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George E. Bohart
Utah State University

John W. MacSwain

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THE LIFE HISTORY OF THE SAND WASP, *BEMBIX OCCIDENTALIS BEUTENMUELLERI* FOX AND ITS PARASITES

By GEORGE E. BOHART and JOHN W. MACSWAIN¹
University of California, Berkeley

This is the first of a series of papers intended to present results of biological studies by the authors on various aculeate Hymenoptera and their parasites. The present study was made at Antioch, Contra Costa County, California, during the summer and fall of 1938, and the spring of 1939. We have found the works of Fabre (1908), Ferton (1923), and Rau (1918) particularly useful in providing a source of corroborative data on the habits of bembicid wasps and we would refer the reader to these papers which are cited in the bibliography.

TAXONOMY AND DISTRIBUTION OF HOST

Bembix occidentalis Fox² was described from Lower California and was based on forms with pronounced yellow maculations. In 1901, from a black specimen Fox described *Bembix beutenmuelleri*³ from Stockton, California. At Antioch (figs. 1-4) specimens show a complete gradation from the yellow type to an entirely black phase. If black forms are later found in Lower California, it will probably be necessary to retain only *Bembix occidentalis* s. str. Other localities for *B. occidentalis beutenmuelleri* include Los Angeles County, California, and Van Sickle Canyon, Oregon (Parker, 1929). This reference also records specimens of doubtful position from Arizona and New Mexico.

HABITAT

The habitat in which this study was made is confined to a few isolated sand dunes east of Antioch, California. The dunes are bounded on the north and east sides by tule marshes and

¹ We would like to acknowledge the assistance of Dr. E. C. Van Dyke under whose direction this paper was prepared; Messrs. E. P. Van Duzee and R. L. Usinger for permission to use material in the California Academy of Sciences; Dr. E. G. Linsley for reading the manuscript and offering suggestions, and Miss Jane M. North for help in gathering field material.

² *Bembix occidentalis* Fox, 1893, Proc. Calif. Acad. Sci. (2), 4: 10.

³ *Bembix beutenmuelleri* Fox, 1901, Journ. N. Y. Ent. Soc., 9: 83.

the banks of the Sacramento River, along the south and west by vineyards. The actual dune slopes are devoid of vegetation and furnish preferred nesting sites. The dunes are relatively permanent in position with a soft, shifting surface layer and a harder packed sub-stratum. Frequent afternoon winds cause a constant movement of this top layer and a consequent covering of burrow entrances. Occasionally a strong wind will remove both the surface layer and sub-stratum to a depth of a foot or more on the windward side and deposit it on the lee of the dune. In some cases wind excavation uncovers and removes living cocoons as well as dead ones from previous years. A complete mortality has been observed in excavated cocoons which have been exposed to the heat of the sun. In addition to this mechanical hazard and to insect parasites, *B. occidentalis beutenmuelleri* in larval state suffers from mold and occasionally as an adult from the predatory attacks of the large asilid fly, *Proctocantha occidentalis* Hine.

In making a study of this species it was found necessary to choose a single large nesting site, since the dunes harbor several colonies whose periods of activity vary. The larger colonies were all located on the slopes of the dunes and only a few isolated specimens made use of the summits.

EMERGENCE

Emergence took place suddenly, a characteristic feature of the wasps of this genus as has been noted by Rau (1918:9) in his study of *Bembix nubilipennis* Cresson. On August 17, 1938, both sexes appeared together and almost immediately commenced what has been called by Rau "the mating dance." This is a rapid zigzag flight a few inches above the ground and within the confines of the colony. At times a male and a female break away from the group in a short rapid flight terminating with a brief contact on the ground. Since this species is both polygamous and polyandrous, the procedure was repeated many times. Often the male and female attempting to leave the "dance" would be followed by one or more additional males causing the attempt to be abandoned or ending on the ground in a brief struggle. The mating period lasted for a week, and during this time no digging was observed. On sunny days flight commenced at about 10 A. M. and reached its peak around noon, after which nearby flowers were visited for nectar, and by 4 P. M. the majority of the wasps returned to their burrows. In contrast to *B. nubilipennis* Cresson both males and females of the present species returned to the burrows for the night, at least at the beginning of the season. This fact was established by opening the burrows in the early evening and taking both sexes from them.

