

## VARIATION AND HOST SPECIFICITY IN THE YUCCA MOTH, *TEGETICULA YUCCASELLA* (INCURVARIIDAE): A MORPHOMETRIC APPROACH

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**ABSTRACT.** Moths presently recognized as *Tegeticula yuccasella* Riley were collected from flowers of *Y. baccata*, *Y. elata*, and *Y. torreyi* from Dona Ana County, New Mexico. All three yucca species occurred sympatrically and only *Y. elata* bloomed later than the other two. A morphometric analysis, using characters of the wings and genitalia and color of the antennae, was carried out on 225 individuals. The data were separated into three groups based on plant host species and analyzed using a stepwise discriminant analysis. Significant separation between the three groups resulted, with only three misclassifications. Three presumed separate taxa were described and compared based on the analysis, although it was not possible from this study to determine their relationship to nominotypic *T. yuccasella*. For this reason, no new specific names are given.

Mutualistic relationships between plants and insect pollinators occur frequently in nature. Insect dependence on the plant for reasons other than a nectar source, however, are much less common. The relationship between the orchid *Stanhopea* and Euglossinae bees, and that between wasps of the family Agaonidae and fig trees, are both examples of highly specific pollination relationships (Dressler, 1968; Ramirez, 1969). In these relationships, specific pollinators exist for closely related species of plants and maintain genetic isolation between the species with which they are sympatric. These highly specific pollination relationships provide a strong basis for speciation and genetic isolation (Baker, 1963).

The mutualistic relationship between the yucca plant and the yucca moth is well known (Riley, 1872; Trelease, 1893; and Rau, 1945). The female moth, with its specialized mouthparts for depositing pollen in the stigma of the pistil, is the only effective pollinator of yuccas. The moth does not obtain nectar from the plant but is dependent upon it for the development of its larvae. The female deposits eggs in the ovary of a flower where the larvae feed on seeds until reaching maturity.

In contrast to the examples above, specific yucca moth pollinators are not known for sympatric and closely related yucca plants, except in yucca moths which pollinate Californian yuccas. Only two moth species are thought to pollinate all other species of yuccas in the United States and Mexico. One of these, *Parategeticula pollenifera* Davis, is known only in southeastern Arizona and Mexico (Davis, 1967). The other moth, *Tegeticula yuccasella* Riley, as presently recognized, is widely distributed across the United States and Mexico.

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Davis (1967) found that variation in the wings and genitalia of *T. yuccasella* was greater than in any other member of the subfamily Prodoxinae. Davis examined individuals from 11 species of yucca across the geographic range of *T. yuccasella* and found that differences in the wing measurements could be ascribed to geographical variation but that differences in the genitalia could not. The variation in the genitalia showed a high correlation with plant host species. Davis proposed that possibly a specific pollinator had evolved for each of the four sections (subgenera) of *Yucca*. *Yucca brevifolia* Engelm. and *Y. whipplei* Torr., which belong to the sections Clistocarpa and Hesperoyucca, respectively, are found in California and have specific pollinators. Davis postulated that *T. yuccasella* was a specific pollinator for the section Chaenocarpa and that possibly a sibling species is in the process of evolving for the section Sarcocarpa.

Southern New Mexico presents an excellent opportunity to examine variation in *T. yuccasella* due to host specificity for two reasons. First, three species of yucca representing two sections of the genus occur sympatrically in the area. *Yucca baccata* Torr. and *Y. torreyi* Shafer are members of the section Sarcocarpa and *Y. elata* Engelm. is a member of the section Chaenocarpa. Second, this sympatry minimizes the occluding effects of geographical variation, and one can concentrate on variation due principally to plant host specificity.

Basic differences that exist in the ecology and morphology of these three yucca species may be important when considering host specificity in plant pollination. The flowers are different in position on the plant, shape, odor, and time of flowering. *Y. elata* bloomed approximately one month later than *Y. baccata* and *Y. torreyi*, which were blooming simultaneously. Since adult yucca moths emerge when yuccas are first blooming, it was possible to collect adults from *Y. baccata* and *Y. torreyi* at the same place and time; whereas, adults from *Y. elata* were collected at the same place but at a different time.

