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1140 W. Orange Grove Ave., Arcadia, California, U.S.A.

BIONOMICS OF *AGATHYMUS* (MEGATHYMIDAE)

KILIAN ROEVER[1]
University of Arizona, Tucson, Arizona

OBSERVATIONS OF ALL THE NAMED AGATHYMUS forms occurring in the United States have convinced me that their bionomics are, in many respects, similar enough to be presented in a general account. Unless otherwise noted the observations on which this study was based refer to the following Arizona forms: *Agathymus neumoegeni* (Edwards), *A. polingi* (Skinner), *A. evansi* (Freeman), *A. aryxna* (Dyar), *A. baueri* (Stallings and Turner), *A. freemani* S. and T., and *A. alliae* (S. and T.).

Variations in bionomics at the species level will be treated in a paper currently being prepared.

ADULTS

The species of *Agathymus* are limited to tropical and subtropical America by the distribution of their food plants, members of *Agave*. The northern distributional limits of the *Agathymus* species lie in southern California, southern Nevada, southern Utah, and central New Mexico. It is expected that these limits will remain fixed because the northern limits of *Agave* are encompassed by this area. The known southern limit presently lies in Panama, but I expect the *Agathymus* are represented in northern South America where agaves are know nto occur. Sixteen named forms are known from the United States with Texas and Arizona containing the greatest number, eight and seven respectively.

The adults, which are diurnal, fly during the late summer and fall months. Their flight is usually very swift and erratic. Numerous feeding observations indicated that only the males feed. Feeding always took place on a damp substrate, i.e., wet sand, mud, fresh manure, or directly from water. I have no evidence that these insects visit nectar sources. An apparent preference was shown for feeding sites located in the shade.

[1] This study was conducted as a partial fulfillment of the requirements for the Master of Science Degree at the University of Arizona.

Continuous feeding was noted for periods up to thirty minutes. In cases where individuals remained at a feeding site for several hours the feeding was discontinuous. While feeding the males continually excreted drops of liquid. The assimilation and excretion of liquid in large amounts suggests that some material in a weak solution may be removed by the insects. It does not seem reasonable that lengthly feeding would be necessary to replace water lost in metabolism. All of the Arizona forms except *A. alliae* and *A. polingi* were taken at water. The former can not be considered a nonfeeder because a suitable substrate was not present where that species was observed. *Agathymus polingi* showed no indication of feeding, even when nearby water sources were attracting *A. aryxna*.

Observations of adults made in colonies of their respective foodplants indicated a given population may be divided in the morning hours as follows: virgin females, gravid females, territorial males, and transient males. Females which were apparently virgin were rarely encountered in the field, but these limited observations indicated that mating took place soon after eclosion if males were available.

The mating procedure of members of the *A. polingi* complex was observed four times and of *A. baueri* once under natural conditions. Based on those matings, plus observations when caged virgin females were released in the wild, the following account of an *A. polingi* mating is regarded as typical. A female was seen flying over a dense patch of the foodplant about two feet off the ground when a male, perched roughly six feet from her line of flight, suddenly gave pursuit. The male was approximately six inches away when the female alighted abruptly, followed closely by the male which landed parallel to her and about one-half inch away. The female half-spread her wings and fluttered them rapidly while the male remained passive with wings held tightly together. After several seconds passed the male curved his abdomen laterally so that his genitalia touched the caudal tip of the female. This behavior was repeated three or four times before the female responded by depressing the central part of her abdomen and exposing her genitalia. The male attached himself immediately, then walked slowly away from the female in an arc of 180°. After slight movements on the female's part the pair came to rest so that the two faced in opposite directions. The estimated time required for courtship and engagement was one minute. Copulation in the field was

noted between 10 and 11 A.M., whereas the copulation of caged specimens generally took place between 8 and 10 A.M., with the matings lasting three to four hours.

Males of all forms, except *A. evansi,* exhibited territorial behavior. Observations of *A. evansi* were limited to transient males and ovipositing females. Territories were all proximate to the foodplant with perches being established on rock outcroppings or on dead and living portions of the foodplant. Territories were obvious from 8:30 A.M. to 1 P.M. During this period the males frequently sat with the forewings opened to approximately 75° and the hindwings held at about 45°, oriented in such a position that the upper wing surface was directly exposed to the sun. Territorial males showed a keen sense of recognition for virgin females and transient males, but rarely left their perches to investigate ovipositing females, *Agathymus* of other species, or other insects passing through their territory. Territory infringement by transient males invariably resulted in pursuit by the territorial male. This pursuit resulted either in both participants leaving the territory in a low-level, linear flight or in a "dogfight" with the participants rising vertically to varying heights. In the case of the low-level flight the male usually returned to the original perch, or one close to it, within a minute. If there was a "dogfight" flight, frequently three or four minutes passed before a male returned to occupy the territory. Based on the rare cases where a wing defect permitted recognition of a territorial male, it appeared that the original occupant returned to his territory after an encounter with a transient.