BURROW CONSTRUCTION

On August 28 several females had commenced digging, while males were numerous and still attempted to mate with them. The females which were digging eluded or fought them off. Burrowing activities started at about 10 A. M. and continued intermittently until about 3 or 4 P. M. Although several trial holes were started by each female, these and the first completed burrow were made in one day. Upon completion, this final hole was used by the female as a place to spend the night, while males probably used the holes from which they had emerged originally.

The burrow shaft is sunk at an angle of 15 to 30 degrees from the horizontal, and to a depth of from 16 to 24 inches. The entrance is oval for a depth of an inch, with surface dimensions of one-half by three-eighths of an inch. The main tunnel is circular and of an average width of three-eighths of an inch. It terminates in an elliptical cell with its dimensions about an inch and a half long and five-eighths of an inch wide at the middle and with its long axis horizontal. The wasp digs by seizing the sand particles in the mandibles and tearing them free from their loose surroundings. The sand particles are then thrown backwards by the spines of the anterior tarsi. Since there is no cementing of sand grains, advantage is taken of areas on the dune which have been denuded of the loose topsoil by the wind. In these bare areas there is a great concentration of nests and the entrances may be communal, serving from two to a probable maximum of six single burrows. An entrance of this type is larger and more irregular than that of a single burrow, but only extends for an inch or two below the surface, at which point the individual holes diverge. Communal entrances are left open at all times, but the individual entrances within may be closed upon departure of the females. When provisioning is started and the egg laid, the wasp habitually covers the nest before each departure. When provisioning has been completed, the burrow is plugged with sand and packed for a depth of two or more inches. While plugging the completed nest, the wasp faces away from her entrance and zigzags back and forth in arcs of increasing radius, kicking jets of sands towards it, which are accurately gauged as to distance and direction. At intervals she interrupts this process to back into her burrow and tamp the sand firm with the end of her abdomen. When the plug has been completed, sand is kicked about indiscriminately to disguise traces of occupation.

FOOD HABITS AND OVIPOSITION

The observation that *Bembix* uses flies for nest provisioning was first made by Latreille and later confirmed by Lepeletier (1841). Females of *B. occidentalis beutenmuelleri* were

first observed provisioning their nests on September 4. The ortalid fly, *Anacampta latiuscula* Loew, was used, necessitating a trip of at least 150 yards to the nearest habitats harboring this species. First egg laying was coincident with this provisioning. Although we were unable to observe the manner in which this species lays her egg, that of a closely related species, *comata* Parker, was discovered attached to the upper wall of the cell immediately prior to the wasp's entrance with the first food. At variance with this is the method followed by *oculata* Latreille, a European species studied by Ferton (1923:91), which attaches its egg to the underside of the fly's wing base. At the same time Ferton also reported that *mediterranea* Handlirsch deposits its egg on the floor of the cell, supporting it with small, conical sand pellets. It seems likely from the above statements that variations in the oviposition habit may be specific characters within the genus.

Ortalids continued to be the exclusive food for the larvae of our wasp until September 18 when females were found with the green bottle fly, *Lucilia sericata* Meigen. This selection, in all probability, was the direct result of the establishment of a pig pen in direct line with the wasp's ortalid search. Also, at about this time, we noted that other flies were being used, a partial list of which follows: *Eristalis latifrons* Loew, *Elophilus latifrons* Loew, *Calliphora erythrocephala* Meigen, two undetermined metopiids, *Musca domestica* Linnaeus, *Stratiomyia laticeps* Loew, *Chrysops* species. It is of interest to note that the genera *Musca*, *Lucilia*, and *Eristalis* were included in the list of prey given for *B. oculata* by Ferton (1923:75).

We observed that whereas the ortalids were invariably immobilized when brought to the burrows, some of the syrphids were apparently merely held in captivity and, when taken, both the wasp and its prey would fly about in the net.

