

NOTES ON PRONUBA AND YUCCA POLLINATION.*

BY PROF. C. V. RILEY.

Partly because of more pressing duties, partly because of a desire to make some special experiments, but chiefly in the hope that (after the fruiting season of the dehiscent *Yuccas* was over, and Mr. Hulst had been able to make more careful observations) he would himself gracefully amend his opinions to accord with the facts, I have deferred answering till now the remarks by Mr. Hulst on pp. 236-238 of vol. ii, *Ent. Amer.* The matter is too important to drop, and I have too much regard for my critic personally, and hope for his future entomologically, not to do what little I can to check an unfortunate tendency to hasty work and conclusion, noticeable in this as in some other of his late writings.

Mr. Hulst "confesses the corn" in reference to my first complaint, and is inclined to blame the report for his misrepresentations—an inclination which would have more of my sympathy were he not editor of the paper.

It is, however, far more important, from the scientific side, that he confess to the justness of my second indictment, and it is to this end that I return to the subject.

Mr. Hulst adheres to his belief "that there must be very extensive fertilization of the dehiscent species of *Yucca* by the agencies of bees and other insects." He does not bring forth a single definite fact or observation of actual pollination to prove or sustain the belief, but rests it on the following grounds:

1st. That Meehan found that the mere application of pollen to the papillose apex of the stigma is sufficient for fertilization.

2d. That he (Hulst) has seen honey-bees within the open as well as the partly open flowers, as also other insects, Aphides and Coccinellidæ being particularly mentioned.

3d. That not one in ten of the capsules subsequently examined by him showed the larva.

4th. That he is informed that dehiscent species of *Yucca* do ripen seeds in Europe.

Such are the negative arguments upon which he rests his belief in the face of all the *facts* I have put on record. Let us consider the former briefly in their order.

1st. My good friend Meehan has written much on the fertilization of

* In explanation of the controversial nature of this communication, it becomes necessary to refer to a dispute on this subject between the Rev. G. D. Hulst and myself in the columns of *Entomologica Americana* during the summer of 1887. The communication is a reply to Mr. Hulst's last publication on the subject, and is presented *verbatim et literatim* as written on my way to Europe in August of that year, and as mailed to him from England. Mr. Hulst is editor of the aforesaid journal, and exercised his editorial prerogative in declining to publish the communication. I have, therefore, concluded to present the paper to the Society, since it discusses matters of considerable scientific interest.

Yucca—much, too, that has not shown the keenest penetration nor the strictest accuracy. But, in candidly admitting his errors when shown to be wrong (as he has done to the writer and, I have reason to believe, to Mr. Hulst, who sought his support in the belief here combated), he has proved himself to be the true naturalist. I am familiar with his experiments, having witnessed the results, and can best express my own opinion by quoting from a letter from the late Dr. G. Englemann (written Jan. 10, 1881), in which among other things he says: * * * “As to Meehan’s operations I have seen myself the fine, large, well-filled pods of *Yucca angustifolia* raised by him by his artificial method. He says he punches an anther into the stigmatic cavity. Whether he or anybody else could distinguish whether the pollen adheres only to the papillose (not stigmatose) apex or gets into the liquor that fills the cavity when the stigma is ready to conceive, is a question (or no question)!” Meehan’s experiments were made on a species in which, as I have elsewhere shown, the stigma is shorter and the stigmatic liquor more abundant than in *Yucca filamentosa*, and it may be that for these or other reasons it is more easily pollinized by hand or by other means than by *Pronuba*. But I have followed up his experiments and made many others during the past seven years, on *filamentosa* and *aloifolia*, with results that convince me that application of the pollen to the papillose apices only is not sufficient to insure fructification, at least in those species. My experiments have been made in the afternoon, evening, and morning; with flowers one day, two days, and three days after opening; with pollen from the same flower or from other flowers either on the same or other racemes; by touching the mere apices with anther or brush, and by forcing the pollen by either conveyance into the stigmatic tube. In these experiments, which have not yet been published, and which it is unnecessary to detail here, I have endeavored to guard against all influences, such as the condition of the plant and the weather, which might affect or vitiate the results. These may be summed up thus:

(1) Dr. Englemann’s limit of time during which fertilization may take place must be extended so as to include the second evening, and even the second morning, after the opening of the flower.

(2) No seed has been produced by merely touching the apices of the stigma with the pollen, though partial fertilization may take place and cause the growth of the fruit for a varying period, generally only three or four days. When the pollen is thrust into the tube (the mode of conveyance making little difference) fertilization is much more certain, but even here is rarely sufficient to produce ripe seed, the upper part of the pod often filling well, but the basal part not filling, and at last withering so that the fruit ultimately falls off before ripening.

The conclusion is inevitable that *angustifolia* is more susceptible to artificial pollination than the species which I experimented with, and that *Pronuba* far excels man in the perfection with which she performs the act. She has the power of fertilizing all the ovules, at which no one will wonder who has carefully watched her, because the act of pollination is normally

repeated several times, first from one of the angles between the apices, then from another, and, as Prof. Wm. Trelease has shown, the tongue is used, in addition to the tentacles, to push the pollen down to the bottom of the tube.

