puncture the ostiole and the air inside equilibrates with the air outside, the female wasps then become active. Galil and Eisikowitch (1974) investigated this further and concluded that it was the available syconial space that determined wasp activity, not CO_2 levels or any other environmental factor. This area needs more attention by researchers.

An examination of B-phase syconia showed that fine, pinkish hairs (with swollen tips) were present on the edges of the ostiolar bracts. This colour was not present in the mature and later stages, since the edges tended to dry up and turn brownish. These hairs may be glandular and contain the attractants which have been the subject of much speculation and research by several workers (Baijnath & Ramcharun, 1981; Barker, 1985; Baijnath et al, 1986; Janzen, 1979). Verkerke (1986) also noted the pink colour in the stigma of *F. ottoniifolia*, and further observed that after pollination and/or oviposition these turned brown.

Ficus capreifolia, being a (gyno)dioecious fig like *F. carica, F. asperifolia* and *F. fistulosa* among many others, had separate hermaphrodite ("male") plants and female plants. Although approximately half of all *Ficus* spp. are (gyno)dioecious plants, only a few species have been investigated in any detail. These include *F. carica* (Condit, 1932; Kjellberg et al., 1987), *F. asperifolia* (Verkerke, 1987) and *F. fistulosa* (Corlett, 1987).

Condit (1932) described *F. carica* with its female trees having long-styled pistillate flowers only, and male trees with short-styled pistillate as well as staminate flowers.

Pistillate flowers of *F. carica* are pedicellate with 5 perianth lobes, a spherical ovary and a cleft stigma. Verkerke (1987) described similar characteristics for *F. asperifolia* with pistillate flowers having pedicellate gall flowers and sessile or subsessile seed flowers, both with 4 to 5 perianth segments and a faintly lobed stigma. The pistillate flowers of *F. capreifolia* were pedicellate (short- or long-pedicellate) with 4 perianth segments (rarely 5), an oval-shaped superior ovary and a large clavate stigma. Sessile seed flowers were also present in *F. capreifolia*. In both the gall and seed flowers of *F. capreifolia*, pedicel lengths and ovary size (gall and seed) had undergone differential growth and increased in size considerably for the different types of pistillate flowers. Pedicel lengths almost trebled (Tables 2 and 3) as the flowers developed from B- to D-phases. This feature allowed the ovaries of the flowers to adjust and fit into the available space within the syconium. Verkerke (1987) stated that the pedicel elongated for some figs (in C phase female flowers of *F. asperifolia)* up to 3mm "for more efficient packing of drupes". Furthermore the ovaries also increased in size (almost double) due to the enlargement of the seeds and/or galls and therefore more space was required to accommodate these increases.

Pistillate flowers of *F. carica* are either short-styled (0,55mm to 0,9mm) in gall flowers or long-styled (1,5mm to 2,0mm) in seed flowers (Condit, 1932). Pistillate flowers of *F. asperifolia* are also short-styled (0,6mm to 0,62mm) in gall flowers or long-styled (1,6mm to 2,4mm) in seed flowers (Verkerke, 1987). In *F. capreifolia* gall flowers had short styles (0,55mm to 0,67mm) and seed flowers had long styles (1,18mm to 1,71mm). There was a clear distinction between the style lengths into short and long, and is referred to as perfect heterostyly. Therefore, while some researchers may not agree, ovipositing wasps could only lay eggs in short-styled gall flowers as their ovipositors were limited in length. Secondary sycophiles, having longer ovipositors, oviposited through the syconium walls and this also limited their ability to oviposit in the short-styled flowers as much of their ovipositor lay in the wall (wall about 1,7mm thick). In this study, the female plant produced figs which produced seeds only and it should be accepted that the style lengths prevented oviposition by pollinating wasps. Male plants produced figs with the pollinating wasps only (a primary sycophile) and no seeds. While these short-styled flowers of the gall fig are pollinated and capable of producing seeds as shown in *F. fistulosa* (Galil, 1973) and *F. carica* (Neeman & Galil, 1978), seeds are not formed because of parasitization by wasps (Neeman & Galil, 1978). Galil & Eisikowitch (1968) and Valdeyron & Lloyd (1979) also suggested that all flowers can form seeds. Verkerke (1987) showed that, in *F. asperifolia*, all flowers that receive a wasp egg also undergo double fertilisation while those that do not receive a wasp egg are arrested in their further development. In those where double fertilisation occurs, the embryo only aborts when the wasp larva enters the embryo sac, while the endosperm survives and probably provides nourishment for the developing embryo (Verkerke, 1987). Therefore as suggested by most fig researchers both figs have normal female flowers. Compton & Nefdt (1990), while working on a monoecious fig species, suggested that female fig flowers, while providing nutrition to the pollinator larvae, fulfil a male function because female pollinator wasps develop in them before collecting and transfering pollen to receptive figs. In this way short-styled female flowers facilitate pollen transfer.

Verkerke (1987) noted that flowers of *F. asperifolia* vary in length due largely to differences in pedicel length. In *F. capreifolia* overall length varied with a mean of 2,67mm to 4,06mm for seed flowers and 1,54mm to 6,33mm for gall flowers, with the variation due largely to the differences in pedicel length also.

The presence of the synstigma has been reported for pistillate flowers in seed figs of all (gyno)dioecious species studied (Verkerke, 1987). The longer styles curved or became hooked at B phase in the seed figs especially to ensure that the stigmatic surfaces became aligned to form the synstigma. The synstigma, by forming a common "platform" ensured that the pollinator wasp would be able to pollinate most (if not all) of the receptive female flowers at the same time. During the B phase (female & receptive) a large number of papillae developed on the upper part of the style and stigma and these papillae became interlinked to facilitate the formation of the synstigma.

Stigmatic surfaces remained separate in gall fig flowers, and the absence of the synstigma may be associated with the non-development of seeds in gall figs. Verkerke (1987) has shown that double fertilisation occurs in all female flowers of *F. asperifolia* that were oviposited and not in the others. This could indicate therefore that in the gall fig pollination of female flowers occurred on a one-to-one basis to avoid the development of seeds in the non-oviposited female flowers. The bright pinkish/purplish colour of the stigmatic surfaces and styles probably again indicated the presence of volatile chemicals which could serve as attractants to the wasps. This strategy probably facilitated both oviposition and pollination.

In all (gyno)dioecious figs studied, staminate flowers are found in the gall fig only and only mature in the D phase. In *F. carica* pedicellate, staminate flowers with 5 perianth lobes and 5 very short-filamented stamens, each with an introrse, two-lobed anther are found (Condit, 1932). *Ficus asperifolia* has 4 to 5 rows of pedicellate staminate flowers with 3 to 4 lanceolate perianth segments, and a single introrse anther with 4 loculi is dorsally attached to a filament (Verkerke, 1987). In *F. capreifolia* pedicellate staminate flowers in 2 or 3 rows with 4 (rarely 5) perianth segments and a single (rarely 2 or more) introrse anther with 4 loculi were found. The large anthers (0,8mm to 1,5mm long) were attached to the enlarged end of the filament at the back and opened by longitudinal dehiscence. All the (gyno)dioecious species above had similar characteristics. The enlarged end of the filament may have provided support for the wasp as it approached the anther to collect pollen.

Verkerke (1987) reported that in *F. asperifolia* the seed figs and gall figs reach a diameter of up to 20mm and 20mm to 26mm respectively. In *F. capreifolia* gall figs reached a mean diameter of 20,6mm (range 16,0mm to 25,5mm) while seed figs reached a mean diameter of 15,1mm (range 13.1mm to 15,8mm). The seed figs in *F. asperifolia* are therefore larger. Seed and gall figs of *F. asperifolia* have about 1700 and 1000 pistillate flowers respectively (Verkerke, 1987). In *F. capreifolia,* there were about 1080 and 1320 pistillate flowers in seed and gall figs respectively. While in *F. asperifolia* the number of pistillate flowers is considerably greater in seed figs than in gall figs. In *F. capreifolia* the gall figs had more pistillate flowers than seed figs. It appears logical to state that the number of flowers producing seeds or wasps plays a significant role in the population dynamics of these species. Therefore it is suggested that, in *F. capreifolia,* the plant could be more efficient as a wasp producer (when compared to *F. asperifolia)* than a seed producer. Considering that *F. capreifolia* studied here exists in a marginal, seasonal habitat, this strategy would be helpful to the survival of the species.

Male syconia of *F. capreifolia* had about 1320 pistillate to 118 staminate flowers. Information on this aspect in (gyno)dioecious figs is lacking. Of interest would be the significance of these numbers in relation to the survival of these figs in their respective habitats. The higher number of flowers in *F. capreifolia* may have improved its chances of survival in the environment. This survival strategy may have been necessary considering the presence of separate male and female functions adopted by the (gyno)dioecious species. The females of the pollinator wasp, upon leaving a male syconium, may have had considerable difficulty in locating a receptive female or male syconium within a short time. Therefore the production of large numbers of galls or even seeds may have improved their chances of survival or subsequent propagation. Although ripe seeds were being produced, there was no evidence of germination of these seeds in the study area.

About 160 (14%) unpollinated pistillate flowers (in seed figs) and 516,8 (35,1%) uninfected pistillate flowers (in gall figs) were located in areas of the figs interior such as the base (V-shaped part), that appeared to be inaccessible or difficult to reach by wasps. Some of these flowers also had not matured sufficiently as seen by the perianth lobes covering their stigmas in the receptive and mature stages. This probably made access to wasps difficult or impossible.

F. capreifolia had an average of 118,7 staminate flowers (range 101 to 150) with a ratio of about 11,1 pistillate flowers to 1 staminate flower. These ratios are comparable to ratios found in other (gyno)dioecious and monoecious species. Verkerke (1987), in *F. asperifolia*, obtained about 1000 female to 100 male flowers (10 :1). Baijnath and Ramchuran (1988) obtained a ratio of 16:1 for the monoecious species *F. burtt-davyii* and Compton and Nefdt (1990) obtained a ratio of 19:1 for the same species. The less female biased ratio of eleven pistillate to one staminate, for *F. capreifolia*, probably reflected the greater efficiency of pollination of the monoecious species where geitonogamous pollination is possible. *Ficus capreifolia* and *F. asperifolia*, both of which are (gyno)dioecious, have similar ratios.

There were 803,6 (61%) gall producing flowers to 516,8 (39%) uninfected pistillate flowers in the gall fig of *F. capreifolia* giving a ratio of only 1,55 gall to 1 uninfected flower. It is possible that the large number of uninfected flowers indicates that pollinators may be limited in their efficacy in oviposition when locating receptive syconia towards the latter part of their life cycle. However an oviposition and gall production range of 25,2% to 88,6% had been recorded for *F. capreifolia*. A range of 74,8% to 11,4% uninfected gall flowers had also been recorded. These values indicated that wasps were capable of ovipositing in a very large number of flowers (range 328 to 1360 galls produced), in possibly ideal conditions. Factors such as reduced viability and activity of wasps may have decreased this efficiency.

There was an average of 921 (85,3%) pollinated to 159,6 (14,7%) unpollinated pistillate flowers in the seed fig of *F. capreifolia*. A seed set range of 77,1% to 90,9% indicated the very high pollination efficiency. A ratio of 5,8 : 1 pollinated to unpollinated flowers indicated that seed figs were well adapted for pollination once a pollinator had entered. The large number of seeds produced must be seen against the small number of seed figs that reached maturity in this marginal habitat. The success of pollination and seed set suggested that pollinator wasps did carry sufficient pollen. Berg (1990) noted the more constant pattern in seed figs and suggested that the differences between gall and seed figs could be related to the differences in phenology and thus nutrient supply.

Bronstein and Mckey (1989) suggested that figs growing at the margins of their tropical range should encounter difficulty in flowering, lowered pollinator survivorship and lowered fig-reproductive success. Bronstein et al. (1990) and Herre (1989) using simulation models, also suggested that about 100 trees would be needed to allow wasp populations to establish and persist. The success of pollination, oviposition and wasp survival also depend on many factors, both internal and external (includes climate). Observations of *F. capreifolia* suggested that being at its marginal limit there were not many plants (about 15 in a 4,5km strip) and only about 6 were producing syconia. Furthermore there were not many syconia on an individual plant (between 20 to 300 at a time). Of the 6 plants that produced syconia the 3 female trees had fig numbers as low as 20 to 100, while 2 male plants produced up to 300 syconia with the third male plant producing between 50 to 100 syconia. These low counts probably indicated the problems experienced by this population at the edge of its range. Bronstein (1989) suggested that in cool dry periods, fig-wasp survival and flight would be strongly limited. She also suggested that (gyno)dioecious species should be better adapted to persist in seasonal environments. While it was difficult to obtain and remove large numbers of syconia for the study, the period was extended for collections and to complete the development study. Hill (1967) reported that in the monoecious fig *F. microcarpa*, which flowers synchronously, up to 100 000 figs may be produced in a single crop. Naicker (1984) reported about 190 000 figs on a single tree of *F. ingens*. Bronstein (1989) maintains that population level asynchrony is essential for wasps to move successfully between trees and for wasps to reproduce, and to prevent the local wasp population from becoming extinct, in which case no tree will reproduce again until wasps recolonise. Adult wasps do not feed and generally survive only a few days (2-4 days for females of the pollinator wasp), and therefore must locate another tree at the correct sexual phase. Population level asynchrony improves the chances of wasp co-existence with

B phase and D phase syconia.

An analysis of a crop of female figs on the female plants of *F. capreifolia* (Table 6) clearly showed the range of syconium sizes from 1,1mm to 17,0mm representing all 4 phases of the female fig life cycle. The success of each would depend on the availability of pollinator wasps when each female syconium reached B phase. Often many of the syconia remained longer at B phase, without being pollinated, and grew to about 10,0mm to 11,0mm before turning yellow and aborting. This obviously reduced the number that passed into the interfloral and mature stages.

There were not many instances or periods during which syconia on both the male and female aborted. In August 1991, over 70% of the receptive (B phase) syconia on plant 10 (male) aborted during a development study. In September 1991, all the syconia aborted on another male tree (plant 9). All the aborted syconia were analysed and showed an absence of pollinator wasps. According to Table 8, there were no ripe syconia on both plants 9 and 10 at that period, although plant 3 which was about 2km away had ripe male figs. It is possible that the distance of 2 km may have been too great for the wasps to remain viable in flight or even the attractants were not strong enough to attract the wasps to the receptive syconia, amongst other possible factors. A large number of trees and syconia may have reduced abortion.

Similarly in June 1992, several female syconia reached the receptive stage and most aborted. At this time all the male plants had ripe syconia and these plants were less than a kilometre away from the female plant. Between June to August/September, cool dry winter conditions prevail, and this may have been further aggravated by an extended drought period. These conditions may have affected the viability of the syconia and pollinators.

It is also possible that crop asynchrony resulted in a smaller number of syconia being receptive together and therefore a weaker chemical signal being sent out to attract the pollinator wasp. Both Janzen (1979) and Bronstein (1987, 1988) proposed that a stronger chemical signal could be sent if crops are synchronised. Windsor et al (1989) suggested factors such as temperature, light, water, seed dispersers and seed predators should affect the optimal timing and reproductive output of figs. They also proposed that since dry and wet seasons are common in tropical regions, figs may respond phenologically to these changes.

Gall figs of *F. capreifolia*, as shown in Table 8, produced syconia asynchronously throughout the year with occasional gaps. There were 2 or 3 periods in a year, after large numbers of syconia were initiated, when gaps were filled by a few syconia being formed on a plant. Seed figs, as shown in Table 7, initiated up to 2 or 3 crops of syconia asynchronously per year. Condit (1932), Kjellberg and

Valdeyron (1984) and Valdeyron and Lloyd (1979) reported that in *F. carica* the gall figs flower throughout the year in 2 or 3 distinct crops, while the seed figs produce one main crop per year. Windsor et al (1989) studied the fruiting patterns of fig species in the subgenus Urostigma and noted great variability in fruiting patterns. They also noted year round fruit initiation with certain species exhibiting peaks which appear to fall between the two major fruiting periods in the forests. Windsor et al (1989) suggested that figs, being less nutritious than other forest fruit, would be easily dispersed by animals when other fruit are unavailable. Foster (1982) suggested that regular fruiting of *Ficus* spp. appear to sustain mammal and bird populations during the months of famine in the late wet season. It is suggested that *F. capreifolia* also played an important role in the ecology of this habitat by providing food for birds, mice and monkeys.

Kjellberg and Maurice (1989) in their model suggested that seasonal conditions may favour evolution towards dioecy as dioecious species are more resilient to strong seasonality, with the male individual tree being selected to maintain the pollinator over the bad season. Survival of the pollinator depended on the fruiting patterns of the male plant of *F. capreifolia*. The presence of ripe syconia (D and E phases) should co-incide with the presence of receptive syconia (B phase) to ensure that pollinator wasp leaving a ripe fig was able to enter a receptive syconium on the same plant (geitonogamous reproduction) or on another plant (xenogamous reproduction). Table 7 and 8 shows that, apart from June, September and October of 1991, both B phase and D/E phases co-incided. During these 3 months of 1991, the presence of the mature interfloral phase ensured the survival of the wasp population and its continuity.

The male fig of *F. capreifolia* had a development cycle of about 130 to 140 days, while the female fig had a cycle of about 120 to 130 days. In both these figs, A and B phases were almost similar and difficult to distinguish. The cycles observed in this study were very much longer than in other reported examples and therefore caused concern. Development studies were repeated, especially for the gall fig in total and for parts of the stages at different times of the year, and the same pattern was obtained throughout. However one male plant produced a shorter cycle of about 100 days during spring/summer when the weather conditions had improved (increase in temperature and rainfall). However a few fruit only were produced in this period. Longer periods for the A (50 days) and C (40 days in seed figs and 70 days in gall figs) phases were recorded in the normal cycles of *F. capreifolia*. Information on the developmental cycles of (gyno)dioecious figs is lacking.

It is suggested that the developmental cycles of the monoecious figs mentioned above are shorter in keeping with their more regular synchronous fruiting patterns and year-round fruiting. In the (gyno)dioecious species, such as *F. capreifolia*, asynchronous crops were produced and the longer developmental cycle with a greater degree of plasticity of the phases may be a strategy for survival of the species. Furthermore, as mentioned previously (at least for the group of plants studied), these plants were growing at the margin of their range and may have adapted to ensure survival of the pollinator and plant populations. Bronstein and Patel (1992) studied phenological patterns in *F. aurea* and found that some syconia remain in A phase, at 3mm diameter, for one week to 8 months with decreasing probability. They also reported that, in winter, the developmental periods take up to 50% longer and that C phase is temperature sensitive. It would be interesting to carry out the developmental studies on (gyno)dioecious fig species growing in a range of climatic conditions to compare their developmental cycles and lengths of specific phases.

REFERENCES

Baijnath,H.,and Naicker,S.,1989. Developmental anatomy of *Ficus ingens* syconia in relation to its wasp faunula. *S.Afr.J.Bot.* 55(4): 409-421.

Baijnath,H., Naicker,S.,and Ramcharun,S.,1986. The interaction of figs and fig wasps,in: Insects and the Plant Surface, pp. 348- 49. Eds. B.E.S. Juniper and T.R.E.Southwood. Edward Arnold Ltd., London.

Baijnath,H.,and Ramcharun,S.,1981. Microscopic observations of the ostiolar bracts in some South African examples of the genus *Ficus* L.(Moraceae). *Proc. Electron micr.Soc.S.Afr.* 11: 135-136.

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

Baijnath,H., and Ramcharun,S.,1988. Reproductive biology and chalcid symbiosis in *Ficus burtt-davyi* (Moraceae). *Monogr.Syst.Bot.Mo.Bot.Gdn.* 25: 227-235.

Barker,N.P.,1985. Evidence of a volatile attractant in *Ficus ingens* (Moraceae). *Bothalia* 15: 607-611.

Berg,C.C.,1989. Classification and distribution of *Ficus*. *Experientia* 45: 605-611.

Berg,C.C.,1990(a). Distribution of African taxa of *Ficus* (Moraceae). *Proc.aetfat.sym.IV,Hamburg*,23a: 401-405.

Berg,C.C.,1990(b).Reproduction and Evolution in *Ficus* (Moraceae):Traits connected with the adequate rearing of pollinators. *Memoirs of New York Botanical Garden*, 55: 167-185.

Bronstein,J.L.,1987. Maintenance of species-specificity in a Neotropical fig-pollinator wasp mutualism. *Oikos* 48: 39-46.

Bronstein,J.L.,1988. Mutualism, antagonism and the fig-pollinator interaction. *Ecology* 69: 1298-1302.

Bronstein,J.L.,1989. A mutualism at the edge of its range. *Experientia* 45: 622-637.

Bronstein,J.L., Gouyon,P.H., Gliddon,C., Kjellberg,F., and Michaloud,G.,1990. The ecological consequences of flowering asynchrony in monoecious figs: A simulation study. *Ecology*. 71b: 2145-2156.

Bronstein,J.L., and Mckey,D.,editors.1989. The comparative biology of figs. *Experientia* 45: 601-680.

Bronstein,J.L., and Patel,A.,1992. Causes and consequences of within-tree phenological patterns in the Florida strangling fig, *Ficus aurea* (Moraceae). *Am.J.Bot.* 79(1): 41-48.

Compton,S.G., and Nefdt,R.J.C.,1990. The figs and fig-wasps of *Ficus burtt-davyi*. *Proc.aetfat, sym.IV, Hamburg*, 23a: 441-450.

Condit,I.J.,1932. The structure and development of flowers in *Ficus carica* L. *Hilgardia* 6: 443-481.

Corlett,R.T.,1987. The phenology of *Ficus fistulosa* in Singapore. *Biotropica* 19: 122-124.

Corner,E.J.H.,1965. Check-list of *Ficus* in Asia and Australasia. *Gdns.Bull., Singapore* 21: 1-186.

Foster,R.B.,1982. The seasonal rhythm of fruitfall on Barro Colorado Island,in: Ecology of a Tropical Forest, pp. 151-172. Eds. E.C. Leigh, A.S. Rand and D.M. Windsor. Smithsonian Institution Press, Washington.

Friis,I.,1990. Distribution patterns of *Ficus* in Tropical N.E. Africa. *Proc.aetfat., sym.IV, Hamburg,* 23a: 407-424.

Galil,J.,1973. Pollination in dioecious figs: pollination of *F. fistulosa* by *Ceratosolen hewitti*. *Gdn.Bull. Singapore* 26: 303-311.

Galil,J., and Eisikowitch,D.,1968(a). On the pollination ecology of *Ficus sycomorus* in East Africa. *Ecology* 49: 259-269.

Galil,J., and Eisikowitch,D.,1968(b). Flowering cycles and fruit types in *Ficus sycomorus* in Israel. *New Phytol.* 67: 745-758.

Galil,J., and Eisikowitch,D.,1968(c). On the pollination ecology of *Ficus religiosa* in Israel. *Phytomorphology* 18: 356-363.

Galil,J., and Eisikowitch,D.,1974. Further studies on pollination ecology in *Ficus sycomorus*. *New Phytol.* 73: 515-528.

Galil,J., and Neeman,G.,1977. Pollen transfer and pollination in the common fig (*Ficus carica* L.). *New Phytol.* 79: 163-171.

Galil,J.,Zeroni,M., and Bar Shalom,D.,1973. Carbon dioxide and the ethylene effects in the co-ordination between the pollinator *Blastophaga quadraticeps* and the syconium in *Ficus religiosa*. *New Phytol.* 72, 1113-1127.

Greuning, J. V. van, 1990. A synopsis of the genus *Ficus* (Moraceae) in Southern Africa. *S. Afr. J. of Bot.*, 56, 599-630.

Herre,E.A.,1989. Co-evolution of reproductive characteristics in twelve species of New World figs and their pollinator wasps. *Experientia* 45: 637-647.

Hill,D.S.,1967. Figs of Hong Kong. Hong Kong University Press.

Janzen,D.H.1979. How to be a fig. *A.Rev.Ecol.Syst.*10: 13-51.

Kjellberg,F., Gouyon,P.H., Ibrahim,M., Raymond,M., and Valdeyron,G.,1987. The stability of the symbiosis between dioecious figs and their pollinators: A study of *Ficus carica* L. and *Blastophaga psenes* L. *Evolution* 41: 693-704.

Kjellberg,F., and Maurice,S.,1989. Seasonality in the reproductive phenology of *Ficus*: Its evolution and consequences. *Experientia* 45: 653-660.

Kjellberg,F., and Valdeyron,G.,1984. The pollination of the fig tree (*Ficus carica* L.) and its control in horticulture. *Acta Oecolog./Oecol.Gen.* 5(4): 407-412.

Naicker,S.,1984. Pollination Biology in *Ficus ingens* (Miq.) Miq.(Moraceae). Unpubl.thesis.

Nair, P.B., and Abdurahiman, U.C., 1984. Population dynamics of the fig wasp *Kradibia gestroi* (Grandi) (Hymenoptera Chalcidoidea, Agaonidae) from *Ficus exasperata* Vahl. *Proc. K. Ned. Akad. Wet.* (C) 87: 365- 375.

Neeman,G.,and Galil,J.,1978. Seed set in the male syconia of the common fig,*Ficus carica* L.(Caprificus). *New Phytol.* 81: 375-380.

Newton,L.E., and Lomo,A.,1979. The pollination of *Ficus vogelli* in Ghana. *Bot.J.Linn.Soc.* 78: 21-30.

Ramirez,B.W.,1987. The influence of the microenvironment, the interior of the syconium, in the coevolution between fig-wasps (Agaonidae) and the fig (*Ficus*). pp. 329-334. In Labeyrie,V., G. Fabres and D. Lachaise (Eds.). Insect-Plants.

Valdeyron,G., and Lloyd,D.G.,1979. Sex differences and flowering phenology in the common fig, *Ficus carica* L. *Evolution* 33: 673-685.

Verkerke,W.,1986. Anatomy of *Ficus ottoniifolia* (Moraceae) syconia and its role in the fig-fig wasp symbiosis. *Proc.K.ned. Akad.Wet.Ser.* C89: 443-469.