In the few cases where males left their perches to investigate ovipositing females they returned to the perches after approach-no closer than two or three feet. With virgin females the males, without hesitation, approached much closer, resulting either in mating within the territory, or a low-level flight into adjoining territories with other males joining the original pair. Under the competitive conditions of the latter case no matings were observed.

In an attempt to determine how the males differentiate between virgin and gravid females, caged females (of *A. baueri* and *A. polingi*) in both conditions were placed near territorial males. These males showed no sign of recognition until the females were released, after which the responses noted previously under natural conditions were duplicated. A theory which

appears to be supported by my observations is that recognition is bidirectional in that while the initial recognition response is made by the male, the receptive female furthers this response by emitting a pheromone when the male approaches.

During the afternoon hours territorial behavior is abandoned, perhaps because the females which emerged that day have mated. The males at that time of day can be classified as transient or sedentary. The sedentary males usually sat in the shade with their wings closed and ignored the transients. In the afternoon the transient males seemed to be those individuals going to and from water or searching for a resting place. I believe many males which occupy fixed territories in the morning become transitory in the afternoon. This belief is founded on the observation that in the afternoon males were often absent from areas they had occupied in the morning. It was not possible for me to recognize the same male in any given territory two days in succession.

Throughout the morning transient males appeared to be those going to or from a food source or males searching for a territory. I saw no indication that these males were seeking females. During peak flight periods several observations such as the following were made:

> After observing, for one hour, the behavior of two males of *A. baueri* which had established territories in a small clearing, they were collected. In the next two hours thirty-four males were taken as they established territories in the clearing. The majority chose the same perches from which the first two males were collected.

That some transients are searching for territories and that a territory selected by one male fits the requirements of many males seems obvious after such observations.

Oviposition by *A. aryxna, A. baueri, A. freemani, A. evansi, A. polingi,* and *A. neumoegeni* was observed under natural conditions, the method being similar for each. Foodplant selection was usually rapid. Females seldom were seen fluttering around a group of plants in an apparent effort to locate a particular site for oviposition. The substratum on which oviposition took place was generally the under surface of a leaf near the tip in the central third of the plant. Tactal contact with the foodplant was not necessary to stimulate oviposition because some females laid eggs while sitting on rocks and branches lying near agaves. Upon alighting the female would remain stationary for a brief period, then curve her abdomen until the tip came in contact with the substratum, after which the abdomen was returned to

its normal position. These movements were made slowly, without a flicking or lateral movement of the abdomen. As the tip was removed from the substratum an abdominal contraction was visible, which resulted in the expulsion of a single egg. The egg, which lacks an adhesive, would then fall to the leaf base or onto the ground. The females always took flight after laying each egg, although they would occasionally return to the same plant several times for oviposition. The final resting place of the egg, if laid when the female is on a plant, is in part determined by the leaf arrangement. The eggs lodge between the leaf bases of those *Agave* with a compact leaf rosette, but usually fall to the ground if the plant has an open leaf arrangement. In the field oviposition was noted between 11 A.M. and 3 P.M. The only previous observation of oviposition under natural conditions differs markedly from mine. Freeman (1951), reporting on *A. aryxna* and *A. evansi* stated, "The method of egg laying was to flick the abdomen from side to side as they flew around the agave plants. The female attempted to flip the egg into the plant; the larvae then would not have to crawl far to arrive at food."

The number of eggs produced and the period over which they are laid can only be surmised from laboratory results. Cage-bred females laid from 80 to 152 eggs, with no clearly defined differences between species. During the first twelve hours after mating the females laid at least half of their eggs. There was a noticeable drop in the eggs produced during the following 48 to 72 hours, but roughly twelve hours prior to death the oviposition rate increased sharply. Death occured from four to five days after mating. An example which I consider typical, based on *A. neumoegeni*, is as follows: 2-12 hours after mating, 70 eggs; 12-83 hours after mating, 18 eggs; 83-100 hours after mating, 25 eggs. The female then died and dissection revealed twelve fully formed eggs still present in her abdomen. Captive females oviposited over a much longer period each day than did females under natural conditions.

The adults are strongly solar positive in that flight activity stops shortly after clouds block the direct sunshine. During such periods the adults sit quietly with wings closed.

