CONTENTS

HOST-DETERMINED MORPHOLOGICAL VARIATIONS IN LECANIUM CORNI
WALTER EBELING

THE ORANGE TORTRIX, ARGYROTAENIA CITRANA
A. J. BASINGER

This Issue Completes Volume 11
<table>
<thead>
<tr>
<th>CONTENTS</th>
<th>PAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Introduction</td>
<td>613</td>
</tr>
<tr>
<td>Description of Lecanium corni</td>
<td>614</td>
</tr>
<tr>
<td>Morphological variability of Lecanium corni</td>
<td>615</td>
</tr>
<tr>
<td>The influence of host-determined phenotypic variations on the synonymy of Lecanium corni</td>
<td>617</td>
</tr>
<tr>
<td>Biometrical experiments with Lecanium corni</td>
<td>618</td>
</tr>
<tr>
<td><strong>Methods</strong></td>
<td>618</td>
</tr>
<tr>
<td>Variations in size and structure of the antennae</td>
<td>619</td>
</tr>
<tr>
<td>Variations in size and structure of the legs</td>
<td>622</td>
</tr>
<tr>
<td>Variations in body proportions</td>
<td>623</td>
</tr>
<tr>
<td>Translocation experiments</td>
<td>626</td>
</tr>
<tr>
<td>Technique</td>
<td>626</td>
</tr>
<tr>
<td>Apricot to Christmasberry</td>
<td>627</td>
</tr>
<tr>
<td>Alder to apricot</td>
<td>628</td>
</tr>
<tr>
<td>Summary</td>
<td>629</td>
</tr>
<tr>
<td>Acknowledgments</td>
<td>630</td>
</tr>
<tr>
<td>Literature cited</td>
<td>631</td>
</tr>
</tbody>
</table>
HOST-DETERMINED MORPHOLOGICAL VARIATIONS IN LECANIUM CORNI

WALTER EBELING

INTRODUCTION

The effect of the host species on the insect phenotype may be said to be:
(1) physical, when the host causes the insect to develop structurally to
conform to certain structural peculiarities of its own, and (2) physio-
logical, when, consumed as food, it affects certain physiological and mor-
phological characteristics of the insect.

The physical effect is exemplified in the case of sessile insects, such as
scales, by distortions of bodily forms induced by their living in furrows
in the bark or by their adapting themselves to parts of plants which do
not allow for normal expansion and growth.

Another physical effect of the host is that which influences the size of
certain insects because of limitations in the amount of available food,
owing to the nature of the host species. Thus, insects infesting seeds,
such as certain weevils, may develop to only a small fraction of their
normal size because the seeds of the host species which they happen to
infest are too small to afford adequate nourishment for normal develop-
ment. The same may be said of parasites attacking insect-host species of
different sizes.

The physiological effect of the host, according to the foregoing classi-
fication, is exemplified by certain morphological variations of Lecanium
corni Bouché on its different host species, which will be discussed at
length. L. corni was selected for this work because it presents such a con-
spicious variety of forms on its various hosts.

1 Received for publication December 4, 1937.
2 Paper No. 388, University of California Citrus Experiment Station and Graduate
School of Tropical Agriculture, Riverside, California.
3 Assistant Entomologist in the Experiment Station.
DESCRIPTION OF LECANUM CORNI

Although an early, detailed anatomical study of the genus Lecanium Burmeister was made by Thro (1903), much confusion has resulted because of the instability of the characters used in the classification of this group (Sanders, 1910). Early workers were not judicious in their choice of structural characters for the classification of Lecanium species. Host plant, color, size, and shape were considered the most important characters for use in classification. The futility of using such indefinite and instable characters for classification is now apparent.

In common with other species of the genus, Lecanium corni is characterized superficially by the convexity of its body and by the brownish color of its derm. Like other species, also, it has an anal cleft, at the base of which is located a pair of anal plates (fig. 1).

