PAPERS READ.

Further notes on the Pollination of Yucca and on Pronuba and Prodoxus. By C. V. Riley, of Washington, D. C.

At the Dubuque meeting of the Association, in 1872, it was my privilege to lay before you the substance of a then unpublished communication to the Academy of Science of St. Louis, embodying sundry facts regarding an interesting and anomalous little moth (*Pronuba yuccasella*, fig. 1), and its connection with the pollination of our Yuccas. The observations were made in the year 1872 and are recorded, with additional facts ascertained in 1873, in the Transactions of the above-named Academy (Vol. III, pp. 55–64 and 178–180), the *American Naturalist* (Vol. VII, Oct. 1873) and my 5th and 6th Reports on the Insects of Missouri. As the facts have never been published in our Proceedings, I will present the more important of them by brief recapitulation.

The moth (fig. 2, *b*, *c*,) has an immaculate white upper surface, and fuscous under surface in both sexes, and rests during the day for the most part within the half-closed flowers, the protective coloring of which serves to conceal it. The male possesses no very marked characters, but the female is most anomalous; *first*, in possessing a pair of prehensile, spinous, maxillary tentacles (fig. 1, *b*) found, so far as we now know, in no other genus of Lepidoptera; *second*, in possessing a long, horny ovipositor (fig. 1, *j*, and fig. 3), adapted to piercing and penetrating — a structure equally exceptional among Lepidoptera: "When the ovipositor is entirely withdrawn, the tip of the abdomen [fig. 3, *a*] presents a truncate appearance, the terminal joint being bluntly rounded at tip, with a slight projection both above and below, and a corrugated ridge dorsally a little in advance of the tip. This terminal joint is very much compressed from the sides, with a few stiff hairs around the terminal borders. The ovipositor issues from the middle of the truncate end, is very fine, tubular, the basal

joint [fig. 3, *b*] beautifully imbricato-granulate, the terminal joint [fig. 3, *d*] perfectly smooth, long and peculiarly constructed at tip, the extreme tip being notched or serrate, and a dorsal membrane, also finely and sharply serrate, running anteriorly from it—the whole recalling in form the caudal and second dorsal fins of the Lamprey (*Petromyzon*). Ventrally along the terminal joint is seen a membranous duct which broadens just in front of the tip and has an outlet from which a soft and extensile oviduct can be extruded [fig. 3, *e*]. The whole structure is, in fact, admirably adapted to cleaving through the fruit of the Yucca and then running into the ovarian cavity."—*Am. En-*

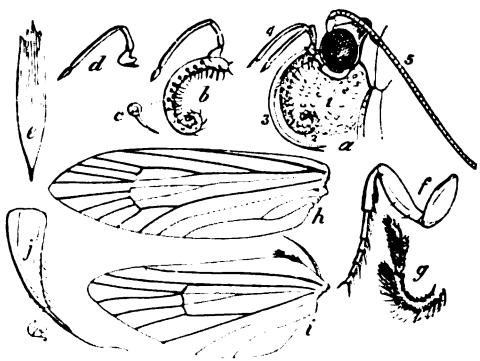

FIG. 1.—PRONUBA YUCCASELLA: Generic characters—*a*, side-view of head and neck of female denuded, showing how the collected load of pollen (1) is held by the tentacles (2); *b*, maxillary tentacle and palpus; *c*, an enlarged spine; *d*, palpus separated; *e*, scale from front wing; *f*, front leg; *g*, palpus; *h*, *i*, front and hind wings denuded; *j*, anal joint of female with ovipositor.

tomologist, III, p. 182.—Within the abdomen the ovipositor divides into four stout, horny rods which extend nearly its whole length, the upper pair being continuations of and aiding in the protrusion of the terminal joint of the ovipositor, the lower pair connected with the basal joint thereof. A careful study of the ovipositors, in the different species of *Pronuba* and *Prodoxus*, characterized in this paper, shows that they are all formed upon the same plan and that their diverse characters are but modifications of this typical form. They all agree in forming a solid piercing organ, which shields the exsertile, membranous oviduct. The nearest approach to such a piercing ovipositor in this Order will probably be found

in some of the *Pyralidæ;* for, in a moth of this family (*Clydonopteron tecomæ*, MS. mihi)[1] the ovipositor is slightly horny and flattened and apparently fitted for slipping under the skin of the pods of *Tecoma* in which its larvæ live. A somewhat similar structure is observable in some species of Pempelia and in *Pyralis olinalis*. In all other Lepidopterous insects known to me the ovipositor, when at all specialized, presents merely a horny sheath, either uniformly horny and cylindrical or having the dorsal and ventral edges more or less membranous and the sides more or less produced and sometimes pointed. In Paleacrita it is extremely elongate and fitted for secreting the eggs under the scales of bark. In some Noctuids, as in Leucania, it is very much compressed from the side, to fit it for secreting the eggs between blades of grass (a form repeated in the Pyralid, *Nomophila hybridalis*); while in others it is produced to a tolerably sharp point to enable the eggs to be thrust in between the scales of a bud, the terminal leaflets of a stem, or into the corolla of a flower. The more typical form of this kind of horny and exsertile ovipositor in the Order may be found in the Ægeriidæ, in which it is admirably adapted for probing the crevices of the bark of the plants in which the larvæ burrow. In the Zeuzerides, as in certain large Australian species, it is flattened to permit the thrusting of the eggs underneath the scales of bark of Acacia and Eucalyptus. In the Castniides (as in *Synemon sophia*, White) we find, again, a special modification, the terminal joint being armed with retrorse spines and having a rather sharp, blade-like tip, compressed laterally; but I know of no other Lepidoptera beyond those mentioned in this paper which have piercing and sawing ovipositors, with an extensile and elastic oviduct issuing from an orifice near and beneath the tip, and the highest living authority on European

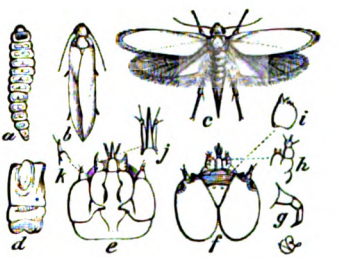

FIG. 2.—PRONUBA YUCCASELLA: *a*, larva; *b*, ♀ moth with closed wing; *c*, do. with wings expanded—nat. size; *d*, side view of larval joint; *e* head of larva, beneath; *f*, do. above; *g*, thoracic leg of same; *h*, maxilla, *i*, mandible; *j*, spinneret and labial palpi; *k*, antenna—enlarged.

[1] Figured and described since this paper was read, in the *American Entomologist*, III, p. 287.

Tineids, Mr. H. T. Stainton, wrote me some years ago that there was no European genus in the family at all analogous to Pronuba in this respect.

