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Aspects of pollination and floral development in *Ficus capensis* Thunb. (Moraceae)

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ABSTRACT

A unique obligatory symbiosis exists between *Ficus capensis* Thunb., and its pollinator, *Ceratosolen capensis* Grandi. Flowers from both aerial and geocarpic syconia may be pollinated and produce seeds. Females of *C. capensis* possess specialized mesothoracic pockets in which pollen is transferred from ripening syconia to receptive ones. A second primary sycophile, *Sycophaga cyclostigma* Waterston, appears to be ineffective in pollination. Several secondary sycophiles oviposit through the syconial wall. Strong sexual dimorphism exists in most sycophilous wasps. All female flowers have the potential to produce either seeds or galls and variation is merely one of gross morphology. Flowering is distinctly asynchronous. Seeds are dispersed by various fruit predators and germinate very easily under warm humid conditions.

RÉSUMÉ

ASPECTS DE LA POLLINISATION ET DU DÉVELOPPEMENT FLORAL CHEZ FICUS CAPENSIS *THUNB. (MORACEAE)*

Une symbiose obligatoire unique existe entre Ficus capensis *Thunb. et son pollinisateur* Ceratosolen capensis *Grandi. Les fleurs des sycones tant aérien que géocarpiques peuvent être pollinisées et produire des graines. Les femelles du* C. capensis *possèdent des poches mésothoraciques spécialisées dans lesquelles le pollen est transféré des sycones en voie de maturation à ceux qui sont réceptifs. Un second insecte sycophile primaire,* Sycophaga cyclostigma *Waterston, semble être inefficace pour la pollinisation. Plusieurs sycophiles secondaires pondent au travers de la paroi du sycone. Un fort dimorphisme sexuel existe chez la plupart des guêpes sycophiles. Toutes les fleurs femelles ont la possibilité de produire soit des graines soit des galles et la variation concerne seulement la morphologie générale. La floraison est distinctement asynchrone. Les graines sont dispersées par divers animaux frugivores et elles germent très facilement sous des conditions humides et chaudes.*

INTRODUCTION

The Cape fig, *Ficus capensis* Thunb.**, has a fairly widespread distribution extending from the Eastern Cape through central Africa as far north as Ethiopia. It commonly occurs in damp areas along stream and river banks and in low-lying depressions. The tree is of moderate size reaching a height of 10–12 metres in the Durban area. *F. capensis* is a member of the sub-genus *Sycomorus* Gasp., and is especially interesting in that it bears both aerial and geocarpic figs (= syconia). A classic case of obligatory mutualism exists between members of the genus *Ficus* L., and small chalcid wasps of the family Agaonidae and several aspects of this study have been reviewed recently (Janzen, 1979). The fig tree is completely dependent on the wasps for pollination and seed production while the wasp completes its ontogeny within the syconium. Since the structure and life patterns of both mutualistic partners are so closely integrated to form a functional system, each pollinator is believed to be species-specific (Wiebes, 1964). The agaonid pollinator of *F. capensis* is *Ceratosolen capensis* Grandi.

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**Dr C. C. Berg of the Instituut voor Systematische Plantkunde, Rijksuniversiteit, Utrecht, Netherlands, has drawn our attention to the fact that *Ficus sur* Forssk. is an earlier published name for *F. capensis* Thunb. He has examined the types and is of the opinion that the two species are conspecific.

MATERIALS AND METHODS

Most of the observations were carried out on an experimental tree located on the campus of the University of Durban-Westville. The developmental cycle of the syconium was monitored by daily measurements of 15 marked syconia. Different stages were gathered and studied in the laboratory. Insects were collected by placing mature syconia in erlenmeyer flasks sealed with muslin cloth. The wingless male wasps were removed by dissecting the syconia and washing in alcohol. Insect behaviour was determined by cutting open syconia and observing under a dissecting microscope. The fate of unpollinated syconia was studied by bagging very young syconia with fine nylon mesh. Conditions of foliage and flowering of 54 trees in and around the Durban area were recorded at 4–5 week intervals over a period of 13 months.

