

Blepharida biology, as demonstrated by the Sacred Sumac Flea Beetle (*B. sacra* Weise)

(Coleoptera: Chrysomelidae: Alticinae)

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Abstract

The complete life cycle and bio-ecology of the Eremian *Blepharida sacra* (Weise), Sacred Sumac Flea Beetle, are described and assumed to apply in most of the basic aspects to all *Blepharida* Chevrolat. An average of ten eggs are laid in an egg packet consisting of hardened fecal material deposited on the branches of the host *Rhus tripartita* (Bernard. da Ucria) Grande. The leaf feeding larvae have a smooth moist skin, anal proleg for attachment, and "threads" of fecal material attached to them as they feed. There is a prepupal period in a tightly sealed cell made from particles of soil and formed several centimeters under the soil surface near the host tree. Pupation subsequently takes place in the same cell.

In Israel the typical population of *B. sacra* in the Judean Desert was studied for four seasons as well as another isolated, more Mediterranean population. Earlier timing of the life cycle was noticed in the latter population as well as a partial second generation. *B. sacra* eggs develop in an average of 16 to 17 days and are laid in the field between September and November in Israel. An egg parasite, *Tetrastichus* sp. (Eulophidae), was recovered from both populations. The average larval development time is approximately 21 days between October and December; a larval parasitic fly, *Meigenia mutabilis* Fall. (Tachinidae), was found in both populations. A prepupal diapause of six to seven months in a sealed subterranean cell is assumed to be an adaptation to the arid environment. After a pupation period of about 16 days, the adults emerge from these cells and feed for a month or two before diapausing from July until September/October, when the host trees sprout new leaves and the beetles copulate and lay eggs.

Introduction

Originally WEISE (1897) described *Blepharida sacra* as a species of *Podontia* Dalman, a related Oriental genus. WEISE (1897) said that it was unexplainable how such a conspicuous beetle could have been undiscovered in the well-traveled area around Jerusalem. The original type series was collected by Dr. Staudinger, a well-known insect collector and Lepidopterist, and, although not indicated on the labels of the type series, were certainly collected in Wadi Qilt which has been the route between Jerusalem and Jericho since ancient times. This seems even more likely since some of the type series had the locality of Jerusalem and some Jericho. Until very recently the only specimens that existed

anywhere in collections, to the best of my knowledge, were the type series: most in the Zoologisches Museum für Naturkunde der Humboldt-Universität, East Berlin; a few in the Museum G. Frey, Tutzing; and one specimen in the Pic Collection of the Museum National d'Histoire Naturelle, Paris. How is it that this largest of the Palearctic (HEIKERTINGER and CSIKI, 1940) Flea Beetles could have gone undiscovered for so long and then avoided notice for another 70 or so years? Presumably the answer involves its biology and ecology.

In fact little was previously known about the biology of any of the many species of *Blepharida* in the world. *Blepharida* is a tropical African genus with at least one valid Nearctic species throughout North America. Several species have been described as *Blepharida* from the northern Neotropics, e. g. Central America, but mostly of them apparently belong to other genera such as the somewhat related *Notozona* Clark (G. SCHERER, in litt.). The Oriental distribution of *Blepharida* is also questionable. Ironically, of all these the most is known biologically about the one non-tropical species of North America, *B. rhois* (Forster) (= *B. dorothea* Mignot). This species has been known for some time to feed on several species of *Rhus* (Sumac) in North America. RILEY (1874) actually gives descriptions of all stages of *B. rhois*, on *Rhus* spp., including eggs – “elongate pellets of excrement . . . containing five or six eggs” and larvae – “. . . besmeared its back with its own excrement”. MORRIS (1916) mentions observing adults and larvae of *B. rhois* on Canada Sumach (*R. aromatica*) and notes the larval appearance as “liquid excrementitious matter . . . slimy coat” and as “one of the most disgusting sights in the insect world”. He also mentions that it feeds in the hottest mid-day sun. The egg parasite *Tetrastichus ovipransus* Crosby and Leonard, 1917, was described from *B. rhois* as well as the tachinid fly larval parasite *Doryphorophaga aberrans* Townsend (1916). PETERSON (1951) also gives a detailed figure and description of the larva of *B. rhois*. FROST (1972) observed and reared young larvae on *Schinus terebinthifolius* (Brazilian Pepper) in Florida, he gives a few notes about the larvae. FROST (1973) added information about other hosts (*Rhus* spp.), oviposition, and a few notes about the life cycle. Despite these various biological notes and descriptions, no complete phenology or life cycle information has been worked out for *B. rhois*.

