

Yucca Moths and Yucca Plants: Discovery of “the Most Wonderful Case of Fertilisation”

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The relationship between yucca plants (*Yucca* and *Hesperoyucca* spp.: Agavaceae) and yucca moths (*Tegeticula* and *Parategeticula* spp. [Lepidoptera: Prodoxidae]) is often cited as a classic example of insect–plant coevolution and, in particular, obligate mutualism (Powell 1992, Thompson 1994, Price 1996, Proctor et al. 1996, Pellmyr 2003). Female yucca moths exhibit morphological and behavioral adaptations that ensure pollination of yucca plants, which have highly modified flowers that reduce the possibility of self-pollination or passive pollen transfer by other insects (Fig. 1). The ovaries of the plants serve as a protected food source for the females’ offspring, which feed on seeds that develop as a result of the pollinating activity of the female moths.

This relationship was first explored by the distinguished entomologist Charles V. Riley¹ (Fig. 2) during the early 1870s, about a dozen years after the 1859 publication of the *Origin of Species*. At the time, Charles Darwin and Alfred Russel Wallace’s revolutionary theory of descent with modification was undergoing vigorous debate, in part because scientists questioned the significance of the role played by natural selection. In addition, most older naturalists (i.e., those of Darwin’s generation) clung to natural theology, which held that organisms were placed on earth for man’s benefit and that their countless and wondrous adaptations evi-

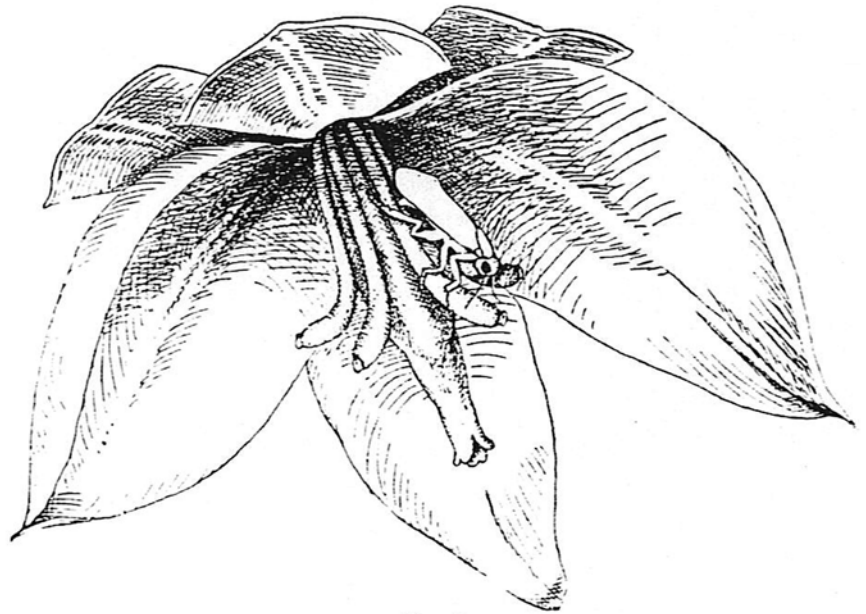


Fig. 1. Illustration by C. V. Riley (1892b) of *Tegeticula yuccasella* (Riley) ovipositing on *Yucca filamentosa*. In this rendering, Riley shows a portion of the petals (top) removed to demonstrate that the anthers point away from the stigmatic tube, making self-pollination highly unlikely.

denced the Creator’s handiwork. In contrast, Darwinian theory, and natural selection in particular, removed all supernatural explanations in accounting for the diversity of life on earth and thus was problematic for many naturalists with strong religious beliefs (Mayr 1982, 1991; Ruse 1982; Bowler 1989; Moore 1993).

This transitional phase in the scientific community’s conception of the natural world was articulated by Riley in his earliest publication on the yucca moth:

Of late years, and more especially since the publication of Mr. Charles

Darwin’s interesting work on the fertilization of Orchids,² we have come to understand more and more the important part which insects play in the fertilization of plants; and the old idea, that color and perfume in flowers were intended for man’s especial pleasure, is giving way to the more natural and philosophic view that they are useful to the plants by attracting the needed insects. (Riley 1873a, p. 57)

¹For biographical treatments of Riley, reputedly the most important entomologist of the 19th century (Sorensen 1995), see Smith and Smith (1996) and Sheppard and Weinzierl (2002).

²Riley made reference here to Darwin (1862).



Fig. 2. C. V. Riley, ca. 1873.

Riley was 27 years old when he read this paper before his fellow members of the Academy of Science of St. Louis.³ A strong advocate of Darwinian theory, Riley rebutted the criticism of many of his colleagues who questioned the validity of the theory. He touted the yucca plant–yucca moth relationship as a remarkable example of Darwinian evolution; and, as the decades passed, Riley’s name and this storied case of plant–insect mutualism became conjoined. Yet Riley might never have become interested in the yucca moth, had it not been dropped in his lap by George Engelmann (Fig. 3), a senior botanist and colleague of Riley who was far from a Darwin enthusiast (Goldstein 1989).

In this article, we revisit the interactions of Engelmann and Riley when both were active members of the Academy of Science of St. Louis. We then focus on Riley’s elucidation of the relationship between yucca plants and yucca moths, an endeavor that engaged him for over two decades and captured the interest of foremost scientists of the 19th century, including Asa Gray, Charles Darwin, and William Trelease. We close with a brief consideration of the more recent findings on this topic.

Engelmann: Biographical sketch and initial yucca observations

George Engelmann (1809–1884) was born in Frankfort-on-the-Main, Germany (Gray 1884, Gray and Trelease 1887, Bek

1929, White 1902, Long 1995), and attended the University of Heidelberg and Berlin University, receiving his M.D. from the University of Wurzburg in 1831. Engelmann’s friends and classmates included Alexander Carl Braun (1805–1877) and Karl Friedrich Schimper (1803–1867), both of whom became well-known botanists, and the renowned naturalist Louis Agassiz (1807–1873), who achieved great stature as a popular lecturer and founder of the Museum of Comparative Zoology at Harvard University.

In 1835, Engelmann relocated to the United States at the request of his uncles, who wished to invest in land in the Mississippi Valley. Engelmann’s emigration facilitated his desire to explore the New World, following in the tradition of famed naturalist and explorer Alexander von Humboldt, who sought to construct a holistic view of nature by teasing out relationships among the natural and physical sciences (Long 1995).

Engelmann eventually settled in St. Louis, Mo., where he became a leading physician. His medical career notwithstanding, Engelmann is a towering figure in the early days of American botany. Regarded as the indisputable authority of the Cactaceae and Coniferae, he also earned recognition as the principal American authority on yuccas, agaves, and American *Vitis* spp. (Rodgers 1944). He traveled to Europe and various regions

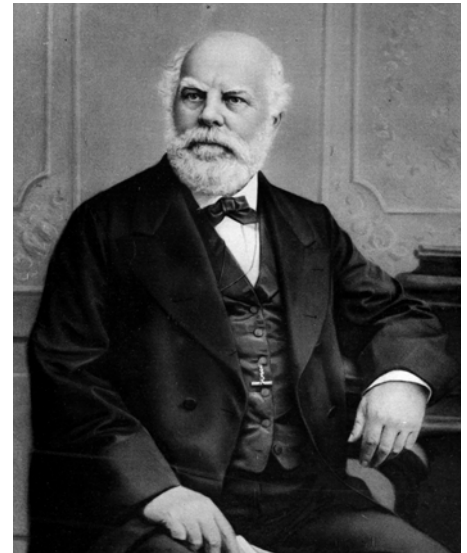


Fig. 3. G. Engelmann (from Gray and Trelease 1887).

of the United States, conducting field excursions and visiting herbaria; and he produced numerous botanical publications, many of them taxonomic/natural history monographs.

In an era marked by U.S. exploration and expansion, Engelmann received botanical specimens for study and classification from numerous federally funded expeditions. For more than 40 years, he contributed to the associated official reports including: C. C.

The genus *Yucca* (Family: Agavaceae) comprises plants native to North and Central America, with approximately half of all yucca diversity occurring in Mexico. Several yucca species have been cultivated in Europe since the late 1500s. *Y. filamentosa*, the pollination of which first captured the attention of Engelmann and Riley, has been naturalized in the United States for more than 150 years. Yuccas are generally associated with arid biomes (chaparral, grassland, shrub desert), but the two southernmost *Yucca* spp. occur in rainforests. According to Pellmyr (2003), *Yucca* taxonomy and systematics are in a state of flux and badly in need of revision, a formidable task because of a historically confused nomenclature, use of horticultural material and cultivars of unknown origin, a lack of herbarium material, and a dearth of phylogenetic analyses.

To view *Yucca* spp. images and distribution maps for the United States, Puerto Rico, and the Virgin Islands, consult the USDA, NRCS PLANTS Database (<http://plants.usda.gov>).

To view a color image of one of the first yucca moth specimens collected by Engelmann in 1872, see the web page by Pellmyr (<http://www.webpages.uidaho.edu/~pellmyr/Firstmoth.htm>); a black and white image appears in Pellmyr (2003).

³Organized in 1856, the academy resided in the bustling portal city to the West and was the center of Missouri’s scientific activity (Hendrickson 1966).

Parry's of the Colorado region and the Rocky Mountains (Parry named a peak in the Rocky Mountains for Engelmann), F. V. Hayden's of the upper Missouri Valley, C. Wheeler's of the territory west of the 100th meridian, A. W. Whipple's of the region westward along the 35th parallel, J. H. Simpson's of the territory of Utah, J. C. Ives's of the Colorado river basin; and the reports of the U.S. and Mexican Boundary Survey and the Pacific Railway Expeditions (Gray 1884; Gray and Trelease 1887; Bek 1929, part 1). In addition to his work as a physician and botanist, and in true Humboldtian fashion, Engelmann also cultivated a serious interest in meteorology and published articles on the altitude of Pike's and Long's peaks in Colorado (Hendrickson 1966).