FLOWERING

1. *The fig flowers*

The small unisexual flowers of *Ficus capensis* are borne in hollow receptacles referred to as figs or syconia. These heart-shaped syconia occur on branched peduncles (Fig. 1A) arising from the trunk and aerial branches as well as from underground wood. Most of the inner surface of the receptacle is lined by female flowers, while relatively few (10–25), male flowers occur in 2 or 3 series around the descending ostiolar bracts. Each staminate flower is simple in structure consisting of 2 (rarely 3 or 4) large stamens enclosed by 3 to 4 perianth

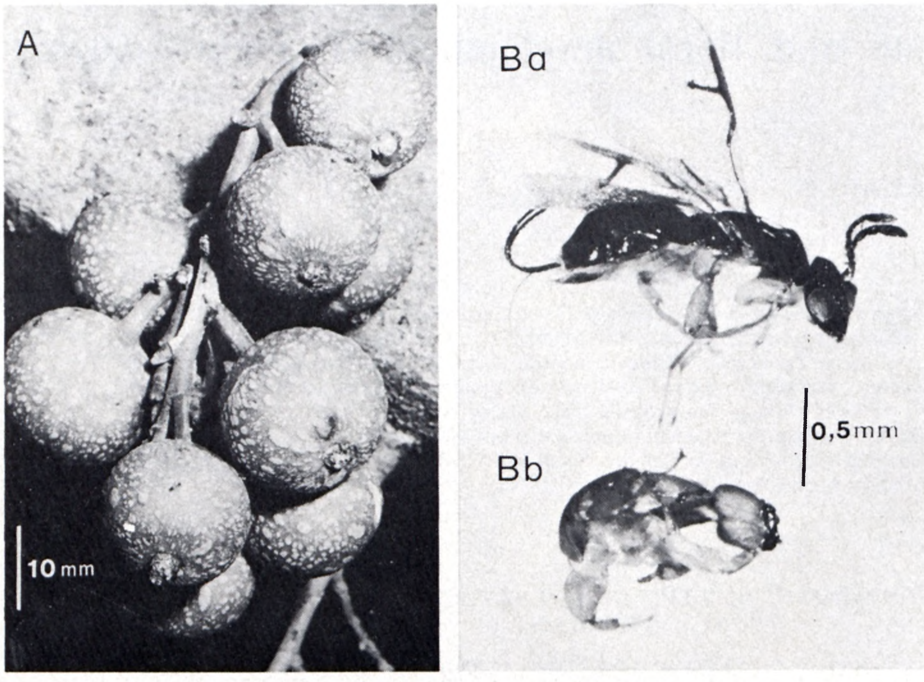

FIG. 1.—Some characters of syconia and pollinators in *Ficus capensis*. 1A, peduncle with several syconia; 1Ba, female and 1Bb, male of the regular pollinator, *Ceratosolen capensis*.

segments. At anthesis, which occurs several weeks after the female flowers are receptive, there is rapid elongation of the filaments so that the anthers protrude out of the perianth. The protogynous nature of syconial development thus effectively prevents selfing within the syconium.

Each female flower consists of a conspicuous ovary with a laterally attached style and 3 reduced perianth segments. The ovary is unilocular with a single large ovule attached laterally close to the stylar region. The flowers may be either sessile or borne on pedicels of varying lengths. Flowers with relatively elongate pedicels are short-styled and are functionally gall flowers. Sessile and short-pedicelled flowers have relatively long styles and are functionally seed flowers. This reciprocal staggering of style and pedicel lengths results in the overall height of all flowers being identical so that their stigmas form a continuous surface or synstigma lining the syconial cavity (Galil & Eisikowitch, 1968a). Each stigma is capitate with a characteristic central depression and short stigmatic papillae.

2. *The developmental cycle of the syconium* (Fig. 2)

The phenophase in *Ficus capensis* requires a period of about 60 days. The five phases of syconial development recognized by Galil & Eisikowitch (1968b) will be adopted in this description.

