with them, but Japanese plants, on the contrary, flourish extremely. Dr. Riley supported Mr. Schwarz, and said it was a well-known fact that Japanese plants flourish better in the east than in the west. His first impression of the Californian flora was that it was European in its character. Referring to the susceptibility of Australian ladybirds to the attacks of enemies, he stated that in Australia birds in general prey upon ladybirds, and in his opinion this was due to the lack of certain protective influences on the part of the ladybirds themselves. The Australian fauna is composed of weak forms. He once more insisted upon the fact that we must not expect good results from miscellaneous introductions of beneficial insects; all the facts concerning them must be known. Mr. Fernow spoke of the introduction of the Douglass spruce into Europe from California and from Colorado. It was found that those from the Pacific coast do not flourish in Europe, while those from Colorado do. He was of the opinion that it was a question of resemblance of climate between the original country and that to which the species was introduced. Dr. Gill said that Prof. Riley's recognition of the European character of the Californian flora is due to the extension of the European flora through northern Asia, making it thus really the flora of an adjoining country. We are accustomed to associate the Indian fauna and flora with the Asiatic idea, but they are in reality quite distinct, and the true European forms extend to the Pacific Ocean at a point above the limit of the Indian life-zone.

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President Ashmead was in the chair and Messrs. Schwarz, Stiles, Stetson, Marlatt, Benton, Howard, Pratt, Linell, Chittenden, Heidemann, Vaughan, Riley, Dodge, and Gill were also present.

—Prof. Riley read the following paper:

ON OVIPOSITION IN THE CYNIPIDÆ.

By C. V. Riley, Ph. D.

Having made a special study of galls and gall insects, and having accumulated a large number of notes on the habits of the

species in different Orders, especially in the Cynipidæ, I have been deeply interested in many of the questions that were treated rather fully by Hermann Adler in his epoch-making work on "Alternating Generations: a biological study of Oak Galls and Gall Flies," published some fifteen years ago. At the time (1881) Lichtenstein published his excellent translation I was in correspondence with him, and also had on several previous occasions the pleasure of joining in some of his observations at Montpellier and in discussing with him some of the questions involved.

One of the most interesting points in the economy of the Cynipidæ is the mechanism of oviposition. It is interesting not only because of the almost universal but erroneous assumption by older authors that Cynipid galls owed their growth to the action of some poison inserted in the plant tissue by the female in the act of oviposition,* but also because of the extremely long, curved and specialized nature of the ovipositor itself and of the difficulty in following all the steps in the act.

A number of years ago, desiring to make some original observations and, if possible, confirm Adler's on the subject of oviposition, as also to endeavor to connect some alternate agamic and sexual forms, I had a series of experiments instituted, placing them in the care of Mr. Pergande. A number of young oak trees of different species, in pots, were obtained for this purpose and to assist observations in the field. Frequent absences from the office, and other pre-occupations, prevented as much personal attention as I had desired to give to the matter, and the experiments were finally allowed to lapse. Some interesting observations, however, have been obtained on the subject of oviposition; and as the results seem to conflict with those obtained by Adler, I have concluded to put them on record, more particularly as an English translation of Adler's celebrated work has recently appeared from the Clarendon Press of Oxford, edited by Charles R. Straton.

Adler goes into details and seems to have made his observations so carefully that one may scarcely doubt the accuracy of his records. For instance, speaking of *Neuroterus lenticularis*, which is the agamous spring form of *Spathegaster baccarum*, he says: "It" (the female fly) "first examines the buds carefully with its antennæ until it finds one that suits it, when it takes up a different position. It advances toward the apex of the bud and pushes its ovipositor down under one of the

*The ingenious dissertations of Walsh on the poison gland and the secretion therefrom (Proc. Ent. Soc. Phil., II, pp. 473-4) very well illustrate how firmly this view was fixed in the minds of naturalists up to that time.

bud-scales. After several attempts, the ovipositor is forced in and glides down under the bud-scales to the base of the bud-axis, which it penetrates from without inwards. This can only be accomplished by imparting to the ovipositor a direction at an obtuse or right angle to the course it followed when entering. The natural curvature of the ovipositor here stands the fly in good stead, but it requires a vast expenditure of time and strength before it can penetrate the heart of the bud."

