FURTHER STUDIES ON THE POLLINATION ECOLOGY OF FICUS SYCOMORUS L. (HYMENOPTERA, CHALCIDOIDEA, AGAONIDAE)

by

J. GALIL and D. EISIKOWITCH

Department of Botany, Tel-Aviv University, Israel

Abstract

The manner of introduction of pollen into the young figs of the sycomore tree (Ficus sycomorus L.) and the pollination act inside the figs have been studied. Unique thoracic pollen pockets have been detected in the body of Ceratosolen arabicus, the legitimate pollinator of F. sycomorus. The existence of these pockets and the behaviour of the wasps in connection with them explain the special role of C. arabicus in the pollination and seed setting of F. sycomorus. The pockets are loaded with pollen prior to escape of the wasp from the almost ripe fig, at the male phase, and are unloaded in the young fig (female phase). Pollination is directly effected by the wasp during egg-laying by the use of its fore legs. The presence of clearly delimited “oviposition areas” of C. arabicus in young figs ensures seed production in long-styled flowers, even in the presence of competitors with long ovipositors. The relationships of the three primary sycophiles of F. sycomorus to each other and to the sycomore tree are discussed.

Introduction

The present paper is the third in a series on pollination ecology and fruit setting in the sycomore fig (Ficus sycomorus L.). For a better understanding of the subject, the reader is kindly referred to the earlier papers in this series (Galil and Eisikowitch, 1968a, b).

In the previous studies on pollination and fruit setting in F. sycomorus several important points remained unsolved, or have not even been properly understood. Thus, for instance, no satisfactory explanation has been offered for the manner of introduction of pollen into the young figs (＝ syconia) at the female phase (B)1). Three species of primary sycophilous wasps are found in F. sycomorus, which enter into the young syconia (phase B) for oviposition (Wiebes, 1968). These are Ceratosolen arabicus Mayr (Agaonidae, Agaoninae), Ceratosolen galili Wiebes (Agaonidae, Agaoninae), and Sycophaga sycomori L. (Agaonidae, Sycophageinae). The mentioned insects are not hairy and carry only a few pollen grains on their surface upon leaving the syconia at the male phase.

1) According to Galil and Eisikowitch (1968a) the developmental phases of figs were named as follows:

Phase A (Pre-female): Young syconium prior to the opening of the ostiole.
Phase B (Female): Ostiolar scales loosen, female flowers ripen, sycophilous wasps penetrate into the syconium and oviposit into the ovaries.
Phase C (Interfloral): Wasp larvae and fig embryos develop within their respective ovaries. Ovaries occupied by the larvae are transformed into galls.
Phase D (Male): Male flowers mature, wasps reach the imago stage, fertilized female wasps leave the syconia via channels bored by the males.
Phase E (Post-floral): Both the syconia and the seeds inside them ripen.
The cleansing movements of their fore and hind legs diminish the quantity of pollen that they carry (Grandi, 1929).

The ostiolar scales of the syconia at the receptive female phase (B) loosen only slightly (Fig. 11, on Pl. 1). The female wasps, upon entering these syconia, push through the narrow slits, the while rubbing their bodies on the ostiolar scales and losing their wings and even the flagella of their antennae at the entrance (Fig. 2). It is not surprising, therefore, that hardly any pollen grains remain on the bodies of the wasps after they enter the syconial cavity. Inasmuch as apomixis has not been detected in F. sycomorus and the unpollinated flowers wither and do not produce seeds, it is impossible to account for the rich seed production of sycomore figs in East Africa.

Although there is no appreciable difference in the amount of pollen carried on the bodies of the three primary sycophiles inhabiting the figs of F. sycomorus, the difference in seed-setting is very significant. Numerous examinations of syconia at phase D have established that seed production in East Africa is invariably connected with the presence of C. arabicus — either alone in the fig or together with one or even both of the other sycophiles. On the other hand, syconia inhabited by C. galili and/or S. sycomori do not produce seeds. This difference between C. arabicus and the other two species is rather perplexing insofar as they all enter the syconia at the receptive phase and would bring pollen if they could carry it.

