BIOLOGICAL AND MORPHOLOGICAL DIFFERENCES BETWEEN **Eriosoma Crataegi** (Oestlund) **and Eriosoma Lanigera** (Haus.)

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Few incidents in the biology of aphides have aroused so great an interest, or have been the subject of so much discussion, as the migration to elm of the woolly aphis of apple in Eastern North America. In every other region of the world, where apples are grown, **Eriosoma lanigera** (Haus.) confines its attention almost exclusively to **Pyrus malus** throughout the year. Alate sexuparae appear among the colonies of apterae in varying degrees of abundance, but it is only in North America, east of the Rockies, that these winged forms are recorded to migrate in the fall to **Ulmus americana,** and there to give rise to several generations. In June of the following year, the wild thorns and mountain ash, share with the apple the attention of the spring migrants, which forsake the elm for these summer host plants.

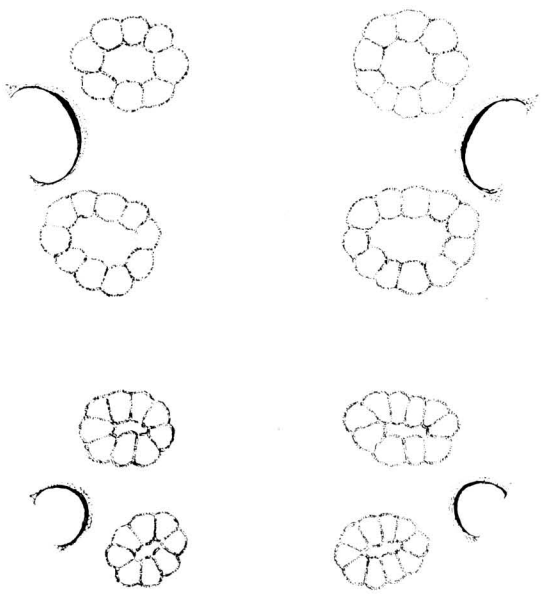

Fig. I.—Above: Waxglands and cornicles of *E. crataegi*
Below: Waxglands and cornicles of *E. lanigera*

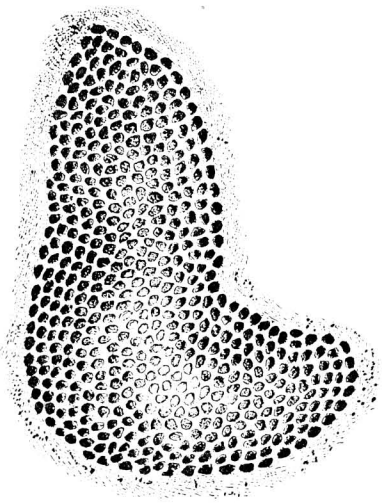

Fig. II.—Waxplate of adult female of *E. crataegi*

In view of this connection with **Ulmus americana,** the woolly aphis of apple has generally been conceded to be of American origin, although

it derives both its generic and specific names from Europe. A serious outbreak of this orchard pest occurred in England as long ago as the close of the eighteenth century and the commonly called "American blight" was first described and named in 1802, in Germany.

E. lanigera appears to have spread through Europe and Asia far more rapidly than in its alleged country of origin. For example, it was well established in India, in 1888, at a time when it was acknowledged to be prevalent in the south of the U. S. A., but was unknown as a pest of apple in the Northern States of the Union. Another woolly aphis was recorded on **Crataegus** in Minnesota in 1887, and this, ten years previously, had been noted on the wild thorns in Ontario under the name of **lanigera,** which it closely resembles.

Oestlund gave specific standing to the woolly aphis of thorn, and despite statements to the contrary, appearing in recent literature, a reference to this original brief description clearly shows that Oestlund considered, in 1887, that his **crataegi** was "evidently not **lanigera.**" His reasons will be discussed later.

While the prevalence and distribution of **lanigera** in North America does not appear to have been general fifty years ago, everything points to the widespread and common occurrence of the thorn aphis. Baker says "that in the north he had seen the insect far removed from orchard trees" while Becker, in the southern State of Arkansas, claims "that by being constantly subjected to attack by woolly aphis, **Crataegus** has acquired a strong immunity to this pest." Likewise in the west, Gillette was sufficiently well acquainted with the thorn aphis in Colorado to remark on its close resemblance to another native species, **Eriosoma americana** Riley, on the native elms.