Referring to *Biorhiza aptera* (which is the agamic form of *Teras terminalis*), he says that the female seeks by preference the greater terminal buds and seeks to bore into them. "The pricking is done in a very different way from that of other gall-flies. After a suitable bud has been found, the fly stops, turns its head downwards, and directs its abdomen to the point of the bud. In this position it inserts its ovipositor somewhat below the middle of the bud, in or upon the tissue from which terminal growth proceeds. After the fly has pushed in its ovipositor it withdraws it, and goes on boring one canal after another in the stratum which the egg is to occupy, until the whole layer is riddled like a sieve. When the operation is finished, the eggs are successively pushed into the pricked canals, where they lie so thickly together that they look like a continuous mass. The amount of work which the fly goes through in laying its eggs in this way is astonishing. After having been occupied for hours in boring these numerous canals, it appeared to me inexplicable that it had as yet laid no eggs; I found, however, that it bores all the canals for their reception before actually laying a single egg. This part of the work requires much time, as to which I have made the following observations.

"On January 27, 1878, a fly was put upon a little oak, and soon began to prick a bud; when it had finished the first bud, it went on without interruption to another, and was altogether eighty-seven hours busily employed laying its eggs. In these two buds I counted 582 eggs."

The process of oviposition in the Cynipidæ is a very elaborate one and has been much written about. Adler gives a most full and elaborate description of the mechanism of the ovipositor, and particularly of the ventral plates and bundles of muscles by which the terebra is worked. The structure of the ovipositor is well known, and its parts homologize with those of the same organ in all Hymenoptera. It consists of a large bristle or seta and of two spiculæ which mortise into it and form the channel down which the egg passes. The seta occupies half the area of a transverse section of the terebra, and the two spiculæ occupy the other half. The seta has two tenons, and a central canal which contains an air vessel, a nerve branch, and some sanguineous fluid.

While appearing like a single piece, it is in reality double or composed of two parts which, indeed, are separated at the extreme base, but otherwise firmly soldered together. The spiculæ are serrate or notched at the tip, and the seta often ends in a slight hook. The two spiculæ play, by means of strong basal muscles, longitudinally up and down, by means of the grooves which embrace the tenons of the seta.

The eggs of Cynipidæ are characterized by having a stalk or pedicel of varying length according to the species, the egg-body próper, according to Adler, being at the apical or anterior end which first issues from the body, and the basal or posterior end being also somewhat enlarged or spatulate. In repose, the ovipositor is concealed within two sheaths, but in oviposition, according to Hartig's views, the spiculæ grasp the egg-stalk and push it to the tip, the fluids being pressed back in the operation, so that they come to be distributed along the stalk or to lie at the opposite or posterior pole of the stalk. The spiculæ then slightly separate at the tip from the seta and extend beyond it so that the apical end of the stalk becomes free. Now, by pressure, the fluid at the posterior end passes through the stalk into the opposite or apical end which is plunged in the plant, the basal portion becoming emptied, the swollen apical end thus remaining in the plant when the ovipositor is withdrawn, filling the distal end of the puncture, which is somewhat enlarged. The empty basal sack of the egg and a portion of the stalk are often left exposed, looking not unlike the empty egg of some lace-wing fly (*Hemerobiid*). In short, Hartig's view, very generally adopted, was that the extensile and ductile egg was driven through the ovipositor itself while this was in the plant, and that the contents of the egg-body were pressed back into the egg-stalk or pedicel during the operation and collected in the posterior end, and only after the apical end had reached the bottom of the puncture did these contents stream back into it.

Adler would refute this view, and draws attention to his own figures on Plate 3, where the eggs and ovipositor are illustrated side by side, all taken from photographs and drawn from the same amplification. These show that the ovipositor is, in every case, longer than the egg itself, the enlarged head of the egg corresponding in direction to the tip of the ovipositor. He argues from this fact that one end of the egg cannot be in the plant tissue while the other is in the canal. He further argues that it is not possible that the whole egg can be received into the ovipositor and glide through it in the way in which Hartig supposed. Let me give in his own words the description of the process which he has followed, particularly on *Neuroterus læviusculus* (the agamic vernal form of *Spathegaster albipes*), while ovipositing in an oak bud.