The internal organization will doubtless show peculiarities corresponding to the external structure; and one feature is worthy of mention, because very noticeable even through the sides of the body when that is rendered in any way transparent. It is a pair of brown, chitinous, radiate structures, each with a darker, circular, central ring, and extending across the third abdominal joint. More carefully studied, the dark circle is seen to represent the end of a hollow, though shallow, cylinder from the sides of which the

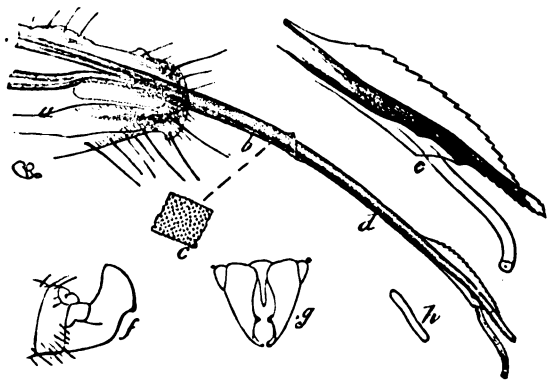

FIG. 3.— Genital characters of Pronuba yuccasella: *a*, tip of ♀ abdomen rendered somewhat transparent; *b*, basal joint of ovipositor; *c*, its sculpture; *d*, terminal joint of same; *e*, tip still more enlarged; *f*, genitalia ♂ from side; *g*, do. from above; *h*, egg.

filaments or spicules radiate as spokes from a hub. These radiate objects seem to distend the walls of a sack, which is evidently the *bursa copulatrix*, as Dr. Hagen has clearly made out in his recent studies of *Prodoxus decipiens*, in which the radiating spicules are fewer, shorter and thicker than in *Pronuba*.

The egg of *Pronuba* (fig. 3, *h*), which is very soft and plastic, is thrust through the pistil or young fruit and into the ovule. The larva (fig. 2, *a*), which is peculiar in possessing no prolegs, feeds upon the seeds, issues from the capsule as it ripens, and hibernates in a tough cocoon underground. The chrysalis (fig. 4) offers characters which enable us to separate the sexes in this state,—

a very unusual occurrence — and is admirably adapted, by means of spade-like dorsal spines, for forcing its way up through the ground, which it does to give forth the moth at the time of the flowering of its food-plant.

In regard to the habits of the female moth, which are more particularly interesting, I shall take the liberty of quoting the original language used:

"Before she [the female] can carry out the maternal task of continuing her race, she must act as foster-mother to the plant in order to insure a proper supply of food to her larvæ, which feed on its seeds. With her maxillary tentacle, so wonderfully modified for the purpose, she collects the pollen in large pellets, and holds it under the neck and against the front trochanters. In this manner she sometimes carries a mass thrice the size of her head. Thus laden, she clings to the top of the pistil, bends her head, thrusts her tongue into the stigmatic nectary, and brings the pollen mass right over its mouth. In this position she works with a vigor that would indicate combined pleasure and purpose — moving her head and body from side to side, and apparently making every effort to force the pollen into the tube. Such is the method by which our Yuccas are fertilized."[2]

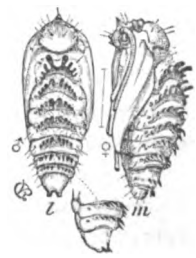

FIG. 4. — PRONUBA YUCCASELLA: *l*, male; *m*, female chrysalis.

Or, again, from the observations of 1873:

"The Yucca flowers are fully opened and perfect during a single evening and night only, and it is during this, the first night of blooming that eggs are consigned to the somewhat prismatic pistil. The pollen grains are not so often expelled, to fall on the inside of the flower, as I had been led to suppose; but almost always remain in an entire lump on the contracted and curled anthers. The moth, consequently, has no difficulty in accumulating her little load of pollen, for a single anther furnishes nearly the requisite amount.

"Once equipped with this important commodity, she may be seen either crawling over or resting within the flower. From time to time she makes a sudden start, deftly runs around and among the stamens, and anon takes position with the body between and the legs straddling some two of them—her head turned towards the

[2] 5th Rept. Ins. Mo., p. 152.

stigma. As the terminal halves of the stamens are always more or less recurved, she generally has to retreat between two of of them until the tip of her abdomen can reach the pistil. As soon as a favorable point is reached—generally just below the middle—the lance-like sheath of the ovipositor, which consists of four converging corneous bristles, is thrust into the soft tissue, held there a few seconds while the egg is conducted to its destination, and then withdrawn by a series of up and down movements. So intent is she upon this work that after the ovipositor once penetrates the pistil the whole perigon may be detached, some of the encumbering petals and stamens removed, the insect brought within the focus of a good lens, and all her movements observed to the greatest advantage, without disturbing her. In this way, I have been able to watch the consignment of hundreds of eggs, and to admire the delicacy and elasticity of the ovipositor proper, which issues from the setaceous sheath in a silk-like thread, almost invisible to the naked eye, and as long as the terminal abdominal joint; and which stretches and bends according as the body is raised or lowered.

"No sooner is the ovipositor withdrawn into the abdomen than the moth runs up to the top of the pistil, uncoils her pollen-bedecked tentacles, thrusts them into the stigmatic opening, and works her head vigorously as I have previously described—the motion being mostly up and down and lasting several seconds. This carrying of the pollen to the stigma generally follows every act of oviposition, so that where ten or a dozen eggs are consigned to a single pistil, the stigma will be so many times be-pollened. The ends of the tentacles, which are most setose and spiny, and which are always curled into the pollen-mass when not uncoiled, must necessarily carry a number of pollen grains each time pollination takes place; and I have noticed a gradual diminution in the size of the collected mass, corresponding, no doubt, to the work performed, which is indicated by the rubbed and worn appearance of the individual—the freshest specimens always having the largest loads.

"While oviposition generally takes place in the manner described, the moth head outward and straddling two stamens, an entirely opposite position must sometimes be assumed, since larvæ and punctures are not unfrequently found in the upper part of the fruit, especially where a single one is stocked with ten or a

dozen larvæ, as is sometimes the case. As the fruit enlarges, the mouth of the puncture forms a slight, discolored depression, more noticeable in some varieties than others; but the passage-way becomes obliterated."[3]

The above are some of the leading facts in the natural history of *Pronuba yuccasella* that can be verified by any one who cares to take the trouble to observe them.

The insect offers, however, such a remarkable instance of special modification of parts to a particular end, and there is such a striking interdependence between it and its food-plant, that Hermann Müller, who, from his extensive studies of the relations between plants and insects, is most competent to speak on the subject, avowed it to be the "most wonderful instance of mutual adaptation"[4] yet detected. The original observations have, as a consequence, been widely commented on. My conclusions have not unfrequently been criticised, and too often, I regret to say, by those who seem not to have taken the trouble to read the original articles. With a view of emphasizing the facts already published and of presenting others recently ascertained, let me briefly consider the criticisms that have been made:

1. Capsules are often found uninfested with the *Pronuba* larva, and several writers have assumed that such could not have been fertilized by the moth and that this last is not necessary to produce fertilization.