In Europe considerable controversy has arisen concerning the method of attack by *Bembix*. Lepeletier (1841) stated that the flies were paralyzed but Fabre (1908, 1:236) and Wesen-burg-Lund described the fly as being dead and crushed or scarred by the wasp's mandibles when brought to the nest. Marchal (1893) took a neutral stand by stating that the method was not precise but very variable. Ferton (1923:74), in what seemed to be conclusive experiments, demonstrated that the flies were not mutilated by the wasp but merely paralyzed and, when exhumed, could be kept alive for as long as fifteen days. At the same time he described the act of paralyzing (1923:77) in which the fly was held by the head, the wasp's abdomen recurving to sting it a little behind the mouth. This process was said to occur either in flight or upon the sand.

The female wasp will occasionally visit flowers for nectar

but apparently does not remain long and soon resumes provisioning activities. After mating the males pass the remainder of their active life at flowers. For this purpose *Eriogonum parvifolium* Sm., *Croton Californicus* (Muhl), and *Heliotropium curassavicum* Linn. are most commonly visited.

HOST DEVELOPMENT

The newly hatched larva feeds upon the first fly provided, chewing and sucking steadily while pouring salivary fluid into it. The fly's abdomen is usually devoured completely whereas the head and thorax may be chewed but are seldom consumed. Provisioning proceeds with the larval development so that flies are brought in at greater frequency as the young wasp increases in size, vigor, and appetite. Apparently, as a general rule, plenty of food is provided since the adult wasps exhibit a very uniform size. Judging from our first records of completed cocoons (September 18) it takes about two weeks for larval development and case formation.

The process of cocoon spinning has been described by Fabre (1908, 1:255) for *B. rostrata* which works in the same manner as *B. beutenmuelleri*. (The size, proportions, thickness, and something of the texture and details of the completed case are shown by the plate figures.) In addition to Fabre's observations on the formation of the cap, we have noted that just prior to its construction, the larva carries the loose ends of silk from the inner wall over the top to the exterior, thus forming a definite line of weakness for later emergence of the adult. Highly characteristic for all bembicids are the small resinous appearing tubercles which resemble minute volcanos or simple craters and are distributed on a single transverse plane throughout the middle of the case. They may be easily observed on the inner wall of the cocoon by the areas of heaviest silk deposition. Rhinehard (1929:36) in a simple experiment with *Sphecius* has demonstrated that these tubercles can act as ventilators since they form the only areas permeable to air. In *B. beutenmuelleri* these pores are tuberculate externally, from four to seven in number, and somewhat unevenly spaced. The cocoon cap, which is provided for the escape of the adult, is illustrated in figure 6. In contrast to *Bembix comata*, *beutenmuelleri* has a silken cocoon lining so heavy that a broken case is held together by it.

Overwintering takes place in the last larval stage which is dormant and commonly termed the prepupa. Under normal circumstances pupation occurs in the late spring and emergence in the late summer, but exposure to the sun causes premature pupation followed by death which may be delayed enough to allow for pigmentation.

PARASITISM BY *DASYMUTILLA SACKENII* (CRESSON)⁴
(HYMENOPTERA-MUTILLIDAE)

A previous biological investigation of *Bembix* parasitism by mutillid wasps was published by Mickel (1928) for *Dasymutilla bioloculata* (Cresson) as a parasite of *Bembix pruinosa* Fox and *Microbembex monodonata* (Say). This paper also includes a comprehensive bibliography of other works dealing with mutillid life histories.

According to Mickel (1928) *Dasymutilla sackenii* (Cresson) ranges throughout the state of California and into bordering areas of Oregon and northern Nevada. This species at Antioch is of a very uniform size (figs. 11-12) which indicates a narrow host selection. However, the general distribution and large number of this mutillid on the dunes makes it seem probable that *B. occidentalis beutenmuelleri* is not its only host. Apparently this same species attains a much greater size in southern California.

The activity range of the adults is from June to November and only worn females are present at the end of the season. The adult is active above ground only in the early morning and late afternoon and usually the only specimens seen during the middle of the day are females actively seeking shade. For this purpose they make use of old open holes remaining from previous years or the shaded areas by banks of sand. The males overlap the daily activity period of the females to a slight extent and have been taken in the middle of the day on vegetation.