"We shall begin with the moment when the fly places its ovipositor on the bud. She always chooses the edge of one of the outer scales as a point of attack, and pushes her ovipositor under it. Then the ovipositor glides under the scales to the base of the bud-axis. Even this first act requires great strength on the part of the fly. We sometimes see it attack the bud repeatedly with its ovipositor before it succeeds in getting it under the scales. It does not succeed with buds in which the scales are closely imbricated, hence it always prefers buds with loose-lying scales. When the ovipositor has arrived at the base it is driven towards the bud-axis, so as to reach the rudimentary leaves; but the path made by the ovipositor is always more or less curved. By making a careful preparation of any pricked bud, the canal can be plainly seen, and the path taken by the ovipositor followed. After the fly has finished the first part of its work, and driven the ovipositor into the centre of the bud, there comes a moment of complete rest, and the fly sits motionless upon the bud. If it is fixed in this position by dipping it into chloroform, nothing is seen of the egg—it still remains in the vagina. Then follows the second part of the work, the pushing of the egg into the bud.

"The egg slips, with its enclosed egg-body, to the base of the ovipositor between the origin of the two spiculæ. The egg-body glides over the point where the two spiculæ embrace the tenon of the seta, since the space remaining open between the two spiculæ is too small to admit it. But the egg-stalk, which follows, slips between the two spiculæ, is seized by them and driven forward; in this way the egg is pushed downwards into the ovipositor, with the egg-body hanging out.

"When at last the egg is about to enter the canal which has been bored into the centre of the bud, it becomes evident that it is impossible for the canal to admit the ovipositor and the egg-body to pass in at the same time. The egg-body is always of much greater diameter than the ovipositor; on this account the ovipositor is next partially withdrawn by the fly, until the pierced canal becomes empty. The egg-body then enters the pierced canal, and the ovipositor follows, pushing it before it. In short, the whole forward motion is dependent on the egg-stalk being propelled by the to-and-fro movements of the two spiculæ, and the egg reaches the end of the bored canal, while the egg-stalk remains lying within it."

To sum the matter up, the operation according to Adler consists of three distinct stages: (1) the canal is first bored, after which the fly rests; (2) the egg is then passed from the ovarium to the base of the ovipositor, the swollen end or body of the egg hanging out, but being pushed along by means of the stalk behind being grasped between the two spiculæ; (3) finally, when

the egg-body reaches the perforation, the ovipositor is partially withdrawn and the whole egg then pushed in till the egg-body reaches the bottom. Adler rightly expresses wonder that this complex procedure should be repeated so often with such great accuracy, and proceeds to describe the tactile hairs connected with the ovipositor which permit her to carry out the operation. He further states that while oviposition on the surface of leaves is, in its nature, easier, the mechanism of oviposition is exactly the same as that in buds.

As already stated, the observations are difficult and can only be made with satisfaction by observing a great number of individuals and by suddenly chloroforming them at different stages of the operation. Adler has done this to some extent, but there are several passages which leave some doubt in my mind as to the complete accuracy of his views. For instance, in controverting Hartig and referring to his (Adler's) figures of the eggs and of the ovipositor, there is no indication as to whether the eggs were taken from the buds after being deposited, or from the ovaries or from the ovipositor. My own experience with these and other ductile and extensile eggs with long egg-stalks would indicate that we have a very varying length of stalk according to these varying circumstances. Therefore, it is rather inaccurate to refer to these eggs as if they had a definite and uniform length as compared with the ovipositor. Moreover, the passages quoted show that the operation varies considerably in different species, his conclusions evidently being based on *Neuroterus lævius-culus*.

Again, any one who will carefully read Hartig will see that Adler has totally misjudged him in assuming that he described the egg as passing down the minute channel of the seta; for Hartig's language, as well as his figures, makes it very plain that he had in mind the actual facts, viz., the passing of the egg down the channel formed by the connection of the two spiculæ with the seta. It is true that he calls the seta the egg-guide (*Eileiter*), and this in truth it is, but he distinctly shows by his figure and his description that it acts as a guide only by the passage which it makes when mortised into the spiculæ, referring particularly to this space (Tab. 1, Fig. 9, *c*) as "die innere Höhlung des Legestachels, in welche das Ei aufgenommen und hindurch geht."*

* Incidentally I may state, as corroborative of Adler's liability to error, that he makes the sweeping assertion that the gall-gnats (Cecidomyidæ) cannot inject an irritating poison into the plant tissue as do the saw-flies (Tenthredinidæ), on the ground that the gall-gnats have no piercing apparatus. He is in good company in making this statement, but I have good

Such are some of the reasons which would make one question the accuracy of Adler's views, and I will now give the record of the observations which would seem to controvert those views and to comport most with those of Hartig, though showing yet a third method.