A or the prefloral phase: This is a period of 3 weeks from the initiation of the syconia until a diameter of approximately 1 cm is attained. The very young syconia are completely covered by tiny scales that are deciduous very early in the prefloral stage. Active growth and development of female flowers occurs during this period.

B or the female phase: The female flowers become receptive when the syconium is 22–24 days old. At this stage, the male flowers are immature and the stamens remain tightly enclosed within the perianth. The ostiolar bracts loosen slightly and females of the legitimate pollinator, *Ceratosolen capensis,* force their way into the syconium through the ostiole. Here they oviposit into short styled flowers and effect pollination of the long styled flowers by the removal of pollen grains from specialized mesothoracic pollen pockets. Usually about 1–3 wasps enter each syconium. These are often damaged as wings and antennal flagella are torn off as they force their way between the ostiolar bracts. In many instances dead wasps were found trapped between bracts. A second primary sycophile *Sycophaga cyclostigma* also enters the syconium during this time and oviposits into female flowers.

C or the interfloral phase: After pollination there is a long interfloral stage lasting approximately 30 days.

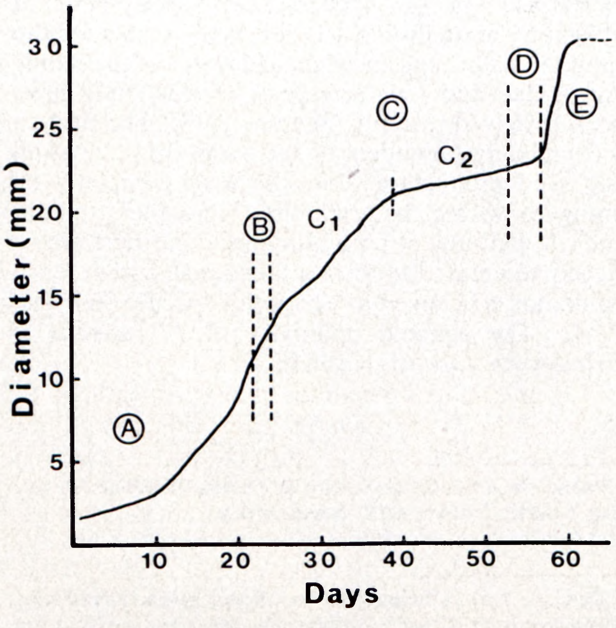

FIG. 2.—Growth curve of the syconium of *Ficus capensis* showing phases in the developmental cycle. A, prefloral; B, female; C, interfloral; D, male; E, postfloral.

During the first half of the interfloral phase (C_1) growth of the syconium continues at a more or less normal rate and is accompanied by rapid hardening of the syconial wall. During the latter half, C_2 growth slows down tremendously so that an increase in diameter of only 2 mm was recorded over a period of 15 days. During the interfloral stage the fig embryos develop in the seed flowers while the wasps pass through the larval and pupal stages in the gall flowers.

D or the male phase: The onset of the male phase, which lasts for 3–4 days, is indicated by a slight softening of the syconial wall. This is often accompanied by a very subtle change in colour from green to olive. The male flowers now attain maturity and the stamens protrude out of the perianth by rapid elongation of the filaments. At the same time the wasps reach the imago stage and the male wasps promptly bite their way out of their native galls. They then actively seek out galls containing female wasps, bite through the walls and fertilize the females within. They are also responsible for detaching anthers from the filaments, so that these become scattered within the syconium. When fertilization is complete, male wasps congregate at the ostiolar end and together bite a neat channel through the bracts to the outside. During this time the females release themselves from their galls by widening the opening made by the male wasps during fertilization. On eclosion, they actively fill up the mesothoracic pockets with pollen from the anthers and eventually leave the syconium through the channel prepared by the male wasps. The blind, wingless males are short-lived and die soon after preparation of the exit channel.

E or the postfloral phase: With the completion of the male phase there is a rapid increase in diameter of the syconium. The syconium wall becomes soft and succulent and changes to an attractive deep red colour with a sweet odour. The postfloral period may last for a maximum of 4 days at the end of which the syconia either fall to the ground or are eaten by various fruit predators.