No observations were made which would indicate the nocturnal resting sites. On two occasions I spent several hours at night in a locality where *A. polingi* and *A. aryxna* were common, but failed to locate the sleeping insects. Brown and

Creelman (1935), reporting on the habits of *Agathymus stephensi* (Skinner) in San Diego County, California, stated that males were found sleeping on the outer branches of bushes at varying heights, but not on the foodplant. It is puzzling that they could only locate the males.

The longevity of adults under natural conditions is not known, but obviously is encompassed by the flight period in a given locality. The observed flight periods range from five to twelve weeks, depending on both the species and population. Caged specimens (males and unmated females) exposed to direct sunlight without access to water survived for as long as ten days, with four to seven days appearing more normal under those conditions. Both males and females survived for two to three weeks under refrigeration at 20 C.

OVA

The eggs of all species are hemispherical with a slightly concave base (Fig. 1). The chorion has a finely granular texture except for the micropylar area which appears smooth. Both external and internal color changes are visible during incubation. A composite account of these color changes, based on the Arizona species, is as follows: The egg at the time of oviposition was a shade of green or yellow, depending on the species. Shortly after being laid a marking in some shade of red developed on the chorion. Within a day after being deposited most eggs were plainly marbled over all parts of the shell. Each egg appeared to have a different pattern. The ground color and marbling became darker with age, maximum color intensity being reached in about six days. By the ninth day the shell began to lose color and internal color changes were visible, particularly the dark head capsule of the developing larva. By the twelfth day all external coloration had disappeared and the color of the larva was visible through the chorion.

Embryological development was completed from nine to twelve days after oviposition, judging from larval characters visible through the shell. Eclosion occurred from twenty-two to fifty-two days after oviposition in all eggs subject to outside temperatures and humidity changes. Eclosion from some ova kept at room temperature occurred from eighteen to twenty-four days after being deposited. Several five-day old eggs of *A. polingi* were refrigerated at 2°C. for three days. Larvae emerged from these eggs four to five days later than larvae from nonrefrigerated eggs laid at the same time. This indicates that

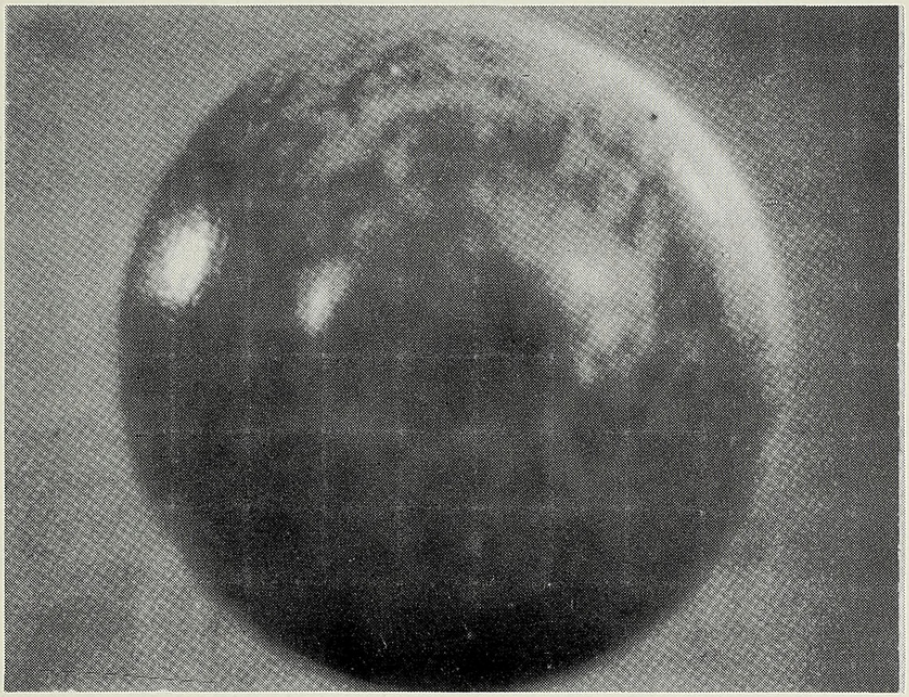


Fig. 1. Dorsal view of *Agathymus baueri* egg.