Verkerke,W.,1987(a). Ovule dimorphism in *Ficus asperifolia* Miquel. *Acta Bot.Neerl.* 36: 121-124.

Verkerke,W.,1987(b). Syconial Anatomy of *Ficus asperifolia* (Moraceae), a gynodioecious tropical fig. *Proc.K.ned.Akad.Wet.* C90: 461-492.

Windsor,D.M., Morrison,D.W., Estribi,M.A., and de Leon,B.,1989. Phenology of fruit and leaf production by 'strangler' figs on Barro Colorado Island, Panama. *Experientia* 45: 647-653.

KEY FOR CHAPTER 1

h - horizontal bract

p - pistillode
pf - pistillate flower

sc - syconial cavity
sf - staminate flower
sw - syconial wall

v - vertical bract

Chapter 2

Developmental fig anatomy and related reproductive biology

Abstract

The developmental anatomy of the male (gall) and female (seed) syconia of *Ficus capreifolia* Del. (Sub-section: *Sycidium*) was studied at both the LM and SEM levels. The structure and development of gall and seed figs were similar from initiation to the receptive phase only. Female figs develop a synstigma and produce normal seeds. Hermaphrodite (male) figs do not develop a synstigma, but instead the female flowers show early embryo and endosperm development.

Key words: *Ficus*, *Sycidium*, Moraceae,(gyno)dioecious, developmental anatomy, seed fig, gall fig, embryo, primordia

INTRODUCTION

Ficus capreifolia is a (gyno)dioecious fig with "male" plants bearing hermaphrodite syconia and female plants bearing female syconia. The plant is functionally dioecious and both their syconia and vegetative parts look similar externally. Male syconia produce ostiolar staminate flowers and short-styled pistillate flowers in the rest of the syconium. Female syconia produce only long-styled pistillate flowers in the syconium. Male syconia provide essentially for the development of fig wasps in their ovaries (galls) and no seeds are produced by them. Female syconia produce seeds only and depend on the wasps released from the male syconia to carry the pollen from the staminate flowers of the male syconia to the receptive pistillate flowers of the female syconia. Pollen is also transferred from ripe male syconia to other receptive male syconia. Morphological characteristics and differences in these plants have already been described in the previous chapter.

Condit (1932) gave detailed descriptions of the anatomy and development of staminate and pistillate flowers, as well as the endosperm and embryogeny in *F. carica*. This extensive and detailed work, by Condit (1932), on a (gyno)dioecious fig represents a cornerstone in fig research and understanding.

Johri and Konar (1956) also presented, with diagrams, descriptions on the anatomy and development of the microsporangia and megasporangia, pollination, endosperm development, embryogeny, seed and fruit set and the germination of drupes in *F. religiosa*. This represents the pioneering work on monoecious figs.

Verkerke (1986, 1987, 1988) reported extensively on the developmental anatomy of *F. ottoniifolia* (monoecious fig), *F. asperifolia* (gynodioecious fig) and *F. sur* (monoecious fig) respectively. Verkerke (1986, 1987) in his work on *F. ottoniifolia* and *F. asperifolia* reported that both seed and gall flowers display early embryo and endosperm development with these eventually disappearing in the gall figs. In his work on *F. ottoniifolia*, he speculated that style firmness rather than style length appears to be the limiting factor for wasp oviposition in fig flowers. Other differences and characteristics in their (*F. ottoniifolia* and *F. asperifolia*) developmental anatomy were reported. In *F. sur*, Verkerke (1988) described the differential development of flower primordia of short- and long-styled flowers in a space stressed environment.

Baijnath and Naicker (1989) speculated on the role of the hairs and presented many diagrams of developmental stages of various parts of the anatomy of the monoecious fig, *F. ingens*.

The developmental cycle of *F. capreifolia* extended over a period of 130 to 140 days for the male syconia and 120 to 130 days for the female syconia. A shorter cycle of about 100 days had been noted in wetter and warmer periods of the year for the gall figs. The development in the male plant followed the five stages as set out by Galil and Eisikowitch (1968(a)) in their studies on *F. religiosa*. However, as seen in Table 1, in the female syconia there were only four phases with the male phase being absent (Valdeyron and Lloyd, 1979). The anatomical changes that were observed will be discussed developmentally for each structure or group of structures.

A closely related pattern emerges from the research presented above, showing great similarities between related plants and even between the monoecious and the (gyno)dioecious species. A discussion of differences in their developmental anatomy and characteristics would add to the limited information available on the anatomy of the figs.

MATERIALS AND METHODS

Male and female shrubs of *F. capreifolia* Del., growing at Umdloti, Verulam (Natal, South Africa), were marked for developmental studies. Successive stages of developing syconia were collected over a two year period and later fixed in FAA for both SEM and LM preparations.

For SEM studies, samples of both seed and gall figs, representing successive stages, were thoroughly washed in water, dehydrated in an alcohol series and critical point dried in the Bio-Rad CPD 750 unit. Portions were trimmed and mounted on stubs before coating in the Polaron SEM coating unit E5000.

Observations were made of the outer wall, inner wall, ostiolar scales and flowers.

For LM studies, samples of both the seed and gall figs, representing successive stages, were thoroughly washed in water, dehydrated in an alcohol series before infiltration and embedding in paraffin wax. Sections of about 10um to 20um were stained in safranin and light green. Longitudinal sections through the median sagittal plane of syconia were made.

RESULTS/OBSERVATIONS

Developmental cycle

The early development of the male and female syconia followed similar patterns and will therefore be considered together.

<u>Table 1</u>: **Phases (P) and approximate dimensions in the developmental cycles of female (seed) and male (gall) syconia of *F. capreifolia***

P	FEMALE SYCONIUM			MALE SYCONIUM		
	DIAMETER (mm)	TIME (days)	PERIOD	DIAMETER (mm)	TIME (days)	PERIOD
A	0 - 9,0	0-50	50	0 - 8,4	0-45	45
B	9,0 - 10,0	50-60	10	8,4 - 9,8	45-55	10
C	10,0 - 12,8	60-100	40	9,8 - 15,2	55-125	70
D	-	-	-	15,2 - 16,8	125-134	9
E	12,8 - 15,8	100-120	20	16,8 - 20,6	134-140	6

Table 1 shows the approximate dimensions and period in the developmental cycles of male and female syconia. These time periods may vary by 5 to 10 days depending on the conditions in the environment. In the gall and seed figs, B (female), D (male) and E (postfloral) phases were very short phases, while A (prefemale) and C (interfloral) phases were long phases.

Syconium and Bracts

The earliest stage observed in the male and female syconia was ca.1,2mm in diameter (ca.7 to 10 days old) and the syconium appeared as a pale green, globose structure (Fig

1a) attached by a short peduncle to the stem. Three large flattened, hairy bracts (Fig 1b) almost fully enclosed the fig. These bracts arose near the base of the peduncle and were shed when the fig reached about 4mm after about 30 days (Fig 1c). Above the level of the peduncular bracts, from the base of the syconium there arose many imbricating bracts which appeared like the overlapping leaves of a "cabbage". At this stage (1,5mm) there was no sign of an ostiole or even a syconial cavity. The outermost imbricating bracts were thicker and covered with more hairs than the inner, shorter, thinner bracts (Figs 1a & 1b). These bracts formed the horizontal bracts. By the 25th day (3,1mm), these bracts differentiated into whorls of horizontal bracts firmly closing off the ostiole. By the 25th day, the vertical bracts which hung loosely downwards into a developing syconial cavity (Fig 1c), developed from just below the point of origin of the horizontal bracts from a ridge on the syconial wall. As the fig enlarged (between 5,1mm to 7,0mm at about the 35th to 45th days), the ostiolar bracts became re-oriented from filling the syconial cavity (Fig 1c) to occupying the upper third of the syconium (Fig 1d), and the ostiolar bracts became more prominent and well developed by the end of the A phase.

Growth of the syconium was rapid during the A phase (Figs 1a, 2a, 2c), with the syconium becoming receptive (Figs 1d,2b) from *ca*.7mm (45 to 55 days in male syconia; 50 to 60 days in female syconia). It continued to grow during

Fig 1(a): SEM view of L/S of A phase male syconium (1,5mm diameter) of *F. capreifolia* showing peduncular bract, ostiolar bracts and hairs
(Bar = 100um)

Fig 1(b): SEM view of A phase male syconium (1,5mm diameter) of *F. capreifolia* showing hairs on peduncular bracts
(Bar = 100um)

Fig 1(c): SEM view of L/S of A phase male syconium (3,1mm diameter) of *F. capreifolia* showing initiation of floral buds, differentiation of ostiolar bracts and shedding of peduncular bracts
(Bar = 100um)

Fig 1(d): SEM view of L/S of B phase male syconium (7,2mm diameter) of *F. capreifolia* showing pistillate flowers in receptive syconium
(Bar = 100um)

the B phase up to *ca*.10,0mm (Figs 2c & 2d). During this phase it became pollinated (female syconia) or infected (female pollinator wasp laid eggs - oviposited in pistillate flowers of male syconia). If either pollination or oviposition did not occur, the syconium turned yellow before aborting. Between 60 to 80 days, in both male and female syconia, the early interfloral stage was reached, and little or no growth in the size of the syconium occurred. After 80 days (late interfloral) there was rapid growth in both syconia up to *ca*.90 days in the female syconia and 105 days in the male syconia (Figs 3a & 3c). Syconia increased in size from *ca*.8,0mm or 9,0mm to *ca*.14,0mm or 16,0mm during the interfloral phase. In the female syconia there was a slower growth rate in the postfloral phase from *ca*.13,0mm or 14,0mm to *ca*.16,0mm in 30 to 40 days (Figs 3b & 3d). In the male syconia there was a sudden increase in size in the male (D) phase, and a very rapid increase in size (17,0mm to 20,0mm) during the postfloral (E) phase. The syconia of both fig types became yellow to purple and softer when ripe.

Syconial initiation was closely linked with the presence of bracts. After the formation of the urn-shaped syconium, from a flattened receptacle surrounded by bracts (Fig 1c), two types of bracts arranged themselves nearer the upper third of the syconium and enclosed the ostiole (Fig 1d).

These ostiolar bracts were of two types, the horizontal bracts which closed off the opening and the vertical

Fig 2(a): SEM view of L/S of A phase of female syconium (5,1mm diameter) of *F. capreifolia* showing development of syconium
(Bar = 10um)

Fig 2(b): SEM view of part of L/S of B phase female syconium (7,2mm diameter) of *F. capreifolia* showing receptive pistillate flowers
(Bar = 10um)

Fig 2(c): SEM view of part of L/S of B phase female syconium (10,0mm diameter) of *F. capreifolia* showing receptive pistillate flowers
(Bar = 10um)

Fig 2(d): SEM view of part of L/S of B phase male syconium (9,2mm diameter) of *F. capreifolia* showing receptive pistillate flowers
(Bar = 10um)

Fig 3(a): SEM view of part of L/S of C phase male syconium (13,4mm diameter) of *F. capreifolia* showing gall flowers (Bar = 10um)

Fig 3(b): SEM view of part of L/S of C phase female syconium (13,7mm diameter) of *F. capreifolia* showing seed flowers (Bar = 10um)

Fig 3(c): SEM view of part of L/S of D phase male syconia (20,0mm diameter) of *F. capreifolia* showing mature galls (Bar = 10um)

Fig 3(d): SEM view of part of L/S of C phase female syconium (14,7mm diameter) of *F. capreifolia* showing mature seed flowers (Bar = 10um) bracts which hung down into the syconial cavity (Figs 1c & 1d). These bracts were spirally arranged in whorls with their free ends overlapping (imbricate) especially the horizontal bracts. The outermost ostiolar bracts were triangular, thicker and hairy with *ca.* 8 to 10 layers of parenchyma cells in their thicker middle region (Fig 4c). The inner horizontal bracts and vertical bracts were glabrous and thinner with *ca.* 5 to 8 layers of cells and showed less cell differentiation (Fig 4b). Only unicellular hairs were present, in the outer horizontal ostiolar bracts, giving these bracts a rough texture (Fig 4c). There were no pluricellular (glandular) hairs in the ostiolar region (Fig 4c). All bracts were enclosed by an inner and outer epidermis with parenchyma cells sandwiched in between. Druses occurred in many parenchyma cells and were more common in the outer bracts. Vascular tissue with spiral thickening occurred in all the bracts with the xylem being better developed in the outer horizontal bracts (Fig 4d). The general appearance and texture of the bracts changed from being green and leaf-like on the outside to being colourless and tepaloid on the inside. Deposition of tannin occurred in a few epidermal cells of the outer ostiolar bracts, especially near the tips of the bracts (Fig 4d). By about the 23rd day, the inner epidermal cells of the bracts were larger than the outer epidermal cells and appeared more isodiametric. By about the 30th day, the outermost ostiolar bracts only, had up to 15 to 20 cell layers and were very thick. The inner bracts remained almost the same with up to 8 layers.

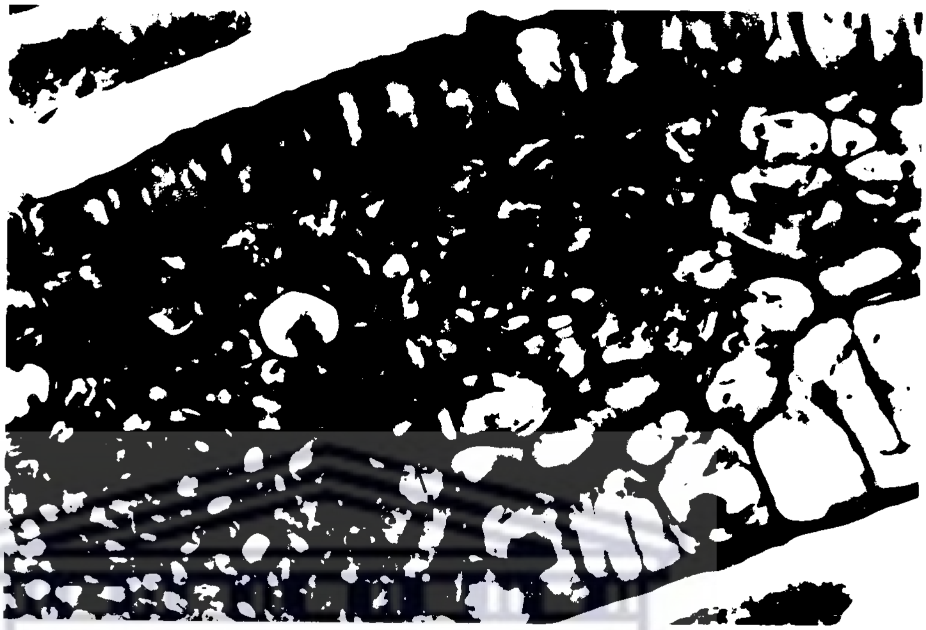


Fig 4(a): LM view of ostiolar bract of male syconium (3,5mm diameter) of *F. capreifolia* showing details with druses and vascular tissue
Bar = 0,05mm

Fig 4(b): LM view of inner horizontal bract of female syconium (4,6mm diameter) of *F. capreifolia* showing details with druses and vascular tissue
Bar = 0,05mm

Fig 4(c): LM view of details of ostiolar bracts of female syconium (4,6mm diameter) of *Ficus capreifolia*
showing hairs
Bar = 0,2mm

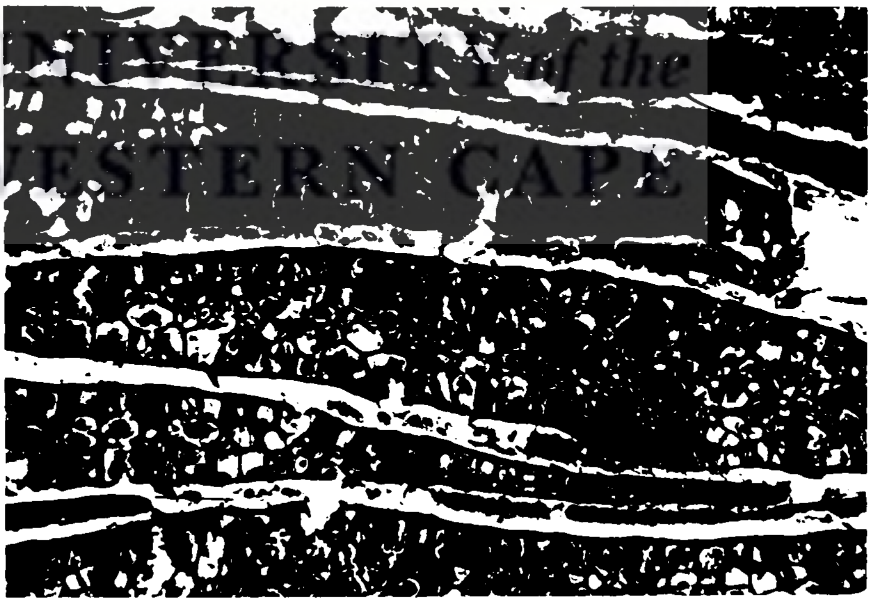


Fig 4(d) LM view of details of ostiolar bracts of female syconium (15,6mm diameter) of *F. capreifolia* showing vascular tissue
Bar = 0,2mm

Vertical bracts had up to 6 layers of cells only. The ostiolar bracts remained firmly closed during A and C phases, but loosened in B phase in both figs and in D phase in gall figs. By D and E phases tannin accumulated in more cells of the bracts.

Epidermal Hairs

The outer surface of the syconium was covered by many unicellular, conical hairs and pluricellular, capitate hairs (Figs 5, 6 & 7). These hairs initially developed as protuberances from the epidermis (Fig 6a) during the early prefemale stages (1,2mm to 1,5mm in 7 to 10 days) and very soon thereafter (by 3,1mm at *ca.* 28 days) covered the whole of the outer syconial surfaces of both the seed and gall figs. The unicellular hairs developed from the epidermal cells in the syconium wall and became surrounded by a collar of 1 to 4 rows of epidermal cells (Figs 5d, 6c & 7c). The pluricellular hairs consisted of a stalk cell and a head of 3 to 4 cells (Figs 5a, 6c & 7a). At first when the fig was small the unicellular hairs lay close together and appeared to be prominent on the walls. As the syconium enlarged (in later A phase from *ca.* 3,1mm to 5,1mm) and the unicellular hairs moved apart, a large number of pluricellular hairs proliferated (Fig 7a) in the spaces towards the end of the A phase (between 5,1mm & 7,2mm at *ca.* 35 to 40 days) in both figs. At this stage the head of the pluricellular hairs became densely stained. After the female phase, many of these hairs collapsed (Fig 7b). The unicellular hairs remained intact.

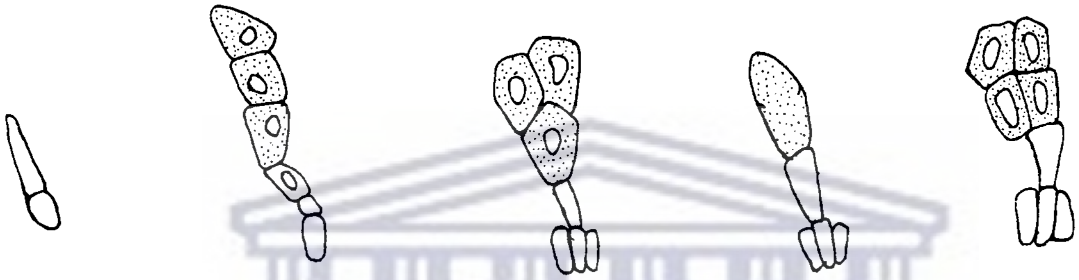


Fig 5(a): Pluricellular hairs on outer walls of male syconium (1,2mm diameter) of *F. capreifolia*

Fig 5(b): Pluricellular hair on outer wall of male syconium (2,6mm diameter) of *F. capreifolia*

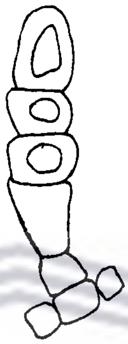


Fig 5(c): Pluricellular hair on outer wall of male syconium (8,1mm diameter) of *F. capreifolia*

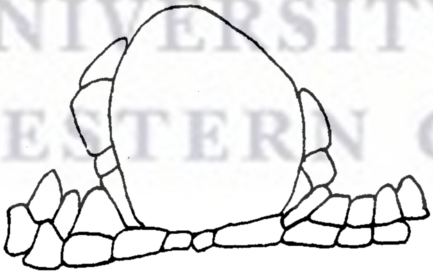


Fig 5(d): Unicellular hairs with surrounding epidermal cells in wall of male syconium (2,6mm diameter) of *F. capreifolia*

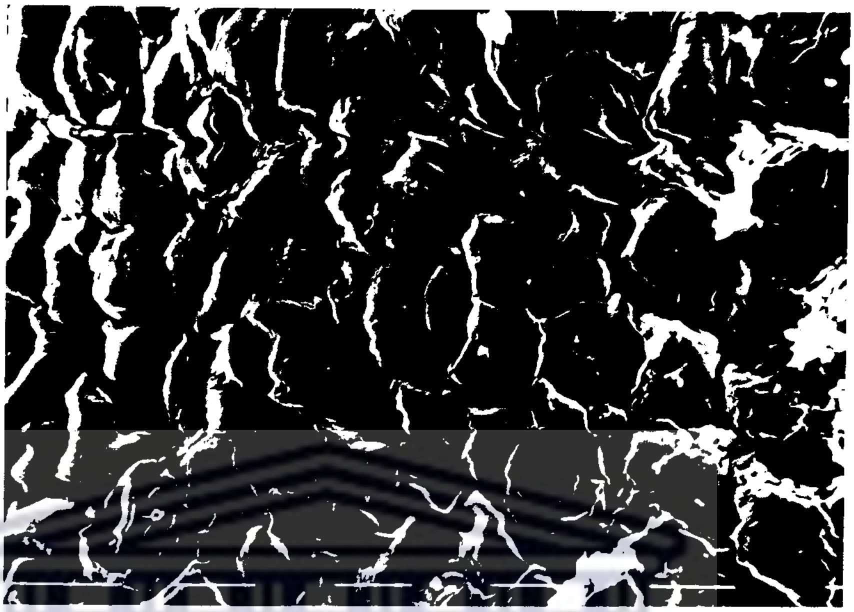


Fig 6(a): SEM view of outer walls of male syconium (1,5mm diameter) of *F. capreifolia* showing hairs absent and stomata present
Bar = 10um

Fig 6(b): SEM view of outer wall of male syconium (3,1mm diameter) of *F. capreifolia* showing pluricellular and unicellular hairs
Bar = 10um

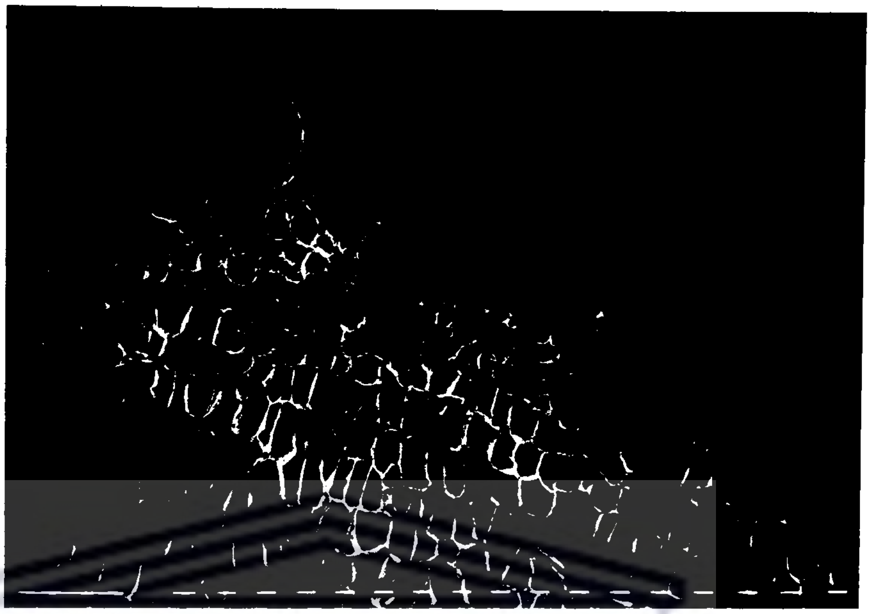


Fig 6(c): SEM side view of A phase male fig (5,1mm diameter) of *F. capreifolia* showing unicellular hair in section
Bar = 10um

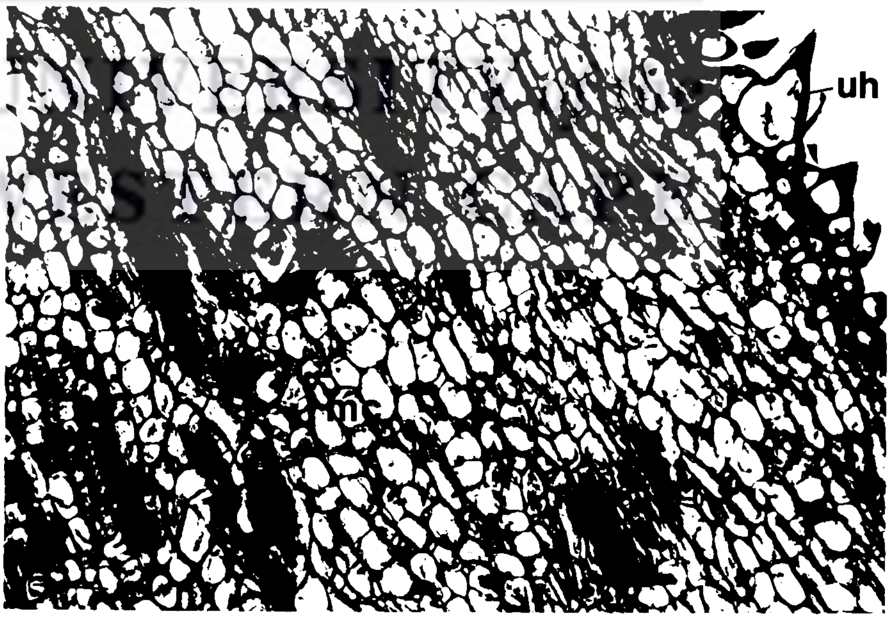


Fig 6(d): LM view of L/S of syconium wall of A phase male fig (10,3mm diameter) of *F. capreifolia* showing hairs, outer and middle cell layers
Bar = 0,2mm

Unicellular hairs also developed from the inner wall when the syconia were *ca*. 5,0mm in diameter (Figs 8a - d). Pluricellular hairs were not present on the inner wall. By the female stage (8,0mm at *ca*. 44 days), a very large number of unicellular hairs were present on the inner wall and even on the pedicels of the flowers. In early C phase (12,3mm at *ca*. 90 days), the hairs on the inner wall became reduced in number as they degenerated. The pluricellular hairs on the outer wall also decreased significantly while the unicellular hairs appeared to flatten out. This trend continued through C and D phases so that only a few hairs remained on the surface (Fig 7d). Towards the latter part of C phase and during D and E phases, a waxy substance appeared on the wall surface almost completely covering the flattened ends of the unicellular hairs (Figs 7c & 7d).