3. *Unpollinated flowers*

Preliminary experiments were carried out to ascertain the fate of unpollinated flowers by bagging young pre-receptive syconia with a fine nylon mesh. At the receptive stage these syconia remained at a constant diameter for almost a week before abscissing. Infected figs of the same age, had during this week increased in diameter and thereafter continued normal development.

From field observations it was noted that figs infected by *Sycophaga cyclostigma* only, continued normal development but without the production of seeds. It is, therefore, apparent that the act of ovipositing stimulated parthenocarpic development of the syconia. This phenomenon is also reported for *Ficus sycomorus* L. infected by *Sycophaga sycomori* L. in the Middle East (Galil, Dulberger & Rosen, 1969). Such unpollinated syconia in *F. capensis* showed a high percentage of empty degenerate flowers.

4. *Asynchronous flowering*

Observation of 54 trees of *F. capensis* over a period of 13 months clearly indicates that the production of syconia is not seasonal. Trees bearing syconia of any developmental stage can be found during every month of the year (Table 1). However, flowering tends to increase slightly from December to April (Table 2). This co-incides with the warm, wet months of the year. Some trees displayed continuous fruiting throughout the year with little or no resting period between crops.

TABLE 1.—Percentage of trees displaying young, mature or ripe stages of syconial development during each month of the year*

Month	Young	Mature	Ripe
June 1980	26	59	15
July	35	70	24
August	22	61	22
September	51	71	23
October	37	70	46
November	37	65	48
December	41	74	39
January 1981	54	78	28
February	41	69	41
March	35	80	22
April	20	57	26
May	22	74	35
June	35	69	28

*For the purposes of this analysis — young = prefloral to female; mature = interfloral to male; ripe = postfloral.

Although each tree usually produces syconia in distinct crops, these may sometimes overlap to such an extent that young, mature and ripe syconia may occur simultaneously on an individual tree. In such instances, subsequent crops are initiated before the original crop has completed the developmental cycle. Furthermore, aerial and geocarpic crops may be initiated independently and may therefore be at different developmental stages at a particular time. The phenomenon of crop overlap (Table 3) and continuous fruiting occurred to a slightly greater extent during the summer period. Trees seem to vary in degree of deciduousness. Whereas some trees appear to be evergreen, others shed their leaves fairly regularly. Unlike the situation reported (Wharton, Tilson & Tilson, 1980) in *F. sycomorus*, no fixed correlation could be established between flowering and leaf drop in *F. capensis*.

5. *The symbionts of the syconium*

The living organisms associated with the syconium are many and include protozoans, yeast, fungi, nematodes, mites, beetle larvae, caterpillars and wasps. The syconium is therefore a very favourable microhabitat harbouring a variety of life forms. However, only the wasps are of direct significance in pollination and seed production. Most of the sycophilous wasps display elaborate sexual dimorphism. The females (Fig. 1 Ba) are active and winged with well developed sensory structures. The males (Fig. 1 Bb) are very much reduced in structure and are relatively pale coloured and wingless. They are often blind or may have vestigial eyes and reduced

TABLE 2.—Numbers of trees bearing syconia during each month of the year, expressed as a percentage of the sample

Month	Jun	Jul	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
%	67	82	72	82	87	80	90	96	91	91	90	87	83

TABLE 3.—Percentage of individual trees bearing young, mature and ripe syconia simultaneously (A). This phenomenon displayed on an exclusively aerial (A^1) or geocarpic (A^2) basis, is also recorded for each month

Month	A	A^1	A^2
June 1980	5,6	1,9	0
July	1,9	0	0
August	5,6	0	0
September	7,4	2,8	1,8
October	13,0	5,6	0
November	11,1	1,9	3,7
December	14,8	9,3	3,7
January 1981	9,3	7,4	3,7
February	13,0	9,3	5,6
March	9,3	7,4	3,7
April	5,6	0	0
May	7,4	7,4	0
June	5,6	0	1,8

antennae. Their most striking feature is a pair of very large, scissor-like mandibles. According to Wiebes (pers. comm.), who has undertaken the identification, the following taxa are involved:

Ceratosolen capensis — Primary sycophile (legitimate pollinator)
Sycophaga cyclostigma — Primary sycophile
Apocrypta sp. — Secondary sycophile
Parakoebelea sp. — Secondary sycophile
Eukoebelea sp. — Secondary sycophile
Sycophila sp. — Secondary sycophile
Camarothorax sp. — Secondary sycophile
Sycoscapter sp. — Secondary sycophile

At least eight species of wasps have been recovered from mature syconia in the Durban area. Most of these are secondary sycophiles (parasites and inquilines) and oviposit through the walls of the syconia. The inquilines do not directly affect seed production since they develop in already induced galls. Females of *C. capensis* and *S. cyclostigma* enter the syconium through the ostiole during the female phase of development. Observations appear to indicate that the main activity period of the former precedes that of the latter by about a day. The entry of females of *S. cyclostigma* into the syconium has been observed on many occasions. Such syconia containing active females of *S. cyclostigma* usually contain dead or dying females of *C. capensis*.

On entry into the syconium the behaviour of these two primary sycophiles is very distinctive. The female of *C. capensis* moves about on the synstigma with the posterior extremity of the abdomen curled downwards. The triangular flap which supports the protrusible ovipositor is held underneath the body in a position perpendicular to the synstigma. At this stage, the ovipositor is only slightly extended and the tip is then positioned into the depression of a stigma. The body vibrates slightly and within a few seconds the ovipositor is completely extended down the style. The tip of the triangular flap now comes to lie in the stigmatic depression. This provides additional support as the prothoracic legs are folded backwards until the distal segments are at the entrance of the mesothoracic pockets. Pollen is then unloaded by a series of 'shovelling' movements which may occur from 3−14 times. Thereafter, the legs are dusted against each other, the ovipositor is withdrawn and the insect moves onto another stigma. Sometimes the ovipositor is only partly inserted into the style and retracted almost immediately. During these trials no pollination movements occur and there is apparently no release of eggs.

The females of *S. cyclostigma* remain very straight and flattened against the synstigma and display no perceptible movement while ovipositing. However, unlike the females of *C. capensis*, they usually tend to withdraw their ovipositors on exposure to light. Thereafter, they appear to make constant attempts to 're-enter' the syconium by crawling through the bracts.

In male or D-phase syconia only the males of *C. capensis* are involved in anther cutting and preparation of an exit channel. On a few occasions ripe syconia without exit channels were dissected to reveal a mass of dead or dying insects. Such syconia were found to contain an exclusive population of *S. cyclostigma*. Aggressive behaviour amongst males (inter- and intra-specific) had been observed on several occasions especially within more crowded syconia.

On eclosion from their native galls, females of *S. cyclostigma* become involved in an elaborate cleansing ritual, commencing with the removal of an antennal moult. Grooming movements of females of *C. capensis* are chiefly restricted to smoothing out of the wings with the use of the pro- and metathoracic legs. There is no antennal moult. The sequence of pollen collecting has not been observed since females of *C. capensis* seek immediate escape on dissection of the syconium. However, females leaving the exit channel always have their mesothoracic pockets laden with pollen grains. Pollen collecting has been observed in some other species of *Ficus*.

6. *Fruit dispersal and seed germination*

The ripe syconia of *F. capensis* are extremely attractive, being deep red in colour and usually occurring in large clusters on elongated peduncles. The walls of the syconia are soft and succulent (water content averages 84,5%) and are favoured by several birds, fruit beetles and possibly bats and other arboreal mammals as a source of food. Seeds are dispersed in this manner. Several species of flies, moths, bugs and hymenopterans are also very active around ripening syconia.

A series of germination trials undertaken in growth cabinets indicated 100% germination in all cases. The most rapid germination and best overall growth was obtained under conditions of high temperature (30°C) and humidity (80%). Seeds subjected to conditions of low temperature (15°C) required several additional weeks for germination.