Another puzzle in the previous studies was seed production within syconia inhabited by both C. arabicus and S. sycomori. On account of its moderate-sized ovipositor, C. arabicus oviposits chiefly into the short-styled flowers, leaving the long-styled ones for seeds. In contrast, the long ovipositor of S. sycomori enables this wasp to occupy all the flowers of the syconium, irrespective of their stylelength. This poses the question as to why many long-styled flowers produce seeds in the presence of a mixed population. Should not Sycophaga occupy all or nearly all of the long-styled flowers, which are left untouched by Ceratosolen? And yet the abundant seed-setting in the syconia with mixed populations clearly indicates that the interrelations between these two species of primary sycophiles are not based solely on the length of the ovipositor.

The aim of the present investigation was twofold: to elucidate the mechanisms whereby pollen is introduced into the syconia, and to observe wasp occupation of the various types of flowers within. For this purpose, a detailed study of the structure of the primary sycophilous wasps and of their behaviour was made, at the various phases of fig development. Only by such study could a better understanding of the interrelations between the wasp species be obtained, and possibly also a solution to the two problems described above.

**Materials and methods**

The majority of the observations and experiments described in the present paper were carried out at Magadi and in Mombasa, Kenya, in the course of two trips (January and August, 1968). In some cases, the syconia and sycophilous wasps of various stages were preserved in 70% alcohol for subsequent study at the Tel-Aviv University.

To locate the “pollen pockets” (see below) in the body of female C. arabicus, intact wasps were stained in various dyes. An alcoholic solution of acid fuchsin was found to penetrate very rapidly into the pollen pockets, staining the contained pollen. After washing each insect in a few changes of water (to eliminate the surplus stain) and
mounting it in lactic acid, the full pockets become clearly visible against the background of its thorax, which remains unstained. Cotton blue penetrates the pockets more slowly: after ten minutes only the pollen grains near the opening are stained. This method is therefore convenient for locating the site of the opening. Under high magnification (× 100) of a dissection microscope, the pollen laden pockets of dried female wasps in ventral view are very prominent even in unstained, unmounted specimens (Fig. 13, on Pl. 1).

For a closer study of the pollen pockets microtome sections, 8 μ thick, were prepared through the thorax of the insect. For this purpose, wasps were fixed in alcoholic Bouin, cut in paraffin embedding and the sections were stained in anilin-blue collagen stain, according to Crossmon (1937). In such sections the pollen grains are clearly visible inside the pockets (Figs. 14, 15, on Pl. 1).

For the observation of the behaviour of wasps during egg-laying, fruiting branches at the end of the pre-female phase (A) were bagged in organdy bags. As soon as the female (B) phase was reached, the already receptive syconia were introduced into plastic boxes together with male-phase (D) syconia and populated with various wasps, as needed. C. arabicus was found to penetrate into the female syconia in the late night hours and in the early morning, whereas S. sycomori penetrated in the evening as well. In syconia cut in half, it was very easy to follow the process of oviposition shortly after penetration: the wasps were intent upon their task and persisted ovipositing even under the strong illumination necessary for observation. To determine the route of the ovipositor shaft inside the pistil, the ovipositing wasps were quick-killed by ether before they could withdraw their ovipositor. They could then be removed together with the pistil and be cleared briefly in chlorax, so as to enable observation of the ovipositor in situ.

In order to study the “oviposition areas” within the syconia, almost ripe figs at the early male phase D (prior to the emergence of the wasps) were bagged individually in transparent cellophane bags. After the wasps emerged from the syconia into the bags the population of each fig became visible. “Monoculture” figs, i.e., occupied by one wasp species only, were used to determine the seed/gall ratios (percentages of seeds, galls and empty flowers) characteristic of each of the primary sycophilous wasps. Figs with a mixed population were used to study separate oviposition areas within one fig.

**THORACIC POLLEN POCKETS IN C. arabicus**

That there is a connection between seed-setting in Ficus sycomorus and the presence of C. arabicus wasps in the figs, was clearly established in our previous studies. Insofar as seed-setting is dependent on pollination, it was reasonable to assume that the insects were implicated in this process. The assumption, however, is offset by the observation that there is hardly any pollen on the external surface of the wasps when they enter the figs at the female phase (B). Although perplexed by these apparently contradictory findings, we were nevertheless convinced that there had to be some structural or behavioural characteristic of the wasps which ensured the introduction of pollen into the fig and the consequent pollination of the female flowers at the proper phase. Undismayed by countless failures to find pollen in the body of the wasps, we tackled the problem anew during our recent visits to East Africa. It is in some way an anticlimax to note that we hit upon the answer to this riddle almost by sheer accident — when a wingless wasp, removed from a young fig at the female phase (B), was stained with cotton blue. At
first there was nothing special about this mounted wasp and as in previous cases, there were no pollen grains to be seen. However, when the mounted wasp was accidentally pressed from above, a dense aggregate of pollen grains appeared at the margin of its body. This initial observation led to the eventual discovery of hidden pollen pockets in the ventral portion of the mesothorax — on both sides of the body (Textfig. 3 and Fig. 13 on Pl. 1). Once found, these pockets were easy to observe and study.
Pockets full of pollen are especially prominent because the pollen grains stain quickly and strongly. Similarly, microtome sections of full pockets are conspicuous due to the typical shape and staining of the pollen grains: these are minute, elliptical bodies, about 10 μ in length, that stain deeply except at the zones of the two polar germ pores which remain unstained (Fig. 1).