On April 20, 1894, my attention was called by Mr. Pergande to several specimens of *Callirhytis clavula* Osten Sacken ovipositing in the buds of *Quercus prinus*. This is a rather large, winged agamic form, which Mr. Ashmead informs me he has actually bred from the *clavula* gall. The same species also oviposits in the buds of *Quercus alba*. The flies were sitting on the buds with the head towards the tip of the bud, and were so absorbed in their work that they scarcely moved or altered their position, even when the twigs were allowed to sweep back with some force. The ovipositor was deeply inserted within the scale-like covering of the buds. On carefully removing the scaly covering of a bud that had been pricked, quite a number of eggs were found in clusters of three or four together, and a few singly, inserted in the tender, new, embryo leaves. It was further found that the eggs were inserted on both the upper and lower surfaces of the leaf and almost entirely hidden by the silvery pubescence of the newly formed leaf. They were attached by a short stout pedicel or stem which, however, upon very careful examination, was found to extend for a great length (six or seven times the length of the exposed egg-body) like a fine thread into the substance of the leaf. The distal or anterior end of the egg-stalk was also somewhat enlarged, looking like a bit of shrivelled skin. The exposed portion of the egg or egg-body was white, glistening, elongate-ovoid or bean-shaped in form and about .2 mm. in length. Two days later, or on the 22d, additional flies were observed ovipositing and the buds were marked. On the 27th

reason to believe, nevertheless, that it is absolutely incorrect. Winnertz, Osten Sacken, and other writers have generalized in this matter from what may be considered the typical Cecidomyidous ovipositor, which is a cylindrical tube, being but a prolongation of the tip of the abdomen. The truth of the matter is, however, that many of the gall-making species have this tip of the abdomen almost as much specialized as in Pronuba among Lepidoptera, ending in a delicate, sharp lance, admirably fitted for piercing the soft tissues of tender vegetation, as I stated in the article on galls in Johnson's Universal Cyclopædia (1876), which Lichtenstein, by a curious error, referred to, in the Introduction to his translation of Adler, as *Le Dictionnaire Scientifique* de St. Louis—a purely imaginary publication. That they insert some special secretion which induces gall growth is also presumable from the fact that in some cases which I have studied the gall forms (as in the Tenthredinidæ) before the larva hatches.

these were examined and it was found that the pedicel had become shorter and stouter, while the anterior or buried end had greatly increased, the exposed portion being now half empty of its contents. Five days later, April 27th, the young leaves had formed from these same marked buds and the eggs were still in position, but mostly empty, and when removed and closely examined it was found that under the epidermis and below the base of the exposed egg-shell there had formed a soft, colorless, globular body, having a yellowish streak internally. This body, probably the first larval stage, is easily detached from the leaf, but no movement could be discerned and the thread-like pedicel had separated from it and disappeared.

So far, there is no trace of a gall or swelling to be seen, although the affected leaves appear more or less crumpled or distorted. May 4th the same leaves were again examined and the young galls had already formed, appearing as slight thickenings of the leaf, but scarcely elevated or prominent. The spot where the egg had been inserted forms a minute depression or hollow in the leaf, with the colorless and shrivelled egg-shell still in position, the cavity thus formed being in an oblique direction to the surface of the leaf. The cell or cells in each gall are removed from the egg-shells about twice the length of these last, but for which there would be little trace as to where the egg entered; they are ovoid or rounded, and each contains a perfect larva, semitransparent or colorless, with a brownish ventral spot. Most of the galls contain three to five cells.

From now on, the formation of the gall is rapid, the substance of the young gall being very juicy and succulent and of a yellowish color, its outer margin or edge being pale pinkish. On May 11th the galls were nearly full grown and proved to be *Callirhytis futilis* O. S., but no flies were reared until the middle of June, and from this time until the last of the month flies in both sexes were continually bred. A number of interesting subsequent observations were made upon this interesting species, but have no especial bearing on this communication. I ought, however, to state that Mr. H. F. Bassett (Psyche, Vol. 5, pp. 235–8, Dec., 1889) has described what is, apparently, the same insect as *Callirhytis radicis*, which he reared from a series of blister-like cavities in the bark of the root of *Quercus alba*, and identified with the fly which he had himself observed ovipositing in the buds of the same oak and producing the gall which gives forth *Callirhytis futilis* Osten Sacken. There is consequently some confusion as to the actual relations of this sexual generation, and either an error as to determination on the part of Mr. Bassett or else an erroneous record of rearing on the part of Mr. Ashmead. I have adopted the former as the more probable. There

is, however, a third explanation, which, if verified by future investigation, would prove to be another interesting discovery in connection with these oak gall-flies, viz., that the same species may indifferently produce a gall on the root or on the twig. When we remember how closely these two parts of the plant are related physiologically and how readily the one in most trees may be converted into the other, such a discovery should not surprise us.