Engelmann first took notice of the genus *Yucca* in 1842, when acquaintances sent him specimens from Texas, northern Mexico, and New Mexico (Engelmann 1873). In the years that followed, he paid particular attention to yuccas on his U.S. and European expeditions. In Europe, he was "first struck with the 'fact' that '[y]uccas do not bear fruit,'" whereas he had seen yucca fruits in some U.S. collections and observed yucca seed pods in St. Louis gardens (Engelmann 1873). He speculated that European yuccas were sterile because of incomplete development of the flowers or problems arising from self-fertilization. However, from the outset he considered the chances of self-fertilization to be remote because the anthers of the yucca flower point away from the stigmatic tube, making it extremely difficult for pollen to fall into this tube (Engelmann 1872, 1873). Engelmann also noted that the glutinous nature of yucca pollen rendered it highly improbable that the pollen could leave the anthers unassisted.

After observing yucca flowers in the United States, Engelmann concluded that "insects (in these *night-blooming* flowers, of course, *nocturnal* insects) must be the agents which introduced the pollen into the tube" (Engelmann 1873, p. 19) and suspected that the pollinator was "a white moth of the genus *Tortrix*" (Engelmann 1872, p. 33). In the summer of 1872, Engelmann passed to his young colleague, C. V. Riley, the insects he found most frequently in the yucca flowers at night.

"Such Theories Would Lead Us Astray"

Given Riley's entomological expertise and proximity to Engelmann, it is not surprising that the latter chose to give the yucca moths to his associate for further investigation. History, however, marks the irony of the event because Riley quickly recognized the unique and mutually adaptive significance of the yucca plant–yucca moth relationship,

which he accounted for unequivocally according to Darwinian principles.

A year before Engelmann gave Riley the yucca moth specimens, the two men sparred over Darwinian evolutionary theory at the 6 March 1871 meeting of the academy. We might imagine the scene: the august Dr. Engelmann, then age 62, a founding member of the academy and its first president (to which post he was re-elected 15 times) versus the young challenger, Riley, age 26, serving at his third meeting as the academy's recording secretary (Goldstein 1989). According to the academy's *Journal of Proceedings*, the exchange unfolded as follows. Dr. Engelmann presented three specimens of a weed that were extraordinarily similar despite their having been collected from St. Louis County, Mo., France, and Italy. This prompted Riley to ask Engelmann how he accounted for the fact that many European plants and weeds had become well established in the United States, yet very few American plants had become established in Europe. Riley added that insects in Europe *vs.* the United States exhibited the same pattern. Engelmann replied that no theory was necessary to explain these phenomena; the answer lay in the "fact that some plants are more vigorous than others" (Anonymous 1868–1877, p. xlii). Then, the *Proceedings* relate that

Mr. Riley undertook to account for it on the Darwinian theory, that from the greater competition and struggle for existence that had gone on in Europe under the civilized conditions of man, their species were, many of them, better able to thrive under similar conditions here than our own indigenous species. Dr. Engelmann feared such theories would lead us astray. (Anonymous 1868–1877, pp. xlii–xliii)

Also present at the meeting was Dr. Frederick Adolphus Wislizenus, age 61, another founding member of the academy and Engelmann's long-time friend, fellow medical practitioner, meteorologist, and botanical explorer. Wislizenus attributed the spread of European plants to the greater space afforded them in the New World, making no mention of Darwinian theory.

This sparring match marks the first of several recorded between Riley and older members of the Academy of Science of St. Louis, who were grappling with Darwin's revolutionary theory. The historian Goldstein (1989) characterized Riley as "an almost combative Darwinian" who intended to "inject Darwinian theory into Academic discussions whenever possible." Given that Riley joined the Academy in 1868, Goldstein speculates that similar disputes may have taken place but went unrecorded by the

academy's earlier recording secretaries because of implicit or explicit censorship.

In his role as president of the academy for 1876, Riley was the first to speak on the topic of evolution (Hendrickson 1972). He presaged the widespread acceptance of Darwinian theory in his presidential address, following the custom of reviewing the previous year's scientific developments:

The visit of Prof. [T. H.] Huxley to America must be looked upon as an event in the progress of evolution in this country—...because he brought in succinct form, and so conspicuously before the public, some of the best arguments in favor of the doctrine. All great truths that oppose long established popular belief must needs belong to the few when nascent...in my humble opinion, the idea of evolution is founded on fact, and, like a gem freed from the deposits which for ages have hidden its lustre, will shine all the brighter as the obstacles which surround it are removed by the light of truth. (Anonymous 1868–1877, p. ccxlvii)

By this time, even Engelmann may have moved somewhat closer to Riley's thinking. At a March 1876 meeting of the academy, Engelmann commented on the ability of certain hybrid oaks to propagate "when removed from the struggle for existence" presented by more hardy competitors (Hendrickson 1972).

Riley Embarks on his Yucca Moth–Yucca Plant Studies

Riley reputedly pursued his research with enormous zeal and dogged determination (Smith 1992, Smith and Smith 1996), traits evidenced by his record of investigations of yuccas and their associated insects. He set to work immediately, examining the behavior of Engelmann's little white moth; and within three months, he reported his initial findings in a paper read before the 21st meeting of the American Association for the Advancement of Science (AAAS) in August 1872.⁴ The next month he presented his paper to the members of the academy; and a few

⁴This particular AAAS meeting is of historical significance in that the Entomological Sub-section was formed, at whose first meeting was discussed Samuel H. Scudder's "Revision of American Butterflies," put forth in advance of his *Butterflies of North America*. According to a report of the meeting, "There was a unanimous expression of regret and disapprobation...at the wholesale and radical changes proposed by this distinguished author in the generic and specific names of the butterflies....The feeling was manifested by all, that changes so radical and so sweeping in the received nomenclature were uncalled for, and would prove of great detriment to the study and popularity of this department of entomology." (Anonymous 1872, p. 183)

months later it was published in the academy's *Transactions* (Riley 1873a), preceded immediately by a report by Engelmann (1873) on the genus *Yucca*.

In his paper, Riley acknowledged his debt to Engelmann for having drawn his attention to the fact that filamentose-leaved species of yucca "must rely on some insect or other for fertilization" (Riley 1873a, p. 59). Riley erected the genus *Promuba* for the yucca moth, described both sexes and the larval stage of *Promuba* (now *Tegeticula*) *yuccasella* (Riley), and related what he had ascertained of the insect's natural history. He observed that male and female moths meet and copulate on the yucca flower. The female then scrapes the pollen from the anthers with a pair of highly specialized, prehensile, hairy tentacles (Fig. 4), modifications of the basal joint of the female's maxillary palps not found in males (Fig. 5). As he explained, "With her maxillary tentacle [palp]...she collects the pollen in large pellets, and holds it under the neck and against the front trochanters...she sometimes carries a mass thrice the size of her head" (Riley 1873a, p.60). Once the female has collected a ball of pollen, 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" (Riley 1873a, p.60).

The female *Tegeticula* moth was the only species that Riley found to be actively engaged in pollinating yucca flowers,⁵ but during the 1872 season, he was unable to witness any females in the act of oviposition. He knew of no Lepidoptera that oviposited by puncturing the flesh of fruit, and found no evidence that any punctures led to eggs nor that eggs were deposited externally. Given this, Riley hypothesized that *T. yuccasella* eggs were inserted into the fruit through the pollen tubes. In addition, because he had examined "hundreds of [yucca seed] capsules" around St. Louis and southern Illinois, of which "not more than four or five percent were uninfested," he conjectured that oviposition immediately followed, not preceded, pollination (Riley 1873a, p. 62).

Reportedly Riley's AAAS paper was "listened to with marked attention, and was followed by an animated discussion" in which Asa Gray, then out-going AAAS President, and others took part (Anonymous 1872). Gray, a renowned Harvard University taxonomic botanist and the most influential American advocate of Darwinian theory (Dupree 1959, Ghiselin 1969), was held in high esteem by Riley. A few years later, Riley sent Gray yucca moth cocoons to help test

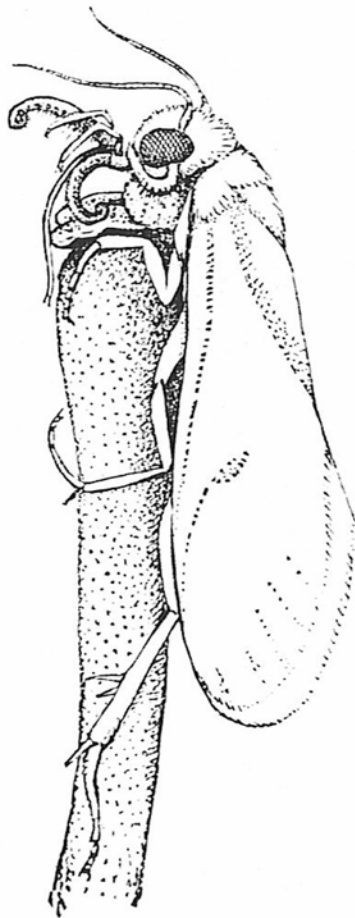


Fig. 4. Female *T. yuccasella* gathering pollen (from Riley 1892b).

his most important yucca-related hypothesis: that yucca moths serve as the sole pollinators of yucca plants.

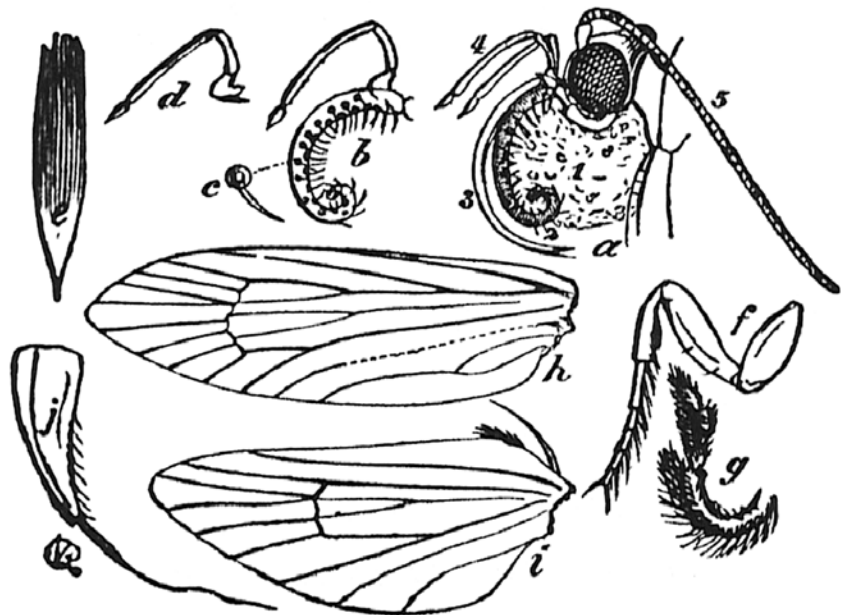


Fig. 5. Illustration by Riley (1873a) from his first yucca moth publication, showing key features of adult *T. yuccasella*: (a) denuded head of female with (1) pollen mass, (b) female maxillary palp with (c) tubercle, (j) ovipositor.