There is thus ample evidence for concluding that the native thorns and elms of North America east of the Rockies have been infested by woolly aphis from remote times. Up to the eventful years 1912-15, when **lanigera's** elm connection was recorded in Maine and Virginia, nothing whatever was known of the biology of the woolly aphis of thorn or of the native **Eriosomae** on **Ulmus americana.** What is known today concerning their migratory habits and host plants is largely due to the discoveries of Dr. Patch in Maine.

Concerning these, the migration of **Eriosoma ulmi** L. between **Ulmus campestris** and **Ribes** was already well known in Europe, when, in 1912, the aphis responsible for the rosette leaf curl of **Ulmus americana** was proved to migrate to both thorn and mountain ash in Maine. In addition to these native summer host plants, the spring migrant from elm rosette readily accepted the cultivated apple.

The rosette aphis was not only found to differ morphologically from **E. americana,** with which it had previously been confused, but in 1915,

Patch was able to prove that this latter species had a cycle entirely its own, between **Ulmus americana** and **Amelanchier.** Still another species of interest, **E. rileyi** Thomas, was shown by Patch's notes to remain on the bark of elm during the summer. This bark aphis, although producing winged forms, appears to dispense with a secondary host plant in America, in much the same way as the bark feeding **lanigera** on apple manages to dispense with the primary host plant in most parts of the world.

In bestowing a name on the rosette aphis, with a known migration to thorn, mountain ash, and apple, Patch, followed by Baker and Becker, was guided by the following indisputable facts; namely, that those specific characters of the antennae, that had served so successfully in separating the **Eriosomae,** failed to separate **lanigera** from **crataegi;** that apple was a host plant common to both; and that **lanigera,** 1802, had obvious priority over **crataegi,** 1887.

Baker, in his well known report, 1915, hesitated to place **crataegi** under the name of **lanigera,** until more was known of the former's biology in its natural environment. It was none the less inferred that **lanigera** was indigenous to America and in its native haunts alternated between elm and thorn, adopting apple when this was introduced. On this new host plant, **lanigera** acquired a new method of perpetuating itself by which it was able, in part, to throw off its dependence on elm. Thus emancipated, it contrived to establish itself in countries where **Ulmus americana** does not exist.

To what extent this modified existence on the adopted host plant in Eastern North America has affected the normal intercourse between native elm and native thorn is a matter that has not been sufficiently enquired into.

It would be interesting to know whether the aphis on thorn is gradually becoming independent of elm in Maine, Virginia, and Arkansas.

With such important information unavailable, it would serve no useful purpose to examine other theories that have been put forward during the last quarter of a century in support, or in refutation, of **lanigera's** elm connection in America. These are set out very clearly and concisely by Greenslade, 1936, who, in addition to presenting a survey of the extensive literature on **lanigera,** gives a digest of the numerous replies received by the East Malling Station, Kent, England, to a widely circulated questionnaire on this subject. Among sceptics, Greenslade cites Carl Borner, 1932, who maintains that **lanigera** confines itself to apple in America as elsewhere, and that the species which migrates to apple, mountain ash, and hawthorn, is **Eriosoma crataegi** Oestlund.

The life history of **lanigera** as studied in Virginia by Alwood, 1898, lends weight to the first part of Borner's contention, and recent observations in connection with the appearance of a woolly aphis of thorn in the Interior of British Columbia indicate in no uncertain manner that this aphis is **crataegi** and is distinct both taxonomically and biologically from **lanigera.**

The significance attaching to certain features of the life history of **crataegi** can best be appreciated by presenting a brief survey of the circumstances leading up to its discovery.

Eriosoma lanigera has been for more than twenty years a common, and at times a noxious pest in the irrigated orchards of the dry belt of British Columbia. Owing to its rapid increase in 1926-27, and accumulating evidence that **lanigera** was instrumental in spreading a cankered condition on the limbs of apple trees, an extensive study of the insect was undertaken in 1928. This has continued since, and has also embraced the study of other gall forming members of the **Aphidinae,** including the **Adelginae.**

In this wider field of research, both the recorded behaviour of **lanigera** in America, and in Europe, have their counterparts in the life history of some of the species studied, where parthenogenesis on the secondary host plant appears to be supplanting a sexual dependence on the primary host. Among species of the **Adelginae,** which like the **Eriosomae,** have the same primary host plant in common, similar difficulties in differentiating between species are encountered, but a much larger number of structures have come into use for taxonomic purposes in studying the **Adelginae** than have hitherto been deemed necessary for separating the **Eriosomae.** Where two insects have similar biologies, one character may be sufficient to prove two separate species, but where there is a wide difference in the biology of two insects, a large number of characters may have to be brought into use before identity can be satisfactorily established.