Syconium Wall and Cavity

The development of the walls of the seed and gall figs were similar. In a 7 to 10 day old syconium (*ca*. 1,2mm diameter) with a wall of *ca*. 0,3mm thick there were 38 to 42 cell layers (Fig 9a). An outer epidermis was covered by a thin cuticle and an inner epidermis lined the cavity of the syconium. The cells in both epidermal layers were cytoplasm-rich and brick-shaped with radial walls being about two times longer than the tangential walls (Fig 9b). There was a 3 to 6 layered hypodermis of unthickened chloroplast-containing cells. These regularly arranged cells were polygonal to isodiametric and increased to *ca*.

Fig 7(a): SEM view of outer walls of male syconium (7,0mm diameter) of *F. capreifolia* showing pluricellular and unicellular hairs
Bar = 10um

Fig 7(b): SEM view of outer wall of female syconium (13,7mm diameter) of *F. capreifolia* showing waxy material, opened stomata and degeneration of hairs
Bar = 10um

Fig 7(c): LM view of outer walls of female syconium (8,7mm diameter) of *F. capreifolia* showing pluricellular hairs, epidermis ,druses and chloroplasts
Bar =0,05mm

Fig 7(d): SEM view of outer wall of male syconium (20,0mm diameter) of *F. capreifolia* showing waxy material & degeneration of hairs
(Bar = 10um)

Fig 8(a): LM view of wall of female syconium (6,0mm diameter) of *F. capreifolia* showing unicellular hairs
Bar = 0,05mm

Fig 8(b): LM view of wall of male syconium (8,7mm diameter) of *F. capreifolia* showing hairs and pistillate flowers with ovary, style and stigma
Bar = 0,5mm

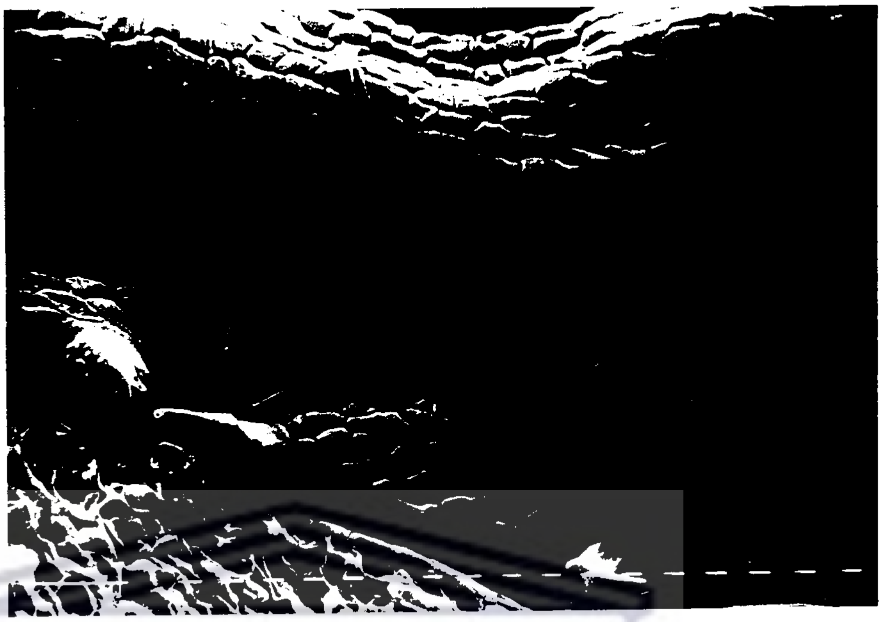


Fig 8(c): SEM view of wall of male syconium (9,2mm diameter) of *F. capreifolia* showing unicellular hairs
Bar = 10um

Fig 8(d): SEM view of wall of female syconium (10,4mm diameter) of *F. capreifolia* showing unicellular hairs
Bar = 10um

6 to 8 layers in mature syconia. The rest of the wall had large and small parenchyma cells with scattered cells containing druses and lacitifers (Figs 7c, 9b & 10a). Many druses were also present in the hypodermal cells. Extensive vascularization of the wall with traces to the ostiolar bracts and flowers were found amongst the parenchyma cell layers (Figs 10b & 10c). Xylem with spiral thickening and well developed phloem tissues were present in many bundles (Fig 10c).

At the 7 to 10 day stage (phase A), when the syconium was essentially made up of bracts, a syconial cavity was lacking. The cavity began to show at *ca.* 2,6mm (23 days) and gradually enlarged as the bracts moved away from the wall. When the syconium reached *ca.* 4,6mm (36 days) in a seed fig and *ca.* 4,8mm (33 days) in a gall fig, a large syconial cavity was present and this continued to open further through the latter part of A phase. It persisted in B phase and closed in C phase. The syconial cavity opened again in D phase in the gall fig, becoming very large (*ca.* 8,0mm at 134 days) in a short time. A syconial cavity did not form in seed figs in the mature and ripe phases. The developing seeds filled up most of the available space in the syconium. A few cells containing tannin appeared in the edges of the outermost ostiolar bracts only. Later (2,6mm at *ca.* 23 days) tannin collected in the peduncular bracts and in a few parenchyma cells of the peduncle. During the interfloral phase, a greater amount of tannin accumulated in the cells of the outer

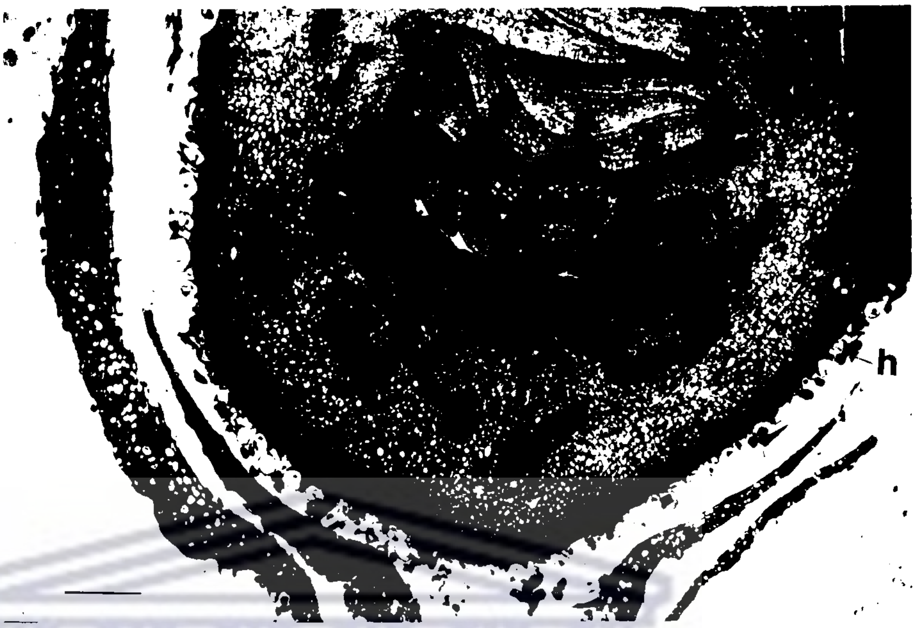


Fig 9(a): LM view of L/S of A phase male syconium (1,2mm diameter) of *F. capreifolia* showing ostiolar bracts, zone of floral development and hairs on outer wall
Bar = 0,5mm

Fig 9(b): LM view of outer wall of male syconium (3,5mm diameter) of *F. capreifolia* showing details of cells
Bar = 0,05mm

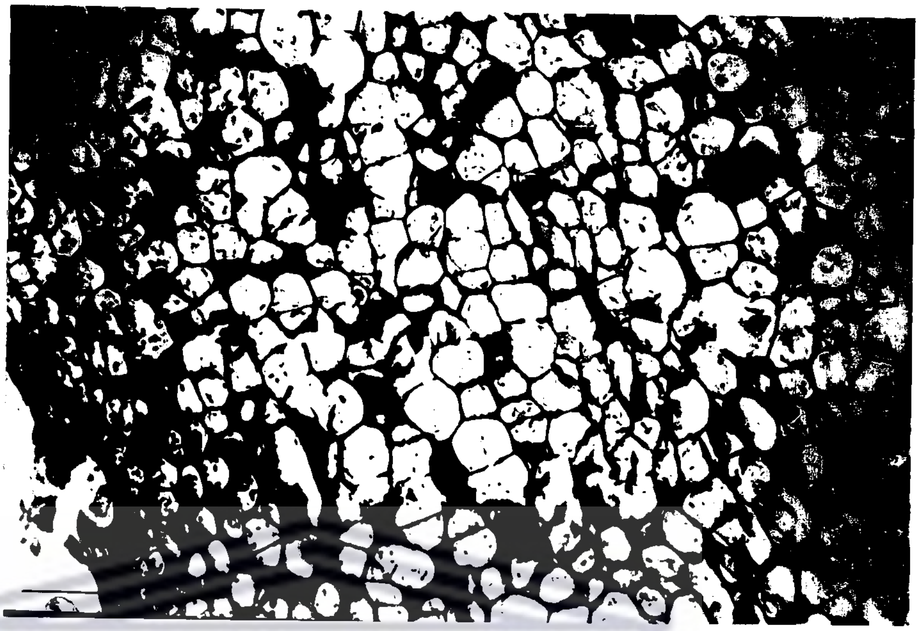


Fig 9(c): LM view of L/S of male syconium (18,0mm diameter) of *F. capreifolia* showing details of highly vacuolated cells and degeneration of hairs
Bar = 0,2mm

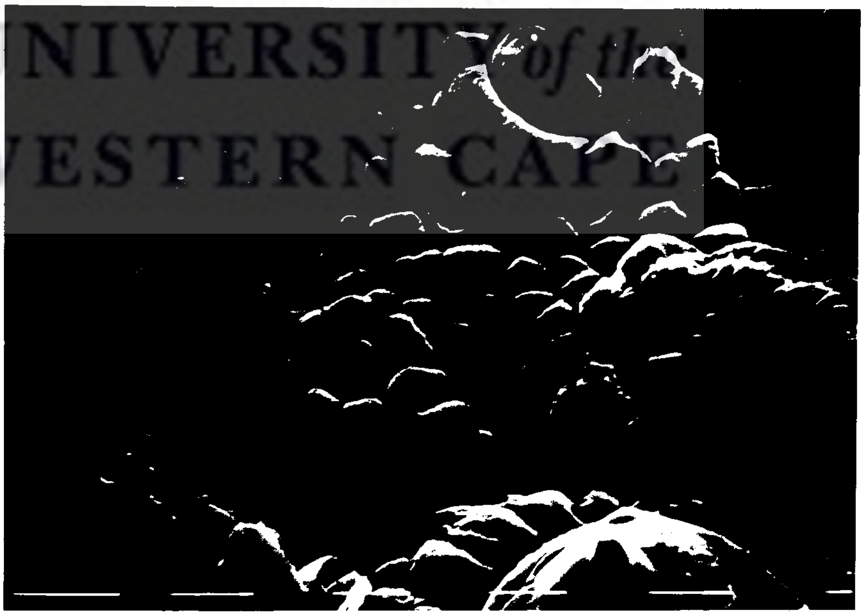


Fig 9(d): SEM view of outer wall of male syconium (7,0mm diameter) of *F. capreifolia* showing stomata and hairs
Bar = 10um

epidermis of the inner bracts, cells of the filament and ovary walls.

The increases in the wall thickness and number of layers were due to increases in the parenchyma zone (with more cells as well as the enlarging of the cells and intercellular air spaces). In the mature and later stages, large (lysigenous type) cavities occurred in the parenchyma layers (Fig 9c). The innermost parenchyma cells were larger and more highly vacuolated from early A phase (Figs 9c & 10d). Epidermal cells increased in size by radial expansion, while the syconial wall grew (as the diameter of the syconium increased) by anticlinal divisions in epidermal cells. Generally the epidermis was a single layer, except for certain areas near the collar of the cells around the unicellular hairs. Both the unicellular and pluricellular hairs appeared as extensions or growths from the epidermal cells (Figs 9 & 10).

The innermost wall layers (of the syconium) and epidermis were not well defined in the earliest stages. This area appeared highly meristematic (very granular and heavily stained) as the floral buds were initiated from this area. Longitudinal rows of cells were produced in early A phase and became more clearly differentiated as the syconium reached *ca.* 4,5mm to 5,0mm in diameter. Towards the latter part of C phase, the outer epidermal cells tended to lose their brick-shape and became more irregular in shape. The hypodermal cells tended to become more parenchyma-like

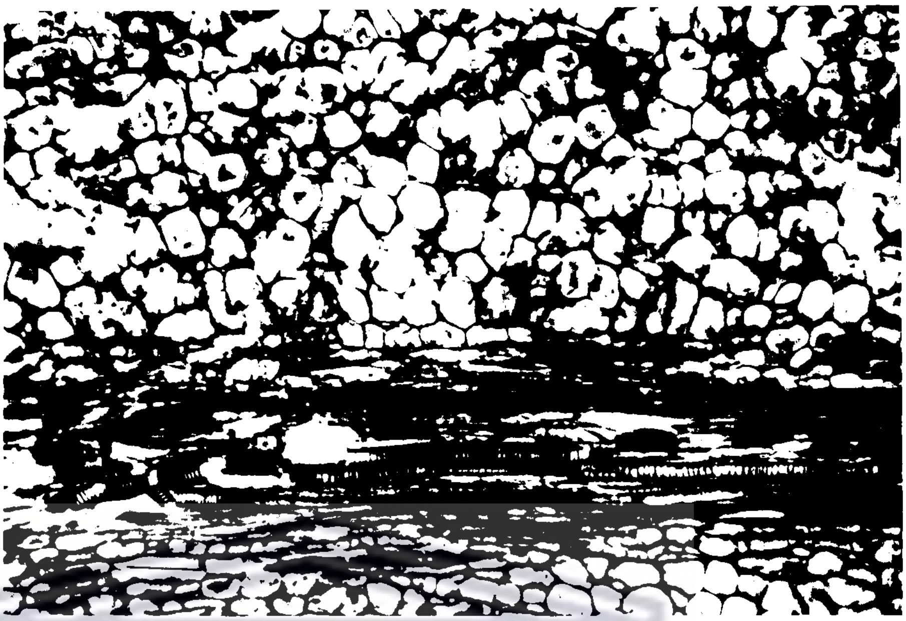


Fig 10(c): LM view of L/S of wall of female syconium (9,7mm diameter) of *F. capreifolia* showing vascular tissues
Bar = 0,2mm

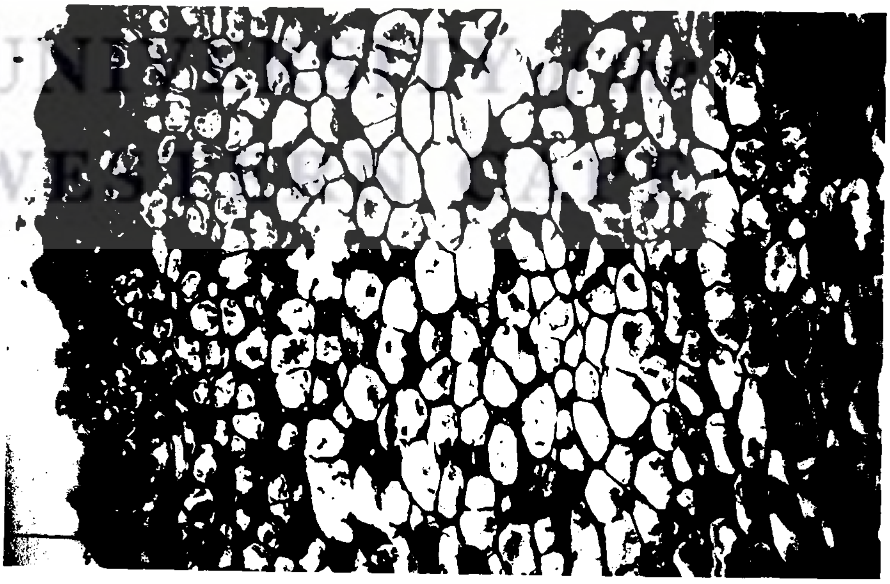


Fig 10(d): LM view of L/S of outer wall of female syconium (15,6mm diameter) of *F. capreifolia* showing degeneration of cellular details
Bar = 0,2mm

with their chloroplasts losing their regular arrangement. As the walls broke down between cells, large (lysigenous type) cavities developed (Fig 9c), and there was a decrease in both druses and laticifers (Figs 9c & 10d) in the walls (at *ca.* 104 days in a gall fig).

By *ca.* 130 days (gall fig 15,8mm), very few chloroplasts remained in the hypodermis. Tannin collected in more cells such as the outer epidermis of the syconium wall, epidermis and other cells of the ostiolar bracts and the parenchyma cells in general.

Stomata in groups only were located in the walls of both figs from syconial initiation. As the epidermis and hairs developed, a collar of ridged cells enclosed each stoma (Fig 9d). Areas occupied by stomata did not have hairs.

Pistillate Flowers

The sequence of development of pistillate flowers in seed and gall figs was similar. Flower primordia were initiated simultaneously from the inner wall of a 7 day old sycone (1,2mm). The dense cytoplast in the cells of the syconial wall became stained heavily and underwent prolific division to form closely packed longitudinal rows of cells (Fig 9a). By the 23rd day (2,6mm), these newly formed cells became grouped to form flower primordia all along the inner surface, which occupied most of the lower two-thirds of the syconium (Fig 11a). A syconial cavity began its formation and the flower primordia developed into buds

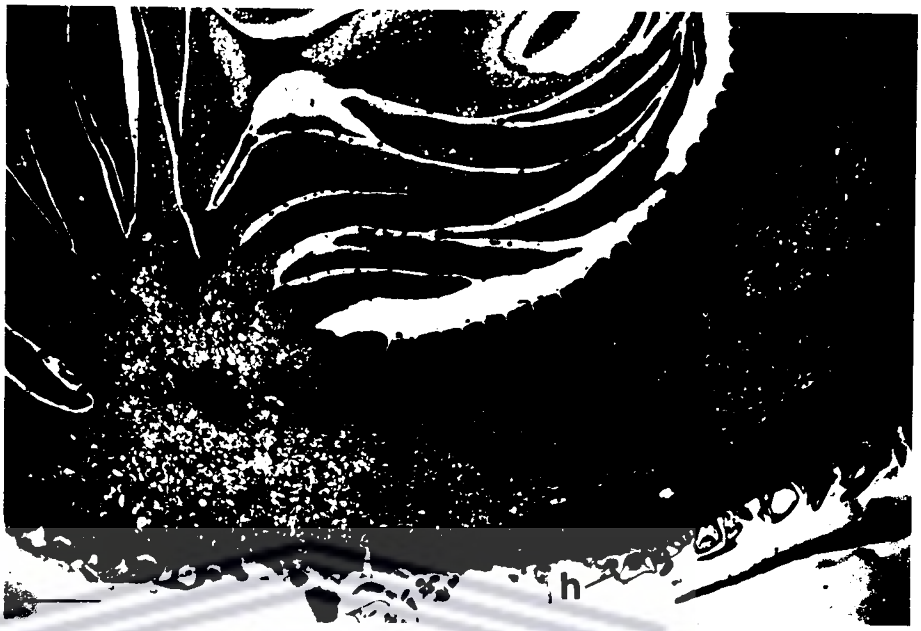


Fig 11(a): LM view of L/S of syconium wall of male syconium (2,6mm diameter) of *F. capreifolia* showing hairs, floral buds and ostiolar bracts
Bar = 0,5mm

Fig 11(b): LM view of L/S of inner wall of female syconium (3,4mm diameter) of *F. capreifolia* showing developing pistillate flowers
Bar = 0,4mm

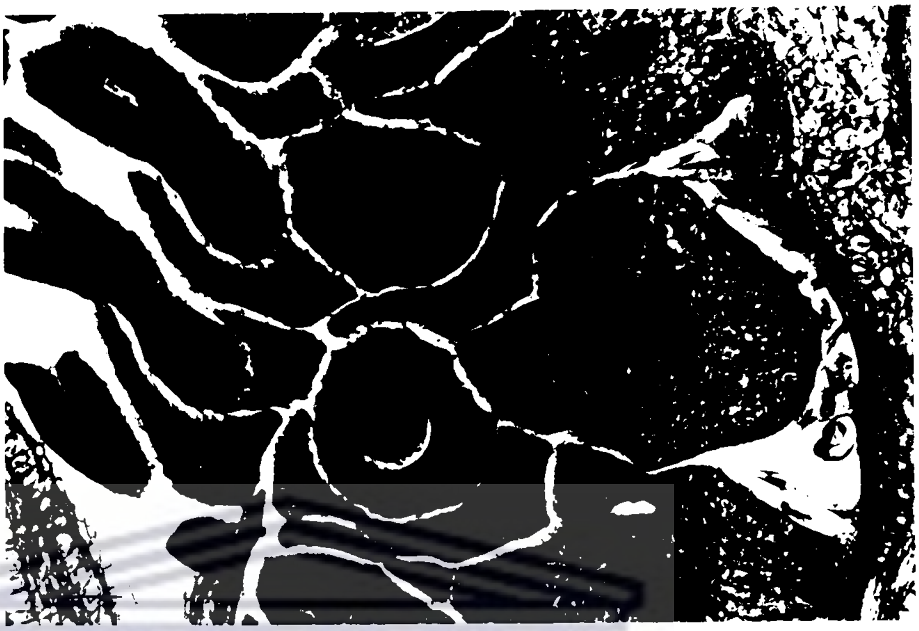


Fig 11(c): LM view of L/S of inner wall of female syconium (4,6mm diameter) of *F. capreifolia* showing developing floral buds Bar = 0,4mm

Fig 11(d): LM view of L/S of developing flower of female syconium (4,6mm diameter) of *F. capreifolia* showing ovary with ovule Bar = 0,05mm pointing into this cavity (Fig 1c). A mature male syconium developed *ca*. 1320 pistillate flowers equally distributed throughout the inner wall of the syconium except in a zone nearer the ostiole where the staminate flowers developed. Female syconia developed *ca*. 1080 pistillate flowers. By the 28th day the floral buds elongated, with the pedicel, perianth segments and style developing first.

The early development of the ovary was noticeable at this stage (Fig 11b). By the 33rd to 36th days, in both figs, pistillate flowers with pedicels, four perianth segments each, ovary with developing ovule, hollow style and a stigma were clearly visible (Fig 11c). The ovary initially developed with 4 to 5 wall layers: an exocarp layer, 2 to 3 mesocarp layers and an endocarp layer (Fig 11d). The superior, stalked, unilocular ovary developed a small cavity surrounding a ball of cells with 3 to 4 layers. The outer wall of the ovary was continuous with the outer wall of the style. The cells of the endocarp elongated radially while some cells of the exocarp were also slightly radially elongated. The mesocarp cells and the rest of the endocarp cells were isodiametrical.

