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A Revision of the Moths of the Subfamily Prodoxinae

(Lepidoptera: Incurvariidae)

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Frank A. Taylor
Director, United States National Museum

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A Revision of the Moths of the Subfamily Prodoxinae (Lepidoptera : Incurvariidae)

Introduction

In 1892, C. V. Riley presented a paper in the third annual report of the Missouri Botanical Garden which summarized all that was then known of the biology and classification of yucca moths. Since that time, surprisingly little interest has been shown in this group of Lepidoptera; consequently, Riley's paper has remained the only comprehensive reference for the group. Unfortunately, this work, as well as several other classic studies of his, are no longer readily available to many biologists. Also, considerable information on general biology and systematics has appeared in recent years which has decreased the scientific merit of earlier efforts. Because of Riley's meticulous manner of observation, however, his biological studies probably will continue to be valuable sources for information regarding these insects.

The primary aim of the present study is to provide a modern, systematic treatment for all members of the subfamily. It is also my intention to summarize all previous information on the life histories of the various species. Thus, in addition to being a specific revision of the Prodoxinae, it is hoped that this study will prove useful as a general reference.

A total of 17 species and one subspecies, representing 5 genera, are recognized as comprising the Prodoxinae. Four species and three genera are described herein for the first time. One species, "*Prodoxus*" *reticulatus* Riley, has been transferred to the genus *Lampronia* of the Incurvariinae, primarily on the basis of characters of the mouthparts and wing venation. The maxillary palpi of *Lampronia reticulata* (Riley), new combination, are considerably shorter than those of typical *Prodoxus*; furthermore, the venation of this species is similar to *Lampronia* in that the outer margin of the discal cell in the primaries is truncate, as compared to the somewhat rounded condition in *Prodoxus* and all other Prodoxinae.

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Review of the Literature

One of the first written accounts of a member of this subfamily appeared in September 1872 as an anonymous report of the American Association for the Advancement of Science meetings of August 21–27, 1872. In that paper, Riley's description (1872a) of a new genus and species, *Pronuba yuccasella,* and its behavior as a pollinator of *Yucca* were briefly outlined. Other naturalists (e.g., Engelmann, 1872a, b) may have observed the general life history of this species prior to 1872, but their findings were published either contemporaneously with Riley's first account or at some later date. Until Riley's death in 1895, the abundant literature which quickly appeared on these insects was primarily the result of this one man. A total of 13 species were described by him as members of this subfamily; two are known now to be synonyms, and one, *"Prodoxus" reticulatus,* has been transferred to the Incurvariinae.

Having been the first to thoroughly investigate the unusual association between the yucca plant and its pollinator, Riley naturally was extremely interested in any subsequent observations that other naturalists might contribute to this special subject. Consequently, if he found the published results of others to disagree with his own, Riley would be unusually prompt in replying and probably at times was more severe in his criticism than was necessary. Such enthusiasm on Riley's part eventually produced some complaint from a few of his colleagues. Chambers (1878a, p. 141), in an attempt to right himself after one barrage of criticism from Riley, made the following observation concerning his critic:

". . . he is the founder of the very interesting genus and species, *Pronuba yuccasella,* and naturally enough seems to feel a sort of paternal solicitude for his scientific progeny; and woe betide the unlucky wight who ventures to trespass on this, his own peculiar demesne, as others beside I, and notably Prof. Zeller and poor Mr. Boll, have feelingly discovered . . . . Indeed, in consideration of the punishment meted out to Prof. Zeller and Mr. Boll, I ought, perhaps, to thank Mr. Riley for letting me off with simply, as it were, an admonitory spank."

What probably disturbed Chambers (and others) more than being the recipient of such barbed remarks, however, was the fact that Riley was usually correct in his arguments.

In 1880a, Riley described another new genus and species, *Prodoxus decipiens,* which he recognized as being related to *Tegeticula yuccasella,* but which differed greatly in its life history. Riley (1880a) originally had suspected that *P. decipiens* was a junior synonym of an earlier species, *quinquepunctella,* which Chambers (1875) had described as a *Hyponomeuta* [sic]; however, he refused to abandon *decipiens* as a specific name, partially because it seemed more applicable, and also because he believed the nomenclatural rules of priority were too extreme. A year later (1881), Riley proposed that the name *quinquepunctellus* be retained for the maculate variety of *P. decipiens;* thus, he still preserved his name for the nominal species. Similarly, Riley (1881) knew that the generic name *Pronuba* was preoccupied, but he continued to use this name in subsequent papers. This proved unfortunate because several contemporary and later authors, undoubtedly influenced by Riley's domination of the subject, likewise used these incorrect combinations for two of our most common moths.

Following the advice of Trelease, Riley (1892a) summarized much of the subject matter included in his previous papers into a single treatise. This reference has remained, to the present day, the most informative source on the Prodoxinae. A year later, Trelease (1893) summed up his observations on the pollination of several southwestern yuccas in a publication which provided original information on the behavior of two species of *Tegeticula, synthetica* and *maculata,* as well as the description of a new melanic form (*aterrima*) of *T. maculata.* At the close of his paper, Trelease presented a general account of the evolution of the yuccas and their pollinators which has been the most significant discussion on the subject.

A brief review of the yucca moths was issued by Dyar (1903b). This three page account contained essentially no biological data but did present for the first time a taxonomic key for the separation of the species. In 1915 an important paper by Busck appeared, describing a new species of *Prodoxus* reared from the flower stalks of *Agave;* thus, it was then established that some members of this group of moths were not restricted to *Yucca* in their feeding habits. The species, *P. barberellus,* which Busck described has been found by the present author to require a new generic placement.

One of the few significant contributions on yucca moths to appear in recent years was also by Busck (1947) and was published in McKelvey's revision of the southwestern yuccas. During the course of her field studies on the genus *Yucca,* McKelvey devoted some effort toward assembling a representation of the insects collected in the flowers. The specimens were sent to August Busck for identification and are now deposited in the collections of the Smithsonian Institution. Due to his death in 1944, Busck was unable to publish the results of his work on the Prodoxinae. McKelvey (1947), however, assembled some of his notes and published them in the second and final part of her revision. The significant part of Busck's notes was a synoptic list of the genera and species of yucca moths. Also of interest in this reference is the host information supplied by McKelvey.

A brief biological review of the common yucca moth, *Tegeticula yuccasella*, was presented by Rau in 1945. This reference summarized Rau's observations and general experiments with this insect over a period of several years. Also included is an annotated list of insects which were encountered in association with *T. yuccasella* within the flowers of *Yucca filamentosa.*

The most recent reference treating yucca moths is that by Powell and Mackie (1966). Because that paper appeared while the present one was in press, it was not possible to incorporate the findings of these authors into this study. Essentially their work involved a biological study of the moths associated with *Yucca whipplei.* This included not only the Prodoxinae but also a few members of the Blastobasidae, Gelechiidae, and Phycitidae; the yucca moths, however, comprise the major part of their paper.

No attempt will be made to summarize all aspects of Powell's and Mackie's interesting study, although it should be noted that there exist two divergences of taxonomic opinion in their treatment as compared to my own. Whereas I have synonymized *Tegeticula maculata apicella* (Dyar) as no more than a color variate of *T. m. maculata* (Riley) and recognize only two subspecies in this complex, Powell and Mackie consider Dyar's subspecies to represent a coast range form, geographically separated from *T. m. maculata.* According to their records the typical form of the species occurs in Tulare and Kern Counties, California, south to Caliente in the foothills north of the Tehachapi Mountains. *T. m. apicella* is reported from San Luis Obispo County, southward through the mountains of Ventura County and on both sides of the San Gabriel Mountains of Los Angeles County, California. Similar to my treatment in the present paper, these authors recognize *T. m. extranea* (Hy. Edwards) as an allopatric subspecies ranging through cismontane Riverside and San Diego Counties, California.

In their presentation of *Prodoxus marginatus* Riley, Powell and Mackie include *P. pulverulentus* as a geographical subspecies, thus differing from previous opinions that these two biological entities represented separate species. As suggested in the present paper, *P. m. marginatus* is the more northern of the two moths and is reported by Powell and Mackie from Tulare, Kern, and San Luis Obispo Counties southward into the transverse ranges, on the desert side of the San Gabriel Mountains and in Cajon Valley, and in cismontane southern California in the Santa Monica Mountains. According to their records, the southern subspecies, *P. m. pulverulentus* ranges southward through San Diego County and probably into Baja California. These authors further state that the two forms meet at an apparent zone of intergradation in the southern San Jacinto Mountains.

Morphology

A thorough morphological study of this subfamily has not been attempted, although certain anatomical areas (e.g., mouthparts, genitalia), due to their obvious importance, have been treated in some detail. Most structures are discussed adequately under the particular genus or species concerned, or in other easily available references and will not be reviewed here. A few structures, however, deserve special emphasis and are discussed in the following paragraphs.

MOUTHPARTS.—Certain modifications of the maxillary appendages have developed in a few species which deserve special consideration. In general, the maxilla is of a primitive type, possessing palpal segmentation similar to the Micropterygidae. The lacinia, however, has been lost, and the galeae extended, but they are still rudimentary in some respects. Each galea is circular in cross section and does not unite with the opposing member to form a common feeding tube, or tongue. A faint, longitudinal line (fig. 40) is present on the median surface of each galea, and it probably represents the rudimentary groove, which, in the higher Lepidoptera, becomes the food canal.

The females of two genera, *Tegeticula* and *Parategeticula*, possess a pair of extremely specialized structures, commonly referred to as maxillary "tentacles," which arise from the base of each maxillary palpus. Until the discovery of *Parategeticula pollenifera*, these structures were believed to exist in no other genus of Lepidoptera except *Tegeticula*. Other genera of Prodoxinae, now unknown, may be found to possess this specialization; however, it is very unlikely that any species not a member of this subfamily will be so equipped, because the maxillary tentacle probably has evolved only once throughout the order.

The homology of the tentacle was studied by Smith (1893), who concluded that it was an extension of the palpifer and was homologous to comparable structures in certain Neuroptera, Mecoptera, and Diptera. Smith's conclusion may be correct, but presently this is difficult to ascertain and will remain so until more comparative work, involving studies of musculature and embryology, can be conducted. It should be emphasized, however, that if the first segment of the maxillary palpus in *Tegeticula* is in actuality the palpifer, then technically the number of palpal segments in the Incurvariidae and related families is one less than is apparent. This would be true because, as defined (Snodgrass, 1935), the palpifer is a lobe of the stripes and not a segment of the palpus. Thus, by following this line of reasoning, the homology as proposed by Smith becomes less acceptable. Primarily for convenience and because its homology is so uncertain, the segment bearing the maxillary tentacle is considered in this paper to be the first segment of the maxillary palpus.

Superficially, the segment bearing the tentacle most resembles a typical palpal segment, especially in the males of *Tegeticula, Parategeticula,* and in all other members of the Prodoxinae. Riley, Trelease, and later authors stated that the males of *Tegeticula* and the females of *Prodoxus* possess a rudimentary tentacle on the basal segment. Such a rudiment is present to a slight degree in both the males and females of *Prodoxus* (fig. 51); however, the base of the second palpal segment is more modified than the basal segment itself.

Crampton (1923) later studied the maxilla of *T. yuccasella* but was unable to homologize the tentacles, providing them with a new name—the palpiprocess. As illustrated by Crampton, the maxillae of *Sialis* (larva) and *Machilis* bore some resemblance to those of female *Tegeticula* in possessing a palpifer which gave rise to a digitate process, referred to by him as the galea.

Examination of the most primitive Lepidoptera offers little toward an understanding of the general problem. A 5-segmented palpus is present in the Micropterygidae which shows no evidence of basal specialization. However, from the basal segment of the labial palpus arises a digitate structure (fig. 53) which Tillyard (1923) has referred to as a sensory process. It does not seem unreasonable to suppose that a similar process could have developed from the comparable segment of the *Tegeticula* maxilla.

On initial examination it may appear that the maxillary tentacles are derived from the lacinia. In the Micropterygidae this appendage is present as a greatly reduced, bluntly pointed process, lying close and slightly based to the similarly reduced galea. Considering the structure and origin of the lacinia in nearly all insect orders, however, there seems little probability that this organ is in any way involved with the maxillary tentacles of *Tegeticula.*

The primary function of the tentacles is to aid the female in gathering yucca pollen; indeed, without these appendages it is evident that pollen can not be collected (see p. 59). In structure the tentacles are tubular and membranous with numerous, short, hooked hairs scattered over the inner surfaces. These hairs engage the pollen as it is gathered and greatly assist in retaining it. Extension of the tentacle is probably by means of fluid pressure with muscular action perhaps playing a major role in retraction.

The labium will be mentioned briefly in this section only in regard to sensory organs located at the apex of the terminal palpal segment.

These organs were first noted in the higher Lepidoptera by Rath (1887, 1888) and in the more primitive groups by Busck and Böving (1914) and Tillyard (1923). In the Micropterygidae (fig. 53) and Eriocraniidae, the sensory area is represented merely by a depression lined with what appear to be rows of sensory cones. A comparable organ, which I consider homologous, is present in the Prodoxinae as a sac-like invagination from the apex of the palpus. In this subfamily, it is best developed in the genus *Agavenema* (fig. 44), being more reduced in *Tegeticula*, *Prodoxus*, and *Mesepiola*. In *Parategeticula* the organ is even less developed and is situated at the apex of the second palpal segment.

Wings.—In addition to venational characters and the distribution of aculeae over the wing surface, another interesting, although often neglected feature in the wings of Lepidoptera is the development of the wing coupling mechanism. The subject has been studied carefully by Braun (1919, 1924) and should be noted here, especially since some interspecific variation apparently exists.

The males of all genera, except *Parategeticula*, characteristically possess a stout, single-spined frenulum (e.g., fig. 45). In *Parategeticula* the frenulum is absent, and the humeral area of the hindwing subsequently has become expanded to compensate for the loss. This rather unique coupling mechanism is assisted in its function by the presence of a row of stout spines arising from the base of the costa.

The frenulum in all females is rudimentary and is represented only by a few short, weak spines at the distal end of the costal sclerite. Beyond this arises a row of spines which vary in structure according to genus and sometimes species. In *Prodoxus*, *Mesepiola*, and *Agavenema*, the spines are approximately the same size, gradually becoming more scalelike outward. The females of *Tegeticula yuccasella* and *T. synthetica* have two or three basal spines of this series greatly lengthened; thus, resembling the true female frenulum of most higher moths. The costal spines of *T. maculata* are generally more similar to those of *Prodoxus*. The coupling apparatus in *Parategeticula* is essentially the same as that described for the males; i.e., with an expanded humeral angle of the hind wing comparable to the condition that exists in the Lasiocampidae.

Male genitalia.—The terminology used in this paper for the components of the male genitalia (figs. 92–94) is essentially the same as that followed by Klots (1956). The application of a few terms is rather uncertain, however, and requires further discussion.

Much of this uncertainty is illustrated by two somewhat different interpretations (Eyer, 1924, 1926; Bastida, 1962) which have appeared on the morphology of the prodoxid genitalia. In her paper, Bastida has shown the presence of a gnathos and has clearly mistaken the tegumen for a combined (?) vinculum and uncus. The gnathos and uncus are characteristically absent in the Incurvariidae; whereas the vinculum is primarily a ventral structure, it is not situated dorsally as indicated by Bastida. An elongate sclerite lying immediately ventrad to the aedeagus was identified correctly by Bastida as the juxta. As evidenced by his illustrations, Eyer (1924) failed to note the presence of this structure and considered it absent. Closely associated with the juxta and located near the inner bases of the valves is a pair of tiny, ovoid sclerites which I have interpreted as sclerotizations within the largely membranous anellus.

The valves are rigidly united at their bases by means of a well developed transtilla; from the latter arise a pair of prominent apodemes. The lateral ends of the transtilla are greatly expanded and form a padlike area at the base of each valve. This entire area (transtilla included) actually may be a development from the costa of the valve. However, I have interpreted these structures to be the labides (as discussed by Klots, 1956), in part because of a rather definite area of weakening, that may represent a former line of fusion, present between labidis and valve proper.

Female genitalia.—As was true for the males, the females of this subfamily possess genitalia very similar to the other members of the Incurvarioidea, particularly with respect to the piercing ovipositor and the single (monotrysian) genital opening. In addition to these features, another interesting modification within this group of moths is the enclosure of the eighth abdominal segment by the seventh. This has developed perhaps as a means of adding rigidity to this part of the abdomen and to aid the ovipositor in its penetrating operation. For further information concerning the structure of this type of ovipositor, the references of Busck (1931) and Klots (1956) may be consulted.

Primarily because of its apparent uniqueness, only one structure of the internal genitalia will be mentioned here. As was pointed out by Busck, the ductus bursa of *T. yuccasella* possesses a membranous enlargement about midway along its length (fig. 131). This sac, which partially is supported by a pair of slender apodemes, has been compared by Busck to the bulla seminalis or receptaculum seminalis (spermatheca) of ditrysian Lepidoptera. Because the primary function of this sac probably is to serve as a temporary storage receptacle for sperm, I have referred to it as the spermatheca even though the true homologies are not known. Apparently, the spermatheca is present to some degree in other Prodoxinae, but is best developed in the species of *Tegeticula*.

Measurements

The wing expanse of all specimens was measured as the maximum distance from the apex of one forewing to that of the opposite wing. In certain instances the length of the forewing is indicated and was measured with the aid of a Bausch and Lomb microscope slide projector and a stage micrometer; an outline of the wing was projected on to paper, marked, and then measured directly with the projected image of the micrometer. A similar method was used to note measurements of the male genitalia and, particularly in the case of the latter, is believed to be quite accurate (within 0.01 mm.).

A few common statistics have been included, particularly in the discussion of *Tegeticula yuccasella,* and will be defined here. The standard deviation (s) was calculated by the method given by Simpson et al. (1960, pp. 84–87), which is based on the ratio:

$$s^2 = \frac{\sum fX^2 - \frac{(\sum fX)^2}{N}}{N-1}$$

where

f=frequency of a given class
X=value of the variate for that class
N=number of observations (total frequency)

The coefficient of variability (C.V.) is an expression of the standard deviation as a percentage of the sample mean and is calculated as:

$$\text{C.V.} = \frac{100s}{\bar{x}}$$

where

$\bar{x}$=sample mean

The procedure followed in determining the statistical significance between certain measurements treated in this paper is that of Snedecor (1956, pp. 244–245, 250), whose test criterion, or F value, is calculated as:

$$F = \frac{\text{mean square of sample means}}{\text{mean square of individuals}}$$

If the computed F value has been found to be significant at the .05 level of probability, it is noted with a single asterisk (*); if its probability lies beyond the .01 level (highly significant), then it is marked with a double asterisk (**).

Systematic Position and Evolution

Originally, *Tegeticula yuccasella* was thought by Riley to be a member of the Tineidae, but upon the discovery of *Prodoxus* and several new species, the family Prodoxidae (Riley, 1881) was proposed. Its affinities were believed to be primarily with the Tineidae and only superficially with the Yponomeutidae. Dyar (1903a) did not treat the yucca moths as a separate family, but placed them in the Tineidae near the genus *Adela*.

Largely on the basis of the female genitalia and presence of aculeae over the wing surface, Busck (1914) recognized the true relationships of the yucca moths to the other aculeate groups and considered them as a distinct family, separate from the Incurvariidae and Adelidae.

Apparently Forbes (1923) was the first to consider the yucca moths as a subfamily of the Incurvariidae. The other subfamily he recognized was Adelinae, which presently is considered to be composed of two distinct families, the Incurvariidae and Adelidae. Handlirsch (1925) likewise treated the Prodoxinae as a subfamily, but included them in the Tineidae; thus, envisioning a large, heterogenous family for this group as did Dyar and numerous, earlier workers. Bourgogne (1951) agreed with the classification of Forbes in recognizing the Prodoxinae as a subfamily of the Incurvariidae.

In the present study I have treated the Incurvariidae as consisting of two subfamilies, the Incurvariinae, sensu strictu, and the Prodoxinae. The Adelidae, which are characterized in part by a more developed tongue, reduced maxillary palpi, and certain secondary adaptations such as elongated antennae and enlarged eyes, may prove to be separate from the Incurvariidae.

It seems certain that the Prodoxinae represent a New World specialization, derived, perhaps, from some primitive and now extinct incurvariine. Morphologically the two subfamilies are very close and at present can not be clearly separated on the basis of the adults. Previously, the principal basis used to delimit these two groups was the length of the maxillary palpi; those of the Prodoxinae were considered longer than those of Incurvariinae (Forbes, 1923). With the discovery of *Agavenema*, however, this character has proven to be of less significance. Instead, there appears to be a gradual reduction in the length of the maxillary palpi through the Prodoxinae and Incurvariinae to such genera as *Chalceopla*, which possesses a greatly shortened, two-segmented palpus. The maxillary palpi of most *Lampronia* are proportionately longer than those of *Agavenema* and more closely approximate the length observed in *Prodoxus*. Other similarities, particularly in the genitalia and wing venation, also exist between the two subfamilies which prevent a clear separation.

These relationships will be discussed further in a future paper treating the New World Incurvariinae.

The principal reasons for recognizing two distinct groups within the Incurvariidae are observed in the larvae. The Prodoxinae characteristically possess larvae which lack prolegs and crochets; thoracic legs are known only in the genus *Tegeticula.* In contrast, at least some remnants of prolegs are believed to exist in all Incurvariinae, in addition to the presence of thoracic legs. The larvae of a few species of European Incurvariinae (e.g., *Lampronia capitella*) are known to bore in plant shoots. Although these particular species are internal feeders, as are all members of the Prodoxinae, their larvae, nevertheless, possess a normal complement of prolegs, at least in the later instars.

At present, it is difficult to summarize the evolution of the Prodoxinae. I believe, however, that some attempt should be made, largely because of the paucity of existing information on this subject, and also as a means of explaining the arrangement of genera presented herein. Considerably more work needs to be performed on the basic morphology of the primitive Lepidoptera, as well as on their life histories. Information from such studies, in connection with the discovery of new species, may greatly modify some of the following speculations. After a study of the Incurvariinae (now in progress) has been completed, it should be possible to discuss more adequately the relationships of the family.

As mentioned previously, the Prodoxinae represents a New World radiation of the Incurvariinae that evolved as borers in certain agavoid plants, the genus *Yucca* in particular. I consider the Incurvariinae to resemble most a possible ancestral group, primarily because of their more archaic distribution (holarctic) and the more generalized form of the larva. At present I regard the genus *Lampronia* as the most primitive component of the Incurvariinae; structure of the head, legs, and wings are the basis for this belief. In addition, certain members of this genus most resemble the Prodoxinae in life history as well as morphology. For example, at least four species of *Lampronia* are known to be internal borers; however, a majority of the known species of Incurvariinae are leaf miners in the early instars and later construct a lenticular case and commence to feed externally.

The suggestion of an internally feeding ancestor for the Prodoxinae is not to imply necessarily that this is the most primitive form of larval behavior in the Incurvariidae, but merely that this habit was an early specialization. Powell (1964) has stated that evolution within the Lepidoptera has preceded from the wood boring habit toward the external feeding habit as a means of adaptive radiation within separate phylogenetic lines. To support this thesis, Powell refers to the Hepialidae, Eriocranioidea, and Incurvarioidea as possible progenitors of the higher Lepidoptera. To the present author, it seems more reasonable to suppose that such groups as the Hepialoidea and Incurvarioidea represent relatively specialized offshoots that were in no way involved with the evolution of the higher (i.e., nonaculeate) Lepidoptera. Morphologically these three superfamilies demonstrate several primitive features, especially in the imago, but their life histories have become specialized within their particular groups. As far as is known, the larvae of the Micropterygidae are external feeders, and it is very likely that this habit has continued into the higher moths and butterflies without passing through any boring stage. Certainly within many families of nonaculeate Lepidoptera, stem and seed boring has evolved as a specialization from externally feeding, ancestral types. It is possible that stem boring in the Incurvariidae was derived, as generally suggested for the Lepidoptera by Hering (1951), from a leaf mining habit, which is so prevalent in Eriocraniidae and in the early instars of many Incurvariinae.

In diagram 1 on page 14, I have summarized the general relationships of the five genera now recognized in the Prodoxinae. As a possible progenitor for the Prodoxinae, I have envisioned (diagram, 1, A) a group which possessed a fruit boring larva with well-developed thoracic legs and some development of abdominal prolegs. The adults possibly may have been pollen feeders similar to the Micropterygidae, although their mouthparts may have become too specialized for such function at this stage of evolution. My decision that *Tegeticula* most nearly represents the ancestral type of the Prodoxinae is not without question, and future findings may modify this decision somewhat. Present information, however, involving not only the morphology of *Tegeticula*, but also its life history, especially as it relates to certain members of the genus *Lampronia*, suggests that *Tegeticula* appeared somewhat earlier in history than did *Prodoxus*.

The larval history of *Lampronia capitella* Clerck is interesting in that it seems to recapitulate the fundamental steps in the evolution of the prodoxine larva. The eggs of *L. capitella* are inserted into the young fruits of *Ribes* during the spring. Upon hatching, the larva feeds for a certain period on the seeds. Then, in June or July, it burrows out of the fruit and spins a case in which it overwinters. Larval feeding is renewed the following spring, but now the half grown larva bores into the buds and also tunnels the young shoots. By April or early May, the larva completes its growth and pupates in the shoot. Similar life histories also have been noted (Ford, 1949) for *L. rubiella* Bjerk, *L. quadripunctella* Stephens, and *L. pubicornis* Haworth.

The transition from a capsular feeding larva to one that bores exclusively in the stem also seems evident within the "marginatus" group of the genus *Prodoxus* (see p. 71). On morphological evidence, the adults of both *Prodoxus marginatus* and *P. pulverulentus* are considered less specialized than *P. aenescens*. It is interesting to note in this regard that the larvae of the former feed primarily in the fleshy part of the young fruit or receptacle, whereas the larvae of *P. aenescens* are restricted to the flower stalk.

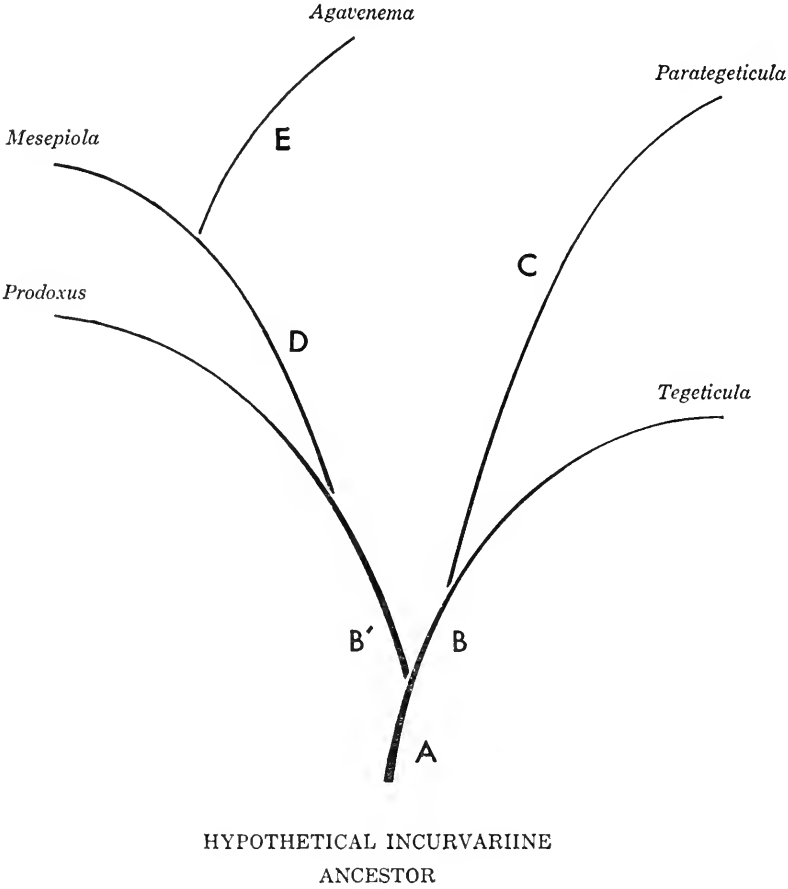


DIAGRAM 1.—Generic relationships of the Prodoxinae.

Other evidence further suggests that *Tegeticula* represents a group more ancient than *Prodoxus*. The larvae of *Prodoxus* are more specialized in that all legs have been lost; the larvae of *Tegeticula*, on the other hand, still retain well developed thoracic legs. A comparison of the prodoxine head also reveals some evidence of specialization. The presence of maxillary tentacles in *Tegeticula* and their apparent reduction in *Prodoxus* probably is of phylogenetic significance; however, as noted on page 7 and in figure 51, any indication of this structure's former presence in *Prodoxus* is slight. Throughout the Prodoxinae an increase in the overall size of the compound eyes is apparent. *Tegeticula* possesses the smallest eyes in the subfamily, whereas *Agavenema*, one of the most advanced genera of Prodoxinae, has the largest pair. Another evolutionary tendency that progresses throughout the subfamily is the reduction of the signum in the female. The rather spectacular, many rayed signa of *Tegeticula* (fig. 136), which superficially resemble the single signum present in *Atteva* (Yponomeutidae), gradually have become reduced through some genera of Prodoxinae and completely lost in the genus *Agavenema*.

One fact which seemingly contradicts *Tegeticula's* apparent antiquity is the absence of insect parasites attacking that genus. Insect parasitism has developed within *Prodoxus*, but perhaps not in *Tegeticula* (see p. 42). This phenomenon suggests that *Prodoxus* may be older than *Tegeticula*, which is not believed to be the case. If no parasites have evolved on *Tegeticula*, then it would seem very likely that the distinctly different life history of this genus, as compared to that of *Prodoxus*, is in some way reponsible for the observed absence of insect parasites.

Two general tendencies (see diagram 1, B and B′) seem to have developed early in the history of the Prodoxinae. One division (B) is characterized by those species which have retained a seed boring larva, or which have become secondarily adapted to a stem boring habit (C). In addition, the members of this division and its predecessors (A) gradually became more intimately associated with the reproductive parts of their hosts, to the extent that pollination was accomplished during the course of oviposition. The possible combination of pollen feeding by the adult in connection with the deposition of eggs in some part of the flower, particularly the pistil, may have initiated occasional or accidental visits to the flower stigma which resulted in the fertilization of the ovules. Early in the history of *Yucca*, other insects probably were responsible for pollination, but with the fusion of the stylar lobes of the pistil and reduction of the nectaries (Trelease, 1893), accidental pollination by these insects or other agencies became less reliable and eventually impossible. Before this stage was reached, however, ancestral *Tegeticula* was completely dependent upon the development of the yucca fruit (i.e., a true seed borer), and had developed the specialized maxillary appendages necessary for pollinating its host. The gradual modifications of the moth's life history (and mouthparts) probably coincided with the gradual changes which occurred in the yucca flower.

Although much remains to be known concerning the biology of *Parategeticula*, this genus is believed to represent a specialized, stem boring group (C), derived from ancestral *Tegeticula*, and completely separate from the phyletic line (B′) which gave rise to *Prodoxus* and its relatives. The eggs of *Parategeticula* are deposited in a very peculiar and unique manner (figs. 33, 34) in the stems of its host. Unfortunately, the habits of the larva are unknown at present. On rarer occasions, the female of *Parategeticula* inserts her eggs into the coralla of the flower. This habit possibly may be a reflection of an earlier time in which the predecessors of this group fed exclusively within the flowers. Morphologically *Parategeticula* presents considerable evidence of its specialized nature. Major among these is the unique ovipositor, which is probably the most modified of any of the plant piercing Monotrysia. The reduced palpi and the loss of the epiphysis and frenulum also should be mentioned in this connection. The retention of the maxillary tentacles, along with a behavior for collecting pollen, indicates the ancestry it has in common with *Tegeticula*. At present it is not known if the females of *Parategeticula* actually complete the pollination sequence, or whether they merely gather the pollen and then move to other parts of the plant for oviposition, without depositing any pollen on the yucca stigma. Because the life history of *Parategeticula* demonstrates less restriction to the yucca flower than does *Tegeticula*, it is possible that the former gradually has acquired a negligible, or less efficient, role in pollination as compared to that witnessed for *Tegeticula*. A present failure for the females of *Parategeticula* to be efficient pollinators probably would be of no great disadvantage, since *Tegeticula* and *Parategeticula* are sympatric, as far as is known, in both time and space. Thus, *Parategeticula*, like the members of *Prodoxus*, may be dependent on the existence of *Tegeticula* for survival.

Division B in diagram 1 is characterized by species that are principally stem borers. No member is believed to have retained a seed boring habit, although some of the less specialized members of *Prodoxus* are known to feed in the fleshy part of the fruit. The genus *Prodoxus* undoubtedly is the most primitive element of this major division, as is indicated by both morphology and host preference. It is possible that this phyletic line diverged from ancestral *Tegeticula* (B) after obligatory pollination already had become an established pattern within the group, and that the loss of this habit accompanied the gradual change in larval behavior. It is also possible, however, that the immediate progenitors of this division never exhibited the specialized pollinating behavior of *Tegeticula*, but that they evolved before this habit had developed.

Division D in diagram 1 represents an important evolutionary step in the history of the Prodoxinae in that plant genera other than *Yucca* were exploited as hosts. Two plant genera are now represented, but more may be discovered as other xerophytic plant groups such as *Nolina, Dasylirion,* and *Furcraea* are investigated. Evidence is beginning to appear to show the possibility of a series of prodoxine genera progressing from *Prodoxus* to *Agavenema.* Each major step in the series may be represented by a distinct genus of moths that feeds, perhaps, on a particular genus of plants. Morphologically, *Mesepiola* is intermediate between *Prodoxus* and *Agavenema;* its life history is unknown, but most likely the larva will be discovered as a borer in *Nolina* or *Agave. Agavenema,* of course, may not represent the terminal group in the evolutionary series; instead, some plant genus such as *Furcraea* may harbor the most specialized stem borer of this phyletic line.

Two species of *Agavenema* are known presently, and future work probably will reveal more. The tremendous success of the genus *Agave* (approximately 275 species), as compared to that of *Yucca* (41 species), immediately suggests the possibility of a somewhat comparable amount of speciation within *Agavenema.* Such a radiation, however, may have never occurred; instead, *Agavenema* may be represented by fewer species than *Prodoxus.* This could be true if (1) *Agavenema* was of relatively recent origin (as is believed), or if (2) the species are not host specific, but feed on a wide variety of *Agave,* and, similarly, if (3) morphological and especially physiological differences between the species of *Agave* are relatively slight (at least within the flower stalk), which, consequently would induce little speciation on the part of the moths. The final answer can be resolved only after a considerable amount of field work has been performed. As a possible parallel, several species of Megathymidae, particularly the genus *Agathymus,* have undergone considerable speciation on *Agave,* and it is likely that *Agavenema,* when better known, will show this also.

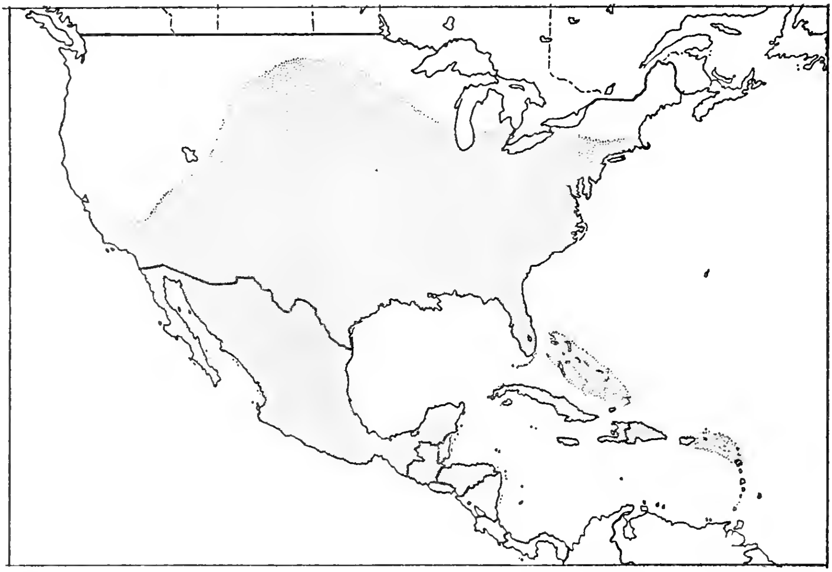
Biology

Distribution.—The apparent center of dispersal for the Prodoxinae has been the Sonoran region of the southwestern United States, particularly southern California and Arizona. California possesses the greatest concentration with a total of 4 genera, 12 species and 1 subspecies; Arizona is next with 9 species but has all 5 genera represented. Only one species, *Prodoxus intricatus,* does not occur in the United States; thus giving a total of 16 species for this country.

Little is known about the distribution of the Prodoxinae in Mexico, although it is probable that all 5 genera are present, at least in the northern states. Representatives of all genera except *Mesepiola* have been collected there and undoubtedly the range of *M. specca* extends into Sonora and perhaps Chihuahua. Five species (including one endemic) are known from Mexico and more can be expected; the total number, however, probably will never exceed a dozen or so, at least not for the yucca feeding species, due to the lack of diversity of *Yucca* in this area. The genus *Agave*, in contrast, has speciated far more and may yield several new species of agave moths.

No records of Prodoxinae have been reported from the West Indies, although potential hosts are present. *Yucca aloifolia* is known from several of the islands, especially of the greater Antilles, but may not be extensively naturalized. Of more significance is the genus *Agave* which is represented by several species native to the West Indies. Consequently, at least some species of yucca moths, or more likely agave moths, may be discovered in this region eventually.

Because the distribution of these insects is less thoroughly known than that of the hosts to which they are restricted, distributional data of the plant hosts should prove meaningful in illustrating the general, or potential, geographic range of the Prodoxinae. Two maps are provided: One to show the possible distribution of yucca moths (i.e., the genus *Yucca*), and a second to indicate the possible occurrence of agave moths (i.e., the genus *Agave*). The data was summarized from several published sources and from specimens in the National

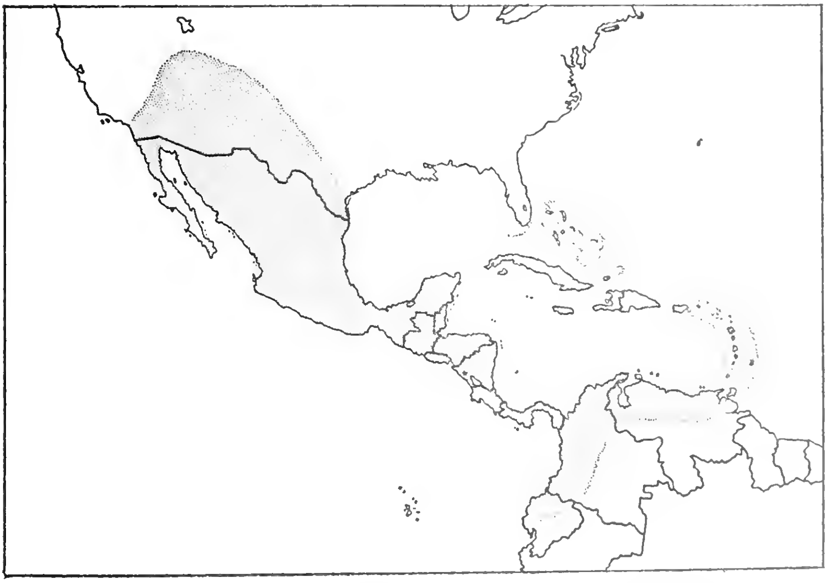


Map 1.—Distribution of the genus *Yucca* (the northern limits of this genus are extended here to conform with the known distribution of the yucca moths).

Herbarium. The extreme northern and southern limits are rather indefinite and in some cases may represent plant populations that have escaped from cultivation, but which now are believed to be naturalized. Through cultivation, the distribution of several species of *Yucca* and *Agave* have become much more extensive than indicated, especially in South America and through the Old World. The moths, however, have not become established in such areas and evidently cannot unless the host is represented by adequate populations that are more or less contingent. Thus, in maps 1 and 2, I have attempted to indicate only the native, or subsequently naturalized, distributions of *Agave* and *Yucca*.

Plant hosts.—Besides *Yucca* and *Agave*, no other genera of plants have been definitely established as hosts for moths of the Prodoxinae. Future investigations may show that some of the larger species of *Nolina* and *Dasylirion* are food plants, as well as certain other plant genera mentioned in the following discussion. In general, these plants are characterized in part as being xerophytic perennials which typically produce a large, pithy flowering stalk and capsular fruits.

Although the genus *Yucca* has received considerable attention from several botanists over the past century, the classification of the group is still in a state of flux, largely because of the extreme amount of variation exhibited by most species. Webber (1953) considered this variation to be of three types: (1) environmental, (2) minor genetical,



Map 2.—Distribution of the genus *Agave* (exclusive of *Manfreda*).

and (3) major genetical. Variations produced by factors which Webber considered as major genetical have caused some of the most serious difficulties in understanding the genus, as this type of variation is expressed frequently in hybrid combinations.

Approximately 41 species of *Yucca* are recognized currently, although, for reasons just stated, the application of several names is questionable. The center of concentration for the genus is the southwestern United States, as evidenced by the presence of 21 species (Webber, 1953) native to this area; previous authors listed as many as 28 to 32 species for the same region. Because no recent, comprehensive reference on *Yucca* is available, several authors were consulted in compiling the list of the species presented in table 1; some of the principal works referred to were those of Trelease (1902, 1920), Small (1933), McKelvey (1938, 1947), Fernald (1950), and Webber (1953).

Webber's study of the southwestern yuccas superficially may appear less thorough than the comparable work by McKelvey; however, I have followed many of the decisions of the former author because his concept of species and techniques employed seem more modern. Several species proposed by McKelvey (e.g., *Y. intermedia, utahensis, verdiensis, campestris, kanabensis*) were considered by Webber to represent certain hybrid complexes and, consequently, were synonymized. In the lists of host plants included in the following taxonomic treatments for each moth, I have retained McKelvey's names, as given in her 1947 paper, in the event that a few may be revived at some future date. Those names which were synonymized by Webber, however, have not been listed in table 1.

I have found it desirable to include a complete listing of all species of *Yucca*, even though several names have not been reported as food plants for yucca moths. This was done primarily because it seems almost a certainty that every plant eventually will be found to harbor at least one, and more probably two, species of moths. Also, because no recent list of yuccas was available, the presence of such a list may prove of some value, especially in reference to certain problems discussed in connection with *Tegeticula yuccasella* (pp. 53–60). Several subspecies of *Yucca* have been proposed, but since the status of these names is even more uncertain than many of the presently accepted species, and because the moths probably are not host specific at this level, subspecific names have been excluded from table 1.

Much of the host information was summarized from the reports of McKelvey (1947). It is possible that all or most of her records were based upon flower captures of the adults rather than upon actual rearings. This is suggested by a lack of any definite statement that rearings were performed, and more significantly by her remark (1947, p. 184) that certain "other" Lepidoptera were collected from

TABLE 1.—*Host records for Prodoxinae*

	Tegeticula				*Parategeticula*	*Prodoxus*										*Mesepiola*	*Agavenema*	
	synthetica	*maculata*	*m. extranea*	*yuccasella*	*pollenifera*	*quinquepunctellus*	*y-inversus*	*coloradensis*	*ochrocarus*	*intricatus*	*sordidus*	*marginatus*	*pulverulentus*	*cinereus*	*aenescens*	*specca*	*barberella*	*pallida*
YUCCA																		
(Section Sarcocarpa)																		
aloifolia				x														
arizonica				x		x												
baccata				x		x	(?)	x										
carnerosana				x														
decipiens																		
elephantipes										x								
endlichiana																		
faxoniana				x		x		x										
filifera				x														
grandiflora																		
jaliscensis																		
periculosa																		
schidigera				x														
schottii				x	x		x		x									
torreyi				x				x										
treculeana				x				x										
valida																		
(Section Clistocarpa)																		
brevifolia	x										x							
(Section Hesperoyucca)																		
peninsularis																		
whipplei		x	x	?				(?)				x	x	x	x			
(Section Heteroyucca)																		
gloriosa				x														
recurvifolia																		
(Section Chaenocarpa)																		
angustissima				x		x												
arkansana				x		x												
baileyi				x														
constricta				x		x												
elata				x		x												
filamentosa				x		x												
flaccida																		
freemanii																		
gilbertiana																		
glauca				x		x												
louisianensis																		
neomexicana																		
pallida				x		x												
reverchoni																		
rigida																		
rostrata																		
rupicola						x												
smalliana																		
thompsoniana																		
AGAVE																		
deserti																		x
palmeri																	x	
NOLINA																		
parryi																?		

the flowers. Flower captures often do indicate the larval food plant for this group of insects, but errors can occur; for this reason, I have noted with a question mark in table 1 any record which I considered dubious.

The systematics of the genus *Agave* is even more complicated than that of *Yucca.* A tremendous variety of morphological types exists which has fostered a great amount of superficial taxonomic activity, resulting in a copious supply of specific names. In his monograph of the genus, Berger (1915) recognized 274 species of *Agave*; approximately 185 species have been described from Mexico alone (Trelease, 1920).

One of the principal factors for the apparent success of *Agave* has been the high development of polyploidy throughout the group. Whereas all species of *Yucca,* as far as known, are diploid (n=30), a euploid series of 2n, 3n, 4n, 5n, and 6n, with a basic number of 30, has been discovered in *Agave* (Granick, 1944). Both autopolyploidy and allopolyploidy probably occur, although more evidence is available to support the latter. A definite correlation exists in *Agave* between polyploidy and vegetative growth, similar to that observed in other plant groups; namely, that the polyploids tend to be more robust and are characterized by leaves which are larger and more succulent than those of the diploids. It seems very likely that polyploidy, in connection with hybridization, has been largely responsible for many of the taxonomic problems encountered in this group of plants.

The center of distribution for *Agave,* in contrast to that of *Yucca,* is situated further south, in Mexico, as indicated by the number of species indigenous to that country. Granick (1944) reached a similar conclusion on the basis of chromosome data. Because diploid forms usually represent the ancestral types in such a group of plants, their heaviest concentration should be near the distributional center for the group. Consequently, one finds several diploid species in Central America but only two such forms as far north as Arizona. Toward the northern limit of its range, *Agave* is represented principally by tetraploids and some hexaploids.

Although *Agave* possesses a many seeded, capsular fruit similar to that of *Yucca,* it is very doubtful that any member of the Prodoxinae has evolved as a seed borer in this plant. It is noteworthy in this regard to mention that the nectaries of the flowers are well developed and quite odoriferous. Consequently, numerous hummingbirds are attracted as well as a great variety of insects (primarily bees and flies), which result in the pollination of the flowers.

The relationships between *Yucca* and *Agave,* which appear relatively close as indicated by the biology of the Prodoxinae, have not been considered so by most botanists in the past. A majority of the botanical texts in current use place *Yucca* and *Agave* in separate families largely on the basis of superficial ovarian structure. *Yucca,* with its superior ovary, is placed usually in the family Liliaceae, and *Agave,* which possesses an inferior ovary, in the Amaryllidaceae.

In 1934 (later revised in 1959), Hutchinson presented a rather revolutionary classification of this group of plants which reflected the most recent opinions of several botanists; namely, that *Yucca* and *Agave* are more closely related than was previously thought. These two genera, along with several others, are recognized by Hutchinson as comprising a single family, the Agavaceae, which is distinct from both the Liliaceae and Amaryllidaceae. Hutchinson emphasized this distinction even further by placing the Agavaceae in a separate order, Agavales, along with the principally Australian family, Xanthorrhoeaceae.