The flight of the male is slow and irregular, a few inches above the ground, and is often interrupted by a collision with bushes. Both sexes, when taken in the net or pursued over the sand, rub the second and third abdominal tergites together producing an intermittent high-pitched squeak. The female also produces this noise while investigating a burrow. She is protected from the return of the owner by her highly sclerotized integument and by possession of a powerful and extremely long sting. This sting is very flexible and is capable of inflicting a series of painful wounds (which on most humans swell for a short time and then subside). The females will enter any hole of suitable size for varying periods of time but in nearly all of these cases finds nothing upon which to oviposit.

The mutillid often appears to sense the presence of a covered burrow and, after scratching in the sand, will uncover the hole and gain access to the pupal cases of the bembicid. According to Mickel (1928) the wasp cuts a small hole in the pupal case with her mandibles and then oviposits on the prepupa

⁴ *Dasymutilla sackenii* (Cresson), 1865, Proc. Ent. Soc. Phila., 4: 385 (*Mutilla*).

within. After oviposition she closes the hole in the case and covers the burrow. Figure 13 illustrates a *Bembix* pupal case which has been exposed by the strong winds at Antioch. In this case the mutillid had attacked the *Bembix* either shortly before or after it was exposed. The host had completed pupation and started pigmentation when attacked by the mutillid larva which consumed it and forced the head and the hard parts of the thorax, legs, and abdominal tergites to the end of the case before spinning its case and entering the prepupal stage. Figure 14 shows another excavated pupal case. Here the mutillid has consumed the prepupal stage of the host as usual and then been forced to an abnormally early pupation due to exposure to the weather. Under ordinary conditions this pupation of the parasite would not take place until the spring or early summer of the following year. In the normal cycle of the parasite the larva, upon hatching from its egg, consumes its host and pushes the indigestible portions of the cap end of the *Bembix* cocoon. Using this detritus as a base the larva spins a loose framework of silk which completely fills the host's case and is loosely attached to the walls. This framework is rapidly built up on the inside into a heavy opaque sheath which is only thinly closed toward the cap end in order to allow for emergence.

From a gross examination the parasitic larva can easily be distinguished from its host by the following characters: smaller in size, a more polished integument, prominent lateral margins of segments, apical tergites strongly cleft as opposed to truncate, and the head smaller with sharper mandibles which are opposed rather than parallel.

The parasitism of *Bembix occidentalis beutenmuelleri* was found to be approximately one percent of the total population on the dune studied. On the other dunes having a different host activity range there may be a higher degree of parasitism. The fact that the greatest mutillid population occurs in localities harboring few *Bembix* seems to indicate that this bembicid is host for only a minority of the mutillids present.

PARASITISM BY ANTHRAX ATRATA LOEW⁵ AND EXOPROSOP
EREMITA OSTEN SACKEN⁶ (DIPTERA-BOMBYLIIDAE)

Bombyliid flies have long been known as parasites of aculeate Hymenoptera. As early as 1864 the German worker, Frauentfeld, reared *Argyramoeba leucogaster* (Meigen) from the nest of *Cemonus* and suggested that the larvae of the parasites must find their own way into the nests as did those of meloids and strepsipterans. The most exhaustive account of parasitism

⁵ *Anthrax atrata* Coquillett, 1887 Trans. Am. Ent. Soc., 14: 171.

⁶ *Exoprosopa eremita* Osten Sacken, 1887, Bull. U. S. Geol. Geog. Surv. Terr., 3: 236.

by flies of this family was made by Fabre (1908) for *Anthrax trifasciata* Meigen, a parasite of the megachilid bee, *Chalicodoma*.

Of the two bombyliid parasites of *B. occidentalis beutenmuelleri*, *Exoprosopa eremita* has been taken in nearly all of the states west of the Rocky Mountains, whereas *Anthrax atrata* is apparently confined to the Pacific Coast states. The wide distributions here demonstrated as contrasted with the comparatively narrow one of *B. o. beutenmuelleri* obviously indicates the existence of other hosts. Also, in our locality, the numbers and habitats of the flies are not in accord with those of the *Bembix*.