⁵Riley (1873a) listed several other non-pollinating insects (Coleoptera and Heteroptera species) that he had collected from yucca flowers.

Tegeticula yuccasella Pupae Described

Riley was anxious to procure *T. yuccasella* pupae for taxonomic purposes. Because the insect overwinters in the larval stage, he attempted to accelerate metamorphosis (i.e., break diapause) by maintaining larvae at about 80° F throughout the winter of 1872–1873. His efforts met with modest success, but in June 1873, he wrote a publication describing the chrysalids of the male and female moth (Riley 1873b).

Meanwhile, the report of his yucca moth presentation at the AAAS meeting had piqued people's interest, such that in his fifth annual report as Missouri state entomologist, Riley (1873c) provided excerpts from letters sent by several readers, relating personal observations of seed production, or lack thereof, by yucca plants. The letters, which had been published in various periodicals, represented diverse geographic regions in the United States and Europe. Thus Riley began the long process of amassing information relevant to his hypothesis about the unique pollinating activity of *T. yuccasella*.

Oviposition and Pollination: Revision of Hypotheses

Riley worked sedulously and with great care, as Pellmyr has commented:

[I]n contrast to the records of most of his contemporaries, there are very few inaccuracies in [Riley's] accounts, simply because of his reliance on empirical observation. In this, he arguably belonged in the exclusive group of exceptional naturalists with

whom he regularly corresponded, such as Charles Darwin, Alfred Russel Wallace, Henry Walter Bates, Thomas Belt, Fritz and Hermann Müller, and Asa Gray. (Pellmyr 2003, p. 37)

By the close of the 1873 summer season, Riley reported his further observations of the oviposition behavior of *T. yuccasella*. As noted earlier, he had initially hypothesized that oviposition occurred after pollination, and that the ovipositor was not used to puncture the fruit of the plant (Riley 1873a). These hypotheses proved incorrect.

In collaboration with Engelmann, Riley (1873d, 1874) discovered that the female's ovipositor does, in fact, puncture the ovary. Over time, the aperture of the puncture forms a depression and, as the fruit enlarges, the oviposition passage becomes obliterated, which explains why Riley was misled by his initial observations. Indeed, only by dipping the pistil in ink a day or two after oviposition and examining the stained tissue under a magnifying lens was he able to trace the passage created by oviposition that led to the egg locus. Riley explained that he could observe the oviposition of hundreds of eggs because once the female selects a suitable site and her ovipositor penetrates the pistil, "the whole perigon⁶ may be detached, some of the encumbering petals and stamens removed, the insect brought within focus of a good lens and all her movements observed to the greatest advantage, without disturbing her" (Riley 1873d, p. 620).

Also contrary to his original hypothesis, Riley determined in the second season that the female first oviposits, and then, "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...up and down" (Riley 1873d, pp. 620–621). He added that the female may deposit two, three, or more eggs before pollination occurs, and he suspected that "the converse of this is equally true" (Riley 1873d, p. 621).⁷

At the conclusion of his paper, he strongly reiterated his view:

[My observations this summer] have convinced me more than ever that *Pronuba* [*Tegeticula*] is the only insect

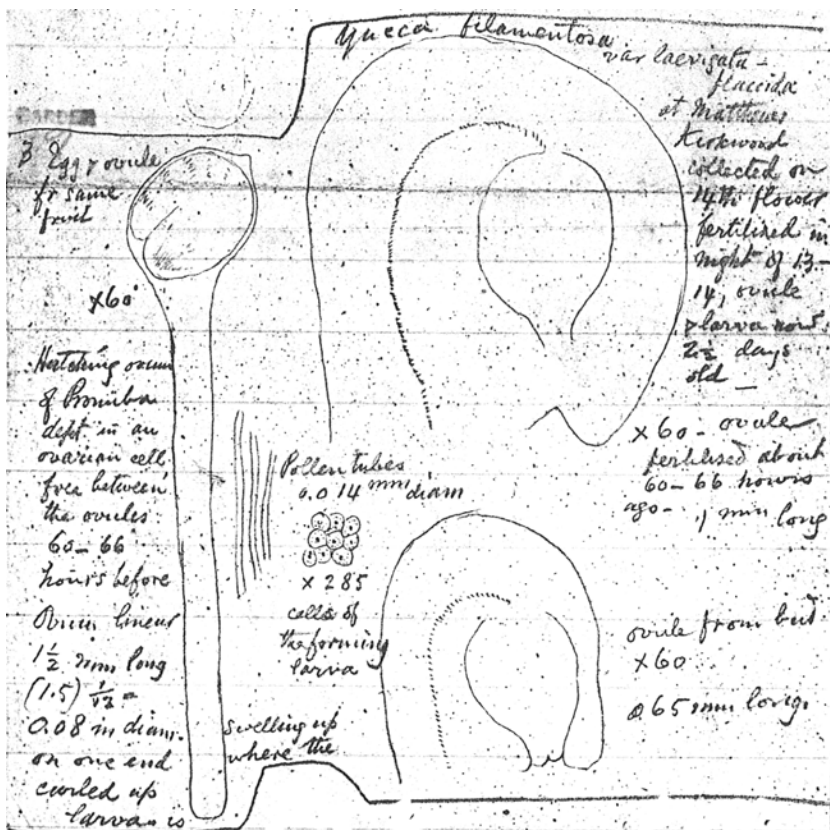


Fig. 6. Engelmann's unpublished sketches, dated July 1873 (Missouri Botanical Garden, William Trelease Professional Papers, Agavaceae, Box 8). Far left, *T. yuccasella* egg, 60–66 hours post-oviposition in *Y. filamentosa*. The elongate egg (1.5 mm long, 0.08 mm diam) holds the developing "curled up larva" at one end. Sketches at right compare relative size and form of an ovule 60–66 hours post-fertilization (top) vs. an unfertilized ovule from a bud (bottom). In the former, the stigmatic tube is closed, whereas in the latter it is still open.

by the aid of which our yuccas can be fully fertilized; for I have studied this fertilization diligently night after night, without seeing any other species go near the stigma. (Riley 1873d, p. 622)

Engelmann's Further Studies of *T. yuccasella* and *Yucca* spp.

During the summer of 1873, while Riley pursued his yucca moth oviposition studies, Engelmann made in situ observations of *T. yuccasella* in various yucca species. His original drawings depict egg morphology and embryonic development of *T. yuccasella* concomitant with early post-fertilization changes in the yucca ovule (Fig. 6). He observed that the developing embryo, with segmentation, is evident at 60–66 hours after oviposition (Fig 7). Engelmann also found that very soon after oviposition, the young seeds "begin to swell up to three or four times the thickness" of the normal seeds and "are thus preparing the sustenance of the young larva, which feeds on one or usually both of them until able to attack the meanwhile more or less developed young seeds" (Fig. 7; Engelmann 1875, p. 211; Riley 1873d).

Engelmann (1875) reported that the stigmatic opening closes immediately after the first night of flowering (Fig. 6). Riley (1873d) thus noted that it is during this one night that female *T. yuccasella* must pollinate the yucca and lay her eggs; subsequently, Riley (1892a) stated that, on occasion, this timeframe could be 1–2 nights. These findings are substantiated in a recent review (Pellmyr 2003).

Influence of Darwin and Gray on Riley's Scientific Conceptualization

The work of Darwin strongly influenced Riley's scientific conceptual framework. He unequivocally supported the Darwinian theory of species origin versus the older view of special creation and immutable species. Moreover, Riley immediately recognized that the mutualism between yucca moths and yucca plants represented "one of the first and strongest examples of evolution by means of natural selection" (Pellmyr 2003, p. 36). Riley openly expressed this opinion at scientific meetings and in publications, and often interpreted his entomological findings in light of evolutionary theory. For example,

⁶"Perigon" (Latin form of "perigone") refers to a flower in which the calyx and corolla (collectively termed the perianth) are not clearly differentiated. (Swartz 1971)

⁷The latter scenario, which has never been documented (Olle Pellmyr, personal communication), would account for the pollination of capsules that contain no larval *Tegeticula* nor evidence of ever having contained any.

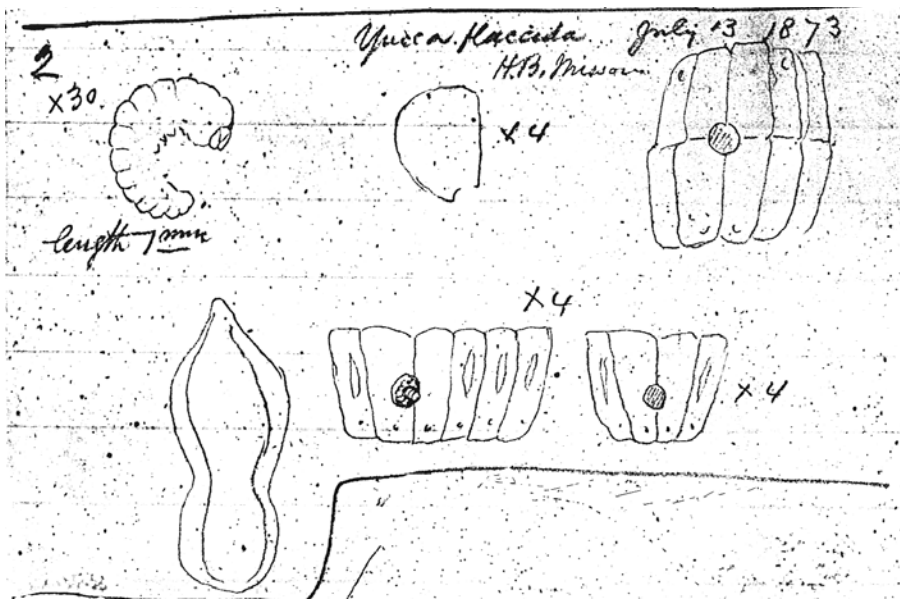


Fig. 7. Engelmann's unpublished sketches, dated July 1873, of *T. yuccasella* development in *Yucca flaccida* (Missouri Botanical Garden, William Trelease Professional Papers, Agavaceae, Box 8). Top left, larva (1 mm in length) at 60–66 hours after oviposition, showing segmentation; top and lower right, seeds with spherical holes from feeding larvae, which eclose from the egg 4–5 days after oviposition. Lower left, seed pod.