Certain cytological evidence also suggests that *Yucca* and *Agave* are closely related. Much of this information has been reviewed by McKelvey and Sax (1933) and Granick (1944) and will be mentioned only briefly in the present discussion. The evidence essentially consists of strong karyotypic similarities between the two plant genera in question. As pointed out by Granick, the "*Yucca-Agave*" karyotype is characterized by a diploid pattern of 10 large chromosomes on the periphery of the metaphase plate and 50 small ones, slightly variable in size, concentrated in the center. The total chromosome number, of course, may vary (as in polyploid *Agave*) but the basic pattern is usually consistent. Because of its relative uniqueness in the plant kingdom, the occurrence of this particular karyotype is believed to be very significant in indicating the basic relationships of certain genera. In addition to *Yucca* and *Agave,* this karyotype has also been found in *Furcraea, Beschorneria,* and *Polianthes,* as well as in an Old World liliaceous genus, *Hosta.*

The present writer concurs with the conclusions of Hutchinson and others in believing that *Yucca* and *Agave* are closely allied. My opinions are derived primarily from the affinities of the moths which have evolved in association with this group of plants. The significance of insect systematics as an indicator for taxonomic relationships of other groups of animals and plants has been realized on numerous occasions. This has been particularly true in situations involving host-parasite associations or host-plant specificity.

In regard to present entomological evidence, the close relationship of *Yucca* and *Agave* are best shown by the apparent evolution of the stem boring Prodoxinae. As discussed on page 17, it is possible that a series of prodoxine genera have evolved, each being restricted to a particular plant genus within the Agavaceae. This evolutionary series, consequently, may reflect, to some degree, the relationships of the hosts. *Prodoxus*, which is restricted to the most primitive genus of the Agavaceae (i.e., *Yucca*), is believed to represent the most primitive stem borer in the Prodoxinae. Likewise, *Agavenema*, which is considerably more specialized than *Prodoxus*, feeds on one of the most advanced members of the Agavaceae, the genus *Agave*. According to Hutchinson, the tribe Polyantheae contains the most specialized elements of the family; thus, the same may hold true for any prodoxines which may inhabit these plants. *Mesepiola* is suspected of being a borer in *Nolina*, a member of a group of plants (Nolineae) which Hutchinson places between the tribes Yucceae and Agaveae. Interestingly enough, these moths, on the basis of their morphology, are intermediate between *Prodoxus* and *Agavenema*. It should be noted, however, at this point that chromosome data do not support the general belief that *Nolina* represents a group that is intermediate between *Yucca* and *Agave*. The karyotype of *Nolina* is very different from the latter complex in possessing 38 somatic chromosomes of varying sizes; an equal number also has been reported for *Dasylirion*.

The close affinities of *Yucca* and *Agave* are also demonstrated by the Megathymidae. In a recent generic revision of this family, Freeman (1958) lists the genera *Aegiale*, *Turnerina*, and *Agathymus* as host specific on *Agave*. All species of the related genus *Megathymus*, except one, feed on *Yucca*. *Megathymus beulahae* Stallings and Turner is interesting in that it is restricted to an unusual *Agave* that resembles a *Yucca*. The remaining genus of the family, *Stallingsia*, is restricted to *Manfreda*, a group of plants formerly considered by botanists to be a subgenus of *Agave*.

In summary then, the relationships of the three known genera of stem boring Prodoxinae suggest that one, relatively homogenous group of plants has been exploited as hosts, and that *Yucca* was the first to be so utilized. Future studies probably will show that additional moth and plant genera are involved in this association, and as a result of such discoveries, the affinities of certain groups within the Agavaceae may become better understood. Other plants, in addition to those already mentioned, which should be investigated as possible hosts for these moths are *Beaucarnea* (Mexico), *Calibanus* (Mexico), *Beschorneria* (Mexico), *Furcraea* (tropical America), *Manfreda* (United States, Mexico, Guatemala), and *Polianthes* (Central America, Trinidad). *Furcraea*, a close relative of *Agave*, may prove particularly interesting in that, like *Agave*, it produces a single, stout flower stalk, which, in *F. longaeva* Zuccarini, may attain a height of 15 meters.

Life history.—The remarkable association of the yucca moths (i.e., *Tegeticula* and *Prodoxus*) with the yucca plant has been known for many years. The life history of *Tegeticula* is analogous in some respects to that of the fig insects of the chalcidoid family Agaontidae, particularly in the fact that unless the pistils of the host are polinated by the insect, no fruit will develop. *Tegeticula*, however, is further remarkable in that the act of pollination, as well as that of pollen collecting, are completely deliberate; whereas, in the fig insects these activities are performed accidentally, due largely to the unusual morphology of the fig flower.

In brief, the female *Tegeticula* first collects, with the aid of her specialized mouthparts, a quantity of pollen from one to several flowers; she then inserts her ovipositor into a yucca pistil and deposits one egg per puncture and a varying number per flower. Usually following oviposition, and sometimes even before this act is completed, she begins to force some of the pollen she is carrying, down the stigmatic tube of the flower. Thus, pollination of the flower is insured, as well as a supply of seeds for the larvae to feed upon.

The association of *Prodoxus* in this relationship is also of some interest, although not nearly as involved as described for *Tegeticula*. The larvae of all species of *Prodoxus* either bore in the main flower stalk, flower pedicel, or in the fleshy part of the fruit. It has been pointed out by Riley (1892a) that, since the flower stalks of at least some species of *Yucca* soon begin to die unless the flowers are pollinated, *Prodoxus* is dependent to a great extent upon the existence of *Tegeticula* for survival. This unusual association may seem to infer that *Tegeticula* necessarily would have had to precede *Prodoxus* in time. *Tegeticula* is believed to be the more primitive group; however, the present dependency of *Prodoxus* upon *Tegeticula* may be a secondary development. This would be true if *Prodoxus* had evolved during the period when *Yucca* was pollinated by diverse agencies (e.g., wind, bees) and not just by females of *Tegeticula*. Thus, ancestral *Prodoxus* could have developed as stem borers in *Yucca*, as the genus *Agavenema* has in *Agave*, independent of any presence of *Tegeticula*.

Because the life histories of various members of this subfamily differ so greatly according to genus, a general review of this subject will be found following the discussion of each genus.

Checklist

1. Tegeticula Zeller
   Pronuba Riley
   Thia Hy. Edwards
   Thelethia Dyar
   Valentinia Coolidge
   1. synthetica (Riley)
      paradoxa (Trelease)

   2. maculata maculata (Riley)
      apicella (Dyar)
      maculata extranea (Hy. Edwards)
      aterrima (Trelease)
   3. yuccasella (Riley)
      alba Zeller
      intermedia (Riley)
      mexicana Bastida
2. Parategeticula Davis
   4. pollenifera Davis
3. Prodoxus Riley
   5. quinquepunctellus (Chambers)
      paradoxicus (Chambers)
      decipiens Riley
   6. y-inversus Riley
   7. coloradensis Riley
      lautus Cockerell
      confluens Cockerell
      rheumapterellus (Dietz)
   8. ochrocarus Davis
   9. intricatus Riley
   10. sordidus Riley
   11. marginatus Riley
   12. pulverulentus Riley
   13. cinereus Riley
   14. aenescens Riley
4. Mesepiola Davis
   15. specca Davis
5. Agavenema Davis
   16. barberella (Busck)
   17. pallida Davis

Subfamily Prodoxinae

ADULT.—Medium to small moths; wing expanse ranging from 8 to 33 mm.

Head: Vesture rough, scales hairlike (figs. 31–32). Antennae simple in both sexes, approximately one-half the length of forewing; scape with pecten absent; basal half typically covered with appressed scales; apical half without scales, usually darker in color, pubescent. Eyes medium to large size; ocelli absent. Chaetosema absent. Tongue reduced, not coiled in repose; the two portions (galeae) free and not appressed to form a single sucking tube; food channel rudimentary. Mandibles present but greatly reduced. Maxillary palpi folded against face, very long, two-thirds or more the length of tongue, usually 5-segmented but reduced to 4 in *Parategeticula;* females of *Tegeticula* and *Parategeticula* with a specialized and a very flexible "tentacle" originating near apex of basal palpal segment; maxillary tentacles absent in females of other genera and in all males. Labial palpi porrect, usually 3-segmented, reduced to 2 segments in *Parate-*

geticula; all of first, and dorsum of second and third segments covered with short, appressed scales; venter of second and first with long, erect, hairlike scales.

Thorax: Loosely covered with hairlike scales. Wings fully scaled and moderately broad; membrane with aculeae evenly scattered over entire surface. Forewings 12-veined; all veins normally separate; an accessory cell present and of large size; base of medius divided within discal cell, forming a large intercalary cell. Hindwings 8-veined; all veins separate except 5 and 6 which may be separate, connate or stalked, intercalary cell present; basal crossvein present between 7 and 8. Frenulum simple in all males except *Parategeticula,* where it is absent; poorly developed or absent in the females. Legs typically with a pectinate epiphysis on foretibia, absent in *Parategeticula;* mesothoracic leg with two tibial spurs, metathoracic leg with four; tarsal claws simple.

Abdomen: Normally cylindrical in all males and laterally compressed in all females except in *Tegeticula synthetica* where it is depressed in both sexes. Seventh segment of all females strongly sclerotized, elongated; seventh sternite largely devoid of scales, brunneous; eighth segment entirely enclosed within seventh.

Male genitalia: Tegumen reduced and hoodlike, apex either evenly rounded or with two setigerous lobes. Uncus and gnathos absent. Vinculum large, V- or Y-shaped, sometimes with saccus greatly extended. Transtilla well developed, rigidly connecting the bases of the two valves; expanded laterally to form a pair of lobe-like enlargements (labides) which are fused to the bases of the valves. Juxta present, usually forming an elongate shield. Anellus largely membranous, with a pair of tiny, darkly sclerotized elements located near inner bases of valves. Valves frequently with spiniferous tubercules; cucullus usually unmodified, sometimes with a row of stout spines. Aedeagus relatively simple and straight; cornuti absent.

Female genitalia: One genital opening present (monotrysia). Ovipositor of the piercing type; apex serrulate, usually spear-shaped; subapical region of ovipositor frequently with a serrated, dorsal ridge; anterior and posterior apophyses usually slender and greatly elongated; bursa copulatrix frequently with a pair of signa, each resembling a stellate cluster; signa vestigial in some species or absent; oviduct greatly lengthened; ductus bursa often enlarged to form a primitive spermatheca.

Larva.—Small, length at maturity usually less than 15 mm. Head small, less than half diameter of prothorax; not depressed, about as high as broad, sometimes partly retracted into prothorax. Body typically stout and cylindrical, usually of a pale green, pink, or white color; without prominent setae. Thoracic legs either present or absent; abdominal prolegs and crochets absent. Seed and stem borers in *Yucca* and *Agave*.

PUPA.—Incomplete, abdominal segments 2–7 free in both sexes; abdomen either finely spined as in *Prodoxus* and *Agavenema*, or with stout processes arising primarily from anterior abdominal tergites (*Tegeticula*). Pupation occurring either in a silken cocoon within host plant, or in a silk and earthern cocoon underground.

Key to the Genera of Prodoxinae

MALES

1a. Foretibia without an epiphysis; frenulum absent; maxillary palpus 4-segmented; labial palpus 2-segmented . . . . **Parategeticula**

1b. Foretibia with an epiphysis; frenulum present; maxillary palpus 5-segmented; labial palpus 3-segmented.

  2a. Apical (third) segment of labial palpus as long as second (fig. 44); fourth segment of maxillary palpus as long as third; wings relatively narrow (fig. 49), hind margin of forewing slightly excavated between veins 1 and 3 . . . . **Agavenema**

  2b. Apical segment of labial palpus less than half the length of second (fig. 42); fourth segment of maxillary palpus twice the length of third; wings broader (fig. 47), hind margin of forewing not excavated.

    3a. Genitalia with posterior margin of valve deeply lobed and usually bearing a few to many short, stout spines in a single cluster (figs. 102, 105–110).

      4a. Medium size moths, wing expanse approximately 15 to 33 mm. Eyes relatively small (fig. 40), vertical diameter less than width of frons. **Tegeticula**

      4b. Small moths, wing expanse less than 15 mm. Eyes larger (fig. 43), vertical diameter exceeding width of frons . . . . . . **Mesepiola**

    3b. Genitalia with posterior margin of valve not deeply lobed, instead evenly curved (fig. 92); spines, if present, never in a cluster, but in a scattered series . . . . **Prodoxus**

FEMALES

1a. Maxillary palpus with a prehensile tentacle arising from basal segment (figs. 40 and 41).

  2a. Foreleg with an epiphysis; maxillary palpus 5-segmented; signum of bursa copulatrix stellate (fig. 136). . . . . **Tegeticula**

  2b. Foreleg without an epiphysis; maxillary palpus 4-segmented; signum not stellate, instead reduced and ovoid (fig. 135). . . . . . **Parategeticula**

1b. Maxillary palpus without a prehensile tentacle (fig. 42).

  2a. Maxillary palpus with fourth segment as long as third (fig. 44); apical (third) segment of labial palpus as long as second; signum absent. **Agavenema**

  2b. Maxillary palpus with fourth segment twice the length of third (fig. 42); apical segment of labial palpus less than half the length of second; signum usually present.

    3a. Apex of seventh abdominal tergite with an uncinate process (fig. 113). **Mesepiola**

    3b. Apex of seventh abdominal tergite simple (fig. 112). . . . . **Prodoxus**

Tegeticula Zeller

Tegeticula Zeller, 1873, p. 232 [type: *Tegeticula alba* Zeller, 1873, monobasic]; 1875, p. 340.—Chambers, 1878a, pp. 161, 163 [synonym of *Pronuba* Riley].—Riley, 1881, p. 639; 1891a, p. 97.—Walsingham, 1903, p. 260; 1914, p. 369.—Busck, 1915, p. 94.—Barnes and McDunnough, 1917, p. 197.—Forbes, 1923, p. 74.—Braun, 1924; pp. 239, 254.—Forbes, 1928, p. 534.—Fletcher, 1929, p. 217.—McDunnough, 1939, p. 109.—Lindinger, 1941, p. 237.—Busck, 1947, p. 182.—Comstock, 1950, p. 599.—Borror and Delong, 1963, p. 432.

Pronuba Riley, 1872a, p. 444 [type: *Pronuba yuccasella* Riley, 1872, original designation and monobasic; preocc., not Thomson 1860]; 1872b, p. 182; 1873b, p. 150; 1873a, p. 55.—Chambers, 1878a, p. 161; 1878b, pp. 141–154.—Riley, 1880a, pp. 141–144; 1880b, pp. 155, 156.—Chambers, 1880b, p. 177.—Riley, 1880d, p. 177; 1880e, p. 182; 1881, pp. 618, 623, 625–629, 637, 639 [*Pronuba* preocc.]; 1883a, p. 197; 1883b, p. 467; 1889a, p. 150; 1891a, p. 97; 1892a, pp. 137 ff.; 1892b, pp. 83 ff.; 1892c, p. 360; 1893a, pp. 43 ff.—Trelease, 1893, pp. 181, 187, 192, 193, 197, 207–208, 211–212, 217, 218, 220–223.—Sharp, 1899, p. 433.—Dyar, 1902 [1903], p. 577; 1903b, p. 102.—Kearfott, 1903, p. 124.—Walsingham, 1903, p. 260 [synonym of *Tegeticula*].—Holland, 1905, p. 441.—Walsingham, 1914, p. 369 [synonym of *Tegeticula*].—Busck, 1915, p. 94 [synonym of *Tegeticula*].—Barnes and McDunnough, 1917, p. 197 [synonym of *Tegeticula*].—Braun, 1919, pp. 356, 362, 363.—Forbes, 1923, p. 74 [synonym of *Tegeticula*].—Handlirsch, 1925, p. 876.—Fletcher, 1929, p. 185 [synonym of *Tegeticula*].—McDunnough, 1939, p. 109 [synonym of *Tegeticula*].—Lindinger, 1941, p. 237 [synonym of *Tegeticula*].—Busck, 1947, p. 182 [synonym of *Tegeticula*].

Promiba [sic] Kirby, 1874, pp. 380, 494 [misspelling of *Pronuba* Riley].—Walsingham, 1914, p. 369.

Thia Hy. Edwards, 1888, p. 181 [type: *Thia extranea* Edwards monobasic; preocc.; not *Thia* Leach 1815, *Thia* Oken 1815, *Thia* Newman 1840].—Dyar, 1893, p. 301 [preocc.; synonym of *Thelethia*].—Meyrick, 1913, p. 29 [preocc.; synonym of *Thelethia*].—Busck, 1947, p. 182 [synonym of *Tegeticula*].

Thelethia Dyar, 1893, p. 301 [type: *Thia extranea* Hy. Edwards, original designation and monobasic]; 1902 [1903], p. 495.—Meyrick, 1913, p. 29.—Busck, 1947, p. 182 [synonym of *Tegeticula*].

Valentinia Coolidge, 1909, p. 112 [type: *Tegeticula yuccasella* Riley, 1872, designated by Fletcher, 1929; preocc.; not Walsingham, 1907].—Forbes, 1923, p. 74 [preocc.; synonym of *Tegeticula*].—Fletcher, 1929, p. 235 [preocc.; synonym of *Tegeticula*].—Busck, 1947, p. 182 [synonym of *Tegeticula*].

TYPE SPECIES.—*Tegeticula alba* Zeller, 1873 (=*Pronuba yuccasella* Riley, 1872a), monobasic.

ADULT.—Relatively robust, heavy bodied moths; wing expanse 15–33 mm.

Head (fig. 40): Eyes small, vertical diameter less than width of frons. Tongue prominent, exceeding length of maxillary palpi. Mandibles relatively prominent. Maxillary palpus 5-segmented; fourth segment doubling the third in length; apical segment minute, apex acute; maxillary tentacle normally arising from basal segment (fig. 50) in female, rarely reduced or absent; basal segment of maxillary palpus unmodified in male (fig. 52). Labial palpus 3-segmented; apical segment short, with a small, terminal sensory gland.

Thorax: Wings (fig. 45) relatively broad, apices subacute, sometimes rounded; all veins normally separate; frenulum prominent, simple in male, usually consisting of 2–3 weak bristles in female. Epiphysis present (fig. 58).

Abdomen: Female with abdomen usually laterally compressed as in other Prodoxinae, depressed in *T. synthetica;* apex of seventh tergite (figs. 115–116) unmodified, without any terminal process.

Male genitalia.—Apex of tegumen bilobed. Vinculum V- to Y-shaped; saccus slightly to well developed. Valves variously lobed; lobes usually bearing short, stout spines. Aedeagus relatively short and robust to elongate and very slender.

Female genitalia.—Apex of ovipositor spear-shaped; a subapical dorsal ridge either present or absent. Apophyses very long and slender. Ductus bursa very long, usually exceeding length of apophyses, with an inflated portion (spermatheca) bearing two, rodlike apodemes; juncture of ductus bursa with oviduct either at spermatheca or more caudad. Signa paired, stellate, with over 40 rays per signum.

Larva (fig. 24).—Head partly retracted into prothorax, concealing rear portions. Body usually pinkish in color, at least by maturity; thoracic legs present, typically 4-segmented, with a single minute apical claw; abdominal prolegs absent. Seed borers in fruit of *Yucca.*

Pupa (fig. 26).—Head with frontal beak greatly reduced. First 7 abdominal tergites with a singly, prominent row of stout spines per segment; those of first tergite greatest in length, then gradually decreasing in length posteriorly. Pupation occurs in an earthen, silk-reinforced cocoon underground (figs. 29–30).

Life History

Egg.—The eggs of the various species of *Tegeticula* are probably at least superficially similar, but only those of *T. yuccasella* have been described. According to Riley (1892a), the egg is threadlike in general appearance, averaging approximately 2 mm in length and less than 0.1 mm in diameter. One end (wherein the embryo develops) is enlarged and gradually tapers posteriorly, forming an elongate pedicel. The eggs of all species are inserted singly into the ovary of the plant host by means of the female's piercing ovipositor.

Larva.—The eggs of *T. yuccasella* reportedly hatch in about a week, giving rise to tiny larvae approximately one mm in length. The newly emerged larva may subsist for a brief period as a sap feeder, but soon enters a developing ovule through the funicular base. Body color at first is a translucent white which becomes in time more yellowish and finally, at maturity, a pinkish to reddish hue. All larvae of *Tegeticula* are characteristic in possessing well-developed thoracic legs and in lacking prolegs.

After entering an ovum, the larva restricts its feeding to the developing seeds. Normally only one locule of the fruit is inhabited by a given larva, and a relatively small number of seeds are destroyed (sometimes less than a dozen). Consequently, it is possible for a single pod, containing well in excess of a hundred seeds, to provide nourishment for several *Tegeticula* larvae. Seldom does this occur, however, because the behavior of the moth is such that rarely are more than a dozen eggs deposited in a single pistil. Trelease (1893) reports (for *T. maculata*) that six eggs—one on either side of each primary septum—are the usual number deposited in a pistil of *Yucca whipplei.* Most eggs do not develop with the result that one seldom finds more than 4–6 mature larvae per pod. In examining over 70 pods of *Y. filifera* from Mexico, the author usually encountered one or two larvae per pod (sometimes none) and rarely over three. Riley (1892a) mentions one exceptional case of discovering as many as 21 larvae within a single yucca pod.

The larva of *T. yuccasella* normally attains maturity in about a month—a period which also corresponds with the usual time required for the seeds of most yuccas to mature. Prior to emerging from the fruit pod, the larva excavates an exit burrow toward the outer surface of the fruit. However, an opening to the outside is not completed at this time, and the larva retreats back to the seeds to continue feeding, thus leaving a thin partition to block the exit. The author observed this activity in specimens of *T. yuccasella,* which were collected from one of the baccate-fruited yuccas, *Y. filifera.* A similar behavior may be true for the other species of *Tegeticula.*

Before the pods begin to harden or dehisce (as is the case with most capsulate yuccas), the mature larva emerges from its host, and, if necessary, lowers itself to the ground by means of a silken thread (Whitten, 1894a). *T. yuccasella* has been observed emerging from the pod at various times of day (usually at night) during or immediately following a period of rain. Rainfall may be the final stimulus inducing the other species to leave the host as well, for then the ground is softened and more easily penetrable. The larva then burrows into the ground and forms a firm, ovoid cocoon (figs. 29–30), consisting of silk, heavily intermixed with soil particles.

Tegeticula yuccasella overwinters in the larval stage and normally does not pupate until the following spring, a few days before the flowering of the yuccas. This general behavior is probably true in most instances for the other species; however, the length of hibernation (or aestivation) for the final larval instar can be quite variable as has been observed for *T. synthetica.* Riley (1892a) reports receiving infested fruit containing larvae of this species in

May, 1888. As soon as the pods were received, the larvae emerged and entered the ground; some of them forming cocoons at this time. A few larvae, however, did not construct cocoons until the end of 1889, or more than a year after they were received. One larva was discovered still living and unchanged inside its cocoon, in August, 1891, or nearly two and one half years from the time it left the fruit. Most of the adults that were reared successfully from Riley's series, however, emerged the following spring in March or April. An even greater extension of the larval stage has been noted for *Prodoxus quinquepunctellus* (see p. 69).

Pupa.—As outlined above, pupation for all species of *Tegeticula* occurs inside an earthen cocoon, underground, and is preceded by a prolonged period of larval hibernation. The actual length of the pupal period is relatively short and probably does not exceed a week or two in most instances.

Structurally, the pupae of *Tegeticula* are characterized by the presence of stout spines arising from the abdominal tergites (fig. 26). A comparison of this heavily-armed form with the smoothly-textured pupa of *Prodoxus* immediately suggests a basic biological difference between these two genera, and, indeed, there is. The presence of these spines in *Tegeticula* probably are of benefit to the pupa in working its way out of its buried, cell-like cocoon, and upwards through the soil until it is at least part way out of the ground.

Adult.—Emergence of the adults usually occurs in the spring, in association with the flowering period of most species of yuccas. It has been observed that the males of *T. yuccasella* emerge slightly earlier than the females. As soon as flight is possible, the moths fly to the nearest yucca flowers, which usually are very near the immediate area of pupation. From then on, the behavior of the female follows a pattern that has proven to be one of the most interesting associations in the animal kingdom.

The exact sequence of events following emergence may vary somewhat; it is probable that, in most instances, the newly emerged female, on reaching the first blossom, begins to gather pollen. Immediately prior to this activity, the moth typically runs about the bases of the stamens and then quickly climbs up the inner side of a filament (Trelease, 1893). With coordinated movements of the head and mouthparts (the maxillary tentacles in particular), she succeeds in scraping pollen from the anther; then with the aid of her forelegs, the pollen is molded into a ball and firmly worked into a natural pocket under the head. Several stamens and more than one flower may be visited before the pollen gathering impulse subsides. Eventually the female climbs a pistil and assumes a position favorable for egg laying (fig. 35).

In *T. yuccasella,* the pistil is penetrated frequently just below the middle. This is not typical for all species, however, for Trelease (1893) has noted that the females of *T. synthetica* pierce the uppermost part of the style and thrust the ovipositor down the stylar channel. In the former case, the location of each puncture is not random, but is carefully selected by the female. This is an area usually where the walls of the pistil are thinnest and, for most moths, normally within one of the deeper (primary) divisions of the young tricarpellate ovary. Insertion of the egg requires approximately one minute. Withdrawal of the ovipositor is often a more laborious task, requiring from forty seconds to as long as three minutes, and is accomplished by a series of pulsating, jerky movements. Through studies of ovarian cross sections, Riley (1892a) has shown that the ovipositor usually enters the locule near the external margin of the ovule and ordinarily does not touch the ovule itself; rarely is an ovule penetrated during oviposition.

Oviposition injury to the young fruit is early noticeable as a dark green, external discoloration in the immediate area of the puncture. As the fruit develops, this becomes a depression, causing the mature pod to exhibit usually a pronounced curvature and median constriction (figs. 18–20), which have been considered by some botanists to be characteristic for this genus of plants. Several experiments clearly have shown that the yucca moth is responsible for these deformations. Most recently, Webber (1953) reported that although several of the yuccas studied by him commonly or always bore constricted fruit, none of the flowers hand-pollinated produced fruit that was in any way deformed. It is evident that fruit constriction results from a failure of the ovules and the surrounding tissue to develop at the oviposition site (fig. 18). It seems very probable that the retardation of cellular growth in this area is due to an inhibitory substance introduced by the moth during oviposition. Ovule abortion, accompanied by later fruit deformation, occurs independently of larval development. Frequently, constricted fruit pods are to be found that show no other evidence of insect injury. Furthermore, successful development of the larva does not seem to accentuate the relative amount of fruit deformation.

Fruit abnormalities are most noticeable for those yuccas (the section *Chenocarpa* in particular) pollinated by *T. yuccasella.* Some plants occasionally may produce undeformed fruit and still be infested with *Tegeticula* larvae. The author has examined well-developed fruits of *Y. baccata* and *Y. elata* (fig. 14) which externally displayed no signs of oviposition injury, but which, upon dissection, revealed the moth's presence. The fruits of *Y. brevifolia* typically exhibit little or no deformity. As pointed out by Trelease, this results because the pollinator (*T. synthetica*) of *Y. brevifolia* normally oviposits in the apex of the pistil; hence the absence of constricted fruit.

It is not known to what advantage, if any, an arrestment of plant growth in the immediate environs of the puncture would provide for the egg or young larva. As discussed earlier, Riley observed the egg to be inserted normally in the locular cavity and frequently on the funicular stalk of the ovule. Largely for this reason, probably, he supposed that rapidly developing ovules could crush any insect egg in close proximity. Considering the shape and size of the egg of *T. yuccasella*, however, this does not seem likely.

Immediately following oviposition, the female climbs to the top of the pistil (if she has not already done so) and commences, amid considerable head and mouthpart movements, to work the pollen into the stigmatic cavity. The behavior of the moth during pollination is very characteristic and easily detectable, even from a slight distance. The entire forward portion of the body of *T. yuccasella* undergoes a series of rapid pumping or bobbing motions, during which time the pollen is not merely deposited on the stigma but is actually forced into the stigmatic tube. Portions of the mouthparts, notably the maxillary tentacles, are held stiffly erect under the head during this activity and appear to function collectively as a kind of plunger or ramrod. For *T. yuccasella*, a series of approximately 10–35 "bobbing" motions are conducted within an interval of usually less than 20 seconds in order to accomplish pollination.

It is possible that the behavioral pattern during pollination differs somewhat between the species of *Tegeticula*. Trelease (1893) has noted that the behavior of *T. synthetica* is similar to that of *T. yuccasella*. For *T. maculata*, however, he observed the female to be slower and more deliberate in her movements while depositing the pollen. Trelease partially attributed this difference in behavior for *T. maculata* to certain unique features in the morphology of its host, *Yucca whipplei*, particularly to the capitate stigma and to the fact that the pollen is formed characteristically in a compact mass, or pollenia.

Pollination does not always follow every act of oviposition. Frequently as many as 3–6 eggs may be inserted into different areas of a given pistil before the female visits the stigma. Following pollination, she then may continue to lay eggs in the same pistil or may leave to visit another flower.

The activity period for the members of this genus may differ greatly depending on the particular species. The activities of *T. yuccasella* commence at about dusk and continue into the early hours of darkness. Copulation normally occurs at this time within the blossoms and probably whenever males come into contact with females. Trelease (1893) has observed the adults of *T. maculata* and *extranea* to be diurnal in their movements. Pollen collecting, oviposition, pollination, copulation, and flight were all noted during the daylight hours. Mention was not made as to when these activities ceased, or if they were continued into the night at a greater or lesser frequency. The behavior of *T. synthetica* is similar to that of *T. yuccasella* in that the moths rest during the days in the flowers and become active toward evening.

As noted by Riley, Trelease, and others, a tendency seems to exist for the females to frequent only the newly opened blossoms of the *Yucca*. This, of course, has a practical advantage in that the females are directed away from flowers which most likely have already been pollinated and supplied with eggs; thus, this may be a means of insuring a more uniform distribution of the larvae. It is not fully understood how the females are directed to fresh blossoms, but in some instances (as observed for *T. synthetica*) the partially unopened condition of the young flower may aid in selection. The relative age difference and degree of flower odor between old and new blossoms may provide the deciding factor for most yucca moths. A desire to imbibe nectar or any comparable plant substance can have no attraction for the moths due to the vestigial condition of their mouthparts. Furthermore, the nectar glands of the yucca flower are reduced in size and open near the base of the pistil. Secretions from these glands do attract some insects but seldom in large numbers. It may be of interest to note here that these insects are not likely to be in any way involved with pollination due to the relative remoteness of the glands from the stigma.

It is interesting to speculate upon the mutual dependency the genus *Yucca* and its pollinators exhibit in their unusual association. Superficially, one appears equally dependent upon the other for survival, and thus display a true symbiotic relationship. In actuality it may be that the yucca moth profits most from this association (at least for the present) and, therefore, demonstrates a greater dependency upon its host.

It seems certain that the great majority of yuccas would never bear fruit if it were not for the deliberate act of pollination performed by the moths. Other insects have been reported visiting the flowers, but none have been observed to act as pollinators. The writer has frequently noted cultivated yuccas in Washington, D.C. which have flowered during the autumn months without ever producing fruits. Similar observations have been reported by numerous authors; whenever the adult moth is not present, then fruiting of yucca usually does not occur. Since the first publication of this association in 1872, however, the fruiting of certain yuccas has been noted in areas where *Tegeticula* was known to be absent. Riley (1891b) refers to such a case in which a yucca (possibly *Y. aloifolia*), cultivated in Australia, produced fruit. Seed pods from this plant showed no signs of oviposition or larval damage. *Yucca whipplei* from southern California repeatedly has been observed to bear fruit without the assistance of *Tegeticula* (Coquillett, 1893; Webber, 1953). This plant was suspected very early by Riley as being capable of selfpollination because of its unique, capitate stigma. *Yucca aloifolia* from the southeastern United States also has been suspected of self-pollination (Riley, 1892a).

Very little evidence has been proposed to demonstrate how great a role apomictic reproduction plays in yucca propagation. Webber (1953) states that except for *Y. brevifolia* and *Y. whipplei*, the southwestern yuccas are not reproducing to any extent by seeds. If such is true, then it would appear that most yuccas could survive indefinitely through vegetative means without need of the moth's presence. In contrast, if all yuccas over a large area failed to bloom for a single year, the population of *Tegeticula* would be precariously reduced, but probably not exterminated because of variances in the length of larval life. Two or three years without flowers being produced, however, most likely would annihilate these moths from a given area, along with any members of the genus *Prodoxus*. Eventually, of course, the moth population would be restored through emigrations from surrounding areas.

Although Webber belittles the significance of seed reproduction in *Yucca*, throughout his paper he emphasizes the important role that hybridization has played in regard to the taxonomic complexity of the genus. Such emphasis, of course, implies yucca production by seeds has been, and perhaps still is, of importance. McKelvey and Sax (1933) likewise have suggested that the perplexing variation and profusion of intermediate forms could be the result of extensive hybridization. Considering the behavior of *Tegeticula*, it would indeed be remarkable if considerable hybridization had *not* occurred between various species of *Yucca*. It need only be remembered that a moth such as *T. yuccasella*, which is fully capable of feeding upon a great variety of *Yucca*, is also just as adept at cross-pollinating its various hosts, and has probably made unconscious attempts to do so for thousands of years. Thus, it is very likely that hybridization has evolved as a common phenomenon within this genus of plants.

NATURAL ENEMIES.—Only one parasite has been reported from a species of *Tegeticula*, and that record is questionable (see p. 42). If insect parasitism does occur, then the frequency is evidently quite low. Although the members of *Tegeticula* are perhaps free from parasites, predators may exert some population control. The author has observed numerous beetle larvae of the family Cleridae inhabiting the seed pods of *Yucca* collected near Monterrey, Mexico. Dr. Donald Anderson of the U.S. Department of Agriculture has identified the predator as a species of *Enoclerus*, probably *spinolae* (LeConte). In the collections of the U.S. National Museum are numerous larvae of *E. spinolae* which likewise were discovered in yucca fruit collected in Mexico.

The larvae (especially the later instars) were found usually in the burrows excavated by *Tegeticula yuccasella* and probably enter the fruit pod through the same vacated burrows. It may be generally stated that most larval Cleridae are predaceous and typically feed upon wood and bark boring Coleoptera. The eggs are laid externally in crevices or in the entrance burrows created by the borers. Upon hatching from the egg, the larva enters the burrows in search of prey.

Numerous other beetle larve (seed borers and scavengers) were also present in the fruit collected near Monterrey, and these probably comprise a major part of the food supply for predators. On no occasion was an *Enoclerus* actually observed feeding on larval *Tegeticula*. Mature moth larvae were sometimes present in the same pod containing *Enoclerus*, and it is possible that these forms are seldom attacked.

Probably the period when *Tegeticula* are most susceptible to predators occurs from the time the larva leaves the fruit to until it has formed a cocoon. Wandering ants undoubtedly prey on many larvae before they are able to burrow underground. Riley (1873a) has reported predation of larvae by ants within the seed capsule at about the time the larva is preparing to leave. Spiders (particularly Thomisidae) and predaceous beetles, which frequently may be seen residing in the yucca flowers, probably attack the adult moths at times. Such examples of predatism have been observed for *Prodoxus y-inversus*.

Also present at times, living as scavengers in the abandoned burrows of *T. yuccasella*, are moth larvae of the family Blastobasidae. Eleven adults, identified as *Holcocera gigantella* Chambers, were reared from the pods of *Yucca filifera* which were collected by the author near Tula, Hidalgo (Mexico). These specimens (fig. 91), although considerably paler than typical *H. gigantella* from the United States (fig. 90), are identical to Chambers' species in regard to the male and female genitalia. Eventually it may be decided that these Mexican moths represent a southern race.

In his original description of *H. gigantella*, Chambers (1876) states that the type series was collected on the leaves of *Yucca*, and that the larva probably will be discovered feeding on some part of the plant. Thus, this prediction has proven correct. In addition to the Mexican material mentioned above, typical specimens of this species (deposited in the U.S. National Museum) have been reared from the seed pods of yucca collected in California; one moth is reported from the fruit of *Y. brevifolia*. The writer has also collected this species in the flowers of *Y. schottii*, as well as to rear it from the fruits.

The young blastobasid larva, perhaps, enters a pod via the exit burrow of *Tegeticula* or some other borer and commences to feed on the seed residue left by the original occupant. Mature larvae frequently can be detected externally by the presence of a silken, frass-covered tube which protrudes about one-half to three-quarters of an inch from the entrance of the burrow. Prior to pupation, the larva leaves the fruit pod and constructs a whitish, silken cocoon in some protective crevice, probably located most frequently near the base of the yucca plant. The length of the pupal period is about two weeks. Other blastobasids probably will be discovered in association with yucca moths, for the habit as a scavenger in plant burrows of other insects is a tendency typical of the family.

Another group of insects that are encountered occasionally in the flowers of *Yucca* are beetles of the family Nitidulidae. The author found larvae of one species, identified by Dr. Anderson as belonging to the genus *Carpophilus*, very abundant in the flowers of *Yucca schottii* (figs. 38–39). The larvae of this unidentified species were first noticed mining the flower petals. The mines are produced in the shape of a linear blotch and usually extend the full depth of the petal. At first the larvae are solitary miners, but as adjacent anthonomes coalesce, several larvae may come to inhabit one large blotch which eventually may occupy the entire petal. An individual larva is not restricted to a single mine; instead, it may leave the original mine to initiate new ones in other parts of the flower at will. As the petals are mined, a gradual decay of these parts commences that often results in a premature dehiscence of the corolla. The larvae may continue to feed in the decaying petals after the flower has fallen, for in this regard they seem very resistant to the adverse presence of decay causing organisms. Usually by this late stage, however, the larvae abandon the petals and commence to burrow in the young fruit. Especially in respect to this latter habit, it is very likely that the larvae of *Carpophilus* and *Tegeticula* are involved in some competition for food.

The larvae of several species of *Carpophilus*, as well as other genera of Nitidulidae, have been reported from the flowers of *Yucca*, particularly *Y. filamentosa*. These records, along with biological notes of the larvae, are summarized by Connell (1956).

Key to the Species of *Tegeticula*

1a. Forewing white or mostly so.
  2a. Forewing entirely white (figs. 86–87) . . . . **T. yuccasella**
  2b. Forewing white, spotted with fuscous (fig. 84) . . . **T. maculata maculata**

1b. Forewing fuscous or nearly so.
  2a. Forewing black (fig. 85), densely scaled; abdomen normal, round in cross section . . . . **T. maculata extranea**
  2b. Forewing light to dark fuscous (figs. 82–83), sometimes with a scattering of greyish white scales; thinly scaled; abdomen depressed. . **T. synthetica**

Tegeticula synthetica (Riley)

FIGURES 29, 82–83, 105, 116, 131, 151; MAP 3

Pronuba synthetica Riley, 1892a, pp. 141 ff., pl. 41, figs. 1–2, pl. 42, fig. 1; 1892b, p. 94; 1892c, pp. 370, 372; 1892d, pp. 305, 307, 308, fig. 14a; 1892e, p. 312, figs. 15–17, 1893a, pp. 46, 53; 1893b, pp. 304, 310.—Trelease, 1893, pp. 181, 196–198, 222, pl. 21, figs. 3–5.—Sharp, 1899, pp. 432, 433, fig. 208.—Dyar, 1902 [1903], p. 577, no. 6576 [synonym of *Pronuba paradoxa*]; 1903b, p. 103 [synonym of *Pronuba paradoxa*].—Handlirsch, 1925, p. 876, fig. 763.

Tegeticula synthetica (Riley).—Barnes and McDunnough, 1917, p. 197, no. 8474 [synonym of *Tegeticula paradoxa*].—McDunnough, 1939, no. 9837 [synonym of *Tegeticula paradoxa*].—Busck, 1947, p. 183 [synonym of *Tegeticula paradoxa*].

Pronuba paradoxa Riley, 1889a, p. 154 [nomen nudum]; 1889b, p. 372 [nomen nudum]; 1891a, no. 5181 [nomen nudum].—Trelease, 1893, p. 196 [synonym of *Pronuba synthetica*].—Dyar, 1902 [1903], no. 6576; 1903b, p. 103.—Kearfott, 1903, no. 7115.—Barnes and McDunnough, 1917, p. 197, no. 8474.—McDunnough, 1939, no. 9837.—Busck, 1947, p. 183.

ADULT (figs. 82–83).—Entire body depressed, thinly scaled, usually appearing very dark due to darkness of exposed cuticula. Wing expanse: male, 17–20 mm; female, 17–21 mm.

Head: Sparsely covered with whitish to light brown scales. Maxillary tentacles fully developed in all females examined. Labial palpi usually thinly covered with a few brownish hairs.

Thorax: Sparsely covered with small whitish scales, dorsum frequently lacking in vesture. Forewings likewise thinly covered with small, narrow, loosely attached scales; females normally lighter in color than males, due to heavier covering of whitish scales; wing scales of male almost entirely fuscous; fringe reduced in length, usually paler than rest of wing. Secondaries similar to forewings in color and scaling, appearing lighter in color if more rubbed; fringe usually white.

Abdomen: Fuscous to light brown above, whitish below; seventh tergite of female (fig. 116) broadly triangular, without an uncinate process.

MALE GENITALIA (fig. 105).—Apex of tegumen with two rounded, setigerous lobes. Outer half of valves deeply divided into two, ventrally projecting, digitate lobes; outer lobe strongly curved, with 0–3 stout, apical spines; inner lobe relatively straight, with 3–6 stout spines concentrated toward apex. Saccus moderately developed.

FEMALE GENITALIA (figs. 131, 151).—Dorsal ridge of ovipositor slightly raised; serrations very minute, exceeding 30 in number; apex of ovipositor rounded, serrulate. Oviduct elongate, greatly surpassing length of apophyses. Junction of ductus bursa with oviduct posterior to spermatheca, as in *T. yuccasella.*

Type.—Lectotype (designated by present author), ♀, Mojave, California, Feb. 4, 1891, through C. V. Riley, USNM 416; in the United States National Museum.

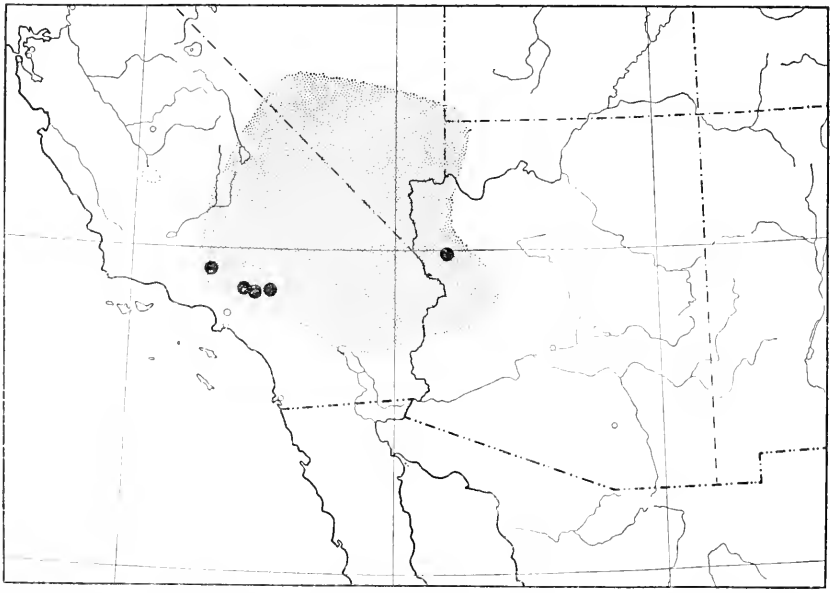
Type locality.—Mojave, Kern Co., Calif. (lectotype).

Recorded host.—"*Yucca brevifolia* Engelmann," Riley, 1892a. Larva bores in seeds of host plant.

Distribution (map 3).—Present records restrict this moth to western Arizona and southern California. In addition to these areas, the host is known also from southern Nevada and the extreme southwestern part of Utah.

Discussion.—Riley first referred to this species (1889a, b) as *Pronuba paradoxa;* but because this name was proposed without any accompanying diagnosis, it can have no taxonomic standing. The species was first described in May, 1892, as *Pronuba synthetica.*

Riley considered *T. synthetica* to represent one of the more ancient members of the Lepidoptera, and, indeed, it may. It should be remembered, however, that certain features, although appearing superficially primitive, may actually represent specializations. For example, the dark, thinly scaled wings and flattened body of this



Map 3.—Distribution of *Tegeticula synthetica* (black circles) and of host plant, *Yucca brevifolia* (shaded area).

species, which so impressed Riley because of their resemblance to certain neuropterous insects of the family Sialidae, very likely are the result of secondary adaptations. This is suggested because such a body form is quite different from that exhibited by the other members of *Tegeticula*. One feature that does indicate *T. synthetica's* early development is its host plant, which is considered generally by botanists to be one of the most primordial elements of the Yucceae.

MATERIAL EXAMINED.—31 ♂♂ and 62 ♀♀.

UNITED STATES: ARIZONA: Mohave Co.: Yucca, ♂, 5 ♀♀, Mar. 14 (USNM). CALIFORNIA: Kern Co.: Walker Pass, 6 ♂♂, 26 ♀♀, Apr. 3 (LACM). Los Angeles Co.: ♀, paralectotype, March, 4 ♂♂, 10 ♀♀, paralectotypes, April, ♂, 4 ♀♀ (USNM). Antelope Valley, 3 ♂♂, ♀, Apr. 3 (LACM). Mojave Desert, Valyermo, 14 ♂♂, 6 ♀♀, Apr. 5 (LACM); ♀, lectotype, 5 ♀♀, paralectotypes, Feb. 4 (USNM). San Bernardino Co.: ♀, paralectotype, April (USNM). Cajon Valley, 2 ♂♂, ♀, April (LACM). Phelan, ♀, Mar. 7 (USNM).

***Tegeticula maculata maculata* (Riley)**

FIGURES 84, 109, 132, 152; MAP 4

Pronuba maculata Riley, 1881, p. 617; 1889a, p. 154; 1889b, p. 372; 1891a, no. 5180; 1892a, pp. 139ff., pl. 42, fig. 2; 1892b, pp. 92ff., fig. 7; 1892c, pp. 367, 368, 370, 372, fig. 66; 1892d, pp. 305, 307, 308, fig. 14b; 1892e, p. 315, fig. 18.—Trelease, 1893a, pp. 181, 198, 210, 212–214, 216, 222, pl. 23, figs. 4–5.—Riley, 1893a, pp. 41ff.; 1893b, pp. 300–305, 308, 310.—Coquillett, 1893, pp. 311, 312.—Dyar, 1902 [1903], no. 6575; 1903b, p. 102.—Kearfott, 1903, no. 7113.

Tegeticula maculata (Riley).—Barnes and McDunnough, 1917, p. 197, no. 8472.—McDunnough, 1939, no. 9835.—Busck, 1947, p. 182.

Pronuba maculata apicella Dyar, 1902 [1903], no. 6575a [new synonymy]; 1903b p. 102.—Kearfott, 1903, no. 7113a.