---

Fig. 1.—Lecanium corni Bouche: A, ventral surface of adult female; B, ventral surface of second instar. a, Antenna; b, mouth parts; c, spiracle; d, spiracular spines; e, spiracular depression; f, marginal spines; g, leg; h, anal ring; i, spines on anal ring; j, anal plates; k, anal cleft; l, derm pores. (X 20.)
More specifically the structural characters of *Lecanium corni*, as it occurs on its more common hosts, such as *Prunus* sp., may be briefly described as follows:

**Adult Female.**—Size 2.5 to 3.0 mm × 4.0 to 6.0 mm; outline from nearly circular to ovoid or cymbiform, moderately convex, dried specimens having a dorsal ridge from which striations radiate to the sides; color reddish brown to chocolate-brown. Antennae usually 7-segmented, 200 to 340 microns long, the 3rd segment being the longest, the 2nd and 4th, 1st and 7th, and 5th and 6th segments being subequal. Legs 325 to 425 microns long, having a fairly definite arrangement of setae (from a lateral aspect usually 5 may be seen on the coxa, 1 on the trochanter, 3 on the femur, 2 on the tibia, and 3 or 4 on the end of the tarsus), with 2 tenent hairs attached on each side of the end of the tarsus, projecting well beyond the claws, the upper tenent hairs longest, practically uniform in thickness throughout, the plates almost twice as long as broad, the caudo-lateral margin little longer than the cephalo-lateral, with 4 fringe setae arranged in two pairs, with 4 apical and 2 subapical setae on each plate. Anal ring with 8 hairs. Derm pores of two fairly distinct sizes, usually single, but often in pairs or multiple, arranged in irregular rows radiating from the center to the margins. Marginal spines short and stout, about 80 microns apart; outer spiracular spines more than half as long as the middle spiracular spine.

*Lecanium corni* has but a single generation a year. In southern California the eggs hatch in early spring. *L. corni* is an active insect for a day or two after hatching. It has the usual appendages, which become fully developed in the second instar (fig. 1, B). In the third and last instar, the insect increases in the size of its body and proboscis only. The antennae and legs of the mature insect cannot be seen from the dorsal aspect, being concealed by the body of the insect.

**MORPHOLOGICAL VARIABILITY OF LECANIUM CORNI**

Many observations have been made concerning the variations in the form and coloration of *Lecanium corni* as it occurs on its many hosts. Ferris (1920) was impressed by the great variation in the external form among individuals of this species. After examining scales from a number of hosts, he states, "There is a very considerable diversity in appearance among specimens from these various hosts, ranging from the large pruinose form on elm to a very small and shiny form on *Arbutus* . . . ."

Marchal (1908) was able to prove that *Lecanium robiniarum* Douglas, described from specimens on black locust, was merely a host form of *L. corni*. He found that when specimens of *L. corni* were transferred from peach trees to a young locust tree isolated from other trees of the same species, their progeny assumed the typical *robiniarum* form. Only four individuals survived to full maturity out of the thousands that hatched from the eggs of the adults transferred from peach trees, but
these had the large size, dark coloring, and the specific appearance of *L. robinarum*. Each individual produced thousands of eggs.

Marchal stated that the foregoing experiment was proof that *Lecan­ium robinarium* is only a variety of *L. corni* by adaptation to the *Robinia* and therefore designated it by the name *L. corni* var. *robiniarum*. It is now known by that name among European entomologists.

Voukassovitch (1930) also produced specimens of *Lecanium corni* var. *robiniarum* by transferring *L. corni* from plum to locust. Other interest-

![Cross sections of dried specimens of *Lecanium corni* Bouché, showing differences in form on various host species. (X 5.)](image)

...ing transformations were found by Voukassovitch to be caused by other host species in further translocation experiments.

Sanders (1909) made some translocation experiments with *Lecanium corni* and stated that "Remarkable changes are wrought in the individual scales when transferred to a new host plant."