in his first yucca moth publication, he wrote:

We have in this little moth a remarkable adaptation of means to an end. There is between it and its food-plant a mutual interdependence which at once excites our wonder, and is fraught with interesting suggestions to those who are in the habit of reasoning from effect to cause. Whether we believe, as I certainly do, that this perfect adaptation and adjustment have been brought about by slow degrees through the long course of ages, or whether we believe that they always were so from the beginning, they are equally suggestive of that same law and harmony so manifest throughout the realm of Nature. (Riley 1873a, p. 63)

In this same paper, Riley elaborated on the adaptive advantages to the yucca plant and the yucca moth: The plant was guaranteed pollination with a high degree of probability, and it lost only a few seeds in return; the insect received a safe larval feeding site. As a good Darwinist (and with clear reference to plant–insect coevolution), Riley accounted for this arrangement on the basis of gradualism, postulating that this mechanism could have resulted in the development of the “peculiarities” present in the plant and the insect:

[I]t is quite easy to conceive, on Darwinian grounds, how both these characters may gradually have been produced in the course of time from archetypal forms which possessed

neither. These peculiarities are, moreover, mutually and reciprocally beneficial, so that the plant and the animal are each influenced and modified by the other, and the same laws which produced the beneficial specialization of parts would maintain them by the elimination of all forms tending to depart from them. (Riley 1873a, p. 63)

Riley recognized the significance of cross-pollination largely because of Darwin's work in this area.⁸ In a paper summarizing his many years of research on the relationship between yucca moths and yuccas, Riley made reference to several of Darwin's botanical publications from the 1860s:

The importance of insects as agents in cross-fertilization was scarcely appreciated, however, until the late Charles Darwin published the results of his researches on *Primula*, *Linum*, *Lythrum*, etc., and his elaborate work on the fertilization of orchids. The publication of these works gave to flowers a new significance and to their study almost as great an impulse as did his immortal “Origin of Species” to the general study of biology.⁹ (Riley 1892a, p. 101)

Riley's early thinking about pollination also drew upon the work of Asa Gray. Riley

cited Gray's 1872 work, *How Plants Behave*, in his first yucca moth publication to support the fact that, typically, the flowers of angiosperms are “curiously and elaborately constructed so as *just not to do* of themselves what must necessarily be done for them in order to prevent degeneracy or extinction of the species,” thereby facilitating cross-pollination (Riley 1873a, p. 57). He pointed out that many plants depend on other organisms to transfer their pollen from plant to plant and stated that the yuccas he had been studying “seem to depend for assistance, so far as we now know, on the single little Tineid [Prodoxid] which I have described” (Riley 1873a, p. 58).

Evidence for the Exceptional Pollinating Activity of *T. yuccasella*

Whether Riley anticipated that his yucca moth research would span two decades and raise the hackles of many a colleague is moot; undoubtedly, he was cognizant from the outset of the enormity of his claim, which he had couched in cautious terms in his first yucca moth publication (Riley 1873a). He admitted that he knew of no other case in which a single insect species was solely responsible for pollinating a given plant, and he had witnessed the discussion that his presentation provoked among his respected colleagues at the 1872 meeting of the AAAS.

Riley based his hypothesis on several lines of evidence: His observation that female *T. yuccasella* was the only insect found actively pollinating the flower; the appearance of the female's highly modified maxillary palps and her behavior regarding pollen collection and deposition; the fact that exclusion of the female moth (by netting) did not result in yucca self-pollination; and the glutinous nature of yucca pollen. He also had additional information from Engelmann, Gray, and others, who reported that yucca plants introduced to northern United States and European gardens where the yucca moth is absent fail to yield fruit and seed, but that pods of wild yucca (*Yucca angustifolia*, [now *Y. glauca*] from the Black Hills of Colorado, *Y. rupicola* from Texas, and *Y. whipplei* from California) show “unmistakable holes of egress of the larvae” (Riley 1873a, p. 64).

In his first yucca publication, Riley expressed hope that “the next blooming-season of our Yuccas will find other eyes than my own watching [*Tegeticula*'s] ways and methods,” because much remained to be discovered about the insect (Riley 1873a, p. 63). Such professional generosity may sound somewhat specious, given the potential im-

⁸Darwin's influence in this regard has been noted by many; see Ghiselin, 1969, Faegri and van der Pijl 1971, Bowler 1990, Proctor et al. 1996.

⁹Riley (1882) articulated the same thoughts in an earlier address to the Biological Society of Washington.

fact of such an extraordinary discovery, but perhaps he believed that the opportunity to obtain corroborating evidence outweighed the possibility of another scientist stealing his thunder. In any event, the most meaningful publications on yucca moths and mutualism would come from Riley, and *T. yuccasella* and other insects closely associated with yuccas would continue to be a part of Riley's scientific investigations for 20 years.

Riley Sends *T. yuccasella* Cocoons to Colleagues

Riley hypothesized that if *T. yuccasella* were the sole pollinator of yuccas, then yuccas that never produce fruit should be found in areas where yuccas had been transported but the moth was absent. He further reasoned that if his hypothesis were correct, introducing yucca moths to areas devoid of moths would yield fruit-producing yuccas. Riley proposed to test the validity of his hypothesis:

It is my intention to obtain a large number of cocoons this year and...distribute them among those who grow the yucca in those parts of this country or in Europe where seed is not produced. (Riley 1873d, pp. 622–623)

During 1873 and 1874, Riley sent larvae (the numbers are shown in parentheses) in their cocoons to Asa Gray, Cambridge, Mass. (150); botanist Jules-Emile Planchon,¹⁰ Montpellier, France (100); botanist Hermann Müller, Lippstadt, Germany (250); Charles Darwin, Down, England (100); lepidopterist Henry Tibbats Stainton, Mountsfield, England (50); and Meade Woodson (whom Riley described as a "great admirer" of *Yucca*), Kansas City, Mo. (100) (Riley 1881). Riley requested that the cocoons be buried in the ground near yucca plants. Darwin, having no yucca plants at his home, sent his insects to Joseph Dalton Hooker, noted botanist and director of the Royal Botanic Gardens, Kew, England.¹¹ Müller's moths hatched, but no ornamental yuccas were in flower at the time (Pellmyr 2003) and the results of the remaining experiments are unknown.

We do know that Riley was mailing yucca cocoons to naturalists until just before his accidental death in 1895. Extant letters¹² that

Riley wrote from 1893 to 1894 indicate that the following correspondents were sent cocoons: Professors M. Valery Mayet and M. Viala (Ecole Nationale Agronomique, Montpellier, France), D. Morris (Assistant Director, Royal Botanic Gardens, Kew, England), T. Hanbury, FRS (Ventimiglia, Italy), and Professor G. L. Goodale (Cambridge, Mass.). Riley asked that the cocoons be placed around yuccas in the filamentose group, or those which typically bloomed in May and June.

Criticism and Confusion: True Yucca Moths, Bogus Yucca Moths, and More

In the years following his first publication on the yucca moth, *T. yuccasella*, Riley encountered much criticism, from botanists and entomologists, who questioned his scientific description of the moth, his observations of its behavior, and his conclusions about its unique relationship with yucca. As we will discuss, many of the disagreements arose because naturalists unwittingly confused *T. yuccasella* with other insect species. Regardless of the reasons underlying a given contentious issue, Riley's record of scientific publications and presentations attest to the considerable time and energy he expended countering those who impugned the accuracy of his findings.

Riley vs. Zeller

The first dispute occurred when Professor P. C. Zeller, an entomologist from Prussia, questioned Riley's assertions that larval yucca moths lack anal prolegs and that the adult female moth collects pollen with her maxillary tentacles. (Pellmyr [2003] has pointed out that Zeller's experience with yucca moths was "limited to three pinned specimens given to him.") Zeller proposed that the female's "tongue" (proboscis) could, by itself, accomplish the task of gathering pollen.

In his rebuttal, a clearly vexed Riley (1876) reiterated his published statement, in which he had indicated that all of his conclusions had been based on careful, repeated observations conducted over the course of three summers. He also took umbrage at Zeller's last sentence¹³: "In my opinion, Riley, while making his most interesting discovery, hasn't seen everything yet; and other observers will be necessary to explain satisfactorily the curious goings-on during reproduction of the moth."

Riley wrote:

...as for the reflection in the last sentence which I have quoted, I am vain enough to believe that there is no

other provocation for it than a certain ill-will on my critic's part. It comes, too, with all the less grace from one who confessedly made hasty and incorrect observations on the position of the species. From one less honored and esteemed, such captious remarks would have received no notice at my hand. (Riley 1876, p. 326, fn.)

In response to his publication, Riley received a personal letter from Zeller¹⁴ that began,

You do me a great injustice by thinking that I wrote the notes on *Pronuba* [*Tegeticula*] with any ill feeling towards you. I am quite convinced that if you had written them in the same manner in opposition to me I would not have felt injured at all, but would only have felt impelled to repeat my observations, for, least of all, do I hold myself to be infallible, but am of the opinion that every observation must go through the crucial test of repetition by several observers before it can be regarded as correct and incontrovertible.

In his letter, Zeller stated that he had asked Stainton for his opinion of the polemic. Stainton replied that Zeller's statements regarding Riley's observations were "truly Zellerian, i.e., a little too dogmatic. You say that it is quite impossible that *Yucasella* can do what R. says it does." Zeller explained to Riley that because "even great investigators, as for example Réaumur, have made mistakes," the remarkable features that Riley had described caused him to question Riley's observations. In closing his letter, Zeller wrote: "As you have up to this time only shown a kind spirit toward me, I cannot imagine at all how I could return it with ill-will." Whether Riley responded to the letter is unknown.