Tegeticula maculata form *apicella* (Dyar)—Barnes and McDunnough, 1917, p. 197, no. 8472.—McDunnough, 1939, no. 9835.

Tegeticula apicella (Dyar).—Busck, 1947, p. 183 [color variety of *T. maculata*].

ADULT (fig. 84).—Wing expanse: male, 16–19 mm; female, 19–23 mm.

Head: White. Maxillary tentacle fully developed in all females examined. Labial palpus entirely white; scaling as in *T. yuccasella*.

Thorax: White, center of dorsum often possessing a single, dark spot. Dorsal surface of primaries largely white, with a variable amount of fuscous spotting at apex, extending into fringe; markings usually from a border around apical third of wing, consisting of approximately 3–13 spots, which tend to coalesce at apex; a conspicuous dark spot usually present at apex of cell and another less frequently present at its base; underside of forewing almost entirely fuscous except for fringe which may or may not be completely white. Secondaries considerably darker than primaries, thinly scaled and semitransparent; scales slender, hairlike, less than one fourth the width of those in forewing, fringe usually white along hind margin, becoming dark towards apex of wing; ventral surface of similar color.

Abdomen: White beneath, brownish above.

MALE GENITALIA (fig. 109).—Apex of tegumen with two small, setigerous lobes. Valves strongly constricted just before apex; posterior margin of cucullus produced into a long, digitate process bearing 2–5 short spines. Saccus moderately developed.

FEMALE GENITALIA (figs. 132, 152).—Apex of ovipositor without serrated dorsal ridge; extreme tip minutely serrulate, sharply angulate. Oviduct relatively short, shorter than apophyses. Spermathecal enlargement present at juncture of ductus bursa with oviduct.

TYPES.—Lectotype (*Pronuba maculata*, designated by present author), ♀, Caliente, Kern Co., Calif., H. K. Morrison, USNM 417; in the U.S. National Museum. Lectotype (*Pronuba maculata* variety *apicella*, designated by present author), ♀, July, Los Angeles Co., Calif., USNM 67708; in the U.S. National Museum.

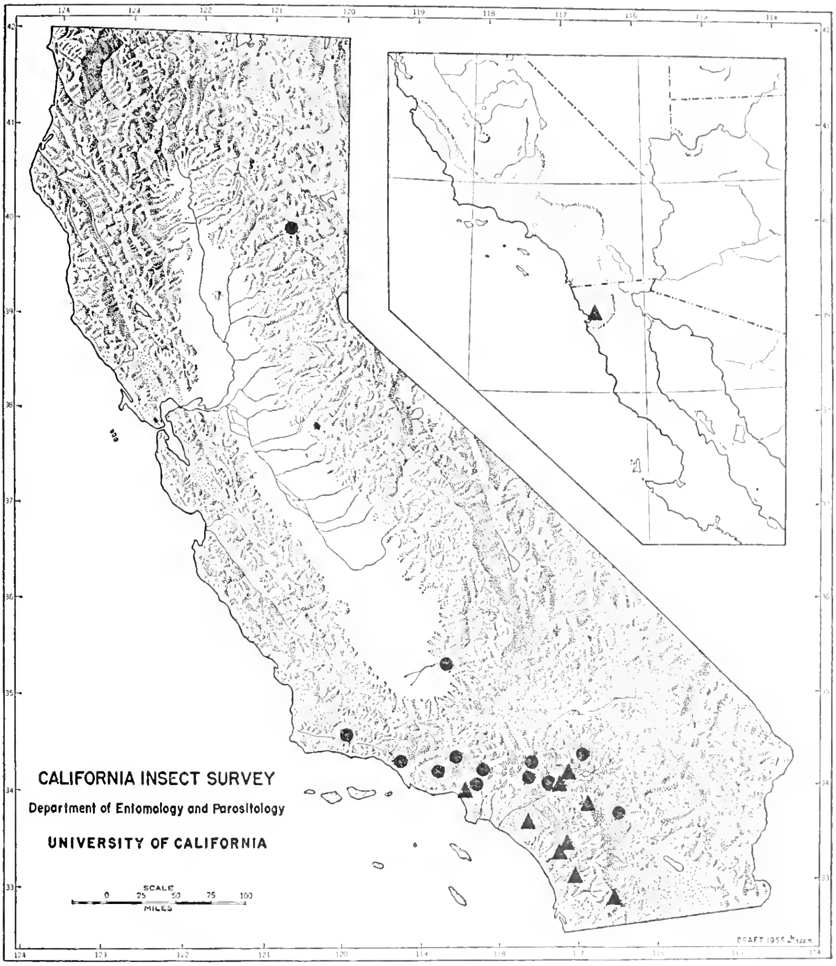
TYPE LOCALITIES.—California: Caliente, Kern Co. (lectotype, *P. maculata*); Los Angeles Co. (lectotype, *P. maculata* variety *apicella*).

RECORDED HOST.—"*Yucca whipplei* Torrey," Riley, 1892a. Larva bores in the seeds of host plant.

PARASITE.—(?) "Braconidae, *Heterospilus koebelei* (Ashmead)," Riley and Howard, 1890.

DISTRIBUTION (map 4).—Presently known only from California. Several specimens of this moth were collected reputedly from Plumas County in northern California; however, this record is questionable, since no species of *Yucca* is native to that area. If the locality as given is correct, then it may be possible that the specimens originated from cultivated plants.

DISCUSSION.—In their list of parasitic Hymenoptera, deposited in the collections of the National Museum, Riley and Howard reported *Heterospilus koebelei* to be a parasite of an undescribed species of *Pronuba* (=*Tegeticula*) from California. Riley later described this moth as *Pronuba maculata*. Because other evidence has cast some doubt as to the validity of this report and because no other species of *Tegeticula* is known to be parasitized, the present writer checked the accession files of the National Museum for additional information concerning the rearings in question. Notations had been entered by "T. Percande" which indicated that no definite association between parasite and host was ever established and that the wasps possibly had emerged from some species of *Prodoxus*. Thus, the above record by Riley and Howard should be regarded with considerable suspicion. It is more likely that *Heterospilus koebelei* is restricted to moths of the genus *Prodoxus* and possibly to those species which I have referred to as the "marginatus" group (see p. 71).



MAP 4.—Distribution of *Tegeticula maculata maculata* (black circles), *Tegeticula maculata extranea* (black triangles), and of host plant, *Yucca whipplei* (shaded area in upper map) (distribution of host modified from McKelvey, 1947).

MATERIAL EXAMINED.—44 ♂♂ and 61 ♀♀.

UNITED STATES: CALIFORNIA: Kern Co.: Caliente, ♀, lectotype, *P. maculata;* 2 ♂♂, ♀, paralectotypes, *P. maculata* (USNM). Los Angeles Co.: ♀, lectotype, *P. maculata* var. *apicella,* July; 3 ♂♂, ♀, June–August, 2 ♂♂ (USNM). Chilao, San Gabriel Mts., 2 ♂♂, 6 ♀♀, May 30 (USNM). Glendale ♂, May 23, ♀, June 28 (LACM). La Tuna Canyon, 3 ♀♀, May 16–17, ♀, July 17; 1200 ft., 2 ♂♂, 2 ♀♀, June 11–17 (USNM). San Francisquito Canyon, ♀, June 7 (USNM). Verdugo, ♀, Feb. 24 (LACM). Plumas Co.: 12 ♂♂, 3 ♀♀ (USNM). Riverside Co.: Palm Springs, ♀, Apr. 22 (LACM). Santa Barbara Co.: San Marcos Pass, ♂, May 14 (LACM). San Bernardino Co.: Camp Baldy, San Bernardino Mts., 4 ♀♀, July 13 (AFB); 10 ♂♂, 24 ♀♀, July 1–23 (USNM). Lucerne Valley, 3 ♂♂, 5 ♀♀, May 26–28 (LACM). Phelan, 3 miles west of, 2 ♂♂, ♀, May 23 (LACM). San Bernardino, ♀, May 1 (LACM). Ventura Co.: Craven's Ranch, Casitas Pass, ♂, ♀, June 23 (LACM). Mortimer Park, Simi Hills, 2 ♂♂, 2 ♀♀, June 4–17 (LACM). Sherwood Lake, Hidden Valley, ♂, May 22 (LACM).

***Tegeticula maculata extranea* (Hy. Edwards)**

Figures 85, 110, 133, 153; Map 4

Thia extranea Hy. Edwards, 1888, p. 181.

Thelethia extranea (Hy. Edwards).—Dyar, 1893, p. 301; 1902 [1903], no. 5538.—Meyrick, 1913, p. 29.—McDunnough, 1939, no. 8639.

Tegeticula extranea (Hy. Edwards).—Busck, 1947, p. 183 [color variety of *T. maculata*].

Pronuba maculata var. *aterrima* Trelease, 1893, p. 216, pl. 23, figs. 1–2.—Riley, 1893a, p. 45; 1893b, pp. 303, 310.

Pronuba aterrima Trelease.—Dyar, 1903b, p. 102.—Kearfott, 1903, no. 7114.

Tegeticula aterrima (Trelease).—Barnes and McDunnough, 1917, p. 197, no. 8473.—McDunnough, 1939, pt. 2, no. 9836.—Busck, 1947, p. 183. [synonym of *T. extranea* Hy. Edwards].

Adult (fig. 85).—Very similar in most respects, except color, to *Tegeticula maculata*. Wing expanse: male, 14–17 mm; female, 16–19 mm.

Head: Almost invariably black, rarely white. Maxillary tentacle fully developed in all females examined. Labial palpus entirely black; scaling as in *T. yuccasella*.

Thorax: Black. Primaries uniformly black above and below. Secondaries hyaline, thinly scaled as in *T. maculata;* fringe completely black, contrastingly darker than rest of hindwing.

Abdomen: Entirely black.

Male genitalia (fig. 110).—Similar to *T. maculata*.

Female genitalia (figs. 133, 153).—Similar to *T. maculata*.

Types.—Lectotype (*Thia extranea* Hy. Edwards, designated by present author), ♂, Los Angeles, Calif., Apr. 4, 1879, 956, cotype ♂, *Thia extranea* Hy. Edwards; in the collections of the Illinois State Natural History Survey. Lectotype (*Tegeticula aterrima* Trelease, designated by the present author), ♀, Arrowhead, Calif., 5606, USNM 67372; in the United States National Museum.

Type localities.—Los Angeles, Los Angeles Co., Calif. (lectotype, *T. extranea*). "From the foothills immediately north of San Bernardino" [Arrowhead], San Bernardino Co., Calif. (lectotype, *T. aterrima*).

Recorded host.—"*Yucca whipplei* variety *graminifolia* Wood," Trelease, 1893. Larva bores in seeds of plant host.

Distribution (map 4).—Current records indicate this subspecies to be somewhat more southern in its range than the nominal species. Presently it is known from the southwestern part of San Bernardino

County and Los Angeles County, southward along the coastal ranges to northern Baja California.

DISCUSSION.—Throughout most of its nomenclatoral history, the subspecies which Henry Edwards originally described as *Thia extranea* was not recognized as a member of the Prodoxinae. Instead, this insect was known as a yucca moth under the name of its junior synonym, *Tegeticula aterrima*. Edwards originally placed *Thia extranea* in the Heterogynidae and stated that it was closely related to *Atychia* Latreille. Dyar (1903a) examined Edwards' series of two syntypes and concluded that *Thelethia* (=*Thia*) *extranea* should be included in the Yponomeutidae. Undoubtedly influenced by Edwards' statement concerning the generic affinities of *T. extranea*, Meyrick (1913) transferred it to the Glyphipterygidae along with *Atychia*. In his checklist, McDunnough (1939) followed Meyrick's decision and placed the monotypic genus *Thelethia* in the Glyphipterygidae. In addition, he included *Tegeticula aterrima* in the Prodoxidae as others had done before him. Perhaps relying solely upon Edwards' description, Busck (1947) correctly associated *Thelethia extranea* as the senior synonym of *Tegeticula aterrima*. With the assistance of Mr. Alex Wyatt of the Chicago Natural History Museum, the author was able to locate one of Edwards' syntypes. Through the cooperation of Dr. H. B. Cunningham of the Illinois Natural History Survey, I was able to examine this specimen and, thus, to confirm Busck's synonymy.

The taxonomic status which I have recognized for *Tegeticula maculata extranea* later may not be found to reflect its true relationship; instead, it may be decided that this moth deserves the status of a distinct species. The fact, however, that *T. m. extranea* represents a melanic derivative of *T. m. maculata* seems certain. Morphologically *T. m. extranea* is identical to its ancestral form in all respects except color and size. These differences, along with distributional peculiarities, suggest a degree of speciation greater than that usually encountered in melanic forms. Primarily for these reasons, I have treated this moth as a subspecies.

Melanism in Lepidoptera has been grouped into three general categories by Kettlewell (1961a): (a) industrial, (b) relict or geographical, and (c) semilethal. The type which *T. m. extranea* demonstrates is apparently that of relict or geographical melanism. Species demonstrating this type of melanism typically occupy rather specialized habitats characteristic of northern climates, such as mountain tops or high latitudes. For example, among those melanic Lepidoptera occurring in the Shetland Isles studied by Kettlewell (1961b), the dark forms invariably were distributed farther north than the lighter forms. In the same reference, Kettlewell (p. 394) further concluded for the North American Lepidoptera that "the farther north samples were collected the higher both the frequency of melanic forms per species became and the number of species exhibiting melanism." In this regard, *T. m. extranea* is further interesting in that its known distribution is apparently more southern than that of the nominal subspecies (see map 4). Unfortunately, other than general locality, relatively little is known of the precise origins for the moths examined in the present study. Considerably more localities need to be sampled, and close attention should be directed toward the gathering of altitudinal data. The latter is particularly important in such a topographically diverse region as the State of California.

As a result of his studies on geographical melanism, Kettlewell (1961b) further separated the insects exhibiting this phenomenon into three groups:

1. Species in which 100 percent of their population is melanic; they have discarded their normal alleles found elsewhere.
2. Species in which the two forms co-exist as a balanced polymorphism.
3. Species in which there is found an indefinite range of forms from black to pale; these presumably reflect either a multifactorial situation, or one in which variable heterozygotes occur.

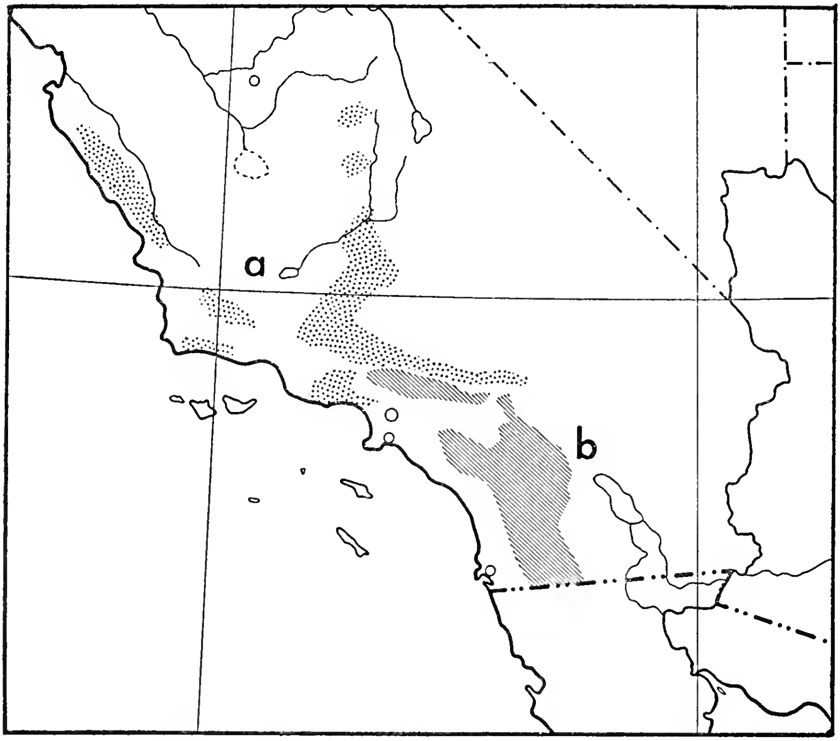
It is apparent that *T. m. extranea* represents an example of the first group. This supposition is based upon the uniform color and relatively distinct size of the subspecies, as well as its distribution. Eighty specimens of *T. m. extranea* and 105 of *T. m. maculata* were examined in the course of this study. Only one individual, a specimen of *T. m. extranea,* showed any evidence of intermediacy. The color of that specimen is entirely black except for the head and collar, which are dusky white. The moth probably represents either a hybrid of the two subspecies, or else a rather unusual variation of *T. m. extranea.*

Perhaps of more significance than color in separating the two subspecies of *T. maculata* is that of size. Consistent differences in size as well as in distribution suggest a greater genetic difference than does color, which in some melanic forms may be under relatively simple genetic control (Ford, 1953). The lengths of the forewings of 30 females were measured for both subspecies (see tabulation below), and the differences were found to be significant ($P = > 0.02$ and < 0.03). A similar size difference has been noted in a British noctuid, *Diarsia festiva* Schiffermüller (Kettlewell, 1961b). The melanic subspecies of this moth is distinguished from the typical form in being smaller as well as much darker. This species, however, demonstrates the normal distributional pattern of most melanic Lepidoptera (geographical type) in that the darker subspecies, *Diarsia festiva* *thulei* Staudinger, occurs to the north in the Shetland Isles, and the typical form is restricted further south to the British mainland.

The forewing measurements of female *Tegeticula maculata* are as follows (see p. 10 for explanation of symbols):

	N	*Length* $\bar{x}$ *(mm)*	*Range (mm)*	*s*	*F value*
T. maculata maculata	30	9.43	8.4–10.1	0.397	
T. maculata extranea	30	7.93	6.9– 8.5	0.395	6.099*

Several botanists (e.g., Trelease, 1893; Haines, 1941; McKelvey, 1947; Webber, 1953) have recognized the existence of two or more subspecies or forms of *Yucca whipplei* in southern California. Opinions vary as to how many entities are involved and to the respective characteristics of each. Vegetative features, particularly growth habits, usually are relied upon for distinction, as well as differences in distribution. It is believed that precise distributional and host records for the subspecies of *Tegeticula maculata* will show correlations in regard to the relationships of the various forms of *Yucca whipplei*. Conversely, additional studies on the systematics of the host should furnish valuable information on the moths. For example, after reviewing the taxonomy of *Y. whipplei*, McKelvey (1947, p. 45) predicted that "with time, one or more floral characters will be found to distinguish two races which even now appear to be geographically separated as far as habit of growth, of itself an important character, is concerned." The known distributions of the subspecies of *T. maculata* strongly support McKelvey's supposition in that evidence is beginning to show that the two moths are restricted to two distinct biotypes of *Y. whipplei*, one of which is more northern in its distribution than the other. Haines (1941) recognized five subspecies of *Y. whipplei* and discussed their ranges in some detail. The status of a few of his subspecies appears doubtful; however, from his key of the various forms it is possible to recognize two distinct groups of *Y. whipplei*. One group is characterized by those plants which produce solitary rosettes and die after fruiting. Under this couplet in his key, Haines included the two subspecies *typica* and *parishii*. The other major group included the subspecies *caespitosa*, *intermedia*, and *percursa*. These plants are characteristic in that they are perennial and produce numerous rosettes; thus, in these individuals only the flower stalk dies after fruiting. Although these fundamental differences were not given special emphasis by Haines, they undoubtedly represent an important division within *Y. whipplei*. This is suggested further by the apparent association of the two subspecies of *T. maculata*. As illustrated in maps 4 and 5, the subspecies *maculata* is apparently sympatric with the "caespitosa" group of *Y.*



Map 5.—Distribution of two major growth forms of *Yucca whipplei* (modified from Haines, 1941) (stippled area [a]=range of *caespitosa* group; lined area [b]=range of *typica* group).

whipplei, whereas the range of *T. m. extranea* corresponds very closely with that of the "typica" group.

The biological relationships of the two subspecies of *Tegeticula maculata* have barely been touched upon. Thus, several interesting problems remain to be investigated which could provide not only a great deal of information concerning the particular relationship treated here, but also of the phenomenon of geographical melanism in general. For example, it would be very enlightening to know what degree of fertility exists between the two forms of *T. maculata*, as well as to know the phenotypical characteristics of any possible hybrids. Also, studies similar to those conducted by Kettlewell (1961 b, c) and Kettlewell and Berry (1961) should be carried out to determine what possible advantages are present that enable the melanic subspecies to occupy a different range—if, in fact, such is verified. The above authors have discovered that bird predatism and temperature factors, especially in association with the flight time of the adults, provide selective advantages for melanic forms under certain conditions. These explanations, however, do not seem to be correlated with what is presently known about the habits of *T. maculata.* As was pointed out on page 35, Trelease (1893) observed both subspecies to be active during the day, which, in itself, is most unusual for this group of moths. After the problem has been studied more carefully, however, it may be found that the activity periods of *T. m. maculata* and *extranea* actually do differ, perhaps in a manner similar to that noted by Hovanitz (1948) for two color phases of *Colias* butterflies. The possibility that the subspecies of *T. maculata* may be host specific on two distinct forms of *Yucca whipplei* strongly suggests that the factors involved in this association are much different from those discovered in other melanic complexes. It seems possible that melanism itself may be of only "neutral" value (e.g., neither decidely advantageous nor disadvantageous) in this particular case, and that it is, instead, closely linked to other more important genetic factors, which are responsible for *T. m. extranea's* host specificity (and distribution) on the *typica* group of *Y. whipplei.*

MATERIAL EXAMINED.—34 ♂♂ and 46 ♀♀.

UNITED STATES: CALIFORNIA: Los Angeles Co.: Los Angeles, ♂, lectotype, *T. extranea,* Apr. 4 (INHS). Orange Co.: Mojeska [east of Santa Ana], 6 ♂♂, 5 ♀♀, May 23 (LACM). Riverside Co.: near Beaumont, ♂, Apr. 23 (LACM). Mt. Santa Rosa [near Temecula], ♀, May 30 (LACM). San Bernardino Co.: Arrowhead, ♀, lectotype, 2 ♂♂, 5 ♀♀, paralectotypes, *T. aterrima* (USNM). San Bernardino, 2 ♀♀, Apr. 30–May 12 (LACM). San Diego Co.: Fallbrook, ♂, Apr. 3 (LACM). Pine Valley, east of, 6 ♂♂, 19 ♀♀, Apr. 24 (USNM). San Pasqual, 14 ♂♂, 12 ♀♀, Apr. 25 (USNM).

Mexico: BAJA CALIFORNIA NORTE: Canon las Cruces [near Ensenada], 3 ♂♂, ♀, Apr. 10 (LACM).

Tegeticula yuccasella (Riley)

FIGURES 19, 24, 26, 30–33, 35, 40, 45, 50, 52, 58, 86–87,
106–108, 115, 134, 136, 154; MAP 6

Pronuba yuccasella Riley, 1872a, p. 444; 1872b, p. 182; 1873b, p. 151, figs. 74, 75; 1873a, p. 56, figs. 1–2; 1873c, p. 178, fig. 3; 1873d, pp. 619–623.—Packard, 1873, pp. 475–476, figs. 128–130.—Riley, 1874a, p. 131, fig. 38; 1874b, p. 208.—Zeller, 1875, p. 340.—Riley 1876b, p. 171; 1876a, p. 325; 1877, p. 568.—Chambers, 1877a [in part], pp. 121, 141; 1877b, p. 148; 1878a, p. 161, 1878b, pp. 141–154.—Riley, 1878, p. 377.—Meehan, 1879, p. 33.—Chambers, 1880a, p. 198.—Riley, 1880a, pp. 141–143; 1880e, p. 182.—Hagen, 1880, p. 128.—Riley, 1880g, p. 263; 1880f, p. 293; 1881, pp. 617, 637, 639 ff., figs. 1–4.—Meehan, 1882, p. 205.—Hagen, 1882, p. 19.—Hulst, 1886, p. 184.—Riley, 1887, p. 233.—Hulst, 1887, p. 236.—Meehan, 1888, p. 274.—Marilaun, 1888, pp. 153–156, figs. 1–5.—Riley, 1891, p. 97, no. 5179; 1892a, pp. 138 ff., pl. 34. figs. 1–4; 1892b, pp. 83 ff., figs. 1, 2, 8; 1892c, pp. 360 ff., figs. 58–61, 67; 1892d, pp. 305–307, fig. 13; 1892e, pp. 312, 313, 315.—Smith, 1893, p. 161, fig. 12.—Riley, 1893a, pp. 42 ff.; 1893b, pp. 301–305, 307, 310.—Trelease, 1893, pp. 181–183, 185, 186, 189, 196, 198, 199, 201, 203–205, 207, 208, 217, 222, pl. 22, fig. 5.—Whitten, 1894a, p. 137; 1894b, p. 376.—Sharp, 1899, p. 432.—Dyar, 1902 [1903], no. 6574; 1903b, p. 102.—Kearfott, 1903, no.

7112.—Holland, 1905, p. 411, figs. 262, 263.—Braun, 1919, p. 362.—Fracker, 1930, p. 61.—Trelease, 1941, pp. 3529, 2530.—Miller, 1949, pp. 135–147.—Comstock, 1950, p. 599 [synonym of *Tegeticula alba*].—Bourgogne, 1951, p. 374 [synonym of *Tegeticula alba*].

Promiba [sic] *yuccasella* Riley.—Kirby, 1874, pp. 380.

Pronuba yuccaella [sic] Boll, 1876, p. 401,

Tegeticula yuccasella (Riley).—Walsingham, 1903, p. 260; 1914, p. 369.—Barnes and McDunnough, 1917, p. 197, no. 8471.—Forbes, 1923, p. 75, figs. 49, 50.—Braun, 1924, p. 238, pl. 23, fig. 5.—Forbes, 1928, p. 534.—Fletcher, 1929, pp. 185, 217 [synonym of *Tegeticula alba*].—McDunnough, 1939, no. 9834 [synonym of *Tegeticula alba*].—Lindinger, 1941. p. 237.—Rau, 1945, p. 373 ff.—Busck, 1947, pp. 180, 181, 182.—Webber, 1953, p. 65.—Peterson, 1956, p. 226, pl. L 58, fig. E.—Imms, 1957, p. 539.—Bastida, 1962, pp. 269–270.

Tegiticula [sic] *yuccasella* (Riley).—Braun, 1924, p. 256.

Tegeticula alba Zeller, 1873, p. 232; 1875 p. 340 [synonym of *Pronuba yuccasella*].—Boll, 1876, p. 401.—Riley, 1876a, p. 325 [synonym of *Pronuba yuccasella*].—Chambers, 1878a, p. 161 [synonym of *Pronuba yuccasella*].—Hagen, 1880, p. 129.—Riley, 1881, p. 639 [synonym of *Pronuba yuccasella*]; 1891a, no. 5179 [synonym of *Pronuba yuccasella*].—Dyar, 1902 [1903] no. 6574 [synonym of *Pronuba yuccasella*].—Walsingham, 1903, p. 260 [synonym of *Tegeticula yuccasella*]; 1914, p. 369 [synonym of *Tegeticula yuccasella*].—Barnes and McDunnough, 1917, p. 197, no. 8471.—Eyer, 1924, p. 309, pl. 29, fig. 2.—Fletcher, 1929, p. 217.—Busck, 1931, p. 201, fig. 1.—McDunnough, 1939, no. 9834.—Lindinger, 1941, p. 237 [synonym of *Tegeticula yuccasella*].—Busck, 1947, p. 182 [synonym of *Tegeticula yuccasella*].—Comstock, 1950, p. 599, fig. 725.—Bourgogne, 1951, pp. 374–375, figs. 364–365.

Prodoxus intermedius Riley, 1881, pp. 635, 639, fig. 11; 1891a, p. 97, no. 5186; 1892a, p. 148, pl. 43, fig. 1; 1893a, p. 49; 1893b, p. 307.—Trelease, 1893; p. 206.—Dyar, 1902 [1903], p. 723, no. 6565; 1903b, p. 103.—Kearfott, 1903, p. 124, no. 7103.—Barnes and McDunnough, 1917, p. 197, no. 8461.—McDunnough, 1939, no. 9824.—Busck, 1947, pp. 181, 182 [synonym of *Tegeticula yuccasella*].

Tegeticula mexicana Bastida, 1962, pp. 259–272, figs. 1–10 [new synonymy].

ADULT (figs. 86–87).—Wing expanse: male, 15–27 mm; female, 20–33 mm.

Head (figs. 31–32, 40, 50, 52): White. Maxillary tentacle normally fully developed in female, sometimes vestigial. Labial palpus with dorsal surface of first and second segments dark brown, scales smoothly appressed; scales of ventral surface white, mostly hairlike and erect; apical segment entirely white.

Thorax: White. Primaries with dorsal surface immaculate white, lustrous; ventral surface and basal fourth of costal margin brown, with a somewhat bronzy iridescense; fringe of both fore- and hindwings white above and below. Dorsal surface of secondaries appearing darker then forewing, due to thinner scaling of former; scales narrow, approximately one-half to two-thirds the width of those in primaries; ventral surface with costal third of wing brownish, posterior two-thirds nearly white.

Abdomen: Pale brown above, white below.

MALE GENITALIA (figs. 106–108).—Apex of tegumen deeply excavate, bilobed, with lobes widely separated. Valves somewhat variable in outline, more constricted beyond sacculus in some specimens than others, with a single, prominent tubercule bearing usually 8–14 short, blunt spines. Saccus variously developed, elongate or moderately so. Aedeagus variable in length, often very long and slender.

FEMALE GENITALIA (figs. 134, 136, 154).—Ovipositor with apex acute; ridge prominently convex, minutely serrulate, number of teeth usually in excess of 30. Oviduct greatly lengthened, exceeding length of slender apophyses; juncture of oviduct with ductus bursa caudad to spermathecal enlargement.

TYPES.—Lectotype (designated by present author), *Pronuba yuccasella* Riley, ♂, June, "C. Mo." [Central Missouri?], USNM 415, genitalia slide no. 867 DRD; in the U.S. National Museum. Lectotype (designated by present author), *Tegeticula alba* Zeller, ♂, Dallas, Tex., MCZ 2922; in the Museum of Comparative Zoology. Lectotype (designated by present author), *Prodoxus intermedius* Riley, ♀, fr. Boll, Dallas, Tex., USNM 418; in the U.S. National Museum. Holotype, *Tegeticula mexicana* Bastida, ♀; in the Instituto de Biología de la Universidad Nacional Autonoma de Mexico.

TYPE LOCALITIES.—"C. Mo." [probably central Missouri] (lectotype, *P. yuccasella*). Dallas, Tex. (lectotype, *T. alba*). Dallas, Tex. (lectotype, *P. intermedius*). El trinquete, Municipio de Villa de Reyes, San Luis Potosi, S. L. P., Mexico (holotype, *T. mexicana*).

RECORDED HOSTS.—"*Yucca angustissma* Engelmann, *Y. arizonica* McKelvey, *Y. arkansana* Trelease, *Y. baccata* Torrey, *Y. campestris* McKelvey, *Y. carnerosana* (Trelease) McKelvey, *Y. constricta* Buckley, *Y. elata* Engelmann, *Y. faxoniana* (Trelease) Sargent, *Y. glauca* Nuttall, *Y. intermedia* McKelvey, *Y. kanabensis* McKelvey, *Y. pallida* McKelvey, *Y. schidigera* Roezl, *Y. standleyi* McKelvey, *Y. thornberi* McKelvey, *Y. torreyi* Shafer, *Y. treculeana* Carriere, *Y. utahensis* McKelvey, *Y. whipplei* Torrey" (McKelvey, 1947); "*Y. aloifolia* Linnaeus, *Y. filamentosa* Linnaeus, *Y. gloriosa* Linnaeus" (Riley, 1892a); "*Y. baileyi* Wooton and Standley" (specimen label); *Y. filifera* Chabaud, *Y. schottii* Engelmann.

DISTRIBUTION (map 6).—Largely due to its ability to subsist on nearly every species of *Yucca* east of the Rocky Mountains, *Tegeticula yuccasella* is the most widely distributed species of the Prodoxinae. In the United States this species occurs as far north as southeastern Canada (southern Ontario) and Massachusetts, west to North Dakota, thence south to southern California. In Mexico, *T. yuccasella* ranges over the Mexican plateau to as far south as Tehuacan in the state of Puebla.

Map 6.—Distribution of *Tegeticula yuccasella* (marginal records are indicated by black circles).

Discussion.—Although my decision may seem somewhat arbitrary, the present lectotype designation for *T. yuccasella* is believed to be reasonably accurate. The difficulty in selecting a lectotype for this name stems from the fact that none of Riley's original, syntypic series (9 males and 15 females) can be positively identified. Riley never fully realized the importance of a type series and consequently was very careless in labelling such specimens or in publishing any data concerning them. Frequently his specimens bear no labels at all, or else they were provided with extremely brief and sometimes cryptic information. The source of Riley's 24 original specimens was never stated, although I have assumed that at least some were collected from Missouri where Riley had been employed during this period as state entomologist. For this reason and also because some syntypes most likely still exist in the collections of the U.S. National Museum, I have selected the above specimen, which bears a Riley locality label, as lectotype. Furthermore, the same specimen had been selected as a type much earlier by August Busck. Even though Busck's unpublished designation was not valid, this specimen probably was regarded by subsequent investigators as typical of the species, due to the type label it bore.

VARIATION.—*Tegeticula yuccasella* occurs commonly over a major part of the North American continent; thus it would not be unusual to encounter a certain degree of morphological variation in such a widely distributed insect; however, the amount of variation observed in the species has proven to be much greater than expected for any member of this group of Lepidoptera. Comparable deviations of so many characters were not observed in the similarly widespread species, *Prodoxus quinquepunctellus,* nor in any other species of the Prodoxinae.

More than one biological entity may be present within the moths currently recognized as *T. yuccasella.* Additional study, involving adequate sampling techniques and the analysis of several characters, will be necessary before this problem can be resolved. Approximately 1220 specimens of *T. yuccasella* were examined in the course of this study; most of these, unfortunately, could not be treated statistically because of the paucity of representative populations, or because of insufficient host information, which apparently is essential for the understanding of the overall problem. A few characters have been treated superfically in this study and are discussed briefly on the following pages. The writer fully intends to pursue these lines of investigation further until a more adequate understanding of this species is attained.

The female genitalia present variances which may or may not have taxonomic significance. The subapical region of the ovipositor normally possesses a small, serrated dorsal ridge (fig. 154) that is characteristic for the species. Occasionally the height of the ridge may vary, but the presence of serrations appears constant. In four females of *T. mexicana* (holotype and three paratypes) from the Mexican state of San Luis Potosi, the ovipositor ridge was much reduced. In a specimen of *T. yuccasella* collected farther south (Tehuacan, Puebla) the ridge was more developed, as was the condition in nearly all females examined from the United States. Because no other significant differences have been established for *T. mexicana,* that species has been treated as a synonym of *T. yuccasella.*

The diameter of the signum also is not constant, with some females having a much larger pair than others. Contrary to what is known concerning the relative development of the ovipositor ridge, the size of the signum seems to be correlated with other morphological characters which may be taxonomically significant. For example, it appears that the diameter of the signum is inversely proportional to the length of the male genitalia (i.e., the longer the male genitalia, the smaller the signum in the female). Furthermore, the distribution of this character may follow that of genitalia length (see table 2) and be directly associated with certain plant hosts. Busck (1947) first noted these variations in the development of the female signum, along with other genitalic characters, but concluded that no relationships were involved and that only one species was represented.

Certain characters of the male genitalia vary to a great extent, but may be relatively constant within a given population. As a

TABLE 2.—*Genitalia measurements of male* Tegeticula yuccasella

Locality	Slide No.	Host	Aedeagus length mm.	Genitalia length mm.
Imperial Co., Calif.	1004	*Y.* "*mohavensis*"	1.65	1.63
Pyote, Tex.	772	*Y.* species	1.51	1.65
Pyote, Tex.	995	*Y.* species	1.67	1.76
Pennsylvania	737		1.79	1.77
C. Mo. [Central Mo.]	867		1.62	1.78
Madera Canyon, Ariz.	1020		1.89	1.83
Tohatchi Mts., N. Mex.	1013	*Y. baileyi*	1.80	1.84
Lucerne Valley, Calif.	1014		1.82	1.85
Beaver Co., Okla.	850	*Y. glauca*	1.68	1.86
Gran Quivira Nat. Monument, N. Mex.	991	[*Y. glauca* complex]	1.59	1.88
Washington, D.C.	996	*Y. filamentosa*	1.69	1.88
St. Petersburg, Fla.	846		1.85	1.90
Mohave Co., Ariz.	1006	*Y. angustissima*	1.77	1.96
Gila Co., Ariz.	849	*Y. elata*	1.78	1.96
Princeton, N.J.	848	*Y. filamentosa*	1.79	1.96
Lucerne Valley, Calif.	847		1.76	1.97
Valencia Co., N. Mex.	840	*Y.* species	1.82	1.98
Valencia Co., N. Mex.	1011	*Y. glauca stricta*	1.90	1.98
Pyote, Tex.	994	*Y.* species	1.80	2.00
Martha's Vineyard, Mass.	987		1.82	2.01
Tehuacán, Puebla, Mexico	984		1.93	2.01
San Antonio (S. of), Tex.	1001	*Y. treculeana*	1.82	2.07
Loraine (W. of), Tex.	1012	*Y. constricta*	1.85	2.08
Devil's River, Tex.	1007	*Y.* "*macrocarpa*"	2.02	2.21
N. of Persimmon Gap and S. of Marathon, Tex.	1010	*Y.* "*macrocarpa*"	2.12	2.40
Hudspeth Co., Tex.	1008	*Y. faxoniana*	2.22	2.51
N. of Persimmon Gap and S. of Marathon, Tex.	1000	*Y.* "*macrocarpa*"	2.34	2.54
Torrance Co., N. Mex.	986	*Y. baccata*	2.65	2.58
Torrance Co., N. Mex.	993	*Y. baccata*	2.64	2.59
Torrance Co., N. Mex.	837	*Y. baccata*	2.65	2.59
Torrance Co., N. Mex.	740	*Y. baccata*	2.75	2.73
Coconino Co., Ariz.	1002	*Y. baccata*	2.89	2.76
Glendale (N. of), Utah	1009	*Y. baccata*	2.77	2.79
Coconino Co., Ariz.	997	*Y. baccata*	2.75	2.80
Torrance Co., N. Mex.	985	*Y. baccata*	2.58	2.82
Coconino Co., Ariz.	1003	*Y. baccata*	2.92	2.89
Coconino Co., Ariz.	998	*Y. baccata*	2.92	2.95

means of illustrating this variation, figures 106–108 are provided to show the size range of the male genitalia, as well as to demonstrate the somewhat intermediate proportions of the lectotype. In addition, the measurements of 37 male dissections are summarized in table 2. The specimens were selected to represent a coverage of the species known distribution and are arranged in the table according to genitalia length, with the lowest values preceding. The length was measured as the distance from the distal apex of the saccus to that of the lobes of the tegumen. Although most localities listed in this table are represented by only one example, this alone can be of some meaning if compared to specimens from such localities as Torrance Co., New Mexico, which present some idea of size variance within a given population.

Three observations are immediately suggested by this preliminary examination. First of all, it will be noticed that the male genitalia exhibit unusual diversity in regard to size. In order to test the homogeneity of the entire sample, the coefficient of variability (C.V.) was calculated and found to be extremely high (18.577). As a means of comparison, the C.V. of other characters, such as wing length, width, and wing ratio (table 3), were found to fall, for the most part, within the normal range of 4 to 6 and never exceeding 7. A

TABLE 3.—*Measurements of female* Tegeticula yuccasella

Localities	Maxillary tentacles			Wing Measurements						
	Normal	Aborted	Aborted %	N	$\bar{x}$ Length (L) (mm)	$\bar{x}$ Width (W) (mm)	$\bar{x}$ $\left(\frac{W \text{ x } 100}{L}\right)$	Range $\left(\frac{W \text{ x } 100}{L}\right)$	s (ratio)	C.V. (ratio)
1. Finleyville, Pa.	4	0	0	4	10.33	3.60	34.88	32.71–36.11	1.492	4.279
2. Highlands, N.C.	5	0	0	5	11.02	3.68	33.41	30.36–35.78	2.080	6.225
3. Philadelphia, Pa.	8	0	0	8	10.80	3.55	32.92	30.36–36.63	1.909	5.797
4. Newark, N.J.	5	0	0	5	10.66	3.50	32.84	31.90–34.29	1.065	3.240
5. Cincinnati, Ohio	8	0	0	8	10.88	3.40	31.23	28.70–34.55	2.141	6.860
6. Gran Quivira Nat. Monument, N. Mex.	16	40	71	56	11.72	3.64	31.12	27.52–34.43	1.798	5.778
7. Clovis, N. Mex.	6	4	40	10	11.78	3.65	31.00	27.50–33.33	1.551	5.002
8. Pyote, Tex.	20	3	13	23	11.09	3.38	30.48	27.52–32.76	1.323	4.340
9. Albuquerque, N. Mex.	9	4	31	13	11.02	3.26	29.73	26.13–33.61	2.015	6.779
10. Texas Co., Okla.	5	0	0	5	11.34	3.20	28.24	26.27–30.00	1.761	6.247
11. Between Alpine and Terlinqua, Tex.	8	0	0	8	11.85	3.25	27.43	26.50–28.57	0.738	2.689
12. Lucerne Valley, Calif.	9	0	0	8	10.11	2.76	27.35	24.78–28.43	1.287	4.706
13. Madera Canyon, Ariz.	23	0	0	23	10.28	2.81	27.31	24.51–30.00	1.221	4.465
14. Torrance Co., N. Mex.	17	0	0	17	11.63	3.06	26.35	21.78–28.07	0.824	3.128

C.V. value greater than 10 usually indicates, for linear, anatomical dimensions of most animals, that the sample was not pure (Simpson et al., 1960). Consequently, the above value of 18.577 strongly suggests, at least on the basis of the male genitalia, that an additional sibling species (or race) may be present within the moths currently recognized as *T. yuccasella.*

A second feature to be noted from table 2 is that the differences observed in the genitalia do not seem to fall into a general or easily defined pattern of distribution. In contrast, another character studied, that of relative wing width, demonstrated a somewhat simpler distribution in that the eastern forms tended to be broader winged than the western. Specimens from several western localities and Mexico exhibited genitalia within a general size range of 1.6 to 2.1 mm, as did all eastern males examined. Interspersed through the southwest, however, are found populations whose males possess more elongate genitalia. For example, the measurements of specimens from four localities in New Mexico are listed in table 2; the males from three of these areas display genitalia of a decidedly shorter length than did those from Torrance County, which, in turn, were comparable in size to certain males from Arizona and Utah. In other words, if two sibling species (or races) are present among our common yucca moth, as suggested by the samples studied in regard to genitalia length, then the two entities probably are closely interwoven in some areas, but not necessarily sympatric in the strict sense.

In close connection with the preceding observation, it will also be noted that there appears to be a correlation between host plant and genitalia length. From the measurements in table 2, two size groups can be recognized arbitrarily; one in which the length ranges from 1.6 to 2.1 mm, and a second ranging in size from 2.2 to 3.0 mm. Specimens reared or collected from *Yucca baccata* consistently exhibited maximum lengths which fell within the latter group. These males also possessed the most slender and elongate aedeagus, a character which is closely correlated with genitalia size.

Other yuccas also have served as hosts for moths tentatively listed in the second group; these species are: *Yucca faxoniana* (Trelease) Sargent and *Yucca "macrocarpa"* (probably equivalent to *Y. torreyi* Shafer of current literature). These three plant species, along with others (see table 1), are included in the section *Sarcocarpa*, which is characterized principally by fleshy, indehiscent fruit. The other three sections of southwestern yuccas possess fruits which ripen as dry capsules. The section *Clistocarpa* is monotypic (*Y. brevifolia*), possesses indehiscent fruit, and apparently never serves as a host for *Tegeticula yuccasella.* The species of the sections *Hesperoyucca* and *Chenocarpa* develop dehiscent fruit and the great majority, if not all, may be hosts for *T. yuccasella.* Members of the *Hesperoyucca* are pollinated by *T. maculata* and *T. m. extranea* and probably not by *T. yuccasella. Yucca whipplei* (of the *Hesperoyucca*) has been listed as a host for the latter moth by McKelvey (1947), but this association is questionable. Five females collected by McKelvey on this plant (probably from flowers) were examined and found to be carrying granular pollen not of the *whipplei* type. Numerous rearing records and pollination observations involving *T. yuccasella* have been noted for nearly all species of the *Chenocarpa,* and it has been established that all plants contained therein are associated with this species of *Tegeticula* and no other.

Considering the botanical classification of *Yucca,* our present knowledge on the biology of *Tegeticula,* and the general variation as observed in the male genitalia, it is tempting to postulate that a specific pollinator has evolved for at least four sections of *Yucca.* The sections *Clistocarpa* and *Hesperoyucca,* as already mentioned, are pollinated primarily and probably exclusively by two distinct species of *Tegeticula.* The members of *Chenocarpa* are frequented only by *T. yuccasella,* and it is possible that a sibling form of that moth has or is in the process of evolving as a specific pollinator for the section *Sarcocarpa.* If ever the existence of such a form is verified, then it most likely will take the name of *T. mexicana.* The type series of this moth was reared from *Y. filifera* Chabaud (=*Y. australis*), which is a member of the *Sarcocarpa.* The diameter of the signum for these Mexican specimens (0.67 mm, N=?) is approximately the same as for females from *Y. baccata*; however, the dimensions of the male genitalia as figured by Bastida (1962), approach more closely those of the lectotype of *T. yuccasella* (fig. 107).

Several factors, in addition to that just mentioned, cast some doubt on a postulation that a sibling form of *Tegeticula* exists, or that such a form is host specific for all *Sarcocarpa.* For instance, two other species listed in table 2, *Y. treculeana* Carriere and *Y. "mohavensis"* (=*schidigera* Roezl), are also members of the *Sarcocarpa.* As shown in table 2, the one specimen examined from *Y. "mohavensis"* possessed the shortest genitalia of the entire series. It is, of course, possible that this host record is a misidentification. This is not likely, however, because this identification, as well as the majority listed in table 2, were made by S. D. McKelvey, an authority on the genus *Yucca.* It is also possible that the moth in question had merely strayed into the flowers of *Y. schidigera,* where it was collected, and was in no way intimately associated with the plant. Also, it must be remembered that the measurements of the male genitalia essentially describe only one character; before any taxonomic division of *T. yuccasella* is made, other characters should be correlated. As noted previously, some correlation may exist between the relative sizes of the male and female genitalia; however, for another character studied, that of relative wing width, similar correlation does not seem to be present. Certain specimens from Arizona (Madera Canyon) and California (Lucerne Valley) consistently demonstrated narrow wings, similar to the moths from Torrance Co., New Mexico, but differed considerably from the latter population in possessing male genitalia of a much shorter length. After several more populations have been surveyed and additional characters studied, such discrepancies may become clarified.