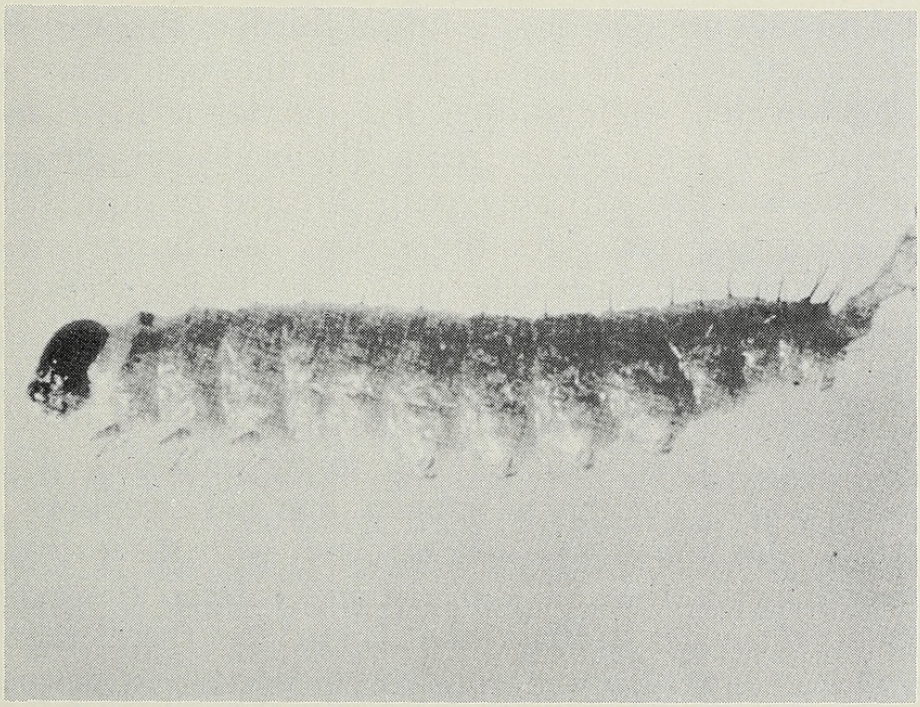


Fig. 2. First instar larva of *Agathymus polingi*.

temperature may play an important part in the time of eclosion under natural conditions. At least some larvae of all the Arizona species of *Agathymus* are known to emerge from the egg during late autumn.

The eclosion process required from one to three days. The first indication that eclosion was about to occur was the appearance of a minute hole in the micropylar area. This hole was slowly enlarged by the larva until the entire micropylar area, as well as part of the surrounding chorion had been consumed, leaving a jagged opening slightly larger than the head capsule. When the hole had reached a size sufficient to permit emergence the larva left the shell within a few minutes. Some lepidopterous larvae are known to consume the entire egg shell after eclosion. *Agathymus* larvae showed no interest in feeding on the chorion after hatching, even under starvation conditions.

LARVAE (Fig. 2)

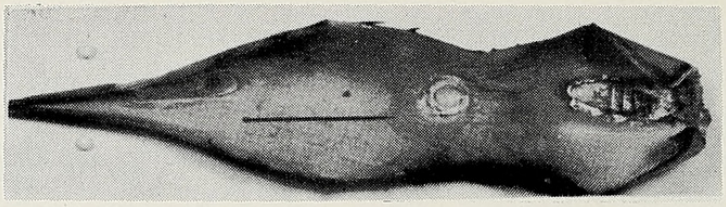
After eclosion the larvae crawled toward the leaf tips. While they crawled they applied a continuous layer of silk to the leaf surface, apparently to gain a better foothold. Larvae which were transferred to a new leaf surface did not maintain their position unless given an opportcnity to construct a silk holdfast.

The larvae did not attempt to feed until they reached the apical half, or more frequently the apical third, of the leaf. Feeding commenced with the excavation in the epidermis of a circular hole which slightly exceeded the larva in diameter. These excavations were most frequently made on the upper surface of the leaf and typically were directed toward the leaf tip. Usually within two days the larvae had burrowed to a depth which concealed them from view. One to five weeks were required to complete the apical gallery. (Fig. 3) The variation in time taken to construct the tunnel resulted, at least in part, from temperature effects on larval activity, the temperature during October and November being quite variable. During tunnel construction the larvae spun a fine silk webbing over those parts of the tunnel wall not involved with the excavation in progress. Despite the silk, sap at times entered the galleries in sufficient quantity to trap the larvae or force them to abandon the burrow. "Sapping out" occurred during periods of warm weather throughout the winter, probably due to sudden increases in sap flow which ruptured the silken tunnel lining. This was frequently noted at lower elevations in southern

Arizona where the temperatures were seldom low enough to result in a continuous state of arrested plant growth. Larvae that were "sapped out" immediately began to construct new tunnels on the same leaf or an adjoining one. Up to eight tunneling attempts resulted before some larvae became established in a dry burrow. Occasionally dead larvae were found clinging to the leaves, likely victims of the weather. First, second, and early third instar larvae were present during the winter in populations where "sapping out" was frequent. Larval growth during the winter seemed to be proportional to the number of galleries a larva was forced to make. At higher elevations the period of arrested plant growth was continuous and "sap outs" were rare. There the larvae over-wintered in the first instar.