In whole-mounts the pollen pockets appear as roughly pear-shaped bodies on both sides of the mesothorax (Figs. 3, 4), with the narrow end pointing backwards. The opening of each pocket is at the narrow end (A in Fig. 4), since it is at this end that staining of the pollen grains commences. Possibly, a second opening (B in Fig. 4) exists near the other end of the pocket, but this opening, if it occurs at all, is probably closed, since no staining of pollen grains was observed to start from this end.

The serial sections (cross- and longitudinal) through the pockets clearly show that they are fully sealed, except for the above-mentioned one or possibly two openings. Each pocket is about 200 μ long, 120 μ wide (maximum width) and about 60 μ thick. Since the dimensions of a single pollen grain are 10 × 6 × 6 μ, a full pocket is estimated to contain 2000—3000 pollen grains.

The only hint as to existence of pollen pockets in fig wasps is found in an article by Grandi (1917), where in a drawing illustrating the sternopleural parts of the meso- and metathorax, the outlines of two empty pockets are clearly seen. Grandi designated these structures as “Parte media sublaterale del mesosterno”. Nothing, however, was said about the pocket-like nature of these organs, or about their function as pollen containers.

The special role of C. arabicus in pollen transfer into the syconia at the female phase (B) and in the consequent seed-setting is fully explained by the pollen-pockets in its body. No such pockets were found in S. sycomori. On the mesothorax of C. galili pockets are discernible, but since in countless preparations these were always found empty, they are not likely to have any functional significance.

Pocket loading

The pollen pockets of C. arabicus are enclosed in a chitinous envelope bearing one or two narrow openings (Fig. 4, A and B). The pollen of F. sycomorus is not exposed, since the anthers remain almost closed even when they are detached by the male wasps in the process of boring the exit tunnels. Under these circumstances, loading of the pollen pockets cannot be attained by mere contact between the body of the insects and the anthers, but rather direct participation of the insects in the loading appears essential.

In order to observe loading of the pollen into the pockets, detached galls containing fertilized females of C. arabicus (i.e., punctured galls with the females still within) were placed in the vicinity of intact anthers. Despite repeated trials, however, the process of pollen loading was not observed. Under these circumstances, apparently, the necessary chain of the insect’s instincts is disrupted, possibly due to cutting of the figs and the strong illumination. Nevertheless, despite failure to observe the act proper, enough data were accumulated as to suggest when and how the loading could occur in the intact fig. Thus, the anthers, which are intact and almost closed when detached from their filaments, later on appear ragged and gnawed along their longitudinal sutures, as if they had been

---

1) A reproduction of Grandi’s original drawing (Fig. iii, 5, p. 16) is given in Fig. 10 of the present paper, where the pockets are indicated as B.
subjected to some external force (Fig. 6). When the female wasps leave the galls and emerge into the syconial cavity their pockets are still empty. Somewhat later, their pockets are already full of pollen. Evidently, the loading of pollen must occur in the meantime. It appears likely that the wasp gnaws open the almost closed anthers and then draws the pollen into its pockets.

EMPTYING OF THE POCKETS: POLLINATION

Immediately upon entering the young syconia at the female phase (B), the female of C. arabicus starts ovipositing into the pistils, one after the other. When the insect reaches the syconial cavity its pockets are full of pollen; when oviposition is over and the insect dies within the fig, the pockets remain intact but are empty, or almost empty. Clearly, the extraction of pollen from the pockets cannot be achieved passively, by the mere rubbing of the insect’s body against the stigmatic surface, but only by directed movements of the wasp, either during oviposition or between successive egg- layoffs.

