FORESTRY COMMISSION.

BULLETIN No. 4.

The Douglas Fir Chermes.

(Chermes cooleyi.)

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The insect *Chermes cooleyi* which forms the subject of this Bulletin lives partly on the Douglas fir and partly on the Sitka spruce. It is not altogether new to Great Britain, having been observed in the New Forest on Douglas fir by Messrs. Henry and Forbes in 1913, but reports received in 1919 showed that it was more widely distributed than had been suspected and was apparently spreading. The Commissioners accordingly decided to investigate the life history of the insect, having before them the example of another Chermes—*C. nüsslini*—which is so destructive to the common silver fir as to make the future use of that tree in this country very doubtful.

Mr. R. N. Chrystal, B.Sc., who had already investigated *Chermes cooleyi* in Vancouver was appointed to enquire into the life history and forest relations of the insect in Great Britain. This work he has carried out under the direction of Dr. Munro, the Commission's entomologist.

The results of the investigation are reassuring from the sylvicultural point of view. Although large numbers of badly infested Douglas firs have been observed, no case of death or serious reduction in vigour has been directly attributable to the attack. Nor has the gall form—which in Vancouver is the dangerous stage—been found on the Sitka spruce, in spite of the fact that ample facilities existed, both in the forest and in the laboratory, for the insect to proceed to gall-formation.

In addition to the main investigation a beginning has been made with the preparation of keys for the identification of the British species of Chermes and the work of future investigators should be considerably facilitated thereby.

The Bulletin has been prepared by Mr. Chrystal in collaboration with Mr. Fraser Story.

R. L. ROBINSON,
Commissioner.

FORESTRY COMMISSION,
July, 1922.

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THE DOUGLAS FIR CHERMES.

(CHERMES COOLEYI.)

CONTENTS.

THE DOUGLAS FIR CHERMES.

(CHERMES COOLEYI.)

CHAPTER I.

This bulletin embodies the results of an investigation into the life history of *Chermes* (*Gillettea**) *cooleyi* Gillette, an American species of the family Chermesidæ, which has made its appearance upon the Douglas fir in this country. Mr. Chrystal was appointed in November, 1920, by the Forestry Commissioners to undertake an investigation which was originally planned to extend over two years but owing to unforeseen circumstances had to be suspended after a period of one year. Sufficient information, however, has been collected concerning the life history of the species in Britain to justify the publication of a bulletin embodying the results of the work done both in this country and in America together with a statement of the important problems remaining to be solved.

The Family Chermesidæ.

The family Chermesidæ to which this insect belongs, forms a division of the super-family Aphidoidea or plant lice which has long been an object of special interest to foresters and entomologists, both as a group of insects injurious to coniferous forest trees, and as showing a variety of highly complicated life cycles.

We owe our present knowledge of the group chiefly to the labours of many Continental workers, of whom three are of special note. The first of these, N. Cholodkovsky, commenced his work in Russia more than a quarter of a century ago, and in 1915 published a monograph on the group in which he dealt very fully with the life histories of all the European species then known, and provided keys for the identification of the sub-genera, and species. In addition he threw much light upon the biological division of the family, discussed in full the theory of migration which he first propounded in 1896, and dwelt upon the question of the importance of these insects as forest pests, and their control by natural and artificial means.

Carl Börner in Germany, commenced his work on the Chermesidæ in 1904 and published his *Monographie über die Chermiden* in 1908. In this monograph in addition to dealing very fully with the phylogenetic status of the family, their external morphology, the life histories of the European species and their systematic relationship, he devoted several chapters to the consideration of the effects of their attacks upon the host trees, the theories of migration advanced by Dreyfus, Nüsslin, Cholodkovsky and others, and the question of control measures.

* In order to prevent confusion in the text, the old generic name Chermes has been retained and used throughout, the more recently created genera appearing in the Keys.

Following this monograph he published a series of shorter papers dealing with the classification of the family.

Paul Marchal in France has studied the life cycles in the genera *Pineus* and *Dreyfusia* and thrown new light upon the monocyclic generations in the pine and silver fir species, and also upon the occurrence of sexual forms in these genera. In Britain, but little attention has been paid to the family, the chief workers on it being Buckton who gave a general account of the British species ; Burdon who dealt with the spruce and larch species and the question of control ; and Steven who in his work upon the spruce and larch species confirmed Cholodkovsky's work on the Continent. In America, Storment, Patch, Gillette, Chrystal and others have contributed to the literature of the group.

General Characters of the Family.

Tables giving a detailed classification of the family, based upon the work of Börner and Cholodkovsky, are given in the Appendix, p. 37. In the text of the bulletin itself only those details of classification which are considered necessary to a proper understanding of the general characters of the family, are included. The following biological characteristics are important :—

(*a*) The Chermesidæ attack coniferous trees exclusively.

(*b*) In a complete life cycle, two different species of host trees are necessary. Upon one of these (the primary host) which is always a member of the genus *Picea*, a deformation of the needles of the twigs results in a peculiar type of gall being formed. On the other or secondary host, which may be a member of any one of the genera *Pinus*, *Larix*, *Abies*, *Pseudotsuga* or *Tsuga*, no such gall is formed, the insects living exposed on the needles, or the bark of the stem and branches.

(*c*) In a complete life cycle five main generations, which are described later, can be recognised. Reproduction in four of these is exclusively parthenogenetic, while the fifth is a sexual generation (Fig. 1, p. 7).

(*d*) Modifications of this complex life cycle may occur, the cycle being confined to one or other of the hosts, in which case the sexual forms are absent or abortive.

Stages of the Life Cycle.

In the past, many different names have been proposed by various authors for the respective stages of the Chermes life cycle. The following description of the principal stages of the life cycle is based on the work of Marchal.

Generation I. The Stem Mother or Fundatrix Vera (Cholodkovsky) on the Primary Host. (*Picea* Sp.).—The fundatrix always hatches from a fertilised egg and passes the end of the summer, autumn and winter seasons in an immature state. She is wingless and extremely prolific, passes through four stages separated by three moults, and settles upon the spruce, either at the base of the buds, on the buds themselves, or on the axis of one of the shoots of the year. In spring a large number of eggs are laid from which the gall-dwelling forms (Generation II.) hatch.

LIFE CYCLES IN CHERMESIDÆ.

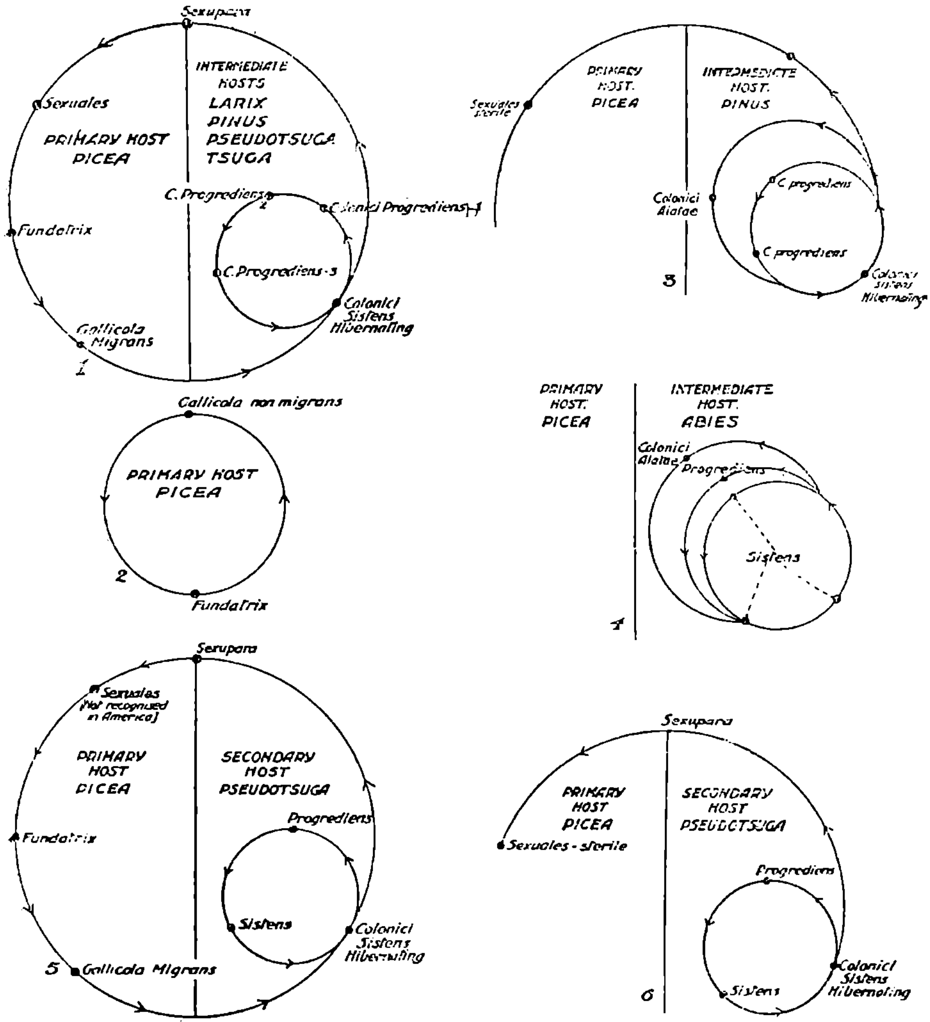

FIG. 1. Typical life cycle of five generations passed on two host trees.

FIG. 2. Life cycle confined to the primary host (*Picea*)—Cholodkovsky's species. *Chermes abietis* Kalt., and *Cnaphalodes lapponicus* Chol.

FIG. 3. Life cycle of *Chermes* (*Pineus*) *pini*. Börner.

FIG. 4. Life cycle of *Chermes* (*Dreyfusia*) *piceæ*. Börner.