Two possibilities are being explored: either 1) a specific pollinator has developed for the section Chaenocarpa and another for the section Sarcocarpa; or 2) a specific pollinator exists for each of the three species of yucca in southern New Mexico. The latter implies that more than one moth species pollinates the section Sarcocarpa.

#### MATERIALS AND METHODS

*T. yuccasella* were collected from newly opened flowers of yuccas from seven cities in the Las Cruces area of Dona Ana County, New Mexico, during the spring of 1979. All collecting was done during the day when individuals were inside flowers and could be easily captured. Moths were normally only found in newly opened flowers; therefore,



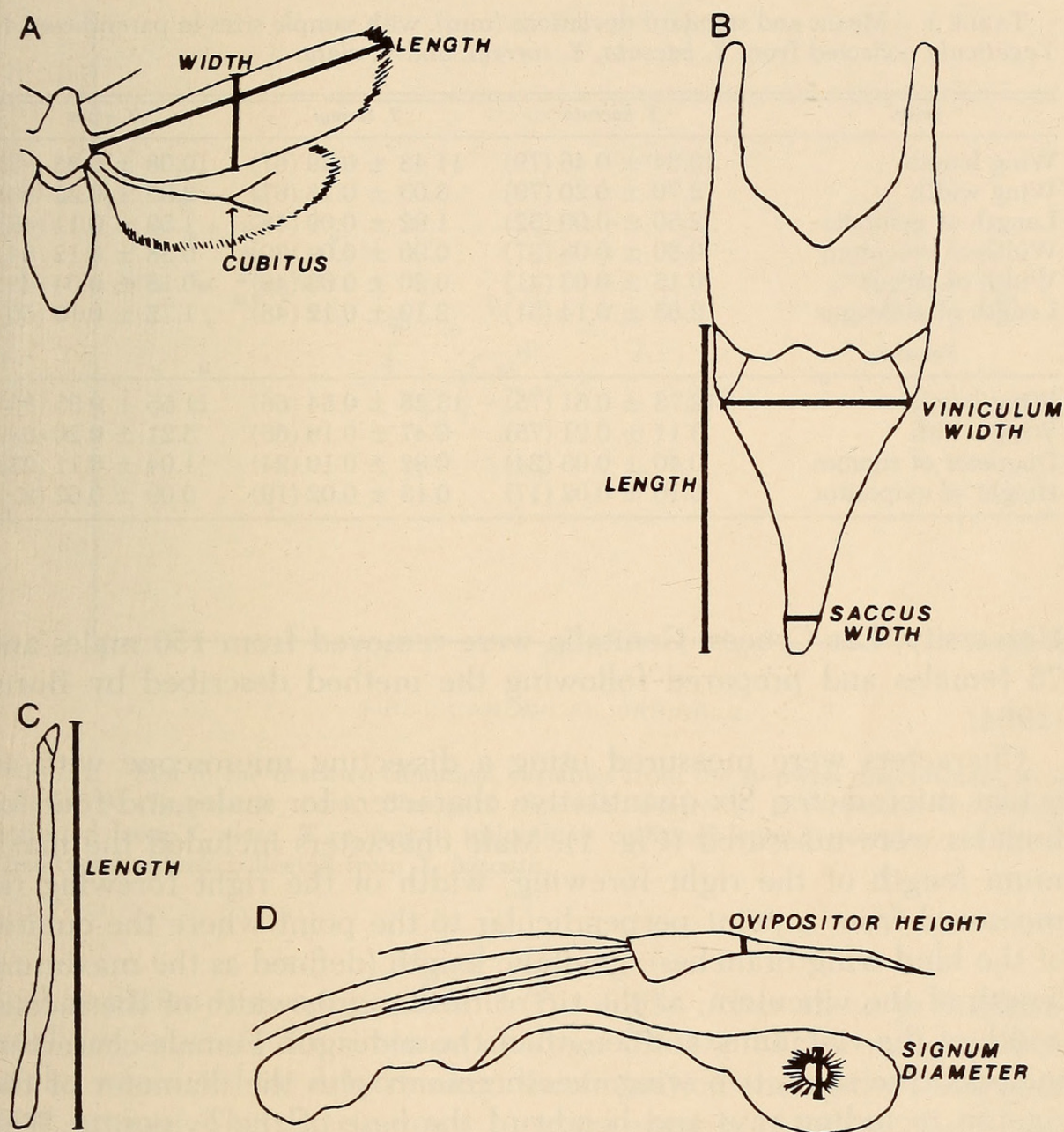


FIG. 1. Morphometric measurements taken from *T. yuccasella*: A, right forewing; B, male genitalia; C, aedeagus; D, female genitalia.

the number of suitable flowers at a given site on a given day was limited. An attempt was made to remove every moth from each plant found to be harboring moths. *Y. baccata* was first noted in bloom on 10 April, and had finished blooming by the last week in April. The first *Y. torreyi* seen in bloom was 14 April, and the last finished blooming by the end of April. *Y. elata* did not begin blooming until the third week in May although a few were observed in bloom until the end of June.

All specimens used in the morphometric analysis are deposited in the Museum of Entomology, Department of Biology, New Mexico State



TABLE 1. Means and standard deviations (mm), with sample sizes in parentheses, for *Tegeticula* collected from *Y. baccata*, *Y. torreyi*, and *Y. elata*.

Males	<i>Y. baccata</i>	<i>Y. torreyi</i>	<i>Y. elata</i>
Wing length	10.64 $\pm$ 0.46 (79)	11.43 $\pm$ 0.49 (67)	10.08 $\pm$ 0.63 (89)
Wing width	2.70 $\pm$ 0.20 (79)	3.05 $\pm$ 0.18 (67)	2.85 $\pm$ 0.22 (89)