The following quotations from the original articles offer a sufficient reply to this objection:

"It is quite possible that the moth may, at times, introduce the pollen into the stigmatic tube without consigning any of her eggs to the fruit, and we should naturally expect to find some capsules uninfested with her larvæ. But I have this year examined hundreds of capsules around St. Louis, and some in South Illinois, and not more than four or five per cent. were uninfested. Sometimes every pod on the same plant had its worms, while at others half the pods on a given panicle would be free from them. From the very large percentage of infested pods, I conclude that oviposition naturally and immediately follows fertilization, unless the moth be disturbed."[5] "While oviposition is generally followed (and not pre-

[3] 6th Rept. Ins. Mo., pp. 133-4.

[4] In correspondence with the writer. See also *Zoologische Garten*, Frankfort, Oct. 1874.

[5] Trans. Ac. Sc. St. Louis, III, p. 62.

ceded, as I formerly supposed) each time by pollination, yet the former sometimes takes place twice, thrice or oftener without the latter being performed; and I suspect that the converse of this is equally true."[6]

2. Yucca occasionally and exceptionally seeds in Europe, and several horticultural writers arguing from this fact, and doubtless without informing themselves of what I had really written, have repudiated any necessary connection between the moth and the flower. A single illustration from a recent editorial in a leading horticultural journal, the London *Garden*, and approvingly quoted in *Vicks' Illustrated Monthly Magazine*, for March, 1880, will suffice:

"I fancy insect agency is talked of in a very unscientific way by too enthusiastic followers of Mr. DARWIN. I remember reading Professor RILEY's dogma that the Yucca could only possibly be fertilized by a certain American insect, and being amused at it because I had seen it fruiting well at the south of Europe, and also in France. Probably we should see it oftener if we had a better climate. I now note what Mr. ELLACOMBE, writing to a contemporary, says: 'There can be no doubt that the Yucca can be fertilized by other means than by the agency of the Yucca moth, *Pronuba yuccasella*. I have more than once had well formed fruit of *Y. recurvifolia*, but the seeds did not come to maturity.' Dr. ENGELMANN, in his *Notes on the Genus Yucca*, says: 'In the botanical garden of Venice I gathered the pulpy pods from a large *Yucca aloifolia*, about fifteen feet high. This was the only Yucca fruit seen by me in Europe, though I have since learned that in other instances, also, though only exceptionally, fruit and good seed have been produced there, principally by the same species, and very rarely by others.' I remember the late Mr. BARILLEE telling me he had raised a great many varieties of *Yucca gloriosa* from seed saved in France. However, this mistake on the part of so good a man as RILEY is good sense compared with what we read on this side as to the influence of insects on the color and odor of plants. The statement by Mr. WALLACE, for example, that showy flowers are scentless, because from their color they are sufficiently attractive to insects, may pass for science with some innocent people, but it seems foolish to those who know even only a few garden plants."

Again let my original language do duty in reply:

"Our Yuccas, on the contrary, *seem* to depend for assistance, *so far as we now know*, on the single little Tineid which I have described, and, for this reason, are among the most interesting of entomophilous plants. At least such is the case with the capsule-bearing species, *i. e.*, those which have dry, dehiscent pods; and I will here premise that my observations have been made upon a filamentose-leaved species in common cultivation about St. Louis, and which Dr. Engelmann takes to be *Y. puberula* or *Y. glauca*.

[6] *Am. Nat.*, Oct. 1873.

"The fructification of such Yuccas as bear fleshy, pulpy fruit, of which *Y. aloifolia* may be taken as the type, has not been studied; but, even with this last mentioned species, the facts, so far as known, strongly indicate that *Pronuba* is principally, if not solely, instrumental in bringing it about. Its seeds are infested with our *Pronuba* larva, though not to the same extent as those of the dehiscent species. It would be premature to speculate until we have further facts; but it is not at all unlikely that the seeds of the fleshy pods are less congenial to the larvæ, and that a smaller percentage [of these] is produced from the eggs consigned to such pods by the moth."[7]

Those parts of the quotation which I have emphasized show little inclination to form sweeping conclusions, not warranted by the facts observed. Again, after bringing together such facts as were then obtainable respecting the seeding of Yucca in different parts of America and Europe, and citing the case of the seeding of *Y. filamentosa*, observed by Mr. T. Smith at Newry in England, in 1868, I wrote:

"These extracts prove that the Yucca moth occurs on Long Island, and around New York, and indicate that other insects occasionally pollinize the flowers. The experience of Mr. Smith, in England, is as interesting as it is exceptional; but until we learn whether or not the work of the larva was manifest, no safe conclusions can be drawn. *Other insects may have been the pollinizers, or Pronuba may have been locally introduced with seed from America.* This last view may not appear very plausible, but if both sexes of the insect were, by some chance, introduced into a locality where Yuccas of blooming age were growing, there is no reason why they should not multiply; and such chance introduction is not impossible, since the larva not unfrequently remains in the capsule after the seed is ripe, where it fastens a number of the riddled seeds together into a sort of cocoon, which might easily pass unnoticed in gathering seed; and, if buried in the ground with such seed, would in time give forth the moth."[8]

And after a second summer's investigation, I further wrote:

"My observations this summer might be extended much in detail. They have convinced me more than ever that *Pronuba* is the only insect by the aid of which our Yuccas can be *fully*

[7] Trans. Ac. Sc., St. Louis, III, pp. 588-9.
[8] 5th Rep. Ins. of Mo. (1872) p. 159.

fertilized: for I have studied this fertilization diligently night after night, without seeing any other species go near the stigma. The stigmatic opening closes after the first night, and I know of no crepuscular or nocturnal species which could collect the requisite amount of pollen and bring it so to bear on the stigma that each ovule would receive the influence of a pollen grain. The species already enumerated as frequenting Yucca[9] are mostly diurnal, and have nothing to do in the work; and wherever I have excluded the moth from the flowers, by enclosing the latter with netting, no fruit has been produced. *I am, therefore, led to believe that the few rare instances of yucca fertilization, in localities where* PRONUBA *may be presumed not to occur, have been brought about by another insect accidentally, or by the stamens reaching an exceptional length, and the anthers being brought into contact with the stigma by the conniving of the closing petals.* I have found the stamens of varying length in the flowers on the same panicle, and in some instances almost as long as the pistil."[10]

The accompanying figure (fig. 5) illustrates a few pistils from the same species of Yucca, and indicates (*a*) a deformity of tolerably common occurrence in which the anthers may easily be brought in contact with the stigma, and also (*b*, *c*, *d*,) varying length of the stamens. I also figure (fig. 6) a flower of *Yucca*