The style developed a 14 to 16 layered wall (Figs 8b, 12d). The outer wall of the style became densely stained by about the 38th day. Projections (papillae) developed from the outer wall layers of the stigma and the upper half of the style in both gall and seed figs (Figs 12 & 13). These papillae, which were finger-like to capitate in

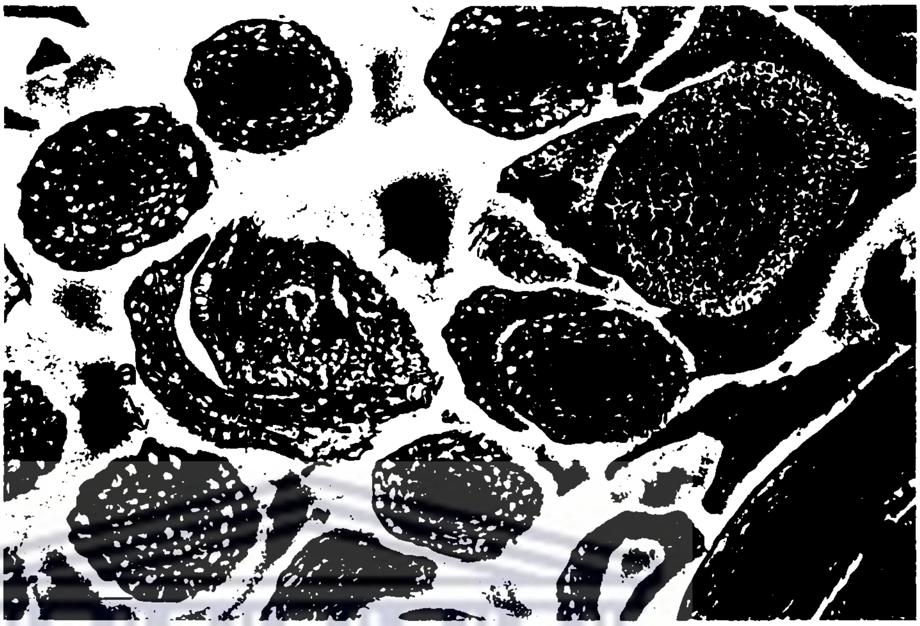


Fig 12(a): LM view of interior of male syconium (6,5mm diameter) of *F. capreifolia* showing floral parts with stigma and papillae
Bar = 0,2mm

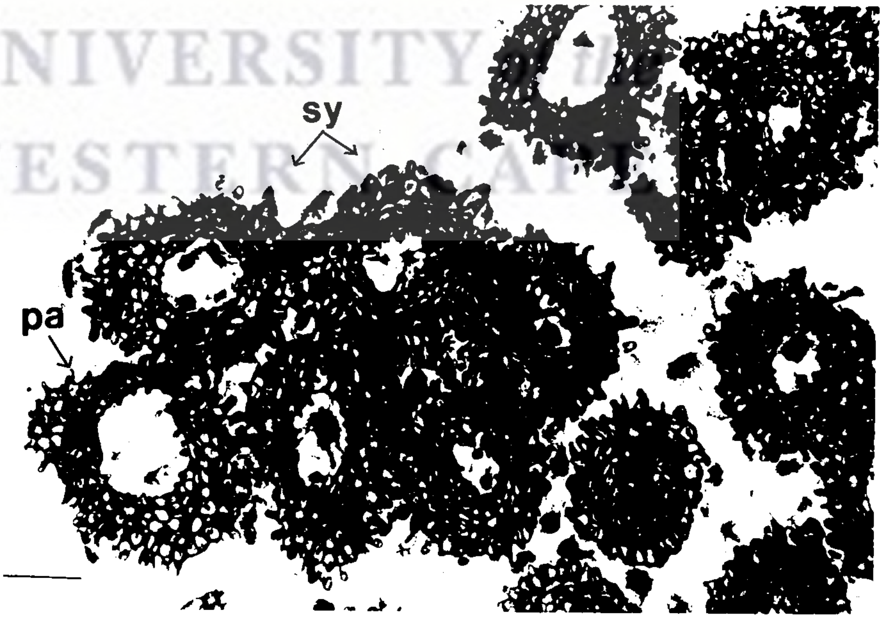


Fig 12(b): LM view of interior of female syconium (9,7mm diameter) of *F. capreifolia* showing synstigma with interlocking papillae
Bar = 0,2mm

Fig 12(c): LM view of interior of female syconium (9,7mm diameter) of *F. capreifolia* showing stylar canals and walls of styles with interlocking papillae in detail
Bar = 0,05mm

Fig 12(d): LM view of L/S of pistillate flowers of female syconium (10,0mm diameter) of *F. capreifolia* showing style and stigma with papillae
Bar = 0,2mm

shape, were prominent by about the 40th day (female - receptive phase). The style remained, with its papillae, firm and intact throughout the female phase and for most of the C phase. A degeneration of the papillae and style firmness occurred towards the end of C phase. These papillae, which at low magnifications appeared to be fine, hair-like structures, were pink to red and very attractive at the end of A phase and during B phase. They became brown towards the end of B phase. Pistillate seed flowers had long (mean length 1,18mm to 1,71mm) styles, while pistillate gall flowers had short (mean length of 0,55mm to 0,67mm) styles.

A slightly-lobed stigma forming a hollow cup-like structure developed fully by *ca*. 40 days (Fig 8b). In the seed fig, the papillae of the stigmatic surfaces came into contact with each other after *ca*. 40 days. This resulted in the formation of the synstigma (Figs 12 a & b). The stigmatic surfaces became aligned to form a common platform as the papillae became interlocked. At this stage (beginning of B phase) they stained red (Figs 12b, c, d and 13a). The papillae of the seed figs were better developed than those of the gall figs. The open ends of some burst papillae were evident in the receptive stage (Fig 13b). By the middle of the C phase (100 to 110 days), the stigmatic surfaces were not so firmly attached to each other. A few scattered druses were located on the outer walls of some styles of gall figs only.

Fig 13(a): SEM view of L/S of pistillate flowers of female syconium (7,2mm diameter) of *F. capreifolia* showing style and stigma with papillae
Bar = 100um

Fig 13(b): SEM view of stigmatic and stylar surfaces of female syconium (10,4mm diameter) of *F. capreifolia* showing papillae
Bar = 10um

Fig 14(a): LM view of L/S of inner wall of female syconium (6,0mm diameter) of *F. capreifolia* showing developing flowers with stigma, style and ovary
Bar = 0,5mm

Fig 14(b): LM view of detail of ovary of pistillate flower of female syconium (6,0mm diameter) of *F. capreifolia* showing ovary wall and ovule
Bar = 0,05mm

The ovule arose from the ovary wall, opposite the insertion point of the style, initially as a projection (Figs 11c & 14a). The ovule in transverse section showed concentric rows of cells and slowly expanded to fill up the loculus of the ovary (Fig 14b). Integuments then developed on the outside of the ovule (dermally) after *ca.* 30 days. By about the 40th day the inner and outer integuments were distinguishable, with the inner integument growing more rapidly than the outer integument. At about this stage the megaspore mother cell divided to produce a linear tetrad from which the embryo sac developed. The ovule with its developing integuments appeared trizonate (Fig 14a). During the receptive stage one end of each ovule became stained red. The hemianatropous ovule was filled with nucellus which rapidly increased as the embryo sac developed in the ovule. The embryo sac contained the embryo and developing endosperm in B-phase.

In both the seed and gall figs the integuments were distinctly 3-layered by the receptive phase. The outer integument had large isodiametrical cells resembling the cells of the endocarp in size and shape. The inner integument had small brick-shaped cells and the cells were smaller than the nucellar cells. The outer layer of the inner integument had larger cells than the two inner layers. These two inner layers of the inner integument had very small flattened cells which were tanninized and loosely arranged in both the gall and seed figs (Figs 14c

Fig 14(c): LM view of detail of ovule in ovary of female syconium (8,7mm diameter) of *F. capreifolia* showing integuments
Bar = 0,2mm

Fig 14(d): LM view of detail of ovule in ovary of female syconium (10,0mm diameter) of *F. capreifolia* after fertilisation
Bar = 0,2mm)

& 16a).The micropyle was formed by the inner integuments. In gall figs, the inner integument was clearly short on the raphal side. Mitotic activity was visible on the raphal side. The wasp egg was deposited together with a drop of fluid (stained red) between the integument and nucellus. At this stage the embryo sac was clearly visible. It was difficult to observe pollen tubes.

After fertilisation, towards the end of B phase (60 days), the development of the seed progressed rapidly with the integuments pulling away from the ovary wall (Fig 14d). The embryo sac developed rapidly becoming filled with the enlarging endosperm and the growing embryo. By the end of the C phase the ovary, which had enlarged considerably, enclosed loosely the almost fully formed seeds. The integuments of the ovule developed into a seed coat around the embryo sac as most of the nucellus was used up. The innermost layer of the inner integument and the outermost layer of the outer integument became tanninized while the other layers disintegrated (Fig 15a & b). The embryo developed two cotyledons and was surrounded by the endosperm. Both the cotyledons and endosperm had a large number of heavily stained globules with those in the endosperm being larger (Figs 15a & b).

Eventually the ripe syconium produced a large number of seeds enclosed in a tanninized seed coat within the pericarp. Most of the other cellular structures became soft and broke up. A sticky mucous-like substance

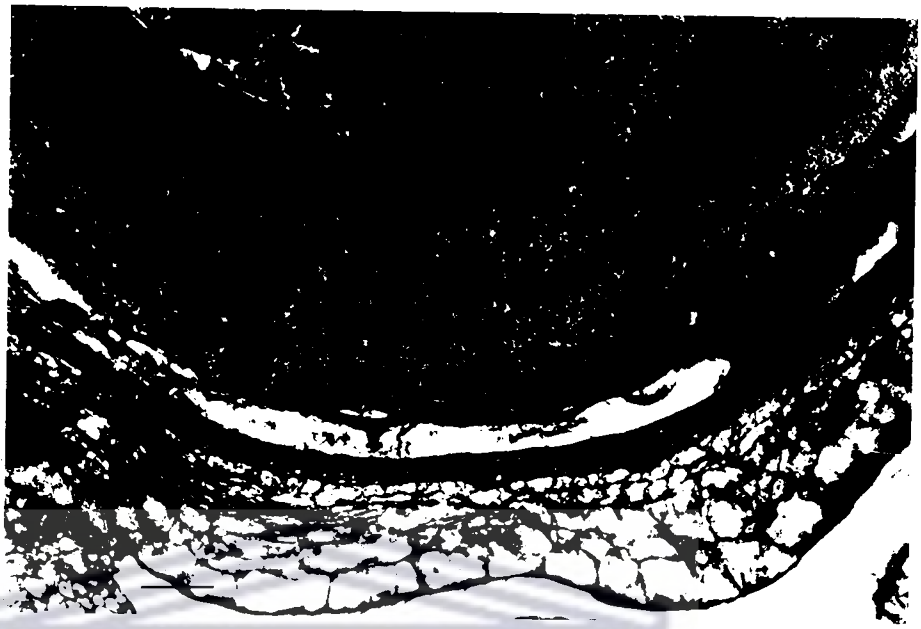


Fig 15(a): LM view of detail of part of ovule in ovary of female syconium (15,6mm diameter) of *F. capreifolia* showing tanninised layers and endosperm
Bar = 0,2mm

Fig 15(b): LM view of detail of part of ovule in ovary of female syconium (16,0mm diameter) of *F. capreifolia* showing tanninised layers and endosperm
Bar = 0,2mm

collected between the seed and the fragile ovary wall and the seeds easily popped out of the ovary with the slightest pressure on its wall.

The development of the female flowers in the gall fig was similar to that of the seed fig up to the end of A phase. The receptive ovary (B phase) had a 4-layered wall with the exocarp having radially elongated cells and isodiametrical mesocarp and endocarp cells as for seed figs (Fig 16a). Mesocarp cells appeared plasm-rich and smaller than the endocarp cells. Ovipositing wasps deposited eggs in the ovary. Wasp eggs together with a purple stained fluid were deposited between the raphe and the nucellus (Fig 16a). By the end of the B phase the wasp larvae had entered the nucellus via the integuments. At this stage there was a considerable amount of nucellar material and the embryo sac was also enlarging (Fig 16a). The larva eventually migrated towards the embryo. The nucellus decreased and disappeared by the end of C phase..

The integuments separated from the ovary wall at the beginning of C phase. During this phase the two mesocarp cell layers and the endocarp layer became flattened and the cells appeared brick-shaped and periclinally elongated. The cells of the integument appeared to lose their regular pattern and appeared to be breaking up. The wasp larva had undergone rapid growth. The endosperm had increased in size but was pushed to one side (Figs 16b & c). The integuments broke down and disappeared completely by the end of the C phase, with the fully formed wasp within the embryo sac. The endosperm tissues soon disappeared and the wasp filled up all the space within the enlarged gall (Figs 16 & 17). Very rapid increase in the size of the gall occurred in a few days at the end of C phase and the beginning of D phase. The ovary wall had an exocarp, 2 to 4 layers of mesocarp and an endocarp. Sclerification of the innermost mesocarp layer occurred by the 135th day and this was completed by the 140th day. Soon after, the wasps departed and large empty galls remained (Fig 17b). Towards the end of A phase and the beginning of B phase a 4-layered ovary wall with 2 mesocarp cell layers was formed (Fig 14b). As the syconium reached the receptive stage, at about the 45th to 50th days, in both figs, the exocarp cells of the ovary increased the size of their cells considerably by stretching radially (Fig 14c). The cells of the mesocarp and endocarp layers appeared isodiametrical and these cell layers together were of the same thickness as the exocarp layer. Gradually the cells of the endocarp and inner mesocarp layers became thick-walled to form the pyrene. The ovary wall became sclerified on the inside forming heavily lignified cells (Fig 15a).

Staminate Flowers

Staminate flowers were found in male syconia in 2 or 3 whorls near the ostiolar region. An average of 118 staminate flowers compared to about 1320 pistillate

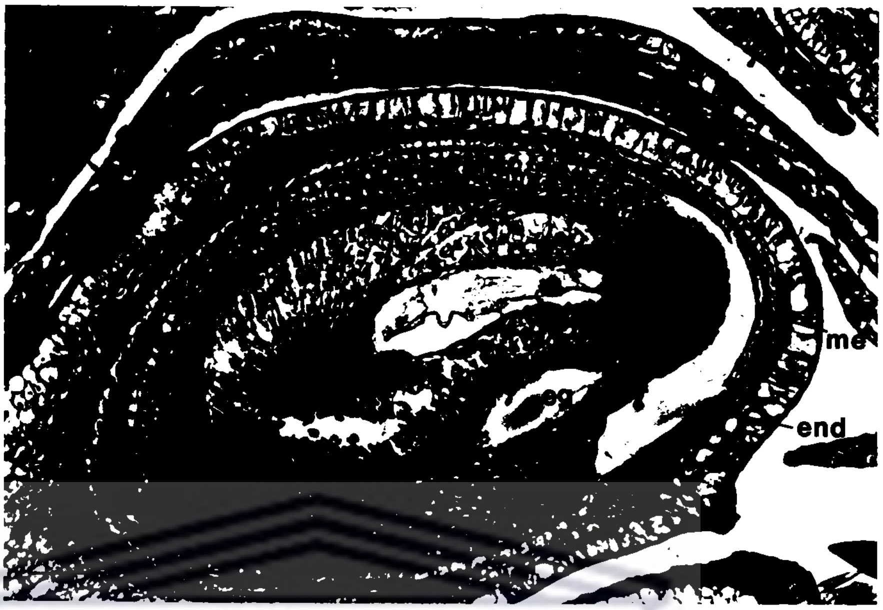


Fig 16(a): LM view of detail of L/S of ovary of male syconium (10,3mm diameter) of *F. capreifolia* showing ovary wall and ovule with egg
Bar = 0,2mm

Fig 16(b): LM view of L/S of male syconium (12,3mm diameter) of *F. capreifolia* showing developing wasp larva
Bar = 0,2mm

Fig 16(c): LM view of L/S of male syconium (14,4mm diameter) of *F. capreifolia* showing enlarging wasp larva
Bar = 0,5mm

Fig 16(d): LM view of L/S of male syconium (15,8mm diameter) of *F. capreifolia* showing maturing wasp larva in gall ovary
Bar = 0.5mm

Fig 17(a): LM view of L/S of ovary of male syconium (18,0mm diameter) of *F. capreifolia* showing developing wasp in gall ovary Bar = 0,5mm

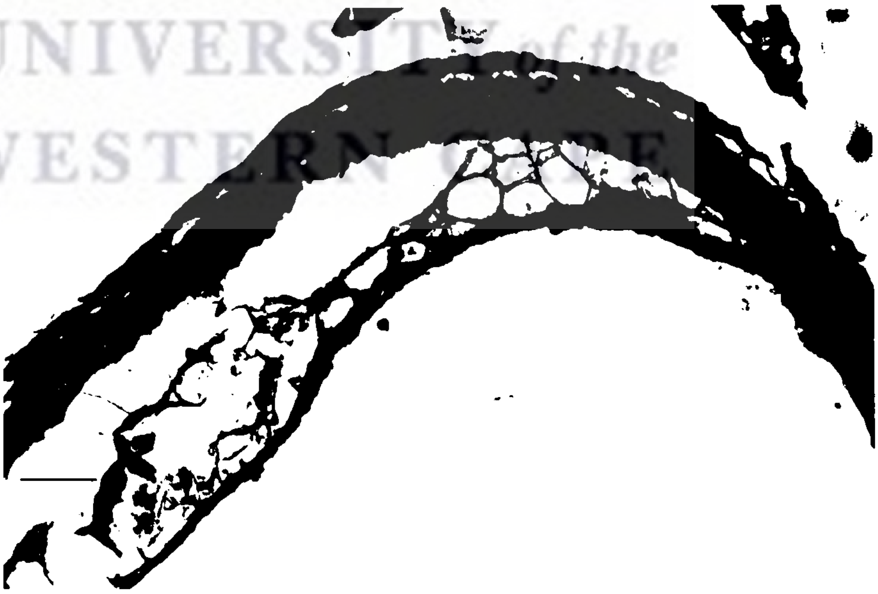


Fig 17(b): LM view of empty gall of male syconium (20,4mm diameter) of *F. capreifolia* showing wall layers of ovary Bar = 0,2mm flowers was present in each fig (ratio of about 1 staminate to 11 pistillate flowers). Each staminate flower had a single stamen (with rarely 2 or 3), 4 to 5 perianth segments and occasionally a rudimentary pistil was present, especially in the marginal locations.

Development of staminate flowers occurred simultaneously with the development of the pistillate flowers in A phase. Primordia were initiated, near the insertion of the ostiolar bracts, in rows, and were covered by the bracts in A phase. Growth of these primordia was arrested until the A phase when further development occurred to form anthers and filaments (Fig 18a). By B phase parts of the perianth, anther and filament had differentiated, although there was little tissue specialisation at this point. By the end of B phase, tissue specialisation occurred with the anther wall formed, the microsporangia with concentric rows of sporogenous tissue, filament and tepals. Each anther was introrse, bithecate with 2 pollen sacs in each theca. By the 80th day (beginning of C phase), the anther wall had an epidermal layer covered by a thin cuticle, an underlying endothecium (with one cell layer) and another 4-cell layer with the innermost layers forming the tapetum. The cells of the tapetum appeared to be very loosely arranged and they surrounded the concentric, large, polygonal, plasm-rich sporogenous tissue cells which remained meristematic (Fig 18b).

The filament was also enclosed by the epidermis with the thicker portion attaching the anthers having cells elongated anticlinally, and the rest being more or less brick-shaped (Figs 18 & 19). Large vacuolate parenchyma, some with druses, and vascular tissue also occurred in the filament. The perianth segments were similar to those of the pistillate flowers in composition (Figs 18 & 19).

By about the 90th day (early C phase), sporogenous tissue produced microspore mother cells. These cells divided to form the tetrads which later developed into the microspores. Pollen grains were present by the end of the C phase (Fig 19a). The anther wall became distorted with the cells becoming irregular in shape. The microspores became surrounded by the glandular (heavily stained) tapetum which broke away from the anther wall. Tannin accumulated in a few cells of the filament. The septum separating the loculi was still present towards the end of the C phase. By the 130th day the longitudinal slits developed in the anther walls and the septum broke down between the loculi (Figs 18 & 19).

Fig 18(a): LM view of L/S of male syconium (8,7mm diameter) of *F. capreifolia* showing development of staminate flowers near ostiolar region
Bar = 0,5mm

Fig 18(b): LM view of L/S of male syconium (10,3mm diameter) of *F. capreifolia* showing bithecate anthers with pollen sacs
Bar = 0,2mm

Fig 18(c): LM view of L/S of male syconium (12,3mm diameter) of *F. capreifolia* showing mature anthers with microspores
Bar = 0,2mm

Fig 18(d): LM view of L/S of male syconium (14,4mm diameter) of *F. capreifolia* showing ripe anthers with pollen
Bar = 0,2mm

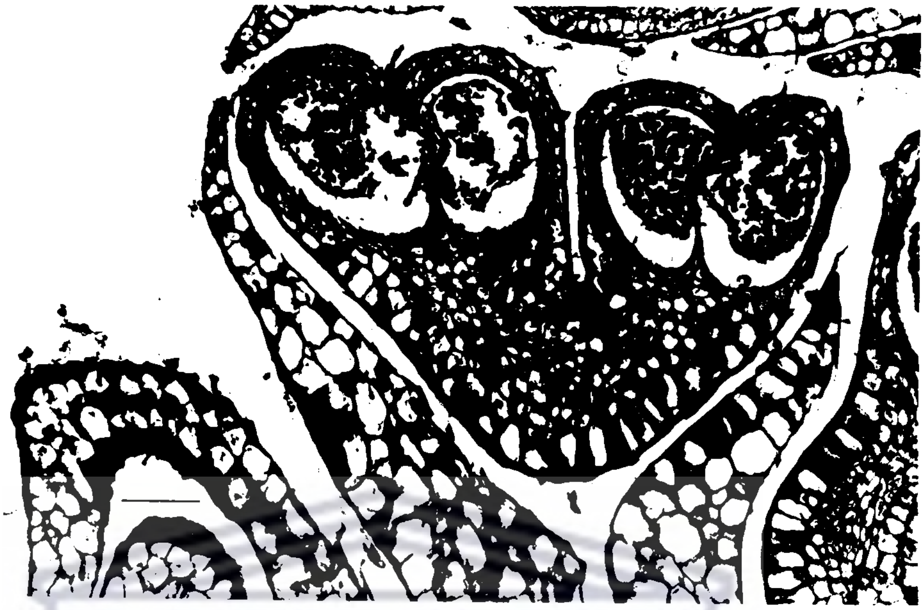


Fig 19(a): LM view of L/S of male syconium (15,8mm diameter) of *F. capreifolia* showing ripe anthers with pollen
Bar = 0,2mm

Fig 19(b): LM view of L/S of male syconium (18,0mm diameter) of *F. capreifolia* showing shrivelling anthers
Bar = 0,2mm

DISCUSSION

The male and female plants of *F. capreifolia* were difficult to distinguish from their prefemale and female phase syconia, as externally, syconia and plants appeared to be identical, with very similar developmental patterns. Plants with C phase syconia could be easily identified by splitting syconia and examining under the microscope. While the plants and syconia may have resembled each other, there are many functional and anatomical differences which may be identified.

Seed figs had shorter developmental cycles (*ca*. 120 days) compared to gall figs (*ca*. 140 days). The shorter cycles of the seed figs may be related to the smaller size of the fig reached and the absence of the male (D) phase. Ripe (E phase) seed figs reached an average size of about 15,1mm compared to an average of 20,5mm for gall figs. The larger size of the gall figs may also be related to the larger size of the wasps, compared to the size of the seeds, and the development of a syconial cavity in D and E phases to facilitate wasp activity and emergence from the syconium. Baijnath and Naicker (1989) reported a 70 to 80 day cycle in *F. ingens*, while Newton and Lomo (1979) recorded a 50 to 60 day cycle for *F. vogelli*. Baijnath and Ramchuran (1983) also recorded a 60 day cycle in *F. sur*. In these three monoecious species, relatively short prefemale stages of 20, 12 and 24 days respectively are reported. A comparison with *F. capreifolia* showed that A phase was longer in both the gall and seed figs with 45 and 50 days respectively, while C phase in both the gall and seed figs was also longer with 70 and 40 days respectively. It is suggested that this *F. capreifolia* sample, growing at the margin of its range and with its asynchronous crops has adopted this strategy, with longer A and C phases, to improve its chances of survival. Bronstein and Patel (1992) studied phenological patterns in *F. aurea* and found that during their developmental cycles some syconia may remain at 3mm in A phase for between 1 week to 8 months. A varying proportion of these syconia (up to 100%) resume growth and within 2 days enter the female phase. They suggested that, because some are in dormant A phase, this put the tree out of its developmental synchrony pattern. They also suggested that there is variation in the length of the developmental periods taking up to 50% longer in winter. They also reported that C phase is markedly temperature sensitive. Bronstein (1989) suggested that durations of fig-reproductive episodes are longer in cooler weather because seeds and wasps develop more slowly then. These arguments were supported by comparing *F. sycomorus* at a site in Namibia and further north in Kenya by Wharton, Tilson and Tilson (1980) and Galil and Eisikowitch (1968) respectively. It may be concluded that developmental cycles for species are not limited in time and that they could exhibit a degree of plasticity which could improve their chances of survival, especially when unfavourable conditions persist in their habitats. It may be concluded that useful information could be obtained by studying the same species in a range of latitudes, habitats and seasons.

The peduncular bracts which enclosed the young syconium probably protected the developing syconium. These abscised once the syconium became completely closed off with its ostiolar bracts, and the syconium was large enough to be self-protecting. The horizontal bracts appeared to enclose, guard and control the entrance (ostiole) to the syconium. This was evident when one considers that this ostiole opened slightly in B phase in both figs and in the D and E phases in gall figs to allow for wasp entrancce and departure respectively. Verkerke (1987) suggests that the bracts open due to a loss of turgor to facilitate the entry of wasps. It is possible that the larger highly vacuolate parenchyma cells and the large radially elongated inner epidermal cells were associated with changes in turgor in the ostiolar bracts. The outer bracts were also thicker than the inner bracts and pubescent to provide protection and possibly attract insects. The vertical ostiolar bracts, by hanging down into the syconial cavity, provided a passage downwards for the entering wasps. The inner bracts are probably thinner because they were not involved in protection. There were also no hairs on them probably because they were not involved in attraction.

Unicellular hairs found on the outer surface of the syconium and outer bracts were probably protective in function. The conical unicellular hairs were robust in appearance and may have contributed to the scabrous nature of the fig surface. This feature may have deterred animals from removing these figs before ripening from the plants. It was shown that when the figs ripened these hairs degenerated and the surface became covered by a waxy material, at which stage the figs may have been available to the animals. Hairs found on the inner surface during B phase mainly, although unicellular in nature, may have been glandular and secreted substances to attract the wasp into the syconium. Pluricellular hairs, which were mostly densely stained, were prolific on the outer syconial wall before and during the receptive phase, and were not present on the inner wall or even on the ostiolar bracts. Baijnath & Naicker (1989) and Verkerke (1986) located pluricellular hairs on the inner surfaces of the syconia during the receptive phase and proposed that these hairs release an attractant for the wasp. These ideas need to be investigated.

Rapid growth of the syconium during A phase may have reduced the chances of physical damage in the environment. Small figs (of 1mm to 2mm in diameter) may have been subjected to more buffetting (by wind) and dessication (in high temperatures) and many were usually lost in this way. Rapid growth in A phase would have also ensured that the fig quickly reached the female phase for pollination and fertilisation, in addition to being large enough to accommodate the wasp that entered in B phase. In early C phase there was little or no visible growth because fertilisation and oviposition may have initiated internal changes in the anatomy and physiology. It is possible that some hormonal changes could have occurred at this stage to prepare for further development. Thereafter growth in the rest of C phase may have been due to the development of food reserves and the increases in size mainly of the wasp larva and the seed in their respective ovaries.