Length of genitalia	2.50 $\pm$ 0.09 (52)	1.92 $\pm$ 0.09 (48)	1.53 $\pm$ 0.11 (49)
Width of vinculum	0.80 $\pm$ 0.08 (37)	0.90 $\pm$ 0.09 (30)	0.88 $\pm$ 0.12 (34)
Width of saccus	0.15 $\pm$ 0.03 (41)	0.20 $\pm$ 0.03 (46)	0.18 $\pm$ 0.04 (43)
Length of aedeagus	2.85 $\pm$ 0.14 (51)	2.19 $\pm$ 0.12 (48)	1.72 $\pm$ 0.13 (50)
Females			
Wing length	12.73 $\pm$ 0.61 (75)	13.28 $\pm$ 0.54 (66)	11.55 $\pm$ 0.55 (86)
Wing width	3.11 $\pm$ 0.21 (75)	3.47 $\pm$ 0.18 (66)	3.21 $\pm$ 0.20 (86)
Diameter of signum	0.40 $\pm$ 0.03 (24)	0.82 $\pm$ 0.10 (24)	1.04 $\pm$ 0.11 (23)
Height of ovipositor	0.10 $\pm$ 0.02 (17)	0.13 $\pm$ 0.02 (19)	0.09 $\pm$ 0.02 (21)

University, Las Cruces. Genitalia were removed from 150 males and 75 females and prepared following the method described by Burns (1964).

Characters were measured using a dissecting microscope with an ocular micrometer. Six quantitative characters for males and four for females were measured (Fig. 1). Male characters included the maximum length of the right forewing, width of the right forewing (as measured from a point perpendicular to the point where the cubitus of the hind wing branches), genitalic length (defined as the maximum length of the vinculum, to the tip of the saccus), width of the saccus, width of the vinculum, and length of the aedeagus. Female characters included the same two wing measurements plus the diameter of the signum including rays and height of the base of the ovipositor. The genital nomenclature follows Klots (1956). In addition to these quantitative characters, a single qualitative character was analyzed: in both males and females the color of the antennae. Seven categories were established: two categories were all yellow or all brown and the remaining five were bicolored as follows: white-black, light brown-black, white-yellow, white-brown, and light brown-yellow.