The very marked differences in external appearances occurring among the scales on different species of hosts are shown in figure 2. This figure indicates the gradation in convexity, which is apparent upon examination of dried specimens from a lateral aspect, from the large, very flattened individuals found on prune, *Prunus domestica* L., to the extremely convex or sometimes globular ones found on madrone, *Arbutus Men­ziessii* Hook. In general, the greatest similarity exists between individuals from hosts which are most closely related—compare the cross sections on the various species of *Prunus* in figure 3 with those on other genera.
An interesting variation from the usual form of _Lecanium corni_ is presented by specimens that developed on maple, _Acer macrophyllum_ Pursh. On this host they are small, very convex, smooth, and of a distinctly light-brown color. In figure 2 is shown the form of the insect from a lateral aspect. This is probably the insect that Ehrhorn (1898) described as _L. crawii_, specimens of which he took from maple in northern California. This insect can be differentiated from the more common forms of _L. corni_ only in superficial appearance. As far as the characters upon which the identification of the species is based are concerned, the form on maple is typically _L. corni_. As in other cases of dispute over the specific identity of scale insects, only translocation of the insects can definitely prove whether the morphological peculiarities of the insect are genetic or merely the result of the influence of the host. Much of this type of work would have been done already were it not for the difficulty of transferring _L. corni_ from one host to another in sufficient numbers to carry an experiment to conclusion.

**THE INFLUENCE OF HOST-DETERMINED PHENOTYPIC VARIATIONS ON THE SYNONYMY OF _LECANIUM CORNI_**

_Lecanium corni_ has been reported in various countries in Europe and North America on about a hundred species of host plants. In many cases it has been described as a separate species on the basis of specimens taken from only a single host. This led to a considerable synonymy of the species. Although _L. corni_ on locust was sufficiently different in appearance from the same species on peach, for instance, to be determined as a separate species, _L. robinia larum_ (see p. 615), Marchal (1908) noted that all gradations between _L. corni_ on locust and _L. corni_ on peach could be found in nature. Thus the form named _L. vini_ Bouche, which occurs on grapes, and the form named _L. wistariæ_ Sign., which occurs on _Glycine_ (soybean), often closely resemble the form on locust. _L. crawii_ Ehrh., which is now considered a form of _L. corni_, was named a new species on the basis of specimens taken from only one host, _Acer macrophyllum_ (see Ehrhorn, 1898). Likewise, the form on _Adenostoma_ has been called _L. adenostomae_ Kuwana. Steinweden (1930), after a careful study of specimens from both maple and _Adenostoma_, as well as other hosts on which _L. corni_ assumes an unusual superficial appearance, says, “Although there are some differences in external appearance, the morphological differences are too slight to separate them from typical _corni_. No further classification seems possible until careful breeding work on a variety of hosts is carried out.”
Marchal (1908) has listed nine European species as synonyms of *Lecanium corni*, to which Sanders (1909) has added twenty-six American species. In working out the synonymy of *L. corni*, Sanders studied the types of all the species he listed as synonyms except four, and in these cases similar topotypic material was examined. He believed, with Marchal, that a very important source of confusion to systematists working on *Lecanium* was the variation in the form and appearance of these insects on their different host plants. Thus he stated:

Moreover, within the last decade or two, many species have been described . . . with but little regard for the individual variations which are bound to appear in insects so absolutely dependent upon the kind and condition of their host plants as are the sedentary scale-insects. It is most unreasonable to expect to find a perfectly formed and fully developed *Lecanium* or *Pulvinaria* on a twig or stem of $\frac{1}{16}$-inch diameter on a starved plant, when the normal form would appear only on the flat surface of a leaf or a large stem in vigorous growth.

Marchal (1908), after commenting on the effect of the host species and the structures of the different parts of the host on the form of *Lecanium corni*, remarks,

Tous ces stades et tous ces aspects divers formaient un ensemble fort disparate, bien fait pour modérer les tendances dangereuses de ceux qui, se cantonnant dans leur cabinet de travail au lieu d’observer et d’expérimenter à l’air libre, multiplient les espèces à l’infini, sans avoir sous les yeux les pièces indispensables pour étayer leur opinion.

The tendency to create synonyms is probably as great among systematists working on other coccids as among those working on the scale insects. Ferris (1918) has long admonished entomologists concerning the unreliability of such superficial and variable characters as waxy secretions and antennal graphs as criteria for the identification of mealybugs because of the great variation found in this group. A large percentage of the synonymy of insects, individuals of which are largely confined to a single host, may be attributable to variations caused by the nature of the host. Other environmental factors, such as temperature and humidity, may be of some importance, but they affect large areas in a more or less uniform way and are more apt to cause an intergradation of phenotypic characters from one area to another. This type of variation is perhaps satisfactorily incorporated into the modern species concept.