There was limited increase in the size of the seed fig in the post-floral phase while the gall fig increased in size significantly. The fully grown wasp (occupying the gall fig ovary), was very much larger than the seed and may have accounted for a part of this difference in size. Ripe gall figs had a syconial cavity which was lacking in seed figs. This cavity provided space for the activity of the emerging pollinator wasps and secondary sycophiles in gall figs. This difference in size may have also been partially due to the presence of a thicker syconial wall in the ripe gall fig (2,2mm) than in the seed fig (1.3mm).

The syconial wall increased from about 38 to 42 layers (0,3mm thick) in a 7 to 10 day old to about 105 layers (2,2mm thick) in a 135 day old gall fig and 80 layers (1,3mm thick) in a 130 day old seed fig. The gall fig wall became thicker with more cell layers than the seed fig wall and this could have been related to the mature gall fig being a larger sphere and therefore needing more cells to provide more support. A 3 to 6 layered hypodermal layer was found below the epidermis in both gall and seed figs. These cells were not sclerified. Verkerke (1986) reported that the hypodermal cells become thick-walled in *F. ottoniifolia*, while Baijnath and Naicker (1989) reported similarly that they become sclerified in *F. ingens*. Both of these are monoecious species, and no such sclerification has been reported for the (gyno)dioecious figs, including *F. asperifolia* whose anatomy was described by Verkerke (1987). From the limited information available, it would appear that this absence of sclerified cells in the dioecious species may be a characteristic difference with some as yet unknown functional significance. It may be related to limiting oviposition by secondary sycophiles through the general wall surface (possibly to ensure that oviposition by secondary sycophiles occurred via the softer ostiolar region to limit oviposition and the amount of oviposition) in the monoecious figs. This could be related to the idea that monoecious figs, being less specialised, have to provide for the production of seeds and pollinator wasps within the same syconium, and therefore excessive or uncontrolled oviposition by secondary sycophiles could reduce its main function(s) and symbiotic role. Dioecious figs, being more specialised with separate seed and gall figs may not be faced with these problems, since no oviposition by secondary sycophiles has been noted in seed figs and the gall fig may have enough space to accommodate the secondary sycophiles. Alternately the presence of the robust unicellular hairs may substitute for the lack of sclerification of the hypodermal layers, and consequently this feature could hinder oviposition by secondary sycophiles through the syconial walls.

A syconial cavity which was initiated when the fig was about 2,6mm (23 days) expanded similarly in both gall and seed figs up to the end of B phase. It closed in C phase as it became filled with galls or seeds. In gall figs only, the cavity opened again in D and E phase to cater for the activity of the wasps. The cavity in B phase provided room for pollination and/or oviposition by visiting females of the pollinator. It opened in D phase to allow for eclosion, mating, pollen collection and emergence of the wasp progeny.

Tannin accumulation occurred more rapidly in cells of both figs towards the end of C phase. Fahn (1974) suggested that these phenol derived compounds may protect the plant against dehydration, rotting and damage by animals. Druses appeared commonly in many cells in the younger stages and decreased in the older stages. The function of this crystalloid substance in cells has not been explained. Lactifers also decreased in the latter stages and this resulted in a decrease in the secretion of latex in the male and postfloral phases.

In the older stages other changes occurred in the fig wall. These included a decrease in the chloroplasts, outer epidermal cells losing their brick-shape to become more irregular, hypodermal cells becoming more parenchyma-like and an increase in vacuolation with large lysigenous-type spaces appearing in parenchyma layers in the syconial wall. This was in keeping with the change in texture of the fig wall from hard to soft and the rapid expansion of the fig. The development of the wall was generally similar to that reported by other workers (Verkerke, 1986 & 1987; Baijnath & Naicker, 1989).

Development of the pistillate and staminate flowers from the inner wall of the syconia occurred similarly for both the gall and seed figs. Flower primordia originated in early A phase and rapidly developed to form long-styled pistillate flowers only in seed figs and short-styled pistillate and staminate flowers in gall figs. Development of the staminate flowers slowed down during late A and early B phases. The development of the staminate flowers was accelerated in late B and in C phases so that its development could keep pace with the development of the wasp progeny in the galls. Similar flower development occurred in seed and gall figs to form an average of 1080 long-styled and 1320 short-styled pistillate flowers respectively. Verkerke (1987) reported that 1700 long-styled flowers and only about 1000 short-styled flowers are formed in seed and gall figs respectively, in *F. asperifolia*. This difference may be associated with environmental forces which direct plants to form more seeds or wasps depending on the success of each partner in the mutualism.

Most of the ovaries of both fig types occupied about two tiers in the A and B phases with this characteristic being more distinct in the gall figs. This layering became more accentuated in the C phase in both figs as the expanding ovaries moved into all the available space. It was a packing strategy made possible by the elongating pedicels which ensured that maximum use was made of the space within a fig. It was shown earlier that mean pedicel lengths in male syconia increased, between B and D phases, from 0,33mm to 1,61mm in short-pedicelled flowers and 0,69mm to 4,4mm in long-pedicelled flowers of *F. capreifolia*. Similarly in female syconia mean pedicel lengths increased, between B and D phases, from 0,34mm to 1,11mm in short-pedicelled flowers and 0,74mm to 2,17mm in long-pedicelled flowers of *F. capreifolia*. This phenomenon has been observed and reported in other figs.

By the 40th day (latter part of A phase) finger-like papillae with slightly bulbous ends arose from the stigmatic surfaces and upper part of the style. These structures may be glandular as their period of formation preceded the transition of the fig from the A phase (prefemale phase) to the B phase (female phase). These structures became fully formed and prominent in the B phase when the fig became receptive, at which stage pollinating wasps were expected to visit the fig, enter via the ostiole and then oviposit in the ovary and/or pollinate the stigma. Furthermore, open ends on papillae had been observed in B phase and this suggested that the ends may have burst to release some substance which could have then attracted the wasps to the receptive fig. Degeneration of these papillae had been observed in C phase and this further indicated that they had a role to play in B phase. The papillae also overlapped and became interlocked during the formation of the synstigma. The papillae of the seed fig stigmata appeared to have a dual role, in forming the synstigma, to facilitate pollination and also probably secrete substances to serve as an attractant. In the gall figs, where no synstigma was present, they probably only released an attractant. Females of the pollinator wasps had large prominent compound eyes. While it is known that wasps respond to shapes and movement and not colours, is it possible for them to be attracted to other cues? The papillae take on a very attractive pinkish colour during the receptive phase. This colour was lost after the receptive phase.

The short-styles (0,55mm to 0,67mm) of the gall flowers were clearly very much shorter than the long styles (1,18mm to 1,71mm) of seed flowers. This difference might be significant especially in preventing oviposition in the long-styled flowers by wasps, with their shorter ovipositors having a mean length of about 0,61mm. Research on monoecious figs shows that oviposition occurs mostly in the shorter-styled flowers. Verkerke (1986),in describing the monoecious fig, *F.ottoniifolia*, suggests that short and thick styles provide better support to an ovipositing wasp, and therefore style firmness and not style length may be the main limiting factor. Verkerke (1987) did, however, suggest that style length may be limiting in *F. asperifolia*. Style firmness may be important for efficient oviposition, but does not seem to be the over-riding factor. Condit (1932) suggested that the insertion and withdrawal of the ovipositor into and out of the stylar canal causes damage and this prevents the growth of the pollen tube in the gall flower styles. There is no evidence for this however. These claims are also made by Neeman and Galil (1978) and Galil and Eisikowitch (1971).

Development of the ovule and ovary followed the pattern already described by earlier workers (Condit, 1932; Johri & Konar, 1956; Verkerke, 1986/7 and Baijnath & Naicker, 1989). A 4-layered ovary wall developed in *F. capreifolia* with the exocarp having some radially elongated cells in early A phase. Verkerke (1987) described only isodiametrical cells in the exocarp of *F. asperifolia* in early A phase. However thereafter the ovary wall development follows the same pattern described for *F. asperifolia* Verkerke, 1987).

Both the inner and outer integuments of the ovule of *F. capreifolia* were 3-layered. In *F. asperifolia*, the seed figs have 3-4 layered integuments and the gall figs have an inner integument of 3 layers and an outer integument of 2 layers (Verkerke, 1987). Baijnath & Naicker (1989) showed 3-layered inner and outer integuments in *F. ingens*.

Condit (1932) described an inner integument with 3 or more layers and an outer integument with 3 to 5 layers for *F. carica* and with the cells of the inner integument being smaller than the nucellus cells. Johri & Konar (1956) reported that both integuments are 3-layered in *F. religiosa*, with the inner integument later becoming 4 to 5 layered in the micropylar region.

The inner integument , which eventually formed the micropyle, grew faster than the outer integument. This has also been shown by Condit (1932) and Verkerke (1986/7). The hemianatropous ovule has a circumvallating inner integument which remains short at the raphal side in the gall fig. Verkerke (1987) has described this aspect in detail explaining how the lack of an inner integument at the raphal end makes it possible for the wasp to lay its egg next to the nucellus. He goes on to explain the presence of elongated cells bordering the raphal strand, which help to direct the ovipositor towards the nucellus, and the plasm-rich endothelium-like raphal epidermis which provides early nourishment for the developing wasp. The present study of the anatomy of *F. capreifolia* lends support to these ideas. Grandi (1961) reported the presence of a brightly coloured fluid deposited with the egg. This fluid, also reported in this study, was also located by Verkerke (1987), and he suggests that the rapid expansion of the nucellus, which occurs immediately after oviposition, may be triggered off by this fluid. Condit (1932) reported that oviposition in *F. carica* also occurs between the inner integument and the nucellus.

The available information suggests that the development of the ovule into a seed, the maturation of the wasp in the gall, oviposition, fertilisation and nourishment followed a similar pattern to that described by Verkerke (1987) for *F. asperifolia*. Therefore, a detailed analysis and explanation of these aspects would be unnecessary here. Both Condit (1932) and Johri & Konar (1956) have made significant contributions in this area also, especially in the field of embryology. Condit (1932) did not describe the proembryo and endosperm development in gall figs of *F. carica*. However Johri & Konar (1956) reported these observations in *F. religiosa*, also suggesting that the larvae could be secreting enzymes or hormones which may have an inhibiting effect on the developing proembryo.

Development of the wall surrounding the wasp was similar to those described by Verkerke (1986 & 1987) for *F. ottoniifolia* and *F. asperifolia*. A pericarp only remained enclosing the wasp while all other layers brokedown. The pericarp had a stretched exocarp layer with sclerified inner mesocarp cells and the endosperm cells.

The drupe became covered by a pyrene. Verkerke (1986 & 1987) described the pyrene as having formed from the thick-walled inner epidermal cells and sclerified sub-epidermal layer by puzzle-shaped cells and suggested that the pyrene protects the embryo.

Both Johri & Konar (1956) and Verkerke (1986 & 1987) have suggested that double fertilisation occurs in both monoecious as well as dioecious figs. Verkerke (1987) concluded that both seed and gall flowers are normal with the developing wasp feeding on the embryo and later the endosperm, thereby preventing seed production. Galil & Eisikowitch (1968b), by excising wasp ovipositors, demonstrated that both long- and short-styled flowers in the monoecious fig, *F. religiosa*, produce seeds. Neeman & Galil (1978) demonstrated seed formation in gall figs of *F. carica* pollinated artificially. Galil & Eisikowitch (1971) also showed that pollen-clean wasps introduced into receptive *F. religiosa* syconia could not initiate endosperm development, resulting in a high mortality rate of the developing wasp larvae. Observations of *F. capreifolia* supported the view that double fertilisation occurred here and that the developing wasp parasitized the gall ovary in order to ensure its survival.

Development of the staminate flower was similar to that reported for *F. asperifolia*, with the plasm-rich sporogenous tissues being formed by the end of A phase (Verkerke 1987). By the end of B phase or early C phase, microspore mother cells were present. Pollen formed in the anther by the end of C phase. Pollen grains were collected by wasps from the pollen sacs split by longitudinal dehiscence. The general organisation and developmental anatomy of *F. capreifolia* was similar in many respects to the descriptions of the (gyno)dioecious fig, *F.*

asperifolia, described by Verkerke (1987). Similarities also existed between these plants and the monoecious figs, as described by Johri & Konar (1956) and Verkerke (1986). Differences between species and between monoecious and dioecious figs existed in terms of size, number, shape and sclerification of parts during their development.

Seed figs differ from gall figs, in the (gyno)dioecious species, in having long-styled flowers, normal integument, embryo and endosperm persisting during development, seed coat, synstigma, pistillate flowers only and seeds (Verkerke, 1987).

BIBLIOGRAPHY

Baijnath,H., & Naicker,S.,1989. Developmental anatomy of *Ficus ingens* syconia in relation to its wasp faunula. *S.Afr.J.Bot*. 55(4): 409-421.

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

Bronstein,J.L.,1989. A mutualism at the edge of its range. *Experientia* 45: 622-637.

Bronstein,J.L., & Patel,A.,1992. Causes and Consequences of within-tree phenological patterns in the Florida strangling fig, *Ficus aurea* (Moraceae). *Am.J.Bot*. 79(1): 41-48.

Condit, I.J.,1932. The structure and development of flowers in *Ficus carica* L. *Hilgardia* 6: 443-481.

Fahn,A.,1974. Plant Anatomy. Permagon Press, New York.

Friis,I.,1990. Distribution patterns of *Ficus* in tropical N.E. Africa. *Proc.aetfat.Sym.IV,Hamburg* 23a: 407-424.

Galil,J., & Eisikowitch,D.,1968a. On the pollination of *Ficus sycomorus* in East Africa. *Ecology* 49: 259-269.

Galil,J., & Eisikowitch,D.,1968b. On the pollination ecology of *Ficus religiosa* in Israel. *Phytomorphology* 18: 356-363.

Galil,J., & Eisikowitch,D.,1971. Studies on mutualistic symbiosis between syconia and sycophilous wasps in monoecious figs. *New Phytol*. 70: 773-787.

Grandi,G.,1961. The hymenopterous insects of the superfamily Chalcidoidea developing within the receptacles of figs. *Boll. 1st. Ent.Univ. Bologna* 26: 1-13.

Johri,B.M., & Konar,R.N.,1956. The floral morphology and embryology of *Ficus religiosa* Linn. *Phytomorphology* 6: 97-111.

Neeman,G., & Galil,J.,1978. Seed set in the male syconia of the common fig, *Ficus carica* L. (Caprificus). *New Phytol*. 81: 375-380.

Valdeyron,G., and Lloyd,D.G.,1979. Sex differences and flowering phenology in the common fig, *Ficus carica* L. *Evolution* 33: 673- 685.

Verkerke,W.,1986. Anatomy of *Ficus ottoniifolia* (Moraceae) syconia and its role in the fig-fig wasp symbiosis. *Proc.Ken.Ned.Akad.van Wetensch.* C89: 443-469.

Verkerke,W.,1987. Syconial anatomy of *Ficus asperifolia* (Moraceae), a gynodioecious tropical fig. *Proc. Kon.Ned.Akad.van Wetensch.* C90: 461-492.

Verkerke,W.,1988. Flower development in *Ficus sur* Forsskal (Moraceae). *Proc.Kon.Ned.Akad.van Wetensch.* C91: 175-195.

Wharton,R.A., Tilson,J.W., & Tilson,R.L.,1980. Aynchrony in a wild population of *Ficus sycomorus*. *S.Afr.J.Sci.* 76: 478-480.

KEY FOR CHAPTER 2

c - chloroplast
co - cotyledon
ct - conducting tissues to flower(s)
d - druse
e - epidermis
eg - egg
en - endosperm
end - endocarp
ex - exocarp
fb - floral buds
fd - zone of floral development
g - gall
h - hair(s)
hd - hypodermis
i - integuments
ii - inner integuments
me - mesocarp
mc - middle cell layers
o - ovary
ob - ostiolar bract
oc - outer cell layers
ov - ovule
ow - ovary wall
pa - papillae
pb - peduncular bract
ph - pluricellular hair
ps - pollen sac
s - style
se - seed
sf - staminate flowers
sm - stigma
st - stoma
sy - synstigma
uh - unicellular hair
vt - vascular tissue
w - waxy material
wl - wasp larva

CHAPTER 3

Pollination Biology and Insects

Abstract

The pollination biology and insects in *Ficus capreifolia* Del. (Sub-section: *Sycidium*) was studied (in the Umdloti area [RSA] at about 29^0S and 31^0E). Male and female syconia were produced asynchronously on separate plants. Females of the pollinator wasp emerged from the male syconia (gall figs) carrying pollen in their mesothoracic pockets. Coxal combs were present. Levels of infection of gall flowers varied from 25% to 86%. A single species of a secondary (2^0) sycophile also oviposited in the gall flowers of male syconia. Of the total number of sycophiles in each syconium, there were 70% females of the pollinator, 19,1% males of the pollinator, 8,1% females of the secondary sycophile and 2% males of the secondary sycophile. The ratio of females to males of the pollinator was 3,7:1 and was close to the ratio of the females to the males of the secondary sycophile of 4,0:1. Females of the pollinator wasp and 2^0 sycophile displayed positive responses to light and negative responses to gravity. Wasp entry, pollination, oviposition and emergence were similar to mechanisms described for other pollinator wasps in monoecious and (gyno)dioecious figs.

Key words: *Ficus, Sycidium*, (gyno)dioecious, mesothoracic pockets, coxal combs.

while producing seeds do not produce wasps or pollen. There is functional specialisation with separate figs for the male and female functions, and therefore these plants are referred to as being structurally (gyno)dioecious and functionally dioecious.

Several research workers suggested that each fig species has a single specific wasp as its pollinator (Baker, 1961; Wiebes, 1963 & 1979; Hill, 1967; Ramirez 1970 & 1974, Janzen, 1979; Lloyd & Kjellberg et al, 1987; Bronstein & Mckey, 1989). Wiebes (1979) suggested that this relationship between the fig and wasp is a result of coevolution. Female pollinator wasps have ovipositors which match the lengths of the styles of fig flowers oviposited by them (Condit, 1932; Ramirez, 1970; Storey, 1975 & 1985). Ovipositors are unable to deposit their eggs in flowers with longer styles, and these flowers generally produce seeds. Generally, about half of the styles are longer than the female ovipositors and this does not allow egg-laying in them (Johri & Konar, 1956; Hill, 1967a; Galil & Eisikowitch, 1971; Ramirez, 1974; Janzen, 1979a). Galil (1973a) also proposed that the ovipositing wasp probably needs the stimulus of the flower ovary on the tip of her ovipositor before she releases an egg.

Generally from one to a few agaonids may enter a single syconium. Frequently more than one or sometimes many agaonids may enter a syconium (Pemberton, 1921; Galil & Eisikowitch, 1969c; Ramirez, 1970a; Janzen, 1979c). Janzen

(1979b) reported that when several agaonids enter a syconium then more long-styled flowers are infected. Murray (1985) suggests that this indicates that there is more competition for oviposition sites.

Unihabited and unpollinated syconia are usually aborted while they are still at B phase (Condit,1947; Galil & Eisikowitch 1968c; Ramirez, 1970a). However it has been shown that, in *F. sycomorus*, a parasitic wasp is capable of preventing abortion when it is present in syconia without seeds or the legitimate pollinator (Galil & Eisikowitch 1968a, 1968b & 1969; Galil, Dulberger & Rosen, 1970). Baijnath and Ramcharun (1983) found that a primary sycophile, *Sycophaga cyclostigma* by ovipositing in *F. sur* is able to stimulate normal development of the syconium without the development of seeds. In the absence of males of the pollinator *Ceratosolen capensis*, to construct exit channels, the entire vespid fauna becomes entrapped and dies.

Female wasps may collect and/or carry pollen actively in coxal and/or sternal corbiculae (Galil & Eisikowitch, 1969; Ramirez, 1969; Baijnath & Naicker, 1989), or passively, if pollen is dusted onto their bodies (Ramirez, 1969; Frank, 1984). Considering the short life span of fig-wasps, a problem that troubles most researchers is how agaonids are attracted to and find their way to distant figs (Bronstein, 1989; Kjellberg & Maurice, 1989; Mckey & Kaufman, 1988; Nadel et al, 1992). Factors such as large

MATERIALS AND METHODS

Mature B phase male and female syconia were split and examined with a dissecting microscope. The behaviour of the wasps at this phase were analysed both in the laboratory and in the field. Receptive syconia were placed under a bell jar with pollinator wasps and observed. Early C phase syconia were also split to determine the number of entering wasps, type of wasps in syconia and other characteristics associated with their entry.

Mature D phase male syconia were split and examined under the dissecting microscope. The syconia were analysed to determine the numbers of oviposited or infected flowers and the number of uninfected flowers (bladders). The emerging wasps were collected, killed in 70% alcohol and counted. Insects were also collected by placing mature D phase and ripe syconia into erlenmeyer flasks sealed with fine nylon mesh. At times, syconia and galls had to be opened to expose the insects.

Wasp behaviour was observed by cutting about one-third to half of the mature D phase syconium away (just before wasp release), covering the laterally opened syconium with a coverslip and observing under a dissecting microscope. Mating behaviour, to pair the wasp types, was also observed.

All wasp types collected were air dried, mounted on stubs, gold-coated and observed with a SEM. Characteristics of male and female wasps were recorded.

Ovipositor lengths, of pollinator wasps and secondary sycophiles, were measured and the results compared with floral characteristics obtained in a previous study.

RESULTS/OBSERVATIONS

An examination of early C phase syconia showed that the ostiolar bracts had suffered partial damage due to the entering wasps. Numerous fragments of body parts, such as wings, antennae and even portions of whole insects, were located amongst the ostiolar bracts. In one instance a clearly formed tunnel was located in the ostiolar region alongside the ostiole. This tunnel had an opening many times larger than the ostiolar opening. In almost every B phase and early C phase syconium opened, a single pollinator wasp was located in the syconial cavity. Often the remains of a second, or even a third wasp lay amongst the bracts. In one case an early C phase syconium which aborted showed the presence of 4 pollinators.

Receptive B phase syconia displayed many characteristics including an abundance of pluricellular and unicellular hairs on the syconial wall, loosening of ostiolar bracts, display of red/pink papillae on the stigma and style, presence of synstigma in female syconia, large number of hairs on the inner ostiolar wall and a relatively large syconial cavity. Although male syconia did not produce a distinct synstigma, all the stigmatic surfaces were more or less at the same level in this phase.

Pollinator female wasps alighted on the male syconium and moved towards the ostiole waving their antennae. Once located, the ostiole was penetrated by the wasp by using its scape and head, aided by its legs. It took the wasp over twenty minutes to penetrate the ostiole. Once inside the syconium the wasp settled on the stigma and made darting motions with its abdomen towards the stigma followed later by movements of its forelegs. The wasp also moved around in the syconium. It was difficult to follow the precise actions of the wasp due to the limited space. Furthermore this behaviour was observed only twice in the male syconia due to the limited number of syconia available for this study. The wasp lost its wings and antennae as it entered the syconium.

Two groups of wasps only, identified as the pollinator wasp and a secondary sycophile, were reared in the male syconia. Although over a hundred ripe syconia were opened over a two-year period, no other wasp type was extracted. The male and female wasps of each group were easily separated by observing mating behaviour and confirmed when some syconia were located without any sycophile being present.

The pollinator female wasp was black, about 1,73mm long (range 1,6mm to 1,9mm), had an ovipositor of about 0,61mm long (range 0,4mm to 0,7mm) and two pairs of wings (Table 1). It had a dorsiventrally flattened, hairy head with a pair of well developed, posterolaterally placed compound eyes, and a pair of ten-jointed antennae. Each antenna had an outwardly pointing curved scape near its proximal end. The distal joints of the antennae were very hairy (Fig 1).

Two large lamellated mandibles were found on the ventral surface of the head. Attached to the well defined dorsoventrally flattened pro-, meso- and metathorax were three pairs of legs and two pairs of wings (Figs 1a & 1b). The second pair of legs was very much smaller and reduced when compared to the fore- and hindlegs. Each foreleg had a depression on the coxa (resembling coxal corbiculae) lined by upright bristles forming a coxal comb. A claw-like structure was also found at the tip of the foreleg. The mesothorax which was larger than the other thoracic segments had two well developed, pollen-filled pockets on its ventral surface. These mesothoracic pockets were elongated antero-posteriorly and lined by bristles at the anterior and posterior ends. Denser bristles were present at the anterior end, and the pocket which was deep at the anterior end became very shallow at the posterior end. These pockets were filled with numerous ellipsoidal, smooth pollen grains. The coxal corbiculae were also filled with pollen but in a single layer only (Fig 2). An enlarged flexible abdomen had a pair of ovipositor valves surrounding a relatively short ovipositor (mean 0,61mm). Scattered amongst the fig pollen, in some specimens only, there appeared to be foreign pollen with rough surfaces and markings.