PATERSON (1943) mentions that *Rhus* is the host of a South African species of *Blepharida*. She also gives some morphological details of the larvae and pupae of that species. SCHERER (1973) gives records of two other South African species feeding on *Rhus*. LEWIN (1912) and NEUWINGER and SCHERER (1978) report that the larvae of two species of *Blepharida* are apparently used by the Bushman tribe of southern Africa for poisoning their darts and arrows. Therefore, until now relatively little was known about the bio-ecology of any of the many *Blepharida* species.

Methods

This study was conducted both in the field and in the laboratory between October 1977 and July 1980 in Israel. Two populations were checked in the field and samples transferred, at different stages, to the laboratory at the Faculty of Agriculture of the Hebrew University of Jerusalem located in the southern coastal plain of Israel. The most typical populations of *B. sacra* exist in the Judean Desert (Wadi Qilt) between Jerusalem and Jericho where large populations of the host (*R. tripartita*) exist. The second population is located in the foothills of western Samaria near the coastal plain at Yarithiv.

This population of the host is evidently a relictual one nearer to the Mediterranean than to its desert range. The environment at the Yarhiv site is more Mediterranean and provides an interesting comparison to the desert environment of W. Qilt. In late October 1977 adults, and some eggs and larvae from Yarhiv, were hand collected from the two populations in the field and brought to the laboratory for rearing. During the entire study fresh or refrigerated branches of the host were provided every two or three days. The larvae and adults were kept in plastic containers (10.5 cm × 10.5 cm with a depth of 6.5, 9.5, or 12.5 cm) with a screen cover. Small petri dishes of soil were provided for pupation. During the 1977–1978 season the beetles were reared in a controlled environment room at the Faculty of Agriculture with a 12 hour day/night light regime and 65% relative humidity at 27°C. During the 1978–1979 and 1979–1980 seasons both populations were also sampled in September/October and the beetles reared under natural conditions of light, humidity, and temperature in the lab at Rehovot. In all three seasons the two field populations were checked once or twice each month between September/October and February and again in the dormant season, June–July. At these times the progress of the life cycle in nature was observed and usually some samples of the various stages were collected to be reared further in the lab. Observations of the different stages were made both in the field and in the lab.

The incubation period for the eggs was determined by daily removal and separation of eggs from cages of newly mated, ovipositing females. The number of eggs per packet and the number of packets per female were counted to obtain approximate averages. The larval cycle was observed daily in the lab. Prepupae were checked periodically for changes; both those in the dirt cells as well as some not given dirt for prepupal cell construction.

Results

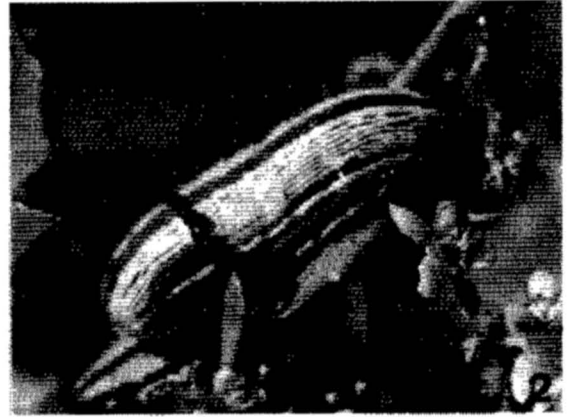
Eggs

The season of egg laying for *B. sacra* begins in late September and continues through October into early November. A few freshly deposited eggs were discovered at Yarhiv on July 12, 1979. The incubation time ranges from 11–19 days with an average of 16–17 days. The eggs are oblong (about 1.0 mm in length), orange, covered with a thin white membrane, and are deposited in “cases” or packets on the branches or twigs of the host tree, especially at the junctures of the branches and twigs or thorns (Fig. 1). These packets are actually made of fecal material of the ovipositing female. Each egg is simultaneously covered with a layer of feces as it is being deposited. This material soon dries into a hard black or sometimes dark brown covering. There are from 2 to 13 eggs in a single packet but the average is 9–10 eggs per packet. I have recorded more than 40 egg packets from a single female (ca. 400 eggs) and probably some females can lay even more. FROST (1973) recorded 94 egg packets per female (ca. 900 eggs per female) for *B. rhois*. There was an apparent tendency in the desert population (W. Qilt) for the egg packets to be deposited most frequently on the older branches rather than the new twigs.