**BIOMETRICAL EXPERIMENTS WITH LECANIUM CORNI**

*Methods.*—After many unsuccessful trials at transferring *Lecanium corni* from host to host, the writer endeavored to determine by statistical studies to what extent, if any, the morphology of the insect is influenced by its various host species as they occur in nature. An attempt was made
to discover whether insects from plants of a given species from identical
and different environments presented any variations in structure. Since
with a single exception, the writer has found *L. corni* only on Christmas-
berry (*Photinia arbutifolia* Lindl.) and apricot (*Prunus Armeniaca* L.)
in southern California, the statistical studies were largely confined to
the insects as they occur on these two hosts.

Christmasberry trees heavily infested with *Lecanium corni* were se-
lected in three widely separated environments, Waterman Canyon, Glen-
dale, and Livermore. Waterman Canyon is located in the San Bernardino
Mountains, California, at an elevation of about 3,500 feet; Glendale is
near the coast in Los Angeles County, California; and Livermore is also
in the coastal region, but about 400 miles north of Glendale. The latter is
not in the native range of Christmasberry, but the tree had been trans-
ferred there from the mountains. Two trees were selected for experimen-
tation in Waterman Canyon in order to determine whether or not trees
of the same species growing in the same environment could differently
affect the morphology of *L. corni*. One tree was selected in each of the
other two environments.

The tree environments present a great diversity of climate in tempera-
ture, humidity, length of seasons, and perhaps other factors. Waterman
Canyon is in a region of repeated snows during the winter months, and,
owing to its elevation, is cool the year round. Glendale is in a mild climate,
ever experiencing snowfall, and with high temperatures during the
summer months. Livermore, which is the farthest north of the three en-
vironments, has a climate warmer than Waterman Canyon but colder
than Glendale, and is, of the three, the most humid and also the most
uniform the year round.

Mature gravid females of *Lecanium corni* were taken from the leaves
of the trees during the spring and summer and were cleared and stained
according to the following technique: The specimens were first boiled in
a 10 per cent caustic-potash (KOH) solution for 10 minutes, then washed
in acidulated water, and immersed in saure fuchsin stain for 20 minutes.
They were then washed in water to remove the excess stain, immersed in
35 per cent, 60 per cent, and 95 per cent alcohol successively, passed
through carbolxylol, and mounted in balsam. Over 2,000 insects were
stained in this manner during the course of the investigation.

*Variations in Size and Structure of the Antennae.*—The expression of
the sizes of the various segments of the antenna in microns or other suit-
able units of measurement is known as the antennal formula. Graphi-
cally expressed, these dimensions are known as an antennal graph.
Antennal formulas and graphs were once used as specific criteria, and
are still extensively employed in the description of insects. Cockerell (1913) mentioned the value of antennal segments in species determination of coccids if sufficient numbers were examined and formulas or graphs were formed so as to include the extremes of variation. Hollinger (1917) and Brain (1915) made use of antennal graphs in their works on scale insects and discussed at length the methods of constructing the graphs. Ferris (1918) discusses antennal graphs in relation to several species of *Pseudococcus*, but says, "Even though it be true that the average graph of any species is relatively constant, this does not aid in the identification of nonaverage individuals... The graphs are neither sufficiently distinctive nor sufficiently constant to be of value in separating species."

Whether antennal formulas and graphs are satisfactory or not in the differentiation of species, they are nevertheless useful in depicting in a comprehensible way the differences existing among the individuals on different host plants provided a large number of antennal measurements are used.

A large number of antennae from scales taken from Christmasberry in Waterman Canyon, Glendale, and Livermore were measured in order to determine the differences in the size and structure of the antennae of the insects on a given host under identical and under different environments. By dividing the mean length of the antenna by the mean length of a single segment (in the present case the fourth segment), a ratio is established which may be called the structural ratio of the antennae of *Lecanium corni* on the particular host plant in question. Variations in the structure of the antennae effected by the host plant may then be measured by the variations in the structural ratio. Table 1 gives the structural ratios of the antennae of *L. corni* taken from different trees of Christmasberry.