The mean ovipositor lengths of the female of the pollinator (Figs 3a & 3b) were considerably lower than those of the female of the 2^0 sycophile, at 0,61mm to 4,97mm respectively. The female of the pollinator had an

Fig 1(a): SEM view of dorsal surface of female of pollinator of *F. capreifolia*
Bar = 100um

Fig 1(b): SEM view of lateral surface of female of pollinator of *F. capreifolia* showing legs and ovipositor
Bar = 100um

Fig 1(c): SEM view of ventral surface of head of female of pollinator of *F. capreifolia* showing compound eyes, mandibles and antennae
Bar = 100um

Fig 1(d): SEM view of antenna of female of pollinator of *F. capreifolia* showing scape and hairs
Bar = 10um

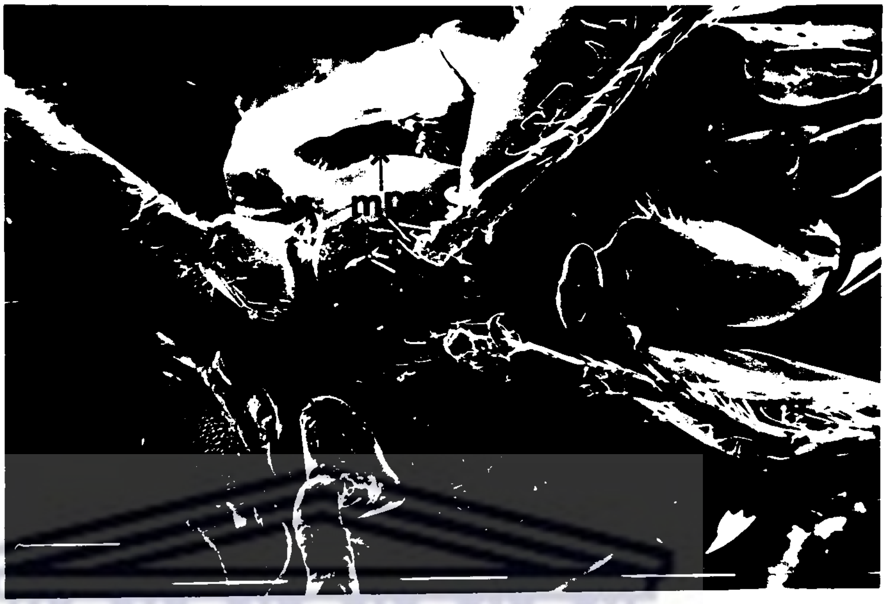


Fig 2(a): SEM view of ventral surface of female of pollinator of *F. capreifolia* showing mesothoracic pockets
Bar = 100um

Fig 2(b): SEM view of ventral surface of female of pollinator of *F. capreifolia* showing coxal combs
Bar = 100um

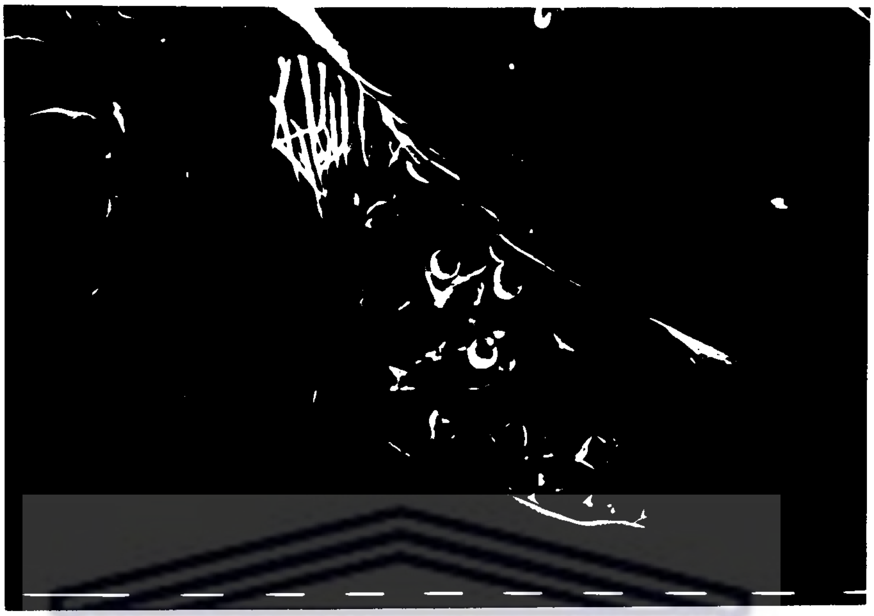


Fig 2(c): SEM view of ventral surface of female of pollinator of *F. capreifolia* showing mesothoracic pocket with pollen, hairs
Bar = 10um

Fig 2(d): SEM view of mesothoracic pocket of female of pollinator of *F. capreifolia* showing pollen
Bar = 10um

ovipositor length less than one-third as long as its body, while the female of the 2^0 sycophile had an ovipositor which is twice as long as its body (Table 1).

Table 1: Mean body lengths (L) and ovipositor lengths (O), in mm, of females of pollinator and secondary (2^0) sycophile of *F. capreifolia* (N = 50)

DIMENSIONS	**POLLINATOR**		**2^0 SYCOPHILE**	
	MEAN	**RANGE**	**MEAN**	**RANGE**
L	1,73	1,6 - 1,9	2,12	1,8 - 2,3
O	0,61	0,4 - 0,7	4,97	4,6 - 5,1
L + O	2,14	1,8 - 2,4	6,89	6,4 - 7,5
RATIO L + O	4,22 : 1		1 : 2,25	

The male pollinator wasp of *F. capreifolia* was brown and wingless. It had a well developed, slightly wedge-shaped, robust body with head, thorax and abdomen. The head was slightly pointed with a pair of antennae reduced to tubercles with just 3 joints, a pair of poorly developed reduced compound eyes and a pair of relatively large, strong mandibles (Fig 4a - d & 5a). The second pair of legs in the male was reduced considerably (Fig 4a), while the first and third pairs had enlarged (powerful-looking) femurs. Claw-like structures appeared at the end of the tarsals of the first and third pair of legs (Fig 5b). A well developed enlarged, highly flexible abdomen curved under the body with the last few segments, which were tapered and retractable (telescopic), forming the solenogaster. The tip of the abdomen may be folded under the body with the tip of the solenogaster being able to

Fig 3(a): SEM view of ventral surface of abdomen of female of pollinator of *F. capreifolia* showing ovipositor
Bar = 100um

Fig 3(b): SEM view of lateral surface of abdomen of female of pollinator of *F. capreifolia* showing ovipositor
Bar = 10um

Fig 4(a): SEM view of dorsal surface of male of pollinator of *F. capreifolia*
Bar = 100um

Fig 4(b): SEM view of ventrolateral surface of male of pollinator of *F. capreifolia* showing abdomen and solenogaster
Bar = 100um

Fig 4(c): SEM view of lateral surface of head of male of pollinattor of *F. capreifolia* showing eye and antennae
Bar = 100um

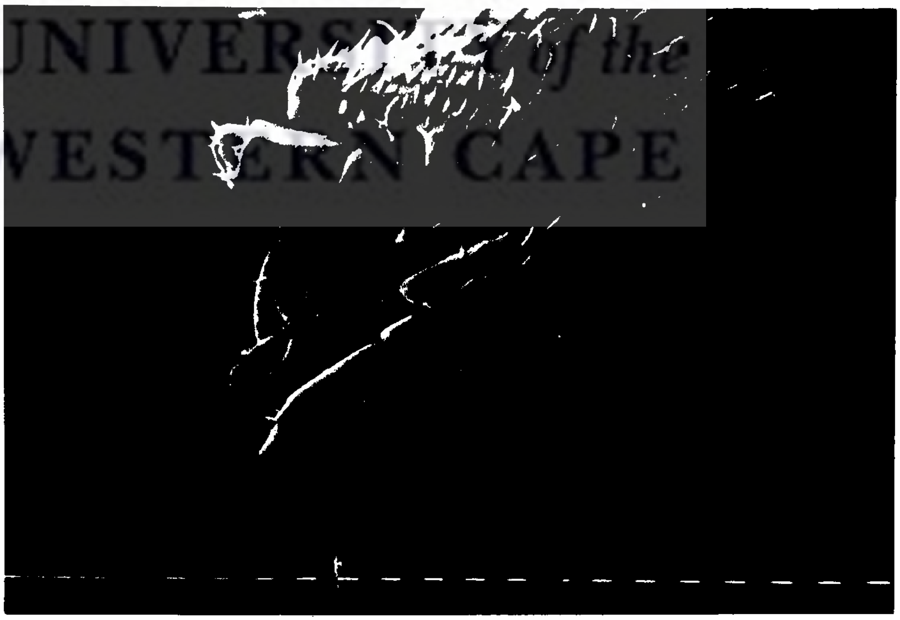


Fig 4(d): SEM view of dorsal surface of head of male of pollinator of *F. capreifolia* showing antennae
Bar = 10um

Fig 5(a): SEM view of ventral surface of head of male of pollinator of *F. capreifolia* showing mandibles
Bar = 10um

Fig 5(b): SEM view of lateral surface of male of pollinator of *F. capreifolia* showing legs
Bar = 100um

extend forwards up to the head and beyond (Fig 4b). The abdomen decreased in size after the copulating activity stops. Fighting was not observed among the male or female pollinator wasps.

The female of the 2^0 sycophile of *F. capreifolia* was brown, had a pair of well developed wings and a narrow elongated body. The head, thorax and abdomen were clearly distinguishable (Fig 6a). The head had a pair of nine jointed antennae and a pair of compound eyes on the dorsal side, and well developed, many-jointed mouth parts on the ventral side. Antennae were covered with thick, long setae and short, thin hairs. Compound eyes were relatively larger and better developed than in the female of the pollinator (Fig 6b). Mandibles were not prominent. Legs were relatively longer than in female pollinators. These wasps were seen to move much faster and were more active (and agile) than the female pollinators. No pollen carrying and pollen were observed on them. The abdomen had a triangular plate on its ventral side and a very long ovipositor extending from its tip (Fig 6a). The female sycophile had a mean body length of 2,12mm (range 1,8 to 2,3mm) and a mean ovipositor length of 4,97mm (range 4,6mm to 5,1mm), with the ovipositor being over two times longer than its body length. This ovipositor was therefore over eight times greater than that of the female pollinator (Table 1).

Fig 6(a): SEM view of lateral surface of female of secondary sycophile of *F. capreifolia* showing legs and antennae
Bar = 100um

Fig 6(b): SEM view of head of female of secondary sycophile of *F. capreifolia* showing antennae eyes and mouth parts
Bar = 100um

The male wasp of the 2^0 sycophile of *F. capreifolia* was brown, wingless, dorsoventrally flattened and wedge-shaped (Fig 7a). Head, thorax and abdomen were clearly defined with a wide head and narrow abdomen. Dorsally on the head there was a pair of 9-jointed antennae with a few hairs and a pair of poorly formed reduced compound eyes (Fig 7c). Ventrally on the head a pair of large, powerful, tooth-like mandibles flanked the other mouth parts (Fig 7b). Three pairs of legs arose from the thorax. The legs were not as large and strong as those of the male pollinator, but they increased in size from the first to the third pair (Fig 7d). An extended solenogaster, as found in the male pollinator, was absent. Some fighting behaviour had been observed between males and between the male and female of the secondary sycophiles.

Table 2: **Mean number of pistillate flowers (P), galls (G), opened galls (OG) unopened galls (UG) and uninfected flowers (UF) in mature male syconia of *F. capreifolia* (N = 20)**

CAT.	**TOTAL**		**RANGE**	**RANGE**
	NUMBER	**%**	**NUMBER**	**PERCENTAGE (%)**
P	1365	100	1253 - 1584	-
G	705,6	51,7	328 - 1360	25,2 - 85,9
OG	477,8	35,0	240 - 984	18,5 - 62,1
UG	227,8	16,7	88 - 376	6,8 - 23,7
UF	659,4	48,3	224 - 972	14,1 - 74,8
DIAM. (mm)	**MEAN**	20,5	**RANGE** 17,4 - 25,0	-

Mature D phase male syconia which had released most of their wasp progeny were analysed for the number of galls (opened & unopened), number of opened galls and the number of unopened galls (Table 2).

The figures in Table 2 do not include the pistillate flowers which remained uninfected/unoviposited. Levels of oviposition may differ with 328 galls only in a syconium of diameter 19,7mm up to 1360 galls for a syconium of diameter 25,0mm. However the smallest mature syconium of the sample, at 17,4mm diameter had 501 galls. Ripe syconia examined in the field showed the presence of many unopened galls and these syconia fell to the ground and were quickly infected by fungi, as they slowly decayed. In this study 51,7% of the flowers were infected. In another study 60,9% of the pistillate flowers were infected.

Of a mean of 1365 pistillate flowers, 705,6 (51,7%) produced galls. Of the infected galls, only 227,8 (16,7%) remained unopened when ripe. Uninfected flowers ranged from 224 to 972 (14,1% to 74,8%).

Table 3: Mean numbers of males (MP) and females (FP) of the pollinator wasp, and males (MS) and females (FS) of the 2^0 sycophile of *F. capreifolia* (N = 20)

WASP	TOTAL	%	RANGE
FP	390,8	70,8	333 - 435
MP	105,5	19,1	84 - 123
FP + MP	496,3	89,9	495 - 682
FS	44,8	8,1	14 - 98
MS	11,3	2,0	4 - 26
FS + MS	56,1	10,1	18 - 12

Fig 7(a): SEM view of dorsal surface of male of secondary sycophile of *F. capreifolia*
Bar = 100um

Fig 7(b): SEM view of ventral surface of head of male of secondary sycophile of *F. capreifolia* showing mandibles
Bar = 10um

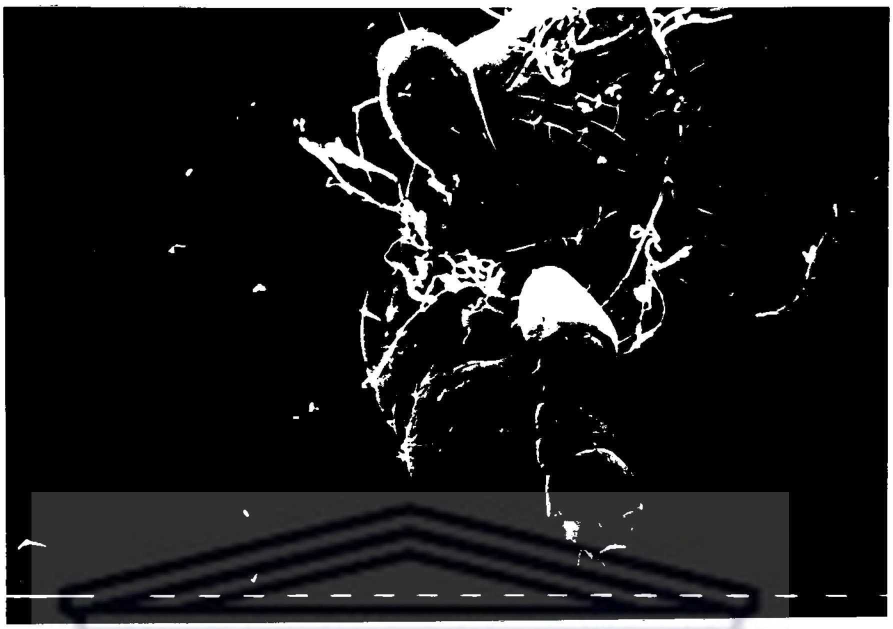


Fig 7(c): SEM view of dorsal surface of head of male of secondary sycophile of *F. capreifolia* showing antennae
Bar = 10um

Fig 7(d): SEM view of ventral surface of male of secondary sycophile of *F. capreifolia* showing legs
Bar = 100um

The number of wasps (female and male pollinators, female and male secondary sycophiles) that emerged from male syconia were analysed (Table 3).

The figures above (Table 3) were for the wasps released from their galls, and collected in flasks, before total ripening of the syconia which had 2^0 sycophiles with distinct marks on their walls. Syconia without 2^0 sycophiles did not have marks on their walls, and further these syconia did not produce more pollinator wasps. In a syconium without 2^0 sycophiles there were *ca*. 318 galls made up of 217 (68,2%) female pollinators and 101 (31,8%) male pollinators. The syconium which had the highest number of 2^0 sycophiles, 98 females and 26 males, also had the highest number of pollinator wasps, with 435 females and 123 males. However the ratio of pollinator wasps to 2^0 sycophiles was reduced from the overall mean of 8,8:1 to 4,5:1 in this syconium. The ratio of female to male pollinators of 3,7:1 was close to the ratio of female to male 2^0 sycophiles of 4,0:1. About 89,9% of the galls were occupied by the pollinators with 10,1% used by 2^0 sycophiles.

Mature D phase male syconia were examined under the dissecting microscope just before wasp release. A portion of the lateral wall was cut away and covered with a coverslip to facilitate viewing of the internal cavity. Male pollinator wasps emerged first after biting through the wall of the ovary with their mandibles. Their first pair of legs were then pushed through the opening over the edges and used to slowly lever the body out of the gall. When an emerging male encountered another wasp (male or female) at its entrance, it quickly withdrew and retreated a bit. It restarted its activity a little later, using its mandibles to bite the edges, widening the hole, before emerging. It took a male wasp from 10 to 20 minutes to emerge fully, and this appeared to be quite an effort for the male wasp. The male pollinator wasp immediately moved in and around amongst the galls, apparently searching out (using its antennae to probe) galls containing female pollinator wasps. Within a short time activity in many more galls was observed and several more male pollinator wasps emerged. As soon as a female was located the male bit an opening near the apex of the female gall, and then inserted its solenogaster through the opening and apparently mated with the female. This act of copulation lasted a short time (few seconds) and the males then departed. The males were observed visiting a few more galls before they appeared to slow down, weaken and even fall between the galls. While in the syconium, the males were fairly active using their strong legs to crawl and even jump (leap) from one gall to another. A few males made their way towards the ostiolar opening and moved through towards the outside and tumbled out onto or off the surface of the syconium.

Female pollinator wasps then pushed their way out through the openings made by the male wasps at the apices of the galls. Females, like the males, used their legs to lever themselves out of the galls. Females also used their mandibles to bite and widen the opening of the gall. The female pollinator wasps immediately crawled over the galls (and males) and moved towards the staminate flowers. They paused at the anthers, seemed to probe with their antennae, moved over the anthers and used their forelegs in swiping/scraping-type movements. Each time the scraping movement was followed by the foreleg disappearing under the body for a while before re-emerging to repeat the sequence. Thereafter, the female wasp spent some time in an elaborate cleansing ritual. It used its foreleg mainly to go over its dorsal body surface, mainly thorax, wings and head. The wasp then made its way towards the ostiolar bracts and proceeded to work its way slowly out through the ostiole and out into the open. Once outside it settled on the syconial surface and once again carried out the cleaning ritual before spreading its wings. In a few moments thereafter it appeared to spread itself, dry up and fly off.

Unopened mature syconia were also examined and observed while in the erlenmeyer flasks. Within a short time (less than a day to a few days), wasp emergence was observed through the ostiole that opened naturally. Often wasp emergence started at night and then continued through the following day or two. Usually wasp emergence started slowly with a few wasps in the first few hours, followed by an acceleration, with peak emergences after about 4 to

6 hours. A few male pollinator wasps emerged first through the ostiole, and this was followed by either the female 2^0 sycophile or the female pollinator. In a few examples the female pollinators only emerged several hours after the female 2^0 sycophiles. In the beginning a female pollinator emerged every 4 to 5 minutes, later every 2 minutes and then every 20 to 30 seconds. Male 2^0 sycophiles remained in the syconial cavity and were not found on the outside when some male pollinators emerged.

In another syconium after *ca*. 2 days the ostiole opened and *ca*. 22 male pollinator wasps and only about 4 female pollinators emerged in over 16 hours. Thereafter, even though the ostiole was physically widened, no more wasps emerged. However, immediately after splitting the syconium, many female pollinators emerged within two hours. By 6 hours there were over 200 wasps in the flask.

An interesting observation concerns the way in which the wasp behaved in the erlenmeyer flasks. When the flask was upright, there was an immediate and rapid movement by almost all the female wasps to crawl up the sides of the glass towards the opening of the flask. Female pollinator wasps even attempted to crawl through the fine openings of the nylon mesh. In many cases their heads became trapped in the nylon mesh. The flask was manipulated to determine whether the wasps were reacting to air at the opening. When the flask was turned over, the wasps immediately moved upwards again towards the broad part of the flask which was facing upwards. Similarly when the flask was lowered on its side the wasps moved away from the base or the neck of the flask to the highest point in the flask. It was also noted that while they instinctively moved upwards, they also tended to aggregate on the side facing the light (artificial or natural). Male wasps did not show any reaction to light.

The male of the pollinators and 2^0 sycophiles lived for only a few hours to a day. Female pollinator wasps lived for 2 to 4 days. Female 2^0 sycophiles lived the longest, remaining viable for *ca.* 4 to 7 days.

In another syconium opened, and placed in a flask before examining under a dissecting microscope, several worm-like larvae were located amongst the flowers. These small (*ca.* 1mm), whitish larvae were transformed into pupae after 3 to 4 days. Pupae appeared brown and *ca.* 2mm long. About 12 days later young fruit flies emerged from the pupae. Caterpillars were also located in one instance between the ostiolar bracts.

DISCUSSION

Wings, antennae and other parts of whole wasp were found amongst the bracts. During the B phase, the ostiolar bracts of *F. asperifolia*, a (gyno)dioecious fig, separated due to a loss of turgor (Verkerke, 1987). Although this facilitated the entry of the pollinator wasps, the ostiolar opening remained small and research on monoecious figs indicated that wasps may lose wings (Verkerke, 1989), wings and antennal flagellae (Baijnath and Ramcharun, 1983) or whole wasps may be trapped in the tunnel (Baijnath and Ramcharun, 1983; Hill, 1967). While mostly one or two wasps may enter most syconia studied, many more wasps may attempt entry, sometimes successfully (Baijnath & Ramcharun, 1983; Bronstein, 1986 & 1988; Ramirez, 1988; Verkerke, 1989; Berg, 1990). Some mechanism may operate, possibly tactile (or even chemical) which may cause the ostiolar bracts to close quickly once one or two wasps had entered. This rapid closure of the opening may result in other wasps being trapped amongst the bracts. However this area needs further investigation.

The characteristics of the B phase receptive syconia, including the presence of glandular hairs on the syconial walls and the papillae of the stigmatic surfaces, possibly provide olfactory signals to the female pollinators. This assumption is supported by the presence of well developed, hairy antennae. Many researchers, working on monoecious figs, have postulated that the hairs on the syconia may be glandular, secreting a specific attractant to attract the female pollinator wasps, which have well developed antennae (Baijnath & Ramcharun, 1981; Barker, 1985; Baijnath & Naicker, 1989; Bronstein, 1989; Janzen, 1989).

Ramirez (1987) suggested that the cleptoparasitic wasp only oviposits in the fig flowers (through the wall of the syconium) containing a female agaonid larva and not in the pollinated female flowers, so that they may feed on the gall tissue. Furthermore, these cleptoparasitic wasps do not oviposit in seed flowers of the (gyno)dioecious figs, indicating once again that there may be some instinctive behavioural pattern or chemical indication for the wasps to avoid the seed figs/flowers. According to Ramirez (1987) the cleptoparasites would need gall tissue to survive. Therefore even if they did enter seed syconia there may be no benefits for them and they would probably die. Verkerke (1987) suggested that the presence of the pollen pocket may ensure only pollination of the oviposited gall flowers, as the production of seeds in unoviposited flowers might strongly compete for space within the syconium. The cleansing behaviour displayed by wasps leaving the syconia, after collecting pollen, may be an instinctive behaviour which enabled them to avoid accidental pollination of the unoviposited pistillate flowers. It is therefore suggested that the absence of the synstigma in the gall flowers may also be necessary to ensure that wasps deliberately pollinate each oviposited gall flower. Therefore ethodynamic pollination of the more

advanced figs, especially the dioecious figs, not only exerted greater control over the acts of pollination and oviposition, but also increased the chances of survival of the wasp larvae. The shallow posterior end (shaped like a ramp) of the mesothoracic pocket would make it easier for the removal of pollen (possibly by a slight shovelling action of the foreleg) from the pocket and its transfer to the stigma during (or just after) oviposition by the pollinator wasp.

Naicker (1984) described in detail the mechanism by which *Platyscapa soraria* wasps may enter the syconia of *F. ingens*. Galil (1977) suggested a 1:1 relationship between *Ficus* spp and its pollinators. Both Verkerke (1989) and Naicker (1984) suggested that the shape of the ostiole may account for the entrance of a particular pollinator with a specific head structure and shape. These ideas concur with the findings in this study.

The pollinator wasp is a primary sycophilic symbiotic wasp and is suitably adapted for pollination and oviposition. A small head and narrow elongated body allowed the wasp to enter the syconium via the narrow ostiole easily. The shape and location of the scape made it a suitable appendage to push aside the ostiolar bracts before the introduction of the head. Serrated mandibles facilitated gripping of the bracts as the wasp forced its way through the bracts. Jointed, highly flexible legs provided leverage and thrust as the wasp entered the narrow tunnel.

The antennal hairs could be receptive to stimuli as the wasp made its way from its natal syconium to a receptive syconium. The location of the antennae and the forward pointing hairs made it difficult for the jointed antennae to survive the forceful entry necessary, and therefore break off.

Only two wasp species were located in these syconia, the pollinator and a secondary sycophile. This may be due to *F. capreifolia* growing at the margin of its range in this study area (Verulam, RSA - 29^0 38'S). Bronstein (1989) stated that although figs may persist in marginal habitats, they do not reproduce well there due to rare migration and frequent extinction of its pollinators. Secondary sycophiles only oviposit in flowers already oviposited by female agaonids. Therefore it is possible that as this plant appeared to be just establishing itself in this habitat also, more wasp types have not had sufficient time to reach these locations. Hill (1967) estimated that most *Ficus* spp. reach reproductive maturity in 10 to 20 years. The introduction of these plants in this area may be flood related or they could have been dispersed by birds. Major flooding occurred in 1977, 1984 and 1987 in large parts of Natal and the study area. Two of these plants have been located in a swamp and a bank established by the flood waters of 1977 and 1984. *Ficus capreifolia* may have entered this area between 9 to 15 years ago.

Ramirez (1974) and Gordh (1975) suggested that cleptoparasites may also be specific. Bronstein (1991) showed that torymid captures at *F. pertusa* are as species-specific as pollinator captures. Galil and Eisikowitch (1968b) also reported the presence of only one 2^0 sycophile, *Apocrypta longitarsus*, in *F. sycomorus*.