FIG. 5.* Life cycle of *Chermes* (*Gillettea*) *cooleyi* Gillette, in America.

FIG. 6.* Life cycle of *Chermes* (*Gillettea*) *cooleyi* Gillette, in Britain.

* In figs. 5 and 6 the term "progrediens" for the first summer generation on the secondary host is inserted provisionally, the sequence of these forms in *C. cooleyi* being still somewhat obscure.

Generation II. The Gall-dwellers (Gallicolæ) on the Primary Host (Picea Sp.).—These emerge in spring, and settle down among the young needles of the bud, on or in the vicinity of which the stem mother is found. Under the influence of the feeding of these gallicolæ, aided by that of the stem mother herself, the spruce bud develops wholly or in part into a gall, the form of which is peculiar to the species. The gall forms pass through four moults separating five stages. When they reach the nymphal state (Stage IV.) the gall opens and from each chamber, which represents the metamorphosed basal portions of the needles, they leave the gall, and moulting for the fourth and last time, they appear as winged forms, which are destined either to remain on spruce and by a shortening of the life cycle give rise to Generation I. *gallicolæ non migrantes*, Cholodkovsky (Fig. 2, p. 7), or to fly to the intermediate host tree (*gallicolæ migrantes*) where they settle upon the needles, commence feeding and lay a considerable number of eggs.

Generation III. The Colonist broods (Colonici) on the Secondary Host, (Pinus, Larix, Abies, Pseudotsuga, Tsuga.) These are usually wingless forms which multiply parthenogenetically upon the secondary host, passing through an indefinite number of generations. The first of these, the progeny of the winged migrants, form Brood I. of the colonici, and were named by Cholodkovsky *fundatrices spuriæ*, or false stem mothers. This brood passes the winter in an immature stage developing in the following spring, when it becomes the starting point for a number of summer broods. The number of these varies according to the season and local climatic conditions.

In certain species of the genera *Pineus* and *Dreyfusia*, Brood I. of the colonici gives rise to a number of winged forms, which confine themselves to the secondary host tree, and give rise to new wingless broods thereon. These winged forms are known as *colonici, alatæ non migrantes* (Figs. 3, 4, p. 7).

Generation IV. The Sexuparæ or Winged Migrants returning to the Primary Host. (Picea Sp.).—Winged individuals forming part of the progeny of Brood I. of the colonici. They are smaller and less prolific than the gallicolæ of Generation II. but exhibit very similar morphological characters. The spring brood (Brood I., colonici) of which they form a part, is dimorphic in character, producing in addition to the sexuparæ, a sister series of wingless forms on the secondary host (Brood II., colonici) and in certain cases *alatæ non migrantes* as described under Generation III. The sexuparæ settle upon the spruce, and there lay a small number of eggs (10–25), which give rise to Generation V.

Generation V. The Sexual Generation on the Primary Host. (Picea Sp.).—The mature individuals are minute wingless forms characterised by having very short rostral stylets, and four-jointed instead of three-jointed antennæ, as in the other wingless forms. The males are more active than the females, they have longer legs and antennæ, and have the abdominal extremity more conical in shape. These pass through four moults as in the case of the winged forms but attain little development. The fertilised female lays a single egg, usually under the scales at the base of the spruce twigs. She dies close by the egg she has just laid, and from which the larva of the fundatrix of Generation I. hatches in a short time.

Description of the Genus Gillettea, Börner.

(Börner. Zool. Anz., XXXIV., pp. 504–506. 1909.)

The following is a translation of Börner's description of the genus.

" Closely related to the genus *Chermes* (*s. str.*) Nüsslin, Börner. In the larvæ of the fundatrix and first colonici broods, the 6th abdominal tergite bears 3 + 3 pairs of hairs and as in the genus Chermes itself, the facets of the dorsal wax glands bear wax tubes.

" The fundatrix larva has antennal and sub-coxal ventral glands. In the colonici larva sub-coxal glands are present only on the middle coxæ, as in the genera *Dreyfusia* and *Aphrastasia*.

" The mature fundatrices of Generation I. and Generation III. have ventral glands at the antennal bases, and on the middle coxæ. The larvæ of the colonici summer broods have a soft integument. The mature stem mothers of the colonici summer broods are to be distinguished by their thicker covering of wool from the winter colonici stem mothers (Generation III.) with their shorter wool.

" The sexupara nymph has normally facetted glands on the vertex and perhaps rudimentary dorsal glands (Gillette). The winged gallicola and sexupara have the head and thoracic gland plates normally facetted and completely developed.

" The above description is based on specimens of *C. cooleyi*, Gillette (fundatrix and gallicola), and var. *coweni*, Gillette (colonici and sexupara)." *

The Species *Chermes* (*Gillettea*) *cooleyi*, Gillette, and *Chermes cooleyi* var. *coweni*, Gillette.

(Gillette. Proc. Acad. Nat. Sci. Philad. 1907.)

This species was first found by Gillette in Colorado in **1903**. He recorded the galls of the insect from a number of localities on the Colorado blue spruce (*Picea pungens* E.) at altitudes of 4,000–8,000 feet, and also upon the Engelmann spruce (*Picea Engelmanni* E.) at higher elevations of 8,000 feet up to the limit of tree growth. At that time he also recorded the receipt of galls from Western Canada on *P. sitchensis* Carr, which he thought were probably those of *C. cooleyi*. Considerable doubt existed at first as to whether the insect was not identical with either *Chermes abietis* L. or *Chermes sibiricus* Cholodkovsky, and specimens of the galls, with the insects themselves were sent to Cholodkovsky, who replied that the insect was neither *C. abietis* nor *C. sibiricus* but a new species.

In his paper on the Chermes of Colorado conifers, Gillette named the new species *Chermes cooleyi*, and described the fundatrix and gallicola generations on two of the spruces mentioned above. He suggested that the gallicolæ migrated to the Douglas fir upon which tree he found what he considered to be the colonici stages. The latter, which he described as *Chermes cooleyi* var. *coweni*, he treated as a variety of the spruce form.

In 1914 Chrystal, in the course of an investigation into the cause of the unhealthy condition of the Sitka spruce (*P. sitchensis*) in Stanley

* "On account of the structural affinity of the two winter larval forms (fundatrix and colonici) and their presence in the same locality, there can be no doubt as to the identity of the two forms one of which was described by Gillette as a variety" (Börner). Chrystal's researches in British Columbia have confirmed this.

Park, Vancouver, British Columbia, found that Gillette's species, *C. cooleyi*, was one of the main causes of the trouble, and made a study of its life history, from which the following results were obtained.

(1) The insect was found on a new primary host, the Sitka spruce.

(2) Experiments proved that the secondary host was the Douglas fir and that Gillette's *Chermes cooleyi* var. *coweni* was the colonici stage of *C. cooleyi.* This confirmed the suggestion made by Börner in 1909, in his description of the new genus *Gillettea*, in which he treated the species *cooleyi* and the variety *coweni* as one.

(3) Sexuparæ were traced back to the spruce, but the sexual stage was missed, although the subsequent stem mother and gall generations were found and studied.

(4) Important evidence was adduced to show the serious damage to the spruce which might ensue from the attacks of the insect. In the case of the Douglas fir no such evidence was clearly established.

CHAPTER II.

Chermes cooleyi in America.

The winter larvæ of the stem mothers (Generation I.) on the Sitka spruce are minute, wingless forms dark brown to black in colour, and may be found hibernating on the spruce twigs. They may occur close to the terminal bud, or at a distance of some inches therefrom. The body of the insect is closely adpressed to the twig, and the setæ are deeply sunk into the tissues, through the bark crevices.

In the month of April these larvæ become active, start feeding, and passing through a series of moults, develop into mature stem mothers. These secrete a large quantity of white waxy wool, under cover of which they commence egg laying (Plate I., Fig. 3). A large number of eggs are laid (300–500) and the young larvæ hatch in about a week, locating themselves at the inner bases of the young needles, which are then just breaking from the bud scales. A gall begins to form and develops rapidly, the whole structure being complete in the course of a few days. The galls of this species vary in length from one and a half to three inches, the size of the gall depending upon the vigour of the shoot attacked. Their general shape is elongate and narrow, and the whole shoot is nearly always affected, the terminal portion being as a rule killed (Plate I., Fig. 1). The colour of the growing gall varies from light green to deep purple. The number of gall chambers varies from forty to over two hundred, and the number of young in each chamber from one to fifteen, although as many as thirty-two have been found in a single chamber. Typically the whole shoot is affected, but cases occur where the shoot is galled on one side only, and badly twisted or bent in consequence. More rarely the terminal portion of the shoot may be galled all round, and the lower portion only half way round.

The galls commence to open about the middle of June, and the nymphs of Generation II. emerge and settling on the spruce needles cast their nymphal coat and become winged. The winged form after a resting period of some hours flies to the needles of the Douglas fir,

PLATE I.

FIG. 1.

FIG. 2.

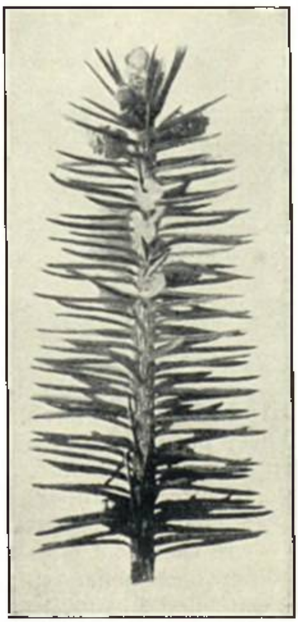

FIG. 3.

FIG. 4.