Six groups were obtained by separating according to the three host species and sexes of the insects. All analyses and programs used were of the BMDP series developed by the Health Science Computing Facility, University of California (Dixon, 1975). Basic statistics (BMDP1D) were carried out for each group to obtain means and standard deviations. Each of the six groups was subdivided by collecting sites and analyzed via analysis of variance (BMDP1V) to test for differences in means among localities. This was carried out to ensure that geograph-



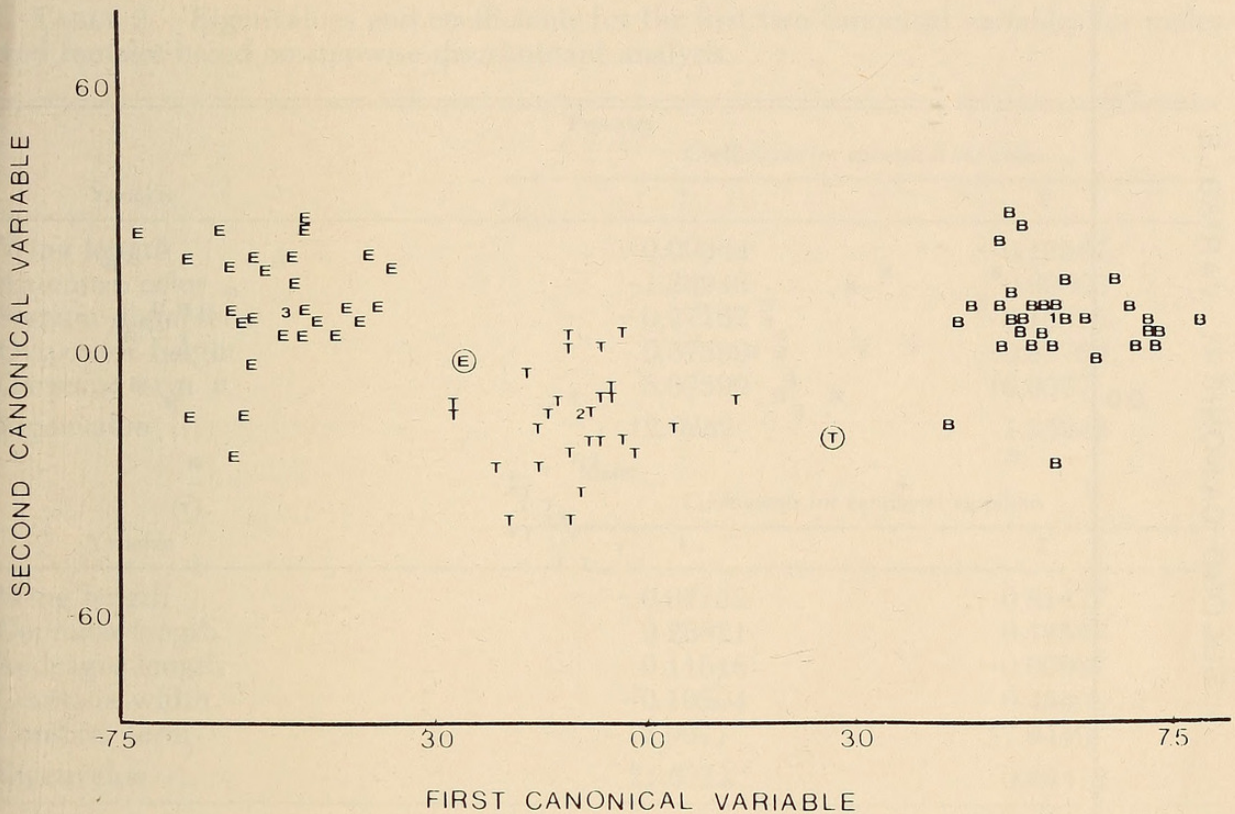


FIG. 2. Plot of the first two canonical variables from the stepwise discriminant analysis for 91 *Tegeticula* males. Numbers represent centroids; **E** represents individuals collected from *Y. elata*, **T** represents individuals collected from *Y. torreyi*, and **B** represents individuals collected from *Y. baccata*.

ical variation was nonsignificant ( $P < 0.05$ ). After these preliminary analyses, separate discriminant analyses (BMDP7M) for males and females were used for determining discrimination among the three plant host groups. The discriminant function used is based on the Mahalanobis  $D^2$  value, a measure of the metric distance between population centroids (Atchley & Bryant, 1975).