The 1222 specimens examined during the course of this study represented a major portion of *T. yuccasella*'s known distribution. Following a casual examination of this series, it soon became evident for both sexes that the eastern forms generally possessed broader wings than the western ones (figs. 86–87). As a means of presenting this variation, 14 localities, consisting of a total of 193 females, were selected to represent the species range (see table 3). These particular localities were chosen because it is believed that most, if not all, constitute definite populations. That is to say, all specimens (for a given locality) were collected at the same site, during the same time period by the same collector. For some locales, host data was also available to associate the material further. The forewings of all examples were measured directly with a stage micrometer by projecting an enlarged outline of the wing onto paper. It is believed that wing measurements performed in this manner are accurate to within 1/20th of a millimeter. To summarize these measurements, the average width-length ratios were calculated (W×100/L) for each locality; the standard deviation (s) and coefficient of variability (C.V.) of the ratios are included in table 3 for comparisons. Most values of C.V. were between 4 and 6.8; some localities exhibited a lower value, reflecting in most instances a small sample size. All data listed in table 3 are based on measurements of female specimens; however, in order to check for possible sexual differences between males and females in regard to wing width, some males were likewise examined. For example, 13 males from Madera Canyon agreed closely with their corresponding females in possessing a mean wing ratio of 28.18.

The general geographic distribution of relative wing width appears more definite than that of genitalia length; although, again, no clear lines of demarcation can be observed. Wing width appears to decrease gradually from east to west, with some overlap in the Southwest. Further collecting may show that the distribution of this character is somewhat similar to that of male genitalia size (i.e., in direct relation to the host plants' distribution), but, for the present, it is difficult to relate, largely due to insufficient host information.

Variation in the development of the maxillary tentacles was first reported by Busck (1947), who consequently synonymized *Prodoxus intermedius*, a moth formerly thought to be distinct from *T. yuccasella* because the females lacked tentacles. The abortion frequency of the tentacles appears somewhat comparable to the length character of the male genitalia in that marked population differences are to be noted. As shown in table 3, the failure for the maxillary tentacles to develop may be a more common occurrence than previously realized. Two populations of adequate size (nos. 13 and 14) showed no tentacle reduction, whereas populations 6 and 8 demonstrated varying degrees of abnormalcy. The series from Gran Quivira National Monument, N. Mex., contained far more abnormal females (71%) than normal; 56 females were examined and 40 were found to have the tentacles either greatly reduced or absent. Usually if these structures are aborted, they are either completely absent or represented by minute stubs, barely visible under low magnification. In a few specimens, the tentacles were more developed (fig. 32) but still considerably reduced in size. In none of these females did the vestigial organs exceed one-third their normal length.

It is usually characteristic (with some exceptions) for field-captured females possessing fully developed tentacles to show some evidence of pollen beneath the head (fig. 31). For example, in the Gran Quivira population studied, all normal females (16) carried large masses of pollen in this position. However, no trace of pollen was found on any abnormal specimens, which suggests not only were the females incapable of collecting pollen, but also, that they had made no attempts to do so. Thus, it may be possible that the general behavior of these moths diverges from the normal pattern. This is not to imply necessarily that fertility barriers of some kind have evolved, for the frequency of abnormal females in the Gran Quivira population has attained a high level. This frequency may not be the result of some factor which is maintained within the population at a certain level, or that has increased over a period of time; instead, it may represent a ratio that fluctuates considerably from one year (or brood) to the next. It would seem that females incapable of pollinating the yucca flower and, thus, incapable of insuring a food supply for their progeny, would in time be selected against, especially if it were possible for the number of such females to comprise eventually a large portion of the population. It should be emphasized, of course, that one normal female is capable of pollinating numerous flowers, and, therefore, able to support the existence of several abnormal individuals. In this way, such populations as that from Gran Quivira could exist, perhaps, indefinitely.

Material examined.—718 ♂♂ and 504 ♀♀.

UNITED STATES: Alabama: Southern Alabama, specific locality unknown, ♀, July (USNM). Arizona: Specific locality unknown, ♂ (USNM). Apache Co.: Lupton, ♀, July 6 (CNHM). Cochise Co.: Bisbee, Mule Mts., ♀, Apr. 18 (USNM). Douglas, ♂, 5 ♀♀, June 8–15 (USNM). Paradise, ♂, ♀, June, 16–23 (USNM). Coconino Co.: 9 ♂♂, 5 ♀♀, May 18 (USNM). Williams, 15 ♂♂, 7 ♀♀, June 5–8 (USNM). Gila Co.: 4 ♂♂, 2 ♀♀, May 10 (USNM), Pinal Mts., 5000 ft., ♂, ♀, May 15–22 (USNM). Mohave Co.: 7 ♂♂, 11 ♀♀, May 12–17 (USNM). Navajo Co.: 3 ♂♂, 10 ♀♀, May 19–20 (USNM). Winslow, ♀, May 8 (USNM). Pima Co.: ♂, June 6 (USNM). Madera Canyon, Santa Rita Mts., 4400 ft., ♂, June 16 (CU). Santa Cruz Co.: 3 ♂♂, ♀, May 6 (USNM). Madera Canyon, Santa Rita Mts., 4880 ft., 13 ♂♂, 23 ♀♀, June 29–July 30 (CU, RWH). Nogales, ♂, ♀, Apr. 19 (USNM). Yavapai Co.: Dewey [Cherry Creek], 6 ♂♂, 5 ♀♀, June 8–23 (USNM). California: Imperial Co.: 2 ♂♂, 2 ♀♀, Apr. 24 (USNM). Los Angeles Co.: Baker, 2 ♀♀, Apr. 30 (USNM). San Bernardino Co.: Barstow, south of, near Box "S" Ranch, 5 ♀♀, Apr. 29 (USNM). Doble, ♂, July (USNM). Lucerne Valley, ♂, ♀, May 7 (LACM); 14 ♂♂, 9 ♀♀, May 7 (USNM). Michel's Cavern, ♂, May 18 (USNM). Moronga, ♀, Apr. 5, ♂, May 11 (USNM). Providence Mts., ♂, 2 ♀♀, Apr. 22–May 8 (USNM). San Diego Co.: Cuyamaca Mts., ♂, Aug. 16 (CU). Colorado: Specific locality unknown, ♂, 2 ♀♀ (USNM). Southwestern Colorado, ♂, ♀ (USNM). Chaffee Co.: Salida, ♂, July 6 (USNM). El Paso Co.: Colorado Springs, Fountain Valley School, 2 ♂♂, ♀, June 12–July 16 (ABK). Monument Park, 2 ♂♂, July 19 (USNM). Ute Pass, ♀, paralectotype, *P. intermedius*, 2 ♂♂, July 18, 3 ♀♀ (USNM). Las Animas Co.: Morley, near, ♀, May 31 (USNM). Park Co.: Como, ♂, ♀, June (USNM). Rio Grande Co.: Between South Fork and Monte Vista, 3 ♀♀, May 28 (USNM). Connecticut: New Haven Co.: New Haven, ♂, June 30 (USNM). District of Columbia: Washington, 2 ♂♂, 2 ♀♀, June 20–23 (USNM). Florida: Highlands Co.: Lake Placid, Archbold Biological Station, ♀, May 14 (CU). Hillsborough Co.: St. Petersburg, 2 ♂♂, ♀, Apr. 22–29, ♀, May, 4 ♂♂ (USNM). Polk Co.: Lakeland, ♂, ♀, May 6 (AMNH); 3 ♂♂, ♀, May 1–7 (USNM). Sarasota Co.: Venice, 2 ♀♀, May 1–7 (USNM). Volusia Co.: New Smyrna, 2 ♂♂, ♀ (USNM). Georgia: Specific locality unknown, ♂, ♀ (AMNH). Charlton Co.: Okefenokee Swamp, Mixon's Hammock, ♂, 2 ♀♀, June 16 (CU). Fulton Co.: Atlanta, ♂, July 7 (ANSP). Illinois: Cook Co.: Arlington Hts., 3 ♀♀, July 2–20 (CNHM). Chicago, 2 ♂♂, ♀, May 27, ♂, 2 ♀♀, July 6–15 (CNHM). Edgebrook, ♂, 2 ♀♀, July 16 (CNHM). DuPage Co.: Downers Grove, 3 ♂♂, 4 ♀♀, July 6 (CNHM). Shelby Co.: Oconee, 2 ♀♀, July 1–7 (USNM). Indiana: Tippecanoe Co.: Lafayette, ♀, June 25 (USNM). Iowa: Monana Co.: Turin, ♂, ♀, June 6 (USNM). Woodbury Co.: Sioux City, 2 ♀♀, June 20 (USNM). Kansas: Douglas Co.: Lawrence, 3 ♂♂, 3 ♀♀, June 15 (LACM). Hamilton Co.: ♀, 3350 feet (CM). Seward Co.: 3 ♂♂, ♀, May 31 (USNM). Maryland: Prince Georges Co.: Capitol View, 2 ♂♂, ♀ (USNM). Massachusetts: Dukes Co.: Martha's Vineyard, ♂, July 5 (USNM). Mississippi: Hinds Co.: Clinton, ♂, May 25 (USNM). Jackson, ♀, May 26 (BrM). Missouri: Specific locality unknown, ♀, May 31 (USNM). "C. Mo." [Central Missouri?], ♂, lectotype, *P. yuccasella*, June, ♂, ♀ (USNM). St. Louis Co.: Kirkwood, 3 ♂♂, 4 ♀♀, June 1–21 (CU); ♀ (ANSP). St. Louis, ♀, June 17 (CNHM). New Jersey: Burlington Co.: New Lisbon, 6 ♂♂, 2 ♀♀, June 26–July 4 (ANSP). Essex Co.: Newark, 5 ♂♂, 5 ♀♀, June 16–26 (AMNH). Mercer Co.: Princeton, 55 ♂♂, 2 ♀♀, June 25 (USNM). New Mexico: Bernalillo Co.: Albuquerque, 15 ♂♂, 13 ♀♀, June 2–27 (LACM); east of, 9 ♂♂, 2 ♀♀, June 6 (USNM). Ft. Wingate, 8 ♂♂, 2 ♀♀, June 1–15 (USNM). Colfax Co.: Raton, ♂, June 31 (USNM); south of, 16 ♂♂, 5 ♀♀, June 4 (USNM). Dona Ana Co.: Aden, ♂, July 12 (CU). Las Cruces, ♀, June 5 (USNM). Guadalupe Co.: Santa Rosa, 5 ♀♀, July 5 (CNHM). Hidalgo Co.: ♂, June 3 (USNM). Luna Co.: Deming, ♀, July 9, ♀, Sept. 1–7 (USNM). Roosevelt Co.: Clovis, 10 miles SW of, 10 ♂♂, 10 ♀♀, June 8 (AMNH). San Juan Co.: Tohatchi Mts., ♂, ♀, May 21 (USNM). Socorro Co.: Gran Quivira National Monument, 84 ♂♂, 56 ♀♀, June 22–July 22 (LACM). Torrance Co.: 74, ♂♂, 18 ♀♀, May 24 (USNM). Valencia Co.: 30 ♂♂, 9 ♀♀, May 22–26 (USNM). New York: Specific locality unknown, ♂, ♀ (USNM). Suffolk Co.: Long Is., ♀ (AMNH). Orient, Long Is., 2 ♂♂, ♀, July 9–13, ♂, Aug. 26 (CU). South Hill, Long Is., ♀, July 11 (CU). Tompkins Co.: Ithaca, 2 ♀♀, July 11–27 (CU). Westchester Co.: Pelham, ♂, ♀, July 3 (ABK). North Dakota: Golden Valley Co.: Beach, 2 ♀♀, June 24 (USNM). Ohio: Cuyahoga Co.: Cleveland, ♀, July 1 (USNM). Hamilton Co.: Cincinnati, 3 ♂♂, 3 ♀♀, June 21–July 7 (AFB); ♂, ♀, June 21–July 1 (CU); ♂, 2 ♀♀, July 1–7 (ANSP); 2 ♂♂, 4 ♀♀, June 21–July 7 (USNM). Oklahoma: Beaver Co.: 4 ♂♂, 3 ♀♀, June 1 (USNM). Noble Co.: 4 ♂♂, ♀, June 2 (USNM). Oklahoma Co.: Oklahoma City, 2 ♂♂, 2 ♀♀, May 22 (USNM). Pennsylvania: Specific locality unknown, 13 ♂♂, 4 ♀♀ (USNM). Allegheny Co.: Edgeworth, ♂, 2 ♀♀, July 11 (CM). Oak Station, 7 ♂♂, 2 ♀♀, June 22–July 16 (CM). Pittsburgh, ♂, ♀, July 6–7 (CM). Sharpsburg, ♂, June 15–21 (CM). Erie Co.: North East, ♂, ♀, July 19–20 (USNM). Philadelphia Co.: Mt. Airy, 4 ♂♂, 8 ♀♀, June 7 (ANSP). Philadelphia, 2 ♂♂, June 8 (ANSP); ♂ (CU). Washington Co.: Finleyville, 3 ♂♂, 6 ♀♀, June 12–July 4 (CM); ♂, ♀, July 2–4 (LACM). South Dakota: Pennington Co.: Bad Lands National Monument, 4 ♂♂, 8 ♀♀, June 27 (CNHM). Tennessee: Hamilton Co.: Chattanooga, 2 ♂♂, 4 ♀♀, June 9 (CNHM). Texas: Specific locality unknown, ♀ (USNM). Bastrop Co.: Bastrop, ♂, June 2 (USNM); west of, 7 ♂♂, 3 ♀♀, May 16 (USNM). Bexar Co.: San Antonio, south of, 3 ♂♂, 4 ♀♀, Apr. 4–5 (USNM). Brewster Co.: 2 ♂♂, Apr. 24 (USNM). Alpine, ♀, Apr. 12 (USNM). Between Alpine and Hovey, 2 ♂♂, ♀, Apr. 10 (USNM). Between Alpine and Terlingua, 7 ♂♂, 8 ♀♀, Apr. 12 (USNM). Marathon, ♂, May 24 (USNM). Persimmon Gap, south of, 2 ♂♂, Mar. 28 (USNM). North of Persimmon Gap and south of Marathon, 14 ♂♂, 3 ♀♀, Mar. 28 (USNM). Callahan Co.: Putnam, 8 ♂♂, 8 ♀♀, May 27 (USNM). Between Putnam and Baird, ♂, May 27 (USNM). Cameron Co.: Brownsville, 14 ♀♀, Mar. 1–15 (USNM). San Benito, ♂, 3 ♀♀, Mar. 16–23 (USNM). Comal Co.: New Brauncels, Edwards Plateau, 2 ♂♂, ♀, May 19 (USNM). Culberson Co.: Van Horn, ♀, May 25 (USNM); west of, 2 ♂♂, 2 ♀♀, Apr. 16 (USNM). Dallas Co.: Cedar Hill, 3 ♂♂, 2 ♀♀, May 28 (USNM). Dallas, ♀, lectotype, *P. intermedius* (USNM); ♂, lectotype, *T. alba* (MCZ). Eastland Co.: Between Ranger and Strawn, ♂, ♀, May 27 (USNM). Howard Co.: Big Spring, 8 ♂♂, 11 ♀♀, Mar. 26, 2 ♂♂, ♀, May 13 (USNM). Hudspeth Co.: 11 ♂♂, ♀, Apr. 26 (USNM). Eagle Flat, 5 ♂♂, 5 ♀♀, Apr. 16 (USNM). Jeff Davis Co.: ♀, Apr. 22 (USNM). [?] Between Alpine and Van Horn, 2 ♂♂, May 25 (USNM). Kleberg Co.: Kingsville, 2 ♂♂ (CU). Mason Co: Mason, ♂. 2 ♀♀, May 14 (USNM). Medina Co.: 2 ♂♂, 7 ♀♀, Apr. 28 (USNM).

Hondo, 4 ♂♂, ♀, Mar. 19 (USNM). Between Hondo and Dunlay, ♀, Apr. 2 (USNM). Near Moon and Devine, ♂, 3 ♀♀, Apr. 4 (USNM). Mitchell Co.: Loraine, west of, 11 ♂♂, 8 ♀♀, May 27 (USNM). Nolan Co.: Sweetwater, 2 ♂♂, 3 ♀♀, May 27 (USNM). Presidio Co.: 2 ♂♂, Apr. 24 (USNM). Marfa, ♂, June 6 (USNM). Shafter, 3 ♂♂, ♀, Mar. 26 (USNM); south of, 5 ♂♂, 2 ♀♀, Mar. 26 (USNM). Terrell Co.: Between Langtry and Sanderson, ♂, Mar. 29 (USNM). Uvalde Co.: Sabinal, ♀, Mar. (USNM). Uvalde, ♂, Apr. 17 (USNM). Val Verde Co.: Del Rio, 20 miles west of, ♀, May 22 (USNM). Devils River, ♂, Mar. 29 (USNM). Ward Co.: Pyote, 23 ♂♂, 24 ♀♀, May 26 (USNM). UTAH: Kane Co.: Glendale, north of, ♂, 2 ♀♀, May 12 (USNM). Between Glendale and Orderville, ♂, May 12 (USNM). Kanab, north of, 2 ♀♀, May 14 (USNM). Washington Co.: St. George, northeast of, 2 ♂♂, ♀, May 9 (USNM); northwest of, 2 ♂♂, 3 ♀♀, May 6 (USNM). VIRGINIA: Fairfax Co.: 6 ♂♂, ♀, June 26 (USNM). WYOMING: Goshen Co.: Torrington, 2 ♀♀, July 10–13 (USNM). Platte Co.: Glendo, ♂, June 25 (USNM). Yellowstone Co.: ♂, ♀, July 16 (USNM).

MEXICO: CHIHUAHUA: Samalayucca, 12 miles south of Chihuahua, 2 ♂♂, 4 ♀♀, July 10 (UCB). HIDALGO: Tula, near ruins, 7500 ft., 6 larvae (USNM). PUEBLA: Tehuacan, 2 ♂♂, April, ♀, July 12 (USNM). SAN LUIS POTOSI: San Luis Potosi, El Trinquete, ♀, holotype, May 25, ♂, 2 ♀♀, paratypes, *T. mexicana*, Apr. 29–July 31 (IB); Santa Rosa, ♂, allotype, May 5, 2 ♀♀, paratypes, *T. mexicana*, May 5 (IB).

CANADA: ONTARIO: No specimens examined, but T. N. Freeman reports (in litt.) that specimens have been collected along the northern shore of Lake Erie at Queenston, Simcoe, and Vineland Station, July 5–29 (CNC).

***Parategeticula*, new genus**

TYPE SPECIES.—*Parategeticula pollenifera*, new species.

ADULT.—Relatively robust, heavy-bodied moth; similar to *Tegeticula* in general habitus.

Head (fig. 41): Vertical diameter of eye equalling width of frons. Tongue similar to *Tegeticula*, exceeding length of maxillary palpus. Mandibles relatively prominent. Maxillary palpus 4-segmented, fourth segment more than doubling length of third; maxillary tentacle present in female, arising from basal palpal segment, reduced in male to a short but prominent stub. Labial palpus 2-segmented; a minute sensory pit present on apex of second segment.

Thorax: Wings (fig. 46) relatively broad, apices evenly rounded. All veins usually separate except 5 and 6 of hindwing which are typically connate. Frenulum absent in male and female; humeral angle of secondaries expanded. Foreleg (fig. 59) with epiphysis absent.

Abdomen: Female with seventh tergite simple (fig. 117); membrane of ninth segment roughened, scurfy.

MALE GENITALIA.—Apex of tegumen with two setigerous lobes. Vinculum V-shaped, saccus only slightly developed. Cucullus with a dense patch of short spines. Aedeagus relatively stout.

FEMALE GENITALIA.—Apex of ovipositor relatively blunt, not spear-shaped. Anterior apophyses stout, broadly expanded posteriorly: posterior apophyses of moderate length, slender. Bursa copulatrix with two ovoid signa present, without rays; ductus bursa short, not exceeding length of apophyses, slight expansion (spermatheca) present at junction with oviduct.

Parategeticula pollenifera, new species

FIGURES 33–37, 41, 46, 59, 88, 89, 111, 117, 135, 155; MAP 7

ADULT (figs. 35, 88, 89).—Wing expanse: male, 24–27 mm; female, 29–31 mm.

Head: White; labial palpus sparsely clothed with slender fuscous scales. Vertex with a pair of short, stout, conical projections.

Thorax: White, lightly intermixed with a scattering of fuscous scales. Primaries dull white, speckled with black (in fresh specimens); thinly scaled, scales of two primary forms: (1) a type which is very abundant, uniformly distributed over wing surface, consisting of usually slender, oblanceolate scales, white in color, and (2) a second type which is sparsely scattered or sometimes lost (in rubbed specimens), consisting of broad, fan-shaped scales, black in color; apices of all scales truncate, or minutely bidentate; fringe very short, whitish; underside similar to dorsal surface except black scales, when present, usually more narrow. Secondaries very thinly scaled, semitransparent, scales whitish and similar to type 1 of forewings except even more slender; black scales usually absent, or if present, very slender.

Abdomen: Vesture relatively sparse, dull white.

MALE GENITALIA (fig. 111).—As described for genus. Valves with an armlike spiniferous lobe arising from near base; margin of cucullus evenly rounded.

FEMALE GENITALIA (figs. 135, 155).—Apex of ovipositor short, stout, usually bicuspidate; dorsal ridge absent. Signa circular, of unequal size with one being extremely reduced and nearly absent.

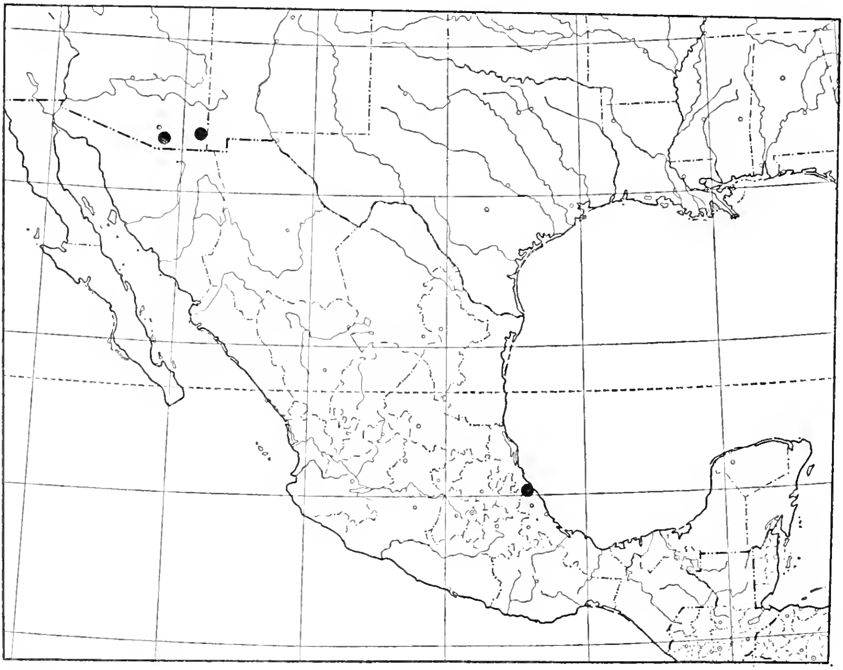
HOLOTYPE.—Bog Spring Camp Ground, Madera Canyon, Santa Rita Mts., 5100 ft., Santa Cruz Co., Ariz., ♀, July 14–26, 1964, D.R. Davis collector, from flowers of *Yucca schottii*, USNM 67375; in the United States National Museum.

PARATYPES.—ARIZONA: Cochise Co.: Southwestern Research Station, Chiricahua Mts., 5400 ft., 3 ♂♂, 3 ♀♀, July 31–Aug. 2, 1964, D.R. Davis collector, from flowers of *Yucca schottii* (USNM). Santa Cruz Co.: Same locality as holotype, 30 ♂♂, 13 ♀♀, July 14–26, 1964, D.R. Davis collector, from flowers of *Yucca schottii* (USNM). Madera Canyon, Santa Rita Mts., 4880 ft., 8 ♂♂, 4 ♀♀, July 3–28, 1959, J.G. Franclemont, R.W. Hodges collectors (CU, RWH); ♂, July 5, 1963, J.G. Franclemont collector (CU); ♀, July 4, 1959, J.G. Franclemont collector (USNM). VERACRUZ: Poza Rica, 7 miles southwest of, 200 ft, Mexico, ♀, July 20–23, 1963, Duckworth and Davis collectors (USNM). Described from a total of 42 ♂♂ and 23 ♀♀.

Recorded host.—*Yucca schottii* Englemann. Larva probably bores in flower stalks of host.

Distribution (map 7).—This species has been collected in two, widely disjunct and dissimilar areas. In northern Veracruz, it has been found near sea level; whereas in southeastern Arizona, it commonly occurs in a much drier habitat at elevations between 4500 and 5500 feet.

Discussion.—The biology of this species, when more fully understood, should prove as interesting as that of *Tegeticula,* especially with regard to its evolutionary significance. The first specimens of *Parategeticula pollenifera* were collected by Drs. J. G. Franclemont and R. W. Hodges in Madera Canyon, Arizona during the summer of 1959. Upon close examination, the author realized that these specimens represented a new genus which probably was involved as a pollinator of some species of southwestern *Yucca,* possibly *Y. schottii.* The moth's role as a plant pollinator was suggested not only by the existence of maxillary tentacles, but also by the presence of pollen masses, held firmly under the head, in nearly all females examined.



Map 7.—Distribution of *Parategeticula pollenifera* (see map 9 for distribution of host).

Yucca schottii was suspected as a possible host because of its distribution and late flowering period, both features of which coincided closely with the occurrence of *P. pollenifera.*

During the summer of 1964, the author made an investigation of the Lepidoptera associated with *Y. schottii* and established not only the host associations of *P. pollenifera,* but also of three other species of yucca moths. With the exception of *Tegeticula yuccasella,* relatively little is known concerning the life histories of these species (viz., *Parategeticula pollenifera, Prodoxus y-inversus,* and *Prodoxus ochrocarus*). Additional studies of all four species, emphasizing their interrelationships as well as the general biologies of each, would be most desirable.

The adults of *Parategeticula pollenifera* are nocturnal in that their activity normally does not commence until 20 to 40 minutes after sunset (approximately 8:00 p.m.). Most activity was noted between the hours of 8:30 and 9:30 p.m. Newly emerged specimens of both sexes usually are observed first within the blossoms, often paired in copulation. Fresh specimens typically are covered with a scattering of large, black scales which give the moths a speckled appearance (fig. 88). These scales, however, are easily lost, so that a great majority of the moths encountered in the field are immaculate (fig. 89). Occasionally the scales can be found adhered to the inner surfaces of the corolla where they had been rubbed off in the course of the moth's movements.

During the early period of emergence, the females engage in pollen collecting and, in all probability, pollination. Pollen collecting was observed by the author, but the final deposition of the spores was not. It is assumed that pollination proceeds in a manner similar to that of *Tegeticula,* although this needs to be confirmed. Following copulation and perhaps pollination, females seldom are encountered within the blossoms at night, although they may be observed crawling over the flower's exterior. Consequently, the great majority of active specimens one sees within the flowers at this later date (mid-July through early August) are males. The females are more apt to be found beneath the blossoms near the center of the panicle, for it is during this period that egg laying principally occurs.

The ovipositor of *P. pollenifera* differs greatly in structure from all other members of the Prodoxinae (fig. 135). This feature early suggested a fundamental difference in life history. Field observations have confirmed my previous suspicions in that the overall behavior of this moth during oviposition is not only unique for the yucca moths but perhaps for the entire Lepidoptera. The eggs are deposited in a single row (fig. 34), usually along the dorsal (lower) surface of the lateral branches of the flower panicle. The diameter of the stems at the oviposition site most frequently ranges from 4 to 7 mm. Prior to egg insertion, the female assumes a transverse position across the upper surface of a branch (fig. 33), in sharp contrast to the vertical or lengthwise position that is characteristic for *Prodoxus* and probably *Agavenema.* She then bends her abdomen under her body and around the stem and commences to scrape a small pit in the plant tissue. During this operation, the movements of the abdomen are quite forceful, while the foreportion of the moth's body remains relatively motionless. Digging is accomplished primarily through a series of lateral or sideway movements of the abdomen, interspersed with irregular, circular motions. Little or no plant tissue actually is removed from the egg pit in the sense of a true excavation; instead, the tissue is merely torn and pushed aside by the ovipositor. After the pit has been excavated to a depth of about 0.5 to 1.0 mm, an egg is deposited in the cavity. Sometimes the egg is placed as deep as 0.5 to 0.7 mm below the surface of the stem, but frequently the pit is more shallow, thus exposing the top of the egg. Immediately following the insertion of an egg in this manner, the moth then steps sideways slightly and commences, without interruption, to dig another pit alongside the first. This procedure is repeated normally until a row of tiny pits has been excavated, each pit being separated by a distance not greater than 1 mm. As mentioned earlier, when the eggs are deposited in a lateral branch, they are always placed on the lower side; however, the exact location often is not along the mid-dorsal line of the stem, but instead, slightly up one side in the direction of the moth's abdomen. Also, the angle of egg insertion usually is not along the radius of the stem, but is slanted at a slight angle to the stem's surface.

The egg (fig. 36) is broadly oval in shape (in sharp contrast to that of *Prodoxus* and, particularly, *Tegeticula*), of an opaque, greenish-white color, and approximately 0.2 to 0.4 mm in length. Its width is usually about one-half its length. As is true for most Lepidoptera eggs that are inserted into plant tissue, the eggs of *P. pollenifera* quickly desiccate if completely exposed due to the presence of a very thin and membranous chorion.

Considering the effort necessary for *P. pollenifera* to accomplish oviposition, one would expect the length of time required for this act to be considerable. In two instances the amount of time consumed during egg laying was noted. In both cases the females were in the process of ovipositing when first observed; thus, the total length of time that elapsed between when they first commenced to lay eggs at the particular site to the time they ceased, is not known. At no time did the moths interrupt their egg laying movements except to move slightly sideways in order to begin the next egg pit. It was also noted that the moths worked slowly downwards as they laid their eggs, from a higher to a lower level on the branch. The first female was observed at 8:42 p.m. on the evening of July 20. At 9:02 p.m. the moth flew away, having spent a total of 20 minutes engaged in oviposition. An examination of the branch revealed a scar 6 mm long containing 12 eggs. On July 22 at 8:35 p.m., a second female was observed depositing eggs. This individual left the site at 8:50 p.m. after laying a total of 10 eggs in a row 5 mm in length. The second female probably would have remained longer at this site had it not been for a light rain which began to fall at this time. Thus, the minimum average time required for the insertion of a single egg in the two examples studied was approximately 1.6 minutes. Considering this information, one can easily conceive that it would have required a moth more than an hour to create some of the egg scars examined.

Sometimes the eggs are deposited in areas of the plant other than the lateral branches of the panicle. Occassionally the scars can be found along the primary stalk. In such areas the scars always are aligned lenthwise (i.e., vertically) along the stem, as is true for the lateral branches. Thus, when ovipositing in the primary stalk, the female assumes a seemingly awkward, horizontal position on the stalk. Perhaps for this reason, fewer eggs are deposited in the main stem as compared to the lateral ones.

A much more remarkable variation of this habit is the deposition of eggs in the flower petals (fig. 37). In such circumstances, the eggs usually are inserted into the outer surface of the corolla and rarely in the inner layers. This indicates that the species seldom enters the flowers to oviposit. The number of eggs deposited at any one site on a petal rarely exceeds five. Probably due to the relative thickness of the petals, the eggs are inserted almost parallel to the epidermis. Immediately surrounding the eggs, a necrotic area begins to develop which eventually appears as a small and somewhat sunken, brownish spot. One female was observed (July 20) ovipositing in the corolla. The moth had assumed a transverse position near the middle of the petal and was in the process of inserting an egg into the dorsal (outer) surface. Because of the reflexed condition of the pedicel, the female rested on top of the flower in a position comparable to that attained when ovipositing in the lateral branches.

As a means of acquiring some idea as to the prevalent site of oviposition, since considerable variation exists, an entire flower panicle was collected (July 26) and examined for egg scars. The results of this examination of egg distribution of *Parategeticula pollenifera* on *Yucca schottii* are summarized below. It can be added that superficial observations of other panicles showed similar patterns of egg distribution.

Oviposition site	*Sites observed*	*Eggs/site (range)*	*Estimated $\bar{x}$ (eggs/site)*
flower petals	9	1–5	3
lateral branches	12	5–49	20
primary stalk	4	3–10	6

Unfortunately, no information is presently available concerning larval morphology or biology. Considering the usual site for oviposition, it seems likely that the larvae are stem borers, although this needs to be verified. Future studies also should be directed toward the discovery of the pupa, since a knowledge of pupal structure and the site of pupation, along with larval information, would greatly elucidate the relationships of *Parategeticula.*

Prodoxus Riley

Prodoxus Riley, 1880a, pp. 141–144 [type: *Prodoxus decipiens* Riley, 1880; monobasic]; 1880b, p. 155; 1880d, p. 177; 1880c, p. 182; 1881, pp. 632, 639.—Hagen, 1882, pp. 19, 20.—Riley, 1883a, p. 197; 1883b, p. 468; 1891a, p. 97; 1892a, p. 145; 1892b, pp. 98ff.; 1893a, pp. 47, 51–53.—Trelease, 1893, pp. 220, 223.—Sharp, 1899, p. 433.—Dyar, 1902 [1903], p. 576; 1903b, p. 103.—Kearfott, 1903, p. 124.—Holland, 1905, p. 437.—Walsingham, 1914, pp. 369, 370 [synonym of *Tegeticula*].—Busck, 1915, p. 94.—Barnes and McDunnough, 1917, p. 197.—Braun, 1919, pp. 353, 356, 359, 361, 362.—Forbes, 1923, p. 74.—Braun, 1924, pp. 239, 249, 253, 254.—Handlirsch, 1925, p. 876.—Fletcher, 1929, p. 184 [synonym of *Tegeticula*].—Braun, 1933, pp. 236, 237, 247, 256, 257.—Brimley, 1938, p. 313.—McDunnough, 1939, p. 109.—Lindinger, 1941, p. 237.—Busck, 1947, pp. 182, 183.—Comstock, 1950, p. 600.—Borror and Delong, 1963, p. 432.

Type species.—*Prodoxus decipiens* Riley, 1880 (=*Hyponomeuta* [sic] *5-punctella* Chambers, 1875), monobasic.

Adult.—Medium to small sized moth, wing expanse 8–23 mm; body moderate to slender.

Head (fig. 42): Eyes medium in size, vertical diameter slightly exceeding width of frons. Tongue slightly surpassing length of maxillary palpus. Mandible present, but minute. Maxillary palpus 5-segmented, fourth segment more than doubling the third in length; maxillary tentacle absent in both sexes. Labial palpus 3-segmented; apical segment one-third the length of second.

Thorax: Wings (fig. 47) relatively broad, apices somewhat acute. All veins normally separate, except 5 and 6 of hindwing which are usually connate. Frenulum present in male, simple. Foreleg (fig. 55) with an epiphysis.

Abdomen: Female with apex of seventh tergite simple (fig. 112).

Male genitalia.—Apex of tegumen either simple or bilobed. Vinculum V-shaped; saccus only slightly developed. Valves relatively simple, either without cucullar spines (and with apex of tegumen simple), or with 3–7 stout spines present on margin of cucullus (and with tegumen bilobed). Aedeagus relatively stout, not greatly elongated.

Female genitalia.—Apex of ovipositor spearlike, dorsal ridge serrate. Apophyses long and slender. A pair of signa normally present, usually stellate, with less than 20 rays, signa absent in *P. intricatus.* Ductus bursa relatively short, usually not exceeding length of apophyses; spermathecal enlargement typically present at union of oviduct.

Larva (figs. 21, 22).—Head usually retracted slightly into prothorax. Body white, often becoming pale green at maturity; apodal. Stem borers in *Yucca.*

Pupa (fig. 25).—Head with a prominent frontal beak. Abdominal tergites finely spined. Pupation occurs in a silken cocoon (fig. 28) within host plant.

Life History

Egg.—As in *Tegeticula,* this stage has been described for only one species, *Prodoxus quinquepunctellus.* Is is likely that the eggs of the other species will be similar. The egg of *P. quinquepunctellus* is characterized as being soft, white, and somewhat variable in shape, but usually compressed and elongate, measuring approximately 0.4 mm in length and less than 0.1 mm in diameter. Both ends are rounded, and no pedicel is present.

The egg is deposited most frequently in the yucca stalk at a depth of about 1–2 mm, but may also be found in the flower pedicel or young ovary.

Larva.—The egg of *P. quinquepunctellus* hatches approximately nine days after oviposition. The larvae of all species are apodal and burrow most frequently into the main flower stalk; some species burrow in the flower stems or in the fleshy parts of the fruit. In the early stages, the larvae are whitish in color, often becoming pale green with maturation. Except for the absence of legs, the mature larvae of most species are of a typical lepidopterous form; those of *P. quinquepunctellus* (fig. 21), however, attain a much greater relative diameter and superficially resemble the larvae of some weevils.

Riley (1892a) noted that the larva of *P. quinquepunctellus* undergoes three molts within the normal growth period of about 30 days. Occasionally the length of the larval period may be greatly extended, as has been observed also in *Tegeticula.* Riley (1894) reported one incident in which larvae of a species of *Prodoxus* had survived for nearly six years. The yucca stems containing these larvae were collected September 20, 1893, by Mr. Albert Koebele. Over five years later (May 17, 1887), the stems were cut open, and two healthy larvae were found in cocoons, along with a large number of larvae which had died previously.

All known members of *Prodoxus* overwinter as last-instar larvae in their burrows. Prior to hibernation, the larva generally excavates a burrow to the outer layers of the stem, leaving a thin partition blocking the future exit. It then retreats back into its burrow and constructs a cocoon of white silk, which is covered externally with larval excrement and tiny plant fragments.

PUPATION.—Pupation occurs in the yucca stalk (or fruit) during spring, prior to the flowering period of the host. The pupal period is relatively brief and probably does not exceed a week or so in length. Immediately prior to adult emergence, the pupa forces its way through the thin partition sealing the exit (fig. 28). After it has pushed itself about halfway out of the burrow, the adult is able to emerge. This activity normally occurs late in the evening, at about dusk.

Structurally, the pupae of *Prodoxus* and *Tegeticula* are quite dissimilar, and are modified in accordance with their different life histories. The pupa of *Prodoxus* (fig. 25) is relatively smooth and lacks the conspicuous dorsal spines of *Tegeticula*. *Prodoxus* further differs in having a frons more projected and conelike. These adaptations probably aid the pupa in forcing its way through the cuticular partition of its burrow, as well as facilitate its emergence from the cocoon.

ADULT.—Emergence of the adults usually occurs in April, May, or early June. The first specimens may appear before any yuccas are flowering and prior to the emergence of *Tegeticula*, but they are most abundant during the flowering period. Copulation has not been observed but probably occurs soon after emergence along the yucca stalk and in the flowers where the adults usually rest during the day.

Immediately prior to oviposition, the female normally settles lengthwise on the yucca stalk with her head directed upward. Raising her abdomen, she then proceeds, usually with some difficulty, to force her ovipositor into the plant. Several abortive attempts may be made over the general surface of the stalk before an area is located where the ovipositor can be inserted. The oviduct and ovipositor of *Prodoxus* are considerably shorter than those of *Tegeticula;* consequently, penetration into the plant is not as deep.

Riley (1892a) reported that the plant tissues surrounding the egg of *P. quinquepunctellus* seem to experience some disorganization through its presence, as in the case of *Tegeticula*. For most species of *Prodoxus,* no serious deformations or retardation of plant growth appear other than a slight discoloration of the stem at the point of oviposition, which later develops into a small scar. The larvae (adult female ?) of *P. y-inversus*, however, have been reported (Riley, 1892a) to induce hard, gall-like swellings in the fruit pods in which they feed.

NATURAL ENEMIES.—Four species of Hymenoptera, representing three families, are known to parasitize members of this genus. *Eudecatoma flammineiventris* (Eurytomidae) has been reared from two closely related moths of the "quinquepunctellus" group, *Prodoxus y-inversus* and *P. quinquepunctellus*. The latter is also parasitized by an ichneumonid, *Calliephialtes notandus*, and a braconid, *Heterospilus prodoxi*. Similarly, *Heterospilus koebelei* is reported to attack two species of the "marginatus" group, *P. marginatus* and *P. aenescens*. *Prodoxus sordidus*, although presently not known to be parasitized, eventually may be found to harbor a distinct species of wasp.

In addition to parasitism, at least one species of *Prodoxus* (see p. 82) is known to be preyed upon by a thomisid spider, *Misumenops coloradensis*, and a clerid beetle, *Enoclerus spinolae*.

EVOLUTION

The relationships of the various species of *Prodoxus* are summarized in diagram 2. This arrangement is based primarily upon host information and morphological characteristics of the male and female genitalia.

An examination of the male genitalia has revealed two groups within the genus *Prodoxus*. One division (A) may be referred to as the "quinquepunctellus" group and is characterized by species with a bilobed or clefted tegumen (fig. 92) and marginal spines on the valves; in contrast, members of the "marginatus" group (A′) exhibit a tegumen with a simple or entire apex (fig. 98) and valves without spines. More significantly, these morphological characters are correlated with important biological differences which, together, indicate an early division (A,A′) within the genus. The phylogenetic sequence of species within each group is somewhat arbitrary, but there seems to be a tendency toward an increase in the amount of scale pigmentation, as well as a gradual reduction or loss of the female signum. Because these tendencies are believed, in part, to represent specializations, *Prodoxus marginatus* and *P. quinquepunctellus* have been considered the most generalized components of their respective groups. Future findings may modify this tentative arrangement considerably.

Present biological information coincides to a remarkable degree with that of morphology in the arrangement of species as presented in diagram 2. If *Prodoxus* originally evolved from a seed boring prodoxine, as is believed, then such a transition probably was marked by certain intermediate steps. Gradually the larva ceased to feed exclusively on seeds, and commenced to burrow through the more fleshy, and probably less nourishing, part of the fruit. Eventually some forms acquired a tendancy to bore into the receptacle and pedicel, and from these parts into the main flower stalk where they developed into true stem borers. Because the larva, at the termination of its growth, was no longer precariously situated in a dehiscent fruit, but instead adequately protected inside the flower stalk, pupation outside of the plant (i.e., underground) was no longer advantageous. Instead, survival of the species was increased when the larvae began to pupate within the yucca stalk. Interestingly enough, the supposed transition of a seed boring habit to one of stem boring is demonstrated, either in part or exclusively, by those species which I have considered to be the least specialized of the genus (viz., *P. quinquepunctellus*, *P. y-inversus*, *P. sordidus*, *P. marginatus*, and *P. pulverulentus*). The larvae of the remaining species are either known or thought to be restricted entirely to the yucca stalk.

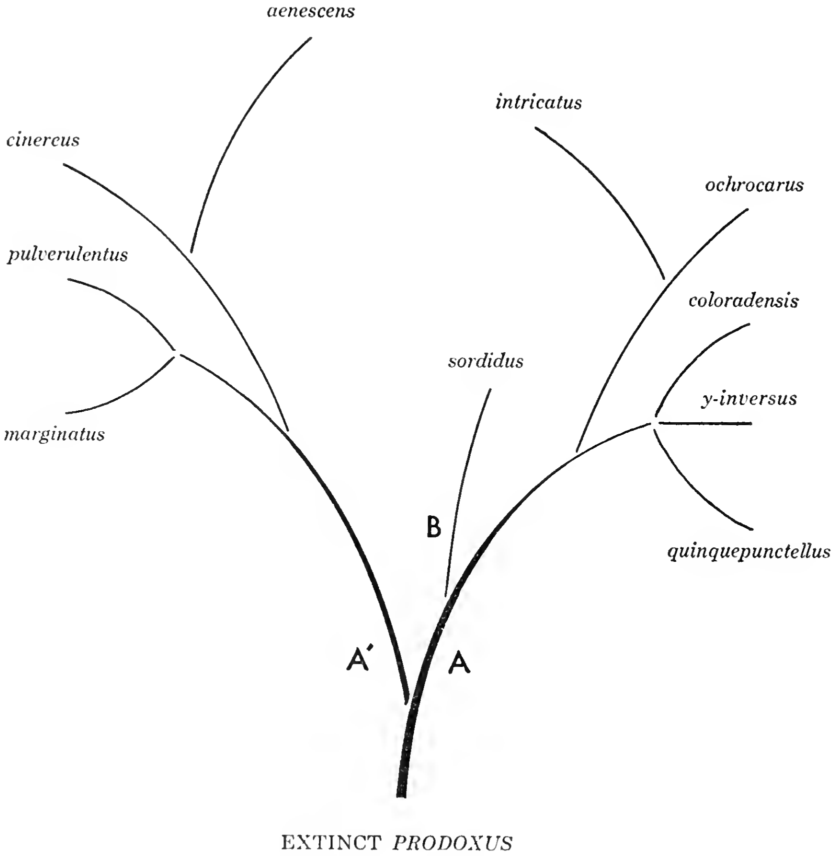


Diagram 2.—Relationships of the species of *Prodoxus*.

The "quinquepunctellus" group (A) is probably the more primitive of the two divisions as indicated by its hosts; its members apparently feed on all species of *Yucca* except the section *Hesperoyucca*. *Prodoxus intricatus* is believed to be the most advanced species within this group, primarily because of the loss of the signum and, perhaps, because of its darker pigmentation. Whether the latter character actually indicates specialization is questionable. It would appear that dark pigmentation has developed as an adaptation to a change in adult behavior, especially if the species were prone to rest on a dark surface when not active. This, however, is not known to be the case; instead, it has been reported that other dark species (e.g., *Tegeticula maculata extranea* and *T. synthetica*) rest in the flowers during the day as do their white relatives.

Prodoxus sordidus represents an early radiation (B) within the "quinquepunctellus" group that is restricted to *Yucca brevifolia*, the sole member of the section Clistocarpa. Morphologically the moth still demonstrates its affinities to the other members of the group by retaining a bilobed tegumen and spiniferous valves. As suggested by its fruit boring habit, this species may be the most primitive member of the genus.

The "marginatus" group (A′) is comprised of four species, all host specific on *Yucca whipplei*. The most generalized member of the group may be either *P. marginatus* or *P. pulverulentus*. These two species are closely related, as evidenced by their very similar male and female genitalia, and by their similar life histories. Primarily on the basis of the genitalia, *P. aenescens* is considered the most advanced of this series. Thus, this position again, curiously enough, is occupied by the darkest extreme in the group.

Key to the Species of *Prodoxus*

1a. Forewing either entirely white or white with black markings.
  2a. Forewing unicolorous, or sometimes with a few scattered, black spots (fig. 61).
    3a. Medium sized moths, wing expanse 12–23 mm; forewing white, sometimes lightly spotted (figs. 60–61); hindwing unicolorous, usually appearing darker than forewing, scales narrow, oblanceolate. **P. quinquepunctellus**
    3b. Smaller species, wing expanse 8–14 mm; forewing unicolorous, white to cream colored (fig. 71); hindwing with costal area fuscous, remainder of hindwing white as in forewing, scales broader, ovate . **P. sordidus**
  2b. Forewing with conspicuous dark markings.
    3a. Forewing with transverse median bands; male genitalia with apex of tegumen bilobed, cucullus with marginal spines (fig. 93).
      4a. Thorax entirely white; forewing variously marked, usually with an inverted Y-shaped band on outer half (fig. 62); dorsal ridge of ovipositor prominent (fig. 138), with approximately 38–44 teeth . . . . **P. y-inversus**

4b. Dorsum of thorax normally with a dark median stripe; markings of forewing variable, usually with a Y-shaped band (not inverted) on outer half (fig. 67); dorsal ridge of ovipositor less produced (fig. 139), more coarsely serrated, with usually 20–25 teeth . **P. coloradensis**

3b. Forewing without transverse median bands; genitalia with apex of tegumen simple, cucullus without spines.