An egg parasite, *Tetrastichus* sp. near *gallerucae* (Fonsc.) (Eulophidae), was recovered from field collected egg packets from both W. Qilt and Yarhiv. The wasps emerged (Oct. 1 to Nov. 13) 1 to 18 days after the eggs were collected. In one unusual case, eggs collected at Yahiv on July 12, 1979 yielded parasites three months later.

Larvae

The larval color is an overall green or yellow, but the details of the pattern (Fig. 2) consist of a series of longitudinal stripes apparently formed by lines of white fat bodies (not



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- Fig. 1: Egg packet of *Blepharida sacra* (Weise) on *Rhus tripartita*.
Fig. 2: Last instar larva of *Blepharida sacra* (Weise) on *Rhus tripartita* (note fecal thread).
Fig. 3: Prepupae and pupa of *Blepharida sacra* (Weise).
Fig. 4: Prepupal/pupal cells of *Blepharida sacra* (Weise).
Fig. 5: Adult of *Blepharida sacra* (Weise) on *Rhus tripartita*.

Malpighian tubules as suggested by PATERSON, 1943) of different thicknesses intermittent with transparent stripes of integument. The widest transparent stripe is mid-dorsally laterad to which is a band of many uneven white lines close together; this is followed laterally by two transparent stripes alternate with two more thickened white lines. A deeper white line can be seen below the most laterad transparent stripe and the most laterad white line passes through all abdominal spiracles. This pattern of longitudinal stripes and lines is quite distinct throughout most of the larval life. The larvae have a smooth, moist, mucous-like skin somewhat similar to a snail. The pronotum is mostly covered by a black chitinized shield. They have a type of fleshy, lobed anal proleg (below the anus) on the tenth abdominal segment that is used for attachment to the substrate when feeding or crawling. Last instar larvae are from 1.2 to 1.4 cm in length. PATERSON (1943) and PATERSON (1951) give some details of larval morphology, including chaetotaxy, for *B. nigrotesselata* Baly from South Africa and *B. rhois* from North America, respectively.

The larvae are found from October to December and sometimes a few in January. The average period of larval development for lab-reared specimens is 21 days. This can be prolonged by at least an additional week under conditions of high humidity. In the field, larvae can be found at several stages of development (instars) in a population throughout most of the season, thus a stagger-effect in development presumably advantageous to the species. The larvae feed in a caterpillar-like fashion eating crescent shaped notches in the edges of the leaves. The larvae have "threads" of fecal material still attached to the anus that protrude 2–3 cm or more posteriorly and often curled over the dorsum (Fig. 2).

A parasitic fly, *Meigenia mutabilis* Fall. (Tachinidae), was recovered from wild-collected larvae of both populations, killed the beetle larvae as they began to prepupate and the fly pupated under the beetle larval skin.

Prepupae

After the mature larvae has terminated feeding it becomes yellowish in color and the larval pattern is less distinct. This is apparently because of the build-up and thickening of the longitudinal lines of fat bodies. Also at this prepupal stage the skin has a much drier appearance and the body becomes stouter with the abdominal segmentation more accentuated (Fig. 3). In the field the larvae that are ready to prepupate presumably wander down from the host tree and enter the soil not far from the base of the host. In the lab, if not offered soil for prepupation, the larvae wander endlessly around the cage and finally come to rest in a quiescent curled prepupal position. When the larvae are offered a small dish of soil they usually enter it and form a hardened, sealed prepupal cell from particles of soil (Fig. 4). This cell is sealed very tightly and presumably preserves humidity inside. When these cells were opened and the prepupae exposed they usually desiccated slowly and did not pupate. In the field such prepupal cells were found more than 6 cm below the soil surface.

Prepupation commences in November through January. Under natural ambient conditions in the lab at Rehovot, the range of prepupation and pupation together is between 192–235 days (6.5 to more than 7.5 months). This is actually a diapause period (almost entirely in the prepupal stage); thus, the prepupal diapause is approximately 6 to 7 months long. However, when reared in a controlled environment in high humidity the period of prepupation ranges from 13–21 days, averaging around 13–15 days, but without much regularity.