### RESULTS

Two hundred and twenty-five moths were measured (Fig. 1). Wing and genitalic characters were quite distinct for each plant host group and are given in Table 1.

Fig. 2 shows the plot of the first two canonical variables for each of the three groups of males. The variables entered in their order of significance were length of the genitalia, wing length, length of the aedeagus, and width of the saccus. Of 91 individuals (the remaining cases were dropped because they contained missing data) there were only two misclassifications, giving an overall percent correct classification of 98.9. Misclassifications are circled on the figure.



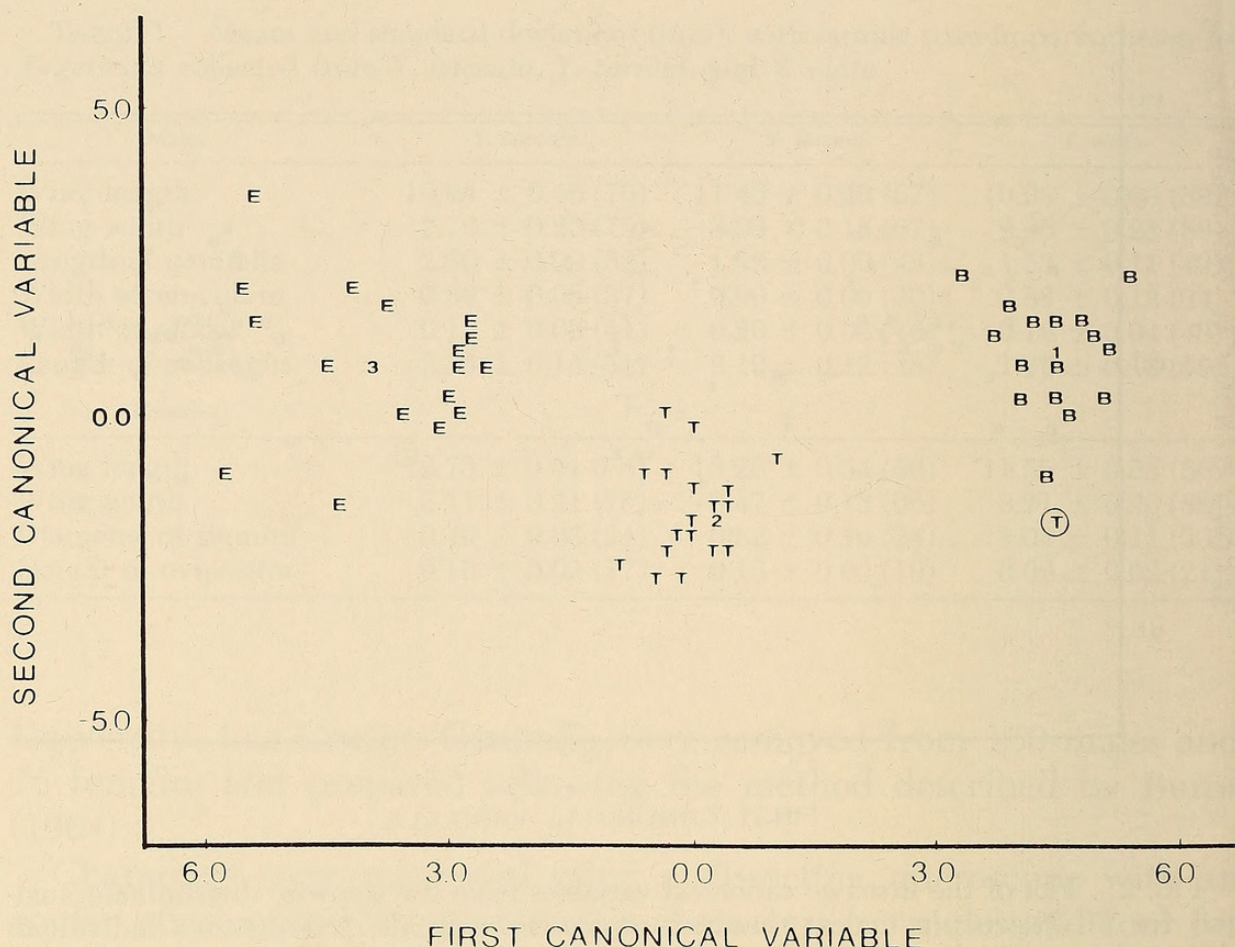


FIG. 3. Plot of the first two canonical variables from the stepwise discriminant analysis for 54 *Tegeticula* females. Numbers represent centroids; **E** represents individuals collected from *Y. elata*, **T** represents individuals collected from *Y. torreyi*, and **B** represents individuals collected from *Y. baccata*.

Fig. 3 shows the plot of the first two canonical variables for each of the three female groups. Signum diameter, antennal color, ovipositor height, and wing length were the characters entered in their order of significance. There was only one misclassification out of 54 individuals, giving an overall correct classification of 98.1%.

Table 2 shows the eigenvalues and coefficients for the first two canonical variables for both sexes. The first canonical variable is the linear combination of characters added that best discriminates among the groups.

A separation of groups of this magnitude with such little misclassification is strong evidence that three distinct taxa are present, especially when coupled with the host-specificity and sympatry data. It appears that three taxa of moths exist in southern New Mexico among populations previously considered to represent one species, *T. yuccasella*. One of the taxa revealed by the discriminant analyses may represent a geographical component of nominotypic *T. yuccasella*. Further re-