4a. Forewing immaculate except for a dark border along outer margin, which is typically reduced in the males to a dark apical blotch (figs. 72, 73) . . . . **P. marginatus**

4b. Outer half of forewing densely irrorated with fuscous (fig. 74). **P. pulverulentus**

1b. Forewing not white, either brownish or fuscous, sometimes with large, yellowish spots.

2a. Forewing dark fuscous, usually with 5–7 pale yellowish spots; male genitalia with apex of tegumen bilobed, cucullus spined (fig. 96); female genitalia with signa present or absent.

3a. Forewing with either 6 or 7 spots present (figs. 68, 69); female with signa absent . . . . **P. intricatus**

3b. Forewing with 5 or fewer spots present (fig. 70); female with signa paired, well developed, stellate (fig. 121) . . . . . **P. ochrocarus**

2b. Forewing unicolorous, brownish or fuscous; male genitalia with apex of tegumen simple, cucullus without spines; female with signa present but reduced.

3a. Forewing fuscous; hindwing lighter in color, semitransparent, thinly scaled, scales hairlike . . . . **P. aenescens**

3b. Forewing light to medium brown; hindwing as dark or darker than forewing, opaque, densely covered with broad scales . **P. cinereus**

***Prodoxus quinquepunctellus* (Chambers)**

FIGURES 21, 28, 42, 47, 51, 54, 55, 60, 61, 92, 118, 137; MAP 8

Hyponomeuta [sic] *5-punctella* Chambers, 1875, p. 7.—Riley, 1877, p. 569.—Chambers, 1878b, pp. 142–154, figs. 1–2.

Prodoxus 5-punctella [sic] (Chambers).—Riley, 1880a, pp. 143, 144 [synonym of *Prodoxus decipiens*]; 1880b, p. 155; 1880d, p. 177.—Chambers, 1880b, p. 177.

Prodoxus quinquepunctella [sic] (Chambers).—Riley, 1891a, p. 97, no. 5182 [synonym of *Prodoxus decipiens*].—Dyar, 1902 [1903], no. 6564.—Kearfott, 1903, no. 7102.—Holland, 1905, p. 438, fig. 255.—Forbes, 1923, p. 74, fig. 44.—Eyer, 1924, p. 309.—Fracker, 1930, p. 61.—Brimley, 1938, p. 313.—Peterson, 1956, p. 226, pl. L 58, figs. F, G.

Prodoxus quinquepunctellus (Chambers).—Dyar, 1903b, p. 103.—Mosher, 1916, p. 46, figs. 26–27a.—Barnes and McDunnough, 1917, p. 197, no. 8460.—Braun, 1919, p. 366, pl. 29, figs. 2, 3, 6; p. 238, pl. 23, fig. 4.—Eyer, 1924, p. 326, pl. 29, fig. 4.—Braun, 1933, pp. 230, 233, pl. 12, figs. 1–2.—McDunnough, 1939, no. 9823.—Busck, 1947, p. 183.—Webber, 1953, p. 65.

Tegeticula quinquepunctella (Chambers).—Walsingham, 1914, p. 370.

Hyponomeuta [sic] *paradoxica* Chambers, 1878b, p. 149.—Riley, 1881, p. 639 [synonym of *Prodoxus decipiens*].

Prodoxus paradoxica [sic] (Chambers), 1880b, p. 177.—Riley, 1891a, p. 97, no. 5182 [synonym of *Prodoxus decipiens*].—Dyar, 1902 [1903], no. 6564 [synonym of *Prodoxus quinquepunctellus*].—Holland, 1905, p. 438 [synonym of *Prodoxus quinquepunctellus*].—Barnes and McDunnough, 1917, p. 197, no. 8460, [synonym of *Prodoxus quinquepunctellus*].—McDunnough, 1939, no. 9823 [synonym of *Prodoxus quinquepunctellus*].—Busck, 1947, p. 183 [synonym of *Prodoxus quinquepunctellus*].

Pronuba yuccasella Chambers, 1877a, p. 121 [misidentification, in part, not Riley 1872].

Pronuba yuccasella Hagen, 1880, p. 128 [misidentification, not Riley 1872].

Prodoxus decipiens Riley, 1880a, pp. 141–144; 1880b, p. 155; 1880c, p. 156; 1880d, p. 177.—Chambers, 1880b, p. 177, [? synonym of *Hyponomeuta paradoxica*].—Riley, 1880f, p. 293; 1881, pp. 630, 637, 639, figs. 7–9; 1882a, p. 62.—Meehan, 1882, p. 207.—Riley, 1882b, p. 272.—Riley and Howard, 1890, p. 350.—Riley, 1891a, p. 97, no. 5182; 1892a, pp. 145 ff., pl. 39, figs. 1–4; 1892b, p. 96, figs. 10–12; 1892c, p. 371, figs. 69–71; 1892d, pp. 305–308, fig. 14c; 1892e, pp. 317, 319; 1893a, pp. 49, 50, 52; 1893b, pp. 307, 309.—Trelease, 1893, p. 206.—Dyar, 1902 [1903], p. 723, no. 6564 [synonym of *Prodoxus quinquepunctella* (sic)].—Kearfott, 1903, no. 7102 [synonym of *Prodoxus quinquepunctella* (sic)].—Holland, 1905, p. 438 [synonym of *Prodoxus quinquepunctellus*].—Barnes and McDunnough, 1917, p. 197, no. 8460 [synonym of *Prodoxus quinquepunctellus*].—Girault, 1920, p. 208.—McDunnough, 1939, no. 9823 [synonym of *Prodoxus quinquepunctellus*].—Busck, 1947, p. 183 [synonym of *Prodoxus quinquepunctellus*].

Prodoxus decipiens variety of *5-punctella* (Chambers).—Riley, 1881, p. 639.

Prodoxus quinquepunctella [sic] variety *decipiens* Riley.—Forbes, 1923, p. 74.

Tegeticula decipiens (Riley).—Walsingham, 1914, p. 370 [synonym of *Tegeticula quinquepunctella*].

ADULT (figs. 60, 61).—Medium to small size; body less robust than in *Tegeticula yuccasella.* Wing expanse: male, 12–19 mm; female, 13–23 mm.

Head (figs. 42, 51): Entirely white. Labial palpus white, with long, erect, hairlike scales arising ventrally.

Thorax: White. Upper surface of primaries usually entirely white, occasionally with 1–14 small, fuscous spots; frequently as many as 12 spots may border the outer margin of the wing, and from 1–5 distributed along the discal cell; underside of wing medium brown. Secondaries less heavily scaled than primaries and usually appearing darker in color; scales elongate, narrow, approximately two-thirds to three-fourths the width of those in forewings; ventral surface with coastal margin darker than remainder of wing; fringes of both wings entirely white.

Abdomen: Entirely white.

MALE GENITALIA (fig. 92).—Apex of tegumen bilobed. Valves with outer margin of cucullus curved outward, bearing usually 3–6 short spines.

FEMALE GENITALIA (figs. 118, 137).—Apex of ovipositor obliquely truncate, shaft relatively stout; dorsal ridge present, usually with 6–8 coarse teeth. Signum stellate, with approximately 10–14 rays.

TYPES.—Lectotype (*Hyponomeuta* [sic] *5-punctella*, designated by present author), ♀, type 1413, Chambers, Tex.; in the Museum of

Comparative Zoology. Lectotype (*Hyponomeuta* [sic] *paradoxica*, designated by present author), ♂, Chambers, Colo., *Pronuba yuccasella;* in the Museum of Comparative Zoology. Deposition uncertain, probably in the U.S. National Museum (syntypes, *Prodoxus decipiens*).

TYPE LOCALITIES.—Bosque Co., Tex. (lectotype, *Hyponomeuta* [sic] *5-punctella*). "Nine miles north of Colorado Springs and thence 5 miles east of the mountains, Colorado" (lectotype, *Hyponomeuta* [sic] *paradoxica*). Bluffton, S.C. (syntypes, *Prodoxus decipiens*).

RECORDED HOSTS.—"*Yucca arizonica* McKelvey, *Y. arkansana* Trelease, *Y. angustissima* Engelmann, *Y. baccata* Torrey, *Y. campestris* McKelvey, *Y. constricta* Buckley, *Y. elata* Engelmann, *Y. faxoniana* (Trelease) Sargent, *Y. glauca* Nuttall, *Y. harrimaniae* Trelease, *Y. intermedia* McKelvey, *Y. pallida* McKelvey, *Y. rupicola* Scheele, *Y. standleyi* McKelvey, *Y. utahensis* McKelvey" (McKelvey, 1947); "*Y. aloifolia* Linnaeus, *Y. filamentosa* Linnaeus, *Y. gloriosa* Linnaeus" (Riley, 1880a, 1892a). Larva bores in fruit and flower stalks of host.

PARASITES.—"Braconidae: *Heterospilus prodoxi* (Riley)" (Riley, 1880c). "Eurytomidae: *Eudecatoma flammineiventris* (Girault, 1920)" and "Ichneumonidae: *Calliephialtes notandus* (Cresson)" (Riley, 1877).

DISTRIBUTION (map 8).—The range of this common species closely corresponds to that of *Tegeticula yuccasella.* It occurs widely over most of the United States from Massachusetts to Florida and west to the Rocky Mountains, where it ranges from south central Montana to southern California. *Prodoxus quinquepunctellus* has been collected in the state of Chihuahua, Mexico, and is also believed to occur in Baja California.

DISCUSSION.—A determination of the types for the various names used for this species was not an easy task, largely because of the careless manner in which the names were first proposed. Lectotypes were selected for two of the names, including the senior synonym, but a selection for the third name, *P. decipiens*, proved impossible due to the absence of properly designated syntypic material.

In his original description of *Hyponomeuta* [sic] *5-punctella*, Chambers (1875) gave no indication of type designation, nor did he state the number of specimens upon which his diagnosis was based. In a later paper (1878b) he stated that the species was described from eight specimens collected in Texas. Through the courtesy of Drs. P. J. Darlington and H. E. Evans, the present writer was able to examine one of these specimens and has designated it as lectotype.

Several of the moths originally identified by Chambers (1877a) as *Pronuba yuccasella* were later described conditionally by him (1878b, p. 149) as *Hyponomeuta* [sic] *paradoxica:* ". . . if it is a *Hyponomeuta*,

MAP 8.—Distribution of *Prodoxus quinquepunctellus* (marginal records are indicated by black circles).

I suggest for it the specific name *paradoxica,* since it cannot be *5 punctella.*" The five specimens constituting this series were described at some length by Chambers and thus were easily recognized by the writer even though they bore no labels identifying them as syntypes of *H. paradoxica.* All five moths possess a handwritten label identifying them as *Pronuba yuccasella,* in addition to a label bearing the collector's name (Chambers) and the locality, "Color[ado]." One specimen, an immaculate male, has been designated the lectotype and the remainder as paralectotypes.

In his description of *Prodoxus decipiens,* Riley (1880b, p. 155) states that the species was "described from 25 specimens, either taken in 1873 from *Yucca* flowers at Bluffton, S.C., or subsequently reared from the flower stems of *Yucca.*" Until the identity and location of this material can be established with some degree of certainty, no lectotype designation is possible. Very likely a few of the syntypes still exist as unlabelled material in the collections of the U.S. National Museum. Even though it is possible that no type material of *Prodoxus decipiens* was available for examination, the status of the name as a synonym of *P. quinquepunctellus* seems unquestionable.

It was early noted by Riley (1892a) that all eastern specimens of *P. quinquepunctellus* were immaculate, whereas the western forms, especially those from Colorado and Texas, were sometimes spotted. The present author likewise has noted the absence of maculate specimens east of the Mississippi River. In addition to Texas and Colorado, I have also noted the spotted form from Arizona, New Mexico, North Dakota, and Utah. This variation probably has little significance as both maculate and immaculate individuals can be observed within the same flower. It is possible that both kinds of individuals may appear within a given brood.

MATERIAL EXAMINED.—1112 ♂♂ and 464 ♀♀.

UNITED STATES: ALABAMA: Mobile Co.: Mobile, 2 ♂♂, 2 ♀♀, May 30 (USNM). ARIZONA: Specific locality unknown, ♂, ♀ (CU). Coconino Co.: ♂, 3 ♀♀, May 18 (USNM). Mohave Co.: 8 ♂♂, 7 ♀♀, May 17 (USNM). Navajo Co.: 22 ♂♂, 17 ♀♀, May 19–20 (USNM). Holbrook, south of, 3 ♀♀, May 9 (USNM). Winslow, 2 ♂♂, 2 ♀♀, May 8 (USNM). Pima Co.: Baboquivari Mts., ♀, June 1–15 (USNM). Yavapai Co.: Dewey [Cherry Creek] 21 ♂♂, 18 ♀♀, June 8–15 (USNM). CALIFORNIA: San Diego Co.: Cuyamaca Mts., ♀, August 16 (CU). COLORADO: Specific locality unknown, ♀ (USNM). Denver Co.: Denver, 4 ♂♂, Mar. 10–June 20 (MCZ); ♂ (USNM). El Paso Co.: Colorado Springs, 2 ♀♀, July 5 (AFB); ♂, ♀, June 21 (ABK); north of, ♂, lectotype, ♂, 3 ♀♀, paralectotypes, *H. paradoxica* (MCZ); Fountain Valley School, ♂, 2 ♀♀, June 15–27 (ABK). Larimer Co.: Fort Collins, ♀, September 19 (USNM). Rio Grande Co.: Between Monte Vista and South Fork, 11 ♂♂, 3 ♀♀, May 28 (USNM). CONNECTICUT: Windham Co.: Putnam, 6 ♂♂, ♀, July 8–August (ABK). DISTRICT OF COLUMBIA: Washington, 86 ♂♂, 42 ♀♀, June 7–27 (USNM); 7 ♂♂, June 14 (LACM). FLORIDA: Specific locality unknown, 21 ♂♂, 14 ♀♀, July 18–30 (USNM); ♂, July 30 (LACM). Highlands Co.: Lake Placid, 13 ♂♂, 5 ♀♀, Mar. 31–May 14 (CU). Polk Co.: Lakeland, ♂, May 1–7 (USNM); ♂, ♀, May 6 (AMNH). Volusia Co.: New Smyrna, 13 ♂♂, May 15 (USNM). GEORGIA: Specific locality unknown, 12 ♂♂, 4 ♀♀, July 18–21 (USNM). Clarke Co.: ♂, June 1 (ABK). Charlton Co.: Okefenokee Swamp, Mixon's Hammock, 7 ♂♂, ♀ June 16 (CU). Chatham Co.: Savannah, 2 ♂♂, ♀, June 21–26 (USNM). ILLINOIS: Cook Co.: Arlington Hts., 10 ♂♂, 5 ♀♀, Apr. 27–June 23 (CNHM). Shelby Co.: Oconee, 10 ♂♂, 16 ♀♀, June 24–July 7 (USNM). KANSAS: Ellis Co.: Ellis, ♂, 2 ♀♀, May 2 (CNHM). Douglas Co.: Lawrence, 12 ♂♂, 3 ♀♀, June 15 (LACM). Seward Co.: 58 ♂♂, 15 ♀♀ (USNM). KENTUCKY: Specific locality unknown, ♂ (USNM). MARYLAND: Cecil Co.: 4 ♂♂, ♀, May 14 (USNM). Prince Georges Co.: Capitol View, 4 ♂♂, ♀ (USNM). MASSACHUSETTS: Dukes Co.: Martha's Vineyard, ♂, July 10 (USNM). MISSISSIPPI: Hinds Co.: Clinton, ♂, 5 ♀♀, May 17–June 3 (BrM); ♀, May 17 (USNM). Jackson, ♂, May 13 (USNM). MONTANA: Yellowstone Co.: Billings, Indian Caves, ♀, June 19 (USNM). NEW JERSEY: Atlantic Co.:

Weymouth, 2 ♂♂, 3 ♀♀, June 8 (USNM); ♂, 4 ♀♀, June 6–9 (ANSP). Burlington Co.: New Lisbon, 5 ♂♂, ♀, May 15–19 (ANSP). [?] White Bog, ♀, July 14 (CU). Essex Co.: Newark, 3 ♂♂, ♀, June 26 (AMNH). Mercer Co.: Princeton, 61 ♂♂, 18 ♀♀, June 25 (USNM). Morris Co.: Green Village, ♂, July 6 (ABK). Ocean Co.: Lakehurst, Wrangle Brook Road, ♂, June 25 (CU). Passaic Co.: Patterson, ♂, July 12 (USNM). New Mexico: Bernalillo Co.: Albuquerque, 5,000 feet, 10 ♀♀, Apr. 4–May 27 (LACM); 19 ♂♂, 2 ♀♀, Apr. 4–May 27 (USNM). Colfax Co.: Raton, ♂, May 31 (USNM). San Juan Co.: Tohatchi Mts., ♂, May 21 (USNM). Socorro Co.: Gran Quivira National Monument, ♀, June 29 (LACM). Valencia Co.: 48 ♂♂, 18 ♀♀, Apr. 22–May 26 (USNM). New York: Suffolk Co.: Long Island, Cold Spring Harbor, ♂, 2 ♀♀, July 17 (AMNH); Orient, ♂, 2 ♀♀, June 7–July 6 (CU). Tompkins Co.: Ithaca, ♂, ♀, July 12 (CU). Westchester Co.: Pelham, ♂, 2 ♀♀, July 1–3 (ABK). North Carolina: Macon Co.: Highlands, 2 ♀♀, July 11–19 (CU). North Dakota: McKenzie Co.: Cartwright, 2 ♂♂, 3 ♀♀, Apr. 2–July 10 (USNM). Ohio: Hamilton Co.: Cincinnati, ♂, July 1 (AFB); ♀, July 1 (CU); 3 ♂♂, ♀, June 23–July 7 (USNM). Oklahoma: Beaver Co.: 6 ♂♂, 10 ♀♀, June 1 (USNM). Noble Co.: ♂, June, ♀ (USNM). Oklahoma Co.: Oklahoma City, ♂, ♀, May 22 (USNM). Texas Co.: 34 ♂♂, 5 ♀♀, May 17–30 (USNM). Pennsylvania: Specific locality unknown, 4 ♂♂, 3 ♀♀ (USNM). Allegheny Co.: Sharpsburg, 7 ♂♂, 2 ♀♀, June 15–July 11 (CM). Washington Co.: Finleyville, 19 ♂♂, 5 ♀♀, June 15–30 (CM). South Dakota: Specific locality unknown, Valya, 3 ♂♂, 2 ♀♀ (MCZ). Pennington Co.: Bad Lands National Monument, ♂, 4 ♀♀, June 27 (CNHM). Texas: Bastrop Co.: Bastrop, 4 ♂♂, 2 ♀♀, June 2 (USNM); west of, 2 ♂♂, 2 ♀♀, May 16 (USNM). Bosque Co.: ♀, lectotype, *H. 5-punctella* (MCZ). Brewster Co.: Alpine, 4 ♂♂, 2 ♀♀, May 23 (USNM). Between Alpine and Marathon, 9 ♂♂, 7 ♀♀, May 23 (USNM). Marathon, 9 ♂♂, 3 ♀♀, May 24 (USNM); south of, 3 ♂♂, ♀, May 24 (USNM). Callahan Co.: Putnam, 16 ♂♂, 5 ♀♀, May 27 (USNM). Between Baird and Putnam, 13 ♂♂, 5 ♀♀, May 27 (USNM). Comal Co.: New Braunfels, 17 ♂♂, 9 ♀♀, May 19 (USNM). Culberson Co.: Van Horn, 22 ♂♂, 7 ♀♀, May 25 (USNM). Dallas Co.: Cedar Hill, 7 ♂♂, 10 ♀♀, May 28 (USNM). Dallas, ♂ (USNM); ♀ (MCZ). Eastland Co.: Between Ranger and Strawn, 33 ♂♂, 24 ♀♀, May 27 (USNM). El Paso Co.: El Paso, ♂, ♀, Apr. 17 (USNM). Howard Co.: Big Spring, 22 ♂♂, 5 ♀♀, May 13–26 (USNM). Between Lamesa and Big Spring, 41 ♂♂, 10 ♀♀, May 13 (USNM). Between Stanton and Big Spring, 40 ♂♂, 6 ♀♀, May 26 (USNM). Hudspeth Co.: ♂, Apr. 26 (USNM). Eagle Flat, near, ♂, Apr. 16 (USNM). Hudspeth, 9 ♂♂, ♀, Apr. 26 (USNM). Jeff Davis Co.: Between Alpine and Van Horn, 14 ♂♂, 7 ♀♀, May 25 (USNM). Martin Co.: Stanton, 8 ♂♂, 2 ♀♀, May 26 (USNM). Mason Co.: Mason, 2 ♂♂, 2 ♀♀, May 14 (USNM). Between Mason and Fredericksburg, 6 ♂♂, 5 ♀♀, May 14 (USNM). Medina Co.: Between Castroville and Hondo, 25 ♂♂, May 19 (USNM). Between Sabinal and San Antonio, 2 ♂♂, Apr. 2 (USNM). Mitchell Co.: Loraine, west of, 32 ♂♂, 10 ♀♀, May 27 (USNM). Presidio Co.: Marfa, 4 ♂♂, ♀, June 6 (USNM); near, 6 ♂♂, 4 ♀♀, May 29–June 4 (USNM). Shafter, 3 ♂♂, ♀, March 26 (USNM); south of, 2 ♀♀ Mar. 26 (USNM). Tom Green Co.: San Angelo, 43 ♂♂, 5 ♀♀, May 14 (USNM); east of, 6 ♂♂, May 14 (USNM). Travis Co.: Austin, ♂, ♀, May 16 (USNM). Uvalde Co.: Laguna, east of Nueces River, 2 ♂♂, Apr. 1 (USNM). Between La Pryor and Uvalde, 7 ♂♂, 6 ♀♀, May 21 (USNM). Between Uvalde and Laguna, 43 ♂♂, 13 ♀♀, May 20 (USNM). Old Road from Uvalde to Eagle Pass, 9 ♂♂, May 21 (USNM). Val Verde Co.: Devil's River, ♂,

♀, Mar. 29 (USNM). Ward Co.: Pyote, 5 ♂♂, 9 ♀♀, May 26 (USNM). Utah: Carbon Co.: Helper, 19 ♂♂, 3 ♀♀, May 10 (USNM). Kane Co.: Glendale, north of, 11 ♂♂, 4 ♀♀, May 12 (USNM). Between Glendale and Orderville, ♂, May 12 (USNM). Uintah Co.: Note, 2 ♀♀, (CM). Washington Co.: St. George, northeast of, 2 ♂♂, 2 ♀♀, May 9 (USNM). Virginia: Fairfax Co.: 8 ♂♂, ♀, May (USNM).

MEXICO: Chihuahua: Samalayucca, 12 miles south of Chihuahua, 4 ♂♂, July 10 (UCB).

Prodoxus y-inversus Riley

Figures 62–63, 93, 119, 138; Map 9

Prodoxus y-inversus Riley, 1892a, pp. 151ff., pl. 43, fig. 5; 1892b, pp. 98, 101, fig. 14; 1892c, pp. 373, 375, fig. 73; 1892e, pp. 316, 319, fig. 19.—Dyar, 1902 [1903], p. 723, no. 6567; 1903b, p. 103.—Kearfott, 1903, no. 7105.—Holland, 1905, p. 439, fig. 258.—Barnes and McDunnough, 1917, p. 197, no. 8463.—Balduf, 1932, p. 56.—McDunnough, 1939, no. 9826.—Busck, 1947, p.184.

Adult (figs. 62–63).—Wing expanse: male, 11–14 mm; female, 14–16 mm.

Head: White. Antenna with basal one-half to two-thirds white; outer one-half to one-third devoid of scales, fuscous. Labial palpus white, ventral hairs brown.

Thorax: White. Upper surface of primaries white with dark fuscous markings which are more developed in female than in male; typically, 2 costal spots are present at base of wing and connected along costa, as well as an inverted Y-shaped band situated in the outer one-third of wing and extending transversely from costa to hind margin; a large apical spot normally present, extending downwards sometimes as a bar to the outer arm of the inverted Y; underside of forewings lightly shaded with fuscous, pattern of dorsal surface clearly visible from beneath. Secondaries pale fuscous above and below, more thinly scaled than primaries, scales hairlike; fringes of fore- and hindwings pale fuscous.

Abdomen: Fuscous above, whitish below.

Male genitalia (fig. 93).—Apex of tegumen bilobed. Outer margin of cucullus evenly curved, bearing usually 4–6 short spines.

Female genitalia (figs. 119, 138).—Apex of ovipositor with dorsal ridge present, abruptly terminating into ovipositor shaft; ridge with approximately 38–44 teeth. Signum stellate, well developed, number of rays usually 12–16.

Type.—Lectotype (designated by present author), ♀, no. 3059, Dec. 5, 1884, USNM 422; in the U.S. National Museum.

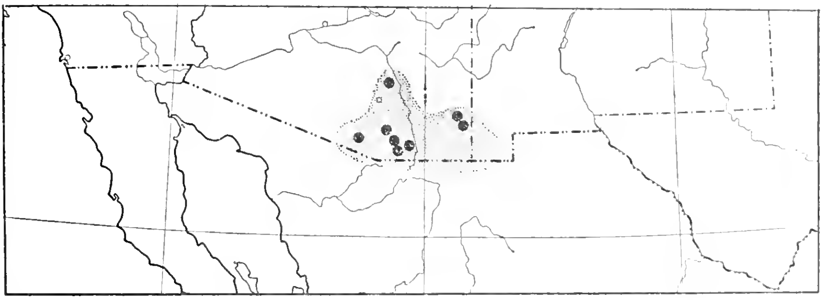
Type locality.—New Mexico (lectotype).

Recorded host.—"*Yucca* sp. (but doubtless *Y. baccata*)" (Riley, 1892a). *Yucca schottii* Englemann. Larva bores in fleshy part of yucca fruit.

PARASITE.—"Eurytomidae: *Eudecatoma flamminneiventris* (Girault)" (Balduf, 1932).

DISTRIBUTION (map 9).—Presently known only from southern Arizona and New Mexico.

DISCUSSION.—The life history of this species is poorly known, but it appears to differ strikingly in some respects from what has been observed in other species of *Prodoxus*. Apparently, the larva, which feeds in the fleshy parts of the yucca fruit, is capable of inducing "hard, gall-like swellings" in the fruit tissue (Riley, 1892a, p. 151). This reaction needs to be studied further, for it seems to differ markedly from the cellular inhibition induced by adult females of the genus *Tegeticula*.



MAP 9.—Distribution of *Prodoxus y-inversus* (black circles) and of host plant, *Yucca schottii* (shaded area).

The cocoon formed by the larva also demonstrates some peculiarity in that it consists of two chambers. Riley has described its structure thusly (1892a, p. 151): "The cocoon, which, as with the other species, is constructed within the burrow, is pale brownish, and resembles an elongate, cylindrical bag, rounded at the base and cylindrical at the apex. When ready to transform, the larva retires to the lower third of the bag and separates it from the upper two-thirds by a dense, tough, delicate whitish layer of silk, thus dividing the cocoon into two unequal chambers."

The author has found *P. y-inversus* abundant in the blossoms of *Yucca schottii* wherever he encountered the plant in flower. This plant undoubtely serves as a host for *P. y-inversus*, because no other yuccas with a comparable flowering period were observed in the general vicinity of *Y. schottii*. With this in mind and also the fact that the moths have never been collected in the flowers of *Y. baccata*, the host record as given by Riley appears questionable.

It is probable that *P. y-inversus*, as well as *P. ochrocarus*, consistently occur rather late in the season, and that they are restricted to the late blooming *Y. schottii*. If this is true, then it would be almost certain that Riley's original series of *P. y-inversus* was collected in the southern part of Hidalgo County—the only area of New Mexico in which *Y. schottii* is known to occur.

When distrubed in the flowers, the adults of *P. y-inversus* are more apt than other yucca moths to abandon the flowers in an attempt to escape. Usually they either drop or fly to the leaves immediately below and quickly move to the leaf axils where they are protected from most predators—including entomologists.

On two occasions, adults of *P. y-inversus* were observed to have fallen prey to a crab spider, identified by Mr. Vincent Roth of the Southwestern Research Station as *Misumenops coloradensis* Gertsch. This spider frequently is encountered in the flowers of *Y. schottii* and probably constitutes a constant menance to *P. y-inversus*. Similarly, this moth is also attacked while resting in the flowers by the adult of *Enoclerus spinolae* (LeConte).

MATERIAL EXAMINED.—138 ♂♂ and 68 ♀♀.

UNITED STATES: ARIZONA: Cochise Co.: Ramsey Canyon, Huachuca Mts., ♀, July 28 (UA). Paradise, 2 miles north of, 5300 feet, Chiricahua Mts., 7 ♂♂, 7 ♀♀, July 7 (USNM). Southwestern Research Station, 5400 feet, Chiricahua Mts., 2 ♂♂, 2 ♀♀, July 31–Aug. 4 (USNM). Pima Co.: Bear Canyon, Santa Catalina Mts., ♀, July 9 (UA). Santa Cruz Co.: Madera Canyon, Santa Rita Mts., 4880 feet, 25 ♂♂, 13 ♀♀, June 29–July 28 (CU, RWH). Bog Spring Camp Ground, 5100 feet, Madera Canyon, Santa Rita Mts., 80 ♂♂, 32 ♀♀, July 11–26 (USNM). Patagonia, 1 mile east of, 11 ♂♂, 3 ♀♀, July 30 (USNM). Peña Blanca Canyon, 1 mile east of, 11 ♂♂, 2 ♀♀, July 28 (USNM). Washington Mts., 7000 feet, ♀, July 12, (USNM). NEW MEXICO: Specific locality unknown, ♀, lectotype, emerged May 12; 2 ♂♂, 5 ♀♀, paralectotypes, emerged May 6–12 (USNM).

Prodoxus coloradensis Riley

FIGURES 64–67, 94, 120, 139; MAP 10

Prodoxus coloradensis Riley, 1892a, p. 152, pl. 43, fig. 6; 1892b, p. 99, fig. 15; 1892c, p. 374, fig. 74; 1892e, p. 316; 1893a, p. 47; 1893b, p. 305.—Cockerell, 1897, p. 142.—Dyar, 1902 [1903], p. 723, no. 6569; 1903b, p. 103.—Kearfott, 1903, no. 7107.—Holland, 1905, p. 440, fig. 260.—Busck, 1906, p. 348.—Barnes and McDunnough, 1917, p. 197, no. 8465.—McDunnough, 1939, no. 9828.—Busck, 1947, p. 184.

Prodoxus reticulatus Riley, 1893b, p. 306 [misidentification; not Riley 1892].

Prodoxus coloradensis variety *lautus* Cockerell, 1897, p. 142 [new synonymy].—Dyar, 1903b, p. 103.

Prodoxus coloradensis lautus Cockerell.—Dyar, 1902 [1903], p. 723, no. 6569a.—Kearfott, 1903, no. 7107a.

Prodoxus coloradensis form *lautus* Cockerell.—Barnes and McDunnough, 1917, no. 8465.—McDunnough, 1939, no. 9828.—Busck, 1947, p. 184.

Prodoxus coloradensis variety *confluens* Cockerell, 1897, p. 142 [new synonymy].—Dyar, 1903b, p. 103.

Prodoxus coloradensis confluens Cockerell.—Dyar, 1902 [1903], p. 723, no. 6569b.—Kearfott, 1903, no. 7107b.

Prodoxus coloradensis form *confluens* Cockerell.—Barnes and McDunnough, 1917, p. 197, no. 8465.—McDunnough, 1939, no. 9828.—Busck, 1947, p. 184.

Incurvaria rheumapterella Dietz, 1905, pp. 37, 92, pl. 1, fig. 4.—Busck, 1906, p. 348 [synonym of *Prodoxus coloradensis* Riley].

Prodoxus rheumapterella [sic] (Dietz).—Barnes and McDunnough, 1917, p. 197, no. 8465 [synonym of *Prodoxus coloradensis*].—McDunnough, 1939, no. 9828 [synonym of *Prodoxus coloradensis*].—Busck, 1947, p. 184 [synonym of *Prodoxus coloradensis*].

ADULT (figs. 64–67).—Wing expanse: male, 8–12 mm; female, 10–14 mm.

Head: White. Labial palpus white, ventral hairs white toward base of second segment, darker at apex.

Thorax: White, usually with a broad, middorsal, longitudinal streak of fuscous; tegulae normally fuscous. Upper surface of primaries white, variably marked with usually 2–4 transverse bands of fuscous extending obliquely, for most their length, from costa to hind margin, frequently forming a Y-shaped mark on outer half of wing (figs. 64–67); fringe white except for fuscous suffusion at apex and tornus; underside of forewing lightly shaded with fuscous, pattern of dorsal surface clearly visible from beneath. Secondaries thinly scaled, semitransparent, scales of membrane hairlike; fringe near apex pale fuscous, becoming whitish toward wing base.

Abdomen: Largely fuscous above with scattered white scales intermixed; entirely white below.

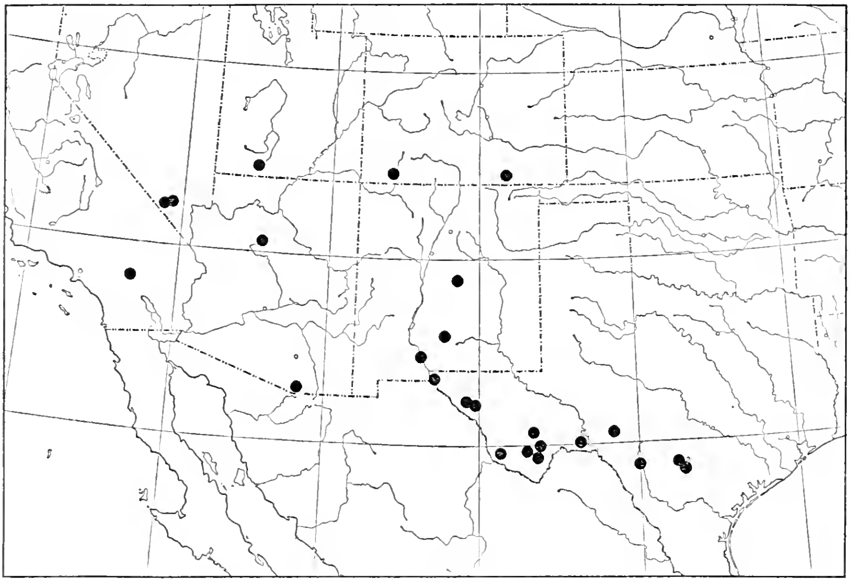
MALE GENITALIA (fig. 94).—Apex of tegumen bilobed. Outer margin of cucullus slightly emarginate, otherwise evenly curved outward; 3–6 short spines present along margin.

FEMALE GENITALIA (figs. 120, 139).—Apex of ovipositor with dorsal ridge present, gradually terminating into ovipositor shaft; ridge with approximately 20–25 teeth. Signum stellate, well developed, number of rays usually 13–16.

TYPES.—Holotype (*Prodoxus coloradensis* Riley), ♂, USNM 425; in the U.S. National Museum. Deposition unknown (variety *lautus* Cockerell and variety *confluens* Cockerell). Lectotype (*Incurvaria rheumapterella* Dietz, designated by present author), ♀, Durango, Colo., no. 199, W. G. Dietz coll.; in the Museum of Comparative Zoology.

TYPE LOCALITY.—Colo. (holotype, *P. coloradensis*). Mesilla Valley, N. Mex. (variety *lautus* and variety *confluens*). Durango, Colo. (lectotype, *I. rheumapterella*).

RECORDED HOSTS.—"*Yucca baccata* Torrey, *Y. faxoniana* (Trelease) Sargent, *Y. standleyi* McKelvey, *Y. torreyi* Shafer, *Y. treculeana* Carrière" (McKelvey, 1947); "[?] *Y. whipplei* variety *graminifolia* Wood" (Riley, 1893a). Larva bores in flower stalk of host.



MAP 10.—Distribution of *Prodoxus coloradensis.*

DISTRIBUTION (map 10).—A rather common species, found over a great part of the southwestern United States, from western Texas to southern California, thence north to southern Nevada and Colorado.

DISCUSSION.—As discussed in the introduction (p. 1), "*Prodoxus*" *reticulatus* has been transferred to the genus *Lampronia* of the Incurvariinae. The evidence necessitating this new placement also indicates that *reticulatus* is in no way associated with plants of the genus *Yucca*. Riley, however, has introduced some confusion into the host relationships of this moth. In one of his last papers on the Prodoxinae, Riley (1893b) reported a female specimen of *P. reticulatus* collected by Trelease at Arrow Springs, Calif., from the flowers of *Yucca whipplei* variety *graminifolia.* Riley further mentioned that the specimen was interesting "in that it shows some variation in the direction of *coloradensis*, especially by the separation of the basal half of the M-shaped band" (1893b, p. 306).

Unfortunately, the present location of Trelease's specimen is not known; otherwise, the confusion introduced by Riley probably could be quickly settled. Because I strongly believe that *reticulatus* is not a yucca moth and because of the superficial similarity which exists between it and *coloradensis*, I regard Riley's note as a reference to the latter species; in other words, a misidentification was made. Furthermore, a consideration of the extreme variation in wing pattern demonstrated by *P. coloradensis*, especially in connection with Riley's statement (quoted above) concerning the specimen in question, greatly amplifies the probability that a specimen of *coloradensis* was wrongly determined.

The possible host record as given by Riley for *P. reticulatus*, therefore, should refer to *coloradensis;* however, it also should be pointed out that since the record represents only an adult capture and not an actual rearing, and because other evidence indicates the host association to be false, *P. coloradensis*, in all likelihood, does not feed in *Y. whipplei*.

Incurvaria rheumapterella was described by Dietz from two female specimens without any indication of a holotype selection. These two specimens are still extant and are deposited in the collections of the Museum of Comparative Zoology in Cambridge, Massachusetts. One specimen, in decidedly poor condition, actually bears a type label, "no. 2873" (as well as a cotype label), and a handwritten label (by Dietz?) which carries the following inscription: "*rheumapterella* Dietz, type." Because this type designation has never been published, however, it is invalid and the specimens have remained as syntypes or cotypes; consequently, it has been necessary to make a lectotype designation. Because of its superior condition, however, I have selected the second specimen (without the type labels) as the lectotype and have designated the poorer specimen as a paralectotype.

Material examined.—81 ♂♂ and 84 ♀♀:

UNITED STATES: Arizona: Coconino Co.: 2 ♂♂, ♀, May 18; Williams, 2 ♂♂, 11 ♀♀, June 7–18 (USNM); ♀, June 6 (MCZ). Santa Cruz Co.: ♂, May 6 (USNM). California: San Bernardino Co.: Morongo Valley, ♀, Feb. 23 (LACM). Colorado: No specific locality, ♂, holotype, *P. coloradensis;* ♂, ♀ (USNM). LaPlata Co.: Durango, ♀, lectotype, *P. rheumapterella*, ♀, paralectotype (MCZ). Las Animas Co.: Morley, near, ♀, May 31 (USNM). Nevada: Nye Co.: Pahrump, 8 ♂♂, 7 ♀♀, April 13–18, ♂, 2 ♀♀, (CM); 19 ♂♂, 23 ♀♀, Apr. 21–24 (LACM). Pahrump, near Charleston Mts., ♀, Apr. 23 (LACM). New Mexico: Dona Ana Co.: Las Cruces, ♂, 2 ♀♀ (USNM); ♂, ♀ (LACM). Otero Co.: Alamogordo, 3 ♂♂, Apr. 8 (ANSP). Torrance Co.: ♂, May 24 (USNM). Texas: Bexar Co.: Between Sabinal and San Antonio, 2 ♂♂, Apr. 2 (USNM). San Antonio, south of, 2 ♂♂, 2 ♀♀, Apr. 4–5 (USNM). Brewster Co.: Between Alpine and Hovey, ♂, Apr. 10: Between Alpine and Terlingua, ♂, Apr. 11: Persimmon Gap, south of, ♂, Mar. 28; north of Persimmon Gap and south of Marathon, 13 ♂♂, 14 ♀♀, Mar. 28 (USNM). Culberson Co.: Van Horn, west of, ♂, 3 ♀♀, Apr. 16 (USNM). El Paso Co.: El Paso, ♀, Apr. 17 (USNM). Hudspeth Co.: Eagle Flat, ♂, ♀, Apr. 16; Sierra Blanca, Indian Hot Springs Rd., 9 ♂♂, ♀, Apr. 15 (USNM). Presidio Co.: Shafter, 3 ♂♂, ♀, Mar. 26: Shafter, north of, 2 ♀♀, Mar. 26 (USNM). Sutton Co.: Sonora, Texas Agricultural Experimental Station, ♀, Apr. 9 (USNM). Terrell Co.: Between Sanderson and Langtry, 2 ♀♀, Mar. 29 (USNM). Uvalde Co.: Laguna, east of Nueces River, 2 ♂♂, Apr. 1 (USNM). Utah: Kane Co.: Glendale, north of, ♂, ♀, May 12 (USNM).

Prodoxus ochrocarus, new species

FIGURES 70, 95, 121, 140; MAP 11

ADULT (fig.70).—Wing expanse: male, 10–12 mm; female, 11–12.5 mm.

Head: Densely covered with whitish to pale yellow hairs. Antenna with scape, pedicel and basal 1–2 segments of flagellum whitish; remainder of flagellum brownish to dark fuscous. Vesture of labial palpus generally light in color, usually more brownish above than below.

Thorax: Largely fuscous above with an occasional suffusion of pale yellow anteriorly; underside whitish to pale yellow. Primaries fuscous, typically with 5 whitish to pale yellow spots distributed as follows in both sexes: one elongate spot arising from wing base and curving to costa; a pair of markings on outer half of costa, the smaller of the two being the most apical; and another pair, similar in size, arising from the hind margin; fringe and underside of forewing fuscous, with dorsal pattern visible from beneath. Secondaries uniformly fuscous, appearing much lighter in color due to thinner scaling; scales narrow, majority less than one-third width of those in forewings.

Abdomen: Dorsal surface fuscous; ventral surface lighter in color, whitish with a slight suffusion of brown.

MALE GENITALIA (fig. 95).—Apex of tegumen bilobed. Outer margin of cucullus evenly curved, usually with 3–6 short, stout spines.

FEMALE GENITALIA (figs. 121, 140).—Ovipositor with subapical ridge slightly raised, gradually terminating into shaft; serrations relatively coarse, approximately 14–19 in number. Signa stellate, well developed, symmetrically paired; each signum with approximately 13–16 rays.

HOLOTYPE.—Bog Spring Camp Ground, 5100 feet, Madera Canyon, Santa Rita Mts., Santa Cruz Co., Ariz., ♀, July 10–26, 1964, from flowers of *Yucca schottii*, D. R. Davis collector, USNM 67373; in the U.S. National Museum.

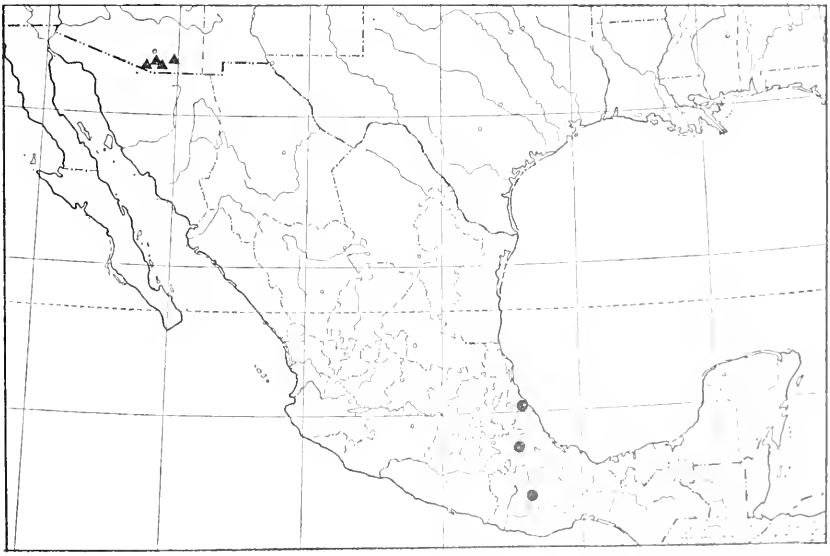
PARATYPES.—ARIZONA: Cochise Co.: Paradise, 2 miles north of, Chiricahua Mts., 5300 feet, 5 ♂♂, 7 ♀♀, July 7, 1964, from flowers of *Yucca schottii*, D. R. Davis collector (USNM). Southwestern Research Station, Chiricahua Mts. 5400 feet, ♂, Aug. 2, 1964, from flowers of *Yucca schottii*, D. R. Davis collector (USNM). Santa Cruz Co.: Same locality as holotype, 25 ♂♂, 5 ♀♀, July 20–26, 1964, from flowers of *Yucca schottii*, D. R. Davis collector (USNM). Patagonia, 1 mile east of, ♀, July 29, 1964, from flowers of *Yucca schottii*, D. R. Davis collector (USNM). Peña Blanca Canyon, 2 miles east of, ♂, July 27–28, 1964, from flowers of *Yucca schottii*, D. R. Davis collector (USNM). Described from a total of 32 ♂♂ and 14 ♀♀.

Recorded host.—*Yucca schottii* Engelmann. Larva probably bores in flower stalk of host.

Distribution (map 11).—At present this species is known from various mountain ranges of southeastern Arizona at an elevation of about 4400 to 5600 feet. Following the distribution of its host, *P. ochrocarus* undoubtedly occurs also in the adjacent area of New Mexico (Hidalgo Co.).

Discussion.—Except for the identity of the host plant, little information is known concerning the biology of *P. ochrocarus*. The species may be found readily during the day or night resting in the flowers of *Yucca schottii*. Frequently the moths leave the flowers to hide or climb about the flower stems. This prevalent habit may suggest that oviposition occurs in the stem and that the larvae are stem borers. If disturbed in the flowers during the day, the moths are very reluctant (in contrast to *P. y-inversus*) to fly away or drop to the leaves; normally they attempt to hide beneath the flowers along the flower stalk. Rarely are the moths attracted to ultraviolet lights, even if the lights are operated within the immediate vicinity of the insects.

The close affinities that probably exist between *P. ochrocarus* and *P. intricatus* are strongly suggested by the systematic relationships of their respective hosts as well as by the striking similarities in general appearance of the two moths. More than likely, *P. intricatus* represents the more recent derivation of the two. *Prodoxus ochrocarus*



Map 11.—Distribution of *Prodoxus ochrocarus* (black triangles) and *Prodoxus intricatus* (black circles).

may be distinguished easily from *intricatus*, the only species of *Prodoxus* that it resembles, by the different maculation of the primaries and the lighter color (thinner scaling) of the secondaries. The conspicuous, pale yellowish head of *ochrocarus*, which somewhat resembles that of *intricatus*, has suggested the specific name for this species.

***Prodoxus intricatus* Riley**

FIGURES 25, 68–69, 96, 122, 141; MAP 11

Prodoxus intricatus Riley, 1893a, p. 50; 1893b, p. 307.
Tegeticula intricata (Riley).—Walsingham, 1914, p. 370.

ADULT (figs. 68–69).—Wing expanse: Male, 13–15 mm; female, 14–16 mm.