Pupae

Pupation takes place within the "prepupal cell". It is rather difficult to observe this change from prepupa to pupa because if the cell is disturbed the developmental cycle is usually unnatural. The pupae are rather normal exarctate chrysomelid pupae, yellow or yellow-green in color (Fig. 3). In the field and in the laboratory under natural conditions pupation takes place during late May until early July. The duration of the pupal stage is approximately 15–17 days; but when reared in high humidity there is a range from 9–21 days.

Adults

The background color of the adult beetles is a dark red-brown. The elytra each have 10 striae (dark red-brown) of deep punctures some of which are convergent subapically. The inter-striae are smooth and yellow in color with irregular amounts of dark red-brown spots in the pattern. Similar spots are also present irregularly along the lateral margins of the elytra. The humeral bossae (shoulders) are smooth with a dark red-brown spot. The pronotum is often somewhat lighter reddish-brown or orange with a sometimes variable pattern, its lateral margins always lighter. The head and entire venter, including the legs, are also colored dark red-brown (Fig. 5). Adult beetles range in length from about 6–8 mm.

In the beginning of the season (September/October) adults can be found in the field in the largest numbers and copulating pairs are common at that time. During copulation the male makes slow and weak lateral movements of the apex of his abdomen apparently using pressure from the hind legs. The female sometimes makes strong and quick lateral movements of the entire body, especially the abdomen, possibly in response to the male or to shake him loose. This behavior is typical of other Alticinae based on personal observations. In the lab multiple copulations between the same pair or of a single female were often observed and copulation often took place at night. Copulations of 30 minutes or more were observed and sometimes the female would feed during copulation. Females would begin to lay eggs within several hours or a day after copulation. The behavioral aspects of copulation have also been observed in the field. By November–December adults are very rarely found and have presumably dispersed and died out. Adults have been kept alive in the laboratory longer but most die soon after copulation and egg laying. The adults emerge from the pupae from May/June until early July at which time they feed lightly and can be found quite commonly. These newly emerged adults were sometimes observed copulating and a few fresh egg packets were found in the field at that time. Also these new adults would copulate frequently when brought to the lab, but no eggs were laid. This phenomenon was observed only with beetles from the Yarhiv population. The newly emerged adults apparently diapause during the hottest driest season (July to September) breaking the diapause in October to feed and reproduce. The adult summer diapause is presumably spent underneath soil and debris near the base of Sumac trees.

Adults eat notches from the leaf edge rather than the round pit-like holes characteristic of Flea Beetles. In October adults and larvae can be found together in the field but the larvae do relatively more damage to the foliage. The adults are often somewhat inconspicuous when they rest or feed on the Sumac trees because their overall reddish brown color is similar to the newer twigs and branches of their host. However, a trained eye can usually find them without much difficulty.

No predators of adult *B. sacra* were observed. Potentially spiders or lizards could be predators, but none of the webs of the several spiders associated with this Sumac contained *B. sacra* remains. It may be possible, as suggested by LEWIN (1912), that *Blepharida* are distasteful or toxic to most vertebrate predators. In the case of birds and some other potential predators the strong jumping ability of Flea Beetles may be the major reason that they are not sought as prey.

B. sacra was tested in repetitions for the length of their jump and maximum records of 67 cm were recorded with approximately 20 cm jumping height also observed. A very interesting phenomenon was also noticed relative to their escape behavior. Very often after a jump the beetles fall to the ground under the Sumac tree, then land on their elytra with the ventral side up and feign death. As mentioned above the entire ventrad is dark reddish brown and this is basically the same color as the senescent leaves of *R. tripartita* that accumulate under the tree – thus, a protective camouflage situation is achieved. This phenomenon was observed numerous times, especially in the W. Qilt desert population.

Blepharida sacra is specific to *Rhus tripartita*. Both larvae and adults were tested on *Rhus coriaria* (L.), the other common species in this region (Middle East), and they would not eat it at all. However, an introduced ornamental tree, the Brazilian Pepper (*Schinus terebinthifolius* Raddi), of the same family was eaten by both larvae and adult beetles. A few young larvae fed on *Schinus* but failed to prepupate. Although this is not a natural host plant, it is known that other species of *Blepharida* can feed on it (FROST, 1972) as well as other *Rhus*-feeding insects (FURTH and HALPERIN, 1980).