[9] I take the opportunity in this connection to elaborate the list given in my 5th Mo. Report (p. 154) of insects known to me to frequent and infest Yucca. COLEOPTERA. Frequenting the flowers and evidently feeding upon the pollen: *Carpophilus yuccæ* Cr., *C. pallipennis* Say, *Euphoria melancholica* Gory, *E. fulgida* Fabr., *Trichius delta* Forst., *Chauliognathus americanus* Forst., *C. marginatus* Fabr., *Strangalia strigosa* Newm., *Typocerus zebratus* Fabr., *Hymenorus densus* Lec., *Anthonomus signatus* Say and many other species of less frequent occurrence. Living in the fruit: *Silvanus quadricollis* Guér., *Carpophilus mutilatus* Fabr., *Epuræa luteola* Er. and a Trogositid larva, presumably of *Trogosita yuccæ* Cr. Living in the dead flower stem: *Hypothenemus hispidulus* Lec. Living under the bark, or boring in the root-stem of the plant: *Carpophilus melanopterus* Er., larva of *Trogosita yuccæ* Cr., larva of *Elophidion* sp. (probably *tectum* Lec.), *Scyphophorus yuccæ* Horn and *Yuccaborus frontalis* Lec. Dr. Horn mentions *Rhigopsis effracta* as feeding on Yucca (Proc. Am. Phil. Soc. XV, p. 37) but the particular part of the plant is not given. LEPIDOPTERA. Living in the flesh of the fruit: an unbred Tortricid larva and exceptionally, the larva of *Prodoxus decipiens* Riley. Feeding on the seeds: larva of *Pronuba yuccasella* Riley and presumably of *P. maculata* Riley. Living in the fresh flower-stems: larva of *Prodoxus decipiens* Riley and presumably of *P. intermedius* Riley, *P. marginatus* Riley, *P. cinereus* Riley, *P. æneseens* Riley. Boring in the root and the root-stem: *Megathymus yuccæ* Boisd. and the variety *coloradensis* Riley and presumably *M. cofaqui* Strecker. Mr. V. T. Chambers mentions that *Holocera gigantella* occurs on Yucca in Colorado. HETEROPTERA. Puncturing and sucking the fruit: *Lygus robiniæ* Uhler, *Orthotylus discoidalis* Uhler, *Cyllocoris scutellatus* Uhler and *Theognis phyllopus* Uhler (*albicinctus* Say).

[10] *Am. Nat.*, Oct. 1873.

aloifolia in which species the stamens reach nearly to the stigma, and in which, were it not for their recurved ends, some of the pollen might fall on the papillose apex of the stigma while the flower hangs or droops.

It is so very plain from the above quotations that, while I have held and still maintain that it is the rule for our Yuccas to be pollinized by *Pronuba*, I have nevertheless admitted that the rule is not without exceptions. The rarity of yucca-fructification in those parts of America or in other countries where the plants are not indigenous and *Pronuba* may be presumed not to occur; the uniform failure to fructify whenever the moth has been excluded from the flowers both in my own experiments and those of Mr. J. M. Milligan[11] and of Mr. Meehan; and the non-fructification, even where the moth exists, of those species which bloom either

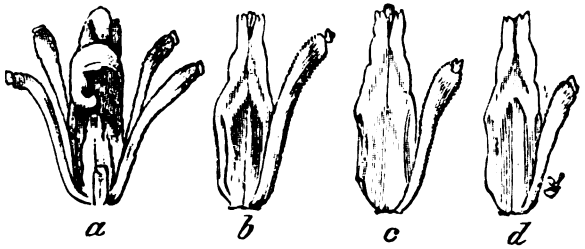

FIG. 5.—Young fruit of Yucca filamentosa, showing (*a*) a deformed pistil and (*b*, *c*, *d*) varying lengths of the stamens.

before or after she appears—all serve to emphasize the rule, and the few exceptions confirm it all the more markedly that (as Mr. Meehan has shown us) the plant is so easily fructified whenever the pollen is brought to the stigma or even to the papillose apex thereof.[12] It would be wonderful indeed, if the plant were not fructified occasionally in some one of the exceptional modes here indicated and more particularly by some of the pollen-feeders like Chauliognathus.

[11] *Am. Nat.*, VIII, p. 749 (1874).

[12] I do not doubt the correctness of Mr. Meehan's observations; yet it is rather singular that the only other recorded experiments of the same kind made in this country, viz., those of Mr. Milligan (see the paper above cited) should give quite different results from those obtained by Mr. Meehan. Mr. Milligan says: "In the three experiments where pollen was used, the pollen was placed as nearly as possible in the same position in each flower, viz., just at the entrance of the stigmatic tube; the result confirms the view taken by Dr. Engelmann in relation to the difficulty of this flower being pollinized by other natural agencies than that afforded by the Yucca moth." In two instances I have tried to fructify *Yucca aloifolia* artificially without avail.

The chances that *Pronuba* may occur in some parts of the world where it had not before existed have also increased by my having, during the years 1873 and 1874, sent to correspondents a number of larvæ in their cocoons with the request that they be buried in the ground near Yuccas. Of those thus sent were 100 to Mr. Meade Woodson, Kansas City, Mo.; 150 to Dr. Asa Gray, Cambridge, Mass.; 100 to Professor J. E. Planchon, Montpellier, France; 250 to Hermann Müller, Lippstadt, Germany; 100 to Chas. Darwin, Down, near London, Eng.; and 50 to H. T. Stainton, Mountsfield, near London, Eng.

FIG. 6.—Flower of Yucca aloifolia fully opened.

3. The accuracy of my observations has been called in question, and notably by Mr. Jacob Boll[13] of Dallas, Texas, who made some himself which seemed to conflict with mine;[14] while much doubt was thrown upon the utility of *Pronuba* to the plant by certain statements made in a paper read by Mr. Meehan at the last meeting of this Association.[15] As I have elsewhere

[13] Deceased since this was written.

[14] *Stettiner Entomologische Zeitung*, 1876, pp. 401-5.

[15] Mr. Meehan's paper "On the fertilization of Yucca" is not published in the Proceedings, but was printed in the *North American Entomologist* for November 1879 (vol. I, p. 33). It is an attempt to rebut the evidence existing as to the benefits derived by plants as species from cross-fertilization, Yucca being used as an illustration. The author lays stress on the *supposed* rarity of the seed moth of Yucca in Colorado and Utah. I say *supposed* because my own experience with Yucca in Colorado (during three

replied to Mr. Boll's strictures,[16] and have more recently considered Mr. Meehan's statements in an article in the *American*

different years), as well as that of others, is in direct conflict with it and shows that the seeds are very generally found wherever a flower-stalk has been thrown up and it has not been prematurely browsed by cattle or cut by man. Mr. Meehan's statements of facts in this matter of insect fertilization have frequently greatly differed from those of others and led him to views in opposition to those generally accepted. In some instances they are pure misstatements or misapprehensions, as in the famous one made before the Association in 1876, viz.: that bees and insect fertilizers of flowers were rare in the Rocky Mountain region where bright flowers abound ("On self-fertilization and cross-fertilization of flowers" *Penn. Monthly*, 1876, vol. 7, p. 834). It was my privilege in answer to this statement to show that the insect fauna of that region was peculiarly rich in pollinizers whether among Hymenoptera, Lepidoptera, Coleoptera, or Diptera, and the experience of extensive collectors in that region, and of Messrs. J. D. Putnam, E. A. Schwarz and H. K. Morrison more particularly, has fully corroborated this view. Dr. LeConte's published papers (Coleoptera of the Alpine Rocky Mountain region; Hayden's Bull. U. S. Geol. and Geog. Surv., IV, p. 447, and V, p. 499), also confirm it. I am not aware, however, that Mr. Meehan has admitted the error whether in the misstatement or the conclusions drawn therefrom. I feel, therefore, that it is desirable to point out the erroneous statements in the article "On the Fertilization of Yucca" to facilitate the doing of which I quote from it the following passages:

[1] "It may be remembered that at our meeting at Buffalo I produced three capsules that had not been produced by this elaborate process, but simply by mere touching of the papillose apex with one of the flower's own polliniferous anthers. Professor Riley was so sure that the seed-vessels could not have been produced in that way, that there must have been some insect agency unknown to me in addition to my work, that at the conclusion of my paper he asked permission to cut open the capsules, sure of being able to show the larvæ in the fruit; but he found them not. I recall these matters to show that I have not misapprehended the position our friends take on this question."