Head: Densely clothed with pale reddish-brown hairs. Vesture of labial palpus fuscous in the female, yellowish to reddish brown in the male. Antenna entirely fuscous.

Thorax: Fuscous. Primaries fuscous, spotted with yellow; pattern sexually dimorphic; in the female, typically 7 spots present: a basal, transverse bar, 3 costal spots and 3 spots along the hind margin; in the male, all spots correspondingly enlarged, 2 apical spots usually uniting to form an oblique streak; fringe and underside of forewing uniformly fuscous, with dorsal pattern faintly discernible from beneath. Secondaries uniformly fuscous, approximately of same shade as primaries; scales broad, approximately one-half to two-thirds width of those in forewing.

Abdomen: Uniformly fuscous.

MALE GENITALIA (fig. 96).—Apex of tegumen bilobed. Outer margin of cucullus rather evenly curved, not blunt, usually with 4–6 short spines.

FEMALE GENITALIA (fig. 122).—Apex of ovipositor with dorsal ridge only slightly produced, gradually terminating into shaft; serrations minute, approximately 40–50 teeth. Bursa without signum.

TYPE.—Lectotype (designated by present author), ♂, Jalapa, Mexico, no. 5762, June 5, 1893, USNM 67752; in the U.S. National Museum.

TYPE LOCALITY.—Jalapa, Mexico (lectotype).

RECORDED HOST.—"*Yucca elephantipes* Regel [=*Y. guatemalensis* Baker]" (Riley, 1893a). Larva most probably bores in the flower stalks of this plant.

DISTRIBUTION (map 11).—Presently known only from the states of Veracruz and Oaxaca of southeastern Mexico, where it reportedly is found, very commonly at times (primarily June), in the flowers of its host. This species often occurs in rather humid, tropical environments and probably ranges further south into Guatemala, where its host, *Yucca elephantipes*, is extensively cultivated.

DISCUSSION.—In the original description of this species, Riley mentions that his series consisted of 20 males and 5 females. The original series, now deposited in the collections of the U.S. National Museum, has been re-examined and found instead to consist of a total of 31 specimens (30 males and 1 female). The discrepancy in the total number may be explained by assuming that the count given by Riley was only an estimated number; an error in sexing the specimens easily could have been made, due to the unspread condition of a majority of the moths and if proper magnification had not been used by Riley in his original examination. I have selected one specimen from the syntypic series for the lectotype and have designated the remainder as paralectotypes.

As now believed, the continued survival of a species of *Prodoxus* in a given area probably is dependent upon the sympatric existence of some moth capable of pollinating the yucca. The reason for this being that unless some fruits are allowed to develop, the flower stalk will wither and die before any stalk-boring *Prodoxus* can complete its larval cycle. Consequently, the distribution of *P. intricatus* also indicates a comparable range for a potential pollinator. The author has collected both *Prodoxus intricatus* and *Parategeticula pollenifera* from the same site near Poza Rica, Veracruz; thus establishing at least some overlap in their ranges. It is possible that the association of these two species extends much further south.

MATERIAL EXAMINED.—42 ♂♂ and 8 ♀♀.

MEXICO: OAXACA—Oaxaca, 8 ♂♂, ♀ (USNM). VERACRUZ—Fortin, 4 ♂♂, 4 ♀♀, June 27–July 24 (USNM). Jalapa, ♂, lectotype, June 5, 29 ♂♂, ♀, paralectotypes, June 5 (USNM). Poza Rica, 7 miles SW of, ♀, July 21 (USNM). Specific locality unknown: ♀ (USNM).

Prodoxus sordidus Riley

FIGURES 71, 97, 112, 123, 142, 143; MAP 12

Prodoxus sordidus Riley, 1892a, pp. 153ff.; 1892c, p. 372; 1892e, p. 319.—Dyar, 1902 [1903], p. 723, no. 6571; 1903b, p. 103.—Kearfott, 1903, no. 7109.—Barnes and McDunnough, 1917, p. 197, no. 8467.—McDunnough, 1939, no. 9830.—Busck, 1947, p. 184.

ADULT (fig. 71).—Wing expanse: male, 8–11 mm; female, 12–14 mm.

Head: White. Labial palpus white to cream colored.

Thorax: Whitish. Upper surface of primaries, including fringe, white to cream in color; ventral surface pale fuscous. Upper and lower surfaces of secondaries mostly white except for fuscous shading along costal margin; fully scaled, scales broad, nearly equal in width to scales of forewing; fringe white.

Abdomen: Pale brown above, white below (fig. 112).

Male genitalia (fig. 97).—Apex of tegumen bilobed. Outer margin of cucullus slightly emarginate, otherwise curved outward and not blunt; usually with 3–6 short marginal spines present.

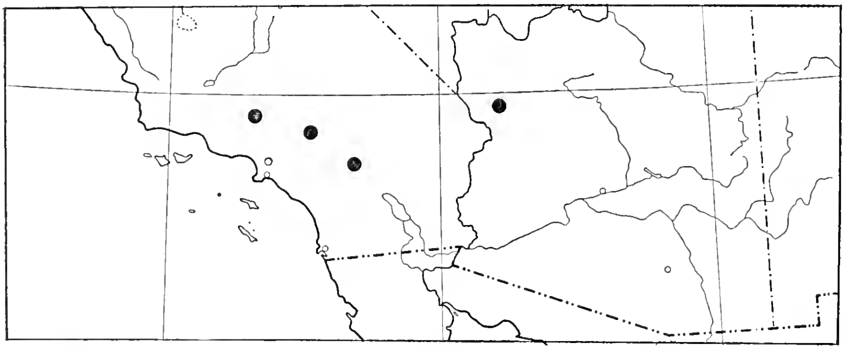
Female genitalia (figs. 123, 142–143).—Apex of ovipositor with dorsal ridge slightly arched, gradually terminating into shaft; ridge with approximately 23–32 teeth. Signum stellate, well developed; number of rays usually 12–16.

Type.—Lectotype (designated by present author), ♀, 2/2, March, Los Angeles Co., Calif., USNM 427; in the U.S. National Museum.

Type locality.—Los Angeles Co., Calif. (lectotype).

Recorded host.—"*Yucca brevifolia* Engelmann" (Riley, 1892a). Larva bores in fleshy part of fruit.

Distribution (map 12).—Presently known only from western Arizona and southern California; however, the moth probably occurs in southern Nevada and the extreme southwestern part of Utah, in association with its host.



Map 12.—Distribution of *Prodoxus sordidus* (see map 3 for distribution of host).

Material examined.—47 ♂♂ and 32 ♀♀.

UNITED STATES: Arizona: Mohave Co.: Yucca, 14 ♂♂, 18 ♀♀, Mar. 14 (USNM). California: Specific locality unknown, 6 ♂♂, Jan. 27 (USNM); 2 ♂♂, 2 ♀♀, Jan. 27–Feb. 20 (LACM). Los Angeles Co.: ♀, lectotype, March, 5 ♂♂, paralectotypes, March–May (USNM). Antelope Valley, 16 ♂♂, 5 ♀♀, Apr. 3 (LACM). San Bernardino Co.: ♀, paralectotype, Apr. 14 (USNM). Adelanto, ♂, 2 ♀♀, Apr. 7 (USNM). Morongo Valley, 3 ♂♂, 3 ♀♀, Feb. 15–16 (LACM).

Prodoxus marginatus Riley

Figures 72–73, 98, 124, 144; Map 13

Prodoxus marginatus Riley, 1881, pp. 635, 639, fig. 12.—Riley and Howard, 1890, p. 350.—Riley, 1891a, no. 5185; 1892a, pp. 147ff., pl. 43, fig. 2; 1892b, pp. 98, 100, fig. 13; 1892c, pp. 373, 375, fig. 72.—Coquillett, 1893, pp. 311, 312.—Dyar, 1902 [1903], p. 723, no. 6566; 1903b, p. 103.—Kearfott, 1903, no. 7104.—Holland, 1905, p. 439, fig. 257.—Barnes and McDunnough, 1917, p. 197, no. 8462.—McDunnough, 1939, no. 9825.—Busck, 1947, p. 183.

Adult (figs. 72–73).—Wing expanse: male, 8–10 mm; female, 10–12 mm.

Head: White. Labial palpus entirely white.

Thorax: White. Dorsal surface of primaries white with dark fuscous scaling at apex; in females this forms a broad margin along termen; in males, dark margin often reduced, sometimes nearly absent; fringe entirely white above and below except for slight apical suffusion of fuscous in female. Secondaries mostly fuscous in female, especially in outer half; hindwing of male lighter in color, mostly white; rather thinly scaled in both sexes, scales narrow, less than half the width of those in forewing; fringe white except for dark suffusion at apex, especially in female.

Abdomen: Usually fuscous above, except for caudal hairs of white; entirely white below.

Male genitalia (fig. 98).—Apex of tegumen simple, not clefted. Valves with outer margin of cucullus relatively blunt and without spines.

Female genitalia (figs. 124, 144).—Apex of ovipositor with dorsal ridge gradually terminating into shaft; ridge usually with 50 minute teeth or more. Signum stellate, well developed, with approximately 10–12 rays.

Type.—Lectotype (designated by present author), ♂, Caliente, Kern Co., Calif., collected by H. K. Morrison, USNM 419; in the U.S. National Museum.

Type locality.—Caliente, Kern Co., Calif. (lectotype).

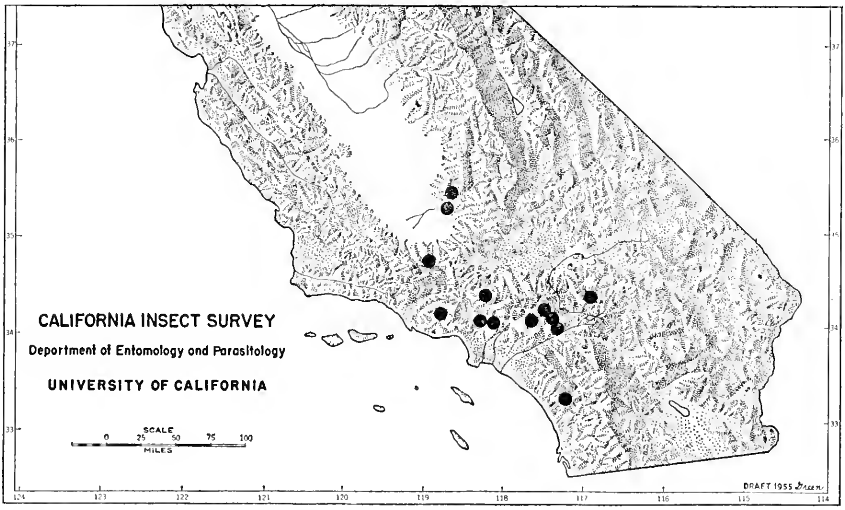
Recorded host.—"*Yucca whipplei* Torrey" (Riley, 1892a). Larva bores in petioles and basal portion of fruit.

Parasite.—"Braconidae: *Heterospilus koebelei* (Ashmead) 1893," (Riley and Howard, 1890).

Distribution (map 13).—Presently reported only from southern California.

Material examined.—56 ♂♂ and 70 ♀♀.

UNITED STATES: California: Kern Co.: Caliente, ♂, lectotype, 2 ♂♂, 2 ♀♀ paralectotypes (USNM). Havilah, 7 ♂♂, 15 ♀♀, June 1–7 (USNM). Lebec, 3 ♂♂, ♀, June 20 (LACM). Los Angeles Co.: ♀, April, 2 ♀♀, July (CU); 17 ♂♂, 16 ♀♀, May–July (USNM). Acton, Mint Canyon, ♀, May 31 (LACM). Big Tujunga Wash, 19 ♂♂, 8 ♀♀, May 7–14 (LACM). Sierra Madre, ♂, May 30 (USNM). San Bernardino Co.: Cajon Pass, ♀, June 12 (LACM). Camp Baldy, San Bernardino Mts., ♀, July 16–23 (LACM); ♂, 14 ♀♀, June 1–July 23 (USNM). Lucerne Valley, 2 ♀♀, May 20–26 (LACM). San Bernardino, 3 ♀♀, May 1–12 (LACM); 2 ♂♂, ♀, May (USNM). Verdemont, ♀, May 9 (USNM). San Diego Co.: Fallbrook, 3 ♂♂, Apr. 3 (LACM). Ventura Co.: Mortimer Park, Simi Hills, ♀, June 4 (LACM).



Map 13.—Distribution of *Prodoxus marginatus* (see maps 4 and 5 for distribution of host).

Prodoxus pulverulentus Riley

Figures 74–75, 99, 125, 145; Map 14

Prodoxus pulverulentus Riley, 1892a, p. 150; 1892b, p. 100; 1892c, p. 375; 1892e, p. 315;—Coquillett, 1893, p. 311.—Dyar, 1902 [1903], no. 6570; 1903b, p. 103.—Kearfott, 1903, no. 7108.—Barnes and McDunnough, 1917, no. 8466.—McDunnough, 1939, no. 9829.—Busck, 1947, p. 184.

Adult (figs. 74–75).—Wing expanse: male, 8–10 mm; female, 8–11 mm.

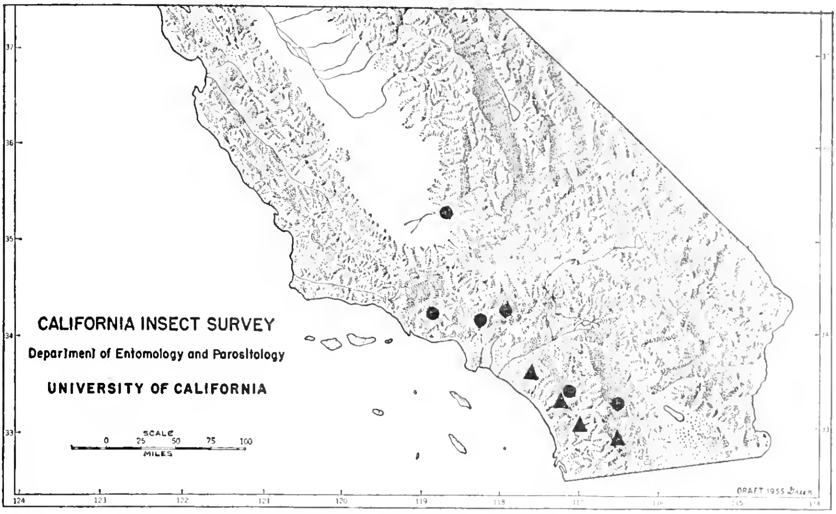
Head: White. Labial palpus entirely white.

Thorax: White. Dorsal surface of primaries white with scattering of fuscous scales, concentrated principally over apical half of forewing; fringe mostly white with scattered mixture of fuscous, especially at apex; ventral surface densely covered with fuscous scales. Secondaries white with fuscous shading along costa to apex, sparsely scaled, scales very narrow, usually less than one-third the width of those in forewing; fringe entirely white except for dark apex.

Abdomen: Pale fuscous above, mostly white below except for posterior patch of fuscous scales.

Male genitalia (fig. 99).—Apex of tegumen simple, not clefted. Outer margin of cucullus bluntly rounded, not spined.

Female genitalia (figs. 125, 145).—Apex of ovipositor with dorsal ridge gradually terminating into shaft; ridge minutely serrulate, with approximately 45–55 teeth. Signum stellate, well developed, with usually 8–12 rays.



Map 14.—Distribution of *Prodoxus pulverulentus* (black triangles) and *Prodoxus cinereus* (black circles) (see maps 4 and 5 for distribution of host).

Type.—Lectotype (designated by present author), ♀, San Diego Co., Calif., May 20, 1886, seed pods of *Y. whipplei*, USNM 426; in the U.S. National Museum.

Type locality.—Santiago, San Diego Co., Calif. (lectotype).

Recorded host.—"*Yucca whipplei* Torrey" (Riley, 1892a). Larva bores in fruit of host.

Distribution.—Presently known only from southern California (map 14).

Discussion.—From casual examination, *P. marginatus* and *P. pulverulentus* appear quite distinct. Comparisons of genitalic structures and life histories, however, indicate their affinities to be very close. Although supporting data is somewhat scant, it is possible that the distributions of the two species are not sympatric, with *P. marginatus* occurring more to the north. If this is so, then it may be further true that the two moths are restricted to the two primary growth forms of *Yucca whipplei* as discussed under *T. maculata extranea*. Largely because the wing patterns of *P. marginatus* and *pulverulentus* appear amply distinct, with no evidence of hybridization nor intermediacy, I have treated them as separate species.

Material examined.—8 ♂♂ and 26 ♀♀.

UNITED STATES: California: Specific locality unknown, ♀, paralectotype; So. Calif., 2 ♀♀, paralectotypes (USNM). Orange Co.: El Toro, ♀, May 17 (LACM). Mojeska [east of Santa Ana], 4 ♂♂, 10 ♀♀, May 23 (LACM). San Diego Co.: Fallbrook, ♂, ♀, Apr. 3 (LACM). Pine Valley, east of, 5 ♀♀, Apr. 24 (USNM). San Pasqual, 2 ♂♂, 5♀♀, Apr. 25 (USNM). Santiago, ♀, lectotype, May 20, ♀, paralectotype, May 20 (USNM).

***Prodoxus cinereus* Riley**

FIGURES 22, 76, 100, 126, 146; MAP 14

Prodoxus cinereus Riley, 1881, pp. 636, 639; 1891a, no. 5184; 1892a, pp. 148ff., pl. 43, fig. 4; 1892b, p. 100; 1892c, p. 375; 1893a, pp. 48, 51, 52; 1893b, pp. 306, 309, fig. 38.—Coquillett, 1893, p. 311.—Dyar, 1902 [1903], no. 6572; 1903b, p. 103.—Kearfott, 1903, no. 7110.—Holland, 1905, p. 441, fig. 261.—Barnes and McDunnough, 1917, no. 8468.—McDunnough, 1939, no. 9831.—Busck, 1947, p. 184.

ADULT (fig. 76).—Wing expanse: male, 9–12 mm; female, 11–15 mm.

Head: Vertex with mixture of white and light brown scales; frons white; labial palpus covered with white scales and brown hairs.

Thorax: Pale brown. Dorsal surface of primaries unicolorous, pale to medium brown, slightly darker in color underneath; fringe brown. Secondaries usually darker than forewings, unicolorous above and below, fully scaled; scales broad, nearly the width of those in forewings.

Abdomen: Medium brown above, pale brown to nearly white underneath.

MALE GENITALIA (fig. 100).—Apex of tegumen simple; lateral margin with a pair of blunt lobes. Outer margin of cucullus evenly curved, without marginal spines.

FEMALE GENITALIA (figs. 126, 146).—Apex of ovipositor with dorsal ridge gradually terminating into ovipositor shaft, not arched; ridge with 19–23 teeth, serrations similar to those of *P. coloradensis*. Signa greatly reduced in size, sometimes barely discernible, usually ovoid in outline.

TYPE.—Lectotype (designated by present author), ♂, Caliente, Kern Co., Calif., collected by H. K. Morrison, USNM 421, genitalia on slide DRD 868; in the U.S. National Museum.

TYPE LOCALITY.—Caliente, Kern Co., Calif. (lectotype).

RECORDED HOST.—"*Yucca whipplei* Torrey" (Riley, 1892a). Larva bores in flower stalk of host.

DISTRIBUTION.—Presently known only from southern California (map 14).

MATERIAL EXAMINED.—80 ♂♂ and 21 ♀♀.

UNITED STATES: CALIFORNIA.—Kern Co.: Caliente, ♂, lectotype; 3 ♂♂, paralectotypes (USNM). Los Angeles Co.: 23 ♂♂, 17 ♀♀, May–June (USNM); 5 ♂♂, 2 ♀♀, May (LACM). Big Tujunga Wash, 42 ♂♂, ♀, May 7–14 (LACM). San Gabrial Mts., 2 ♂♂, June 9 (LACM). Riverside Co.: Mt. Santa Rosa [near Temecula], ♂, May 30 (LACM). Ventura Co.: Hidden Valley, Sherwood Lake, 3 ♂♂, ♀, May 22 (LACM).

***Prodoxus aenescens* Riley**

FIGURES 77, 101, 127, 147; MAP 15

Prodoxus aenescens Riley, 1881, pp. 636, 639.—Riley and Howard, 1890, p. 350.—Riley 1891a, p. 97, no. 5183; 1892a, p. 149; 1892b, p. 100; 1892c, p. 375;

1893a, p. 49; 1893b, p. 307.—Coquillett, 1893, pp. 311, 312.—Dyar, 1902 [1903], no. 6573; 1903b, p. 103.—Kearfott, 1903, no. 7111.—Barnes and McDunnough, 1917, p. 197, no. 8469.—McDunnough, 1939, no. 9832.—Busck, 1947, p. 184.

Adult (fig. 77).—Wing expanse: male 9–11 mm; female, 9–15 mm. Head: Whitish with a few scattered brown hairs; labial palpus white, intermixed with dark brown hairs.

Thorax: Ventral half whitish, dorsum fuscous. Upper and lower surface of primaries unicolorus, brownish to fuscous, with a somewhat metallic bronze luster. Secondaries very sparsely scaled, semitransparent, scales hairlike; fringe of both wings brownish.

Abdomen: Completely fuscous in male; fuscous above in female, ventral half either fuscous or whitish.

Male genitalia (fig. 101).—Apex of tegumen simple, not clefted. Valves relatively slender, somewhat constricted near middle, with a prominent lobe arising from sacculus; outer margin of cucullus rounded, without spines.

Female genitalia (figs. 127, 147).—Apex of ovipositor with dorsal ridge prominently arched, gradually terminating into ovipositor shaft; ridge with approximately 17–21 teeth. Signum reduced to a minute bar-shaped sclerotization which may or may not be forked at one end.

Type.—Lectotype (designated by present author), ♀, Caliente, Kern Co., Calif., collected by H. K. Morrison, USNM 423; in the U.S. National Museum.

Type locality.—Caliente, Kern Co., Calif. (lectotype).

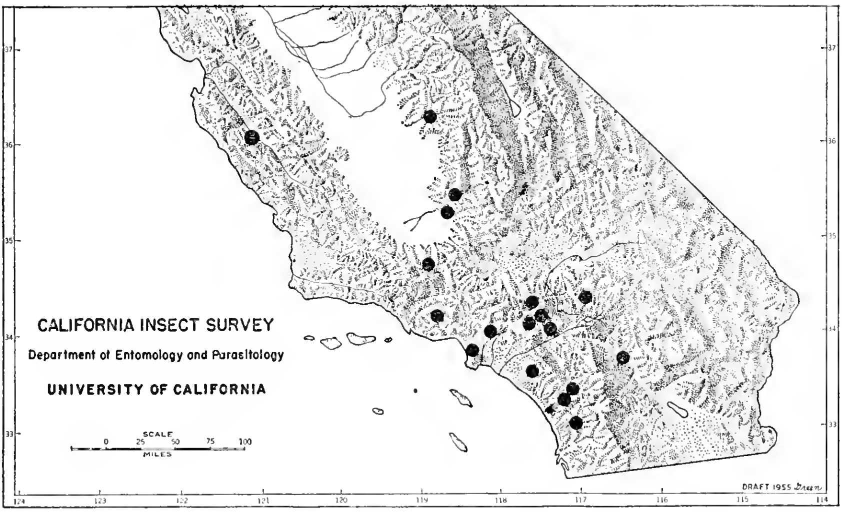
Recorded host.—"*Yucca whipplei* Torrey" (Riley, 1892a). Larva bores in flower stalk of host.

Parasite.—"Braconidae: *Heterospilus koebelei* (Ashmead)" (Riley and Howard, 1890).

Distribution (map 15).—Presently known to occur only in southern California.

Material examined.—142 ♂♂ and 149 ♀♀.

UNITED STATES: California: Kern Co.: Caliente, ♂, paralectotype (LACM); ♀, lectotype, 2 ♂♂, 3 ♀♀, paralectotypes (USNM). Havilah, 10 ♂♂, 16 ♀♀, June 1–15 (USNM). Lebec, 35 ♂♂, 9 ♀♀, June 20 (LACM). Los Angeles Co.: 4 ♀♀, July (LACM); 6 ♂♂, 6 ♀♀ (USNM); 8 ♂♂, 7 ♀♀, May–July (USNM). Los Angeles, ♀, June 22 (USNM). Sierra Madre, 3 ♂♂, ♀, May 30 (USNM). Monterey Co.: Arroyo Seco, 2 ♂♂, ♀, May 17 (USNM). Orange Co.: Mojeska [east of Santa Ana], ♂, 3 ♀♀, May 23 (LACM). Riverside Co.: Mt. Santa Rosa [near Temecula], ♂, May 30 (LACM). Palm Springs, ♂, 9 ♀♀, March (USNM). San Bernardino Co.: Cajon Pass, 2 ♂♂, 2 ♀♀, June 12 (LACM). Camp Baldy, San Bernardino Mts., ♀, July 13 (AFB); 4 ♂♂, 13 ♀♀, June 24–July 23 (USNM). Lucerne Valley, 4 ♂♂, 13 ♀♀, May 7–26 (LACM); ♂, ♀, May 7 (USNM). Phelan, 3 miles west of, ♂, 3 ♀♀, May 23 (LACM). San Bernardino, 6 ♀♀, May 28 (LACM); 35 ♂♂, 15 ♀♀, May 1–12 (USNM). San Diego Co.: Fallbrook, ♂, ♀, Apr. 3 (LACM). San



Map 15.—Distribution of *Prodoxus aenescens* (see maps 4 and 5 for distribution of host).

Pasqual, 5 ♀♀, Apr. 25 (USNM). Tulare Co.: Three Rivers, 20 ♂♂, 23 ♀♀, May 7–21 (USNM). Ventura Co.: Mortimer Park, Simi Hills, 3 ♂♂, 5 ♀♀, June 17 (LACM). Sherwood Lake, Hidden Valley, ♂, May 22 (LACM).

Mesepiola, new genus

Type species.—*Mesepiola specca*, new species.

Adult.—Relatively small, slender bodied moths; similar to *Prodoxus* in general habitus.

Head (fig. 43): Eyes large, vertical diameter approximately 1.5 times the width of frons. Tongue prominent, similar to that of *Prodoxus* in size, greatly exceeding length of maxillary palpi. Mandibles minute, rounded. Maxillary palpus 5-segmented, segmentation similar to that of *Prodoxus;* fourth segment doubling third in length; maxillary tentacle absent in both sexes. Labial palpus 3-segmented, apical segment one-half the length of second; sensory invagination present at apex of distal segment.

Thorax: Wings (fig. 48) similar to *Prodoxus*, relatively broad, apices somewhat acute; all veins normally separate except 7 and 8 of forewings and 5 and 6 of hindwings which are usually connate; frenulum simple in male, prominent. Epiphysis present (fig. 56).

Abdomen: Seventh tergite of female with a prominent, uncinate appendage (fig. 113).

Male genitalia.—Similar in general structure to *Agavenema*. Apex of tegumen bilobed; a pair of tiny, sclerotized spots near middle of dorsal membranous area. Vinculum somewhat V-shaped; saccus broad, indistinctly set off from vinculum. Valves with sacculus produced into a prominent, setigerous lobe; beyond sacculus, valve constricted, with a relatively broad lobe, bearing a dense row of stout spines, arising from ventral margin. Aedeagus relatively stout, not greatly elongated.

FEMALE GENITALIA.—Apex of ovipositor spear-shaped; dorsal ridge nearly obsolete, with serrations few in number. Apophyses long and slender. Signum paired, reduced in size. Ductus bursa of moderate length, approximately equalling the free portions of the anterior apophyses in length.

Mesepiola specca, new species

FIGURES 43, 48, 56, 78, 102, 113, 128, 148; MAP 16.

ADULT (fig. 78).—Wing expanse: male, 8–10 mm; female, 8–12 mm.

Head: White; lateral (outer) surface of labial palpus usually pale brown, inner surface and most of apical segment white; second segment with several brownish, hairlike scales concentrated toward apex.

Thorax: White. Dorsal surface of primaries white, speckled with fuscous; fringe entirely white; undersurface uniformly pale fuscous. Secondaries darker, pale fuscous, more thinly scaled than primaries; scales relatively broad, approximately one-half the width of those in forewing.

Abdomen: Pale brown above, white below; apex of seventh tergite in female with a broad, uncinate process (fig. 113); abdomen of male unmodified.

MALE GENITALIA (fig. 102).—As described for genus. Saccus only moderately lengthened; combined length of saccus and vinculum slightly exceeding that of valve.

FEMALE GENITALIA (figs. 128, 148).—Serrations of dorsal ridge very minute, reduced in number to less than eight. Signum minute, somewhat stellate, with a few, extremely short rays of irregular lengths.

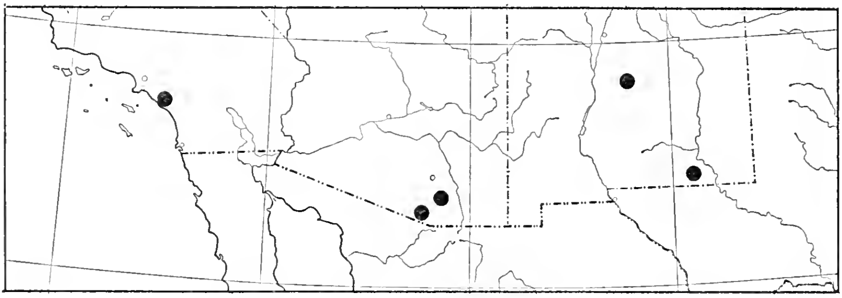
HOLOTYPE.—Bog Spring Camp Ground, Madera Canyon, Santa Rita Mts., 5100 feet, Santa Cruz Co., Ariz., female, July 10–26, 1964, D.R. Davis collector, USNM 67753; in the U.S. National Museum.

PARATYPES.—ARIZONA: Santa Cruz Co.: Same locality as holotype, 2 ♂♂, 16 ♀♀, July 10–26, 1964, D.R. Davis collector (USNM). Madera Canyon, Santa Rita Mts., 4880 feet, 6 ♂♂, 63 ♀♀, July 2–Aug. 23, 1959, R.W. Hodges collector (CU, RWH); ♂, 2 ♀♀, July 9–Aug. 10, 1959, R.W. Hodges collector (USNM). Peña Blanca Canyon, ♂, ♀, Aug. 26, 1959, R.W. Hodges collector (CU, RWH); ♀, July 27–28, 1964, D.R. Davis collector (USNM). CALIFORNIA: Orange Co.: El Toro, ♀, May 17, 1938, collected by C. Dammers on flowers of *Nolina parryi* (USNM). NEW MEXICO: Eddy Co.: Carlsbad National Park, ♀, June 24, 1939, A. Braun collector (AFB).

Carlsbad, 50 miles south of, along highway 180, near Guadalupe Canyon, 2 ♂♂, ♀, June 26, 1964, J.R. Eyer collector (JRE); 5 ♂♂, June 26, 1964, J.R. Eyer collector (USNM). Socorro Co.: Gran Quivira National Monument, 6600 feet, ♀, July 1–3, 1964, D.R. Davis collector (USNM). Described from a total of 17 males and 88 females.

RECORDED HOST.—None. Larva possibly may be a borer in *Nolina* or *Agave.*

DISTRIBUTION (map 16).—This species ranges rather widely through the southwestern United States from New Mexico west to southern California. More than likely, it also occurs in certain areas of northern Mexico.



MAP 16.—Distribution of *Mesepiola specca.*

DISCUSSION.—An interesting structure exists in the females of *M. specca* that is apparently unique for the family. This is a peculiar, strongly sclerotized, hooklike process projecting from the apex of the seventh abdominal tergite (fig. 113). It is unlikely that such a process has developed without serving some function; possibly, some use may be made of it during oviposition. For example one obvious advantage for which it might be used would be to engage some part of the host plant so as to anchor the moth better during insertion of the ovipositor.

The life history of *Mesepiola specca* is not known, although there is reason to suspect that the larva may be a borer in the flower stalks of *Nolina.* This suspicion is based primarily upon a single female specimen collected by Charles Dammers near El Toro, Calif., in the flowers of *Nolina parryi.* Such records of the adults can be misleading at times, although often they are of some significance for the Prodoxinae. During the summer of 1964, the author searched for prodoxine larvae in the flower stalks of *Nolina microcarpa* S. Watson over parts of southeastern Arizona, as well as in the stalks of a related plant, *Dasylirion wheeleri* S. Watson. No evidence of larvae were found, although one female moth of *M. specca* was collected during the day on the flowers of *Dasylirion wheeleri.*

Considering the relationships of the plants, one may suspect the genus *Manfreda* as a possible host. On the basis of karyotypic information (see p. 24), as well as other characters, the Nolineae do not appear closely related to either *Yucca* or *Agave*. On the other hand, *Manfreda* is considered very close to the *Agave* and formerly was placed in that genus. It is also interesting to note here as a possible parallel that one of the five genera of Megathymidae recognized by Freeman is restricted to *Manfreda*. Present distribution records of *M. specca*, however, do not indicate *Manfreda* as a probable host. *Manfreda* occurs widely over the southeastern United States and Mexico, but its range is rather limited in the southwestern United States. No specimens of *M. specca* have been collected east of New Mexico, although more intensive efforts may reveal the moth as a part of our southeastern fauna.

Mesepiola specca typically occurs in association with certain members of the Agavaceae, particularly the genus *Agave*. It is possible that *Agave*, or certain elements of it, is the food plant for this moth. However, in nearly all observable features, *M. specca* represents a form intermediate between *Prodoxus* and *Agavenema*, thereby intimating that its host may be some plant intermediate between *Yucca* and *Agave*. Such a prospective plant group, of course, may not exist. In regard to most characters of the head, particularly the mouthparts, *M. specca* closely resembles the genus *Prodoxus;* however, it is somewhat intermediate in respect to the relative development of eyes. Likewise, the male genitalia of this species is strikingly similar in structure to that of *Agavenema;* but the female genitalia is decidedly more close to *Prodoxus*.

The intermediacy of this insect has suggested the generic name *Mesepiola*, which literally means "intermediate moth"; the specific epithet, *specca*, is derived from the Anglo-Saxon word for speckled.

Agavenema, new genus

TYPE SPECIES.—*Prodoxus barberellus* Busck, 1915.

ADULT.—Body slender, medium to small size, wing expanse 11–25 mm.

Head (fig. 44): Eyes large, vertical diameter nearly doubling width of frons. Tongue very reduced, less than length of maxillary palpi. Mandibles minute, apex evenly rounded. Maxillary palpus 5-segmented; third and fourth segments of equal length; maxillary tentacle absent in both sexes. Labial palpus 3-segmented; apical segment enlarged, equalling the second in length, with a well-developed, apical, sensory pit extending inwards about one half the length of segment.

Thorax: Wings (fig. 49) relatively narrow, apices acute. Forewing with all veins separate, hind margin slighly excavate between 1b and 2. Hindwing with 5 and 6 stalked about half their length; frenulum simple in male, prominent. Epiphysis present (fig. 57).

Abdomen: Elongate, slender; seventh tergite of female simple (fig. 114).

Male genitalia.—Tegumen with apex bilobed; a pair of tiny, sclerotized spots near middle of dorsal membranous area. Vinculum Y-shaped; saccus well developed, elongate. Valves with sacculus produced into a large, rounded lobe; beyond sacculus, valves greatly constricted, with a prominent, digitate lobe, bearing a dense crown of stout spines, arising from ventral margin. Aedeagus elongate, slender.

Female genitalia.—Apex of ovipositor spear-shaped, with a serrated, dorsal ridge. Apophyses very long and slender. Signa absent. Ductus bursa very short, less than half the length of the apophyses; spermathecal evagination present at juncture with oviduct.

Larva (fig. 23).—Head slightly retracted into prothorax. Body white in early instars, usually becoming pale green at maturity; apodal. Stem borers in *Agave*.

Pupa (fig. 27).—Head with a frontal beak similar to *Prodoxus*. Abdominal tergites each with a single row of minute spines. Pupation occurs in a papery cocoon within host plant.

Life History

Relatively little is known about the biology of this group of moths. In general, their life history appears to bear close resemblance to that of most stem boring members of the genus *Prodoxus*.

The egg, as far as known, is always inserted into the stem, and the entire larval stage is passed as a borer in the soft pith of the agave flower stalk. Prior to pupation, the larva constructs an exit tunnel toward the outer surface of the stem, leaving a thin partition intact to block the future exit. The overwintering stage has not been noted, but it is probably the last larval instar.

Pupation takes place inside a somewhat papery cocoon, constructed in the burrow usually just under the surface of the stem (fig. 27). When ready to emerge, the pupa forces its way through the thin partition blocking the exit of the burrow until its body has protruded about two-thirds its length from the stem; after this position has been attained, the adult emerges. Recently infested stalks can sometimes be observed with numerous pupal remains protruding in this fashion.

The distribution of this genus is undoubtedly much more extensive than is indicated by present records. The author has collected numerous larvae of a species of *Agavenema* from the flower stalks of a large agave, 7 miles east of Galeana, Nuevo Leon, Mexico. As of this writing, no adults have emerged; consequently, the identity of the moth remains unknown.

Key to the Species of *Agavenema*

1a. Forewings heavily streaked with fuscous (fig. 79); male genitalia relatively short (fig. 103), combined length of vinculum and saccus approximately twice that of valve; dorsal ridge of ovipositor coarsely serrated (fig. 149), number of teeth less than 25 . . . . **A. barberella**

1b. Forewings paler, lightly streaked with fuscous (fig. 80); male genitalia elongate (fig. 104), combined length of vinculum and saccus 2.5x or more that of valve; dorsal ridge of ovipositor, finely serrated (fig. 150), number of teeth more than 30 . . . . **A. pallida**

***Agavenema barberella* (Busck), new combination**

Figures 23, 27, 44, 49, 57, 79, 103, 114, 129, 149; Map 17

Prodoxus barberella [sic] Busck, 1915, p. 93.

Prodoxus barberellus Busck.—Barnes and McDunnough, 1917, p. 197, no. 8470.—McDunnough, 1939, p. 109, no. 9833.

Adult (fig. 79).—Wing expanse: male, 11–19 mm; female, 12–21 mm.

Head (fig. 44): White. Labial palpus primarily brown above, white below, with a few brown hairs normally arising from apex of second segment.

Thorax: White. Dorsal surface of primaries white with scattered, longitudinal streaks and spots of brownish fuscous; more heavily marked than in *A. pallida;* underside lightly shaded with fuscous, pattern of upper surface visible from beneath; fringe mostly white except for darkening near tornus. Secondaries pale fuscous in color above and below, thinly scaled, majority of scales hairlike, those along margin and at apex of wing much broader; fringe pale fuscous.

Abdomen (fig. 114): Pale fuscous above and below, with admixture of whitish scales underneath, especially posteriorly.

Male genitalia (fig. 103).—Apex of tegumen slightly clefted, less so than in *A. pallida.* Saccus relatively short as compared to following species, combined length of vinculum and saccus approximately twice that of valve.

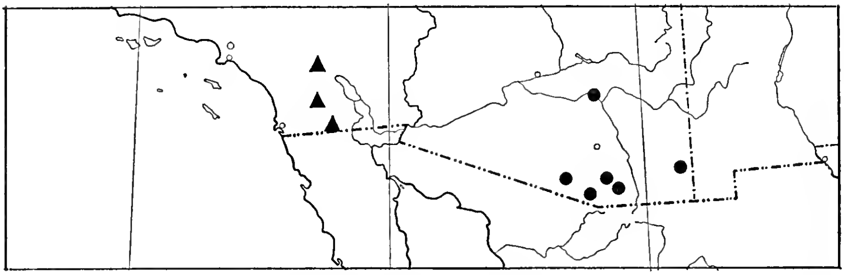
Female genitalia (figs. 129, 149).—Apex of ovipositor with dorsal ridge rather coarsely serrated; number of teeth usually 18–23. Apophyses not as elongate as those of *A. pallida.*

Type.—Holotype, ♀, USNM 19290; in the U.S. National Museum.

Type locality.—Ray, Ariz., 4400 ft. (holotype).

Recorded host.—"*Agave palmeri* Engelmann" (Busck, 1915). Larva bores in flower stalk of host.

Distribution (map 17).—Presently reported only from southern Arizona; however, the host plant is known to occur also in New Mexico and Sonora (Mexico).



MAP 17.—Distribution of *Agavenema barberella* (black circles) and *Agavenema pallida* (black triangles).

DISCUSSION.—As discussed under the following species, the forewings of 37 female specimens of *A. barberella* were measured and compared to those of *A. pallida.* The great majority (29) of these 37 specimens were reared from the flower stalks of *Agave palmeri,* collected near Ray, Arizona; the remaining 8 females were collected at lights in Madera Canyon, Santa Cruz Co., Ariz. The latter moths ranged somewhat larger in size (6.8–9.4 mm) than did the reared specimens (5.5–7.8 mm), but were very similar in regard to all other characters examined. The mean difference in wing length between the two populations was found to be significant (F=5.47*) although not highly so.

Because this degree of difference may be due, in part, to an inadequate sample, especially from Madera Canyon, and since these two populations are essentially identical in all other respects (including valve-genitalia ratio), only one species has been recognized in the material examined.

MATERIAL EXAMINED.—91 ♂♂ and 47 ♀♀.

UNITED STATES: ARIZONA: Cochise Co.: Portal, 4 miles west of, Chiricahua Mts., 5300 ft., 5 ♂♂, Aug. 3–6 (USNM). Southwestern Research Station, Chiricahua Mts., ♀, May 9 (UA). Pima Co.: Baboquivari Mts., ♀, Sept. 1–15 (USNM). Pinal Co.: Ray, ♀, holotype, Mar. 2; 43 ♂♂, 34 ♀♀, paratypes, Mar. 3–17 (USNM). Santa Cruz Co.: Madera Canyon, Santa Rita Mts., 4880 ft., 42 ♂♂, 8 ♀♀, July 2–Aug. 22 (CU, RWH). Bog Spring Camp Ground, 5100 ft., Madera Canyon, Santa Rita Mts., ♀, July 22 (USNM). Patagonia, 1 mile south of, ♂, July 29 (USNM). Peña Blanca Canyon, ♀, Aug. 8 (CU).

Agavenema pallida, new species

FIGURES 80, 104, 130, 150; MAP 17

ADULT (fig. 80).—Wing expanse: male, 17–22 mm; female, 21–25 mm.

Head: White. Labial palpus largely brown above and white below with a few brown hairs arising from apex of second segment.

Thorax: White. Dorsal surface of primaries white with scattered, longitudinal streaks and spots of brownish fuscous; less heavily marked than in *A. barberella;* some specimens with forewings almost entirely white; fringe usually white, sometimes with pale shading near tornus; ventral surface lightly shaded with fuscous. Secondaries pale fuscous above and below, thinly scaled; majority of scales hairlike, those along margin and near apex broader.

Abdomen: Pale brown above except for posterior tuft of white hairs, whitish below with admixture of brownish scales.

MALE GENITALIA (fig. 104).—Apex of tegumen bilobed, more prominently so than in *A. barberella.* Saccus very elongate, longest in family; combined length of vinculum and saccus approximately 2.5 times or more that of valve.

FEMALE GENITALIA (figs. 130, 150).—Apex of ovipositor with dorsal ridge gradually terminating into ovipositor shaft; serrations finer and more numerous (32–37) than in *A. barberella.* Apophyses the most slender and elongate of subfamily.

HOLOTYPE.—Mason Valley [La Puerta Valley, near Julian], San Diego Co., Calif., ♀, emerged Apr. 26, 1939, reared from *Agave deserti,* L. M. Martin (LACM).

PARATYPES.—CALIFORNIA: Riverside Co.: Pinyon Flat, 16 miles SW Palm Desert, 20 ♂♂, 19 ♀♀, emerged Apr. 9–May 20, 1963, JAP no. 63 D 10, reared from *Agave deserti,* J. Powell collector (UCB); 2 ♂♂, 2 ♀♀, emerged Apr. 7, 1963, JAP no. 63 D 10, reared from *Agave deserti,* J. Powell collector (USNM). San Diego Co.: Same locality as holotype, 14 ♂♂, 28 ♀♀, emerged Apr. 24–May 5, 1939, reared from *Agave deserti,* L. M. Martin collector (LACM); 2 ♂♂, 2 ♀♀, emerged Apr. 26–May 1, 1939, reared from *Agave deserti,* L. M. Martin collector (USNM). Jacumba, 5 miles east of, 44 ♂♂, 23 ♀♀, emerged March–May 10, 1963, JAP no. 63 C 31, reared from *Agave deserti,* Chemsak and Powell collectors (UCB); ♂, ♀, emerged Apr. 15–20, 1963, JAP no. 63 C 31, reared from *Agave deserti,* Chemsak and Powell collectors (USNM). Described from a total of 83 ♂♂ and 76 ♀♀.

RECORDED HOST.—*Agave deserti* Engelmann (from specimen labels). Larva bores in flower stalk of host.

DISTRIBUTION (map 17).—At present, this moth is known only from southern California; the host plant, however, also ranges into western Arizona and Baja California.

DISCUSSION.—This species closely resembles the preceding one in certain respects, but several differences exist which are believed to be of specific importance. Most easily, *Agavenema pallida* may be separated from *A. barberella* by the former's larger size and paler color. Furthermore, the male and female genitalia of *A. pallida* are proportionately more elongate than those of *barberella.*

As an indication of the size differences between *Agavenema pallida* and *barberella,* the lengths of their forewings have been summarized below (for explanation of symbols, see p. 10). In addition, the populations of *A. pallida* were tested for an F value against the combined samples of the two recognized species, and the differences were found to be highly significant (**). The females of *A. pallida* originated from three localities in southern California (see paratype data), and all were reared from *Agave deserti.* The 37 specimens of *Agavenema barberella* represent two localities in southern Arizona; 29 females were reared from *Agave palmeri,* whereas the host of the remaining 8 moths is not known.

	N	*Length* x (*mm*)	*Range* (*mm*)	*s*	*F value*
A. barberella	37	7.06	5.5– 9.4	0.859	
A. pallida	46	10.26	8.9–11.4	0.706	7.028**

Three specimens, deposited in the collections of the United States National Museum, resemble *A. pallida,* in all respects except in color pattern; their forewings, instead, are heavily marked (fig. 81) as in *A. barberella.* The specimens were collected near Paradise, Cochise Co., Ariz. and bear no information as to host. For now, it seems preferable to leave these unnamed until additional specimens can be collected, and the host plant discovered.

From the rather superficial information presented above and in the preceding discussion under *A. barberella,* it should be evident that considerable work remains to be done in this genus of moths. The taxonomic key included in this paper, of course, should prove adequate for essentially all known specimens of *Agavenema,* but future collecting may show the systematics of this genus to be far more complicated than now indicated. The relatively large sample of moths reared from *Agave deserti* exhibit a high degree of uniformity and are believed to represent a distinct species (*A. pallida*). The situation, however, is not so clear in those specimens collected from southern Arizona; instead, considerably more variation is to be noted, especially in regard to overall size. Future investigations, involving all species of *Agave,* eventually may reveal the existence of several sibling species or food plant races of *Agavenema.* Such a situation would not be surprising, considering the comparatively rapid rate at which the host plants may have speciated.

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Figures 1–155

Figure 1.—*Yucca schottii*, height approx. 5 ft., a member of the section *Sarcocarpa*, Chiricahua Mts., 5300 ft., 2 miles north of Paradise, Ariz. (photographed July 8, 1964).

Figure 2.—*Yucca schottii*, Santa Rita Mts., Madera Canyon, Ariz., 5100 ft., [illegible] July 22, 1964.