Discussion

Until recently *Blepharida sacra* was only known from the Judean Desert (Wadi Qilt) in the original description (WEISE, 1897) and type series. SCHERER (1972) recorded it from the Red Sea coast of Sudan. It is an Eremian (Saharo-Arabian) faunal element and presumably feeds on the same host, *Rhus tripartita*, in Sudan as in Israel. The host and the beetle seem to have a relictual distribution and this biogeographical relationship is discussed elsewhere (FURTH, in preparation).

The deposition of the eggs in a packet of fecal material is an interesting and rather unusual practice for Alticinae or any beetle. Evidently it serves to protect the delicate eggs from the elements of climate as well as to hide them to some degree from potential predators, especially those using visual search. Such a packet of eggs can be firmly attached to the most optimum locations on the host even before the full foliage has developed. In late September 1978, at W. Qilt the first larvae of the season were found on one of the few Sumac trees with any leaves at all and with more leaves than others in the area. The same tree had the only new egg packet of *Thaumetopoea jordana* (Staudinger), also a specific feeder on *R. tripartita* (FURTH and HALPERIN, 1980). Therefore, specialists locate and oviposit on the host trees, that have the first foliage, through visual and/or chemical cues. The tendency (not yet statistically measured) of *B. sacra* egg packets to be deposited on the older, tougher, thorned branches or twigs rather than the newer soft growth may indicate a relatively recent behavioral selective pressure on these beetles in desert populations because of the heavy grazing pressure by domestic goats and sheep. Thus, eggs on more protective parts of the host are less likely to be eaten by grazing animals. This egg packet de-

position is certainly characteristic of the genus *Blepharida*; however, the location of the packet on the host varies (FROST, 1973 and FURTH, in preparation). There is another interesting aspect of these egg packets in that they remain on the host tree for at least one year and probably in some cases for several years. Therefore, even in the season when no live stages of the beetle may be evident on a Sumac tree population, careful searching can discover the presence or absence of beetle populations through the occurrence of old egg packets.

The overall greenish color of the larvae provide a good general camouflage. The "fecal threads" always attached to the larvae (Fig. 2) and those threads that periodically break off are quite good indicators for discovering and locating feeding larvae. These threads are usually very dry but attached to a moist section held within the larva's anus. This fecal thread possibly serves for efficient water reabsorption from the feces and is an adaptation to arid environments. The moist skin of the larvae may be a type of prevention from desiccation, an aid for respiration or excretion, or an overall protective feature against predators. The number of instars was difficult to determine; however, presumably there are either three, as indicated by PATERSON (1943) for a South African species, or four as noted by RILEY (1874) for *B. rhois* in North America.

Perhaps one of the most striking aspects of the biology of *B. sacra* is the very long diapause between prepupa and adult (6.5 to 7.5 months). Most of this diapause is spent in the prepupal stage and because the average actual time of pupation is approximately 16 days, the prepupal diapause is about 6 to 7 months in duration. This prepupal diapause is evidently an adaptation to the desert or arid existence of *B. sacra* and its host *R. tripartita*, even though some of this diapause overlaps with the wet winter months and some in the dry yet cooler spring. The harshest (hot) season (July through September) is spent as an adult, which may be better able to withstand the summer desert heat, in a second diapause. It is interesting to note that another specific feeder on this *Rhus* host, *Thaumetopoea jordana* (Staudinger), also has an exceptionally long pupal diapause (6-8 months or more) during the harshest season, presumably an adaptation to the desert environment (FURTH and HALPERIN, 1980).

The two populations of *B. sacra* that were studied are located in quite different ecosystems. Wadi Qilt is typical of the Judean Desert with low diversity, sparse, xerophilic vegetation and with a very hot spring and summer (April til October), and a low average annual precipitation (ca. 145 mm) occurring mostly in November til March. Wadi Qilt is the type locality for *B. sacra* and is the typical and most widespread present-day environment for this beetle as well as its host *Rhus tripartita*. Yarhiv is often referred to as Coastal Plain; however, the location of *R. tripartita* populations is actually in the western foothills of Samaria which has a different ecosystem than true coastal plain. At Yarhiv the vegetation is more that of the Mediterranean garigue with more diverse, mesophilic species of plants than at W. Qilt. Also, at Yarhiv the spring and summer (May til September) is less hot and the average annual precipitation is higher (ca. 560 mm) occurring primarily from November until March. During the four seasons of this study of *B. sacra* most of the field observations were made at both localities, usually within a week of each other. It was apparent that some constant difference in the timing of the beetle's life cycle existed between these two localities. The population at Yarhiv was approximately two to three weeks more advanced in development than the population of W. Qilt. This is presumably due to the climatic differences of these two localities mentioned above.