Riley vs. Boll

Jacob Boll of Dallas, Tex., attempted to refute Riley's oviposition and pollination findings with assertions based on cursory observations and a poorly designed experiment. Moreover, Boll had never bothered to read Riley's yucca moth publications and eventually admitted to Riley that he "knew absolutely nothing of [Riley's] writings on the subject except what he learned through Prof. Zeller's notice" (Riley 1877, p. 572). Unlike Riley, Boll (1876) made no effort to observe the behavior of the moth under field conditions, but instead he had caged female yucca moths with cut yucca flowers that had apparently already been fructified. Boll also put forth the fallacious notion that the fe-

¹⁰Planchon collaborated with Riley on grape phylloxera research (Smith 1992).

¹¹Darwin to Hooker, 7 April 1874 (Cambridge University Library, classmark DAR 95:321).

¹²Missouri Botanic Gardens: William Trelease papers.

¹³"Meines Erachtens hat Riley bei seiner höchst interessanten Entdeckung noch nicht Alles gesehen, und noch andere Beobachter werden erforderlich sein, um die sonderbaren Vorgänge bei der Fortpflanzung der Motte ganz genügend zu erklären."

¹⁴Missouri Botanic Garden, William Trelease professional papers, Box 8, folder 1; letter dated 3 April 1876.

male yucca moth used pollen or stamen hairs to seal her oviposition puncture. He further opined that the exclusive fertilization of yuccas by yucca moths had not been proven and that “internal fertilization, if one should take this for such, would belong to the realm of fable” (cited in Riley 1877, p. 573). Riley called Boll’s publication “palpably superficial and erroneous” (Riley 1877, p. 570) and concluded with a biting rejoinder:

Mr. Boll should increase his knowledge by perusing what has been written on the fertilization of flowers by insects. He should also learn something more than he has done in this instance of a subject he intends to treat, and especially of observations which he has undertaken to criticize. Investigations, however instigated, should be carried on, not under the warping influence of individual motive, but solely for the love of truth and knowledge. (Riley 1877, p. 573)

Riley vs. Chambers

Another clash occurred in 1877, when V. T. Chambers published his account of the Tineina of Colorado in Hayden’s Geological and Geographical Survey of the Territories. Chambers (1877) claimed that he had discovered a “spotted version” of adult *Pronuba* [*Tegeticula*], thereby bringing into question Riley’s taxonomic description of the moth’s front wings as “uniformly silvery-white.” Chambers sent all of his specimens to Hagen at Harvard, a few of which were forwarded to Riley, whose incredulity upon examining the specimens is evident in this passage:

...what is more remarkable, they are one of Mr. C.s’ own described species—[*H*]yponomeuta *5-punctella*. Of the six specimens submitted to me, there was but one *Pronuba* [*Tegeticula*], and that was immaculate, as the species always is. ...I have reared upward of 500 specimens of *Pronuba* [*Tegeticula*], and have it from South Carolina, Texas, California, Colorado and Missouri, and there is never the faintest tendency to maculation. (Riley 1877, p. 569)

To make matters worse, Riley was asked by Hagen not to denude the specimens and, as a result, was incorrect in his identification of the “spotted” *Tegeticula* as *H. 5-punctella* Chambers. Riley would eventually be in a position to correct his error and, in so doing, erect a new genus.

As fate would have it, in July 1879, Riley had occasion to pass through Dallas, whereupon he visited Boll, who had bred what he thought to be *T. yuccasella* from the flower stem of *Y. rupicola* (Riley 1880a). Upon examining the insects, Riley determined that

Boll’s moths were not, in fact, *T. yuccasella*, but a closely related species. One month later, Riley attended the annual meeting of the AAAS held in Saratoga, N.Y. There he announced to the Entomology Club that he had likely discovered the cause of the discrepancy between his findings and those of Boll and Chambers—namely, that the moths the latter two had been observing were *Prodoxus decipiens* Riley¹⁵ (Lepidoptera: Prodoxidae) (Riley 1880b) (Fig. 8). Although very similar in appearance to the yucca moth, *P. decipiens* oviposits on the flower stem and is not a yucca pollinator (Fig. 9).

Ever the careful observer, Riley had reported the presence of the then-unnamed *P. decipiens* in his first yucca moth publication. He wrote of finding “a smaller white, apodous larva” in the pulp of *Y. aloifolia*, “sometimes in considerable numbers,” which “occasionally gnaws into the seed from the outside,” adding that this larva has hymenopterous affinities and that its legless character “will at once distinguish it” from larval *Tegeticula* (Riley 1873a, p. 59, fn.).

In the publication that derived from his presentation at the 1879 AAAS meeting, Riley (1880a) pointed out the various ways

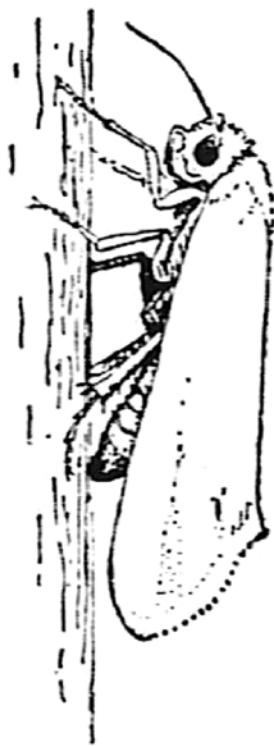


Fig. 8. Female *Prodoxus decipiens* Riley ovipositing in a yucca flower stalk (from Riley 1892a).

¹⁵The genus name derives from the Greek, “judging of a thing prior to experience” (Riley 1880b, p. 155, footnote).

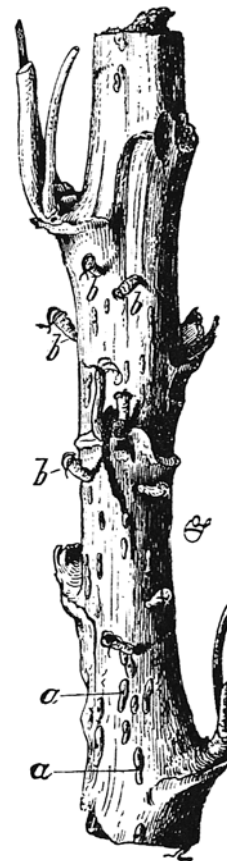


Fig. 9. Riley’s rendering of a yucca flower stem with (a) oviposition scars and (b) pupal exuvia of *P. decipiens* (from Riley 1892a).

in which *Prodoxus* differed from *Tegeticula*: The adults show an inclination to maculation, and the female lacks the characteristic maxillary tentacles; the larvae are legless; and there are differences in the chrysalis, male genitalia, and habits of the two species.

In addition, having been unable to examine Chambers’s “supposed spotted *Pronubas* [*Tegeticula*], the types of which are in the Cambridge [Harvard University] museum,” Riley conjectured that the specimens would turn out to be *Prodoxus*, based on Chambers’s description of its habits and his depiction of the pattern of maculation. He openly expressed his displeasure with the carelessness of Chambers’s scientific work:

We assumed that Mr. Chambers had made a proper reference in describing his *Hyponomeuta 5-punctella*, but we are now perfectly satisfied that he had not, since many specimens of *Prodoxus* agree exactly in maculation with his description and figure. More careful study plainly shows that *Prodoxus* does not even belong to the same family, but must be placed with *Pronuba* [*Tegeticula*] in the *Tineidae*. ...Mr. Chambers...has published some 14 pp. of matter containing many

interesting but irrelevant facts, and more that is funny than convincing when it comes to the point at issue. He brings forward no fresh evidence except such as he calls circumstantial, and admits that he does not 'pretend that they [the arguments] are conclusive of the question, especially when opposed to the positive statements of so competent an observer'. (Riley 1880a, p. 143)

Recent research has revealed another twist in the *P. decipiens* story. For many years, this species was considered synonymous with *P. quinquepunctellus* (Chambers) (Chambers 1875). However, Althoff et al. (2001) have shown *P. decipiens* to be a distinct species, ranging from the eastern United States westward to central Texas; Riley's *P. decipiens* series derived from South Carolina. *P. quinquepunctellus* occurs in the southwestern United States into the northern Great Plains states; Chambers's *P. quinquepunctellus* specimens were from Colorado. These two sister taxa are sympatric in central Texas (Althoff et al. 2001). It is also worth noting that although Riley (1880a) stated that a few *P. decipiens* larvae are found in the fruit, this observation has not been corroborated and whereas certain prodoxids are gall-makers in fruit, no species is known to do both (Olle Pellmyr, personal communication).

Riley vs. Meehan

Mr. Thomas Meehan, botanist and editor for *Gardeners' Monthly*, also attended the 1879 AAAS Saratoga meeting. He gave a paper in which he reported that although he had observed *T. yuccasella* to be abundant at the time of flowering of *Y. glauca*, the plant never produced fruit unless he artificially pollinated it. Based on this, he concluded that *T. yuccasella* must not pollinate *Y. filamentosa* as Riley had claimed.

Riley (1877) had known since 1876 that *T. yuccasella* adults typically appear 2–3 weeks after *Y. glauca* blooms and that this yucca species rarely produces seed. He informed Meehan at the AAAS meeting that the moths in question most likely were *P. decipiens*. Riley added that the one time he did observe a few seeds in *Y. glauca* in St. Louis was when it had bloomed a bit later than usual; upon inspection, he found that the capsules contained *T. yuccasella* larvae. As if to further frustrate Riley, Meehan, like Chambers, had sent his specimens (living larvae) to Hagen,¹⁶ who initially thought them to be Coleoptera; once they had pupated, Hagen realized his error. At the time that Riley's paper (1880a) went to press, Hagen

had been unwilling to send Riley any of Meehan's specimens for identification because, Hagen explained, he had been studying them and was "about to publish it" (Hagen 1880). As we shall see, Riley would once again find himself defending his findings (this time to Darwin) because of Meehan's flawed scientific work and unfounded assertions.

Riley Erects Prodoxidae; Hagen Misidentifies *P. decipiens*

In 1878, Riley resigned his post as the first state entomologist of Missouri to become the head federal entomologist in Washington, D.C., the position he held (except for a 2-year hiatus) until 1894, the year before his death. During that time, Riley briefly revived the *American Entomologist* as a new series and, with L. O. Howard, co-edited a new journal, *Insect Life*, published by the Bureau of Entomology, USDA. He also was founder and first president of the Entomological Society of Washington [D.C.] and a founding member of the Biological Society of Washington [D.C.], both of which published their own *Proceedings*. Thus, much of the ensuing yucca-related controversy was recounted by Riley in the pages of these periodicals and at his presentations at AAAS meetings.