The first step in this prolonged study of **lanigera** was naturally an enquiry into probable host plants. Thorns are abundant in most parts of the Interior, but these native kinds are distinct from those in the east. No native elms exist west of the Rockies, but a number of these have been introduced, most of the older trees having been imported from Shenandoah, Iowa, in 1897. Both English and American elms are numerous in some localities, while one, or both species, are absent in others. There is nothing to indicate that the presence, or species, or proximity of elm, have any influence whatever on the extent or degree of infestation of apple by **lanigera.**

A failure to find rosettes on elm during 1928-1936, coupled with the complete freedom of the native thorns and mountain ash from woolly aphis attack, confirmed an opinion, very soon formed, that **lanigera** did

not follow, in British Columbia, the biological development claimed for it in the East.

In Vernon, alate sexuparae appear in the autumn as they do in Europe, and after an unusually mild winter, some of the hibernating forms developed into sexuparae in May, 1932, and deposited abnormal sexforms. Some of these had perfect and others partially developed rostra. Two viviparous alates and one pupal form were found in different years during the mid summer months, but in the fall, every effort to procure the sexes and egg on elm, by the sleeving in of numerous normal sexuparae, proved unsuccessful.

Due to many factors—among which may be cited better methods of control, the natural increase of predators as infestation reached its peak, and the successful dissemination and establishment of the parasite **Aphelinus mali** Hald.—there has been a marked decline in woolly aphis infestation since 1933. It has, indeed, become quite difficult to obtain material for study in the vicinity of the laboratory at Vernon.

In July, 1935, two small yet remarkable infestations, about three-quarters of a mile apart, were discovered on the wild thorn. One of these infestations was conveniently situated in the insectary yard, just a step from the laboratory. This yard is only about 30 feet square, yet manages to contain several young apple trees which, in previous years, had shown a decided susceptibility to attack by **lanigera.** On the east side, the yard is bounded by a thorn hedge. This, in turn, is flanked on the south by an apple tree, and on the north by an American elm. This elm is but one of many in the neighbourhood.

Thousands of alatae of **lanigera** have been sleeved in on this elm in the yard without procuring a rosette, and the same tree has been constantly visited from year to year to study the life history of **E. americana** which is well established between imported American elm and the native **Amelanchiers.**

The entire absence, during the last few years, of any sign of lanigera on the apples in the insectary yard did not permit this July infestation on thorn merely to be regarded as one of those rare escapes of **lanigera** to kindred host plants noted by Marchal in France. The time of the year, and the local absence of **lanigera,** strongly suggested a migratory aphis. Accordingly, this infestation was left unmolested until August, when a number of sexuparae were procured and sleeved in on the elm to test the truth of the above assumption.

In the following spring, several rosettes made their appearance not only on the elm in the yard but on others in the neighbourhood. The rosette aphis was observed in 1936 and 1937 to copy faithfully the development recorded in the East, and was found to agree in every detail with the characters described and depicted by Patch and others for

the rosette aphis during its sojourn on elm. The subsequent discrimination in selecting the summer host plant was not however in accordance with the behaviour of the migrant from rosette which in Maine, accepts apple readily.

During the past two years infestation had so increased that rosettes on American elm could be counted in hundreds in the spring of 1937. Infestation has been picked up on thorn a considerable distance from known elms, while thorns on vacant lots in close proximity to elm have been severely affected. During this rapid spread of the insect on elm and thorn, the apple trees in the yard and neighbourhood have remained entirely free from any woolly aphis attack. Strange to say, cage tests indicate that the rosette aphis has no inclination at present to go to apple. This, however, is no reason for presuming that it will not incidentally establish itself on apple in the future.

A curious, and precocious instinct for the normal host plant was displayed in one cage test, where in addition to thorn, the rosette aphis was offered Transcendent Crab, which variety is highly susceptible to **lanigera.** The crab was entirely neglected, the migrants, as in other tests, choosing to settle on the leaves of the thorn. There they deposited their yong which crawled away to settle on the base of the stem. In the test under consideration, a number of pupal forms prematurely left the drying up leaves of the rosette interned in the cage, and were found—not on the leaves of the thorn, the natural objective of the adult—but with their stylets inserted in the stem among the progeny of the migrant.