The two species considered here, although members of different genera, appear to behave so similarly that a separate discussion is unnecessary. Considerable gaps in our knowledge and observations have made it as yet impossible for us to distinguish between the larvae of the two species.

The flies do not become active until the dunes are warmed by the late morning sun and become inactive again by 3 or 4 p. m. Since their delicate pubescence and fragile wings (which are held outstretched) would prevent them from spending their dormant period within burrows, it is probable that it is spent on vegetation. During their active hours the females are to be seen largely on bare sand areas, hovering over burrow entrances and darting from one hole to another. As our close scrutiny on these areas revealed few males and no mating, it can be assumed that copulation takes place away from the dunes, probably near the flowers where the males were observed to spend most of their active time. Feeding from flowers is apparently accomplished while settled with the wings held horizontally and nearly at right angles to the body. This method is in contrast to that used by the long tongued bombyliines which sip nectar while hovering in front of the blossoms.

The oviposition habits may be readily observed since this function occurs above ground at the lip of the burrow. The female is most often seen hovering from a few inches to less than an inch above an open hole, advancing slowly until near the opening while flipping the tip of the abdomen at intervals downward and forward toward the entrance, then flying slowly backward. This action apparently throws the eggs close to or within the opening as has been reported by other authors. After making several motions toward the burrow with her abdomen, the bombyliid moves a few inches to one side of the hole and settles on the sand. Upon completion of this act the fly then returns to the air and resumes her search for other open burrows.

Fabre (1908, 1: 189-223) was the first to consider the hypermetamorphism of bombyliid larvae in detail. He first acted on

the inference that the newly hatched larva must make its own way to the wasp's cell, and so discovered the active first instar of *A. trifasciata* which he carefully described and figured (1908, 1: 205). This larva demonstrated a most decided "tropismic" activity in attempting to burrow downward from whatever point it was placed. This activity would not only explain the migration of a larva to the shallow cells of *Chalicodoma*, but also the much deeper ones of *Bembix*.

When once within the cell of its host, the young larva waits until the *Bembix* has entered the prepupal stage before attacking it. This waiting period was stated by Fabre to occur with *A. trifasciata* and is inferred by us to be the case for *A. atrata* and *E. eremita* since we were unable to find evidence of attack except on prepupae. (The authors have also noted this phenomenon in the case of bombyliid attacks on osmiine bees.) The first moult leaves the larva maggot-like, without bristles, and with the head region retracted. In this condition it is unable to progress in any direction but, being beside its source of food, can apply its head to the body of the larval wasp and apparently suck the body fluids of the latter through the intervening membrane. The host remains alive throughout this process as is shown by its lack of discoloration. The time lapse from the first attack, through the gradual shriveling of the host until it is reduced to an empty skin fragment, was for Fabre's fly about one fortnight. Fabre's description of the process of feeding and the appearance of the repleted fly larva for his *Anthrax* could serve equally well for the two species of the present study. The creamy mottled appearance caused by collections of fatty tissue beneath the skin is highly characteristic and immediately distinguishes a bombyliid larva. Overwintering is undergone by the mature larva and pupation takes place in the summer.

Pupation occurs within the *Bembix* cocoon and transforms the bombyliid (fig. 9) into a heavily sclerotized, reddish pupa with numerous abdominal spines and hairs and a bizarre head armature. Prior to complete development of the imago within the pupal case, the pupa darkens and becomes active. Fabre was able to observe *A. trifasciata* utilizing the spines of its head to break its way out of the stony wall of the *Chalicodoma* cocoon. We have observed the pupae of several species of bombyliids using a corkscrew motion in attempting to penetrate the cotton plugs of the vials in which they were kept. In the case of *Bembix* the pupal fly must not only break its way through the cocoon but also push to the surface of the sand where it thrusts its head and thorax above ground. In this position the imago emerges by splitting the pupal case longitudinally along the back of the head and thorax. Empty cases may be seen in the early autumn following emergence still in the same position.