In 1881, a seminal paper by Riley appeared in the *Proceedings* of the AAAS,¹⁷ which he sent to Darwin (discussed later). In this publication, Riley summarized his yucca-associated findings to date; quoted extensively from the criticisms by Meehan and Boll of his work and his rebuttals thereof; described several new yucca-associated insect species (*Pronuba* [*Tegeticula*] *maculata*, *Prodoxus intermedius* [now *Tegeticula intermedia*] (Riley); see Pellmyr 1999], *Prodoxus marginatus*, *Prodoxus cinereus*, and *Prodoxus aenescens*); noted that G. H. Horn had informed him that the name *Pronuba* was preoccupied in Coleoptera and if so, then Zeller's *Tegeticula* would take precedence; and erected a new family, Prodoxidae, which stands today.

Riley (1881) also set the record straight on two points of taxonomic interest. First, he corrected his earlier misidentification of the specimens that Chambers had sent to Hagen—having finally been given permission to denude some of Chambers's specimens, Riley identified them as a 5-spotted form of *P. decipiens*, thereby supporting the validity of his earlier conjecture (Riley 1880c). Second, Riley reported Hagen's admission to having mistaken *P. decipiens* for *T. yuccasella*; thus, Hagen's then-recent publication (1880),

in which he claimed to have bred *T. yuccasella* from yucca flower stems, was in error.

Riley's abstract for the 1882 AAAS meeting resounded with confidence that his latest findings would finally silence his critics:

This paper records some recent experiments and observations which establish fully and conclusively the fact that *Pronuba* [*Tegeticula*] is necessary to the fertilization of the capsular Yuccas. It describes for the first time how the pollen is gathered and collected by the female *Pronuba* [*Tegeticula*]. The act is as deliberate and wonderful as that of pollination. Going to the top of a stamen she stretches her tentacles to the utmost on the opposite side of the anther, presses the head down upon the pollen and scrapes it together by a horizontal motion of her maxillae. The head is then raised and the front legs are used to shape the grains into a pellet, the tentacles coiling and uncoiling meanwhile. She thus goes from one to another until she has a sufficiency. (Riley 1883, p. 467)

Riley (1883) reported several other important findings: He confirmed Engelmann's conclusion that the stigmatic apices of certain *Yucca* species are impotent and that the flower morphology of *Y. aloifolia*, the only species known to self-fertilize, is such that the flowers can achieve this task; he demonstrated that the irregularities in yucca pods, then considered a character state by botanists, are attributable to *Tegeticula* oviposition punctures (Fig. 10); and he determined exactly where and how the egg of *Tegeticula* is oviposited by examining the internal anatomy of the yucca ovule and the ovipositor of *T. yuccasella*. His new findings notwithstanding, if Riley believed that he had at last quelled the yucca moth controversy, he was indeed mistaken.

Riley vs. Hulst

In 1886, the Reverend George D. Hulst instigated what would become a contentious debate with Riley. Hulst, editor of the journal *Entomologica Americana*, argued in its pages that honey bees must be extensive fertilizers of yuccas because he had observed honey bees "plentiful about the flowers," the majority of yucca seed capsules he examined gave no indication of the presence of *Tegeticula* larvae, and yuccas are sometimes fertile in foreign countries (Hulst 1886). In response, Riley began by underscoring the depth and breadth of his yucca moth studies:

For over 16 years now I have very carefully studied the habits of *Pronuba* [*Tegeticula*] in connection with *Yucca*, not in one locality alone but in nearly

¹⁶According to Hagen (1880), Meehan sent the specimens at Engelmann's request.

¹⁷This paper was read by Riley at the 1880 AAAS meeting (Anonymous, 1880).

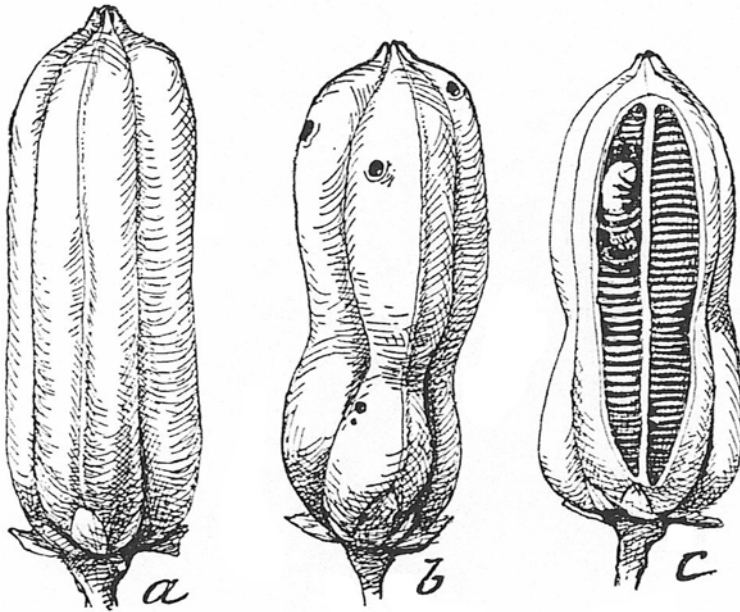


Fig. 10. Illustration by Riley (1892a) of mature pods of *Y. angustifolia* (now *Y. glauca*): (a) artificially pollinated (thus lacking punctures and constrictions due to oviposition), (b) pollinated by *Tegeticula* (showing oviposition punctures, constrictions, and larval exit holes), (c) larva within the pod.

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...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. (Riley 1888, pp. 151)

Riley also contrasted Hulst and “his good friend” Meehan, stating that the latter had written much on the fertilization of *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. (Riley 1888, p. 150–151)

Riley pointed out that Meehan had been working with *Y. glauca*, whose flower morphology and abundant stigmatic liquor likely made it more susceptible to artificial pollination; a quote from a letter of Engelmann to Riley supported this assertion. Riley also cited the research of his trusted colleague, botanist William Trelease, who had shown that female *Tegeticula*, in the act of pollinating, repeats the process several times, “first from one of the angles between the apices, then from another, and...the tongue¹⁸ is used, in addition to the tentacles, to push the pollen down to the bottom of the tube” (Riley 1888, p. 152).

In addition, Riley (1888) provided more recent evidence to discount Hulst’s belief that honey bees could serve as pollinators of yuccas. He had those in his employ (L. O. Howard, T. Pergande, O. Luger) observe more than 200 yucca stalks at the USDA in Washington between 9 and 10 a.m., and no honey bees were seen around the flowers. Riley noted that he himself had seen a single bee on two occasions, but each time it merely probed the flower on its outer base and flew off without entering it. Furthermore, Riley noted, these findings had been corroborated by Professors Cook and Beal at Michigan State Agricultural College (now Michigan State University).

Lastly, Riley related the findings of Trelease (1886), who reported that the stigmatic cavity of *Y. filamentosa* is not nectariferous and that the small amount of nectar it secretes is

every State east of the Rocky Mountains where that genus occurs either indigenously or by introduction. I have also had occasion to study it in many places in Europe in which it is cultivated, and the results have been published in several papers. (Riley 1887, p. 233)

Riley continued, stating that he had seen neither honey bees nor other nectar-feeding Hymenoptera frequenting yuccas and that this was not surprising, given certain characteristics of the flowers—they are half-closed in the daytime, opening when bees are done foraging, and their glutinous pollen would not stick to hirsute Hymenoptera. He reiterated that years earlier, he had listed the insect species found in yucca flowers and that his associates and others had corroborated his findings. In response to Hultz’s criticism that *T. yuccasella* larvae are not always found in the fruit, Riley emphasized that pollination can (albeit rarely) occur without oviposition, and that sometimes the eggs may fail to hatch successfully or the larvae may perish (in which cases the fruit bear evidence of oviposition activity). Riley cited his earlier publications, which provided substantiating evidence in response to others who also had questioned his findings, to rebut Hulst’s other criticisms.

Unconvinced by Riley’s reply, Hulst (1887) wrote a rejoinder that was printed immediately beneath Riley’s response. Hulst persisted in his belief that honey bees could act as yucca pollinators because the flowers

remain open until 10 a.m., and “business hours for honey bees begin long before that time” (Hulst 1887, p. 237). He added that Meehan’s work with artificial fertilization suggested that self-fertilization in yuccas was possible.

The beleaguered and clearly annoyed Riley penned his response in August 1887, while en route to Europe, and mailed it to Hulst from England (Riley 1888, p. 150, fn.). But according to Riley, Hulst “exercised his editorial prerogative in declining to publish [Riley’s] communication...” (Riley 1888, p. 150, fn.), which prompted Riley to send his response to the *Proceedings* of the Entomological Society of Washington. Riley explained that he had deferred in his response to Hulst mostly because he had hoped that Hulst “would himself gracefully amend his opinions to accord with the facts” because the yucca fruiting season had ended, and he would have been “able to make more careful observations” (Riley 1888, p. 150). Riley then countered each of Hulst’s arguments in full, stating that he had “followed up on [Meehan’s] experiments, and made many others during the past seven years, on [*Yucca filamentosa* and *aloifolia*.” At a time when relatively few entomologists were performing experiments of any sort, Riley’s brief description of the pollination experiments he conducted speak to his scientific acumen and the thoroughness of his approach:

My experiments have been made in the afternoon, evening, and morning, with flowers one day, two days, and three days after opening; with pollen

¹⁸Trelease (and Riley 1873a) was incorrect, as the “tongue” is not used to pollinate, but is held straight out above the tentacles. However, he subsequently described its proper position during pollination for *T. synthetica* (Trelease 1893).

located at the base of the pistil or the petals, not near the stigma. Riley stated that he had corroborated Trelease's findings "by dissection [of the pistil] and study of the insects seeking this scant nectar" (Riley 1888, p. 154).