There is, notwithstanding, both grave misstatement and misapprehension. Having known a few pods to develop from the last and topmost flowers of *Y. angustifolia* at St. Louis with evidence that *Pronuba* was the fertilizer (see Trans. Ac. Sc. St. Louis, III, p. 570), I stated the fact and made the point that the pods which Mr. Meehan exhibited might after all have been fertilized by *Pronuba* and that I should not be surprised to find its larvæ within them. It never entered my mind to be "sure" that the flower could not be pollinized through human instrumentality, or to be "sure" of finding the larvæ in the pods, and the misconstruction of the remarks is quite unjustifiable.

[2] "At the conclusion of this address, delivered at the Saratoga meeting of the American Association, Professor C. V. Riley made some remarks which unfortunately I did not hear. The newspaper reports make him say that I was mistaken in the insect I found in *Yucca angustifolia*, that it was not *Pronuba yuccasella*. I have called Professor Riley's attention to this and have asked for a correct note of what he did say, but have only the reply that he is 'not answerable for a newspaper report.' It remains then only for me to say in reply to the "newspaper report" that at the outset of my observations on *Yucca angustifolia*, I sent one of the insects caught to Professor Riley asking: 'Is this certainly *Pronuba yuccasella*?' and he replied that it was."

It remains only for me to remark on the above that I was never guilty of the discourtesy to my friend implied in the first quotation from my correspondence, but that in stating that I could not be answerable for newspaper reports which I had not seen, I also expressed my willingness, in order to avoid misapprehension, to write out my criticism of the paper if the author would send me the MS. In reference to my determination as *Pronuba yuccasella* of a specimen sent me by Mr. Meehan, it was not preserved because pressed and spoiled in the letter, so that I cannot now verify my determination. *Prodoxus decipiens* being unknown to me then, my determination may have been erroneous, or there may have been some error in the fact stated by my correspondent which, in this instance, was not our author but his son, Mr. Jos. T. Meehan. That there was an error somewhere is rendered probable by the facts recorded in the present paper.

[16] Trans. Ac. Sc. St. Louis, III, p. 571; *Stettiner Ent. Zeitung*, 1878, p. 377.

Entomologist for June last (vol. III, p. 142) entitled "The true and the Bogus Yucca Moth," it suffices here to state that the strictures and statements of both gentlemen resulted from mistaken identity, and that the conflicting experiences are explained by the existence of a moth which I have named *Prodoxus decipiens* and which, while bearing a very deceptive general resemblance to *Pronuba yuccasella*, yet differs essentially in structure and habit.

Prodoxus decipiens[17] was first announced by me before the Entomological Club of the Association at its Saratoga (1879)

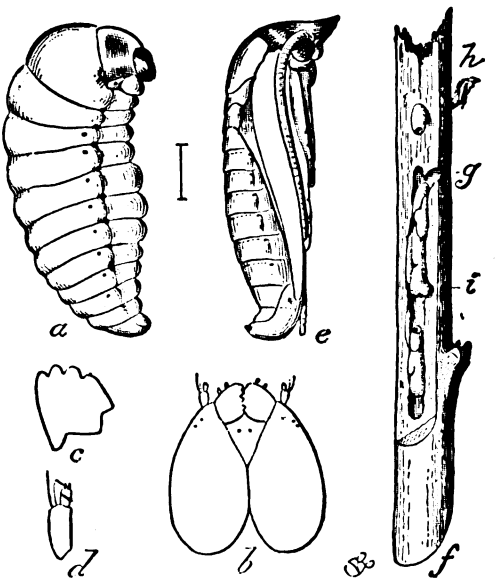

FIG. 7.—PRODOXUS DECIPIENS: *a*, larva; *b*, head from above; *c*. *d*, left jaw and antenna; *e*, pupa; *f*. infested stem cut open to show the burrows, castings, cocoons and pupa shell (*h*)—all enlarged but *f*, the hair line between *a* and *e* showing natural length.

meeting. It breeds either in the flower-stem or in the flesh of the fruit of different species of Yucca and is common through the Southern states, both on *Yucca aloifolia*, *Y. rupicola* and *Y. gloriosa*. In the West it is found on *Y. angustifolia*, while at Washington I have found it not uncommon on the different cultivated forms of *Y. filamentosa*. It also occurs around Philadelphia and has been bred by Dr. H. A. Hagen and by myself from larvæ

[17] *American Entomologist*, III, pp. 153 and 182.

infesting the flower-stems of *Y. filamentosa* grown in Mr. Meehan's grounds, thus furnishing strong presumptive evidence that the moths which Mr. Meehan assumed to be *Pronuba yuccasella*, and which he found upon *Y. angustifolia* long before the flowers of *Y. filamentosa* had opened, were in reality the *Prodoxus* or Bogus Yucca Moth, as I surmised would be the case in my comments upon his paper at the meeting of the Association a year ago. Its occurrence there weakens the inference which Mr. Meehan drew in his paper that, because *Pronuba* did not pollinize *Y. angustifolia*, therefore it did not pollinize *Y. filamentosa* and entirely nullifies the conclusions in the following paragraph from that paper in which, moreover, as in the affirmation (without a

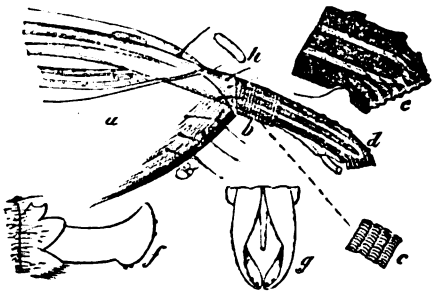

FIG. 8.—Genital characters of Prodoxus decipiens: *a*, tip of ♀ abdomen rendered somewhat transparent; *b*, basal joint of ovipositor; *c*, its sculpture; *d*, terminal joint of same; its tip more enlarged; *f*, genitalia of ♂ from side; *g*, do. from above; *h*, egg.

particle of proof) that the moth feeds on other flowers, there are some very unscientific statements.