FIG. 1. Galls of *C. cooleyi* Gillette, half natural size (after Britton).
FIG. 2. Sitka spruce in Stanley Park, Vancouver, B.C., heavily galled by *C. cooleyi* (original).
FIG. 3. Egg masses of stem mother or fundatrix of *C. cooleyi* on blue spruce (*Picea pungens*), half natural size (after Gillette).
FIG. 4. *C. cooleyi* on Douglas fir in spring, natural size (original).

To face p. 11.

PLATE II.

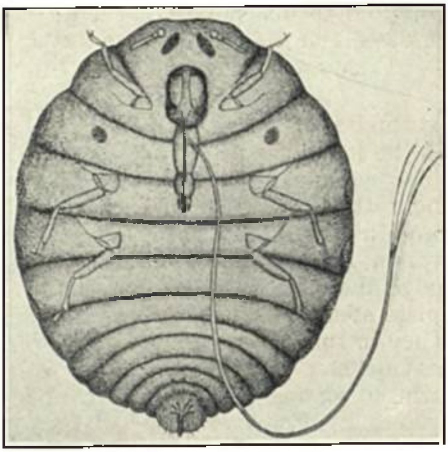

FIG. 1.

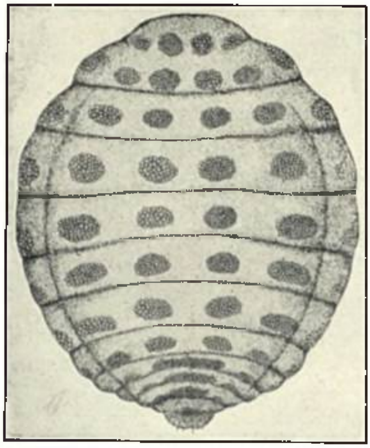

FIG. 2.

FIG. 3.

FIG. 4.

FIG. 1. Adult stem mother or fundatrix of *C. cooleyi* on Sitka spruce. Ventral aspect. x 49 (after Gillette).

FIG. 2. Adult stem mother or fundatrix of *C. cooleyi* on Sitka spruce. Dorsal aspect. x 49 (after Gillette).

FIG. 3. Winged sexupara of *C. cooleyi* egg-laying on needle of Sitka spruce. x 13 (original).

FIG. 4. Winged Sexuparæ of *C. cooleyi* on Sitka spruce. x 5 (original).

and settling there, lays from one hundred to one hundred and fifty eggs. The eggs hatch in six or seven days, and the young larvæ settle upon the undersides of the needles, and remain undeveloped until the following spring.

These larvæ constitute the first brood of Generation III., the colonici on the Douglas fir. Early in the following spring (May), they develop into stem mothers on the needles, and lay a small number of eggs (30–60), which hatch in about three weeks. This brood is dimorphic in character ; those emerging first pass through a nymphal stage to winged sexuparæ of Generation IV., which fly back to the needles of the Sitka spruce, and lodge there ; those appearing later develop into a spring brood of wingless stem mothers, which remain on the needles of the Douglas fir. They in turn give rise to a summer brood of wingless forms which do not develop into mature adults in the same year (Fig. 7, p. 13). The winged sexuparæ which fly to the spruce, after settling down on the needles lay a small number of eggs (10–25), which hatch in about a week.

Beyond this point the life history of the species in America may be considered as uncertain in so far as no sexual generation has been observed. Chrystal's observations in Britain, however, have shown that a sexual generation does exist in this species, and it is believed that this generation is the immediate connecting link between the migration from the Douglas fir to the Sitka spruce, and the establishment of a fundatrix stage thereon, leading to gall production. Further work on this species in America will almost certainly result in the discovery of this connecting link in that country and thus clear up that portion of the life history, which both in Gillette's work in Colorado, and that of Chrystal in Stanley Park, Vancouver, was not completely elucidated.

Chermes cooleyi in Britain.

Chermes cooleyi Gillette was first noticed in this country by A. C. Forbes and Augustine Henry in the New Forest, July 1913, upon the needles of the Oregon Douglas fir, but it was not definitely identified until the summer of 1919, when material was sent to the Bureau of Entomology, U.S. Department of Agriculture, Washington, where it was identified as *Chermes cooleyi* var. *coweni* Gillette, the colonici generation of *Chermes cooleyi* Gillette. All specimens of Chermes on Douglas fir in Britain received during this investigation have proved to be this species.

Methods of Investigation including Laboratory Technique.

The life history studies were carried out in the following ways :

A. *Laboratory.*—Experiments were conducted in the laboratory using infested twigs of Douglas fir, which were kept in tubes of water in glass cages. This method proved quite suitable for limited periods of a month or thereabout, but could not be carried on over longer periods owing to the fact that the material lost vigour after that time, and the development of the insects was affected. These experiments were started in January 1921, and as the temperature in the laboratory was higher than that out of doors, they were especially useful in anticipating development in the field. For example the first moults of the winter larvæ were observed in the laboratory, in the middle of February, and from that date onwards a close watch was kept on the outdoor and field experiments and their progress more or less anticipated.

B. *Outdoor Experiments at Kew.*—For the study of the life history under natural conditions Douglas firs seven years old, infested with *Chermes cooleyi*, were planted in the experimental plot at Kew early in January 1921. Along with these, Sitka and Norway spruces were planted, the whole being enclosed in cheese cloth cages. These experiments enabled the following phases of the life history to be observed :—

(1) The commencement of activity in the first-stage larvæ of the colonici in the spring ;

(2) The study of the individual moulting periods of these larvæ, the behaviour of the adult stem mother (fundatrix spuria), including egg laying and the emergence of the young larvæ of the colonici (Brood I.).

(3) On the appearance of winged forms in May, special experiments upon their migration were started in the cages, from which satisfactory data were obtained, enabling the subsequent behaviour of the sexuparæ (Generation IV.) to be studied upon the Sitka spruce, and the existence of a sexual form to be determined.

C. *Field Experiments.*—Field controls were obtained at Midhurst, Bagshot, Watford and elsewhere, and field notes were made during visits in the winter, spring and summer to plantations of Douglas fir and Sitka spruce in the south and west of England, and during the autumn in Scotland. Further valuable information was received in reports sent in by correspondents, and by the Commissioners' officers situated in various parts of the country.

Laboratory Technique.—The following methods were employed in the preparation of mounts for the microscope :

(1) *Börner's Method.*—The specimens were immersed in 70 per cent. alcohol, and dehydrated through 90 per cent. and absolute alcohols, this process occupying about half an hour. The specimens were then passed into sulphuric ether, to dissolve out the fatty material, and left in this medium for 24 hours. From the sulphuric ether they were brought from absolute, through 90 per cent., 70 per cent., 50 per cent. and 30 per cent. alcohols respectively to distilled water, passed into weak caustic potash, left for 6 hours, and brought into distilled water again. Glycerine was then added slowly until the mixture reached 70 per cent. glycerine, in which solution they were finally mounted.

(2) *Speyer's Method.*—Börner's method, while excellent in many ways, is a very long process. In the case of the larger winged forms the body of the insect has to be opened before preparation, and furthermore glycerine mounts are not permanently satisfactory. Speyer in a paper on the life history of the larch Chermes proposed the following method, which has been employed in the present work.

The living insect is placed upon a glass slide with a cover glass over it, a few drops of sulphuric ether are then run under the cover glass, and the solution allowed to evaporate until the pressure of the glass upon the body of the insect, forces out a quantity of the body contents, which escape through the body wall and the extremity of the abdomen.

The slide is then flooded with absolute alcohol, and the cover glass carefully removed. As sulphuric ether " fixes " the body of the insect, and prevents folding and distortion of the integument the insect is found after the cover glass is removed adhering flatly either to the slide or to the cover glass itself. If it is sufficiently cleared at this stage, it may be mounted at once in Canada balsam, especially when dealing with very minute specimens. If, however, further clearing is desired the specimen may be passed through the alcohols into distilled water, cleared in 2 per cent. potash for three hours, washed in distilled water and passed again through the graduated alcohol to absolute. To the latter a few drops of terpineol are added, the specimen cleared in pure terpineol and mounted in Canada balsam (Xylol).

This process has been found to be much shorter than that of Börner and the final mounts are quite satisfactory and more permanent.

Life History of the Species.

The life history studies of the species in Britain were commenced in the month of November, 1920, the winter brood of Generation III. on the Douglas fir being taken as a starting point. At this time the insects were found only as first stage larvæ which occurred mostly upon the undersides of the needles, their flat bodies closely adpressed to the needle surface, and their setæ inserted through the stomata. They appeared as minute oval-shaped forms, dark brown to black in colour, with a fringe of stout white waxy threads surrounding the body margins, but with only faint traces of white wool upon the dorsal surface. Under the microscope the body was seen to be heavily chitinised, the plates upon the head and thorax appearing smooth and shining. Examination of Douglas firs at Midhurst on November 24th showed a few larvæ situated upon the upper surface of the needles, a condition also found at Watford. The majority of the larvæ were located along the median groove, but some were found upon the general surface. A few larvæ were found settled upon the shoots at the bases of the needles.

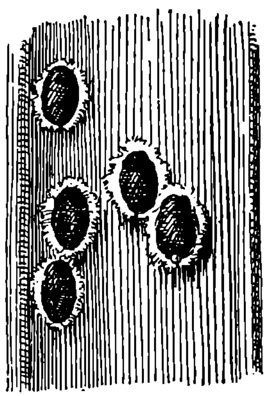

FIG. 7. *C. cooleyi.* Young larvæ of colonici sistentes on needle of Douglas fir. x 12 (original).