Without doubt (and understandably so), what most infuriated Riley was Hulst's allegation that "[to] Dr Engelmann...we are indebted for the discovery of the fact that *Pronuba* [*Tegeticula*] is an agent in the fertilization of *Yucca* (though he did not work out the history which Prof. Riley has done so well)..." (Hulst 1887, p. 236). Regarding this, Riley remarked: "Whatever may have led Mr. Hulst to make this assertion, it is simply untrue...." Riley acknowledged that it was quite likely he might never have studied the yucca moth had Engelmann not called it to his attention, but he correctly asserted that Engelmann had "made no observation whatever upon insect pollination." Riley continued:

The discovery that *Pronuba* [*Tegeticula*] 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....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. (Riley 1888, pp. 153)

With the remark that he had "already devoted more time to Mr. Hulst's opinions than they justify," Riley recapitulated his denouncement of Hulst's assertions. He concluded,

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* [*Tegeticula*] nor *Pronuba* [*Tegeticula*]-like insect exists, to find the plant modified to more readily permit self-fertilization sooner than to find *Apis mellifica* the pollinating agent, the opinion...of Mr. Hulst, to the contrary notwithstanding. (Riley 1888, p. 154)

Darwin: "It is the most wonderful case of fertilisation"

On 7 April 1874, Darwin wrote to J. D. Hooker, the celebrated botanist and one of his closest friends, about the yucca moth-yucca plant relationship as elucidated by Riley, stating: "It is the most wonderful case of fertilisation ever published."¹⁹ By this

point in time, Darwin was well acquainted with Riley's work because the latter had sent him copies of his Annual Report of the Missouri State Entomologist. Indeed, according to Darwin's son, Francis, and A. C. Seward, "These reports were greatly admired by Mr. Darwin, and his copies of them, especially of Nos. 3 and 4, show signs of careful reading." (Darwin and Seward 1903, p. 385, fn. 2).

Darwin (1876) cited Riley's yucca work in his book, "*The Effects of Cross and Self Fertilisation in the Vegetable Kingdom*;" and soon after its publication, Meehan sent Darwin a letter calling into question the significance of Riley's findings. Meehan wrote that Gray had admitted in a letter to him that "there is far more self fertilization among flowers than he [Gray] had supposed." Meehan added that although only *T. yuccasella* can fertilize the yucca, "as you are no doubt aware, the *Pronuba* [*Tegeticula*] fertilizes the flower with its own pollen,—and it seems to me a great mystery why the plant should not be arranged to use any itself, and not be necessitated to have insect aid in the use of its own pollen."²⁰

Subsequently, when Riley sent Darwin a copy of his 1881 AAAS publication, he received the following response from Darwin:²¹

I must write half a dozen lines to say how much interested I have been by your "Further Notes" on *Pronuba* [*Tegeticula*], which you were so kind as to send me.—I had read the various criticisms, & though I did not know what answer could be made yet I felt full confidence in your result, & now I see I was right.—What an inaccurate man Mr. Meehan is! His Epitaph ought to be "He retarded natural science in the U. States as much as any one man advanced it." ...If you make any further observation on *Pronuba* [*Tegeticula*]—it would I think be well worth while for you to observe whether the moth can or does occasionally bring pollen from one plant to the stigma of a distinct one for I have shown that the Cross-fertilisation of the flowers on the same

plant does very little good; & if I am not mistaken you believe that *Pronuba* [*Tegeticula*] gathers pollen from the same flower which she fertilizes—.

In his reply,²² Riley clarified his findings regarding *Tegeticula* and cross fertilization²³:

My language is perhaps ambiguous on this point, but in fact she not only pollinizes with the same load of pollen different flowers on the same panicle, but often flies from plant to plant. I have never seen her gather the pollen, but have watched her thus go from flower to flower and from plant to plant during a single evening and with one and the same load.²⁴

In the same letter, Riley voiced a harsh assessment of Meehan's scientific prowess:

His trouble is that he has not been so trained that he can appreciate a truth whether it conflict with his own opinions or not. There is a bias in most everything he writes or says, and he is especially fond of controverting generally-accepted doctrine, upon his own observations—oft-times insufficient and even inaccurate. He is, withal, unfair, not to say, untruthful.

In exasperated tones, Riley recounted at length what had transpired between him and Meehan. Riley had visited Meehan at his invitation during the summer of 1881, when *Y. glauca* was finishing flowering and *Y. filamentosa* was about to commence doing so. Riley observed numerous *P. decipiens* ovipositing into the stems of *Y. filamentosa*. Riley also had collected several hundred moths, every one of which he determined to be *P. decipiens*, as he subsequently informed Meehan. To Riley's surprise, that August, Meehan read a paper in Cincinnati in which he reported that he had collected from a single *Y. glauca* flower 17 moths, 4 of which were *Prodoxus*, the remainder being *Tegeticula*. Because *Y. glauca* were not fertilized, Meehan inferred that *Tegeticula* was incapable of pollination. When Riley asked who had identified the moths, he was informed that Meehan had sent them to Hagen the day after Riley's visit. A patently annoyed Riley continued,

[Meehan] made no mention whatever of my visit or my determinations

¹⁹Darwin to Hooker, 7 April 1874 (Cambridge University Library, classmark DAR 95: 321). In a letter to C. V. Riley, Hermann Müller echoed Darwin, calling it "the most wonderful instance of mutual adaptation" yet detected. (Private letter to C. V. Riley, cited in [Riley 1881, p. 623, fn. 4])

²⁰Meehan to Darwin, 1 July 1877. (Cambridge University Library, classmark DAR 171: 112)

²¹Darwin to Riley, 28 Sept. 1881. (Cambridge University Library, classmark DAR 147: 303)

²²Riley to Darwin, 18 Dec. 1881. (Cambridge University Library, classmark DAR 176: 158)

²³Pellmyr et al. (1997) state that Riley erred in his assertion that yucca moths do not perform geitonogamous pollinations and provide evidence to the contrary.

²⁴Trelease corroborated this finding (letter from Trelease to Riley, quoted in Riley 1892a, p. 125).

[emphasis Riley's]...[Hagen] knows little outside of Neuroptera and only the year before had made a most unpardonable blunder in pronouncing certain moths which he had bred from Yucca stems to be *Pronuba* [*Tegeticula*] *yuccasella* where afterward he confessed they were *Prodoxus*, and one would suppose that a fair man seeking only truth would have at least put my own determinations, in relation to genera of my own creation, along side of Hagen's.

Riley noted that Hagen had determined the moths to be males, adding that "males are not so easily distinguished as the females and Hagen may again have blundered; but even if he was correct the explanation is simple." Riley continued, stating that *Tegeticula* males often emerge before the females and that, as *Y. filamentosa* had not yet bloomed, the males likely took refuge in the few remaining *Y. glauca* flowers. He added,

But nothing is more certain, from a series of experiments and observations which I made this past summer, than that *Prodoxus* female oviposits in the stem and that her race is run essentially by the time the plant begins to bloom, for she can only successfully oviposit in the tender stem and perishes in the act when attempted after the flowers begin to open and the stem gets hard; further that she is absolutely incapable of pollinizing and never attempts it.

Approximately six months after Riley penned this letter, Darwin died on 19 April 1882, and one month later, the Biological Society of Washington, D.C., held a memorial meeting in his honor that was attended by an estimated 700 people. Riley and several other prominent members of the Society, including its president, Major John Wesley Powell, delivered addresses.

In his presentation, Riley (1882) proclaimed Darwin's greatness, enumerating his many original contributions to and insights into the entomological world. Riley closed with a heartfelt remembrance of the two occasions (in 1871 and 1875) on which he had visited Darwin at his residence in Down:

Going to him as a young entomologist with no claim on his favor, he seemed to take delight in manifesting appreciation...an interest in natural science was an open sesame to his generous soul. His consideration, without aggression, was the secret of the gratitude and respect which all felt who had the honor to know him, either personally or through correspondence. (Riley 1882, pp. 79–80)

Final Years: Riley's Work with Trelease and Others

Riley maintained a steadfast interest in the complex of moths associated with the genus *Yucca* through the last years of his life. Extant letters²⁵ indicate that in February 1893, Riley wrote to J. T. Mason (Houston, Texas, Land & Trust Co.) expressing his keen interest in obtaining a *Tegeticula* species that he felt certain must be associated with *Y. filifera*, a large tree yucca of northeastern Mexico; Riley had evidence of the moth's existence from seed pod samples. A few months later, Riley wrote Mason to inform him that the plant specimen he had sent Riley was most likely *Y. guatemalensis* [now *Y. elephantipes*] and that the associated moth was a new species, which Riley named *Prodoxus intricatus* (Riley 1893). Riley added,

I am quite confident that further intelligent research will give us an interesting form of *Pronuba* [*Tegeticula*] in this *Yucca guatemalensis* [*elephantipes*] and if you have a chance of studying *Y. filifera* you will undoubtedly secure a number of interesting species of the family, of both genera, *Pronuba* [*Tegeticula*] and *Prodoxus*. The *Pronuba* [*Tegeticula*] associated with *filifera* must be a large and interesting species and I am quite sure will prove different from any of the three so far characterised [*sic*].

Recently, *Parategeticula elephantipella* Pellmyr & Balcázar-Lara was described and appears to be the exclusive pollinator of *Y. elephantipes* (Pellmyr and Balcázar-Lara 2001); information on *Y. filifera* pollination remains incomplete (Olle. Pellmyr, personal communication).

Riley collaborated with other professional scientists in his investigations. He gave J. B. Smith (1893) *Tegeticula* specimens to investigate morphological homologies between their maxillae and those of other insects. As chief entomologist, USDA Division of Entomology, Riley directed one of his field agents, D. W. Coquillett, to observe the behavior of female *T. maculata* on *Y. whipplei* in southern California (Coquillett 1893). The flower stalk of this yucca species can reach spectacular heights (Fig. 11). Riley had a particular interest in *Y. whipplei* because he thought that certain of its traits might facilitate ordinary pollination, yet he knew that *T. maculata* serves as a pollinator (Riley 1893). Riley also described several *Prodoxus* spp. from *Y. whipplei* and, in recent times, Powell (1992) cited *Y. whipplei* and its associated prodoxids as one of the two most complex yucca/yucca moth systems.

In his final years, Riley worked closely with botanist William Trelease, first appointee to the George Engelmann Professorship of the Henry Shaw School of Botany, Washington University, St. Louis, and first director of the Missouri Botanical Garden, founded by Shaw (White 1902, Rodgers 1944). Trelease (1886) corroborated Riley's earlier findings on yucca moth oviposition and pollination, calling it "a case without parallel", and at his urging, Riley (1892a) compiled a comprehensive review of his 20 years of yucca moth studies.