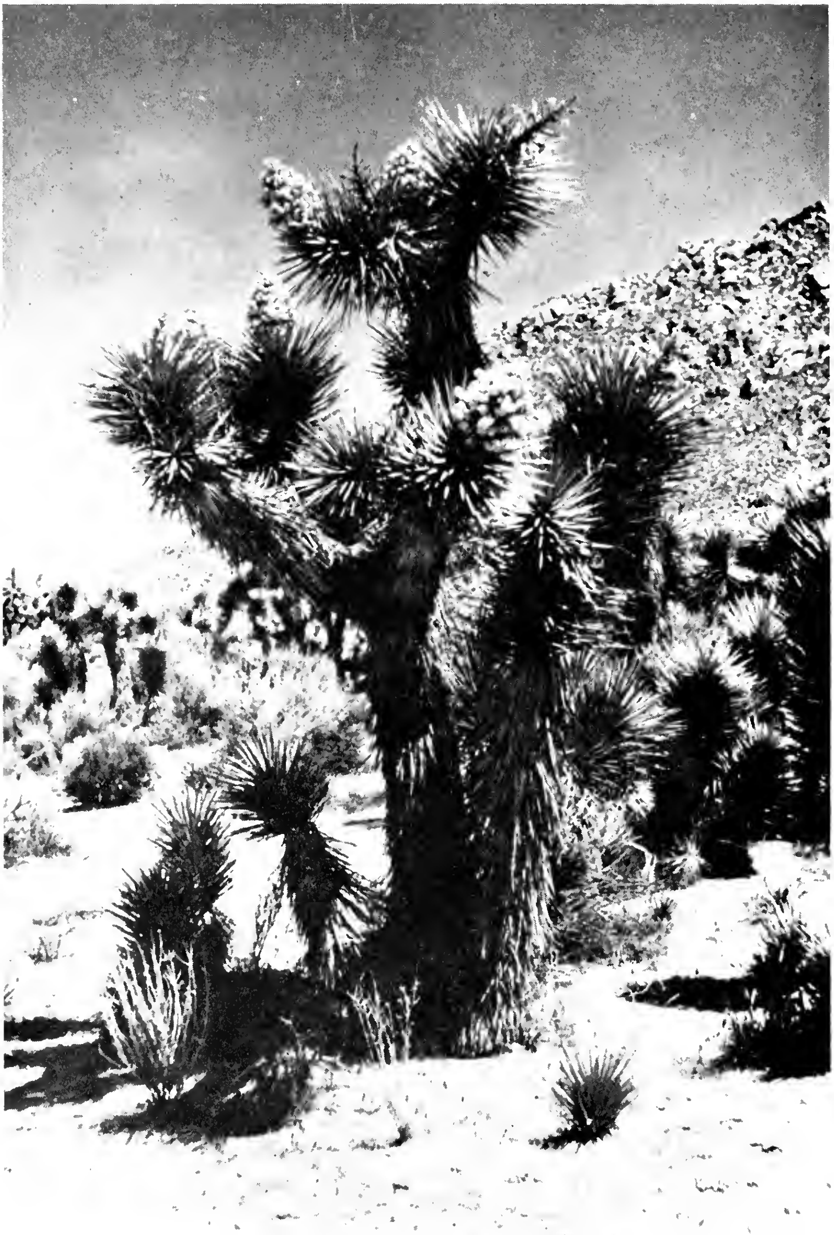


FIGURE 3.—*Yucca brevifolia*, a member of the section *Clistocarpa*, Kern Co., Calif., 16 miles south of Weldon (photographed Apr. 26, 1964, by J.A. Powell). This species is known to attain a height of 18 m. or more.

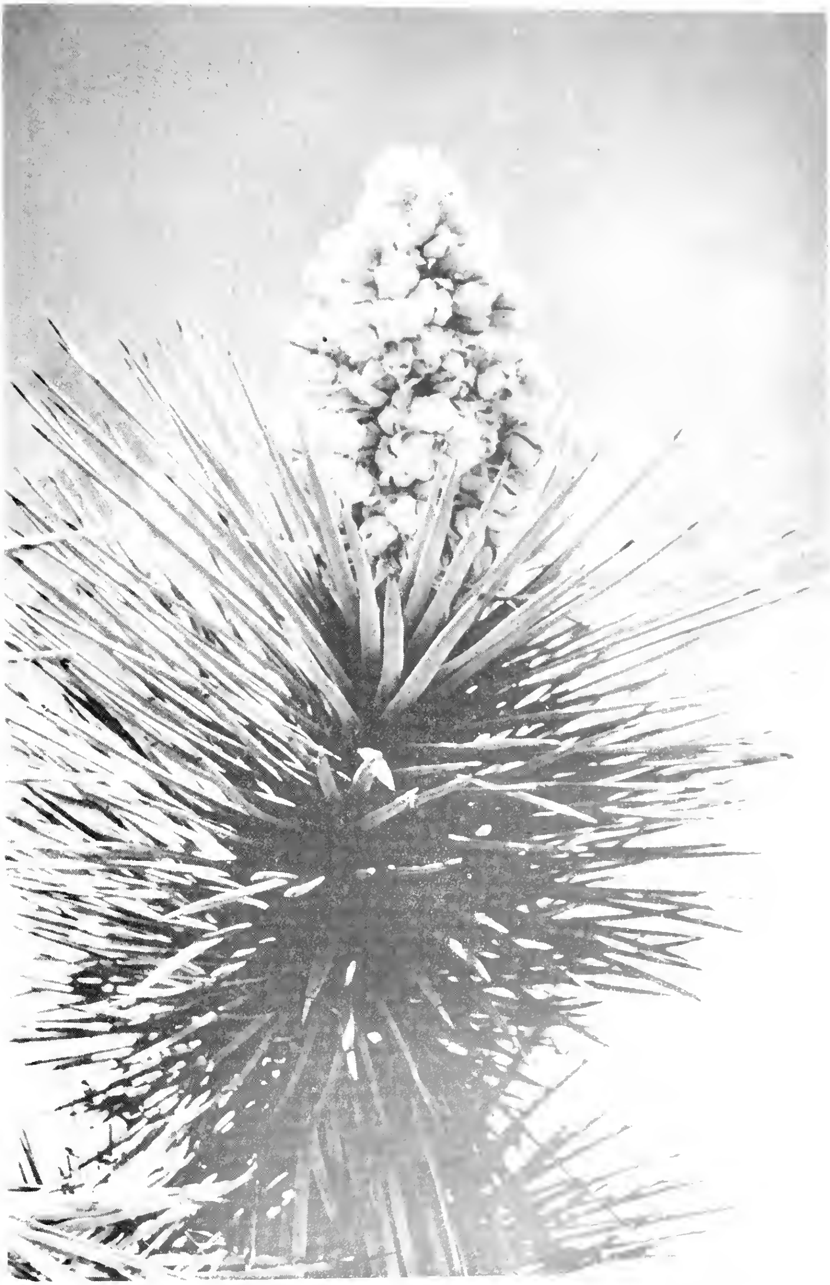


Figure 4.—*Yucca brevifolia*, Kern Co., Calif., [illegible] Apr. 26, 1964, by J. A. [illegible]

FIGURE 5.—*Yucca whipplei*, a member of the section *Hesperoyucca*, Kern Co., Calif., 1 mile east of Caliente (photographed May 15, 1963, by J.A. Powell).

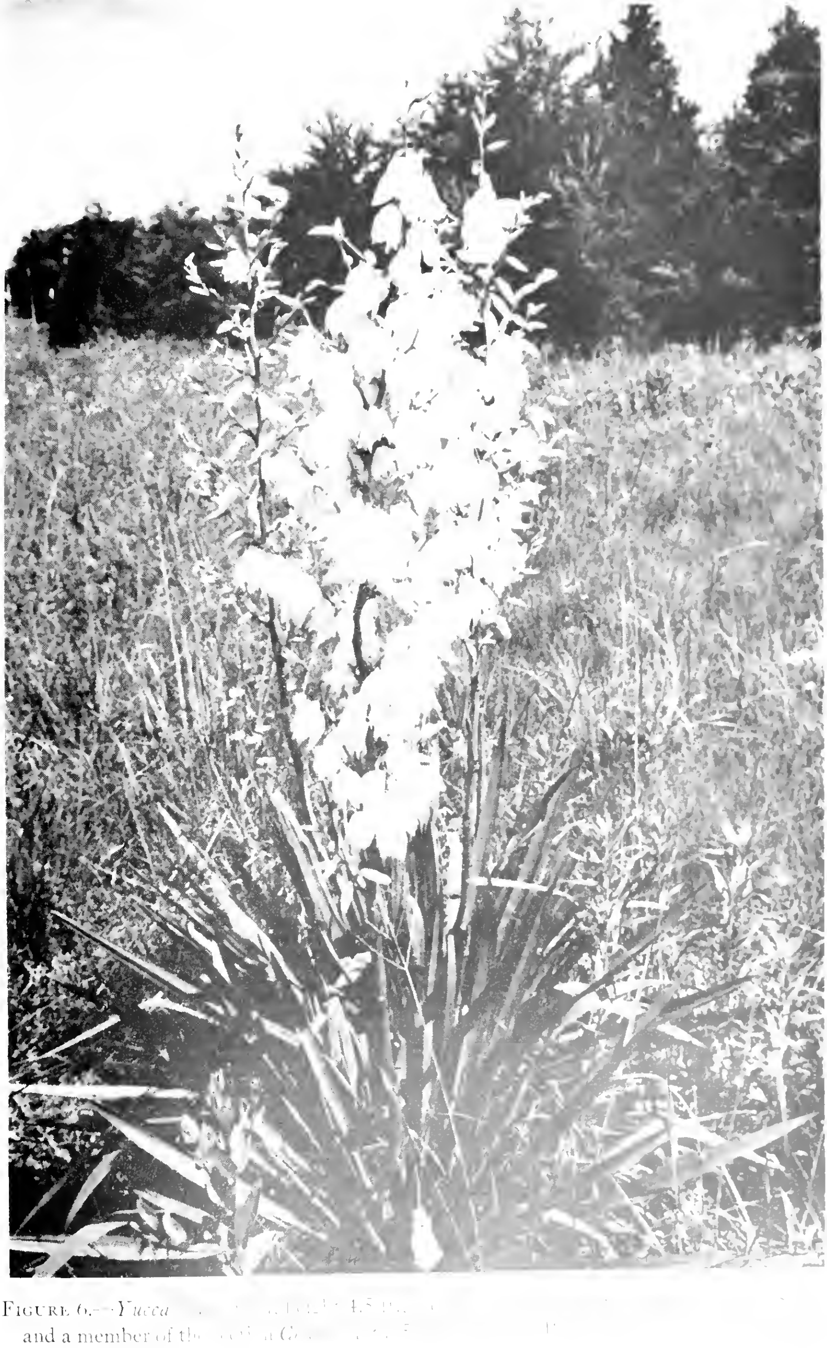


FIGURE 6.—*Yucca* [illegible] 4.5 [illegible]
and a member of the [illegible]
June 20, 1963.)

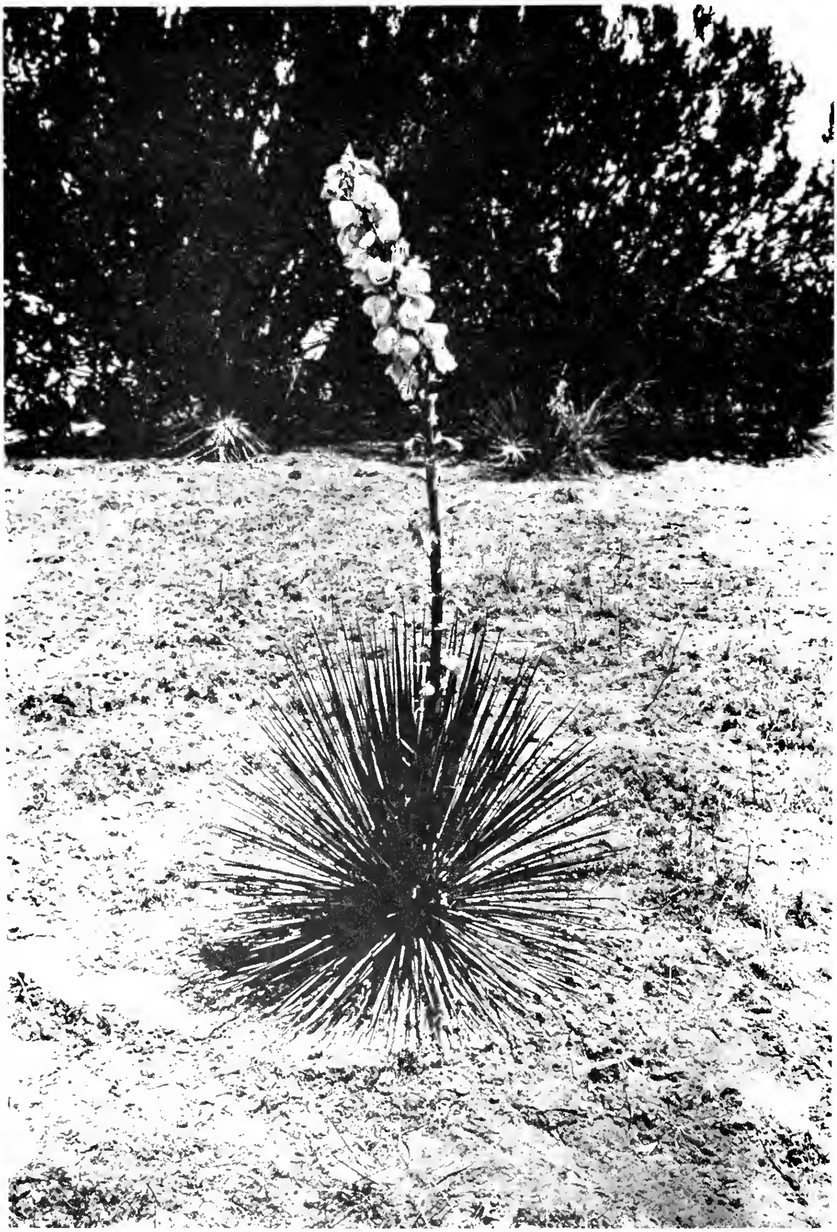


FIGURE 7.—*Yucca glauca* complex, height approx. 4 ft., a member of the section *Chaenocarpa*, Gran Quivira National Monument, N. Mex., 6600 ft. (photographed July 2, 1964).

FIGURE 8.—*Agave palmeri*, Chiricahua Mts., Cave C[illegible] P[illegible]tographed July [illegible], 1[illegible]4[illegible].

FIGURE 9.—*Dasylirion wheeleri*, height approx. 15 ft., a relative of *Yucca* and *Agave* and a possible host for some member of Prodoxinae, Peña Blanca Canyon, Ariz. (photographed July 28, 1964).

FIGURE 10.—Santa Rita Mts., Ariz., type locality for three new species of Prodoxinae (Madera Canyon, near center of picture; Mt. Wrightson, "Old Baldy", highest peak in the Santa Ritas, 9432 ft., left of center).

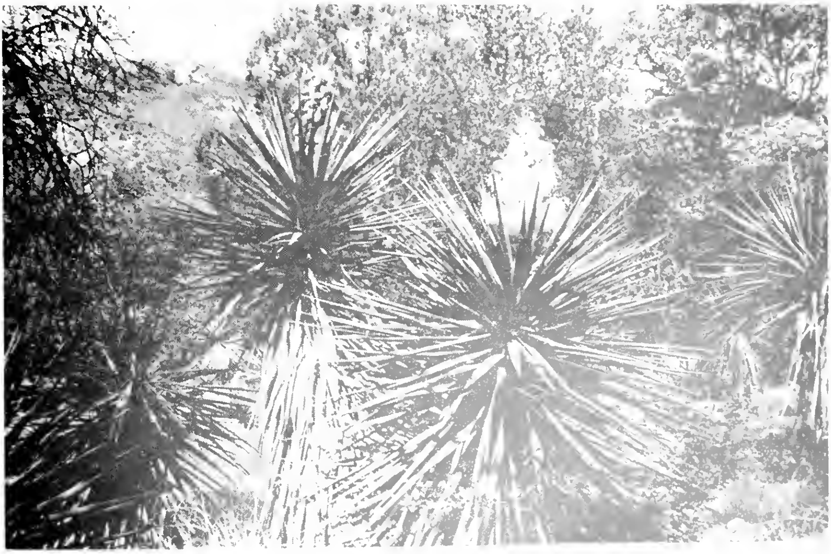


FIGURE 11.—*Yucca schottii*, plants with flowers and fruits, [illegible] Madera Canyon, Ariz., 5100 ft. (photographed July [illegible]).

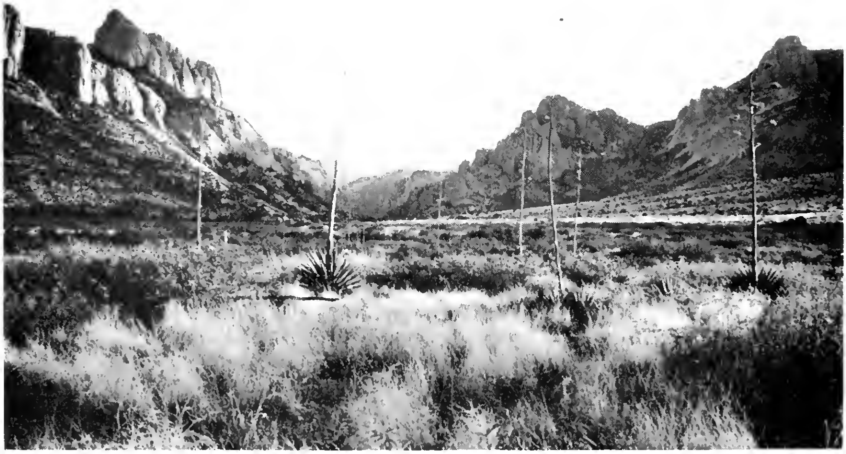
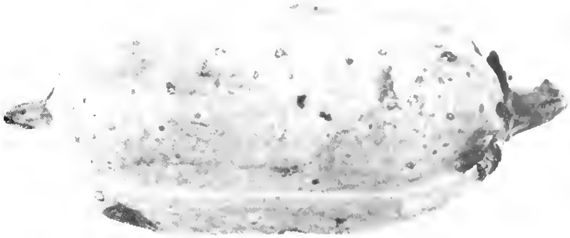


FIGURE 12.—*Agave palmeri* at entrance to Cave Creek Canyon, Chiricahua Mts., Ariz. (photographed July 6, 1964).

FIGURE 13.—*Nolina microcarpa*, close relative of *Dasylirion* and possible host for some member of Prodoxinae (photographed July 5, 1964, near Tyrone, N. Mex.).



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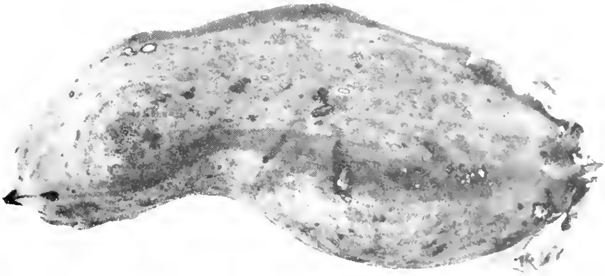

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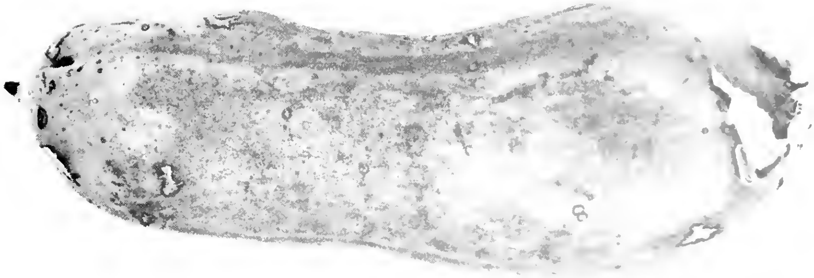

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FIGURES 14–16.—Yucca fruit, approx. actual size: 14, [illegible]
15, 16, [illegible]

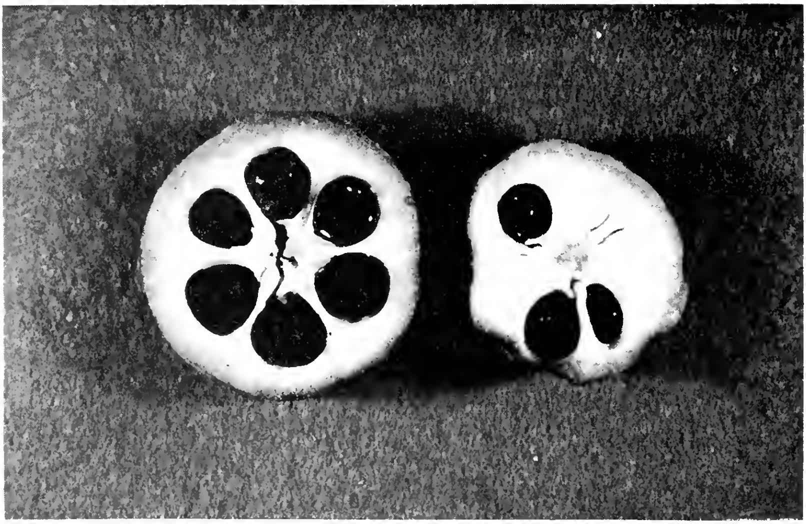


FIGURE 17.—Fruit of *Yucca baccata*, cross sections, diameters 1.5 and 1.25 in. respectively: Left section (normal) taken below oviposition site; right section taken just above.

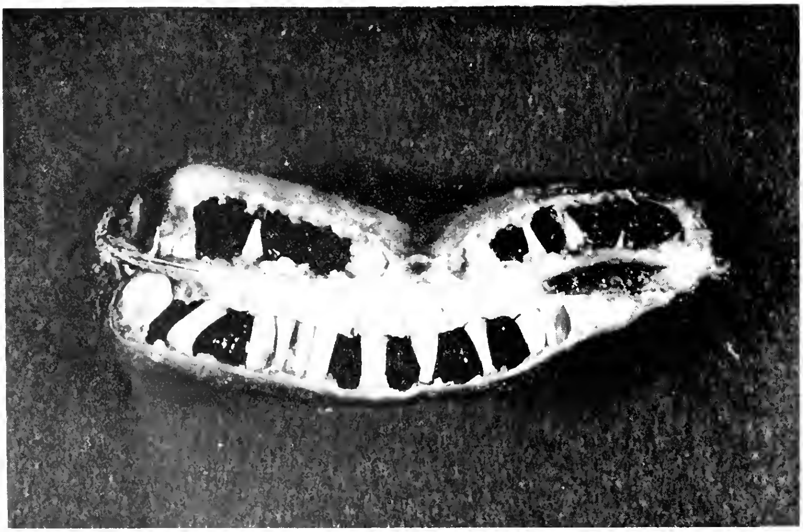


FIGURE 18.—Fruit of *Yucca filifera*. longitudinal section, length 3.25 in. (note growth inhibition and ovule abortion at oviposition site).

FIGURE 19.—Fruit of *Yucca schottii* with larva of *Tegeticula yuccasella*, in situ, length 3.25 in. (the larva has developed immediately below oviposition site and has eaten part of the fruit core).

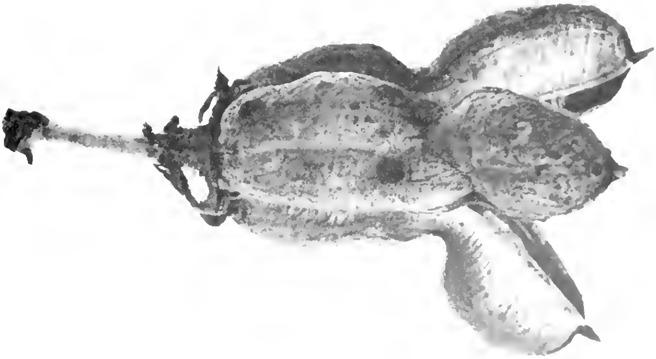


FIGURE 20.—Dry, dehiscent fruit of *Yucca* [illegible], length of pod 1.5 [illegible] emergence openings of *Tegeticula yuccasella*).

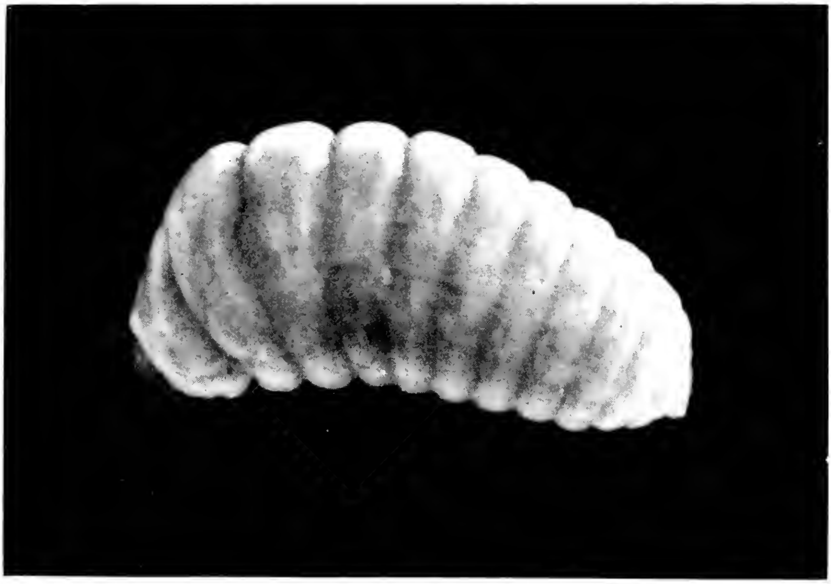


FIGURE 21.—Larva of *Prodoxus quinquepunctellus*, lateral view, length 6 mm.

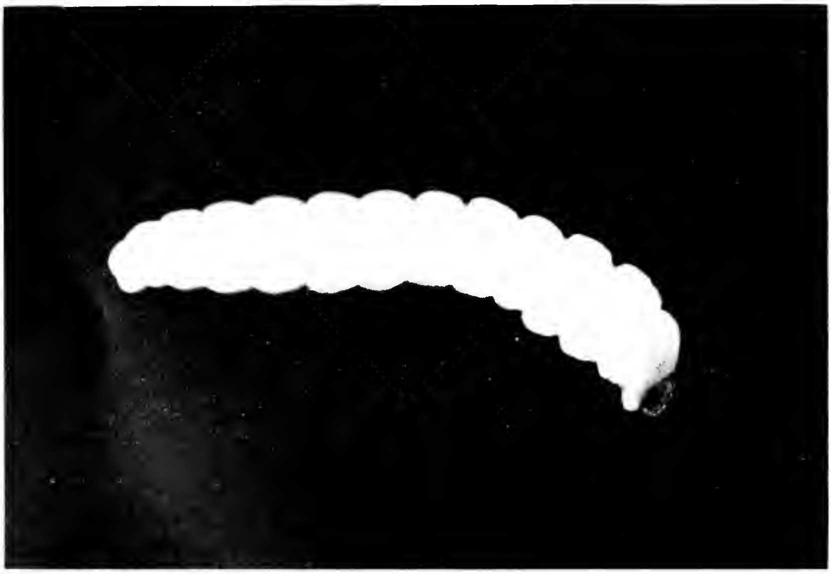


FIGURE 22.—Larva of *Prodoxus cinereus*, lateral view, length 10 mm.

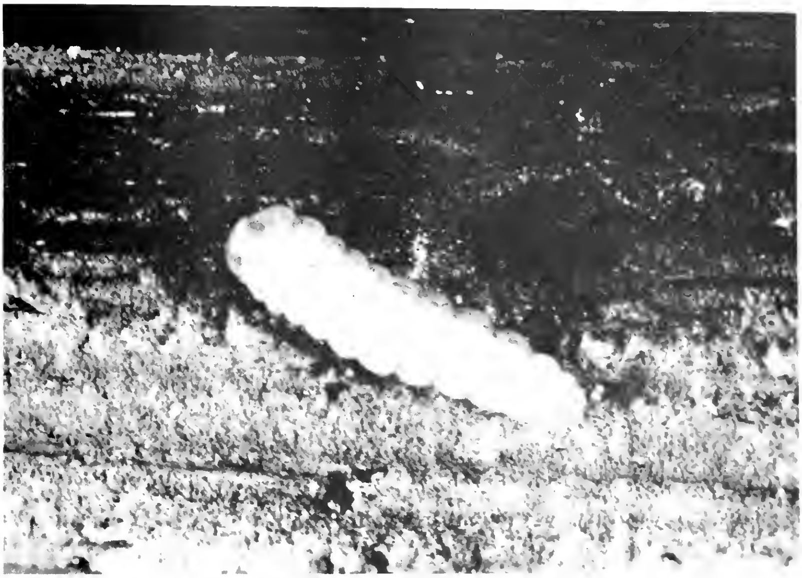


FIGURE 23.—Larva of *Agavenema barberella*, dorsal view, length 9 mm.

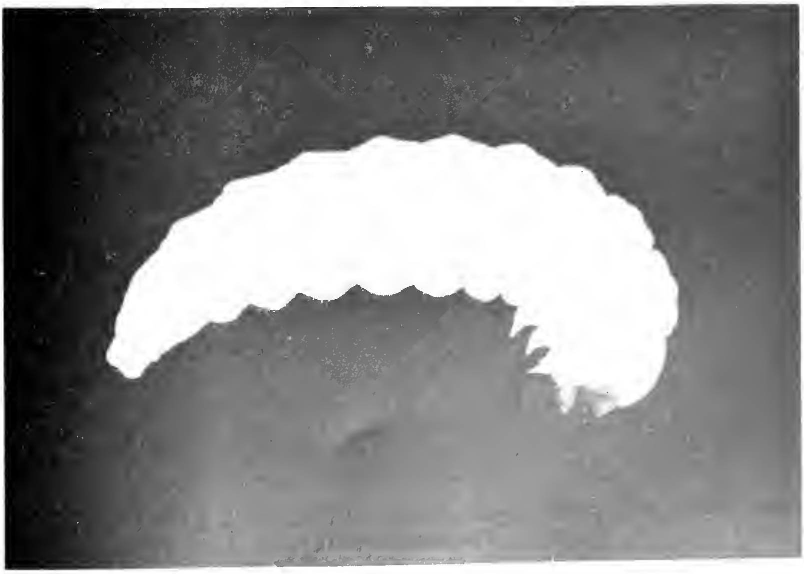


FIGURE 24.—Larva of *Tegeticula yuccasella*, lateral view, length [illegible]

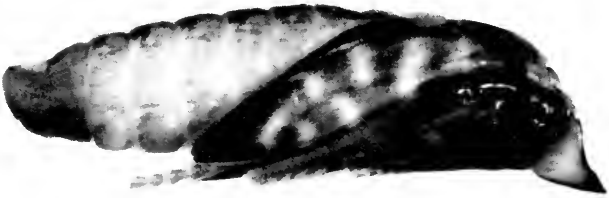


FIGURE 25.—Pupa of *Prodoxus intricatus*, lateral view, length 6 mm (note prominent frontal beak).

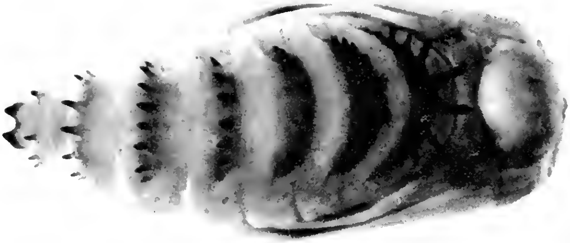


FIGURE 26.—Pupa of *Tegeticula yuccasella*, dorsal view, length 9 mm (note prominent abdominal spines).

FIGURE 27.—Pupal skin (after emergence of adult) and cocoon of *Agavenema barberella*, in situ, length of pupa 4 mm.

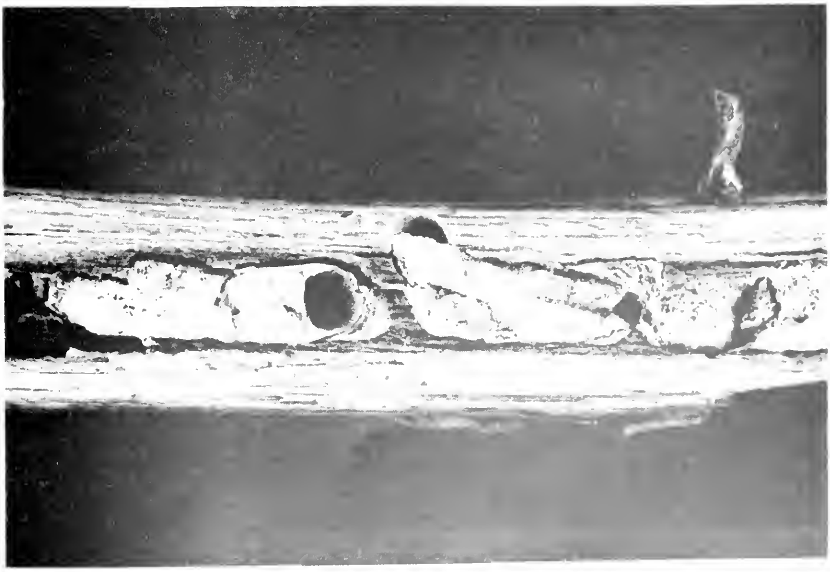


FIGURE 28.—Pupal skin (after emergence of adult) and cocoon of *Pr* [illegible] in situ, diameter of stem 8 mm.

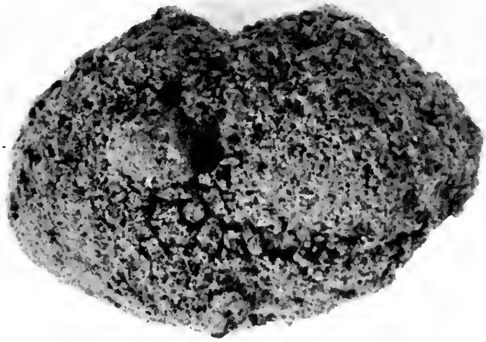


FIGURE 29.—Cocoon of *Tegeticula synthetica*, length 9 mm.

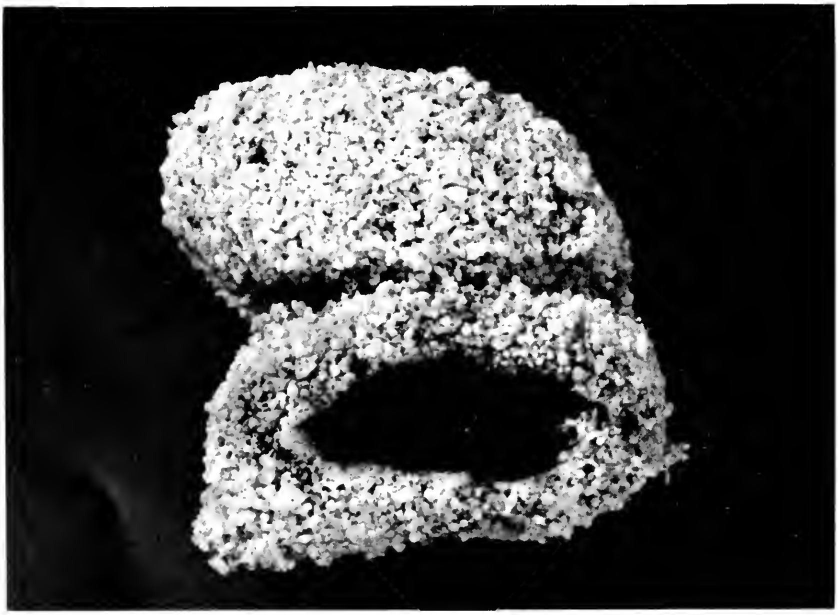


FIGURE 30.—Cocoons (2) of *Tegeticula yuccasella*, length 16 mm.

Figure 31.—*Tegeticula yuccasella:* normal female with large mass of pollen enclosed by two elongate processes beneath head; lower process is tongue (galea), upper (see arrow) is maxillary tentacle.

Figure 32.—*Tegeticula yuccasella:* female with vestigial maxillary tentacle (see arrow) and no trace of pollen.

FIGURE 33.—*Parategeticula pollenifera:* female in act of ovipositing on lateral flower stalk of *Yucca schottii.*

FIGURE 34.—Egg scars of *Parategeticula pollenifera* on flower stalk of *Yucca schottii* (tops of eggs barely visible).

FIGURE 35.—*Tegeticula yuccasella* in act of depositing [illegible] within blossom of *Yucca* [illegible].

FIGURE 36.—Egg of *Parategeticula pollenifera*, in situ, with surrounding plant tissue removed, length of egg 0.4 mm (photographed by A. Peterson).

FIGURE 37.—Eggs of *Parategeticula pollenifera* in flower petal of *Yucca schottii* (photographed by A. Peterson).

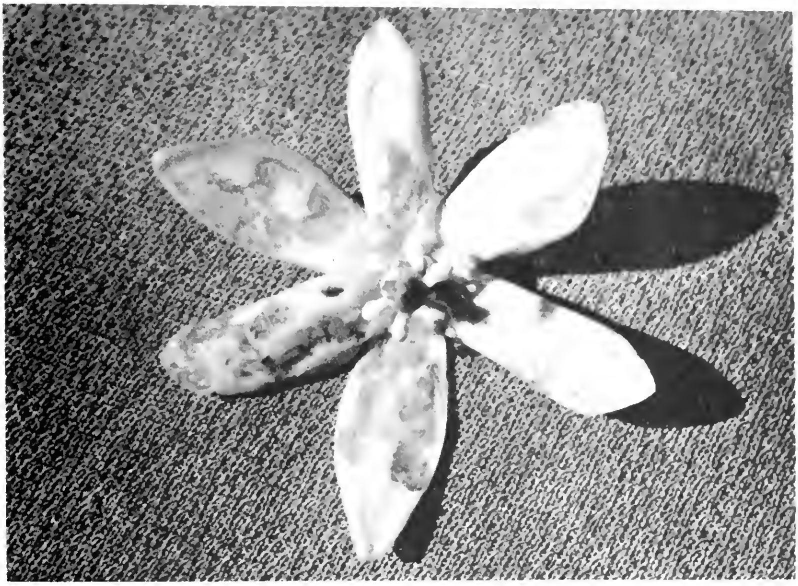


FIGURE 38.—Flower of *Yucca schottii* showing petal mines (anthonomes) of beetle, *Carpophilus* species (Nitidulidae) (see page 38 for discussion).

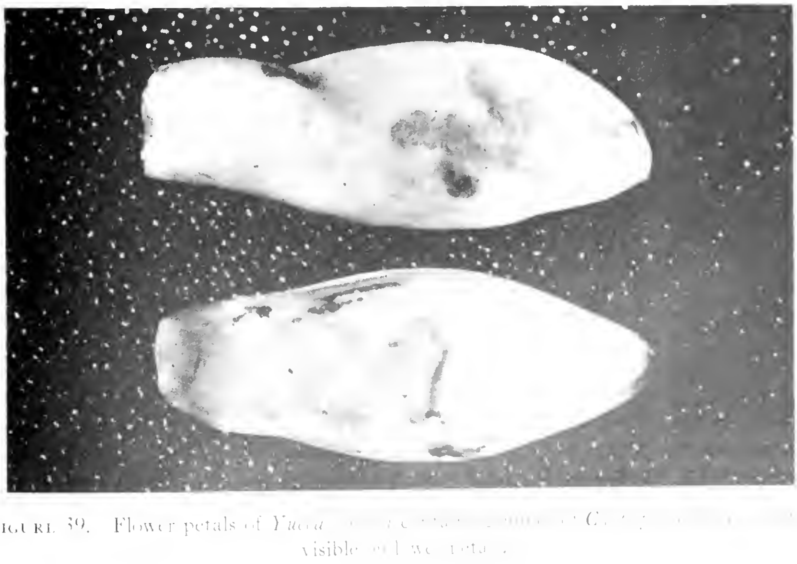
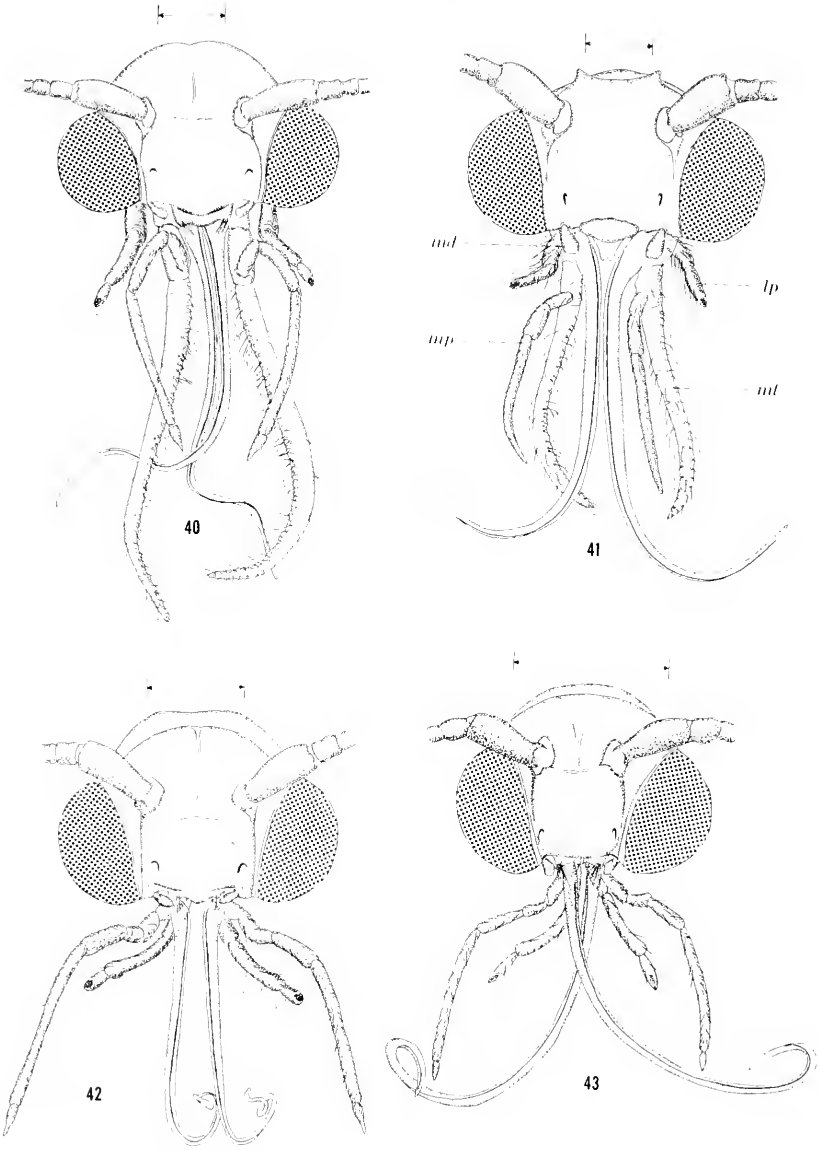
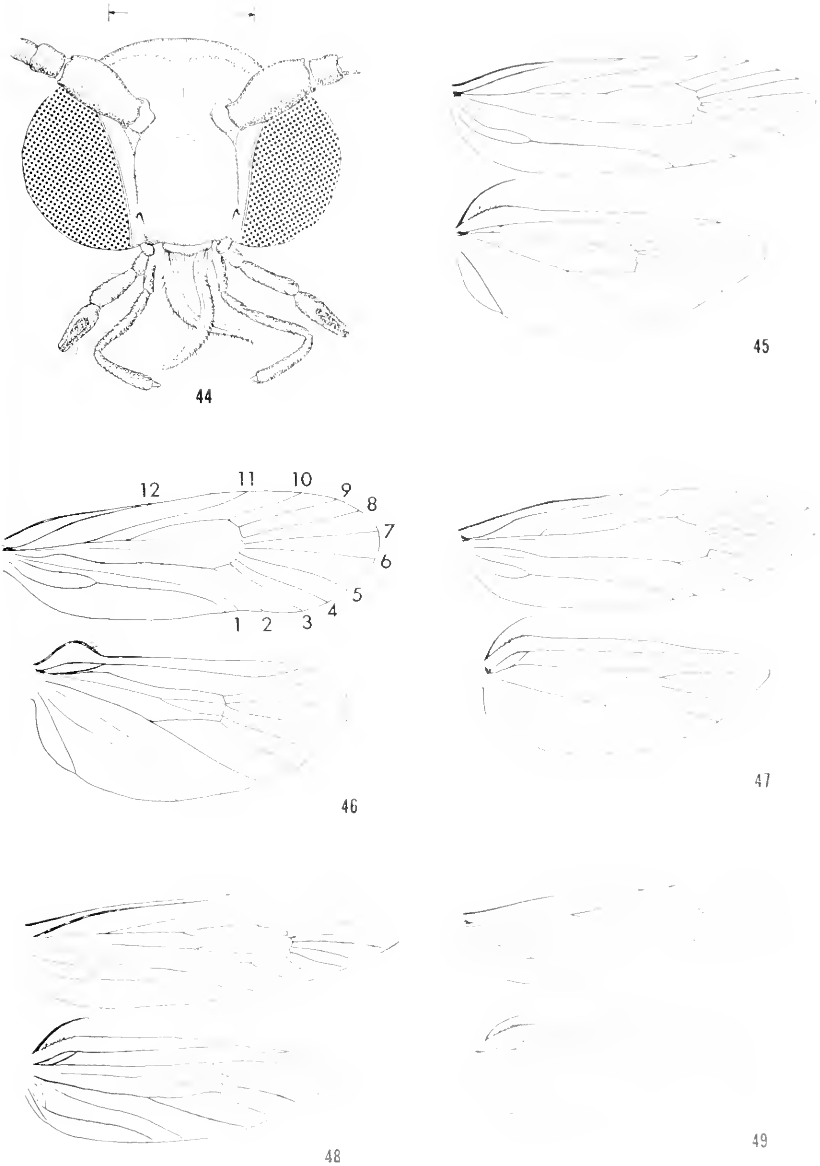


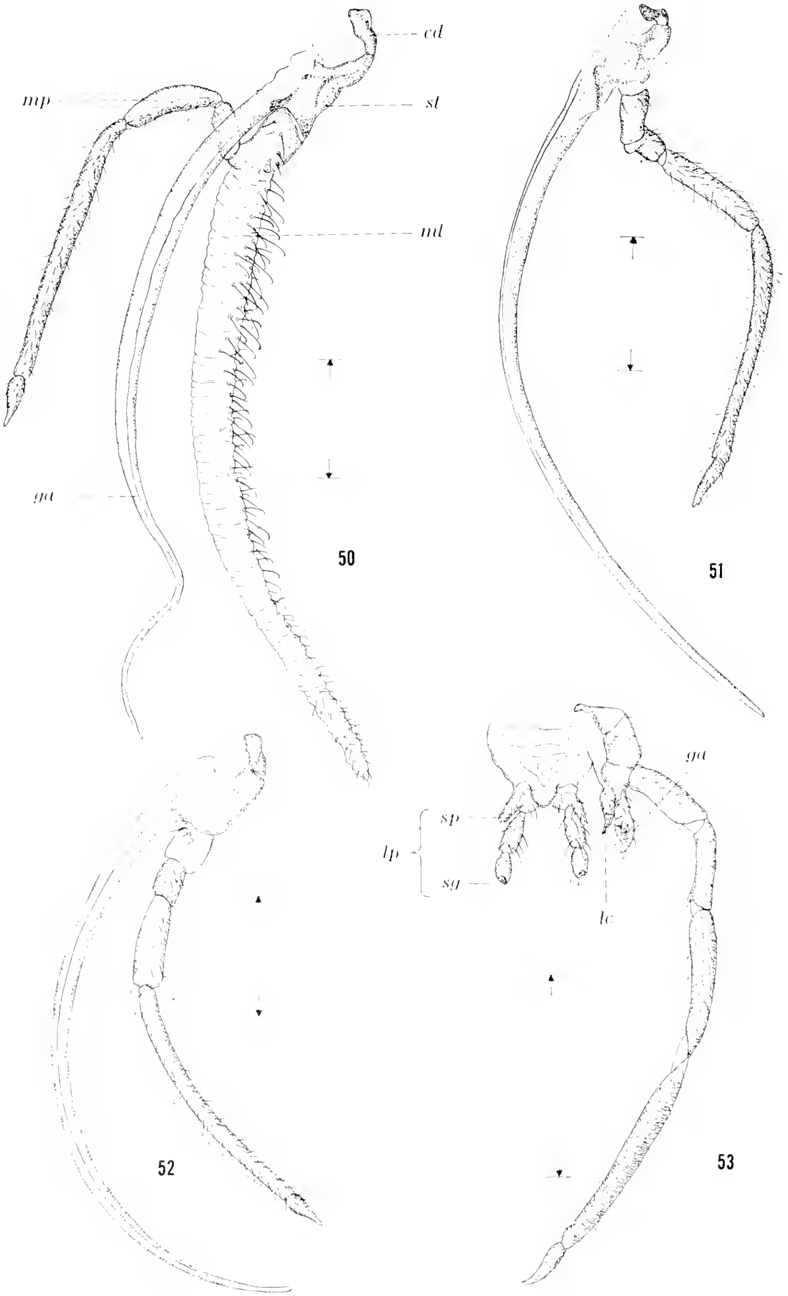
FIGURE 39. Flower petals of *Yucca* [illegible] *C*[illegible] visible on lower petal.