Oviposition by C. arabicus. — Numerous observations on the behaviour of female wasps inside the syconial cavity convinced us that the act of pollination is so integrated into the oviposition process that it is not possible to understand the one without the other. In general aspects, the oviposition process of C. arabicus is similar to that of Blastophaga pseudes L. of the common fig, as described by Grandi (1929). However, in view of the fact that no pollen pockets have been described for B. pseudes and since the actual pollination act has not been observed previously, we deem it appropriate to describe the entire process of oviposition-pollination as it occurs in C. arabicus. The wasp stands firmly on its six legs. As in Blastophaga, the urosternites, which cover the abdomen from below, diverge downwards, forming a broad flap at right angles to the abdomen. Initially flat or somewhat convex (Fig. 7) the flap folds lengthwise forming a triangular, gutter-like body which serves to support and guide the ovipositor shaft during oviposition (Figs. 8, 9, 16). At this stage the shaft is liberated from the ovipositor valves (see also Snodgrass, 1935) and becomes contained within the triangular flap, ready for oviposition (Fig. 16). The valves do not participate in egg-laying, but extend backwards and upwards from the tip of the abdomen. The probing for the appropriate oviposition site is carried out by the tip of the shaft, which moves back and forth within the gutter-shaped, thickened, distal part of the triangular flap. When the proper site is located, the shaft sinks into the shallow depression at the centre of the round stigma and moves downwards along the collenchymatous, conductive tissue of the style. When the shaft penetrates into the pistil the wasp trembles, lowers its head towards the stigmatic surface and energetically bites the stigmata within reach.

Pollination. — Toward the end of oviposition a special event occurs, which has not been observed in B. pseudes. A few seconds before the withdrawal of the ovipositor shaft, the fore legs of the wasp fold back simultaneously or alternately until the tarsi and pulvilli touch the lower margins of the pollen pockets (Fig. 16). Now the wasp lowers its legs and moves them delicately to and fro, caressing the stigmatic surface below. These actions may be repeated several times.

From the entrance of the female wasp into the fig till its death within it, no other action of the wasp has been detected which may suggest pollen extraction from its pockets. Inasmuch as these pockets ultimately are empty, it follows that the described movements of the fore legs are truly pollination movements and indeed, on several occasions, pollen grains were detected on the tarsi and pulvilli.
Fig. 11. Longitudinal section through an open ostiole of Ficus sycomorus (X 9). Fig. 12. Young sycomore fig, at the end of phase B, with a wreath of Sycophaga wings at the entrance (X 3). Fig. 13. Ventral aspect of Ceratosolen arabicus, showing pollen-laden pockets (dry material, X 20). Fig. 14. Cross-section through the mesothorax of Ceratosolen arabicus, showing pollen pockets (X 150). Fig. 15. Longitudinal section through a pocket of Ceratosolen arabicus (X 250).

J. Galil & D. Eiskowitz: Pollination of Ficus sycomorus
Oviposition duration. — The described pollination movements are very swift. A few seconds later, the female wasp withdraws its shaft out of the pistil and retracts it into the triangular flap. The ovipositor valves do not enfold the shaft between successive egg-layings.

A single episode of oviposition, from insertion of the shaft to its withdrawal, lasts 50 to 70 seconds, rarely up to 100 seconds. Frequently, however, brief insertions of the shaft, which last 5 to 15 seconds, interpose between the regular oviposition episodes.
Such insertions almost never include pollination movements. In several instances, the pistils involved were measured and found to be long-styled. In contrast, the pistils involved in ordinary oviposition episodes were generally short or medium-styled. Apparently, then, mere stingings of the pistils can occur, which are not accompanied by oviposition.

Oviposition by *C. galili*. — The oviposition of *C. galili* is quite similar to that of *C. arabicus*. Here, too, the triangular flap guides and supports the shaft, whereas the valves do not participate in the oviposition. During this process, the insect bites the stigmata much the same as does *C. arabicus*, but the pollination episodes are always missing.