All larvae resumed feeding with the advent of warmer temperatures in the spring. Growth was rapid as first, second, or early third instar larvae either enlarged the apical galleries where they had over-wintered, or made new ones, generally directed toward the leaf tip. During the third instar the larvae left the apical galleries and crawled to the base of the leaves where another tunnel was made. The basal tunnel was always located in the lower quarter of the leaf and directed downward toward the caudex. The choice of the upper or lower leaf surface for the entrance to the basal tunnel depends on the species of *Agathymus*. The remaining stadia were passed in the basal tunnel. "Sapping out" often resulted when basal galleries were being established. Larvae that were "sapped out" of basal galleries usually failed to establish new galleries, a high mortality thereby resulting in some populations.

As soon as a larva was concealed in the base of a leaf it proceeded to enlarge the gallery to several times its own width. Although the gallery was constantly being enlarged during the remainder of the third, throughout the fourth, and early in the fifth instar, the entrance remained small, being kept only large enough to facilitate defecation. The viscid, dark brown frass expelled from the basal galleries contrasted sharply with the relatively dry, light green frass often produced when feeding occurred in the apical galleries. The viscid frass accumulated around the entrance, where it hardened, possibly offering the larva some protection from natural enemies. For a number of years it was thought that some *Agathymus* species did not deposit frass outside the burrow entrance. It is now known that all the species occurring in the United States deposit a large



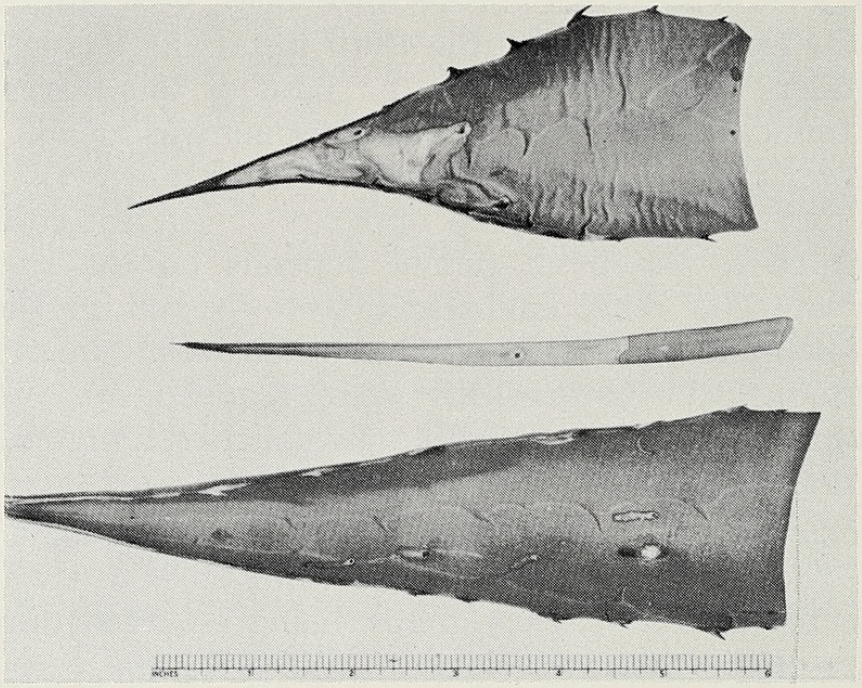


Fig. 3. A leaf of *Agave parryi* showing the apical gallery, trapdoor, and basal tunnel made by *Agathymus neumoegeni.*

Fig. 4. Looking into a large plant of *Agave parryi* containing four trapdoors made by *Agathymus neumoegeni* larvae. The adults have emerged from three of the burrows. Note the frass accumulation beneath the trapdoors.

Fig. 5. Apical galleries made by 1st and 2nd instar *Agathymus* larvae. Top: *A. neumoegeni* in *Agave parryi.* Middle: *A. polingi* in *Agave schottii.* Bottom: *A. aryxna* in *Agave palmeri.*

quantity of frass outside the burrow which is usually dispersed by summer rains before pupation occurs.