Pronuba yuccasella, the Yucca Moth, has for years abounded on my flowers of the *Yucca filamentosa*. It has not been known to visit any other plant than Yucca. *Yucca angustifolia* begins to flower from three to two weeks and its blossoming is all over before *Yucca filamentosa* begins to open. The facts now adduced show that the moths exist weeks before the flowers bloom with which they have been so intimately connected, feeding of course on other flowers, and would perhaps make use of other fruits as depositaries for their eggs if Yucca should not exist. At any rate the facts weaken any belief we may have that the Yucca and Yucca Moth, through the long ages, have become mutually adapted to each other through a fancied mutual benefit.

The accompanying figures will sufficiently indicate the structural peculiarities of *Prodoxus decipiens* and how markedly it differs from *Pronuba yuccasella* in the larva (fig. 7, *a*) having no legs (lacking even the thoracic legs which belong to the latter); in the pupa (*e*), among other differences, lacking the series of

dorsal spade-like projections; in the form of the claspers in the male moth (fig. 8, *f*, *g*); in the much stouter and differently shaped ovipositor of the female (fig. 8, *b*, *d*); and especially in her lacking the maxillary tentacles. Oviposition has not yet been observed, but stems that have been badly infested are usually covered with small elongate-oval scars or swellings with a depression along the middle as at fig. 9, *a*. These are undoubtedly the scars of the wounds made by the ovipositor, though comparatively few of them show evidence of having led to an egg or a larva. I cannot better set forth the differences in the two insects, whether in structure or in habit than by quoting the concluding portion of the article in the *American Entomologist* above alluded to:

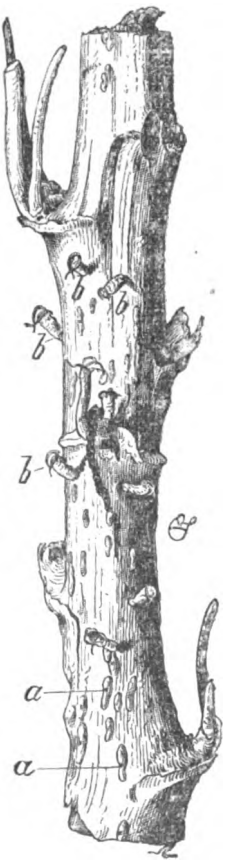

FIG. 9.—Flower stem of Yucca, showing scars made by female Prodoxus decipiens in ovipositing (*a*, *a*) and pupal exuvia protruding (*b*, *b*, *b*,).

"The larva of *Prodoxus* never quits the stem in which it lives. It eats comparatively little, packing its pale, buff-colored excrements very tightly in its burrow, and spinning as winter approaches a neat cocoon of white silk covered on the outside with its castings [fig. 7, *f*]. Prior to forming its cocoon, a passage way is always made to the outside of the stem, leaving but a very thin covering [fig. 7, *g*]. In issuing, the chrysalis pushes half way out, very much as is the case with all other Lepidopterous endophytes [fig. 7, *h*; fig. 8, *b*]."

* * * "Who, studying these two species in all their characters and bearing, can fail to conclude that, notwithstanding the essential differences that distinguish them not only specifically but generically, they are derivations from one and the same ancestral form? *Pronuba*, depending for its existence on the pollination of the flower, is profoundly modified in the female sex in adaptation to the peculiar function of pollination. *Prodoxus*, dwelling in the flesh of the

fruit or in the flower-stem, and not depending upon the fructification of the plant, is not so modified, but has the ordinary characters of the family in both sexes. In the former, the larva quits the capsules and burrows in the ground: it has legs to aid it in its work, while the chrysalis is likewise beautifully modified to adapt it to prying through the ground and mounting to the surface. The latter, on the contrary, never quitting the stem, has no legs in the larva state, and in the chrysalis state is more particularly adapted, by the prominence of the capital projection, to piercing the slight covering of the stem left ungnawed by the larva. The former is very regular in its appearance as a moth at the time of the flowering of *Yucca filamentosa*, a fact which would indicate that it was modified while living upon that species and had a range coëxtensive with it and other species blooming simultaneously. The latter appears earlier, as the food of its larva is earlier ready. Which of the two insects is the older in time, or whether the divergence from some archetypal form has been simultaneous, is a matter of opinion which those interested in evolution will decide for themselves one way or the other, or according as knowledge increases. That other species of both these genera will yet be discovered, there can be but little doubt."

Since the preceding quotation was written I have detected a species of *Prodoxus* which is still more closely related to *Pronuba yuccasella*, and have obtained another species of *Pronuba* and several of *Prodoxus*, collected upon Yucca (species unknown) at Caliente, Kern Co., Cal., by Mr. H. K. Morrison. The insects seem to be not uncommon there, but Mr. Morrison searched in vain for other species.

PRONUBA MACULATA n. sp.—Expanse, ♀ 21.5 mm; ♂ 17.8 mm. *Head* white, eyes black, mouth parts yellowish but very sparsely clothed with white scales; antennæ yellowish, the tips fuscous, sparsely clothed with scales on the basal half only; maxillary tentacle (fig. 10, *mt*) yellowish, the base green, large, more swollen and with the notch or elbow near the base more distinct than in *yuccasella;* maxillæ bristly (in *yuccasella* they are nearly smooth). *Thorax* white: primaries (fig. 10, *pr*) with the upper surface opaque white, bordered with from 10-12 black spots (when all are present) of varying size and running from just beyond the middle of the wing to about the inner angle; the disk with 5 spots, 4 of them in a line from base to apex, the 2d and 3d rather farthest apart, the 5th, or middle one, below and nearest the 3d from the base; under surface deep fuscous, intensified around the borders and with the spots of upper surface barely indicated; fringes white: secondaries transparent, being

very slightly covered with elongate fuscous scales, thickening on the borders, especially toward apex; fringes faintly fuscous: legs white, tarsi very sparsely clothed and yellowish except at extreme tips which are more fuscous. *Abdomen* white beneath, fuscous above. Integument of head yellowish, of thorax and coxæ black or blackish. Terminal abdominal joint in ♀ short and thick, obliquely truncate from beneath (fig. 10, *a*) bare, honey-yellow with its base black; ovipositor stout, decurved, the terminal, horny joint (fig. 10, *tjo*) broad and rounded at the tip and its edge finely denticulate. Claspers of ♂ short and abruptly curved upward as in *yuccasella*, but armed with only one tooth and this tooth greatly lengthened and preceded by a deep excavation (fig. 10, *c*.).