While excavating for *Bembix* cocoons, we found approximately one bombyliid larva for every hundred cases opened. This low percentage of parasitism may possibly be explained by the habit of the *Bembix* in keeping its entrance covered both while on hunting expeditions and after complete provisioning. Since the fly will oviposit only on open burrows, its effective period is reduced to the times when the *Bembix* is in its burrow.

PARASITISM BY *PHYSOCEPHALA AFFINIS* WILLISTON⁷
(DIPTERA-CONOPIDAE)

Physocephala affinis Williston occurs throughout temperate North America and the West Indies. It is the commonest and most widespread member of the genus in North America, but is most abundant in the western United States. On the pacific slope there is but one other recognized species in the genus *P. burgessi* Williston. At Antioch, California, where this study of *P. affinis* was made, *P. burgessi* is not found.

To our knowledge this is the first study of and the second record of *Physocephala* parasitism of *Bembix*. Published records for other insects include those of Meijere (1903: 145-146, 163-164) citing *Bombus*, *Apis*, *Megachile*, *Xylocopa*, and *Vespa* as hosts. This work also contains an excellent summary of conopid biology as known at that time. In this country Plath (1934: 60) and Van Duzee (1934: 315) have reported parasitism on *Bombus* and on *Apis* respectively. Townsend (1935: 147) records *Bembix*, *Philanthus*, *Eucera*, *Halictus*, and *Sphingonotus* as additional genera both from original observation and as gleaned from previous publications. His paper includes an excellent morphological discussion of the larva and puparium of *Physocephala sagittaria* (Say).

P. affinis as a parasite of *B. occidentalis beutenmuelleri* has only one brood a year. This was demonstrated by the discovery of living puparia in the abdomens of *Bembix* of the previous year during the earliest period of host activity. Several hundred puparia were collected during the nesting season of the wasp, and only those taken at the beginning of the season yielded adult flies during the same season. The capture of numerous specimens of *P. affinis* several months prior to the time of *Bembix* emergence would also seem to indicate that the fly has other hosts.

On our dune it was observed that the time of emergence of *P. affinis* lagged behind that of *Bembix* by two weeks. The period of activity lasted until the early days of October. Only the females appeared in abundance on the dunes, flying low over the sand and occasionally resting on it. The males were found on the surrounding flowers, mainly *Eriogonum* and *Heliotropium*, where the females sometimes joined them. Mating takes

⁷ *Physocephala affinis* (Williston), 1882, Trans. Conn. Acad., 4: 339 (*Conops*).

place about the flowers during the warmest part of the day and continues throughout the major portion of the season. Males pursue the females and alight upon their backs, accomplishing copulation in this position. The pairs remain in contact for several minutes, often flying when disturbed, and only separating when captured.

Soon after mating the female returns to the dunes to oviposit on the *Bembix* which are at this time provisioning their nests. At this early period it is the male bembicid which bears the brunt of the attack since the females spend a large part of the time underground or on hunting expeditions. So successful is this attack that it is a major factor in the disappearance of the male wasps. Knowing the population and approximate sex ratio on our dune, the above conclusion was easily made from the great numbers of parasitized male bodies uncovered in later digging.

The conopid lurks about the nesting site, making repeated swoops at the passing wasps. This procedure is continued until the fly succeeds in following the flight path of the host. The chase, if successful, ends with the fly alighting on the back of its victim and after a short tussle on the ground, inserting an egg between its abdominal tergites. The organs which make this possible are the powerful and highly specialized sternal plates of the parasite. Even when able to follow the complicated flight of the wasp, the fly does not always succeed in oviposition since the wasp often turns rapidly and strikes its tormenter to the ground. In this case the wasp does not follow up its advantage by killing the parasite but flies off, leaving the conopid to recover and continue its activity. At other times, when seized, the wasp may succeed in dislodging the conopid before oviposition has been accomplished.