2d. I have made careful search the past summer, and have had my associates, Messrs. Howard, Pergande, and Luggler, assist in the search for honey-bees in or about the *Yucca* flowers in Washington. There were over 200 stalks under observation, most of them of easy access on the grounds of the Department of Agriculture. Neither of the three gentlemen mentioned detected any bees, but I succeeded on two occasions, and each time between 9 and 10 a. m., in finding a single bee flying about the flowers. In neither case did the bee make any attempt to enter, but in each it probed around the outer base of the flower in search for nectar, and soon left evidently without being able to get much. These facts I record, not in any way to cast discredit on Mr. Hulst's statement, but rather to show how very different from his own has been my experience in this direction, both in St. Louis and Washington. Not that I place much faith in the constancy of bees, which are known to be somewhat fickle in their tastes according to season or colony, a fact that may account for the difference in our experience, as may also the presumption that *Apis mellifica* is more abundant in Brooklyn than in Washington, or, again, the known fact that *Yucca angustifolia* is less scant in nectar than its filamentose congener. Be that as it may, our *Apis* has plainly, so far as observed, been after nectar, and has shown no disposition whatever to go near the stigma, and this fact is, as I have learned, corroborated by Professors Cook and Beal, of the Michigan State Agricultural College, where, for the first time this year, they have observed honey-bees about the *Yucca* flowers. It is further corroborated by experiment which I made this summer of confining bees to the flowers within a gauze enclosure.

As for pollination by other insects, *Chauliognathus pennsylvanicus*, which feeds on both pollen and the nectar, is the most common species found in the flowers, and by virtue of these habits and its peculiarly modified mouth-parts, is most to be suspected; yet I have carefully watched it for years, only to be convinced that it never either assists or competes with *Pronuba* in the act of pollination.

3d. This argument has already been disposed of in my previous communication (vol. ii, p. 238, summary iv), and it is only necessary to add, that until Mr. Hulst is more exact, and will tell us what proportion of his pods containing no larvæ also showed no signs of oviposition (*i. e.*, how many were perfect without sign of puncture or constriction or irregularity about the middle), we shall not even know how many the little moth pollinized without getting a chance to perform the other (to her) important act.

4th. This is contrary to my own experience in Europe, and to all authoritative record familiar to me, and until Mr. Hulst gives us his authority and the evidence, it were sheer waste of time to further discuss the point.

I have thus disposed of all the valid arguments brought forward by Mr.

Hulst to sustain his position on this matter. I may briefly notice, however, a little satire which he indulges in at my expense, and a quite irrelevant assertion which happens also to be incorrect.

As one deeply interested in apiculture and a practical bee-keeper twenty-seven years ago, it was, perhaps, unpardonable in me not to qualify the statement about bees not being attracted to white flowers. Both Müller, in his "Alpenblumen," and Lubbock, in "Ants, Bees, Wasps," etc., have shown that bees prefer blue and purple to white flowers, and this is what was meant on the face of my language, so to speak; but Mr. Hulst has naturally made the most of the *lapsus*, and scored a point where every other point is against him.

The assertion which I would call attention to, and which is entirely beside the question at issue, is that "we are indebted to Dr. Engelmann for the discovery of the fact that *Pronuba* is an agent in the fertilization of *Yucca*."

Whatever may have led Mr. Hulst to make this assertion, it is simply untrue, and the facts, which I may as well put on record here, are these: In June, 1872, Dr. Engelmann, who then knew full well that *Yucca* needed extraneous aid in fertilization, called my attention to this fact, and to the further fact that insects, especially white moths and soldier-beetles (*Chauliognathus*), were common in the flowers. He made no observations whatever upon insect pollination, but wished me to study the question. The discovery that *Pronuba* was the agent was my own, as were all the subsequent discoveries in reference to the insect made that year; but they were always communicated to him, and often shared with and witnessed by him. My first paper on the subject was read in August, 1872, before the A. A. A. S., at its Dubuque (Iowa) meeting, and presented to the Academy of Sciences of St. Louis at the meeting for September 2, 1872. Dr. Engelmann's "Notes on the genus *Yucca*" were presented to the same Academy September 16, 1872. Both papers are printed in vol. iii of the Transactions of the Academy, Dr. Engelmann's preceding, because leading up to mine. In his paper Dr. E. says: "The *suspected* insects were handed over to my friend Mr. C. V. Riley, who thereupon took up the zoölogical part of the investigation, the surprisingly interesting results of which are detailed by him in the succeeding paper" (Trans., etc., iii, p. 19), and I distinctly express my indebtedness to him "for drawing my attention to the fact that the plants of this genus must rely on some insect or other for fertilization." It is quite probable that but for Dr. Engelmann's suggestion I should never have made the investigations, and he should share with me whatever honor attaches to the discovery. If this is what Mr. Hulst means his language is unfortunate. Dr. Engelmann was, during my residence in St. Louis, at once my friend, companion, and master in natural history matters, and I have too much reverence for his memory to allow to pass unchallenged what he himself would repudiate were he still among us. As soon as I had learned that *Pronuba* was the agent he sent a brief announcement to the Bulletin of the Torrey Botanical Club (vol. iii, No. 7, July, 1872, p. 33) rather hastily

referring to the insect as "a white moth of the genus Tortrix," and in a subsequent communication (*ibid.*, August, 1872, p. 37) he corrected the error and recorded some further facts in the life-history of the insect. In neither case was there any claim of individual discovery of the entomological facts, and these announcements must be read in the light of his subsequent more deliberate language which I have quoted.