On the whole, however, these conditions were unusual, and typically the underside of the needle is the settling place of the winter form. The numbers of larvæ found upon the needles varies greatly. At Midhurst, on November 25th, from two up to twenty were counted on the infested needles, but these numbers were exceeded by the colonici of the summer generations which, at Watford, amounted to over thirty upon heavily infested needles. At the point where the larva was feeding a white blotch appeared upon the needle, and this blotching is evidently characteristic of the attack of the insect upon Douglas fir. The months of November, December and January were passed without any sign of activity on the part of the larvæ. In the warm atmosphere of the laboratory a few larvæ began to feed and moult about the middle of February, and passed through three moults to the adult stage in seventeen days, being found mature, and with a few eggs on March 3rd. This was well in advance of the outdoor conditions, development in the cages in the open at Kew not commencing until March 15th and in the field developing larvæ were found at Knightwood Enclosure in the New Forest on March 17th.

The moulting periods were studied both in the laboratory and in the field, and showed a duration of five to eight days for the second stage, and five to seven days for the third stage, the duration of the stages showing considerable variation in length dependent upon temperature, condition of the needles, and general vigour of the tree. The whole period from the first moult up to the commencement of egg laying was from fifteen to twenty-one days. The larva when about to moult withdraws the setæ from the needle, and is often found upon its back during the moulting process, the skin splitting down the centre of the head and thorax. After each moult the secretion of wax upon the dorsal surface becomes more abundant, this being due to the increase in number of the wax producing glands upon that surface. In the first stage larvæ, those concentrated upon the vertical plates of the head, and the marginal plates surrounding the body, are the most productive. In the later stages the dorsal plates upon the hind margin of the head, the thoracic region, and the first few segments of the abdomen show many wax producing glands.

The third moult reveals the mature stem mother or *fundatrix spuria*. She secretes a moderate quantity of flocculent white wool, under cover of which the eggs are laid. The eggs are oval in shape, about ·25 mm. in length, light yellow-brown in colour, dusted over with fine white powder, and as in other Chermesidæ, are firmly anchored to the needle by a thin white thread. The first eggs were found in the open at Kew on April 1st, laboratory material showing eggs about a month previously. Those stem mothers which were in shaded places on lower branches commenced oviposition first. Forty to sixty eggs were laid by each stem mother, and the period of hatching was from twenty-two to twenty-seven days. The first larvæ hatched out-of-doors at Kew on April 27th (material from Murthly, Perthshire, received about this time showed winter larvæ in the third stage, and stem mothers with a few eggs, but no spring forms). The young larvæ are bright yellow in colour and show a less heavily chitinised integument than the winter form. They seek the new shoots, settling upon them even before the bud scales are properly cast off, as was observed at Watford in May. Early in May the majority of the winter forms were full grown and oviposition was general. On May 14th the young larvæ of the colonici (Summer Brood I.) were in the second and third stages, and nine days later, on May 23rd, a fourth stage larva was found at Parkend, Dean Forest, showing wing pads.

This, the first indication of a dimorphic brood, was confirmed by the observation on May 24th at Watford, of a winged sexupara upon the Douglas fir. Estimates of the numbers of the winged sexuparæ of this generation on the one hand, and the wingless forms upon the other, confirmed the results previously obtained by Gillette and Chrystal in America, namely that about half the individuals develop into sexuparæ, and the rest into the stem mothers of the colonici (Summer Brood I.). The latter were mature and laying eggs at this time (May 24th) (Plate I., Fig. 4). The stem mothers of this brood, which was studied almost entirely from material obtained from Watford, settled down upon the needles of the Douglas fir, and as they produced wool in much greater abundance than the winter form, soon appeared like balls of white wool upon the needles. They commenced oviposition about May 28th, forty to sixty eggs being laid, similar in character to those laid by the winter form. The period of hatching was from twenty two to twenty four days, and on June 22nd the young larvæ appeared. These larvæ settled down on the needles and assumed the winter form.

In America this brood had remained as first stage larvæ throughout the summer, autumn and following winter, until development commenced again in the spring. Later they developed into stem mothers and resumed the cycle upon the Douglas fir, along with the hibernating progeny of the winged migrants of the previous year, from the Sitka spruce. In Britain, individual insects of this brood were observed during the summer of 1921 at Watford. The first observation was made on June 22nd on which date the newly hatched larvæ were settling on the Douglas fir needles. The observations were continued at intervals during July, August, September and October, and it was found that in all cases the larvæ assumed the winter form and remained unchanged.

It is apparent from the above records, that this late summer brood is one and the same with that first observed in November 1920, and that the cycle on the Douglas fir consists of two broods.

The Sexupara Generation.—The nymphs of this generation are reddish brown in colour, but the entire body is lightly covered with a fine white powder. The wing pads are dark brown to black in colour, the legs and antennæ pitchy. The nymphal coat splits down the head and thorax, and the process of emergence takes about ten minutes, the cast skin being left hanging upon the needles. The newly-emerged winged form remains for some hours upon the needles of the Douglas fir before taking wing.

Experiments were conducted at Kew, both in the laboratory and in the outdoor cages, to settle the question of migration, branches of Douglas fir laden with developing winged forms being caged up with Douglas fir, Sitka spruce and Norway spruce. These gave satisfactory results. In the laboratory on June 3rd, sexuparæ were found settling on two- to three years old needles of Sitka spruce; they produced much wool and laid eggs. A few which visited the Norway spruce did not settle down, produced no wool and died without laying eggs.

In the open about the same dates large numbers of sexuparæ settled down freely upon the Sitka spruce, produced much wool and commenced egg laying (Plate II., Figs. 3 and 4). The Norway spruce was left practically untouched. There was no question of the existence in this case of the non-migrant winged forms which Marchal found in *Chermes nüsslini* and *Chermes pini*. The winged forms of *C. cooleyi* were not seeking to settle upon the Douglas fir but were true sexuparæ.

Additional evidence in support of these observations was obtained in the field at Midhurst, Sussex, during the month of June, by the discovery of sexuparæ upon the Sitka spruce which upon careful microscopic comparison with those at Kew were found to be morphologically identical. At the same time a comparison by microscopical examination of the various winged Chermes found upon the Sitka spruce showed that *C. cooleyi* could readily be distinguished from other Chermes by structural characters. Furthermore, a careful search on the Douglas fir at this time revealed no trace of any winged form on the needles, and confirmed the absence of winged non-migrants. These results were valuable in that they supplied more data bearing upon the question of return migration to the Sitka spruce than had previously been obtained in America, and thus established the identity of *Chermes cooleyi* var. *coweni* with the form on the spruce host.

Upon settling on the spruce needles, the winged sexupara secretes much wool from the head and abdominal regions. The wings are arched roofwise over the back, and the eggs are almost completely hidden by the protecting wool. The eggs are elongate and pointed, very small, brown in colour and slightly powdered. The total number laid varies from ten to twenty five, the latter number being found in material from Dunster, Somerset, on June 9th. The Sexuparæ were present in numbers by the end of May, and were settling freely upon the Sitka spruce by the end of the first week in June, the migration finishing by the end of that month.

The Sexual Generation on the Sitka spruce.—The first eggs of this generation were laid on June 3rd and hatched on June 12th Other observations showed a hatching period of from ten to twelve days. The young larvæ are bright red in colour, elongate-oval in shape, and show no wool, the body being smooth and shiny, and sparsely covered with fine hairs. Development takes about a month, and there are five stages separated by four moults, but not all of these have so far been studied in detail. Although the period of development is long, the increase in size from the first larval stage to the adult is extremely small, and is indeed a feature of this generation. Towards the end of the first week in July the first mature sexual form, a male, recognised by its elongate shape, was found at Kew, and a few days later the female form, less elongate in shape, was found on material from Midhurst, together with several males. From this time onwards the study of the sexual generation was somewhat difficult. At Kew, many males were found, but no females, while at Midhurst also, males were numerous, but in spite of the examination of a large amount of material no female was ever found settling and ovipositing. It was soon realised that here lay the real centre of importance in the life history of *Chermes cooleyi* in this country, inasmuch as the failure of the sexual generation on the Sitka spruce precluded the possibility of gall formation, and prevented possibly serious injury being done to that tree. Further study of this problem is necessary but meanwhile the following summary of observations is given.

The mortality in the young stages of this generation is very great, and seems to be connected with the fact that the larvæ which leave the protection of the mother's wool and commence wandering over the needles usually perish. On many of the spruce twigs examined, great numbers of the larvæ in the second and third stages were found lying brown and shrivelled upon the needles. This condition was observed not only in the cages at Kew, but also in the field at Midhurst. Of the mature forms the males seem to be the more numerous, but considering the amount of material examined, even they were comparatively rare. Failure to locate more than a single female cannot at present be explained, the sexual forms by reason of their bright red colour being easily seen, but further research in this matter must be carried out before any more definite statement can be made. In seeking for an explanation for the apparent scarcity of the mature sexual forms the following theories are suggested as a basis for future work. Both at Kew and at Midhurst, numbers of *Acarina* (mites) were found running actively up and down the spruce twigs on which the sexuparæ and their young were feeding. From a knowledge of the predaceous habits of this group in relation to Coccidæ (scale insects) it might be assumed that they were the enemies attacking these larvæ, which were under the shelter of the mother's wool. When mature it is possible that the males by reason of their superior activity, escape injury more readily than the females, which are much slower in their movements. Future observations upon this point will probably open up a problem in animal parasitism, of considerable interest and importance. The rôle played by the *Acarina* in the control of certain Coccidæ is well known, and Tothill in a paper upon the predaceous mite *Hemisarcoptes malus* Shimer, and its relation to the control of the Oyster Shell Scale *Lepidosaphes ulmi* L., points out, that this mite is the most important single factor in the natural control of the scale. Although in this instance the mite is chiefly predaceous upon the eggs, it has been recorded both from Europe and America as preying upon the growing and mature insects.