TABLE 2. Eigenvalues and coefficients for the first two canonical variables for males and females based on stepwise discriminant analysis.

Variable	Females	
	Coefficients for canonical variables	
	1	2
Wing length	-0.00364	-0.12587
Antennae color	-1.23943	0.69803
Signum diameter	-0.27162	-0.15915
Ovipositor height	0.37599	-0.88764
Constant term	8.37599	16.0337
Eigenvalue	12.0282	1.55944
Variable	Males	
	Coefficients for canonical variables	
	1	2
Wing length	-0.04152	-0.21477
Genitalia length	0.23821	0.12548
Aedeagus length	0.11516	-0.09967
Genitalia width	-0.19504	-0.49490
Constant term	-17.9077	17.9449
Eigenvalue	21.6712	0.89412

search needs to be conducted to determine the hierarchic ranking of the three taxa. Therefore, I include a diagnosis of each below without proposing formal names.

COMPARISON OF TAXA STUDIED

*Tegeticula* ex *Y. baccata*: Head white, with antennae usually white for the first half of length and black to tip, or occasionally antennae appear completely black due to wear; maxillary tentacle fully developed and labial palpus brown; thorax white; forewings white dorsally except for almost black fine line along proximal half of length of costal vein; forewings dark gray ventrally except for white fringe; length of the forewings 9.43 to 11.7 mm in males and 11.43 to 14.14 mm in females; hind wings dark gray dorsally, hind wings dark gray ventrally for costal one-third of length and lighter posterior two-thirds; fringe of hind wing gray, occasionally white; abdomen pale brown dorsally and white ventrally. Genitalia (Fig. 4): tegumen bilobed with lobes widely separated; saccus elongate and narrow; aedeagus elongate and slender, length 2.4 to 3.1 mm; ovipositor with convex minutely serrate ridge with slightly more than 30 teeth; height of the base of the ovipositor intermediate between other two species; signum and rays small with diameter 0.32 to 0.47 mm; number of rays exceeds 20.

This form was only collected from newly opened flowers of *Y. baccata* with the exception of six individuals collected on *Y. torreyi* flowers. These six individuals emerged after all available *Y. baccata* flowers were gone and *Y. torreyi* was the only yucca in bloom.