From the facts given in this case, although the act of oviposition was not carefully followed, it is yet obvious that the eggs could not have been inserted in the manner described by Adler. The facts as already suggested comport more with the conclusions of Hartig, though they indicate quite a different method of oviposition than that described by either, in that the fluid egg-contents are not passed from one pole to another rapidly during the act of oviposition as described by Hartig, but very gradually, the process not being completed till just before the hatching.

Again, a small, black, wingless species (*Biorhiza nigra* Fitch, subsequently described as *B. politus* by Bassett) is not infrequently found, during late winter, under the shelter of bark scales, and oviposits, during late winter, in the terminal buds of *Quercus alba* and *Q. obtusiloba*. The ovipositor in this case, as in most cases where eggs are laid in dormant buds, is thrust down between the bud-scales until it reaches the soft latent cell tissue toward the centre of the bud. And here it is easy to observe, by removing the scaly coverings, that the pedicel or stalk only, which is about ten times as long as the egg-body, is inserted in the leaf tissue, and the enlarged portion or egg-body is at first external, being pressed and somewhat flattened by the surrounding leaf-scales.*

In still a third case, of a small black inquiline (*Ceroptus politus* Ashm.), oviposition was observed by Mr. Pergande in the midrib of *Quercus rubra*, May 20, 1884, and in this case, as my notes show, the egg is thrust down into the puncture made by the terebra in the midrib until not a vestige of the egg is visible, the pedicel being very short.

There is, therefore, good reason for believing that oviposition in these insects follows no uniform system, and there is a serious question whether Adler's rejection of Hartig's views is justified.

* This fly produces, according to experiments made for me by Mr. J. G. Barlow of Cadet, Mo., an undescribed vesicular bud-gall, from which issues a small black-winged bisexual species (*Dryophanta vesiculoides* MS. mihi). The gall produced by this and from which the apterous agamic generation comes is not yet known, though it will probably be a leaf-gall similar to that of *Acraspis erinaceæ* Walsh.

In connection with Adler's views as to oviposition, he concludes from his own studies that the main purpose of the stalk is, by its posterior end remaining at the surface of the puncture, to supply oxygen to the egg-body in the plant tissues; but that this is also an erroneous conclusion is, I think, made manifest by some of the facts just stated. That the function of the egg-stalk is, rather, to facilitate the otherwise difficult mechanical operation of the passage of the egg down a narrow and elongate ovipositor in the manner indicated by Hartig is supported by the fact that the puncture is often closed at its mouth, as also from what we know of the similar oviposition in other orders of insects. The facts, for instance, connected with the oviposition of *Pronuba yuccasella*, where the egg is thrust deep into the ovarian cavity of the Yucca pistil, bear out this view. The egg, in this case, as it passes down the ovarium has not a definite pedicel or stalk, but becomes a mere thread in passing through the ovipositor (the nature of which precludes any external outlet during the passage), and the fluids gradually concentrate in the apical or anterior end as the embryo develops. Moreover, it is passed into the ovarian cavity of the pistil and has no connection through the pedicel with the exterior wound, which is closed before the larva hatches.

The paper was briefly discussed by Messrs. Marlatt, Ashmead, and Benton. Mr. Marlatt said that the mere fact that observations on this point are so difficult is sufficient in itself to explain any discrepancies. Mr. Ashmead expressed himself as inclined to accept the observations of Dr. Riley. In referring to dimorphism, he said that he was satisfied that the wingless species of the genera Acraspis and Biorhiza are agamic forms of some winged bisexual forms. He thinks, for instance, that there is a connection between Dryophanta and Acraspis. In Florida the winged bisexual form of Belonocnemus occurs on the roots of live oak, the agamic form appearing on the leaves in the fall.

—Mr. Marlatt read the following paper:

THE HIBERNATION OF NEMATIDS, AND ITS BEARING ON INQUILINOUS SPECIES.

During the summer and fall of 1894 large quantities of saw-fly galls on willow were collected for me by Mr. E. L. Horton, of East Steamburg, N. Y. These belong to both of the genera of Nematinæ (Euura and Pontania), the larvæ of which develop in galls on twigs or on leaves of willow. The experience