Prior to moulting the larvae sealed the entrance with silk, which was removed when feeding was resumed three or four days later. Through the first four instars and part of the fifth the larvae were primarily pulp feeders, but during the latter part of the fifth instar the larvae appeared to be exclusively sap feeders. The tunnel reached maximum size shortly after the onset of the fifth instar, but the lowest portion of the burrow was kept free of silk and sap entered freely. Sap feeding was suggested because the larvae were often seen with their mouthparts in proximity to the sap accumulation at the base, but actual feeding was not observed. Feeding in the basal gallery may last from one to three months, varying both within and between species. The physiological condition of the plant, particularly sap flow, is believed to play an important part in the rate of larval development.

The division of feeding between the young larvae in the apical galleries and the older larvae in basal tunnels is not understood, but can perhaps be explained by the sap content in different parts of the leaf. I would expect first instar larvae to experience greater difficulty in establishing a dry overwintering gallery in the leaf base, with its concentration of water storage cells, than in the drier apical section. Spangehl (1933), working with *Agave parryi* var. *huachucensis* (Baker) Little, sampled sections from the apical, central, and basal portions of a leaf to determine the percentage of water (by weight) contained therein. His results were: apical section, 75%; central section, 85%; and basal section, 96%.

The directions a burrowing larva takes do not appear to be motivated by the food supply, but by negative and positive geotropism for the early and late instars respectively. This was demonstrated by inverting the foodplant and observing the change in direction of tunnels made by the larvae.

When mature the larva silked over the tunnel base and constructed a silk plate in the tunnel entrance, slightly below the leaf surface. This plate sometimes had plant matter incorporated in it. The combination of silk applied by the larvae and a rigid wound cambium formed by the plant around the tunnel wall, provided dry burrows in which the larvae underwent a quiesent period. Larvae in this resting stage responded to tactile stimuli, but were far less active when disturbed than were active-

ly feeding larvae. Quiescence lasted from two to twenty weeks. Larval activity was resumed during July, August, or September, depending on the population. The termination of quiescence appeared to be a response to lower temperature. Larvae kept in an air conditioned room terminated quiescence more rapidly than did larvae exposed to a higher outdoor temperature. No feeding occurred after the quiescent period.

The two characteristic larval activities between the termination of quiescence and pupation are the production of a white, soapy-textured powder and the construction of a trap door. The powder, which looks like asbestos under magnification, is produced on the ventral surface of the seventh and eighth abdominal segments. Dethier (1942) stated that four large rectangular areas, composed of simple unicellular glands lying just beneath the cuticle, secreted the powder. In noting the hydrofugic property of this secretion, he stated that its chief purpose was to create a dry environment for the pupa. The mature larvae of two other megathymid genera, *Megathymus* and *Stallingsia,* are known to produce this hydrofugal substance. Dr. H. W. Kircher of the University of Arizona obtained an infrared spectrograph of the powder produced by *Megathymus yuccae arizonae* Tinkham, for me. His results show that it is probably a ketone with approximately thirty-five carbon atoms. The spectrum is similar to that of stearone. The aid to survival contributed by this powder is questionable. The larvae of two agave-feeding genera in the Megathymidae, *Aegiale* and *Turneria,* do not powder their burrows (Stallings & Turner, 1958). Furthermore, I have found five living pupae of *A. polingi* and three of *A. stephensi* in burrows with no evidence of powder, indicating that survival is possible in these species when the powder glands do not function. It would appear that the silk and wound cambium making up the tunnel walls and the silk covering the entrance are alone effective in preventing the accumulation of moisture within the burrows.

The construction of a trap door over the entrance followed powder secretion (Fig. 4). Before making the trap door the larva removed the silk plug constructed prior to quiescence. It then proceeded to enlarge the narrow entrance to the diameter of the tunnel. In enlarging the entrance the remaining plant matter was dropped outside the tunnel as each bite was removed, very little being ingested if one may judge by the small amount of frass produced. Upon smoothing the perimeter of the hole

the larva applied the hydrofuge powder around the exit. The larva accomplished this by backing to the base of the burrow, turning around, then backing to the exit, where the powder was applied by pressing the glandular area to the tunnel wall and rotating the posterior portion of the abdomen. From time to time the larva would crawl down the tunnel, turn around, and return to the exit headfirst, where it further distributed the powder with the aid of the spinneret. In making the "door" the larva started at the upper edge of the hole, applying silk in a semi-circular pattern. The silk produced was in a much thicker strand than was used to line the burrow walls during the feeding period. Another property of trap door silk was that it remained viscid for several seconds after secretion so that it actually flowed into the adjoining strands and created a relatively smooth plate. Because the silk remained plastic the larva was able to smooth over weak places in the structure. The holes, measuring from four to nine mm. in diameter, were covered within thirty minutes, but the larvae could be seen through the transparent cover applying more silk to the inner surface. Only a weak attachment to the leaf existed at the perimeter of the trap door. From one to three days were required before the trap door acquired the color that is characteristic of the various species complexes.