The migration from elm to the secondary host plant is much as complete as it is in the East. The migration from thorn to elm is likewise complete, whereas **lanigera's** migration from apple in the East is at best only partial. Not only has it been ascertained that **Crataegus columbiana,** and **C. douglasii,** show no sign of infestation until the migration from elm is well advanced, but it is proved, beyond doubt, that all the late generations on thorn develop wings. There are no apterae left on the secondary host plant (which are abundant in the case of **lanigera** on apple) to make an early infestation of thorn possible.

Should the migrants from elm adopt apple and mountain ash, besides thorn, as they do in the East, a complete return of their descendents to elm is to be anticipated in the fall. There are no grounds for believing that the adoption of other kindred host plants during the summer could, without some mutation occurring, alter fixed habits which are identical in character to those displayed by **americana** between elm and **Amelanchier.** Apple trees infested by elm migrants and also by **lanigera** would thus reveal a partial migration to elm as noted by Baker, 1912, in an extract of a letter published by Patch, 1916.

Dissections show that the alates that migrate to elm from thorn

contain a larger number of sexforms than those that stay on apple. This is remarked on by Schoene and Underhill, 1935. The males of the virile elm sexuparae outnumber the females more than two to one. The opposite is the case in the impotent sexuparae on apple. Experiment shows that the males of the elm-thorn aphis are born first, while under similar conditions, the females of the apple aphis are the first to be deposited.

Turning to an examination of structural differences, it has to be admitted that except for the greater proportional length of the male antennae of **crataegi,** there are no differences in these appendages that have specific value in other stages. There are other characters, however, that are not only sufficient to give **crataegi** specific standing, but in addition indicate that the relationship of these two aphides is not nearly as close as the study of the antennae alone would lead one to believe.

Fig. 1 shows at a glance a considerable difference in the size and shape of the waxglands, taken from the same area, of the same instar, of both species. The individual pores are alike in character in all the **Eriosomae** studied, but the arrangement of the pores is peculiar to different species. In **lanigera,** the pores are not arranged in an open circular ring, enclosing an extensive area, but are pressed together, so that their inner sides are nearly touching. This closed type of waxgland is specific for **Eriosoma lanigera** in British Columbia.

The open, ring-like nature of the waxglands of **crataegi** is constant throughout the descendents of the foundress on elm. This open, ring-like waxgland is depicted by Baker as typical of the viviparous female on apple, presumably derived from elm, and by Patch as typical of the second generation actually on elm.

Accompanying this difference in the arrangement of the waxpores, there is also a marked difference in the size and shape of the cornicles. Both **lanigera** and **ulmi** have small circular cornicles, while the larger oval cornicles are common to both **crataegi** and **americana.**

The above two characters are sufficient to separate the apterae of **lanigera** and **crataegi,** except in the early instars where cornicles are absent.

The differentiation between the sexuparae is more difficult, for the waxpores are vestigial in the winged forms, and only the difference in the cornicles remains. No one long accustomed to **lanigera's** variations, could fail to be conscious of something very different on first beholding the sexuparae of **crataegi** under the binocular. This difference is partly due to size, spread of wing, and a more delicate tracing of the wing veins. Colour, however, is the chief difference. Although colour can rarely be relied on for separating species, it is very constant for groups.

For example, when **crataegi, lanigera, ulmi,** and **americana,** are mounted side by side in gum chloral, which preserves and accentuates the natural colour, the abdomen and stigma of the forewing of crataegi are the same vivid green of **americana.** The abdomen of **lanigera** is the reddish hue of **ulmi,** and in both the latter alatae, the stigma is not green, but the same dull brown. The adult males of **crataegi** and **americana,** are also green, whereas, the males of **lanigera** and **ulmi** are yellow.

Structural differences in the wings of all the **Eriosomae** are slight, with some variation occurring in the same species. All have the single forked median of the forewing obsolete at its base, a character on which Hartig, 1841, erected his genus **Schizoneura,** which recently has been superseded by Leach's less constructive **Eriosoma,** 1818, which has priority.