*Tegeticula* ex *Y. elata*: Head white, with antennae brown, yellow or bicolored white-brown; maxillary tentacle usually fully developed and labial palps brown; thorax white; forewings white dorsally except for fine black line along costal vein; forewings tan ven-



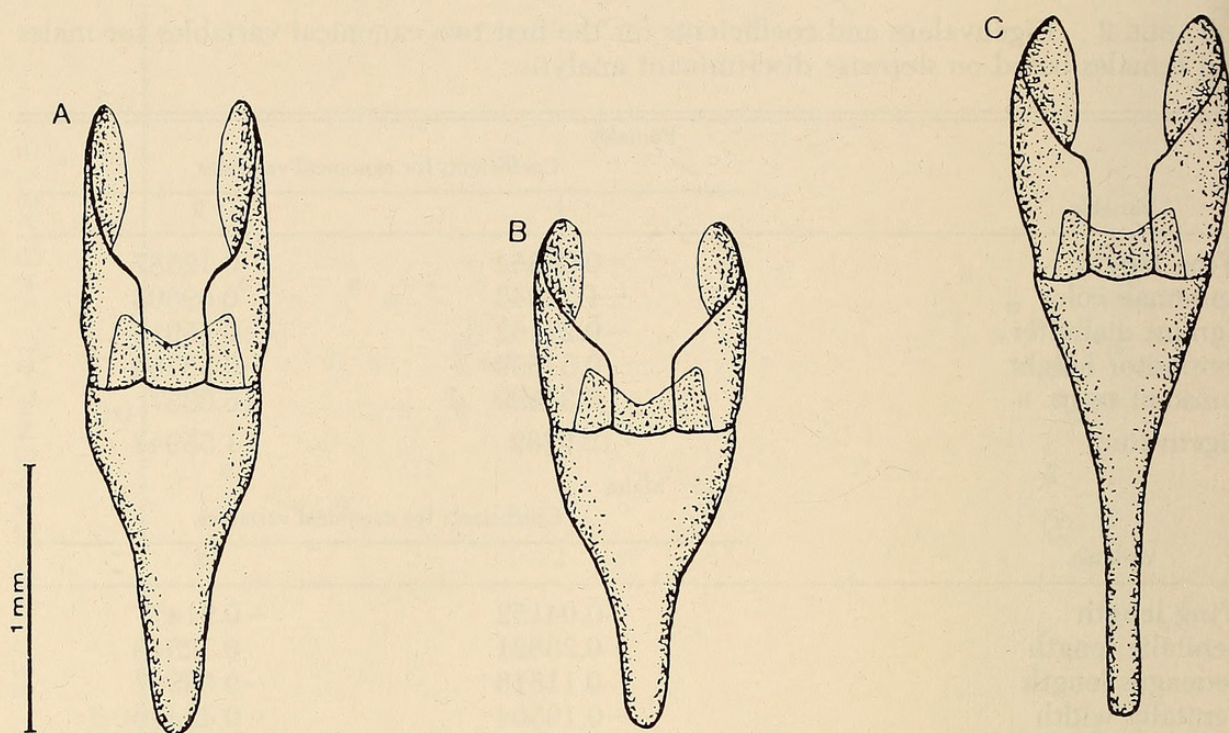


FIG. 4. Drawings of male genitalia: A, *Tegeticula* ex *Y. torreyi*; B, *Tegeticula* ex *Y. elata*; C, *Tegeticula* ex *Y. baccata*.

trally except for white fringe; occasionally white extends into margin of wing slightly; length of forewings 8.57 to 11.86 mm in males and 10.07 to 13.29 mm in females; hind wings tan to almost white dorsally; hind wings brown ventral costal one-third of length and white posterior two-thirds; fringe on hind wings white; abdomen white dorsally and ventrally. Genitalia (Fig. 4): tegumen bilobed with lobes widely separated; saccus much shorter and wider than in *Tegeticula* ex *Y. baccata*; aedeagus also much shorter, length 1.4 to 2.0 mm; ovipositor with minutely serrate ridge with slightly more than 30 teeth; height of the base of the ovipositor lowest of the three species; signum and rays largest in diameter of the three species, diameter 0.90 to 1.30 mm; number of rays exceeds 20.

This form was collected in newly opened flowers of *Y. elata*. This was the only available yucca species in bloom at the time these moths were active.