The differences in the size and structure of the antennae (see table 1) are within the limits of experimental error. This experiment implies that the mean size and structure of the antennae of *Lecanium corni* on different trees of Christmasberry remain practically constant under similar or diverse environmental conditions.

Specimens of *Lecanium corni* were also selected from three environments—Fullerton, Anaheim 1, and Anaheim 2—on the twigs of apricot. In Fullerton, California, the first environment, the insects were selected from two trees about 25 feet apart. The second and third environments were about 2 miles apart in Anaheim, California, and are designated as Anaheim 1 and Anaheim 2. Here the insects were selected from a single tree. The differences in the environmental conditions of the regions in
TABLE 1

SIZE AND STRUCTURAL RATIO OF THE ANTENNAE OF LECANIUM CORNI TAKEN FROM
DIFFERENT TREES OF CHRISTMASBERRY AND OF APRICOT

<table>
<thead>
<tr>
<th>Environment</th>
<th>Number of antennae</th>
<th>Mean length of antenna, microns</th>
<th>Mean length of 4th segment, microns</th>
<th>Structural ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>From different trees of Christmasberry</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Waterman Canyon, tree 1</td>
<td>662</td>
<td>291.92±0.44*</td>
<td>52.36±0.17</td>
<td>5.57</td>
</tr>
<tr>
<td>Waterman Canyon, tree 2</td>
<td>658</td>
<td>291.34±0.45</td>
<td>52.77±0.15</td>
<td>5.52</td>
</tr>
<tr>
<td>Glendale</td>
<td>391</td>
<td>290.71±0.51</td>
<td>54.10±0.17</td>
<td>5.48</td>
</tr>
<tr>
<td>Livermore</td>
<td>96</td>
<td>285.83±2.02</td>
<td>53.10±0.40</td>
<td>5.57</td>
</tr>
<tr>
<td>From different trees of apricot</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fullerton, tree 1</td>
<td>663</td>
<td>239.25±0.65</td>
<td>38.49±0.12</td>
<td>6.21</td>
</tr>
<tr>
<td>Fullerton, tree 2</td>
<td>545</td>
<td>234.90±0.46</td>
<td>37.92±0.16</td>
<td>6.19</td>
</tr>
<tr>
<td>Anaheim 1</td>
<td>129</td>
<td>243.54±0.87</td>
<td>40.05±0.31</td>
<td>6.08</td>
</tr>
<tr>
<td>Anaheim 2</td>
<td>170</td>
<td>239.60±0.77</td>
<td>38.40±0.27</td>
<td>6.24</td>
</tr>
</tbody>
</table>

* Throughout the tables in this paper, mean and probable error of the mean are given, the latter calculated from the formula, probable error = \( \pm \frac{0.6745\sigma}{\sqrt{n}} \).

which specimens of *L. corni* were taken from apricot are not so great as the differences in the environmental conditions of the regions in which the insects were taken from the Christmasberry. With the exception of the two adjacent trees in Fullerton, however, the trees are sufficiently

TABLE 2

SIZE AND STRUCTURAL RATIO OF THE LEGS OF LECANIUM CORNI TAKEN FROM
DIFFERENT TREES OF CHRISTMASBERRY AND OF APRICOT

<table>
<thead>
<tr>
<th>Environment</th>
<th>Number of legs</th>
<th>Mean length of leg, microns</th>
<th>Mean length of tibia, microns</th>
<th>Structural ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>From different trees of Christmasberry</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Waterman Canyon, tree 1</td>
<td>134</td>
<td>399.78±1.20</td>
<td>77.22±0.35</td>
<td>5.18</td>
</tr>
<tr>
<td>Waterman Canyon, tree 2</td>
<td>105</td>
<td>394.05±1.21</td>
<td>75.60±0.38</td>
<td>5.21</td>
</tr>
<tr>
<td>Glendale</td>
<td>189</td>
<td>398.64±0.61</td>
<td>77.54±0.23</td>
<td>5.14</td>
</tr>
<tr>
<td>Livermore</td>
<td>100</td>
<td>394.50±1.38</td>
<td>76.44±0.41</td>
<td>5.16</td>
</tr>
<tr>
<td>From different trees of apricot</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fullerton, tree 1</td>
<td>97</td>
<td>362.35±1.04</td>
<td>65.30±0.38</td>
<td>5.55</td>
</tr>
<tr>
<td>Fullerton, tree 2</td>
<td>105</td>
<td>359.85±1.07</td>
<td>64.33±0.33</td>
<td>5.59</td>
</tr>
<tr>
<td>Anaheim 1</td>
<td>121</td>
<td>366.95±0.78</td>
<td>64.34±0.23</td>
<td>5.70</td>
</tr>
<tr>
<td>Anaheim 2</td>
<td>144</td>
<td>360.49±0.88</td>
<td>64.05±0.24</td>
<td>5.63</td>
</tr>
</tbody>
</table>
distant from one another to obviate the possibility of their harboring populations of scales of immediately common ancestry.