PUPAE

Pupation takes place in the basal tunnel from one to two weeks after the trap door is completed. In the majority of the tunnels examined the pupae rested in the lower parts, separated from the base only by the exuviae. In rare cases the pupae were suspended by a few silk strands placed between them and the base. A few silk strands were generally present between the pupa and the trap door.

Movement of the pupae was evident only when they were disturbed. In contrast, the pupae of *Megathymus* show an adept ability for movement up and down their burrows through rotation of the abdomen and use of the cremaster as a brace. Pupil movement in the *Megathymus* is primarily a response to temperature changes; during warm weather the pupae move to the tunnel apex, while in cold weather they rest near the base. *Megathymus* tunnels have aerial and subterranean sections; therefore, it would be reasonable to expect significant temperature differences in the various portions of the tunnels. *Agathymus* tunnels are short in comparison to *Mega-*

thymus tunnels; as they are in most cases entirely above ground only slight temperature variation would be expected in different parts of a burrow.

Eclosion of the adults occurred from three to seven weeks after pupation, usually between the hours of seven and ten A.M. The adult leaves the pupal case through tranverse and longitudinal splits made in the head and thoracic region and then crawls up the tunnel to the trap door. By putting pressure on the trap door it ruptures the silk strands attaching the door to the leaf and causes it to swing open on a silk hinge or to fall off (Fig. 5). No silk digesting substance is produced. The adult next crawls onto the leaf surface where the wings are expanded to full size, usually within fifteen minutes. From one to two hours additional are required before the wings have attained sufficient rigidity to permit flight. In populations from which a large number of adults were reared most of the females emerged at a slightly later date than the males. However, the emergence dates of males and females overlapped to a certain extent and the first adult to emerge was sometimes a female.

NATURAL ENEMIES

The most obvious natural enemies of *Agathymus,* if we do not include physiological reactions of the foodplant, are other insects, particularly dipterous and hymenopterous parasites. A frequently encountered dipterous parasite was *Phorocera texana* Aldrich & Webber (Tachinidae). This fly was reared from *A. Aryxna, A. baueri, A. freemani, A. evansi,* and *A. chisosensis* (Freeman). Simpson (1957) did not record this tachinid from Arizona.

Townsend (1936) states, "The females of the *Phorocera* . . . deposit more or less incubated eggs directly on the host." But the life histories of many *Phorocera* are not known. Several tachinid genera are known to show variation in the type of reproduction and this may also apply to the *Phorocera.* Ingestion of the eggs appears to be the least probable method of parasitism because of the limited feeding *Agathymus* larvae do on the leaf surface. The deposition of eggs or maggots on the host is a possibility, although larvae are usually concealed in their galleries and no flies were observed near a gallery entrance. It is quite likely that maggots are deposited near the tunnel entrance where they can seek out the host in the burrow or attach thmselves to larva when it defecates. I have not dissected gravid flies to determine whether they were bearing maggots

and/or eggs. Observations show the maggots emanate from the host during July, August, or September, and pupate in the burrow. The flies emerge about three weeks after pupation and have no difficulty in pushing open the trapdoor. The parasitized larvae often survive long enough to construct a trap door, but usually fail to powder their tunnels. Host larvae yielded from one to eight maggots. The occasional parasitized larvae that pupated never produced more than two maggots. Fall emergence of the flies, before *Agathymus* larvae are available as hosts, seems to indicate that other hosts are used. *Phorocera texana* was described from a series reared on *Melitara* (Phycitidae, Lepidoptera) taken at three localities in south-central Texas (Aldrich & Webber, 1924). I found no other host records.

A sarcophagid was also found to be an *Agathymus* parasite. This fly represented a new genus and was described by Dr. H. J. Reinhard (1963) as *Erucophaga triloris*. I reared it from *A. neumoegeni, A. aryxna, A. baueri, A. freemani,* and *A. florenceae* (Stallings & Turner).

Many of the Sarcophagidae are scavengers during the larval stage, but the fact that parasitized larvae were encountered in burrows where the trap door was tightly closed indicates that this fly attacks living larvae. Sweetman (1958) states that most parasitic sarcophagids are larviparous, but a few deposit fully incubated eggs. Those that I collected pupated within the burrow, the adults emerging during September and October. Adult sarcophagids were often seen walking around on agave leaves, but the deposition of eggs or maggots was not observed. These flies showed a reluctance to fly and when disturbed usually ran to the underside of a leaf.