![Fig. 17. Route of ovipositor shaft of *Sycophaga sycomori*](image_url)

Oviposition by *S. sycomori*. — The oviposition of *S. sycomori* differs markedly from that by *Ceratosolen* spp. It rather resembles the egg-laying of *Parakoebelia glomeratus* Ansari as described by Ansari (1966). Making due allowance for the differences between primary and secondary sycophiles, the oviposition process in these two species proceeds along the same main lines. The ovipositor valves support and conduct the shaft during egg-laying. The wasp rises high on its hind legs and projects the ovipositor far behind. After locating the proper oviposition site the wasp moves backwards, inserting the long ovipositor into the pistils. During oviposition the wasp lifts its head high above the syn-
stigma, and no biting movements are discerned. As can be expected, the pollination act is missing entirely. The course of the ovipositor is peculiar: it penetrates the margin of one stigma and proceeds along the style of the neighbouring pistil, eventually disappearing inside the ovary (Fig. 17). The egg is ultimately deposited inside the embryo-sack (Rosen, 1965) and not between the inner integument and the nucellus, as reported for various Agaoninae (Grandi, 1929; Galil and Eisikowitch, 1968a). A single oviposition episode lasts 2½ to 4 minutes, and does not include any extraneous insertions of the shaft. The prolonged oviposition of S. sycomori is certainly a drawback in its competition with C. arabicus, since the latter can lay two or three eggs for every one of the former.

Oviposition areas

During the observations on oviposition in young syconia at phase B (carried out at Mombasa and Magadi in January, 1968) our attention was drawn to peculiar yellow patches on the inner surface of the figs. In these patches the stigmata turned yellow and stood out conspicuously from the snow-white surface of the synstigma. These yellow patches were continuous and included all the flowers, the short- as well as the long-styled. Such yellow areas were especially pronounced in syconia inhabited by a single specimen of C. arabicus or C. galili.

The nature of these yellow patches was soon clarified by observations of the oviposition, when it was found that the stigmata of F. sycomorus turn yellow as a result of wounding. Evidently the movements of the wasps on the stigmatic surface, which involve also biting and puncture of the pistils, eventually produce yellowing, especially in the hotter months of the year, when chemical changes proceed quickly. Mere walking of the wasp, however, does not cause prompt yellowing of the stigmatic surface. The pattern of these yellow areas indicates that oviposition is not scattered, but rather concentrated in one area, which gradually enlarges as oviposition proceeds. In figs occupied by Sycophaga only, such yellow areas were not detected while the wasps were alive. This is probably attributable to the different behaviour of Sycophaga during oviposition.

In B-phase syconia it is possible to ascertain the continuity of oviposition only by the yellow areas. When the figs are opened the wasps become restless and tend to wander over the stigmatic surface and change the site of oviposition. But if the concept of oviposition areas is correct, it ought to be confirmed by the distribution patterns of seeds and galls (seed/gall ratios) in mature or almost mature syconia at the male phase (D). And this is actually the case. As the three primary sycophiles differ in their capacity to occupy the long-styled pistils and in their ability to cause seed-setting in monoculture figs, quite different seed-gall distribution patterns are achieved, as follows (Fig. 18):

1. Figs containing C. arabicus only: Most long-styled flowers produced seeds. Medium-styled flowers produced galls and seeds in similar numbers. Almost all short-styled flowers produced galls.

2. Figs containing C. galili only: No seeds. Most long-styled flowers remained empty and withered. Most medium-styled flowers produced galls, the remainder were found empty. Almost all short-styled flowers produced galls.

3. Figs containing S. sycomori only: No seeds. Almost all the flowers in the fig produced galls. When occupation was high, the percentage of empty flowers was insignificant. When occupation was low, many flowers remained empty.
Fig. 18. Diagrammatic illustration of the distribution of seeds, galls and empty flowers in pieces of figs at phase D, occupied by Ceratosolen arabicus, Ceratosolen galili and Sycophaga separately. Beneath the diagram, percentages of the same, calculated from a great number of figs.

The above data were collected by examining normal syconia populated by one wasp species only, in which the galls and the seeds, if any, developed normally. Abnormal cases, usually occurring at the end of a given fig generation, were not taken into consideration. The inquilines, which are generally found in the figs of F. sycomorus, have not been included, because they occupy the already existing galls and do not interfere with seed-setting (Galil and Eisikowitch, 1968a).

On the basis of the above data it is very easy to delimit the oviposition areas occupied by each species separately, in syconia with a mixed population. Especially prominent, according to seed/gall ratio, are the separate areas in figs inhabited by C. arabicus and S. sycomori. In cases of partial occupation, many empty flowers remain between the occupied areas.