Data for scales on apricot similar to those secured in the preceding experiment are also summarized in table 1. As in the case of *Lecanium corni* on Christmasberry, a considerable uniformity in the structure of the antennae of insects on different trees of the same species was found.

Variations in Size and Structure of the Legs.—By use of the ratio of

![Antennae of Lecanium corni Bouche from different hosts and different environments: A, B, C, on Christmasberry—A from Waterman Canyon, B from Glendale, and C from Livermore; D, E, F, on apricot—D from Fullerton, E and F from Anaheim. (A–F, X 150.) Right, dorsal aspect of L. corni, showing relative size of an average individual on Christmasberry (G) and on apricot (H). (G, H, X 6.)](image)

the length of the leg to the length of the tibia as a structural ratio, a uniformity is observed among individuals of *Lecanium corni* taken from Christmasberry in different environments, as is shown in table 2 for Waterman Canyon, Glendale, and Livermore.

In a similar way, it can be shown that the ratio of the length of the forelegs to the length of the tibiae is also practically constant when the specimens are taken from different apricot trees in similar and diverse environments. The data showing this morphological constancy are also given in table 2.
By comparing the structural ratios of the antennae and legs of *Lecanium corni* on Christmasberry with the structural ratios of the antennae and legs of *L. corni* on apricot, the variations in the structure of these appendages caused by the two host species can be readily appreciated. The structural ratios for the antennae of the scales on the former host range from 5.48 to 5.57, while on the latter host they range from 6.08 to 6.24 (table 1). Corresponding ratios for legs range from 5.14 to 5.21 on Christmasberry, and on apricot from 5.55 to 5.70, respectively (table 2).

When the *t* test for significance (Snedecor, 1937) was applied, the differences in the means of the structural ratios between the insects on the two host species were found to be highly significant.

Variations in Body Proportions.—While the insects taken from Christmasberry have longer antennae and legs than those taken from apricot, they are nevertheless much smaller in total length, measured from the anterior to the posterior tip of the derm. This striking structural inconsistency is shown in table 3 and, for antennal length and body length, in figure 3.

The ratio of the difference of the means to its own standard deviation is especially significant as indicating the probability of the statistical significance of the difference of the means, that is,

\[ \frac{M_1 - M_2}{\sigma_{(M_1 - M_2)}} \]

when \( \sigma_{(M_1 - M_2)} = \sqrt{\sigma_1^2 + \sigma_2^2} \)

The following figures are computed in the above manner, and show the high degree of statistical significance of the data: For length of the antennae on the two hosts,

\[ \frac{M_1 - M_2}{\sigma_{(M_1 - M_2)}} = 97.62 \]

The corresponding figures for the length of the legs and the length of the bodies are, respectively, 24.05 and 41.18.
According to conventional standards in taxonomic work, if the source of the insects were not known, the structural differences between \textit{Lecanium corni} on Christmasberry and \textit{L. corni} on apricot shown by the foregoing data might legitimately be construed to indicate that the insects on these two hosts are distinct species. The translocation experiments cited later prove definitely, however, that the differences found between the insects on these two hosts are caused by the differences in the plants themselves.