The following extract from Marchal's account of the sexual generation of *Chermes pini*, is also noteworthy in this connection. Discussing this generation he writes,* " The evolution of the sexuales takes place in a most complete and regular fashion upon *Picea orientalis*. The young larvæ are protected and kept in place by the woolly secretion of the sexuparæ, which is more abundantly produced upon this species (*P. orientalis*) than upon the Norway spruce (*P. excelsa*). At the same time, even upon *Picea orientalis* a large number of sexuales become dispersed while still immature and thus leaving the wool which shelters them, they soon perish. Others again show arrested development in one stage or another, and perish without its being possible to assign any definite cause of death. This mortality, the percentage of which varies according to the tree, or even the twig concerned, cannot be attributed in every case to physiological feebleness in the sexuales, by reason of the rudimentary condition of the sexual reproduction in *Chermes pini*. It is due in many cases to the agency of natural enemies of the Chermes, and particularly to the little acarinids, which easily pass unnoticed on account of their minute size, and often to the presence of parasitic disease. Upon the Norway spruce for which *C. pini* is much less well adapted than for the Oriental spruce, the sexuales perish in enormous numbers during development, but a certain number of females reach their full development upon these trees."

The Stem Mothers and Gall Generations.—Owing doubtless to the failure of the sexual generation no young larvæ of the stem mothers were observed on the Sitka spruce at Kew and Midhurst. Accordingly the

* **Paul Marchal. Cont. à l'étude de la biologie des Chermes. Ann. des Sci. Nat. Zool. IXe Serie, pp. 256–257**

question of the existence of the spruce generations was approached from another standpoint, and a search was made in the field for typical galls of *Chermes cooleyi* on Sitka spruce, and for the winged forms migrating from Sitka spruce to Douglas fir. The search for these was carried out over an extended period lasting from the early spring to late summer, so that if *C. cooleyi* galls existed, their period of opening, together with the migration of the winged forms from Sitka spruce to Douglas fir was amply covered.

No galls on Sitka spruce approaching the *C. cooleyi* type were found, although many galls were examined from nearly all parts of the country where *C. cooleyi* occurs. In every case the galls examined were either those of *C. abietis* or *C. strobilobius*. The variation in size and form of the galls was considerable, being dependent on the size and vigour of the shoots attacked. As in America the condition of the shoots had been found to play an important part in modifying the general shape of the galls of *C. cooleyi*, particular attention was paid to this point in determining the species responsible for the gall concerned. In every case, however, the general shape and manner of growth of the galls remained fairly true to the *C. abietis* and *C. strobilobius* types, and differed markedly from that of *C. cooleyi*. Furthermore, an examination of the stem mother which had given rise to the gall, confirmed the identification arrived at.

At the same time observations made on Douglas fir in various parts of England and Scotland showed no trace of winged migrants, and even at Midhurst, where Douglas fir and Sitka spruce occur in close proximity, careful observation during June, July, and part of August revealed no sign of this generation.

These observations at Midhurst were the more important in that sexuparæ of *C. cooleyi* were numerous on the Sitka spruce, indicating a successful migration from the Douglas fir to the Sitka spruce, and further showing that the distance between the two hosts of *C. cooleyi* played no part in the failure of the migration of the winged forms (if they occurred) from the Sitka spruce to the Douglas fir. In this connection, observations made in Vancouver upon the migration of this species showed that the winged forms from the Sitka spruce would in many cases fly for a considerable distance, and settle upon isolated Douglas firs.

The evidence collected so far then would appear to confirm the failure of the sexual generation upon the Sitka spruce, and to show that in Britain the life cycle of *C. cooleyi* is incomplete, lacking the gall-forming generations on the spruce. Accordingly the life cycle of *C. cooleyi* in Britain, may be graphically represented as in Fig. 6, p. 7.

Distribution of Chermes cooleyi.

In America.—Since Gillette's discovery of this species in Colorado in 1903, it has been found on Douglas fir in California, is known to be widely distributed on both Douglas fir and Sitka spruce in the coast region of British Columbia, and in 1917 its galls were reported on Colorado blue spruce (*P. pungens*) from New Haven, Conn., U.S.A.. No further data are available as to whether it is increasing, to what extent it occurs, or whether it is appearing in new localities.

In Britain.—Although *Chermes cooleyi* was first recorded in this country in 1913, there is reason to suppose that its introduction took place considerably before that date. It is almost certain that it was introduced into this country on nursery stock, indeed no other medium of introduction is possible as the entire life cycle of the insect is confined to the green portions of the plant.

In England the insect is more generally distributed in the south and west, than in the midlands and north. In Scotland there is one record of its occurrence at Dawyck in Peeblesshire, and three from Perthshire, namely Callander, Murthly and Dunkeld. It is interesting to note that the insect apparently does not extend further north, nor has it been found on the west coast. There are no records of its occurrence in Ireland.

Mode of Dispersal.

The study of this aspect of the *C. cooleyi* problem has been a matter of considerable difficulty, and may be considered under two heads:

(1) *Direct Dispersal.*—By means of winged individuals flying from Douglas fir to Sitka spruce, and *vice versa*;

(2) *Indirect Dispersal.*—By transport on nursery stock, or by means of wind, birds, insects, &c.

(1) *Direct Dispersal.*—So far observations have shown no winged form from Sitka spruce settling upon the Douglas fir, during the course of the life cycle. This indicates that the gall stage upon the Sitka spruce does not develop in this country, and in consequence precludes the possibility of dispersal by winged migrants. No dispersal of *C. cooleyi* therefore takes place by migration of the insect from the spruce to the Douglas fir.

Two other possible means of direct dispersal remain namely, (1) In crowded plantations where the branches of the trees are closely interlaced, the young may crawl from one tree to another, and infection may be spread throughout the whole area; (2) The possible presence of non-migrating winged forms in spring, as described by Marchal in the case of *Chermes pini* (see p. 8). Again, the absence of any winged forms on the Douglas fir, and the strictly limited, and truly dimorphic character of the first colonici summer brood rules out any possibility of dispersal by such means. That is to say that no spread of *C. cooleyi* from Douglas fir to Douglas fir takes place by the action of the Chermes itself. The dispersal of the insect must therefore take place by indirect means.

(2) *Indirect Dispersal.*—That the insect is conveyed from one part of the country to another on nursery stock cannot be doubted. This mode of dispersal is the means of transporting the insect not only from one nursery to another, but from the nursery into young plantations, and gardens, and thus in many cases establishing new centres of infestation in districts which have been free from the insect hitherto. The patchy nature of the distribution of the insect in this country clearly suggests dispersal by this means.

As regards other means of infection, the part played by the wind in the dispersal of insects has long been recognised, and the following records from the American literature are of interest in this connection. Webster, for example, regards wind as one of the most important agents in the spread of the San José Scale *Aspidiotus perniciosus* Comst., in the orchards of the middle west of America. Infested trees, he states, planted in clean orchards soon infect those adjoining, the wind being the principal carrier, as is shown by the infestation proceeding in the direction of the prevailing wind.

Felt, writing of the Elm Scale, *Gossyparia spuria* Modeer, and the Woolly Maple Scale, *Pulvinaria innumerabilis* Rath., also mentions the importance of wind as a carrier of infection.

In the case of *Chermes cooleyi* the following recent observations are of interest. During a visit to Dunster, Somerset, in June last, it was found that young Douglas fir seedlings growing under the shade of the mother trees, were infected by needles which fell down from the mother tree with the Chermes still upon them The Chermes eggs, protected by the woolly covering, remained quite fresh, even after the fallen needles were brown and dead. It was also observed that infected needles were wind-borne from old trees to young ones standing at a little distance. Examples of this occurred in a wood where there were several large trees of Douglas fir infected with Chermes, with young natural regeneration below. The wool of the Chermes along with the eggs, was found in several cases caught upon branches, one of which was not that of a Douglas fir, but of a species of *Cryptomeria*. In young plantations also it was proved that infested trees affected healthy ones in close proximity to them, even where their branches were not actually touching, and in the same place, these young trees had also been infected from older and taller trees near by.

With respect to the part played by birds and mammals, in the dispersal of the insect, no direct evidence has been obtained in the present case, and indeed examination of the literature shows how little is known of this phase of the problem.

The following notes on the dispersal of certain species of scale insects by animals, taken from Felt's " Insects affecting Park and Woodland Trees," throw some light upon the subject, and indicate the lines of inquiry which might be followed in the present case.

Writing of the Woolly Maple Scale, *Pulvinaria innumerabilis* he calls attention to the fact that birds, insects and even spiders, are often unconscious agents in the spread of the scale, owing to the active young crawling upon them. In the case of the Elm Scale *Gossyparia spuria*, he says that its rapid distribution in cities is probably largely due to the agency of birds, particularly the English sparrow. Again, referring to the San José Scale, *Aspidiotus perniciosus*, he states that men and horses working in infested orchards, are often responsible for the carriage of the scale from one part to another.

CHAPTER III.

The Sexual Generation in the Chermesidæ.

The existence of a sexual generation in the Chermesidæ was first discovered by Blochmann in 1887, in *Chermes viridis* Ratz. He studied the generation in some detail, and described pairing and egg laying. He found the males were much more active than the females, the latter usually hiding themselves away in a bark crevice or under a bark scale, soon after pairing. For this reason the males were found in greater numbers than the females. He was uncertain as to whether one or more fertilised eggs were laid by the female, but it is now known that only one egg is laid.

Since Blochmann's time the sexual generation in the European species of Chermesidæ has been studied by Cholodkovsky, Nüsslin, Börner, Marchal and others, and as a result of their researches the European species of the family may be divided into groups according to the behaviour of the sexual generation as follows:—

A.—Species in which a complete sexual generation is normal; the female after pairing lays a single fertilised egg under a bark scale. From the egg hatches the young larva of the stem mother generation on the spruce.