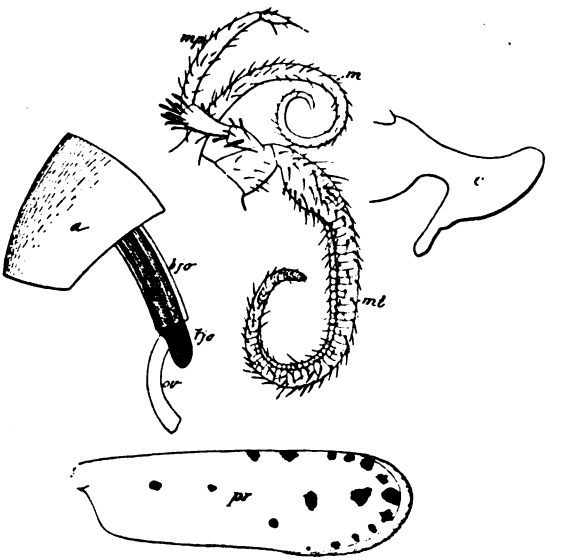

FIG. 10.—PRONUBA MACULATA: *a*, tip of female abdomen; *bjo*, basal joint of ovipositor; *tjo*, terminal joint do.; *or*, oviduct; *m*, maxilla; *mp*, max. palpi; *mt*, maxillary tentacle; *c*, clasper of male from side; *pr*, front-wing showing arrangement of spot—hair line showing nat. size.

Examination of the venation in one male shows that marginal veins 7 and 8 arise from the transverse vein independently of the discal branch of the subcostal vein and that the upper fork of the independent discal veinlet is wanting.

In one of the male specimens only 4 of the spots on the border of the primaries are present, and in this specimen as well as in one other male and one female, the second discal spot is absent.

Described from 2 ♀♀ 5 ♂♂, collected in California by Mr. H. K. Morrison.

Easily distinguished from *P. yuccasella* by the smaller size, the spots

on primaries, the broader maxillary tentacles and shorter, blunter ovipositor; and by the male claspers being deeply excavated before the tooth which is greatly elongated.

PRODOXUS INTERMEDIUS n. sp. ♀.—Expanse 28.5 mm. Coloration as in *Pronuba yuccasella* and immaculate specimens of *Prodoxus decipiens*. Basal joint of the maxillary palpi not provided with a tentacle, but having a slight tubercle at the tip. Apical joint of the abdomen (fig. 11, *a*) shaped as in *Pronuba yuccasella*, but slightly deeper and possibly a little thicker. Ovipositor (fig. 11) shaped as in *Pronuba yuccasella*, but slightly stouter, more acuminate at tip and with the serrations of membrane finer and more numerous. The sculpture of basal joint shows like very fine punctations in regular rows.

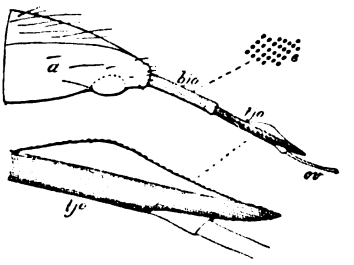

FIG. 11.—PRODOXUS INTERMEDIUS: *a*, anal abd. joint of female; *bjo*, basal jt. ovipositor; *s*, its sculpture; *tjo*, terminal jt. do.; *ov*, oviduct.

Described from 2 ♀♀ from Texas (Boll), and 1 ♀ from Ute Pass, Col., July 18, 1877 (Riley).

In the specimen from Ute Pass there is a short rounded process just before the apex of the abdomen on the under side. As this, together with the space just above it, is very thin I consider it to be the result of some injury, such as a pinch of the forceps, which the specimen may have suffered while fresh. (This flattened portion is indicated by a dotted line in the figure.)

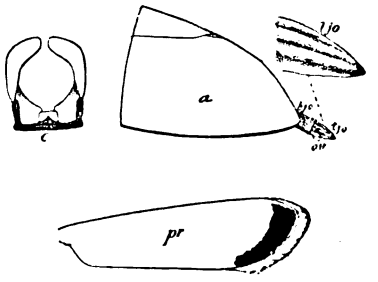

FIG. 12.—PRODOXUS MARGINATUS: *a*, anal abd. jt. of female; *bjo*, basal jt. ovipositor; *tjo*, terminal jt. do.; *ov*, oviduct; *c*, claspers of male from above; *pr*, front wing—hair-line showing nat. size.

PRODOXUS MARGINATUS n. sp.—Expanse 10 mm. Color white, the clothing of body very sparse, especially on the abdomen, and showing more or less distinctly the integument which is dark brown often with an æneous tinge. Antennæ bare towards tip and yellowish. Primaries (fig. 12, *pr*) satiny white with a terminal black band of varying width; under surface fuscous, almost black on costal and posterior borders; fringes white. Secondaries white with a broad costal and apical fuscous shade; under surface concolorous; fringes white. Apical abdominal joint of ♀ blackish, slender, very obliquely truncate above, the tip blunt-pointed (fig. 12, *a*). Ovipositor short and stout; the horny terminal joint gradually narrowed to the pointed tip, the upper edge very finely and acutely

serrate (fig. 12, *t j o*). Claspers of ♂ (fig. 12, *c*) not dentate, their form much concealed by scales, the large arms broad and of nearly uniform width; large upper basal piece obtusely angulated in the middle.

Described from 3 ♀♀ and 4 ♂♂ collected in California by Mr. H. K. Morrison.

PRODOXUS CINEREUS n. sp. ♂.—Expanse 12 mm. Head, thorax, legs and apical ventral joints whitish. Primaries ashy; secondaries and under surface of all the wings brown with a cinereous reflection. Tip of maxillary palpi and apical third of antennæ black; the integument of body black. Claspers (fig. 13, *a*, *b*,) dark testaceous, similar in form to those of *decipiens* but without teeth; large upper basal piece broadly rounded or subtruncate; the smaller piece beneath it of similar shape.

FIG. 13.—PRODOXUS CINEREUS: male claspers (*a*) from above; and (*b*) from side.

Described from 7 ♂♂, collected in California by Mr. H. K. Morrison.

PRODOXUS ÆNESCENS n. sp.—Expanse, ♀ 14.7 mm.; ♂ 11.2 mm.—14mm. General color bronzy, the primaries with a distinct purple reflection. Under surface of thorax, the coxæ and the femora clothed with white scales. Head whitish, with scattered black hairs; labial palpi with black hairs; 4th and 5th joints of maxillary palpi and the antennæ, except at the base, black. Integument black. Apical abdominal joint ♀ (fig. 14, *a*) swollen as in *P. decipiens* and obliquely truncate from above, but the tip is also truncate from beneath and the lower border is slightly excavated. Ovipositor short and stout, very broad; the upper

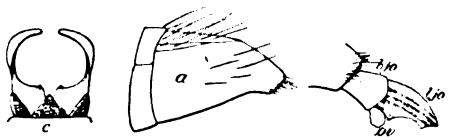

FIG. 14.—PRODOXUS ÆNESCENS: *a* anal abd. jt. of female with ovipositor retracted; *bjo*, basal jt. ovipositor; *tjo*, terminal jt. do.; *ov*, oviduct; *c*, claspers of male from above.

border of the horny terminal joint (fig. 14, *t j o*) thin, arched and finely serrate, the tip obliquely truncate beneath and at the base of the truncation forming a small, thin tooth, the base beneath forming a blunt tooth, the border between these teeth retuse. Claspers of ♂ (fig. 14, *c*) with no teeth on the arms beneath; the arms more slender than in *cinereus* and narrowed more abruptly near the base; the broad basal part with a small tooth at the apex within. Large upper basal piece forming a stout process at the apex.