In conclusion, having already devoted more time to Mr. Hulst's opinions than they justify, let me add that another year's study of *Yucca* fertilization has not only served to confirm all that I have hitherto written, but still further to enhance the importance of *Pronuba* to the plant and the intelligent nature of her unique performances. Prof. Wm. Trelease, who has made the only other careful observations on the subject which have come to my notice, has demonstrated (Bull. Torrey Bot. Club, Aug., 1886, pp. 135-141) that the stigmatic liquor is not nectariferous, but that the slight amount of nectar associated with the flowers is secreted in thin pockets formed by the partitions that separate the three cells of the pistil, and which open externally by a contracted pore from which the nectar is poured through a capillary tube (enclosed by the closely applied, but not outwardly united, lobes of the ovary) to the base of the pistil, so that nectar-feeding insects seek it not about the stigma, but at the base of the pistil or of the petals, whether within or without. I have fully verified Trelease's statements by dissection and study of the insects seeking this scant nectar, and endorse his conclusion that while the observations serve to disprove any positive value of their nectar in the pollination of *Yucca* flowers, they add to the importance of *Pronuba* by showing that the acts of collecting the pollen and transferring it to the stigma are performed voluntarily and without food compensation as I was at first inclined to believe.

I have lately had the pleasure of studying *Yucca whipplei* in California and the remarkable tree-yucca (*Y. brevifolia*) in the Mojave desert. The former is pollinized by *Pronuba maculata* Riley, and the latter by a most remarkably modified and adapted species which I expect to describe as *Pronuba paradoxa*.

Thus everywhere in the United States where *Yucca* nominally fruits we find it associated with its *Pronuba*.

I await with interest and curiosity any new discoveries in this connection, but, so far as present knowledge justifies anticipation, I should expect, where neither *Pronuba* nor *Pronuba*-like insect exists, to find the plant modified to more readily permit self-fertilization sooner than to find *Apis mellifica* the pollinizing agent, the opinion of Mr. E. L. Layard, of New Caledonia (who first expressed it in 1880; *Nature*, vol. xxii, p. 606), and of Mr. Hulst, to the contrary notwithstanding.

On board the "City of Rome," Aug. 22, 1887.

Mr. Schwarz said, commenting on Müller's statement that bees do not visit white flowers, that Müller was not speaking of food flowers at the time, but what he calls bee flowers.

Mr. Howard thought that Prof. Riley's experiments, confining bees with *Yucca* which they did not touch, were conclusive.

Mr. Smith said that the habits of an insect in one locality are not necessarily the same as in another. Both Mr. Hulst and Prof. Cook had seen bees on *Yucca*. On Long Island he had found *Lachnosterna* in great abundance on blackberry blossoms. Mr. Townsend had found them in Michigan with similar habits. He had this season failed to find a single specimen on the flowers near Washington, though there were plenty of beetles all around.

Prof. Riley reasserted the similar fact regarding bees, which were often very capricious, but showed that, where they do visit the *Yucca* flowers, they have nothing to do with fertilizing them, and, even in artificial pollination by man, perfect fruit can only be obtained when the pollination is done as fully and carefully as it is done by *Pronuba*.

Prof. Riley read the following paper :

TWO BRILLIANT AND INTERESTING MICRO-LEPIDOPTERA NEW TO OUR
FAUNA.

By C. V. RILEY.

I have had for some time, as a part of the material which I have turned over to the National Museum, two small moths of exceptional brilliancy and beauty, which are new to our fauna and which I took occasion to study while in Europe last autumn. As a rule, I do not care to present isolated descriptions of species, but in both these instances there are special reasons for departing from this rule, as the first is one of the largest and prettiest of the Tineina, having a superficial Tortricid habitus, and the second is interesting as belonging to a small group essentially exotic, which has been placed by authors both in the Tineidæ and the Tortricidæ, and which virtually is a somewhat interesting form belonging rather to the lower Noctuidæ. I name them in honor of two of our most capable and most worthy micro-lepidopterists, and in each case with permission.

SETIOSTOMA FERNALDELLA n. sp.—Expanse, 12-13 mm. General colors, vivid pea-green, yellow, and metallic bronze. *Head*, vivid pea-green, approaching in some instances to olivaceous; face and palpi paler, more yellowish. *Thorax* of the same vivid green, somewhat more yellowish on the borders, but especially on the collar, which is separated from the mesothorax by a fine black suture. Primaries of the same vivid green at basal third, posteriorly limited by a straight line which slightly obliques outwardly