B.—Species in which the sexual generation does not usually develop, and consequently no stem mother and no gall generation occur on the spruce.

C.—Species in which the life cycle is curtailed and confined to the primary host, the gall generation being developed from a parthenogenetic source.

As examples of Group A, the following species may be cited: *Chermes viridis* Ratz. *Cnaphalodes strobilobius* Kalt. *Chermes pectinatæ* Chol. *Chermes sibiricus* Chol. *Chermes nüsslini* Börner, and *Chermes pini* var. *orientalis* Dreyfus.

In Group B may be cited *Chermes piceæ* Börner, *Chermes strobi* Hartig, and probably *Chermes cooleyi* Gillette in Britain.

In Group C, Cholodkovsky recognises two species *Chermes abietis* Kalt. and *Cnaphalodes lapponicus* Chol. as representing this type of life cycle.

The Incomplete Life Cycle and related Phenomena.

Nüsslin and Carl Börner working on *Chermes piceæ* Ratz. described the sexual generation as impotent. In 1908, however, Börner suggested that the name *Chermes piceæ* had been applied to two distinct species, *C. piceæ* Ratz., proper, and another which he described and named *Chermes nüsslini*. In 1913 Marchal studying the life histories of these two species, found that while *C. nüsslini* passed through a full cycle of five generations upon *Picea orientalis*, and *Abies* spp., *C. piceæ* on the other hand confined its cycle to the intermediate hosts *Abies pectinata* and *Abies Nordmanniana*. In the same paper Marchal showed that the species *Chermes pini* Börner, consisted of two biological races, one of which he called *Chermes pini* var. *orientalis* Dreyfus, and the other *Chermes pini*. In his studies of the life histories of these species, he found that the former, a native of south eastern Europe (Caucasus), passed through a normal two-year life cycle of five generations on *Picea orientalis* and *Pinus sylvestris*. The latter, however, confined itself to the pine, and no gall generation appeared.

In the case of *Chermes strobi* Hartig, Marchal also found an incomplete life cycle, but succeeded in tracing the sexuparæ to *Picea nigra* Link., the black spruce, a native of eastern North America. From these sexuparæ he succeeded in rearing mature sexual forms which however proved to be all females, and the cycle was interrupted in consequence. Marchal had already noticed this phenomenon of unisexuality, in the life history of *Chermes pini*, and he called it "spanandry" (scarcity of males). He considered it so important that he made a special study of it in these two species.

In the case of *Chermes pini* he found that even when large numbers of females were settling on the Oriental spruce the males were so rarely present that the sexual generation was almost entirely non-productive, and that furthermore even when a male was present, and pairing took place, the fertilised egg did not develop, and the life cycle came to an end In the case of *Chermes strobi* upon the black spruce his results were even more definite, no males appearing in this case. From these results Marchal concluded that climatic factors, the condition of the host, and the forest conditions generally, were probably the underlying causes, which, affecting the species in different ways, determine for any given locality whether a species shall pass through the normal life cycle, or show a retrograde form of cycle with the sexual generation non-fertile, and the life cycle restricted in consequence to the secondary host

The Sexual Generation in America.

It is significant that the American literature on *Chermes* contains no reference to sexual generations. That such generations exist in America must be regarded as certain, and confirmation of their occurrence, and a study of their behaviour will throw light on several interesting problems. Whether for example, there exists in *C. strobi* in America, a race comparable to *C. pini-orientalis* in Europe, and whether the sexual generations of such species as are common to both continents, *e.g.*, *C. viridis*, behave in the same, or in a different manner, are points not only of scientific interest, but of considerable practical importance. Again, if in *C. strobi* a race equivalent to *C. pini-orientalis* exists on *Picea nigra* in America, as from the occurrence of a gall, we have every reason to believe is the case, there are good grounds for assuming that the factors governing the existence of this race, and therefore determining the success of the sexual generation, are climatic. For example, the dry hot summers of eastern North America probably partly account for the successful production of a fertile sexual generation. In support of this it may be remarked that in Britain, the dry, warm summer of 1921 was very favourable to the successful migration of the *Chermes* generally, and doubtless had some effect upon the generation following. As far as *C. cooleyi* is concerned, and for reasons already given, it is practically certain that a sexual generation exists in America. So far no evidence exists, which will enable us to explain the failure of this generation in Britain, but that it cannot be attributed to "spanandry" is certain, the males being found to be much more numerous than the females, a condition which is the reverse of that which Marchal's term denotes.

CHAPTER IV.

Relations of Chermes cooleyi to the Forest.

In America, Gillette does not record any extensive damage to the Sitka spruce as a result of the attack of *Chermes cooleyi*, and does not appear to have made a special study of it from that point of view. Chrystal's work in Stanley Park, Vancouver, on the other hand, showed that the insect may be a serious enemy of this tree, as the following account of a special enquiry into the general condition of the Sitka spruce in that area shows. In this survey it was found that in places, Sitka spruces of all ages, and varying in height from ten to over a hundred feet, had suffered severe attack by *C. cooleyi*. On heavily infested trees the galls were found upon the leading shoots of all the side branches, the attack progressing from the lower branches upwards (Plate I., Fig. 2). In the majority of cases the entire shoot was destroyed, and as a result of many observations on trees which had suffered for a number of years, it was found that they showed marked diminution in the vigour of the new shoots and corresponding reduction in size of the galls produced. As the old galls remain on the bare, dead shoots for some years after the attack, the steady weakening of the new growth, and the reduction in size of the galls are very pronounced. It was estimated that *Chermes cooleyi* was the primary insect enemy of about 75 per cent. of the Sitka spruces, no account being taken, except in one special instance referred to below, of any predisposition to insect attack on the part of the spruce, owing to fungus disease or physiological causes. The above percentage figure is noteworthy inasmuch as there were two other insects present as factors in the situation, and the question as to which of the three was the primary enemy was carefully investigated.

The first of these was the Green Spruce Aphis *Myzaphis abietina* Walk., a species which feeds upon the needles of the spruce, and may cause serious defoliation of the tree. This insect was studied in England by Theobald in 1914, and recorded as destructive to several species of spruce, under park conditions. In 1915 Prof. Wilson, of Corvallis, Oregon, U.S.A. recorded the aphis as harmful to Sitka spruce in the Pacific Coast region. In Britain during the last few years, the importance of this insect as a forest pest has been more and more widely realised, and the following remarks are therefore of interest.

The spruce aphis was studied both in Stanley Park, Vancouver, and in the Beacon Hill Park, Victoria, Vancouver Island. In the latter area it was proved that several Sitka spruces had been killed by this insect, and that others were in a serious condition. In Stanley Park, however, it was found that spruces which had been attacked solely by the aphis, a few years before the date of the enquiry, were recovering their vigour in most cases, and would probably regain their healthy condition. On the other hand, in the case of trees attacked both by aphis and by *C. cooleyi*, although the aphis was a powerful secondary factor in weakening the trees by hastening their defoliation and thus making recovery doubtful, the Chermes was obviously the primary enemy.

The second insect enemy in Stanley Park was a bark beetle *Dendroctonus obesus* Mann., which was found locally prevalent in certain areas on large Sitka spruces. These spruces were heavily infested by *C. cooleyi*, but there was little doubt that the attack of the Chermes was induced by adverse soil conditions, which had weakened the trees. The Chermes was undoubtedly the first insect invader here, as dying Sitka spruces heavily galled by Chermes, but so far unattacked by the beetles, were common in the neighbourhood of beetle-infested trees, showing that the beetle attack was a secondary one and only beginning to spread from tree to tree.

Several European workers have demonstrated the importance of the damage done by certain species of Chermes in weakening the host tree, and thus rendering it subject to bark beetle attacks. Nüsslin quoting observations made by Oberförster Geutner in Silesia (1843), speaks of the attacks of *Chermes piceæ* (?*nüsslini*) on silver fir sixty to seventy years of age. These trees which had at one time been growing vigorously were so reduced by the attack of the Chermes, that the bark became loosened, and injurious bark beetles, which had not hitherto been observed, appeared to complete the work of destruction.

As regards the damage done to the Douglas fir by *C. cooleyi*, Gillette states that although he has seen trees in parks discoloured as a result of the presence of the insect, he has never seen a tree killed by it. In the survey of Stanley Park, attention was also paid to the condition of the Douglas fir in relation to Chermes attack, and the final results failed to show any evidence that *C. cooleyi* was a dangerous enemy of the tree in that region. It must be stated however that the experience gained in America refers only to older trees, and that the effects arising from the attacks of the insect in nurseries and young plantations have not been studied in that country.

In Britain, as already stated, the gall stage of *C. cooleyi* on the Sitka spruce is so far unknown, and the importance of a study of the sexual generation, to establish the presence or absence of the gall stage on the Sitka spruce is again emphasised.

Further, a study of the sylvicultural conditions of the Sitka spruce and their relation to Chermes attack in general would undoubtedly yield results of the greatest interest, as there is no doubt that soil and climatic conditions, the presence of fungus and other diseases, the origin of which may or may not be specifically known, play a large part in the initial process of weakening the tree and rendering it susceptible to the attacks of Chermes. In otherwise healthy plantations at Bagley Wood, Oxford, and in the Forest of Dean, an examination of patches of young Sitka spruce badly galled by *Chermes abietis* and *Cnaphalodes strobilobius* indicated that the soil conditions played a decisive part in predisposing the trees in these patches to severe attack.

In the case of the Sitka spruce in Stanley Park, although no detailed observations were made as to the physiological conditions, the opinion was formed that the unhealthy state of the spruce in that area was favourable to *C. cooleyi*, and made rapid spread of the insect possible.