*Tegeticula* ex *Y. torreyi*: Head white, with antennae yellow or bicolored white-yellow; maxillary tentacle fully developed and labial palpus brown; thorax white; forewings white dorsally except for fine black line along costal vein; forewings gray ventrally with white fringe; gray lighter than in *Tegeticula* ex *Y. baccata*; length of forewings 10.43 to 13.00 mm in males and 12.14 to 14.57 mm in females; hind wings light gray ventrally, costal one-third of wing darker gray than posterior two-thirds; abdomen pale brown dorsally and white ventrally. Genitalia (Fig. 4): tegumen bilobed with lobes widely separated; saccus elongate but not as much as in *Tegeticula* ex *Y. baccata*; saccus wider than *Tegeticula* ex *Y. baccata*; aedeagus elongate and slender, length 2.0 to 2.8 mm; ovipositor with minutely serrate ridge with slightly more than 30 teeth; height of the base of the ovipositor intermediate between the other two species; signum and rays only slightly more narrow than *Tegeticula* ex *Y. elata*, diameter 0.43 to 0.93 mm; number of rays exceeds 20.

This form was collected from newly opened flowers of *Y. torreyi*. *Y.*



*baccata* was also in bloom at the same time but no individuals were collected from that plant.

### Species Diagnosis

The characters that are best for distinguishing among the three moths are antennal color, wing color, abdomen color, male genitalia length and width, aedeagal length, signum diameter, and height of the base of the ovipositor. The genitalia and wing measurements given by Davis (1967) for *T. yuccasella* are highly variable and overlap those of these three moths in each case and cannot be used to separate them. It should be noted that the measurements taken by Davis included individuals collected from *Y. baccata*, *Y. elata*, and *Y. torreyi* in southern New Mexico and probably do not all represent *T. yuccasella*.

### DISCUSSION

The results of this study support the hypothesis that a single species of moth exists for each of the three species of yucca in southern New Mexico. The data do not support Davis' hypothesis (1967) that one species exists for each of the sections of the genus *Yucca*. *Tegeticula* ex *Y. baccata* and *Tegeticula* ex *Y. torreyi* both have hosts within the section *Sarcocarpa* and are quite distinct morphologically. *T. yuccasella* as described by others, then, is a composite species. The study also implicates that in the Las Cruces area, one of these three moths may represent a subspecies of nominotypic *T. yuccasella*. To answer this question, additional studies similar to this one need to be carried out at other localities between southern New Mexico and Missouri (the collection locality for the holotype of *T. yuccasella*). Moreover, analyses of yucca moths and their hosts over broader geographic ranges may identify additional species of *Tegeticula*.

Justification for assigning specific status to these three taxa would stem from morphological distinctness and fidelity to species of yucca. Samples collected from the same locality can be either individual variants of the same species or else different species (Mayr, 1969). In deciding between the two alternatives, it is important to examine characters such as the genitalia which are not subject to a great deal of individual variation and look for intermediacy between the groups. If differences among groups are found consistently in unrelated characters, specific rank is further implicated (Mayr, 1969). All three groups from this study are sympatric and show differences in the genitalia, as well as other very different characters such as wing length and antennal color. No individuals with intermediate characters were found and this indicates an absence of gene flow, particularly between moths collected



on *Y. baccata* and *Y. torreyi*, where blooming times were simultaneous. Temporal isolation appears to exist among the *Y. elata* group and the two previous groups, because blooming times and thus time of moth emergence are a full month apart. Since moths only live two to three days, overlap between breeding periods is not possible. Therefore, blooming times serve as a principal mechanism for isolating the *Y. elata* group from the other two groups in the area. Following the above criteria, moths taken from the three plant host species are themselves distinct species.

Six *Tegeticula ex Y. baccata* were collected from flowers of *Y. torreyi*. Two of these were included in the discriminant analysis and account for misclassifications. These moths emerged in an area where all the *Y. baccata* had finished blooming and *Y. torreyi* was the only available flowering yucca. This shows that, although moths usually maintain host specificity, individuals potentially can and do use alternate yucca hosts if the preferred host is unavailable. The fact that these individuals were observed in the presence of *Tegeticula ex Y. torreyi* further supports the conclusion that there is no gene flow between the two because no intermediates were observed.

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