The egg hatches soon after being layed and the immature larva migrates to the haemocoel where it pierces and sucks the non-vital organs in the region of the second abdominal segment by means of its two mouth hooks. The body of the larva lies in the same planes as the host, with the head region elongate and turned down toward the venter. This orientation is maintained throughout the pupal stage, making it necessary for the emerging adult to sever the connection between the propodeum and abdomen of its host. At any time in mid-season it is possible to collect *Bembix* containing all stages of larvae. To our knowledge there have been no cases of multi-parasitism although it seems unlikely that all wasps would escape or be immune from more than one attack. It is more probable that it is physiologically impossible for more than one larva to develop. From all external appearances the *Bembix* suffers no ill effects from the early development of the larva but with the later consumption of the fat bodies and crowding of the gonads the life span is shortened.

Pupation of the fly occurs only when the host is in the burrow and brings about the immediate death of the wasp. We observed one exception in which a *Bembix* was found writhing on the sand incapable of coordinated movement and this specimen contained a full grown larva which completely filled the abdominal cavity. Underground death of the host is probably of vital importance to the well being of the fly puparium which might otherwise suffer from the attack of predators or from dessication. However, the puparia are remarkably resistant to drying and have been found alive after several weeks of exposure to the sun and wind. The *Physocephala* puparium has prominent stigmal plates and a tri-lobed construction (fig. 18) and is thus easily distinguishable from those of other dipterous parasites.

The percentage of parasitism of any free ranging adult insect is exceedingly difficult to determine. *P. affinis* must parasitize from twenty-five to fifty percent of the *Bembix*, judging from the number of living wasps examined for parasitic larvae and the number of dead wasps containing puparia. However, the effect of this high percent of parasitism on the host population is relatively slight because the majority of those parasitized are males. In addition, even when females are attacked they are able to continue their activities for some time.

CONCLUSIONS

Bembix occidentalis beutenmuelleri Fox in the vicinity of Antioch, California, prefers sand dunes as a nesting site. The flight period of a single colony in 1938 was from August 17 to the latter part of November. A mating period of a week was followed by nest construction. Burrows were sunk to an angle of 15 to 30 degrees and to a depth of 16 to 24 inches and each terminated in a single horizontally placed cell provisioned with several species of flies, the most important of which were *Anacampta latiuscula* Loew and *Lucilia sericata* Meigen. The most important parasites at this locality appear to be *Dasymutilla sackenii* (Cresson) (1%), *Anthrax atrata* Loew and *Exoprosopa eremita* Osten Sacken (together about 1%), and *Physocephala affinis* Williston (25-50%).