Too much stress then cannot be laid upon the importance of collecting data from sample plots, with a view to the close study of the sylvicultural requirements of this tree. Such studies aided by the further knowledge of the life history of *C. cooleyi* will prove more valuable than any attempts at artificial control measures, which, while feasible in the case of isolated trees in parks and gardens, are usually quite out of the question in the forest.

As regards the Douglas fir, Henry and Flood in their paper on the genus state that *C. cooleyi* has not so far been found in Britain on the Colorado Douglas fir, *P. glauca*, although several records are published in America of its occurrence on that tree. Henry strengthens his evidence on this point by stating the remarkable fact that in plantations composed of both the Oregon and the Colorado Douglas firs in close association with each other at Bagley Wood, Oxford, and East Liss, Hants, the Chermes which occurs on the Oregon Douglas fir has not spread to the other species. This question has been studied in the course of the present investigations, and the results tend to confirm Henry's observations both as regards the plantations he specifically mentions, and many other areas. *C. cooleyi* does, however, occasionally settle on the Colorado Douglas fir, but is never found in numbers on that tree.

The reasons for this comparative immunity of the Colorado Douglas fir from attack by *C. cooleyi*, are unknown, but the following suggestions may be offered :—

(1) The presence of a continuous layer of thin wax on the upper and lower surfaces of the needle, coupled with a thick walled epidermis, in *Pseudotsuga glauca*, may prove to be sufficient protection, preventing the Chermes feeding on the needles.

(2) Henry and Flood in the above-mentioned paper, describe two kinds of oil obtained from the needles of the Oregon and Colorado Douglas firs respectively, namely geraniol from the former, and pinene from the latter. It is possible that the presence of the pinene in *P. glauca* may be distasteful to the Chermes, and render the needle immune from its attacks.

Feeding Habits and Nature of Injury.

Feeding Habits.—Generally speaking, *C. cooleyi* occurs upon the undersides of Douglas fir needles. The larvæ are most closely congregated in the lower and more shaded parts of the tree, especially the parts of the branches nearest the main stem. This, however, is not always the case, as plantations of Douglas fir in the Forest of Dean showed heavy infestation of Chermes almost to the tops of the trees, but it is uncertain whether in this case the density of the stand did not play some part in rendering the tops more suitable from the point of view of shade, and thus encouraged the insects to settle there. In most cases which have been investigated, the Chermes were more prevalent upon the lower and middle branches, and in young trees on the needles of the stem itself.

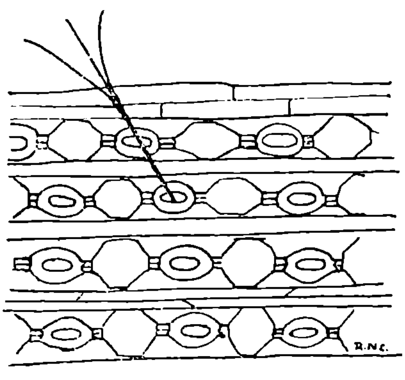

FIG. 8. *C. cooleyi*. Surface view of under side of Douglas fir needle, showing entry of larval stylets into the tissue, through a stoma. x 375 (original).

A study of the feeding habits of the Chermes has shown that, when lodged on the underside of the needle, the larvæ invariably insert their stylets into the tissue through the stomata (Fig. 8). It was found in every case examined that after passing through the epidermis, the stylets travel almost directly to the vascular bundle. They pass through the endodermis of the bundle, and seek the albuminous cells adjacent to the phlöem which contain highly organised food materials (Fig. 10). When lodged on the upper surface of the needle, the larvae apparently find no difficulty in penetrating the thick-walled epidermal layer, the stylets passing through this in the region of the common wall between two cells traversing the inner walls, and thence passing to the vascular bundle (Fig. 9). The stylets frequently pass through the cell walls on their way through the tissue, but quite as often make their way between the cells, especially when traversing the endodermal layer, as several specimens show.

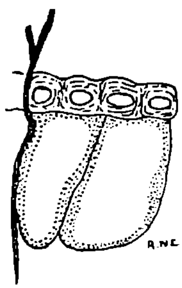

Fig. 9.

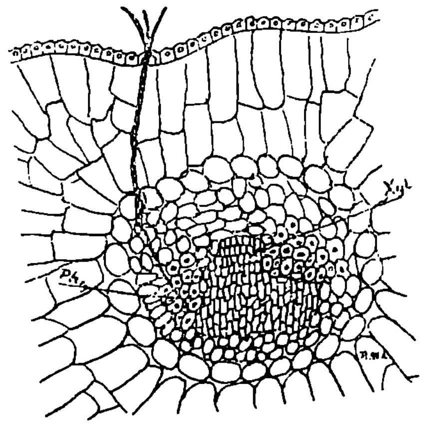

Fig. 10.

FIG. 9. *C. cooleyi*. Transverse section through upper surface of Douglas fir needle, showing larval stylets passing through the thick-walled epidermis. x 375 (original).

FIG. 10. *C. cooleyi*. Transverse section through Douglas fir needle showing larval stylets passing through a stoma into the needle tissue and seeking the albuminous cells adjacent to the phlöem of the vascular bundle. Xyl=xylem. Ph=phlöem. x 106 (original).

In this connection it is interesting to note that Hargreaves found in the Greenhouse White Fly, *Aleyrodes vaporariorum* West., that the larval stylets sought the phlöem cells of the vascular bundle, and his description of the passage of the stylets through the leaf tissue applies to *C. cooleyi* in several particulars.

Nature of Injury.—Trees severely attacked by *Chermes cooleyi* show the needles much bent and wilted, presenting a similar appearance to those of *A. Nordmanniana*, attacked by *Chermes nüsslini*. The injured needles are covered with white blotches, a feature not uncommon in the case of the feeding of other forms of Chermes on the needles. *C. cooleyi* on the secondary host is confined to the needles, shows no tendency to become a bark feeder, and does not cause any deformation of the buds such as occurs in the case of *Chermes piceæ* var. *bouveri*. In consideration of the effect of the feeding of the insect upon the Douglas fir, it may be stated at the outset that the amount of research done upon this question so far does not justify any definite conclusions being drawn, but recent research shows that in older plantations the feeding of *C. cooleyi* on the needles does not seem to have a serious effect upon the general vigour of the trees. Even in heavily infested plantations except for the abundant wool secreted by the insect, nothing abnormal is noticeable in the health and appearance of the trees.

Further investigation into the effects of *C. cooleyi* on trees growing under unfavourable conditions, may reveal this Chermes as a dangerous pest, but so far this has not been established. No sickly or dying Douglas fir trees have been found either isolated or in plantations, the condition of which could be directly attributed to the attacks of *C. cooleyi.*

In dense woods of Douglas fir it was found that *C. cooleyi* occurred chiefly on the trees near the margin and was not present to any appreciable extent in the centre of the plantation.

In young plantations, say, from ten to twenty years of age, which had been badly attacked by *C. cooleyi* for some time, it was found that the trees resisted the attacks of the Chermes, which had considerably decreased in numbers. This has been noticed at Swinley, Berks., at Surrey Hill, Bagshot, and in a plantation near Murthly, Perthshire. The most critical stage in the life of the Douglas fir with respect to injury by Chermes, appears to be in the nursery and just after a plantation is formed. It is at this time more than any other that the baneful influence of the Chermes attack is to be feared, and for this reason further study of the effect of the attack on young trees is recommended. With regard to this aspect of the Chermes problem Steven has stated the case generally in his paper on the spruce and larch species, but so far as one can see from a study of the literature of the group in this country, no special attention has been given to it by other writers. It has not been possible to go fully into this matter in the present investigation. The problem is one which will require several years for its solution, and involves careful sifting of data in order to ascertain to what extent *C. cooleyi* affects the health of Douglas fir in the nursery, and whether the attack of the insect has any retarding influence upon the young plant when first put out in the plantation.

Types of Injury to the Secondary Host Trees in the Chermesidæ.

These may be divided into the following groups :—

A. Leaf-feeders.

B. Bark-feeders.

C. Gall-producers.

A. *Leaf-feeders.*—As a rule injury to the tree by these forms is not considered serious. Cholodkovsky remarks, however, that *Chermes funitectus** Dreyfus may cause serious damage to a species of hemlock (*Tsuga*) by feeding upon the needles. Chrystal has

* *Chermes funitectus* Dreyfus, was discovered in Germany in 1888 on *Tsuga canadensis.* Cholodkovsky (1915) considers it to be synonymous with *C.* (*Dreyfusia*) *nüsslini* Börner. Marchal (1913) has expressed some doubt as to the accuracy of Dreyfus' identification of the host tree of the species as *Tsuga canadensis.*

observed a Chermes on western hemlock *Tsuga heterophylla* in Stanley Park, Vancouver, which agreed with the original description given by Dreyfus of his species *C. funitectus*. This species was found causing considerable damage to the western hemlock and in a few cases large trees were observed to have been completely defoliated by it. This species fed upon the bark of the young shoots quite as much as on the needles, at the bases of which the insects were most often found, and this habit was probably the main cause of the damage done.

B. *Bark-feeders.*—*Chermes nüsslini* Börner, *Chermes piceæ* (Ratz., Börner).

Previous to Börner's paper of 1909, in which he treated *C. nüsslini* and *C. piceæ* as distinct species, the Chermes found on silver firs of all ages were treated, both from the biological and the systematic standpoint as one species, *C. piceæ* Ratz. It is uncertain therefore to which of these species Nüsslin referred in his work on the silver fir Chermes, an insect he regarded as a very destructive pest, being supported in this opinion by Börner. Probably, however, *C. nüsslini* was the species chiefly concerned in the attacks on younger trees, and on the young shoots of older trees, *C. piceæ* being mostly confined to the main stem and larger branches.