Graphs showing the differences in the structure of the antennae and legs of \textit{Lecanium corni} on Christmasberry and on apricot are shown in figures 4 and 5. It is obvious from an examination of the graph that the ratios of the segments to one another are different on the two hosts. The differences in the antennae of the insects taken from Christmasberry and from apricot are also shown in figure 3.
It may be argued that differences in the structure of the appendages may occur concomitantly with differences in their length, irrespective of the species of host from which the insects were taken, but we have not found this to be true. Appendages of the smallest insects on Christmasberry, which averaged the same in length as the average appendages of the insects on apricot, did not have the structural peculiarities of the latter, but conformed closely to the structure of the average appendages of the insects on Christmasberry. Structural differences, then, are independent of the absolute dimensions of the appendages, but are due rather to the differences in the species of hosts from which the insects bearing the appendages were taken.

The relative sizes of the antennae of *Lecanium corni* on Christmasberry and on apricot are graphically illustrated in figures 6 and 7. When individuals from these two hosts are combined in one frequency distribution for antennal length, a markedly bimodal curve results (fig. 6). When the distributions for the two hosts are plotted separately, the two curves closely approximate the "normal curve," and overlap only slightly (fig. 7).
Fig. 6.—Bimodal curve resulting when individuals of *Lecanium corni* from two host species, apricot and Christmasberry, are combined into one frequency distribution for antennal length.

Fig. 7.—Slightly overlapping "normal curves" resulting when individuals of *Lecanium corni* from apricot (left) and Christmasberry (right) are placed in their respective frequency distributions for antennal length.

**TRANSLOCATION EXPERIMENTS**

*Technique.*—The effect of the host species on insect morphology has been determined in the past by biometrical methods and by translocation experiments. In the case of *Lecanium corni*, the latter method presents certain difficulties. Repeated attempts to transfer *L. corni* in nature from one host plant to another over a wide range of temperatures and with many species of host plants have been successful in only a single instance. Translocation was effected more successfully in the laboratory.
The method of translocation in either case has consisted of attaching twigs of one host heavily infested with gravid females or newly hatched larvae of _Lecanium corni_ to another host. When the twigs of the first host begin to dry, the young larvae (those hatched before the twig was transferred or those resulting when eggs of the females on the old host hatch) crawl off and attach themselves to their new host.

Thousands of insects have thus migrated in the course of the experiments from Christmasberry and apricot to Christmasberry, apricot, prune, peach, locust, willow, potato, and _Malva_. On all but the last three hosts, the transferred larvae have developed in the usual manner throughout the summer and fall on the leaves of their hosts, but have usually failed to make a successful migration from the leaves to the twigs and branches before the abscission of the leaves at the approach of winter—even when they are transferred from one plant to another of the same species.

The difficulty encountered in transferring _Lecanium corni_ is not surprising, in view of the fact that Voukassovitch (1930) reports that only two or three individuals per thousand were successfully transferred by him in Yugoslavia, where conditions for survival appear to be unusually favorable.

_Apricot to Christmasberry._—In the spring of 1933, large numbers of apricot twigs heavily infested with gravid _Lecanium corni_ were fastened to uninfested Christmasberry shrubs in Orange County Park, California. Enormous numbers of young scales settled on the Christmasberry leaves, and of these a considerable number migrated to the branches in the fall. In the spring of 1934, 21 mature scales were found on the shrubs infested the previous fall. These were removed, cleared, and stained according to the method previously mentioned, and microscopic measurements were made of antennae and legs of these individuals. The mean antennal formula in microns was found to be 40.6, 47.9, 60.8, 55.0, 23.9, 24.2, 46.5, and the leg formula, 66.8, 159.9, 109.9, 77.5. By comparing these formulas to corresponding formulas for _L. corni_ on Christmasberry, as established by previous investigations (see figs. 4 and 5), it can be seen that they coincide remarkably well, both in structure and size. The scales transferred from apricot to Christmasberry had developed not the apricot-form characteristics of their progenitors, but the typical characteristics of the Christmasberry form. Because of the tremendous mortality of insects, the possibility of selection is not excluded. However, the mortality appears to be just as great when the larvae are settling on the host plant or host species upon which their progenitors have lived for generations.
Alder to Apricot.—On June 17, 1934, the writer found *Lecanium corni* infesting a number of alder (*Alnus rhombifolia* Nutt.) trees in the upper reaches of San Antonio Canyon in the Sierra Madre Mountains of southern California. These insects were small and very convex in form, a great contrast to the apricot form of *L. corni* (fig. 8). A comparison of the shape of *L. corni* on alder and apricot was made by measuring the height and length of all insects and calculating a structural ratio (fraction of height over length) for the insects on each host. An idea of the difference in the structure of the bodies of the insects on the two host species can be obtained by comparing the structural ratios (see table 4).