Described from 3 ♀♀ and 8 ♂♂ collected in California by Mr. H. K. Morrison.

From the above descriptions it is evident that we already have represented, in the few species so far known, various gradations between the more typical ovipositor of *Pronuba yuccasella* on the one hand and that of *Prodoxus decipiens* on the other. It would also seem that the curious maxillary tentacle possesses simply generic and not Family value. *Prodoxus intermedius*, agreeing so closely with *Pronuba* in all respects except in lacking these tentacles, shows us how insects of different genera may become similarly modified in special parts by similarity of function of such parts; for we may with tolerable safety assume that *intermedius* breeds in the fruit of the plant and probably in the seed as does *yuccasella*, existing largely through the intervention of this last since it has itself no special means of pollinizing.[18] The male of this species is not positively known; but two specimens taken at Ute Pass, Col., on the same day with the female, and two others taken at the Monument Park the next day, differ from the ♂ of *Pronuba yuccasella* only in the somewhat greater expanse.

Hitherto rather than hastily found a family on a single species even where there are good structural characters not covered by former characterizations of the Family, I have been unwilling to separate *Pronuba* from the TINEIDÆ in the group TINEINA, with which family it has most affinities in its venation and well developed maxillary palpi. But with the addition of other species and another genus science will be best served by the establishment of a distinct family which I would call PRODOXIDÆ. The family characters will then be:

Imago with the head rough; labial palpi of moderate size and curved upward; maxillary palpi long, elbowed, 5-jointed, the basal joint either protuberant or modified into a prehensile tentacle; anal joint of female compressed from the sides, bare and horny; ovipositor extensile, the terminal joint horny, in one piece and adapted to piercing and sawing; egg very soft, elongate and flexile; larva

[18] The assertion of Dr. H. A. Hagen in a recent number of the *Canadian Entomologist* (July, 1880) that moths which he bred from the flower-stem of Yucca were typical specimens of *Pronuba yuccasella* and possessed its curious maxillary tentacles, might strengthen the idea that these organs were structures of dimorphic value only, but Dr. Hagen has since admitted to me that he was entirely wrong and that his moths were typical specimens of *Prodoxus decipiens*. I need only record the fact, without further comment. Indeed Dr. Hagen has made some beautiful studies of the anatomy of *decipiens* which strengthen and emphasize the differences between the two insects.

either without prolegs or entirely apodous; chrysalis with a strong capital thorn.

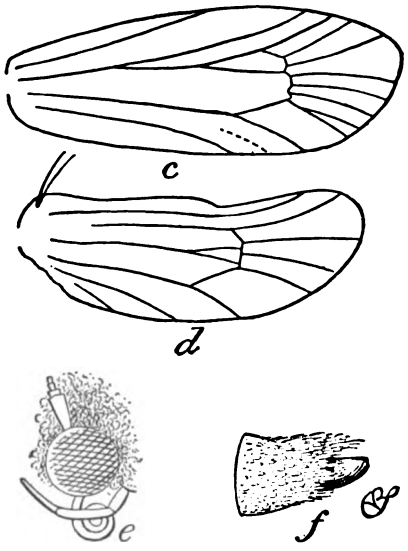

FIG. 15.—HYPONOMEUTA MALINELLA: *c*, *d*, venation of female front and hind wings; *e*, head with tongue, labial palpus and part of antenna; *f*, tip of abdomen.

From the HYPONOMEUTIDÆ with which it has strong general resemblances, the family is at once distinguished not only by the anal characteristics, but by the different venation and by the possession of maxillary palpi. In the typical *Hyponomeuta* the antennæ are more serrate, the head more finely and closely scaled, the palpial joints differently proportioned, the tip of abdomen does not extend beyond the scales, the front wings lack the forked disco-longitudinal vein and the internal vein is simple, not forked at base. The hind wing is usually notched on costa and shows the frenulum in the ♀ more distinctly, in two bristles. The accompanying figures will show (fig. 15) the pterognostic characters, trophi and anal abdominal joint of a ♀ *H. malinella* Zeller, a common European species feeding on Apple, and (fig. 16) the slightly varying venation of *H. multipunctella* Clem., one of our own species. The larval habits are also quite different. From the GELECIDÆ the PRODOXIDÆ are readily distinguished by the rougher head the presence of maxillary palpi, the wing characters and the larval characters and habits.

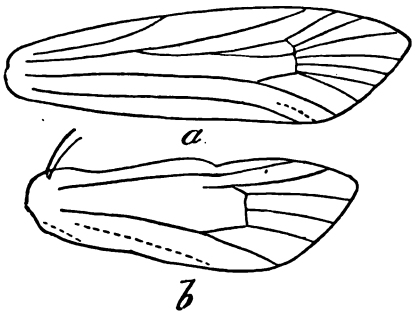

FIG. 16.—HYPONOMEUTA MULTIPUNCTELLA: *a*, *b*, venation of front and hind wings.

We have thus:

Family PRODOXIDÆ.

Genus PRONUBA.[19]

P. YUCCASELLA Riley, Trans. St. L. Ac. Sc., III (1872), p. 56. *Tegeticula alba*[20] Zeller, Verh. d. zool.-bot. Ges., XXIII, (1873), S. 232 (Sep. p. 32).

P. MACULATA[21] n. sp.

Genus PRODOXUS.

P. DECIPIENS Riley, American Entomologist. III (1880), p. 155. *Hyponomeuta 5-punctella*[22] Chambers, Canadian Entomologist, VII (1875), p. 7.

Hyponomeuta paradoxica Chambers (Journ. Cincinnati Soc. Nat. Hist., Oct., 1878, p. 9.

P. INTERMEDIUS n. sp.

P. MARGINATUS n. sp.

P. CINEREUS n. sp.

P. ÆNESCENS n. sp.

[19] This name seems to be preoccupied in Coleoptera, as I am informed by Dr. Geo. H. Horn that it is used by Thomson in his Classification of the Longicorns, 1860, p. 241. In this event Zeller's *Tegeticula* will take precedence.

[20] Zeller described from the ♂ only, but I have examined his type in the Cambridge Museum of Comp. Zool. and verified the fact that it is ♂ *P. yuccasella* and not *Prodoxus decipiens*.

[21] This is quite different from the supposed spotted specimens of *Pronuba yuccasella* which Mr. Chambers found in Colorado (See *American Entomologist* III, p. 143), all of which that are in existence and which I have carefully examined being spotted forms of *Prodoxus decipiens*. The maculation in these last, though variable, is on a different pattern.

[22] A recent reëxamination of the type in the Cambridge Mus. of Comp. Zool. leaves no question as to this being a 5-spotted form of *Prodoxus decipiens*. The figures, given in the Journal of the Cincinnati Soc. Nat. Hist., are somewhat inaccurate in detail and are turned completely around, so that what is given as the costa is the inner border. I would retain my own name for the immaculate form and relegate 5-*punctella* as a variety name to the 5-punctate form which seems to most prevail in parts of Texas.