One of the main characters, which Oestlund relied on in giving distinction to the thorn aphis, was that the median vein of the alate was not obsolete, but continued to its base. This feature is very constant in the alates taken on thorn, but is more apparent than real, the basal part of what was conceived to be the vein being tracheal. Newly emerged sexuparae of both **lanigera** and **americana** display this feature, which disappears as the wings become more mature. The alates of **crataegi** leave the thorn as soon as the wings are in a condition for flight. The alates of **lanigera** linger, and often feed on the apple, sometimes dropping the sexforms in the colonies of apterae. This difference in the maturity of the wings, accounts for this feature of the median noted by Oestlund as being constant in **crataegi** on thorn, and only occasional in **lanigera.**

As shown by the photographs of Patch, the curve of the radial sector of **crataegi** is slightly deflected downwards at the extremity, while in **lanigera** the curve usually continues on its upward course. The radial sector in both **lanigera** and **ulmi** is not inserted as close to the base of the stigma as is the case with **crataegi, americana,** and **rileyi.** This relative position of the radial sector to the base of the stigma is of interest, because Scudder contends that this particular character separates the ancient and modern aphides of the New World from those of the Old.

There are also a number of campaniform sensillae scattered along the thick subcosta between the base of the anal and the stigma. These are more numerous in **crataegi** than in **lanigera.** Similar sensillae are found in groups at the base of the wings of both species, and are singly represented on the distal segment of the tarsus and the second segment of the antennae. Two pairs of these sensillae are found on the trochanter and others are found on the femur. These sensillae are common to other families besides the **Eriosomae.**

A difference in the antennal lengths of the male has already been noted. The average length of 10 males of **crataegi** is .274 mm. as compared to Baker's measurements of .181 mm. for **lanigera** and .209 for **lanigera** in Vernon. This difference is most significant in segments III and IV. Baker's measurements and those in Vernon, show that the male and female antennae are much the same in length, whereas the male of **crataegi** has consistently longer antennae than the female, averaging .274 and .212 mm. respectively.

The only difference in the eggs of the two species is that the egg of **crataegi** both on elm and under artificial conditions is deposited with a covering of woolly excretion, while very little wool surrounds the egg of **lanigera.** The sexforms exude only a very small quantity of woolly material, the waxglands being vestigial, and the profuse covering of the egg is derived from a special, and hitherto unrecorded structure, appearing only in the adult oviparous female. This is one of a pair of perforated waxplates, shown in Fig. 2, occupying the position of the cornicles in the viviparous forms. These plates only appear after the last moult, at a time when the egg practically occupies the whole cavity of the body and thus obscures these structures. After the egg is deposited, the shrunken abdomen of the female can be pressed out in mounting, and these perforated waxplates, yellow in colour, are brought into view. Although more prominent in **crataegi,** these plates are present and function to some extent in **lanigera.** They are also observed to be vestigial in **americana** where the eggs are entirely destitute of covering.

In many respects **lanigera** might be morphologically regarded as a degenerate off-shoot of **crataegi,** but there is one character, that has considerable specific value, which debars the acceptance of such a view. In all its five stages, the female of **lanigera** has a rudimentary labium, represented by a crescent-shaped thickening of the cuticle on which are clustered four or five hairs on tubercles. Hence, the mouthparts of the female are not so vestigial as those of the female of **crataegi,** where hairs and vestiges of a labium are entirely wanting.

It will, nevertheless, be evident that the above morphological differences are not as pronounced as biological differences. Had **crataegi** been as general, in 1928, as it is likely to become in the near future, there can be little doubt that rosettes on elm would have confused the issue of early investigations.

The late arrival of **crataegi,** probably from some source where the habit of going to apple had not, or could not, be acquired, together with the local absence of **lanigera** in the neighbourhood, as a disturbing factor when **crataegi** was discovered, have all been advantages denied to other workers who have assisted in clearing up a highly controversial question of long standing.

Although corroboration of the main facts in this paper must be awaited from the East before this vexed question of **lanigera's** connection with the elm is finally settled, there is one general fact beyond dispute. This is, that the only part of the world where **lanigera** is said to migrate to elm is North America, where a definite migration is proved to exist between the native elms and thorns by a woolly aphis.

This aphis in British Columbia is proved to be as independent of apple, as **lanigera** has been proved to be independent of elm in every part of the world except North America, east of the Rockies.

On the basis of the antennae, a remarkable and perhaps an unique case of resemblance exists between two species that are separable by characters which do not point to a close relationship.

There is every assurance that the species studied on apple since 1928 in Vernon, British Columbia, is **Eriosoma lanigera** (Haus.) and equal assurance that the recently introduced woolly aphis on thorn, alternating between elm and thorn, is not **lanigera.** There is no option but to consider the latter aphis to be **Eriosoma crataegi** (Oestlund) and therefore distinct.

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