Coxal corbiculae and mesothoracic pockets located on the ventral surface of the body of the pollinator wasps were involved in active (ethodynamic) loading and carrying of pollen, and the deliberate pollination of *F. capreifolia*. The shallow coxal corbiculae may suggest that only a limited amount of pollen was carried in the coxa, and the greater amount was carried and stored in the deeper part of the mesothoracic pockets. Bristles/setae may have reduced the loss of pollen during the movements of the wasp. The shape of the mesothoracic pockets made it easier for the tips of the forelegs to slide into and out of them during loading and unloading of pollen. Claw-like structures at the tips of the forelegs may have helped in scooping out pollen grains from the pollen sacs and corbiculae. Some pollen grains adhered to the body surface, suggesting that these grains may have been slightly sticky, which may also account for the fact that the grains did not fall out of the pockets. This also made it necessary for the cleansing behaviour of the wasps to remove the pollen from its body surface. The presence of these corbiculae was first reported by Galil and Eisikowitch (1969a) and Ramirez (1969).

In *F. capreifolia* gall figs, the short-styled pistillate flowers had style lengths varying from 0,4mm to 0,7mm with a mean of 0,55mm in B phase and 0,67mm in D phase. The mean ovipositor lengths of 0,61mm, varying from 0,4mm to 0,7mm, of the pollinator wasp were slightly larger than the mean style lengths of the short-styled flowers. The range of ovipositor lengths corresponded with the range of style lengths. This clearly indicated that most pollinator wasps could easily oviposit in the short-styled flowers. In seed figs, long-styled flowers had style lengths varying from 0,9mm to 2,0mm, with a mean length of 1,18mm (in long-pedicelled), 1,34mm (in short-pedicelled) and 1,71mm (in sessile) in pistillate flowers. These style lengths all exceeded the ovipositor lengths of the pollinator wasps and would have therefore been impossible for oviposition to occur. Furthermore, it is generally accepted that the egg was laid between the nucellus and the inner integument and therefore the ovipositor must be able to place the egg in this position. Even an ovipositor which was fractionally short would find it almost impossible to accomplish its task successfully. Naicker (1984) reported that in *F. ingens*, style lengths vary from 0,44mm to 2,0mm while the ovipositor lengths of the pollinator wasps ranged from 0,6mm to 1,2mm, making a range of possibilities from accessible to inaccessible. Compton and Nefdt (1990) suggested that in *F. burtt-davyi*, 83% of the ovules could be easily reached by the ovipositors of the pollinator wasp, *Elizabethiella baijnathi*. Baijnath and Ramcharun (1983) reported that a percentage of the ovaries in *F. capensis* remain beyond the reach of the ovipositors of the primary sycophiles (mainly pollinator wasps). Verkerke (1986 & 1987) suggested that style width and style firmness may be more significant than style length in preventing pollinator wasps from ovipositing in certain flowers. If this idea were to be accepted one would have to seriously question the need for the seed figs having developed distinctly longer styles. However this study clearly indicated that style length was a significant factor in determining whether a flower receives an egg or not. Style firmness may have facilitated the process by providing a suitable platform for the wasp to accomplish its task of oviposition and pollination.

While the male pollinator wasp had a clearly sclerotized head with well developed mandibles, they have not been used for fighting. Instead the mandibles were strong enough to enable the wasp to bite its way out of its natal gall. Both their eyes and antennae had been reduced because these wasps carry out their activities in a small, restricted, dark environment. The short antennae may have been adequate to enable them to locate the female galls for copulation. The highly flexible, elongated abdomen ending in a solenogaster was well adapted for copulation. Murray (1990) suggested that the large abdomen may be used for the storage of sperms. The abdomen decreased in size after completion of copulation because of the depletion of the stored sperms.

In the female of the 2^0 sycophile, the 9-jointed antennae, with well developed hairs, and well developed compound eyes accounted for its ability to move more rapidly than the female pollinator wasps. These wasps also lived much longer outside the syconium and there was a need for well developed sense organs. Their antennae had two types of hairs, long and short types, while the female pollinators had a single type only. It is possible that some sort of functional specialisation may exist because of this difference. Mature B-phase syconia were usually between 8,0mm to 10,0mm in diameter while the ovipositor lengths of these 2^0 sycophiles varied from 4,6mm to 5,1mm with a mean of 4,97mm. Most syconia could therefore be easily penetrated via the wall and most ovaries would be easily accessible.

Males of the 2^0 sycophile had more flattened bodies than males of the pollinator wasp. Their mandibles were better developed also and this may account for the fighting behaviour observed occasionally. Frank (1987) reported that wingless, parasitic males frequently use their dangerous mandibles in fighting, while the wingless agaonids have harmless mandibles and never seem to fight. Joseph (1958) and Hamilton (1979) also reported similar observations. Ramirez (1970) noted aggression between females during oviposition.

There was no relationship between size of the syconium and the number of galls present. Male syconia had an average of 1365 pistillate flowers with a range of 1253 to 1584. While the average infection lies above 50%, it ranged from a low of 25,2% to a high of 85,9%. While this indicated that the pollinator wasps were capable of infecting most of the pistillate flowers, this may not have possibly occurred because of the number of eggs available, pollinator viability, flower receptivity and maturity, timing of oviposition, viability of eggs, number of pollinators entered, level of infection by parasites, climatic and environmental conditions, amongst others. All these factors above may be affected by their own circumstances also, such as, adequate fertilisation of females by males, time elapsed between emergence of females and location of receptive syconium, or other related events. Murray (1985) stated that the number of eggs produced is related to the size of the insects and size of the syconia. Many fig researchers reported that female agaonids produce between 100 to 400 eggs (Abdurahiman & Joseph, 1976; Grandi, 1961; Michaloud et al, 1985; Murray, 1985; Pemberton, 1921). Newton and Lomo (1979) suggested that in *F. lutea* one wasp may lay eggs in about 50% of the flowers.

From the earlier discussion, we see that the level of infection of pistillate flowers depended on many factors. The presence of 2^0 sycophiles could also influence the ratio of pollinator and parasitic wasps produced. Although the infection of flowers by parasites increased, the number of pollinator wasps did not decrease. Instead the ratio did decrease from 8,8:1 to 4,5:1. Secondary sycophiles are regarded as parasites because they only oviposit in galls occcupied by agaonid larvae and feed on them. This would imply that syconia having a larger number of agaonid larvae could be a home for a larger number of 2^0 sycophiles, with the ratio being reduced as a result.

In *F. capreifolia*, the average ratio of female to male of the pollinator of 3,7:1 represented a range of 22-47 male pollinators per 100 females. Joseph (1984) reported that for most species there are equal numbers of males and females. Naicker (1984) recorded 16-56 males per 100 females of *P. soraria* (in *F. ingens*), Joseph (1984) recorded 9-18 males per 100 females in *B. psenes* (in *F. carica*) and Galil and Eisikowitch recorded 20-78 males per 100 females of *B. quadraticeps* (in *F. religiosa*). Nair and Abdurahiman (1984) recorded 25-40 males per 100 females in *F. exasperata*, Abdurahiman and Joseph (1976) recorded 30-40 males per 100 females in *F. hispida* and Ibrahim (1985) recorded 10-25 males per 100 females in *F. carica*. *Ficus carica*, *F. hispida* and *F. exasperata* are (gyno)dioecious members. While there is a wide variation in possible numbers, in *F. capreifolia* an average of 27 males per 100 females may signal a bias towards the rearing of female pollinators to improve the chances of pollination and oviposition. Galil and Eisikowitch (1971) suggested that the ratio of male to female is sufficient to ensure fecundation of females. Herre (1987) postulated that the wasps had the ability to alter brood sex ratios in response to different local mate competition situations. Bronstein (1986 & 1988) suggested that syconia entered early tend to have many more foundresses. Galil and Eisikowitch (1971) found that the inhabitation of figs such as *F. religiosa* by pollenless females results in many dead female larvae in the syconia, which causes an increase in the male to female ratio from 0,4 to 3,9 males to each female. Galil (1990) suggested that this clearly indicates a shortage of food in these ovaries. A ratio of 31 males to 100 females was recorded in a syconium without 2^0 sycophiles in *F. capreifolia*. Michaloud et al (1985) showed that when more females colonize syconia then sex ratios rise in favour of males.

Female sycophiles, with a range of 14-98 wasp offspring per syconium, had an infection rate of about 8%, range from 21-29 males per 100 females in *F. capreifolia* (ratio 4 female to each male). Male 2^0 sycophiles constituted about 2% of the wasp population. Infection by 2^0 sycophiles ranged from 0% to 18%. Bronstein (1988b) found that in *F. pertusa* crops, parasites comprise 52% of all wasps reared. Joseph (1984) reported 50-75 males per 100 females for parasitic wasps. It is possible that the lower male to female ratio in *F. capreifolia* was a further indication of problems experienced at this marginal habitat or even a shortage of food for the larvae.

The retreat within the gall of the male agaonid when encountering another male wasp showed its non-aggressive nature. The emergence of the male agaonid from its gall by biting an opening with its mandibles, its seeking out of females and mating behaviour after biting an opening at the apex of the female gall was similar to the descriptions presented in papers by Baijnath and Ramcharun (1983), Baijnath and Naicker (1989) and Murray (1990). Male pollinator wasps instinctively moved towards the ostiole, and some emerged through to the outside. This act may have helped to change the composition of air within the syconium, by reducing the CO_2 levels (Ramirez, 1987). Ramirez (1987) suggested that this change causes the release of the female agaonids. Whether female pollinator wasps moved instinctively towards the anthers or were attracted by scents is an area that needs further research. Pollen loading into their coxal corbiculae and mesothoracic pockets was similar to descriptions of earlier workers (Galil et al, 1973; Galil, 1973a; Galil & Eisikowitch, 1969b & 1974; Galil & Snitzer-Pasternak, 1970; Naicker, 1984).

Male pollinator wasps emerged before female pollinator wasps as they had well developed mandibles to bite their way out of their natal galls and also later assist the females by biting an opening in the female galls for them to emerge more easily. Furthermore, since the males were wingless and less agile than the females, it was easier for them to mate with the females while the females were still in their galls. This setup increased the chances of fertilisation. Bronstein (1991) found that in a few unpollinated and pollinated syconia lacking male agaonids, mature wasps die in the sealed syconium. Galil and Eisikowitch (1968) and Hamilton (1979) noted that generally non-pollinators do not assist in constructing the exit passage. The role of the male agaonid was therefore crucial to the emergence of both the female pollinator (agaonid) and the female 2^0 sycophile (torymid). In the absence of the male agaonid, both female pollinators and 2^0 sycophiles may have become trapped and died within the syconium. Galil and Eisikowitch (1965 & 1968) and Joseph and Abdurahiman (1978) reported that male agaonids cut holes through the syconial wall to the outside. This has also been reported subsequently by Baijnath and Ramcharun (1983), Verkerke (1986) and Baijnath and Naicker (1989) among others. Verkerke (1987), working with the (gyno)dioecious fig *F. asperifolia*, noted that there are no holes cut and the males emerge via the opening formed when the ostiolar bracts loosen. It was suggested that generally in monoecious figs exit holes were cut in the syconium wall because the ostiolar bracts did not loosen. This may have been necessary to avoid the dessication and/or infection of the seeds if the bracts had loosened. The hole could have been sealed by the fig once the wasps had departed. In the (gyno)dioecious figs, since seed figs and gall figs existed separately this safeguard may not have been necessary and the ostiolar bracts of the gall fig could have loosened for wasp emergence. Of significance is the fact that the ostiolar bracts of the seed fig did not loosen in the ripening process. They remained firmly closed, having opened only in the B phase. Seed figs did not harbour any wasps, only seeds, and therefore their ostiolar bracts remained firmly closed as their seeds matured and ripened.

Both the females of the pollinator wasp and the 2^0 sycophile reacted negatively to gravity and positively to light. This instinctive behaviour ensured that the wasp moved towards the ostiolar region to facilitate emergence and improved the chances of pollen collection, wasp emergence and survival. Ripe figs faced upwards with their ostioles pointing towards the sun and this accounted for the above reactions of the females of the pollinator and the 2^0 sycophile to light and gravity.

Male wasps had very short life spans because of their limited functions. The act of biting through the walls of their natal galls and the wall of the female gall, copulation and their struggle through the ostiole were probably energy consuming acts, and therefore with no further purpose they died. Females of the pollinator wasp lived longer in order to accomplish the tasks of location of receptive syconia, pollination and oviposition. Due to their inability to feed, they could have only survived a few days. Females of the 2^0 sycophile lived longer probably because they oviposited only after the agaonids and could only complete their life cycles after the female pollinators. Nair and Abdurahiman (1984) and Janzen (1979) have suggested that wild wasps (wasps free in envioroment) may live for up to 30 days. Berg (1990) noted that in captivity wasps may live for a few days. Ramirez (1988) noted that agaonid females have a lifespan of less than 3 days. Joseph (1958) cited a longevity of 2-3 days for *B. psenes*, while Grandi (1920) kept several for 4-5 days. Bronstein (1989) however suggested that their lifespan is shorter in the wild.

The syconium also acted as a suitable microhabitat for not only wasps, but also fruit flies, butterflies, fungi and ants. Several workers have reported a variety of insects and other organisms associated with ripening figs (Compton & Disney, 1991; Nadel,Frank & Knight, 1991). Lachaise (1977) and Lachaise, Tsacas and Couturier (1982) noted the presence of drosophilid flies associated with tropical figs.

BIBLIOGRAPHY

Abdurahiman,U.C. and Joseph,K.J.,1976. Observations on the biology and behaviour of *Ceratosolen marchali* Mayr (Agaonidae, Chalcidoidea, Hymenoptera). *Entemon* 1: 115-121.

Baijnath,H.,and Naicker,S.,1989. Developmental anatomy of *Ficus ingens* syconia in relation to its wasp faunula. *S.Afr.J.Bot*. 55(4): 409-421.

Baijnath,H., Naicker,S.,and Ramcharun,S.,1986. The interaction of figs and fig wasps. *In*: Insects and the Plant Surface, pp. 348- 49. Eds. B.E.S. Juniper and T.R.E. Southwood. Edward Arnold Ltd., London.

Baijnath,H.,and Ramcharun,S.,1981. Microscopic observations of the ostiolar bracts in some South African examples of the genus *Ficus* L.(Moraceae). *Proc.Electron micr.Soc.S.Afr*. 11: 135-136.

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

Baker,H.G.,1961. *Ficus* and *Blastophaga*. Evolution 15: 378-379.

Barker,N.P.,1985. Evidence of a volatile attractant in *Ficus ingens* (Moraceae). *Bothalia* 15: 607-611.

Berg,C.C.,1989. Classification and distribution of *Ficus*. *Experientia* 45: 605-611.

Berg,C.C.,1990. Reproduction and Evolution in *Ficus* (Moraceae):Traits connected with the adequate rearing of pollinators. *Memoirs of New York Botanical Garden*, 55: 167-185.

Bronstein,J.L.,1986. Coevolution and constraints in a neotropical fig-pollinator wasp mutualism. Ph.D. Dissertation. Univ.of Michigan. Ann Arbor, USA.

Bronstein,J.L.,1988a. Fruit production in a monoecious fig: consequences of an obligate mutualism. *Ecology* 69: 207-214.

Bronstein,J.L.,1988b. Mutualism, antagonism and the fig-pollinator interaction. *Ecology* 69: 1298-1302.

Bronstein,J.L.,1989. A mutualism at the edge of its range. *Experientia* 45: 622-637.

Bronstein,J.L.,1991. The non-pollinating wasp fauna of *Ficus pertusa*: exploitation of a mutualism? *Oikos* 61: 175- 186.

Bronstein,J.L., and Mckey,D.,editors.1989. The comparative biology of figs. *Experientia* 45: 601-680.

Boucek,Z., Watsham,A., and Wiebes,J.T.,1981. The fig wasp fauna of the receptacles of *Ficus thonningii* (Hymenoptera, Chalcidoidea). *Tijdschr.Ent.* 124: 149-233.

Compton,S.G., and Disney,R.H.L.,1991. New species of *Megaselia* (Diptera: Phoridae) whose larvae live in fig syconia (Urticales: Moraceae), and adults prey on fig wasps (Hymenoptera: Agaonidae). *Journal of Natural History*,25: 203-219.

Compton,S.G., and Nefdt,R.J.C.,1990. The figs and fig-wasps of *Ficus burtt-davyi*. *Proc.aetfat,sym.IV, Hamburg*, 23a: 441-450.

Condit,I.J.,1932. The structure and development of Flowers in *Ficus carica* L. *Hilgardia* 6: 443-481.

Corlett,R.T.,1987. The phenology of *Ficus fistulosa* in Singapore. *Biotropica* 19: 122-124.

Frank,S.A.,1983. Theoretical and Empirical Studies of Sex Ratios, Mainly in Fig Wasps. Master's Thesis, University of Florida, Gainesville.

Frank,S.A.,1984. The behaviour and morphology of the fig wasps *Pegoscapus assuetus* and *P.jimenezi*: descriptions and suggested behavioural characters for phylogenetic studies. *Psyche* 91: 289-308.

Frank,S.A.,1987. Weapons and Fighting in Fig Wasps. *Tree,vol 2*, no.9: 259-260.

Galil,J.,1973. Pollination in dioecious figs: pollination of *F. fistulosa* by *Ceratosolen hewitti*. *Gdn.Bull. Singapore* 26: 303-311.

Galil,J., Dulberger, R.,and Rosen, D.,1970. The effects of *Sycophaga sycomori* L. on the structure and development of the syconia in *F. sycomorus* L. *New Phytologist*, 69: 103-111.

Galil,J., and Eisikowitch,D.,1965. Pollination of flowers in *Ficus religiosa* L. *Tera Ve Aretz*. 1: 1-16.

Galil,J., and Eisikowitch,D.,1968(a). On the pollination ecology of *Ficus sycomorus* in East Africa. *Ecology* 49: 259-269.

Galil,J., and Eisikowitch,D.,1968(b). Flowering cycles and fruit types in *Ficus sycomorus* in Israel. *New Phytol.* 67: 745-758.

Galil,J., and Eisikowitch,D.,1968(c). On the pollination ecology of *Ficus religiosa* in Israel. *Phytomorphology* 18: 356-363.

Galil,J., and Eisikowitch,D.,1969. Further studies on the pollination ecology of *Ficus sycomorus* L. (Hymenoptera, Chalcidoidea, Agaonidae). *Tijdschr. Entomol*. 112 (1): 1-13.

Galil,J., and Eisikowitch,D.,1971. Studies on mutualistic symbiosis between syconia and sycophilous wasps in monoecious figs. *New Phytol*.70: 773-783.

Galil,J., and Neeman,G.,1977. Pollen transfer and pollination in the common fig (*Ficus carica* L.). *New Phytol*. 79: 163-171.

Galil,J., and Snitzer-Pasternak,Y.,1970. Pollination in *Ficus religiosa* L. as connected with the structure and mode of action of the pollen pockets of *Blastophaga quadraticeps* Mayr. *New Phytol*. 69: 775-784.

Galil,J., Zeroni,M., and Bar Shalom D.,1973. Carbon dioxide and ethylene effects in the co-ordination between the pollinator *Blastophaga quadraticeps* and the syconium in *Ficus religiosa*. *New Phytol*. 72: 1113-1127.

Godfray,H.C.J.,1988. Virginity in haplodiploid populations: a study on fig wasps. *Ecol.Ent*. 13: 283-291.

Gordh,G., 1975. The comparative external morphology and systematics of the neotropical parasitic fig wasps genus *Idarmes* (Hymenoptera: Torymidae). *Univ.Kansas Sci. Bull.*, 50: 389-455.

Grandi,G.,1920. Studio morfologico e biologico della *Blastophaga psenes* (L.) *Boll.Lab.Zool.Portici* 14: 63-204.

Grandi,G.,1961. The hymenopterous insects of the superfamily Chalcidoidea developing within the receptacles of the figs. Their life history, symbiosis and morphological adaptations. *Boll.Inst.Entomol. Univ.Bologna*, 26:1-13.

Hamilton,W.D.,1979. Wingless and fighting males in fig wasps and other insects, p.168-220. *In* Reproduction, Competition and Selection of Insects. M.S. Blum [ed.]. New York: Academic Press.

Herre,E.A.,1987.Optimality, plasticity,and selective regime in fig wasp sex ratios. *Nature* 329: 627-629.

Hill,D.S.,1967. Figs of Hong Kong. Hong Kong University Press.

Ibrahim,M.,1985. Contribution a une approche evolutive de la symbiose entre *Ficus carica* L. et *Blastophaga psenes* L. Thesis Montpellier.

Janzen,D.H.,1979a. How many babies do figs pay for babies? *Biotropica*, 11: 48-50.

Janzen,D.H.1979b. How to be a fig. *A.Rev.Ecol.Syst.*10: 13-51.

Janzen,D.H.,1979c. How many parents do the wasps from a fig have? *Biotropica*, 11: 127-129.

Johri,B.M. and Konar,R.N. 1956. The floral morphology and embryology of *Ficus religiosa* Linn. *Phytomorphology* 6: 97-111.

Joseph,K.J.,1958. The biology of *Philotrypesis caricae* L.;Parasite of *Blastophaga psenes* L. (Chalcidoidea). *Proc. XV Int. Cong.Zool.* 21: 662-664.

Joseph,K.J.,1984. The productive strategies in fig wasps (Chalcidoidea: Hymenoptera), a review. *Proc. Indian Natn.Sci.Acad.*, (B) 50: 449-460.

Joseph,K.J., and Abdurahiman,U.C.,1978. Oviposition behaviour of *Ceratosolen fusciceps* Mayr. (Agaonidae: Hymenoptera) and the mechanism of pollination in *Ficus racemosa* L. *J.Bombay Nat. Hist.Soc.* 78: 287-289.

Kuttamathiathu,J.,1958. Recherches sur les chalcidiens, *Blastophaga psenes* (L.) et *Philotrypesis caricae* (L.), du Figuier (*Ficus carica* L.)- *Ann. Sci.Nat.*20: 197- 260.

Kjellberg,F., Gouyon,P.H., Ibrahim,M., Raymond,M., and Valdeyron,G.,1987. The stability of the symbiosis between dioecious figs and their pollinators: A study of *Ficus carica* L. and *Blastophaga psenes* L. *Evolution* 41: 693-704.

Kjellberg,F., and Maurice,S.,1989. Seasonality in the reproductive phenology of *Ficus*: Its evolution and consequences. *Experientia* 45: 653-660.

Lachaise,D.,1977. Niche separation of African *Lissocephala* within *Ficus* Drosophilid community. *Oecologia* (Berlin) 31: 201-214.

Lachaise,D.,Tsacas,L., and Couturier,G.,1982. The Drosophilidae associated with tropical African figs. *Evolution*, 36: 141-151.

Mckey,D., and Kaufmann,S.C.,1988. Naturalization of exotic *Ficus* species (Moraceae) in south Florida. *Proceedings of the Symposium on Exotic Pest Plants, Miami, Florida.*

Michaloud,G., Michaloud-Pelletier,S., Wiebes,J.T., and Berg,C.C. 1985. The co-occurrence of two pollinating species of fig wasp and one species of fig. *Proc.K.Ned.Akad.Wet.Ser.* C.88: 93-119.

Murray,M.G.,1985. Figs (*Ficus* spp.) and fig wasps (Chalcidoidea, Agaonidae): hypotheses for an ancient symbiosis. *Biol.J.Linn.Soc.* 26: 69-81.

Murray,M.G.,1990. Comparative morphology and mate competition of flightless male fig wasps. *Anim. Behav.*, 39:434-443.

Nadel,H., Frank,H.J., and Knight R.J.(jr.),1992. Escapees and Accomplices: The Naturalization of Exotic *Ficus* and their Associated faunas in Florida. Florida *Entomologist* 75 (1): 29-38.

Naicker,S.,1984. Pollination Biology in *Ficus ingens* (Miq.) Miq. (Moraceae). Unpubl.thesis.

Nair,P.B., and Abdurahiman,U.C.,1984. Population dynamics of the fig wasp *Kradibia gestroi* (Grandi) (Hymenoptera Chalcidoidea, Agaonidae) from *Ficus exasperata* Vahl. *Proc.K.Ned.Akad.Wet.* (C) 87: 365-375.

Neeman,G.,and Galil,J.,1978. Seed set in the male syconia of the common fig,*Ficus carica* L.(Caprificus). *New Phytol*.81: 375-380.

Newton,L.E., and Lomo,A.,1979. The pollination of *Ficus vogelli* in Ghana. *Bot.J.Linn.Soc.* 78: 21-30.

Pemberton,C.E.,1921. The fig wasp in its relation to the development of fertile seed in the Moreton Bay Fig. *The Hawaiian Planters' Record*, 24: 297-319.

Ramirez,B.W.,1969. Fig wasps; mechanism of pollen transfer. *Science* 163: 580-582.

Ramirez,B.W.,1970. Host specificity of fig wasps (agaonidae). *Evolution* 24:681-691.

Ramirez,B.W.,1974. Coevolution of *Ficus* and Agaonidae. *Ann.Missouri Bot. Gard.* 61: 770-780.

Ramirez,B.W.,1987. The Influence of the Microenvironment - The Interior of the Syconium- in the Coevolution between Fig Wasps (Agaonidae) and the Fig (*Ficus*). pp. 329-334. In Labeyrie, V., G. Fabres and D. Lachaise (eds.). Insect-Plants.

Ramirez,B.W.,1988. Parasitic relationships among chalcidoid fig-wasps and the syconia of *Ficus* (Hymenoptera: Chalcidoidea). In: Gupta,V.K.(ed.), Advances in Parasitic Hymenoptera research. E.J. Brill, Leiden, pp. 345-350.

Storey,W.B.1975. Figs. In J. Janick and J.B. Moore [eds.],Advances in fruit breeding, 568-589. Purdue University Press, West Lafayette, IN.

Storey,W.B.,1985. *Ficus carica*. In A.H. Halevy [ed.]. *CRC handbook of flowering*, Vol.III CRC Press, Boca Raton, Fl.

Ulenberg,S.A., and Nubel,B.K.,1982. Oviposition of *Apocrypta* fig wasp parasites (Hymenoptera: Chalcidoidea: Torymidae). *Proc.K.Ned.Akad.Wet.Ser. C.* 85: 607-614.