7. *Some interesting observations*

Normally very enlarged galls contain individuals of *Sycophila* sp. or *Camarothorax* sp. These thick walled galls usually occur in groups and, because of the great increase in size, their walls become angular as they coalesce. On a few occasions such enlarged galls were found to contain 5–9 females of *Apocrypta* sp. In another instance 13 females of *S. cyclostigma* emerged from such an enlarged gall. It is not known whether these developed from numerous eggs that were deposited into a single ovary or whether they were a result of polyembrony. However, a male and female wasp were also dissected out of a slightly enlarged ovary. Although these were embryonic, the female could be identified as belonging to the genus *Apocrypta*. The male could not be recognized with any certainty. The fact that these were of separate sexes indicates that they developed from separate ova.

A very unusual find on the experimental tree was the discovery of two 'seed syconia' (1 aerial and 1 geocarpic). These syconia had ripened completely but displayed no exit channels. On dissection, seeds were discovered in both seed and gall flowers and there was a complete lack of insects. These seeds germinated normally. Since selfing within the syconium is excluded, the origin of these seeds is uncertain. If the flowers from these syconia were in fact pollinated by sterile females, remains of the insects would have been found. The only remaining suggestion appears to be that the seeds were produced by some form of parthenogenesis.

DISCUSSION

Flowering in the genus *Ficus*, must involve a tremendous output of energy since each crop of syconia produces many thousands of flowers. Much of this energy becomes spent in the maintenance of a supply of pollinators. Hence, flowering represents a compromise between seed production and the provision of an adequate supply of pollinators. It is therefore of obvious advantage to produce large numbers of small reduced flowers. Seed and gall flowers have evolved as a long term safety mechanism to effectively maintain this fine balance between the production of seeds and pollinators. However, it is important to note that the variation between seed and gall flowers is essentially one of gross morphology and there is no bimodal distinction between them. Occasionally, seeds occur in short styled flowers, whereas fairly long styled flowers produce galls. The continuous range of style lengths does ensure that a percentage of the ovaries remains beyond the reach of the ovipositors of the primary sycophiles. This was determined by measurement of random samples of 200 styles of female flowers and wasp ovipositors.

The developmental cycle of the syconium of *F. capensis* is very similar to that described for *F. sycomorus* (Galil & Eisikowitch, 1968b). However, the very rapid increase in diameter of the syconium during the ripening or postfloral phase has not been emphazised by previous workers. Furthermore, the interfloral phase may be differentiated into two equal sub-phases (C_1 and C_2). During the first half of the interfloral phase (C_1) growth continues at a more or less normal rate while during the second half (C_2) increase in size of the hard green syconia is negligible. C_2 may therefore be regarded as a resting period during which the seed walls harden considerably and the wasps pupate within their galls.

Asynchronous flowering in *F. capensis* ensures that receptive stages of figs are always available for infection by wasps that leave the male or D-phase syconia. This is essential since wasps are believed to be non-feeding and fairly short lived. Females of *C. capensis* survived in the laboratory for periods of 35–50 hours. Sometimes only a single branch on a tree may bear syconia and this usually represents less than 10% of the normal crop. This 'false fruiting' helps to ensure the availability of some syconia in between normal crops, so that, pollinator supplies are successfully maintained. It is interesting to note that the presence of such syconia has also been observed for *F. natalensis* Hochst., in the Durban area.

Although outbreeding may be the general rule in the genus *Ficus*, crop-overlap could result in wasps from male phase syconia pollinating female phase syconia on the same tree. The occurrence of crop-overlap has not been reported by previous workers but close observation might reveal that this is of a more widespread occurrence. Certainly, some inbreeding must occur in populations of *F. capensis*. Since each species has become so specialized a degree of inbreeding can be an advantage in the maintenance of the species. In general, there appears to be a slight increase in fruiting during the warm rainy season with many trees fruiting continuously or displaying degrees of crop overlap. Hence, there will be an ample build-up of seeds and pollinators during this period.