Trelease (1892) also performed morphological studies of several yucca species, and detailed his pollination and oviposition studies of *T. maculata* on *Y. whipplei* and *Tegeticula synthetica* (Riley) on *Yucca brevifolia* (commonly called the Joshua tree) (Trelease 1893). Riley (1892a, 1893) quoted extensively from these studies, including Trelease's unpublished findings. In his research, Trelease was assisted by his wife, Julia Johnson Trelease, who made behavioral observations of the moths and rendered illustrations of pollination and oviposition.²⁶ Trelease also collected several *Prodoxus* species (*P. coloradensis* Riley, *P. reticulatus* [now *Greya reticulata* (Riley)]; see Davis et al. 1992], *P. cinereus*, *P. aenescens*, *T. intermedia*) from various yuccas and sent them to Riley, who detailed their morphology (Riley 1893).

²⁶William Trelease Papers, #2560, Division of Rare and Manuscript Collections, Cornell University Library.



Fig. 11. *Yucca whipplei* in bloom. (from *Insect Life* 1893).

²⁵Missouri Botanical Garden, William Trelease professional papers, Box 8, Folders 1 & 2.

In February 1894, Riley wrote Trelease of a possible joint trip to Mexico; three months later, he wrote that he was clearing out his USDA office in preparation for his replacement, L. O. Howard.²⁷ Soon thereafter, Riley was named Honorary Curator of Insects, U.S. National Museum, and on 14 September 1895, he died suddenly following a bicycling accident.

Interested readers seeking the single best review by Riley on prodoxids and yuccas can do no better than to peruse his paper written for the Third Annual Report of the Missouri Botanical Garden (Riley 1892a).²⁸ This comprehensive work provides extensive excerpts from his earlier publications, taxonomic descriptions for *Pronuba* [*Tegeticula*] and *Prodoxus* spp., and some of Riley's unpublished observations. It also contains 10 plates, each featuring several illustrations, including renderings of the ovipositor of *T. yuccasella* (Fig. 12), and microscopic sections of *Y. filamentosa* pistils with *Tegeticula* eggs and larvae in situ (Fig. 13).

Current Research and Closing Remarks

After Riley had worked for several years on various yuccas and their associated moths, he stated that there was "little doubt" that other species of *Pronuba* [*Tegeticula*] and *Prodoxus* would be discovered (Riley 1880a, p. 145). A dozen years later, he recognized that there was still "much yet to learn of the pollination of other species of *Yucca*", and he predicted that "all the [yucca] species which are sufficiently distinctive in characters and in range, may be expected to have special *Pronubas* [*Tegeticula*] associated with them" (Riley 1892b, pp. 95–96).

Since then, knowledge of the complex of prodoxids associated with yuccas has increased significantly and Riley's predictions have been validated. In his revision, Davis (1967) described two new *Prodoxus* species and *Parategeticula pollenifera*, a yucca pollinator. Currently there are 78 described species of Prodoxidae; of these, 11 are *Prodoxus* and 4 are *Parategeticula* and, until recently, 3 were *Tegeticula* species: *T. synthetica* (Riley), *T. maculata* (Riley), and *T. yuccasella* (Riley) (Pellmyr 2003). However, *T. synthetica* is believed to contain two species and *T. maculata* may comprise several (Pellmyr 2003).

In his recent systematic revision of the *yuccasella* complex north of Mexico, Pellmyr

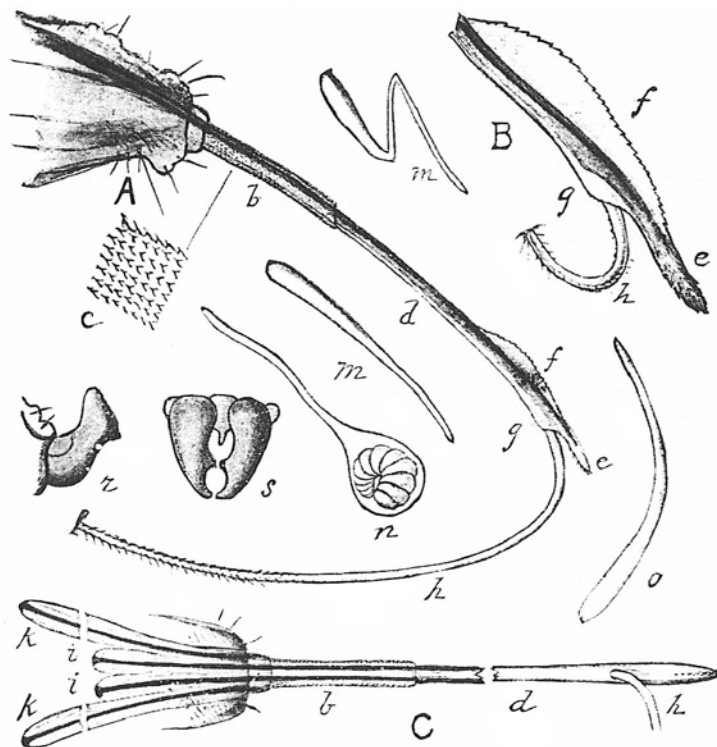


Fig. 12. Masterly renderings from Riley (1892a) of *T. yuccasella* ovipositor: (A, c) file-like surface of (b), the ovipositor base; (h) extended oviduct; (B) partial enlargement of (A); (C) ventral tip of abdomen with (k) muscular attachments. Also shown are eggs from the yucca pistil (m) and the mature ovary of the moth (o), the developing embryo (n), and the male genital claspers (r, s).

(1999) reported that *T. yuccasella* comprises at least 13 species, of which 2, *T. intermedia* (Riley) and *T. corruptrix* Pellmyr, are "cheater yucca moths," that is, moths that coexist with yucca pollinators and oviposit into the fruit, but do not engage in yucca pollination. Females of these species lack the

maxillary tentacles needed for pollination (Pellmyr 1999, Pellmyr and Krenn 2002). (Because he viewed the female's tentacles as an absolute requirement for placement in *Tegeticula*, Riley misidentified *T. intermedia* as a bogus yucca moth, naming it *Prodoxus intermedius*.)

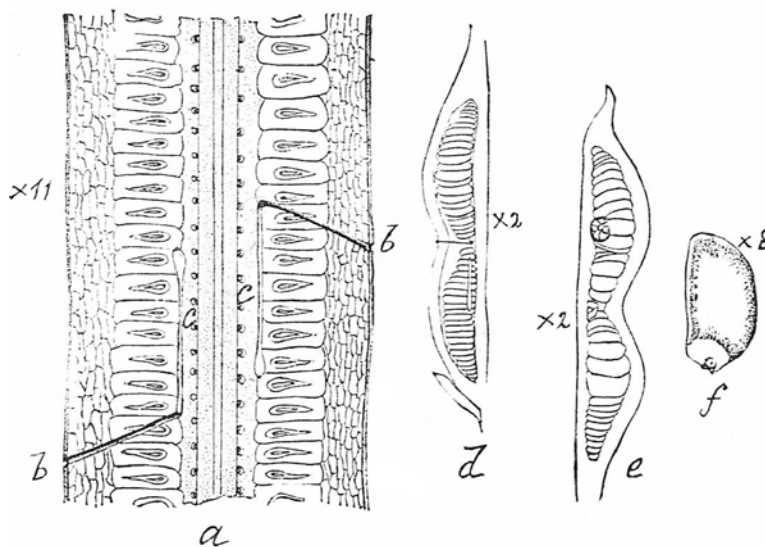


Fig. 13. Microscopic views of *Y. filamentosa* and *T. yuccasella* (from Riley 1892a): (a) longitudinal section through pistil, (b) oviposition punctures, (c) elongate eggs in situ, (d, e) larvae in situ. Also shown is a seed (f) at 13 days after oviposition, with a young larva visible at the funicular base.

²⁷William Trelease Papers, #2560, Division of Rare and Manuscript Collections, Cornell University Library.

²⁸For a condensed version of this publication, see Riley (1892b).

Riley demonstrated remarkable pre-science as he considered the phylogeny and evolutionary biology of yucca-associated moths:

Who, studying these two species [*T. yuccasella* and *P. decipiens*] 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?...Which of the two insects is oldest in time, or whether the divergence from some archetypal form has been simultaneous, are matters of opinion which those interested in evolution will decide for themselves one way or the other, or according as knowledge increases. (Riley 1880a, pp. 144–145)

According to Pellmyr's recent review (2003), prodoxids colonized yuccas about 41.7 million years ago. Soon thereafter, the three genera (*Tegeticula*, *Parategeticula*, and *Prodoxus*) underwent rapid diversification. Together, these genera exhibit a species diversity greater than 20 times that of their sister group, *Mesepiola*, which are nonpollinating seed parasites (Pellmyr and Krenn 2002).

In his review of yuccas and yucca moths, Powell (1992) argued that "insect biologists and ecologists failed to recognize the highly complex nature of this coevolutionary relationship until recently," stating that little research was done in the 70 years following Riley's work. He listed several areas ripe for further investigation, and the recent treatment of this topic by Pellmyr (2003) provides an informed measure of the advances that have been made in the decade since Powell's review, including ideas relevant to the evolution of obligate mutualism.

Speculation about the possibility of non-yucca moth pollinators of yuccas continued to be raised a century after Riley's death, yet, according to Pellmyr (2003), the only yucca species for which there is even "moderate support" for such came from Trelease (1893), who performed pollinator exclusion experiments on *Y. aloifolia*. Pellmyr (2003) argues that carefully executed experiments would settle the recurring question of yucca copollinators.

Our review of the first two decades of yucca moth research provides a window on mid- to late 19th-century entomology, when the discipline broadened from a purely descriptive enterprise (taxonomic and life history studies) to include research aimed at the practical application of scientific knowledge. At the same time, Darwin's theory of evolution emerged, providing a conceptual frame-

work within which to pursue research of both sorts. Great naturalists like Riley recognized this and strove to use valid scientific approaches to test their hypotheses, but at times they labored in the midst of colleagues less gifted and far less rigorous in their empiricism. Riley's powers of observation, clarity of reasoning, and abundant self-confidence served him well in rebutting his relentless critics. With the writings of Darwin and Gray laying the theoretical groundwork, and the collaborative efforts of Engelmann, Trelease, and others providing the needed botanical expertise, Riley synthesized a corpus of knowledge on a fascinating case of coevolution. The majority of his findings have withstood the test of time for more than a century, and yuccas and yucca moths continue to be a vibrant area of research, perhaps the greatest testament to Riley's labors.

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