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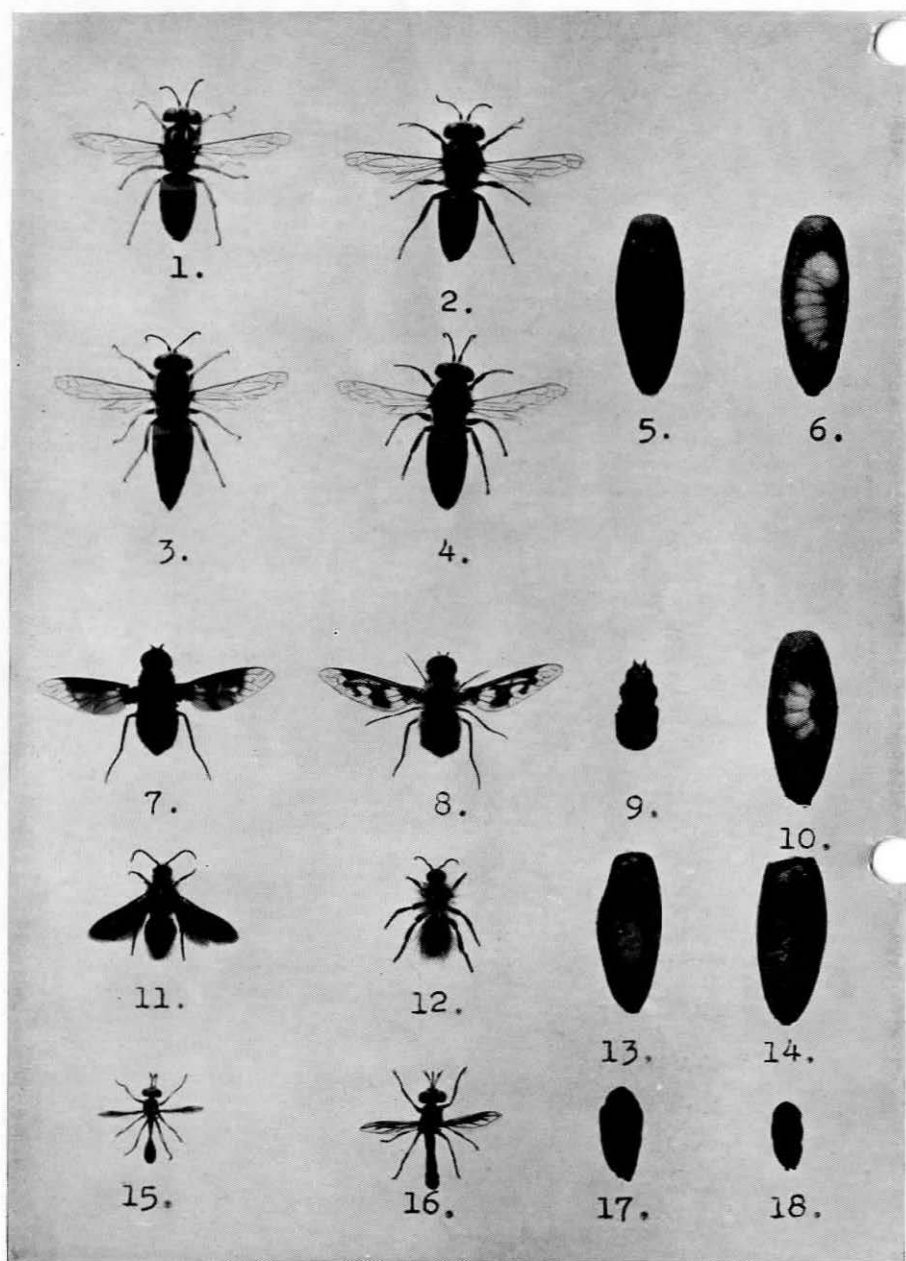


PLATE 16

Bembix occidentalis beutenmuelleri Fox and its parasites.

EXPLANATION OF PLATE 16

All figures natural size.

- Fig. 1. *Bembix occidentalis beutenmuelleri* Fox. Female, fasciate color phase.
- Fig. 2. *Bembix occidentalis beutenmuelleri* Fox. Female, black color phase.
- Fig. 3. *Bembix occidentalis beutenmuelleri* Fox. Male, fasciate color phase.
- Fig. 4. *Bembix occidentalis beutenmuelleri* Fox. Male, black color phase.
- Fig. 5. *Bembix occidentalis beutenmuelleri* Fox. Whole cocoon.
- Fig. 6. *Bembix occidentalis beutenmuelleri* Fox. Cocoon opened to show mature larva.
- Fig. 7. *Anthrax atrata* Coquillett. Female.
- Fig. 8. *Exoprosopa eremita* Osten Sacken. Female.
- Fig. 9. *Exoprosopa eremita* Osten Sacken. Pupa.
- Fig. 10. *Bembix occidentalis beutenmuelleri* Fox. Cocoon opened to show mature bombyliid larva.
- Fig. 11. *Dasymutilla sackenii* (Cresson). Male.
- Fig. 12. *Dasymutilla sackenii* (Cresson). Female.
- Fig. 13. *Bembix occidentalis beutenmuelleri* Fox. Cocoon opened to show mature larva of *Dasymutilla sackenii* (Cresson). With half spun cocoon.
- Fig. 14. *Bembix occidentalis beutenmuelleri* Fox. Cocoon opened to show adult *Dasymutilla sackenii* (Cresson). Female *in situ* in its cocoon.
- Fig. 15. *Physocephala affinis* (Williston). Male.
- Fig. 16. *Physocephala affinis* (Williston). Female.
- Fig. 17. *Bembix occidentalis beutenmuelleri* Fox. Abdomen with basal segment removed to show *Physocephala affinis* (Williston). Puparium *in situ*.
- Fig. 18. *Physocephala affinis* (Williston). Puparium.