The developmental cycles of the wasps and the syconia are, of necessity, perfectly synchronized. The behavioural patterns of the pollinating wasps viz. pocket filling and pocket emptying ensures successful pollination of receptive flowers. There are two basic reasons for *S. cyclostigma* being ineffective in pollination. Firstly, there are no specialized pollen carrying structures and secondly, the elaborate grooming behaviour of the females reduces the probability of pollen adhering to the body of the insect. On the other hand, pollination by *C. capensis* is very successful since it is a deliberate act resulting from a distinct behavioural sequence. It is important to note that pollination of a few flowers by *S. cyclostigma* cannot be totally excluded. However, the fact that syconia containing exclusive populations of *S. cyclostigma* were completely seedless does indicate that this insect does not affect pollination. Although syconia with unpollinated flowers normally abort, they may persist and ripen if infected by *S. cyclostigma*. Non-infected flowers in such syconia degenerate rapidly. Unlike reports on *S. sycomori* (Galil, Dulberger & Rosen, 1969) in the Middle East, the males of *S. cyclostigma* do not engage in the preparation of an exit channel. Therefore, in the absence of males of *C. capensis*, the entire vespid fauna remains entrapped and perishes within the syconium.

Most of the secondary sycophiles in *F. capensis* are believed to be inquilines i.e. they do not induce gall formation but parasitize existing galls. As such, they do not influence the number of seeds produced per syconium. However, they are unwelcome as they might parasitize galls of *C. capensis* thus causing reduction of the population. Individuals of *Sycophila* sp. and *Camarothorax* sp. develop in enlarged galls with thickened angular walls. These galls usually occur in clumps with gall formation occurring in both short and long styled flowers. It therefore appears that these genera of secondary sycophiles are able to induce gall formation. The elaborate sexual dimorphism present in most sycophilous wasps is lacking in *Sycophila* sp. and *Camarothorax* sp.

The ratios of the different species of wasps occurring in the syconia tend to vary greatly. This would obviously be influenced by availability of the different species of wasps during the receptive and interfloral periods when egg-laying occurs. It is therefore not uncommon to find a crop producing a high percentage of a particular species and exceptionally large populations of *S. cyclostigma* were observed on a number of occasions. Population ratios also vary from one syconium to another within a single crop. In general, however, end of crop syconia produce a very poor population of primary sycophiles. Such syconia mostly contain secondary sycophiles with *Apocrypta* sp. being very common. Since these syconia develop slightly later than the main crop, there are at any one time only a few at the correct interfloral phase for infection by secondary sycophiles. As a result of this, these syconia become heavily infected with the eggs of the available inquilines which then develop at the expense of the primary sycophiles.

A particularly interesting feature in *F. capensis* is the production of geocarpic syconia. These may occur at the soil surface, but are very often buried in the subsurface layers. It was found that geocarpic figs become pollinated and produce viable seeds. Clear knowledge as to how the pollinating wasps gain access to these syconia is completely lacking. Corner (1978) has speculated that wasps might burrow, that geocarpic syconia become exposed by activity of other larger animals, or, that syconia only become buried after pollination has taken place. The last suggestion cannot be accepted for *F. capensis* as young prereceptive syconia may be truly geocarpic. In all cases studied, a colony of ants was found to be associated with the geocarpic syconia. The likelihood of wasps reaching the syconia through the ant burrows thus cannot be totally outruled. However, it is definitely known that ants are predators of fig wasps. As wasps leave male phase syconia through the ostiole they are often snatched up by the waiting workers. These workers may later enter the syconium and carry out the wingless male wasps. Therefore, if wasps had to gain access to the syconia through the ant burrows, they may only do so when ant activity is at a standstill.

The pollination syndrome of the genus *Ficus* probably represents one of the most unique animal-plant relationships existing in nature. The pollination movements of the insects appear to have no short term advantage to the pollinating wasps and is an instinctive behavioural sequence (Galil & Eisikowitch, 1969). One of the most interesting unanswered questions in the pollination story is what attracts the wasps to the syconium. It is very likely to be an olfactory stimulus that attracts the correct pollinator. At present the possibility of investigating the chemical nature of the various components of the syconium is being undertaken. The only other well documented case of ethodynamic pollination is that of the Yucca plant and its pollinating moth (Riley, 1892).

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