FIGURES 40–43.—Frontal view of female heads: 40, *Tegeticula yuccasella;* 41, *Parategeticula pollenifera* (lp=labial palpus, md=mandible, mp=maxillary palpus, mt=maxillary tentacle); 42, *Prodoxus quinquepunctellus;* 43, *Mesepiola specca.* (Scale=0.5 mm.)



FIGURES 44–49.—Frontal view of female head and wings: [illegible] 45, *Tegeticula yuccasella*; 46, *Parategeticula pollenifera*; 47, *P*[illegible]; 48, *Mesepiola specca*; 49, *Agavenema* [illegible]. (Scale 0.5 mm.)



FIGURES 50–53.—Maxillae: 50, *Tegeticula yuccasella*, female (cd=cardo, ga=galea, mp=maxillary palpus, mt=maxillary tentacle, st=stipes); 51, *Prodoxus quinquepunctellus*, female; 52, *Tegeticula yuccasella*, male; 53, *Micropteryx aureatella*, male, maxilla, and labium (ga=galea, lc=lacinia, lp=labial palpus, sg=sensory gland, organ of vom Rath; sp=sensory process). (Scale=0.5 mm.)

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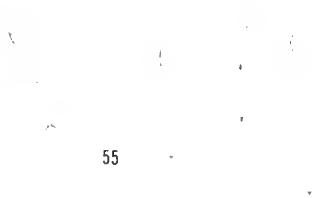

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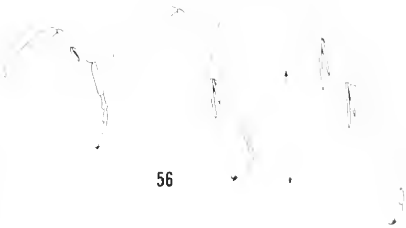

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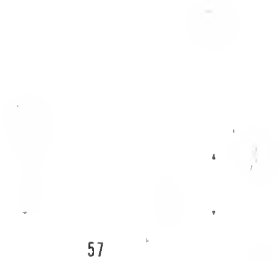

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FIGURES 54–59.—Legs: 54, *Prodoxus quinquepunctellus*, [illegible]; 55, *Prodoxus quinquepunctellus*; 56, *Mesepiola specca*; 57, [illegible]; 58, *Tegeticula yuccasella*; 59, *Parategeticula pollenifera*. (Scale 1.0 mm.)

FIGURES 60-67.—Adults

60. *Prodoxus quinquepunctellus*, female, Highlands, North Carolina, length of forewing 10 mm.
61. *Prodoxus quinquepunctellus*, female, between Ranger and Strawn, Tex., length of forewing 8.5 mm.
62. *Prodoxus y-inversus*, female, Madera Canyon, Santa Rita Mts., Ariz., length of forewing 7 mm.
63. *Prodoxus y-inversus*, male, Madera Canyon, Santa Rita Mts., Ariz., length of forewing 6 mm.
64. *Prodoxus coloradensis*, male, Pahrump, Nev., length of forewing 5 mm.
65. *Prodoxus coloradensis*, male, Pahrump, Nev., length of forewing 5 mm.
66. *Prodoxus coloradensis*, female, Pahrump, Nev., length of forewing 6 mm.
67. *Prodoxus coloradensis*, female, Pahrump, Nev., length of forewing 6 mm.

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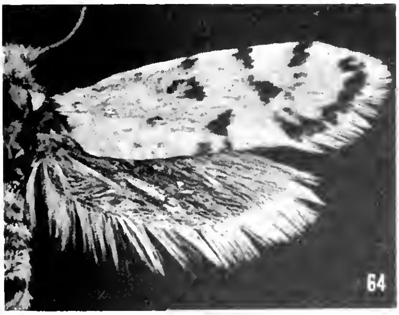

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FIGURES 68-75.—Adults

68. *Prodoxus intricatus*, female, Fortin, Mex., length of forewing 7 mm.
69. *Prodoxus intricatus*, male, Fortin, Mex., length of forewing 6 mm.
70. *Prodoxus ochrocarus*, male, paratype, Madera Canyon, Santa Rita Mts., Ariz., length of forewing 5 mm.
71. *Prodoxus sordidus*, female, Calif., length of forewing 6 mm.
72. *Prodoxus marginatus*, female, Los Angeles, Calif., length of forewing 4.5 mm.
73. *Prodoxus marginatus*, male, Los Angeles, Calif., length of forewing 4 mm.
74. *Prodoxus pulverulentus*, female, Calif., length of forewing 5 mm.
75. *Prodoxus pulverulentus*, female, Mojeska, Calif., length of forewing 4.5 mm.


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FIGURES 76–83.—Adults

76. *Prodoxus cinereus*, male, Los Angeles, Calif., length of forewing 5 mm.
77. *Prodoxus aenescens*, female, Los Angeles, Calif., length of forewing 6 mm.
78. *Mesepiola specca*, female, paratype, Madera Canyon, Santa Rita Mts., Ariz., length of forewing 5.5 mm.
79. *Agavenema barberella*, female, holotype, Ray, Ariz., length of forewing 7 mm.
80. *Agavenema pallida*, female, holotype, Mason Valley, Calif., length of forewing 11 mm.
81. *Agavenema* species, female, Paradise, Ariz., length of forewing 11 mm.
82. *Tegeticula synthetica*, male, Antelope Valley, Calif., length of forewing 8 mm.
83. *Tegeticula synthetica*, female, Valyermo, Calif., length of forewing 10 mm.


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FIGURES 84–91.—Adults

84. *Tegeticula maculata maculata*, female, La Tuna Canyon, Calif., length of forewing 9.5 mm.
85. *Tegeticula maculata extranea*, male, Mojeska, Calif., length of forewing 7 mm.
86. *Tegeticula yuccasella*, female, Highlands, N.C., length of forewing 12 mm.
87. *Tegeticula yuccasella*, female, Madera Canyon, Santa Rita Mts., Ariz., length of forewing 10 mm.
88. *Parategeticula pollenifera*, female, paratype, Madera Canyon, Santa Rita Mts., Ariz., length of forewing 14 mm.
89. *Parategeticula pollenifera*, male, paratype, Madera Canyon, Santa Rita Mts., Ariz., length of forewing 12 mm.
90. *Holcocera gigantella*, female, San Bernardino Co., Calif., length of forewing 14 mm.
91. *Holcocera gigantella*, female, pale form, Tula, Hidalgo, Mexico, length of forewing 13 mm.


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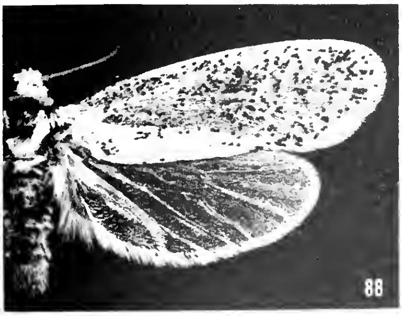
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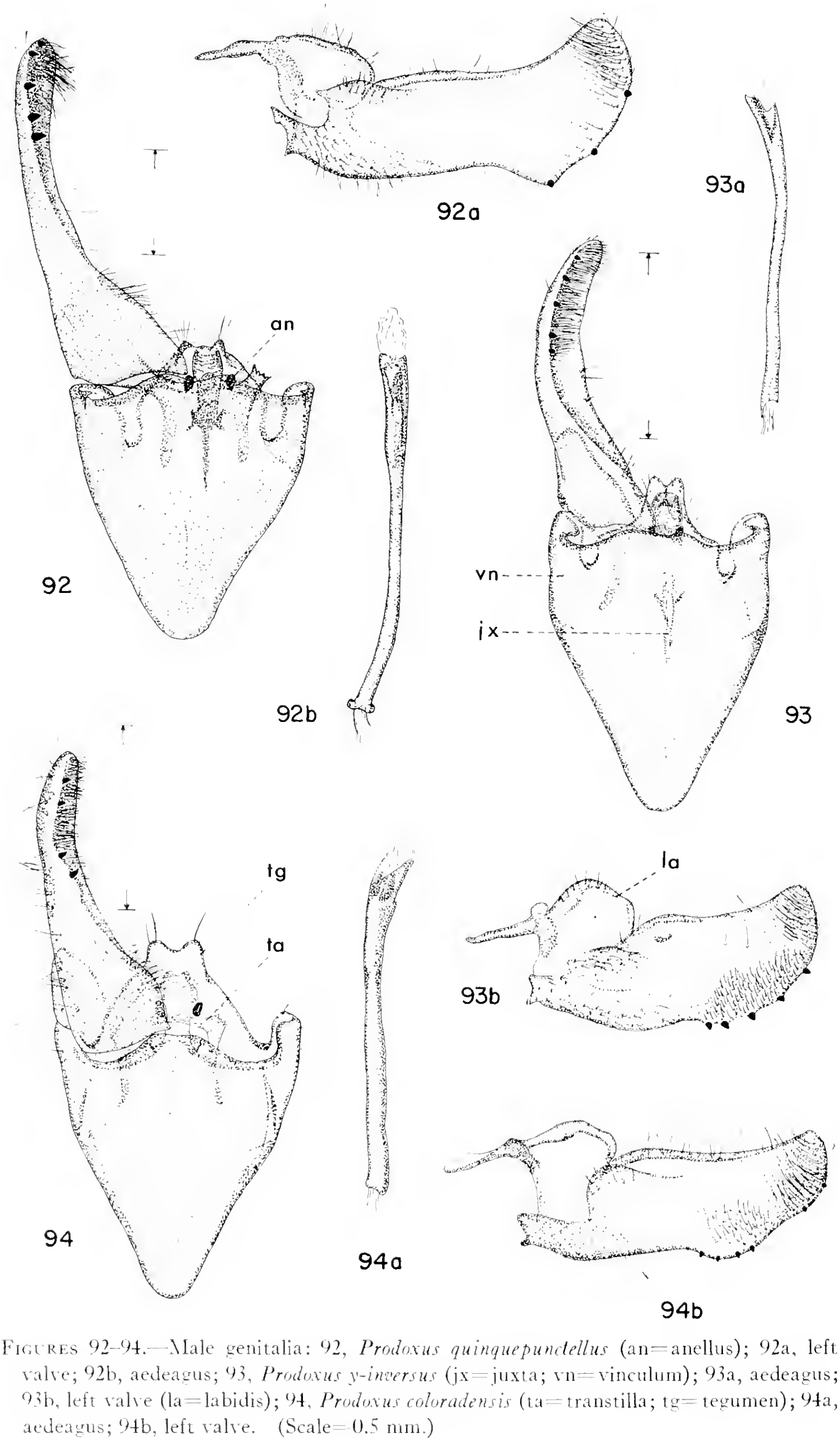
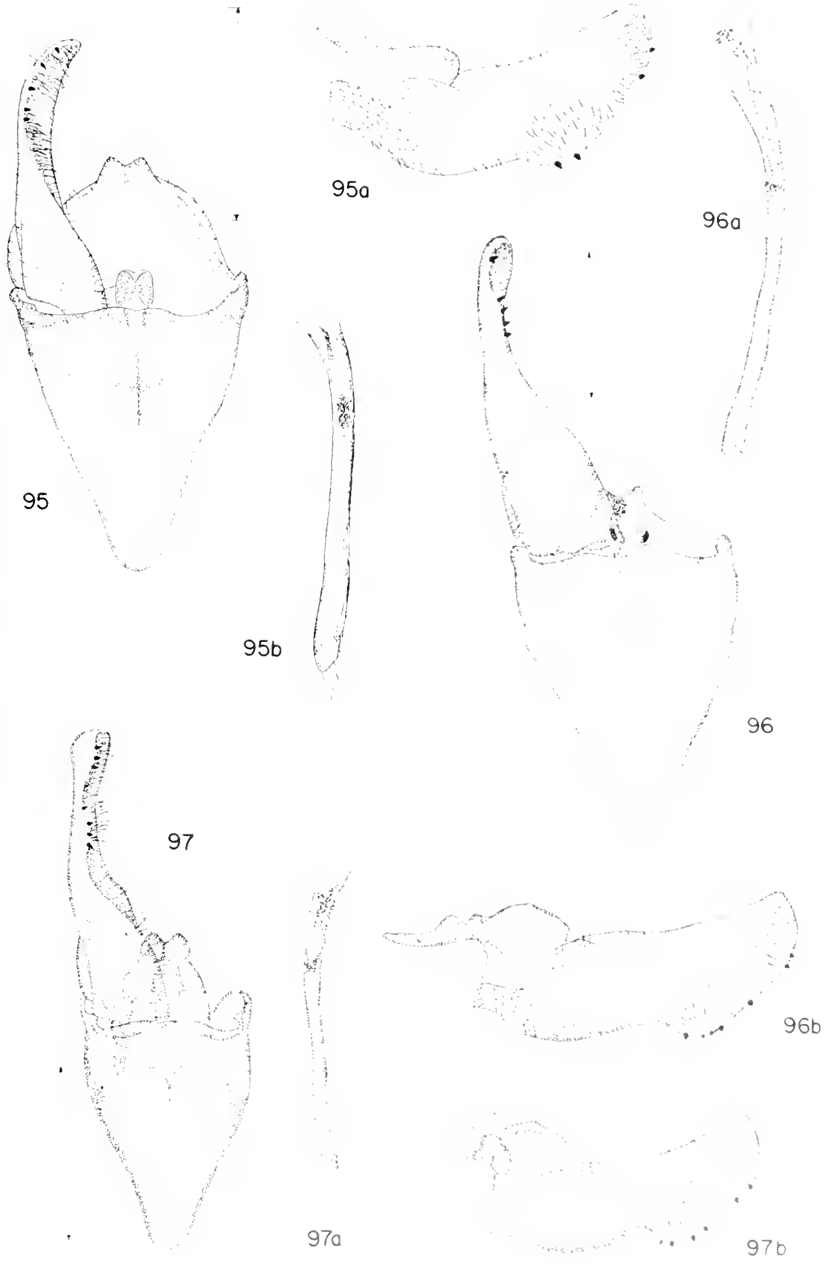
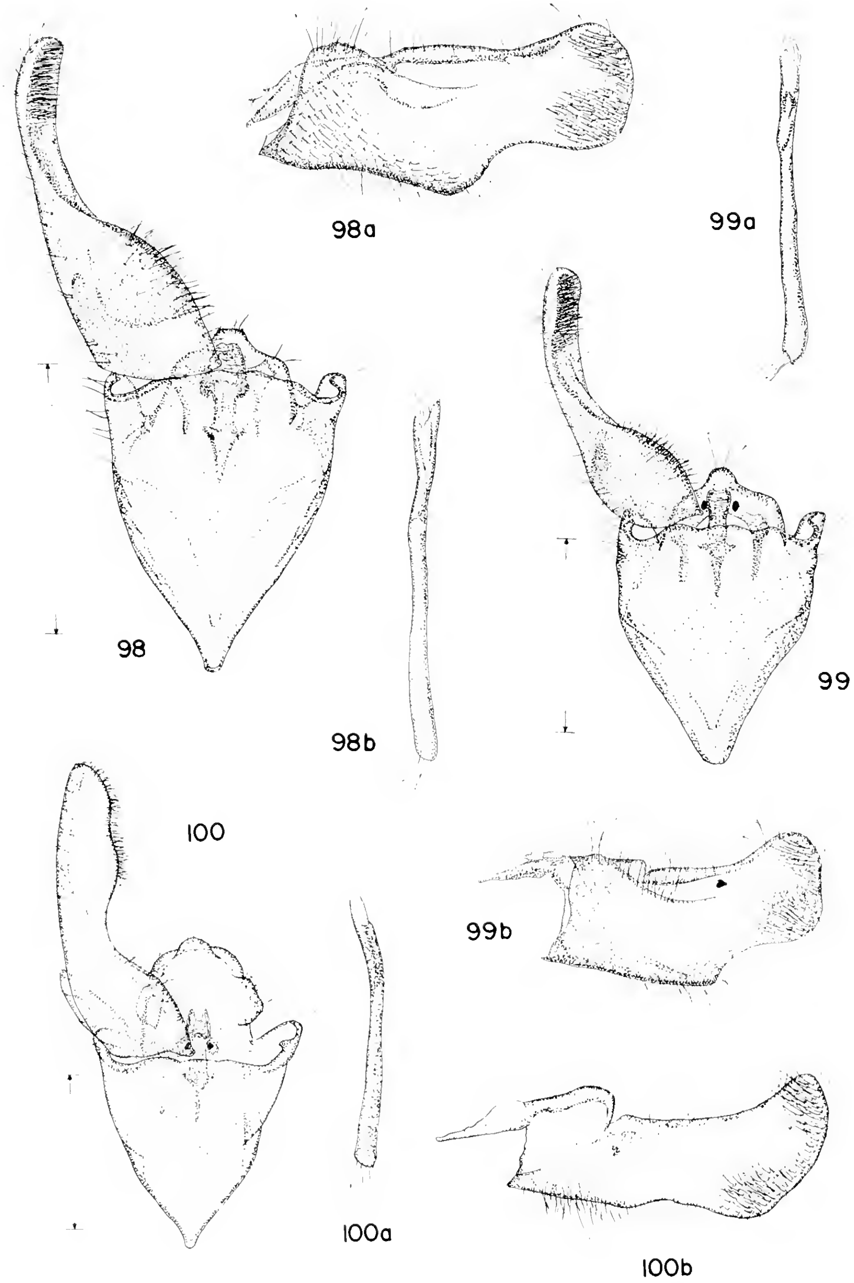


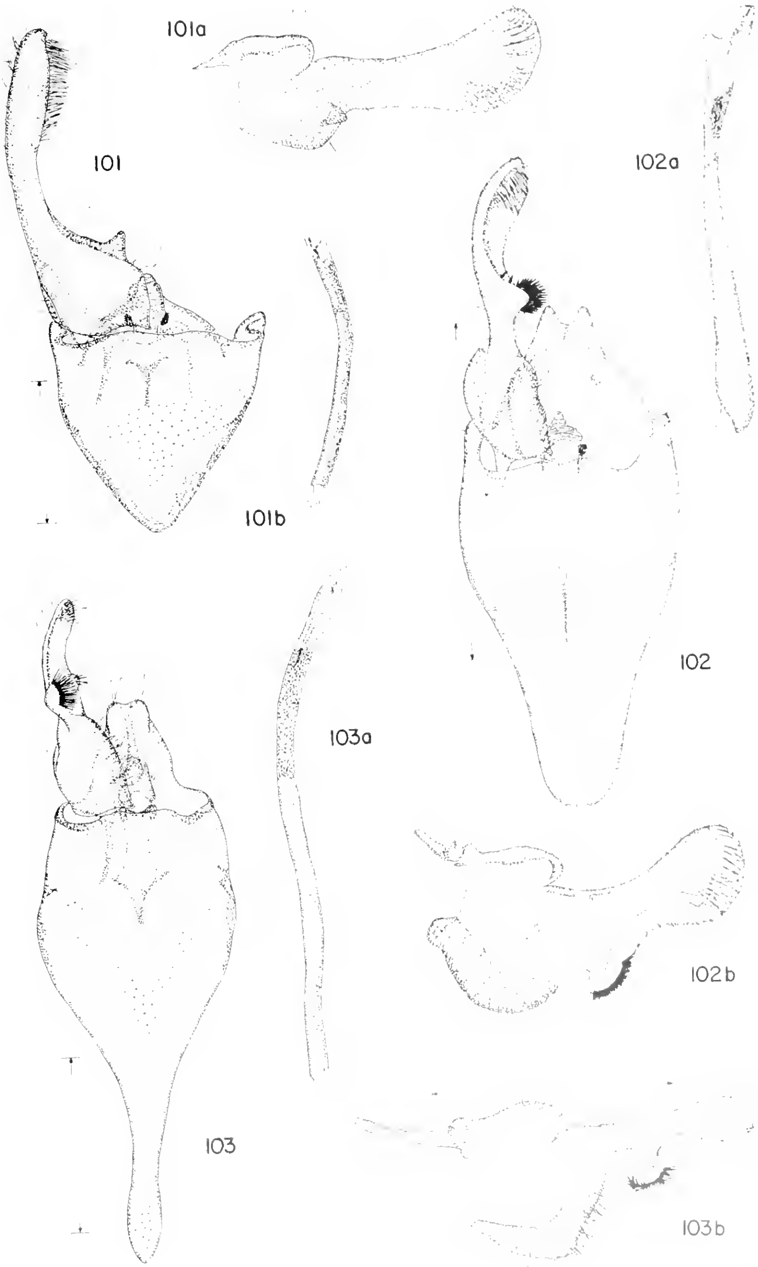
FIGURES 92–94.—Male genitalia: 92, *Prodoxus quinquepunctellus* (an=anellus); 92a, left valve; 92b, aedeagus; 93, *Prodoxus y-inversus* (jx=juxta; vn=vinculum); 93a, aedeagus; 93b, left valve (la=labidis); 94, *Prodoxus coloradensis* (ta=transtilla; tg=tegumen); 94a, aedeagus; 94b, left valve. (Scale=0.5 mm.)



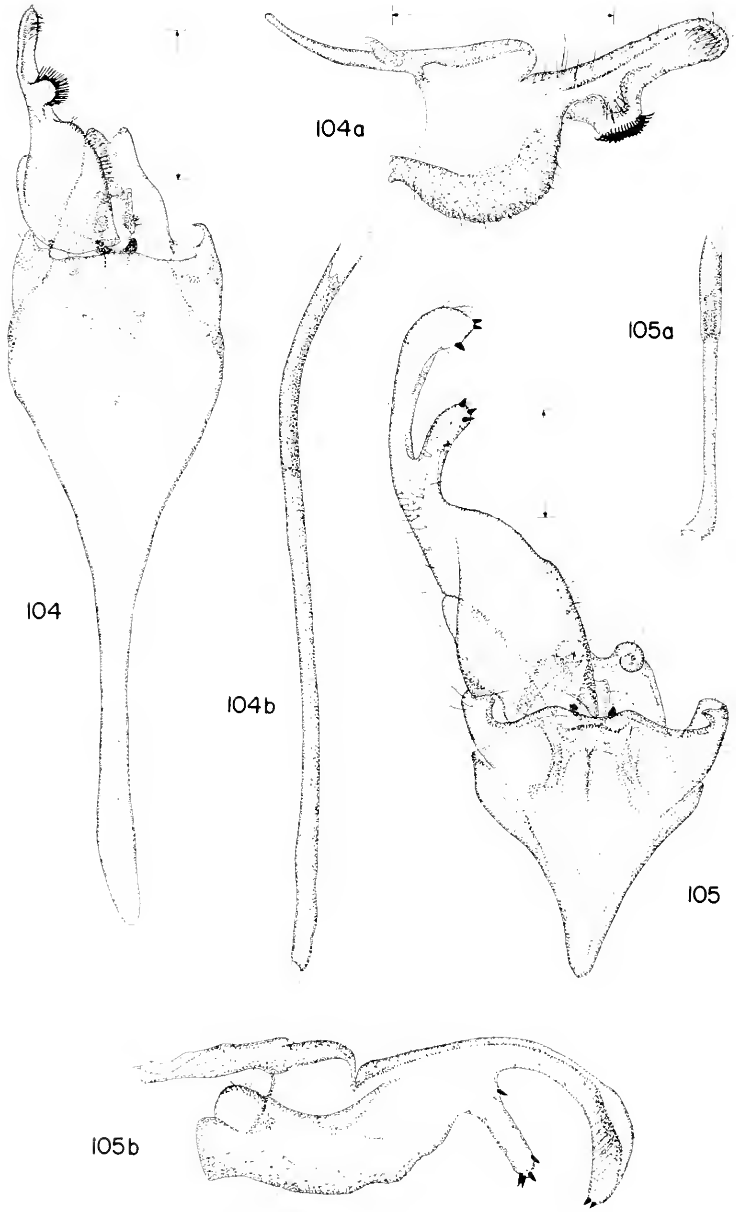
FIGURES 95-97.—Male genitalia: 95, *Pr*[illegible]; [illegible] aedeagus; 96, *Prodoxus intricatus*; 96a, aedeagus; 96b, left valve; 97, *Pr*[illegible]; 97a, aedeagus; 97b, left valve. (Scale 0.5 [illegible])



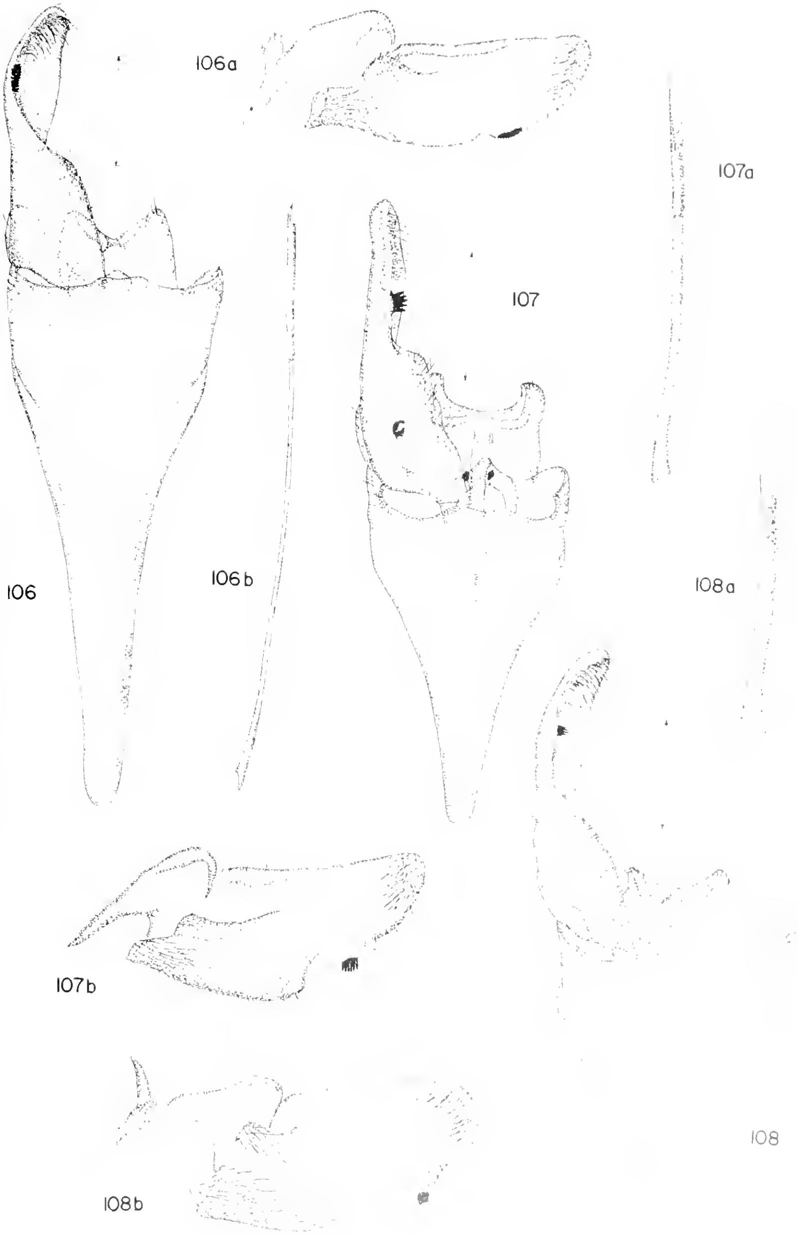
Figures 98–100.—Male genitalia: 98, *Prodoxus marginatus;* 98a, left valve; 98b, aedeagus; 99, *Prodoxus pulverulentus;* 99a, aedeagus; 99b, left valve; 100, *Prodoxus cinereus;* 100a, aedeagus; 100b, left valve. (Scale=0.5 mm.)



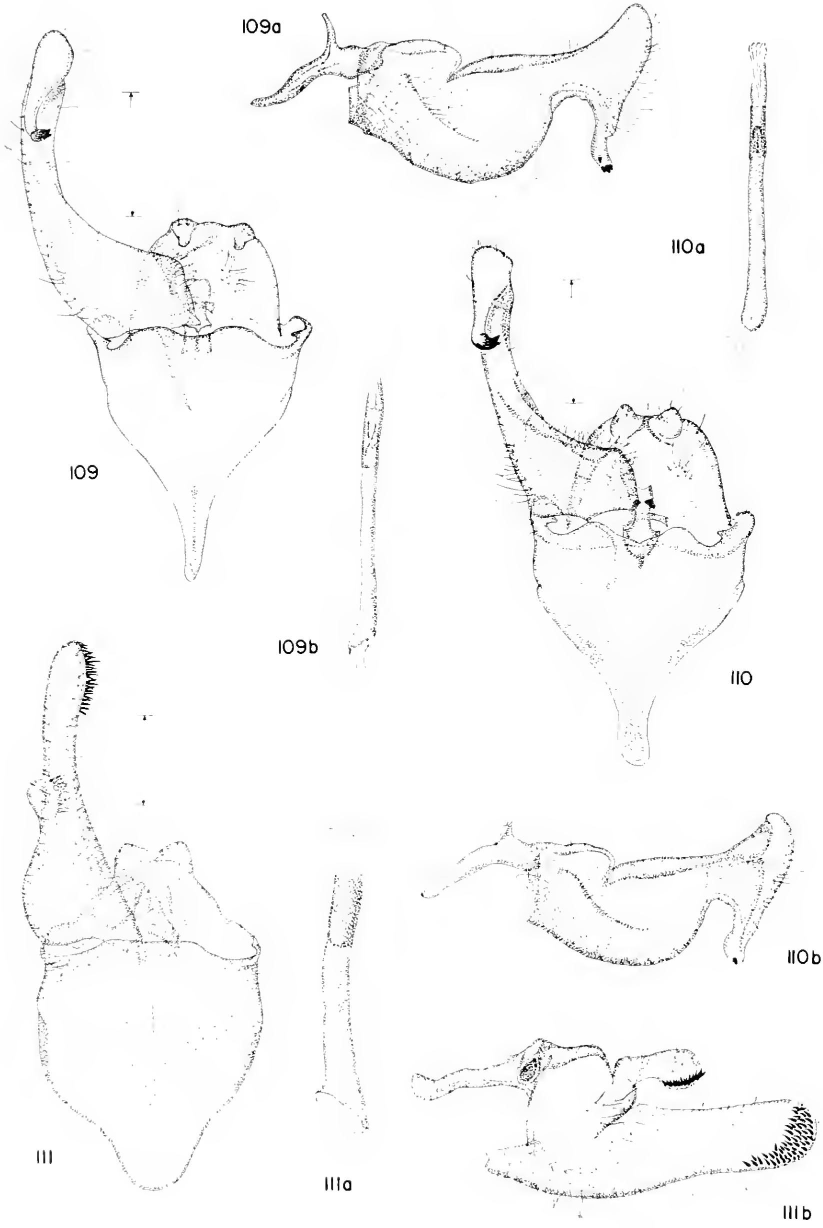
Figures 101–103.—Male genitalia: 101, *Pr[illegible] [illegible]*; 101a, left valva; 101b, aedeagus; 102, *Mesepiola specca*, paratype; 102a, aedeagus; 102b, left valva; 103, *Agavenema barberella*, paratype; 103a, aedeagus; 103b, left valva. (Scale = 0.5 mm.)



FIGURES 104–105.—Male genitalia: 104, *Agavenema pallida*, paratype; 104a, left valve; 104b, aedeagus; 105, *Tegeticula synthetica;* 105a, aedeagus; 105b, left valve. (Scale=0.5 mm.)



FIGURES 106–108.—Male genitalia. *Te*[illegible] DRD [illegible] 40[illegible] Co., N. Mex.; 106a, left valve; 106b, aedeagus; 107, [illegible] DRD slide 867, Central (?) Mo.; 107a, aedeagus; 107[illegible]; 108, [illegible] Pyote, Tex.; 108a, aedeagus; 108b, left valve [illegible]



FIGURES 109–111.—Male genitalia: 109, *Tegeticula maculata maculata;* 109a, left valve; 109b, aedeagus; 110, *Tegeticula maculata extranea;* 110a, aedeagus; 110b, left valve; 111, *Parategeticula pollenifera,* paratype; 111a, aedeagus; 111b, left valve. (Scale=0.5 mm.)

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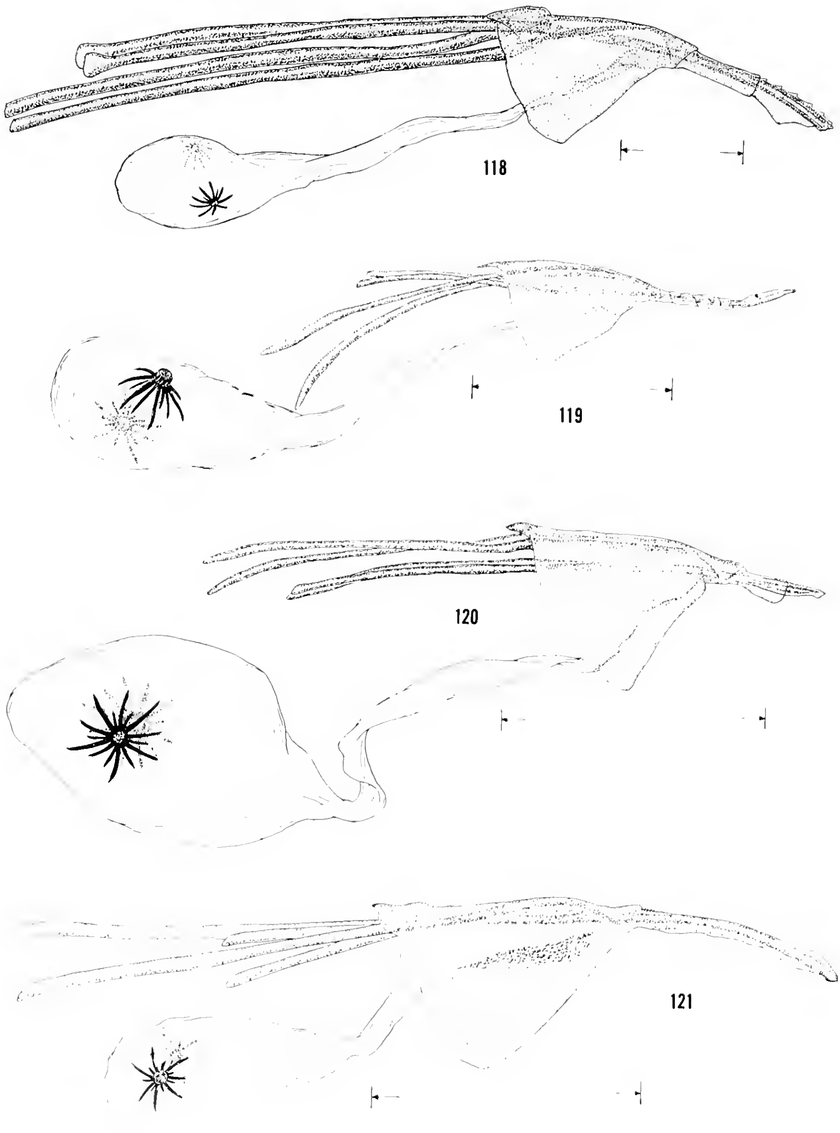
FIGURES 112–117.—Seventh segment of female abdomen, lateral view: 112, *Prodoxus sordidus;* 113, *Mesepiola specca*, paratype; 114, *Agavenema [illegible]*, paratype; 115, *Tegeticula yuccasella;* 116, *Tegeticula synthetica* (dorsal view); 117, *Parategeticula pollenifera*, paratype.



Figures 118-121.—Female genitalia: 118, *Prodoxus quinquepunctellus;* 119, *Prodoxus y-inversus;* 120, *Prodoxus coloradensis;* 121, *Prodoxus ochrocarus*, paratype. (Scale= 1.0 mm.)

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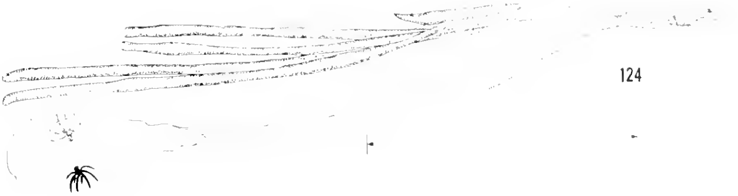

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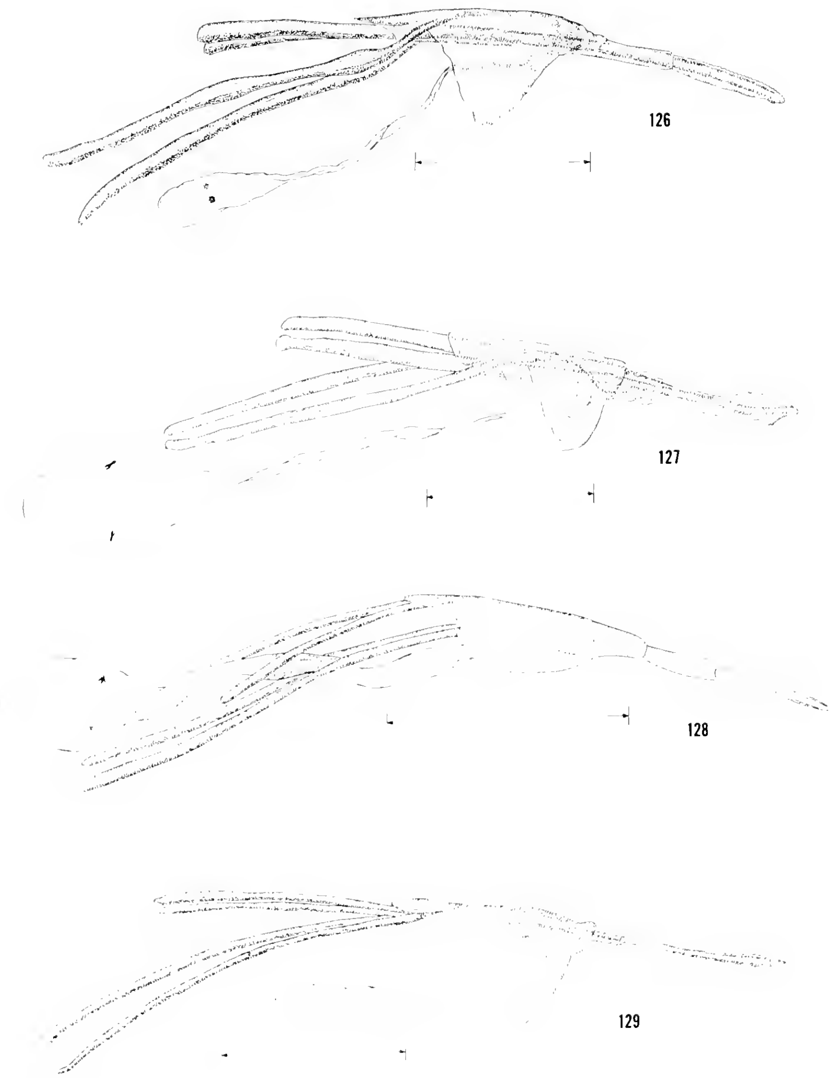
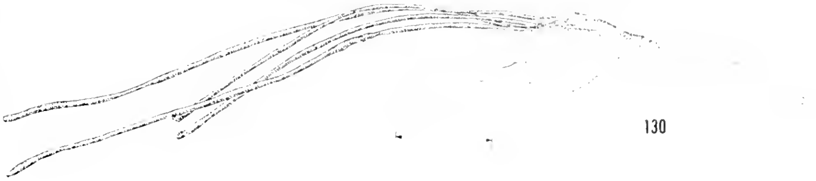
FIGURES 122–125.—Female genitalia: 122, *Prodoxus intricatus;* 123, *Prodoxus [illegible]*; 124, *Prodoxus marginatus;* 125, *Prodoxus pulverulentus.* (Scale 1.0 mm.)



FIGURES 126–129.—Female genitalia: 126, *Prodoxus cinereus;* 127, *Prodoxus aenescens;* 128, *Mesepiola specca*, paratype; 129, *Agavenema barberella*, paratype. (Scale=1.0 mm.)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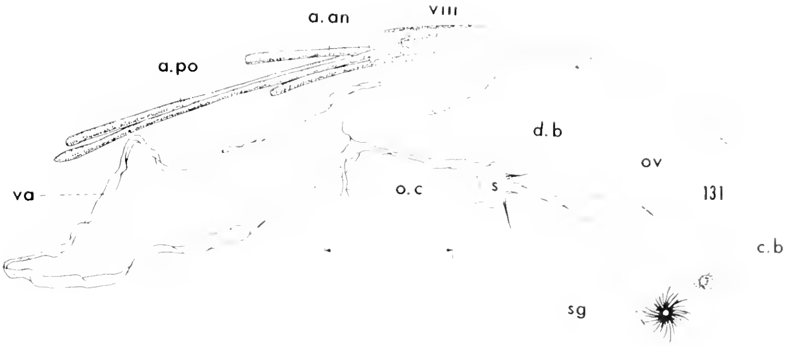
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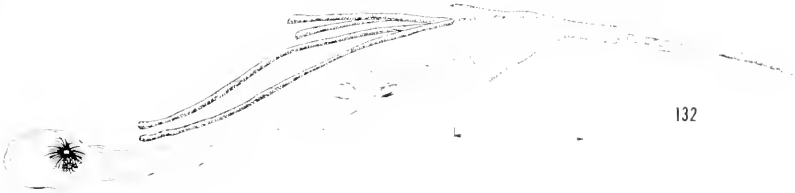
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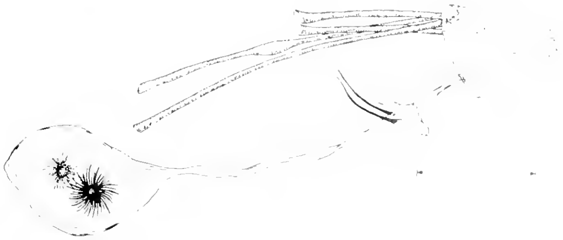
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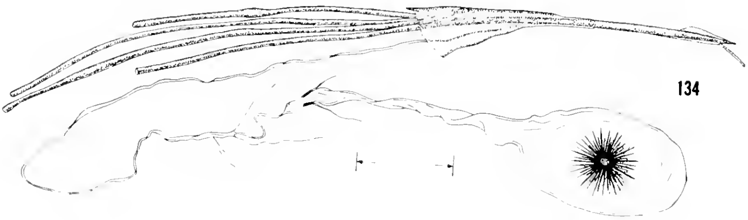
FIGURES 130–133.—Female genitalia: 130, *Agavenema pallida*, paratype; 131, *T. synthetica* (a.an=apophysis anterior; a.po=apophysis posterior; c.b=corpus bursae; d.b=ductus bursa; ov=ovipositor; o.c=oviductus communis; s=spermathecal duct; sg=signum; va=vagina; VIII=eighth abdominal segment); 132, *T. maculata maculata*; 133, *Tegeticula maculata extranea*. (Scale=1.0 mm.)



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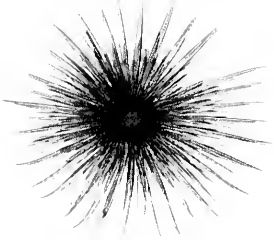

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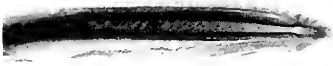

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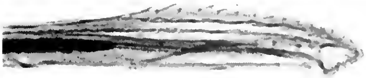
FIGURES 134–139.—Female genitalia: 134, *Tegeticula yuccasella;* 135, *Parategeticula pollenifera*, paratype; 136, signum of *Tegeticula yuccasella;* 137, *Prodoxus quinquepunctellus*, apex of ovipositor; 138, *Prodoxus y-inversus*, apex of ovipositor; 139, *Prodoxus coloradensis*, apex of ovipositor. (Scale=1.0 mm.)



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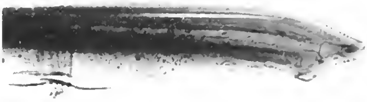

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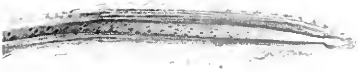

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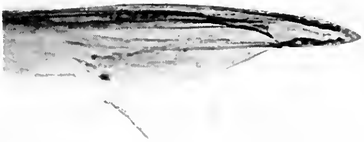
FIGURES 140–147.—Apex of ovipositors: 140, *Pr*[illegible], paratype; 141, *P*[illegible] *intricatus;* 142–143, *Prodoxus sordidus;* 144, *P*[illegible]; 145, *P*[illegible]*lentus;* 146, *Prodoxus cinereus;* 147, *Prodoxus ae*[illegible].



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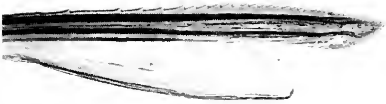

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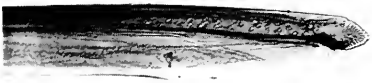

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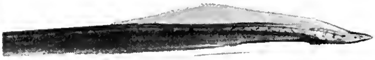

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FIGURES 148–155.—Apex of ovipositors: 148, *Mesepiola specca*, paratype; 149, *Agavenema barberella*, paratype; 150, *Agavenema pallida*, paratype; 151, *Tegeticula synthetica;* 152, *Tegeticula maculata maculata;* 153, *Tegeticula maculata extranea;* 154, *Tegeticula yuccasella;* 155, *Parategeticula pollenifera*, paratype.

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[Names of new genera and species in italics, page numbers of principal accounts in boldface]

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