A new wasp, described by Dr. C. F. W. Muesebeck (1963) as *Bracon agathymi* was reared from *A. neumoegeni, A. florenceae, A. mcalpinei* (Freeman), *A. diabloensis* Freeman, *A. aryxna, A. mariae* (Barnes & Benjamin), and *A. alliae.* This insect was frequently encountered as a parasite of the *A. neumoegeni* complex, but was rarely encountered on other species. On three occasions during May and June female braconids, presumably *B. agathymi,* were seen walking around entrances to laval tunnels. Oviposition was not observed. I assume the host is parasitized when it defecates because the wasp's ovipositor does not appear long enough to penetrate the leaf and burrow wall. When fully grown the braconid larvae leave the host and form a dense cocoon cluster. The cocoons, numbering from ten to forty

tightly plug the tunnel. Emergence occurred during June, August, and September. Larvae parasitized by this branconid either powdered their burrows and made typical trap doors; constructed weak, discolored trap doors and failed to powder the burrow; or died in the fourth instar.

Another wasp, determined by Dr. Muesebeck as similar to *Apanteles megathymi,* is to be described. This insect was reared from *A. stephensi* and an undescribed *Agathymus* which occurs in western Arizona. It is clear that the host-parasite relationships contribute no aid to clarifying the taxonomic status of *Agathymus* at the species level when the aforementioned cases are used.

Predators of *Agathymus* larvae were rarely encountered. Two beetles, probably *Cymatodera oblita* Horn (Cleridae), were reared from *A. aryxna* and *A. baueri.* Two carabid larvae were taken while feeding on *A. polingi* larvae, but attempts to rear them failed. Small ant colonies were sometimes encountered in the basal tunnels, but it was not possible to determine if they entered the burrows as predators or became established after the original occupant died of other causes. While checking an *A. stephensi* population near Palm Springs, California, I noted that a number of burrows with trap doors had been gnawed into and the larvae or pupae removed. Only those burrows with a trap door on the under surface of the leaf were affected. Judging from the dung below those burrows the predator was a mouse.

Several insects, not to be considered enemies, were found in association with abandoned tunnels. Weevils of the genus *Scyphophorus* used the burrows to gain an entrance to the caudex of the agaves. A eumenine wasp, *Rygchium pratense* (Saussure), constructed mud-lined cells in old tunnels. Cells constructed of masticated plant matter made by bees of the genus *Ashmeadiella* were also encountered.

Diseased larvae were frequently found, but the causal agent was not determined. Four *A. freemani* larvae taken near Baddad, Yavapai Co., Arizona, were covered with a fungus (*Metarrhizum*?) that produced green conidia. It was not possible to determine whether this fungus caused larval mortality or was merely a saprophyte.

No examples of cannibalism were noted, even when a large number of first instar larvae were closely confined. Larvae at times would chew through the wall of an adjoining tunnel while

making their basal galleries. Under these circumstances a silk partition was made and feeding resumed.

As is to be expected, the mortality rate varied widely at the population level. The highest mortality rate due to natural agents was encountered in an *A. florenceae* population near Mt. Locke in the Davis Mountains of Texas. An examination of 350 basal tunnels in late May yielded the following: 311 tunnels approximately three cm. in length which gave evidence that third or fourth instar larvae had been "sapped out" and had failed to become established elsewhere on the plant; 20 dead fourth instar larvae trapped by sap; six diseased larvae with symptoms suggesting a polyhedral wilt; eleven larvae actively feeding as evidenced by fresh frass deposits at the burrow entrance; and two tunnels which were sealed in such a manner as to indicate that they contained moulting or quiescent larvae. Two feeding larvae and one quiescent larva were removed for preservation and ten living larvae left. On a large plant which contained six living larvae a female *Bracon* was observed running around a frass pile at the entrance to a tunnel. This parasite did not attempt oviposition during the fifteen minutes of observation, so was then collected. During September, four months after they were first located, I checked the ten living larvae, with the following results: three tunnels contained braconid cocoons, three contained larvae covered with a fungus, three contained pupae which later produced adults, and one tunnel contained a puparium from which a sarophagid later emerged. The mortality of fourth and fifth instar larvae attributable to the braconid varied from 0 - 63% in Arizona populations of *A. neumoegeni*. Mortality caused by *Phorocera texana* varied from 24 - 90% in *A. freemani*, 6 - 40% in *A. baueri*, and 0 - 45% in *A. aryxna*, based on larvae collected and held for rearing in the fifth instar.

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