### Table 4
**Differences in the Structural Ratios of Adult *Lecanium Corni*, Taken from Alder and Apricot Trees**

<table>
<thead>
<tr>
<th>Host</th>
<th>Number of individuals</th>
<th>Height</th>
<th>Length</th>
<th>Height/Length</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alder</td>
<td>200</td>
<td>2.29</td>
<td>3.29</td>
<td>0.696</td>
</tr>
<tr>
<td>Apricot</td>
<td>200</td>
<td>2.10</td>
<td>5.27</td>
<td>0.398</td>
</tr>
</tbody>
</table>

By plotting the heights of the scales taken from alder and apricot as ordinates and the lengths as abscissas (fig. 9), it was found that the points representing the individuals from the two hosts were confined to two distinct areas in the coordinate system. Thus again two host forms of a species are structurally distinct, with greater structural differences than are sometimes found between distinct species.

A number of *Lecanium corni* from alder were transferred to apricot trees growing in a laboratory at temperatures varying from 70° to 80° F
throughout the life cycle of the insects, and some of these reached maturity in the spring of 1935. These correspond closely in size and structure to scales normally occurring on apricot (fig. 10). Again, variation in structure was definitely correlated with the host species.

SUMMARY

A scale insect, *Lecanum corni* Bouché, was selected as the subject for experimentation on the effect of the host species on the morphology of insects because of the great morphological variation in this species on its various host plants in nature.

A detailed description of *Lecanum corni* is given. Its structural variability is greatly influenced by various host species. Much of the synonymy of *L. corni* has resulted from the confusion arising from its host-determined morphological variability.
On the basis of certain structural ratios, such as the ratio of the length of the antennae to the length of the body, ratios of the lengths of antennae or leg segments to one another or to the length of the entire appendage, and the ratio of the height of the entire insect to its length, certain morphological differences in *Lecanium corni* have been evaluated statistically.

Individuals of *Lecanium corni* taken from apricot (*Prunus Armeniaca* L.) have large bodies and short appendages; those taken from Christmasberry (*Photinia arbutifolia* Lindl.) have small bodies and long appendages. The antenna and leg formulas, which show the ratios of the lengths of the segments of these appendages to one another, are also different on the two hosts. When individuals from the two hosts are combined in one frequency distribution for antennal length, a markedly bimodal curve results. When the distributions for the two hosts are plotted separately, the curves each closely approximate the “normal curve” and overlap only slightly.

Adult insects were transferred from apricot to Christmasberry in the field, and their progeny developed the structural characteristics of the Christmasberry form of *Lecanium corni*.

On alder (*Alnus rhombifolia*) the ratio of height to length of *Lecanium corni* is 0.696; on apricot it is 0.399. Progeny of adult insects transferred from alder to apricot in the laboratory developed the structural characteristics of the apricot form.

ACKNOWLEDGMENTS

The present paper is a portion of a dissertation entitled, “The Influence of the Host Species on Insect Biology,” submitted as a partial fulfillment of the requirements for the Ph.D. degree at the University of California, and, as such, was reviewed and criticized by Professors H. J. Quayle, H. S. Smith, S. F. Light, and W. M. Hoskins, and by Dr. H. B. Frost. Later, the paper was reviewed and criticized by Dr. A. E. Emerson, of the University of Chicago, and by Dr. J. W. Lesley and Professor E. B. Babcock. To all these the writer wishes to acknowledge his appreciation.
LITERATURE CITED

BRAIN, C. K.

COCKERELL, T. D. A.

EHRHORN, E. M.

FERRIS, G. F.

HOLLINGER, A. H.

MARCHAL, P.

SANDERS, J. G.

SNEDECOR, G. W.

STEINWEDEN, J. B.

THRO, W. C.

VOUKASSOVITCH, P.