Valdeyron,G., and Lloyd,D.G.,1979. Sex differences and flowering phenology in the common fig, *Ficus carica* L. *Evolution* 33: 673-685.

Verkerke,W.,1986. Anatomy of *Ficus ottoniifolia* (Moraceae) syconia and its role in the fig-fig wasp symbiosis. *Proc.K.ned. Akad Wet Ser.* C89: 443-469.

Verkerke,W.,1987(a). Ovule dimorphism in *Ficus asperifolia* Miquel. *Acta Bot.Neerl.* 36: 121-124.

Verkerke,W.,1987(b). Syconial Anatomy of *Ficus asperifolia* (Moraceae), a gynodioecious tropical fig. *Proc.K.ned.Akad.Wet.* C90: 461-492.

Verkerke,W.,1989. Structure and function of the fig. *Experientia*, 45: 612-627.

Wiebes,J.T.,1963. Taxonomic and host preferences of Indo-Australian fig wasps of the genus *Ceratosolen* (Agaonidae). *Tijdschr. Ent.* 106: 1-112.

Wiebes,J.T.,1966. Provisional host catalogue of the fig wasps (Hymenoptera Chalcidoidea). *Zool. Verth* 83: 1-44.

Wiebes,J.T.,1979. Co-evolution of figs and their insect pollinators. *Ann. Rev. Ecol. Syst.* 10: 1-12.

KEY FOR CHAPTER 3

a - antenna
ab - abdomen

ce - compound eye
cx - coxal combs

he - head

m - mandible
mp - mesothorax pocket

ovi - ovipositor

sc - scape
sg - solenogaster

th - thorax

GENERAL DISCUSSION AND CONCLUSIONS

The members of the genus *Ficus* display a complex mutualistic relationship between pollinating wasps and fig syconia. Research has shown that the act of pollination has a significant effect on the development of the syconia, flowers and wasps.

About half of the 750 spp. of *Ficus* are (gyno)dioecious. This study was undertaken because of the limited amount of work that has been done on the (gyno)dioecious fig species (*ca*. 1% have been studied in some detail). Research on the following species has been undertaken:- *F. carica* (Condit, 1932/47; Galil & Neeman, 1977; Kjellberg et al., 1987; Kjellberg & Valdeyron, 1984; Neeman & Galil, 1978; Valdeyron & Lloyd, 1979), *F. asperifolia* (Verkerke,1987a /1987b), *F. exasperata* (Nair & Abdurahiman, 1984) and *F. fistulosa* (Corlett, 1987).

Except for some work by Greuning (1990) on the taxonomic status of the only two Southern African representatives of the (gyno)dioecious fig species, *F. capreifolia* and *F. pygmaea*, no detailed work has been done previously on the (gyno)dioecious figs in South Africa.

Some work has been done on the pollination biology of a few monoecious fig species in South Africa (Baijnath & Ramcharun, 1981, 1983 & 1988; Baijnath & Naicker, 1989; Compton & Nefdt, 1990). However much work needs to be done on the other fig species, especially their phenology, insects and pollination biology in South Africa.

The major part of this study focussed on the morphology, phenology, anatomy, insects, pollination and reproductive behaviour of *Ficus capreifolia*. Several important findings from this research have been documented in Chapters 1, 2 and 3. A few of these will be highlighted in the following paragraphs.

Figs are mainly tropical to sub-tropical in distribution, found between 35°N and 35°S latitudes mainly. *Ficus capreifolia* was located at 29°S and 31°E in this study. Together with *F. pygmaea* they are the only (gyno)dioecious members at this southern location in South Africa. Questions regarding their migration to these habitats and the influence of climate on their survival need to be further investigated. It would be interesting to investigate the phenology and pollination biology of this plant in a more natural environment, especially in areas where the populations are better established, such as in N.E. Africa.

The location of these plants along the sandy river banks and their ability to grow much better alone indicated their role as pioneer plants. Other fig researchers were interested in this idea at the Fig Symposium in Bergen (per. comm. May, 1994). Very soon after these plants stabilised the banks other plants including grasses invaded this niche and partly affected the growth of these plants. Berg (1990b) noted that most of the fig plant species are located in more or less open, unstable areas and this supports the idea of figs being pioneer plants. The ecology of this plant needs further investigation so that local developers and planners could make use of these plants in the control of erosion along river banks and similar localities.

The reproductive success of these plants depend on the presence and survival of a population of pollinator wasps concurrently with the development and production of syconia. In the absence of pollinator wasps, abortion of syconia often occurred during the female stage. This problem arose during the development studies, especially during the dry, cold or even very hot months. These studies had to be repeated during more favourable conditions. Conditions such as wind, temperature, distance between plants and lifespan of pollinator wasps, among other factors, may have affected successful wasp transfer, pollination and oviposition. Bronstein (1989) suggests that in cool dry periods, fig-wasp survival and flight will be strongly limited.

Pistillate flowers had 4 perianth segments, an oval laterally-flattened ovary and a large clavate stigma. Short-pedicelled and long-pedicelled flowers were present in gall flowers, while sessile, short- and long-pedicelled flowers were present in seed flowers. Pedicels increased in length up to three times from B- to D phases in the flowers. Verkerke (1987) reported similar characteristics for *F. asperifolia* with 4 or 5 perianth lobes, a spherical ovary and a cleft stigma. *Ficus asperifolia* also had pedicelled gall flowers and sessile or sub-sessile seed flowers. Verkerke (1986, 1987b) also reported observing increases in pedicel length, after oviposition had occurred, and suggested that they provided for a more efficient packing of the drupes.

Perfect heterostyly, with short-styled pistillate flowers in gall figs and long-styled pistillate flowers in seed figs, was present in *F. capreifolia*. Mean ovipositor lengths of the females of the pollinator wasps clearly indicated that oviposition would have been possible only in the ovaries of the short-styled flowers of the gall figs. Female syconia produced seeds only and this clearly showed that oviposition was prevented because the styles in these pistillate flowers were too long. Verkerke (1986) suggested that style firmness may be a more important factor than style length as a limiting factor for oviposition in the female flowers of *F. ottoniifolia*. He suggested that the shorter, thicker styles provided better support to an ovipositing wasp - hence short styles had a better chance of receiving wasp eggs.

A synstigma was formed in seed figs through an interlinking of the papillae on their stigmata and upper stylar regions. This may be a functional specialisation to ensure that gall figs become more efficient as wasp producers through the avoidance of competition from seed production. This strategy may be necessary to guarantee the success and survival of this symbiosis.

Staminate flowers in 2 to 3 rows, with 4 perianth segments and a single introrse anther were located near the ostiole. Longitudinal dehiscence allowed the wasp to access the pollen more easily from the anthers by using a scraping movement of its foreleg.

Male trees produced more syconia (50 to 300 per tree) and more often (2 to 3 times per year) compared to female trees (20 to 100 syconia, mostly once a year). Gall figs also produced more pistillate flowers than the seed figs. These statistics suggest that wasp production in larger numbers and more often is important to the survival of the population (and species?) in this marginal, seasonal habitat. The presence of separate male and female syconia with different functions, and xenogamous pollination coupled with all the problems that the wasps could encounter in moving between the syconia, make it necessary for the higher floral production. Bronstein and Mckey (1989) suggested that figs growing at the margins of their range should encounter difficulty in flowering, lowered pollinator survivorship and lowered fig-reproductive success.

Gall fig plants produce syconia asynchronously throughout the year with occasional gaps within individuals. These gaps are closed at the population level, sometimes by the presence of a few syconia only on certain plants. This type of asynchronous syconial production prevented local extinction of wasps, thereby improving the chances of wasp co-existence with B-phase and D-phase syconia. Bronstein (1989) maintains that population level asynchrony is essential for wasps to move successfully between trees and for wasps to reproduce.

Seed figs produced from 1 to 3 crops of syconia asynchronously per year. Gaps in syconial production occurred at both individual and population levels. Continuous seed production, though essential for propagation of the species, is not crucial to the survival of the symbiosis. In the absence of gap closure in the male figs, wasp production and survival will be adversely affected resulting in problems for this population to carry out pollination. Figs which are formed will abort at B phase.

This study also showed that *F. capreifolia* had long developmental cycles (120 to 140 days) and long A and C phases. This plasticity in phenological patterns improved the possibility of overlap between B and D phases and successful reproduction. Windsor et al. (1989) suggest that factors such as temperature, light and water, amongst others, could affect the optimal timing and reproductive output of figs. They also propose that since wet and dry seasons are common in tropical regions, figs may respond phenologically to these changes. Bronstein and Patel (1992) found that in *F. aurea* some syconia may remain dormant in A phase for up to 8 months. They also noticed a variation in developmental periods and that C phase was temperature sensitive. Bronstein (1989) suggested that durations of fig-reproductive episodes are longer in cooler weather because seeds and wasps develop more slowly then. A study of the same species in a range of seasons, habitats and latitudes should become an exercise for future fig-researchers (on a co-operative basis).

Light microscope (LM) and scanning electron microscope (SEM) analysis of the developmental stages revealed many intersting anatomical details in *F. capreifolia*. These included information on the bracts, hairs, syconial wall, syconial cavity, cellular inclusions, pistillate flowers, staminate flowers, style, papillae, ovule, ovary and anther amongst others.

The large highly vacuolated parenchyma cells and the large radially elongated inner epidermal cells may have been associated with changes in turgor in the ostiolar bracts. Unicellular hairs which were conical and robust contributed to the scabrous nature of the outer surface of these figs. Unicellular hairs were also found on the inner surface of the syconial walls during B phase only and these could have been glandular. This needs further investigation. Pluricellular hairs, found abundantly on the outer syconial surface during the receptive phase, may have been glandular and responsible for secreting the attractant for the wasp. This area has been the subject of much speculation and will also come under further scrutiny in the near future. Although Verkerke (1986) has reported the presence of pluricellular hairs on the inner wall of *F. ottoniifolia* (a monoecious fig), he has remained silent on this feature in *F. asperifolia*. Could their absence on the inner wall be a characteristic in the (gyno)dioecious species?

Ripe gall figs developed a syconial cavity which catered for the activities of the emerging wasps after eclosion. Naturally as this activity is lacking in ripe seed figs, no cavity is present.

While the gall fig developed a thicker syconial wall than the seed fig, both had unsclerified hypodermal layers containing chloroplasts. Thick-walled (sclerified) hypodermal layers have been reported in the monoecious species *F. ingens* (Baijnath & Naicker, 1989) and *F. ottoniifolia* (Verkerke, 1986). No such sclerification has been reported for (gyno)dioecious figs, including *F. asperifolia* (Verkerke, 1987b). The absence of sclerification in the hypodermal layers of the (gyno)dioecious figs may also be a characteristic that differentiates the (gyno)dioecious and monoecious figs. This feature may be necessary in the monoecious figs to limit oviposition by 2° sycophiles into its syconial cavity via the softer ostiolar region only. The (gyno)dioecious figs may not encounter this problem since the gall fig is specialised and large enough to cater for the production of both 1° and 2° sycophiles. Alternately, the robust unicellular hairs could have substituted for the lack of sclerification. Both *F. capreifolia* and *F. asperifolia* belong to the section *Sycidium* and have scabrous leaf and fig surfaces.

Descriptions of the development of pistillate and staminate flowers are included in this research. Similar flower development occurred in both seed and gall figs in A and B phases. The development of the papillae emphasises its relationship to receptivity in the female phase of fig development. An investigation needs to be done to extract/isolate the chemical secreted by the papillae.

The pattern of development of the ovary and ovule was similar to that described by Verkerke (1987b) in *F. asperifolia*. A few differences existed in terms of size, number, shape and sclerification of parts.

Wasp characteristics, wasp behaviour and the fig-wasp relationships in *F. capreifolia* have also been described in some detail in this research. Antennae in the females of the pollinator wasp are hairy and well developed. This suggested that they may be sensitive to chemicals, such as those secreted by syconial hairs and the papillae.

A combination of ethodynamic pollination, presence of pollen pockets and cleansing behaviour may be behavioural patterns to avoid accidental pollination of unoviposited pistillate flowers in gall figs. The shallow posterior end of the mesothoracic pocket made pollen removal easier for the wasp.

Only two wasp species were located in the syconia of *F. capreifolia*, a pollinator and a secondary (2^0) sycophile. While it is generally accepted that the fig-wasp relationship is a specific 1:1 relationship (Galil, 1977) between the fig and its pollinator, one to several specific 2^0 sycophile species may inhabit a fig syconium. The presence of a single 2^0 sycophile may be associated with the idea that this species is growing at the margin of its range and is not yet well established in this habitat. Further these 2^0 sycophiles may not have had sufficient time to reach these locations. Galil and Eisikowitch (1968b) also reported the presence of only one 2^0 sycophile, *Apocrypta longitarsus*, in *F. sycomorus*.

The pollinator wasp and the 2^0 sycophile species of *F. capreifolia* have been sent for identification to entomologists in France. Although other researchers have named the pollinator wasps for *F. capreifolia* in their taxonomic studies, their descriptions do not fit the descriptions of the wasps presented in this research. A further complication is that the same wasp has been named for *F. asperifolia* and *F. exasperata* as the pollinator.

This situation will be investigated in *F. capreifolia* as soon as the correct identity is received.

The females of the pollinator wasp possess coxal combs and mesothoracic pockets which accounted for ethodynamic pollination. There was a mean of 27 males to 100 females suggesting a bias towards the rearing of females to improve the chances of pollination and fertilisation. Galil and Eisikowitch (1971) suggested that the ratio of males to females was sufficient to ensure fecundation of females. Herre (1987) postulated that the wasps had the ability to alter brood sex ratios in response to different local mate competition situations. A ratio of 31 males to 100 females was recorded in a syconium without 2^0 sycophiles in *F. capreifolia*.

Observations of the behaviour of the wasps both within and outside the syconia were carried out and some very interesting results obtained. Generally wasp emergence from their galls, copulation and pollen loading were similar to the descriptions of earlier workers (Galil et al., 1973; Galil, 1973a; Galil & Eisikowitch, 1969b & 1974; Galil & Snitzer-Pasternak, 1970; Naicker, 1984). It has been observed that the 2^0 sycophiles emerged via the ostiole once the males of the pollinator wasp had opened the ostiole in *F. capreifolia*. This has also been reported for *F. asperifolia* (Verkerke, 1987b). No holes were cut in the walls of (gyno)dioecious figs. Holes were cut in the walls of monoecious figs (Galil & Eisikowitch, 1965 &

1968a; Joseph & Abdurahiman, 1978; Baijnath & Ramcharun, 1983; Verkerke, 1986 and Baijnath & Naicker, 1989). It is suggested that, because the ostiolar bracts did not loosen in D phase, the cutting of the wall is necessary to avoid dessication, infection or predation of the seeds in monoecious figs. This hole could be sealed, to limit the use of the syconium by insects (such as flies) for egg-laying or other activities, once the wasps had departed. This characteristic is not necessary in the (gyno)dioecious figs because wasps and seeds are produced in separate figs.

The results also showed that both the females of the pollinator and the 2° sycophiles reacted negatively to gravity and positively to light, thus facilitating their movements towards the ostiole.

As this work represented the first on a (gyno)dioecious fig species in Southern Africa, the data obtained on phenology and morphology was very enthusiastically received by fellow fig researchers at the International *Ficus* Symposium in Bergen, Norway, in May 1994. Many of the researchers including Judith Bronstein, Finn Kjellberg, Steve Compton and Daniel Lachaise showed great interest in the work and offered their expertise in reviewing the material and assistance in its publication. Bronstein's interest was focussed on the phenological data as she was involved in this area in her own work, on *F. pertusa* and *F. aurea*, in the United States of America.

Kjellberg, working in France, has worked mainly with *F. carica*, which is the most researched of the (gyno)dioecious figs in Europe. *Ficus carica* is the common edible fig which is extensively cultivated, and therefore much information is based on research on the cultivated crop. Kjellberg is keen to use this data on a comparative basis with *F. carica*. Compton, who has worked in South Africa with *F. burtt-davyi* and is now based in England, has shown an interest in the species from an ecological point of view and has requested that this area be pursued further with more statistical data. Lachaise showed an interest in the wasps and took the samples to colleagues in France for their identification.

Future research on this fig/section could focus on the following areas:

1. Phenological and morphological work on *F. pygmaea*.
2. Behaviour of insects and pollination biology in *F. pygmaea*.
3. Comparison of *F. capreifolia* and *F. pygmaea*, since these two plants are related and found in Southern Africa.
4. Study of *F. capreifolia* in a more natural habitat, and the comparison with this research to identify the influence of other factors on the mutualism.
5. The completion of the identification and description of the wasps in *F. capreifolia*.
6. The comparison of *F. capreifolia* with a monoecious

Southern African fig growing in close proximity in similar conditions.

7. Isolation of the fig-wasp attractant and its identification.
8. An investigation of the ecological, economic and biological importances of fig plants in Southern Africa.

From the list of suggested areas for future research and the enthusiasm of the international researchers, it is evident that this field is wide open and is in need of more funding and a larger pool of active researchers. Of the 24 recognised species of South African figs only a few have been studied/examined in detail.

Figs constitute a major source of food for animals in the forests and in the wild. Asynchronous fruiting ensures that figs become available throughout the year and therefore is one of the few food sources available to animals (birds, bats, monkeys and mice) when other plants are not fruiting. These fig plants also play an important role in disturbed areas and could be of importance in soil reclamation programmes.

ACKNOWLEDGEMENTS

I wish to thank my promoters, Dr H. Baijnath (UDW) and Prof. C.T. Johnson (UWC), for their guidance, support, assistance, criticism and encouragement throughout this study. My sincere thanks go to Mr S. Naicker (SCE) for initially assisting me in setting up this study. Further thanks go to Mrs Y. Naidoo (UDW) and Miss V. Hansen (Natal Technikon) for their assistance and support during my SEM and LM work respectively. My thanks also go to my colleagues, friends and family for their assistance and support at all times. I am indebted to my wife and children (Hamsha, Sashika and Paroshen) for assistance on the the field and their continued support, encouragement and numerous sacrifices made on my behalf.

GENERAL BIBLIOGRAPHY

Abdurahiman,U.C. and Joseph,K.J.,1976. Observations on the biology and behaviour of *Ceratosolen marchali* Mayr (Agaonidae, Chalcidoidea, Hymenoptera). *Entemon* 1: 115-121.

Baijnath,H.,and Naicker,S.,1989. Developmental anatomy of *Ficus ingens* syconia in relation to its wasp faunula. *S.Afr.J.Bot.* 55(4): 409-421.

Baijnath,H.,and Ramcharun,S.,1981. Microscopic observations of the ostiolar bracts in some South African examples of the genus *Ficus* L.(Moraceae). *Proc.Electron micr.Soc.S.Afr.* 11: 135-136.

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

Baijnath,H., and Ramcharun,S.,1988. Reproductive biology and chalcid symbiosis in *Ficus burtt-davyi* (Moraceae). *Monogr.Syst.bot.Mo.Bot.Gdn.* 25: 227-235.

Berg,C.C.,1989. Classification and distribution of *Ficus*. *Experientia* 45: 605-611

Berg,C.C.,1990(a). Distribution of African taxa of *Ficus* (Moraceae). *Proc.aetfat.sym.IV,Hamburg*,23a: 401-405.

Berg,C.C.,1990(b).Reproduction and Evolution in *Ficus* (Moraceae):Traits connected with the adequate rearing of pollinators. *Memoirs of New York Botanical Garden*, 55: 167-185.

Bronstein,J.L.,1989. A mutualism at the edge of its range. *Experientia* 45: 622-637.

Bronstein,J.L., and Mckey,D.,editors.1989. The comparative biology of figs. *Experientia* 45: 601-680.

Bronstein,J.L., and Patel,A.,1992. Causes and consequences of within-tree phenological patterns in the Florida strangling fig, *Ficus aurea* (Moraceae). *Am.J.Bot.* 79(1): 41-48.

Compton,S.G., and Nefdt,R.J.C.,1990. The figs and fig-wasps of *Ficus burtt-davyi*. *Proc.aetfat,sym.IV,Hamburg*, 23a: 441-450.

Condit,I.J.,1932. The structure and development of Flowers in *Ficus carica* L. *Hilgardia* 6: 443-481.

Condit,I.J.,1947. The fig. Waltham, Massachusetts: *Chronica Botanica*.

Corlett,R.T.,1987. The phenology of *Ficus fistulosa* in Singapore. *Biotropica* 19: 122-124.

Corner,E.J.H.,1965. Check-list of *Ficus* in Asia and Australasia. *Gdns.Bull., Singapore* 21: 1-186.

Friis,I.,1990. Distribution patterns of *Ficus* in Tropical N.E. Africa. *Proc.aetfat.sym.IV,Hamburg*,23a: 407-424.

Galil,J.,1973. Pollination in dioecious figs: pollination of *F. fistulosa* by *Ceratosolen hewitti*. *Gdn.Bull. Singapore* 26: 303-311.

Galil,J.,1977. Fig biology. *Endeavour* 1: 52-56.

Galil,J., and Eisikowitch,D.,1965. Pollination of flowers in *Ficus religiosa* L. *Tera Ve Aretz*. 1: 1-16.

Galil,J., and Eisikowitch,D.,1968(a). On the pollination ecology of *Ficus sycomorus* in East Africa. *Ecology* 49: 259-269.

Galil,J., and Eisikowitch,D.,1968(b). Flowering cycles and fruit types in *Ficus sycomorus* in Israel. *New Phytol.* 67: 745-758.

Galil,J., and Eisikowitch,D.,1968(c). On the pollination ecology of *Ficus religiosa* in Israel. *Phytomorphology* 18: 356-363.

Galil,J., and Eisikowitch,D.,1971. Studies on mutualistic symbiosis between syconia and sycophilous wasps in Monoecious figs. *New Phytol.* 70: 773-783.

Galil,J., and Eisikowitch,D.,1974. Further studies on pollination ecology in *Ficus sycomorus* II. Pocket filling and emptying by *Ceratosolen arabicus* Mayr. *New Phytol.* 73: 515-528.

Galil,J., and Neeman,G.,1977. Pollen transfer and pollination in the common fig (*Ficus carica* L.). *New Phytol.* 79: 163-171.

Galil,J., and Snitzer-Pasternak,Y.,1970. Pollination in *Ficus religiosa* L. as connected with the structure and mode of action of the pollen pockets of *Blastophaga quadraticeps* Mayr. *New Phytol.* 69: 775-784.

Galil,J., Zeroni,M., and Bar Shalom D.,1973. Carbon dioxide and ethylene effects in the co-ordination between the pollinator *Blastophaga quadraticeps* and the syconium in *Ficus religiosa*. *New Phytol.* 72: 1113-1127.

Greuning, J. V. van, 1990. A synopsis of the genus *Ficus* (Moraceae) in Southern Africa. *S. Afr. J. of Bot.*, 56, 599-630.

Herre,E.A.,1987. Optimality, plasticity and selective regime in fig wasp sex ratios. *Nature* 329: 627-629.

Herre,E.A.,1989. Co-evolution of reproductive characteristics in twelve species of New World figs and their pollinator wasps. *Experientia* 45: 637-647.

Hill,D.S.,1967. Figs of Hong Kong. Hong Kong University Press.

Ibrahim,M.,1985. Contribution a une approche evolutive de la symbiose entre *Ficus carica* L. et *Blastophaga psenes* L. Thesis Montpellier.

Joseph,K.J., and Abdurahiman,U.C.,1978. Oviposition behaviour of *Ceratosolen fusciceps* Mayr. (Agaonidae: Hymenoptera) and the mechanism of pollination in *Ficus racemosa* L. *J. Bombay Nat. Hist. Soc.* 78: 287-289.

Kjellberg,F., Gouyon,P.H., Ibrahim,M., Raymond,M., and Valdeyron,G.,1987. The stability of the symbiosis between dioecious figs and their pollinators: A study of *Ficus carica* L. and *Blastophaga psenes* L. *Evolution* 41: 693-704.

Kjellberg,F., and Valdeyron,G.,1984. The pollination of the fig tree (*Ficus carica* L.) and its control in horticulture. *Acta Oecolog./Oecol.Gen.* 5(4): 407-412.

Naicker,S.,1984. Pollination Biology in *Ficus ingens* (Miq.) Miq. (Moraceae). Unpubl.thesis.

Nair,P.B., and Abdurahiman,U.C.,1984. Population dynamics of the fig wasp *Kradibia gestroi* (Grandi) (Hymenoptera Chalcidoidea, Agaonidae) from *Ficus exasperata* Vahl. *Proc.K.Ned.Akad.Wet.* (C) 87: 365-375.

Neeman,G.,and Galil,J.,1978. Seed set in the male syconia of the common fig, *Ficus carica* L.(Caprificus). *New Phytol*.81: 375-380.

Okamoto,M., and Tashiro,M., 1981. Mechanism of pollen transfer and pollination in *Ficus erecta* by *Blastophaga nipponica*. *Bull. Osaka Mus. Nat. Hist.* 34: 7-16.

Valdeyron,G., and Lloyd,D.G.,1979. Sex differences and flowering phenology in the common fig, *Ficus carica* L. *Evolution* 33: 673-685.

Verkerke,W.,1986. Anatomy of *Ficus ottoniifolia* (Moraceae) syconia and its role in the fig-fig wasp symbiosis. *Proc.K.ned.Akad Wet Ser.* C89: 443-469.

Verkerke,W.,1987(a). Ovule dimorphism in *Ficus asperifolia* Miquel. *Acta Bot.Neerl.* 36: 121-124.

Verkerke,W.,1987(b). Syconial Anatomy of *Ficus asperifolia* (Moraceae), a gynodioecious tropical fig. *Proc.K.ned.Akad.Wet.* C90: 461-492.

Verkerke,W., 1989. Structure and function of the fig. *Experientia*, 45: 612-627.

Windsor,D.M., Morrison,D.W., Estribi,M.A., and de Leon,B.,1989. Phenology of fruit and leaf production by 'strangler' figs on Barro Colorado Island, Panama. *Experientia* 45: 647-653.