The distribution patterns of the galls and seeds in various parts of a fig inhabited jointly by C. arabicus and S. sycomori clearly indicate that the concept of oviposition arrived at on the basis of the yellow patches in B syconia — is correct. In other words, seed production in these figs is not the result of random dispersal of pollen but is strictly connected with well-defined areas. The above findings point to the fact that the syconium is not a homogeneous unit but is rather divided into separate areas, small or large, according to the nature and number of sycophilous wasps which enter it at the receptive female phase (B). Only precise charting of the entire inner surface of the fig can fully reflect the relationships between the wasps which develop within it.
Discovery of the pollen pockets in *C. arabicus* and the special behaviour of the wasps which is associated with or derived from their presence, brings us nearer to a better understanding of what really happens within the figs. The presence of such pockets fully explains the successful introduction of pollen into the young figs. The pollen transport is ensured by a chain of instincts involving attraction of the female wasps toward the anthers before they leave the syconia at the male phase D (Galil and Eisikowitch, 1968c), loading of the pockets with pollen extracted from the almost closed pollen sacks and ultimately the deposition of the pollen on the stigmata during oviposition.

The pollen sources within the sycomore fig are restricted in view of the small number of detached anthers in the syconial cavity at phase D. The loading of pollen directly from the anthers into the pockets prevents wastage and appears to be essential. Evidently, our previous concept (Galil and Eisikowitch, 1968a) that pollen transport is effected by passive dusting of the wasps with pollen during their passage along the exit tunnel bored through the syconial wall — is not correct.

The presence of thoracic pollen pockets is not unique to *C. arabicus*. In cursory examinations carried out recently, similar pockets have been observed in several other sycomophilous wasps which inhabit *Ficus* species of various sections (*Ceratosolen capensis* Grandi, inhabiting *F. capensis* Thunb.; *Blastophaga quadriceps* Mayr, inhabiting *F. religiosa* L.; *Blastophaga tonduzi* Grandi, within the figs of *F. hemsleyana* Standley). These observations are only preliminary but they suggest that thoracic pockets may be a common means of pollen transport in the legitimate pollinators of various *Ficus* species.

The relationship of *C. galili* to the sycomore fig is of a special interest. The fact that *C. galili* belongs to the Agaoninae and to the genus *Ceratosolen*, naturally raises the possibility that this wasp is a mutualistic symbiont of the sycomore, as are its relatives. However, observations carried out in the course of the present study disproved this idea completely. The female *C. galili* has pollen pockets and its behaviour during oviposition is similar to that of *C. arabicus*. However, several fundamental differences exist between these two species. In repeated tests, the pockets of *C. galili* were always found empty, and the specific pollination movements have not been observed. It appears, therefore, that the pollen pockets of *C. galili* are not functional and that the instincts associated with them are extinct, so that figs inhabited by *C. galili* are seedless. We may conclude then, that *C. galili* is a parasite of *F. sycomorus* and a competitor of *C. arabicus*, which is the only mutualistic symbiont of the tree.

The relationship of *S. sycomori* to *F. sycomorus* is easier to understand. From all aspects, morphological as well as ethological, this wasp is a parasite of the sycomore and a competitor of the legitimate pollinator. Wiebes (1966) noticed the relation of *Sycophaga* to *Eukoebelea* and proposed to include both genera in the family Torymidae, tribe Sycophagni, as contrary to the usual classification (Grandi, 1963; Wiebes, 1961), which includes the *Sycophaga* in the Agaonidae. The present observations on the mode of oviposition and the route of the ovipositor also bear out the peculiarity of *Sycophaga*, and offer further justification for its inclusion in the Torymidae.

All the female flowers in the sycomore fig, the short- as well as the long-styled ones, are fertile and may produce seeds under suitable conditions. The stigmata of all the flowers produce a continuous surface (the synstigma) and there are no grounds for believing that the *C. arabicus* females are able to distinguish between short- and long-

View This Item Online: https://www.biodiversitylibrary.org/item/89667
Permalink: https://www.biodiversitylibrary.org/partpdf/66355

Holding Institution
Harvard University, Museum of Comparative Zoology, Ernst Mayr Library

Sponsored by
Harvard University, Museum of Comparative Zoology, Ernst Mayr Library

Copyright & Reuse
Copyright Status: In copyright. Digitized with the permission of the rights holder.
License: http://creativecommons.org/licenses/by-nc-sa/3.0/
Rights: https://biodiversitylibrary.org/permissions

This document was created from content at the Biodiversity Heritage Library, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at https://www.biodiversitylibrary.org.