Probably related to the environmental differences between these two localities is the fact that newly emerged adults collected in the summer at Yarhiv (July 12, 1979) often copulated and some laid viable eggs that apparently produced a relatively small population of larvae (some mature larvae were found in early October 1979) which probably completed development and pupated; thus, a partial second generation. However, the extent and success of this second generation needs to be investigated further. The fact that this phenomenon occurs only at Yarhiv may be further evidence of the importance of environmental influence. RILEY (1874) mentions that a second generation (partially overlapping) of larvae occurs in North America and spends the hotter months of the summer in the ground before emerging as adults in September.

This is the first study of the complete life cycle and field ecology of any species of the genus *Blepharida*. Some aspects of the biology and life cycle of *B. sacra* such as location of egg packet deposition, long prepupal and adult diapause, relictual distribution, are adaptations to this beetle's association with its specific host's (*R. tripartita*) distribution and ecology as well as with the harsh desert or arid environment. It is proposed that the common name for *B. sacra* (WEISE) be Sacred Sumac Flea Beetle. This beetle is a specific feeder on *Rhus tripartita* which is a desert adapted species throughout most of its range, unlike most of the species of *Rhus* (Sumac) in the world. Many other aspects of the biology of *B. sacra* are assumed to be generally applicable to all *Blepharida* species, such as: the deposition of egg packets made from hardened fecal material; the basic anatomy and behavior of the larval stage, e. g. moist smooth skin, anal proleg for attachment, and fecal threads produced and attached to the feeding larvae; the tightly-sealed subterranean prepupal/pupal cell; and certain aspects of adult mating and feeding behavior. Yet other traits of *Blepharida* need to be investigated further to determine if they are species specific or pan-generic in nature, e. g. poisonous or distastefulness of larvae and adults.

Blepharida is a tropical African genus with apparently an outlying species in the Nearctic. Those species recorded as *Blepharida* from the Neotropics probably belong to the related genus *Notozona* or to other genera (SCHERER, in litt.). The closest relatives of *Blepharida* are *Calotheca* Heyden (considered as a subgenus of *Blepharida* by some, HEIKERTINGER and CSIKI, 1940) from the Ethiopian Region and *Podontia* Dalman and *Ophrida* Chapuis from the Oriental Region. Of the related genera evidently *Podontia* is the closest to *Blepharida*, based on morphology and biology of all stages. It is no surprise that WEISE (1897) first described *B. sacra* as a *Podontia*, because it was the first species of these related genera that he came in contact with; later, in the early 1900's, WEISE began to publish more about African *Blepharida*. He apparently considered Palestine as closer to the Asian fauna anyway; thus, *Podontia* was a logical mistake, especially because the Asian species of *Podontia* were known long before the African ones. In fact, the African species of *Blepharida* were first considered to be *Podontia* (HEIKERTINGER and CSIKI, 1940). *Podontia* and *Blepharida* are quite similar in their adult and larval morphology (TAKIZAWA, 1978). In addition, the host of *Podontia* is also *Rhus*, in some cases also other genera of Anacardiaceae (TAKIZAWA, 1978); a very important mutual character. It is still premature to try to decipher the phylogeny of *Blepharida* because further morphological and biological studies are needed on the above-mentioned and any other related genera. Tentatively it could be said that at least *Blepharida* and *Podontia* form a monophyletic Paleotropical group and that possibly the New World *Blepharida* spread there before the separation of Africa and South America.

Acknowledgements

I would like to thank Dr. Gerhard Scherer for helpful information about *Blepharida* and related genera. Some of this research on *Blepharida sacra* was conducted during a Postdoctoral Fellowship at the Faculty of Agriculture of the Hebrew University of Jerusalem, from 1977 to 1979.

I would also like to thank Prof. J. Kugler (Tel Aviv University) for identification of the tachinid larval parasite and Dr. Z. Boucek of the British Museum (Natural History) for the identification of the eulophid egg parasite.

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Angenommen am 1. 10. 1981