Cholodkovsky in a recent paper, stated that he found *C. nüsslini* causing much damage to young *A. Nordmanniana* in Switzerland. The attacks of the insects caused extensive withering of the young shoots and thin branches in trees of all ages. The younger trees were often completely destroyed, but older trees did not suffer so badly.

Boas in Denmark, investigating the injury to silver fir caused by *Chermes*, stated it as his opinion that the two species, *nüsslini* and *piceæ*, were not distinct, but merely biological races of a single species. He found that the soil conditions played a large part in determining the severity of attack, that in good soil the attack gradually diminished, but that where the soil was poor it was continued over a long period, and finally caused the death of the trees. Kotinsky in America, records *C. piceæ* as killing old trees of Balsam fir (*A. Balsamea* Miller) at New Haven, Conn., U.S.A.

Very little work has been done on these species in Britain, but investigations made in the silver fir plantations at Inverliever, Argyllshire, this summer, showed that *C. nüsslini* was apparently responsible for much damage to the silver fir in that locality. It is believed, however, that there exists at the same time in that area, a problem of soil conditions, which when fully investigated in conjunction with that of the Chermes will throw much light upon the conditions under which this species can be a serious enemy to young silver fir in this country.

Chermes viridis and *Cnaphalodes strobilobius.*—These two species, in the opinion of Börner and others, may cause much damage to the larch, by feeding on the bark of that tree.

Chermes pini Koch.—This species is well known as an enemy of young pines, both in this country and in central and southern Europe.

Chermes strobi. Hartig.—The injuries caused to the Weymouth pine, *Pinus Strobus*, are well known both in Europe and America.

C. *Gall-producers.*—This type of injury to the secondary host, was first described by Cholodkovsky in 1903 for *Chermes piceæ* var. *bouveri* Chol., on *Abies nobilis* var. *glauca.* It was found in this species that the sucking of the insects caused swellings upon the stem and young shoots. This injury was considered by Cholodkovsky to be a form of gall production similar to that on the primary host (*Picea*), but Nüsslin, while admitting that the cause of the malformation was identical in the two cases, stated that morphologically the two types of gall were distinct.

CHAPTER V.

Control Measures.

NATURAL ENEMIES.

Cholodkovsky mentions the following natural enemies of the Chermesidæ. Hymenopterous parasites of the family *Chalcididæ.* Dipterous larvæ of the family *Syrphidæ* or hover flies, Coleopterous larvæ of the family *Coccinellidæ* or ladybirds, Hemipterous larvæ of the family *Anthocoridæ* or tree bugs, various acarids or mites, and casual enemies such as the caterpillars of sawflies and moths, which destroy the Chermes while feeding.

Escherich quotes Keller,* on the importance of the Arachnida (spiders and mites), in the control of Chermes and allied insects. Keller found that the winged gall forms of *C. strobilobius* on emerging from the galls, were destroyed in large numbers by hunting and web-spinning spiders belonging to various genera. He furthermore observed that the Phalangidæ or harvestmen, arachnids closely allied to the true spiders, sought out and destroyed the egg-laying winged females of *C. strobilobius*, devouring the egg mass together with the softer portions of the hind body of the insect. Thus he states that one female phalangid was responsible for the destruction of a considerable number of the Chermes, and their eggs.

In the case of *C. cooleyi* in America, Gillette records syrphid larvæ attacking the insects when exposed on the needles, but states that he has never seen them attacked, when sheltered in the gall chambers. In Stanley Park, however, syrphid larvæ were observed on several occasions feeding upon the Chermes pupæ in the gall chambers, as well as upon the forms exposed on the needles.

Gillette also records the yellow and black ladybird beetle, *Harmonia picta* Drury, as feeding on this species on Douglas fir. In Stanley Park the webs of numerous spiders were observed on affected shoots, but no detailed records of their relations to the Chermes were made. There the most numerous of all the predaceous enemies were the syrphid larvæ, which were often present in large numbers. In Britain very few natural enemies of *C. cooleyi* have been seen.

ARTIFICIAL CONTROL MEASURES.

A. *In Plantations.*—There are no means at present by which *Chermes* attacks can be directly controlled in established plantations. The use of sprays has been recommended by some authorities, but the cost of this operation would be very high, the operation itself

* Keller, C. Untersuchungen über die forstliche Bedeutung der Spinnen. Schweiz. Zeit. für Forstwesen. 1883–1881.

would be a difficult and tedious one, requiring repetition to ensure good results, and is from the forester's point of view impracticable. On the other hand, while direct control is practically impossible much can be done in an indirect way, to reduce the effects of the insect's attacks. *Chermes cooleyi*, and in fact all the *Chermes* species, are usually most injurious in plantations where the soil conditions are unfavourable to the species planted, and there are good reasons for thinking that this will ultimately be accepted as one of the fundamental principles governing Chermes attacks. Accordingly in plantations where *C. cooleyi* infestation is severe, the first step towards reducing it should aim at the improvement as far as practicable of the soil conditions by drainage or other means. Again in the formation of plantations, *Chermes* attacks can be prevented by selecting Douglas fir only for those portions of an area which are clearly suited to its requirements.

B. *In Nurseries : Spraying.*—Infested beds of Douglas fir may be cleared by means of a nicotine or paraffin spray. If the operation is to be successful, however, it is essential that a fine force sprayer should be employed, and that the spray used should be thoroughly emulsified. Care must be taken to see that the men employed in the operation pay special attention to the undersides of the needles, where the majority of the *Chermes* feed.

Formulæ for two efficient sprays are as follows :—

(1) *Nicotine Emulsion.*

Nicotine, 98 per cent. ...	¾ oz. to 1 oz. (fluid measure).
Soft soap	½ lb.
Soft water	10 gallons.

Dissolve ½ lb. of soap in 4 pints of boiling water, allow the solution to cool, and then add ¾ oz. (fluid) of 98 per cent. nicotine. Stir well, and keep in a well-corked bottle or jar. To use, take 1 (fluid) oz. of the concentrated solution, and make up to 1 pint with soft water.

(2) *Paraffin Emulsion.*

Paraffin	2 pints.
Soft soap	1 lb.
Soft water	10 gallons.

Dissolve the soft soap in one gallon of boiling water, and while the solution is still hot, add the paraffin. Churn the mixture very thoroughly. Before use make up to 10 gallons with soft water, and again mix thoroughly.

Dipping.—Young plants may be dipped in a solution of 1 lb. soft soap to 1 gallon of water, just before despatch to the planting area. This method has already been used by the Forestry Commission, and has proved effective in destroying the Chermes. It has not, however, proved entirely successful from the forester's point of view, as treated plants tend to suffer from heating in transit. It is probable that this was due to lack of sufficient drying after dipping, but no definite information can be given on this point. On the whole, the measure is only to be recommended where no other means are available.

The Control of Chermes cooleyi in Parks and Gardens.—In the case of individual trees in parks and gardens, where the Chermes attack is so severe as to weaken the tree or render it unsightly, spraying is to be recommended as a practical measure. Suitable sprays for the purpose, have already been mentioned above. From the study of the life history of the Chermes on the Douglas fir, it has been found that the best time to apply the spray is during the month of March, when the winter larvæ are in their second and third stages, in which, owing to their tender condition and lack of woolly covering, they are more vulnerable than at any other period. Spraying should be repeated once or twice at intervals of a week or ten days.

Fumigation of Nursery Stock infested by Chermes.—The question of the control of Chermes on nursery stock by fumigation with hydrocyanic acid gas, was touched upon by Steven in his work on the spruce and larch Chermes, and a recent paper by Sasscer and Borden in the United States deals with the use of the same fumigant in the control of greenhouse pests, In the course of the present investigation an enquiry was commenced into this method of control, and experiments were started based upon the results already obtained by the authors mentioned above. This work has, however, been interrupted, and the results are so far not sufficiently definite to warrant inclusion.

Summary of Results.

(1) *Chermes* (*Gillettea*) *cooleyi* Gillette, hibernates upon Douglas fir as a first stage larva. Development commences in early spring, and the first mature stem mothers may begin oviposition early in April. This brood is dimorphic, about half of the young developing into winged migrants, and the rest into wingless forms on the Douglas fir.

(2) The winged migrants mature about the beginning of May, and fly to the Sitka spruce, settle on the needles, and lay a small number of eggs. From these eggs hatch the larvæ of the sexual generation. This generation has not hitherto been described for *Chermes cooleyi* either in Europe or America.

(3) Both male and female sexual forms have been found in Britain, but they have failed to produce offspring.

(4) No gall stage on the Sitka spruce has been found, and no winged gall form has been observed settling on the needles of the Douglas fir.

(5) There are two broods on the Douglas fir, an early summer brood, and a late summer brood which remains on the needles as first stage larvæ, over the winter.

(6) The species is widely distributed in the south and west of England, and is recorded from a few localities in the midlands and north. In Scotland its distribution is local, and it is so far unknown in Ireland. The species has been present in the country for a number of years, and was undoubtedly introduced on nursery stock, by which means it is now very largely spread. Wind dispersal is, however, known to occur, and other means of infection are not unlikely.

(7) The insect has not so far proved a serious enemy of the Douglas fir in established plantations. In consequence of its being confined solely to the needles, it has not that capacity for damage which is possessed by *Chermes* (*Dreyfusia*) *nüsslini* Ratz. on the silver fir.

(8) The importance of the Chermes as an enemy of plants in the nursery, and newly formed plantations is uncertain.

(9) The amount of woolly secretion visible on infested trees in any given area, bears no relation to the amount of damage done.

(10) The natural enemies of this Chermes do not seem to play a prominent part in its control. Artificial control measures can only be employed in the case of nursery plants and ornamental trees.

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APPENDIX.

Records of Seasonal Stages in the Life History of *Chermes* (*Gillettea*) *cooleyi* Gillette in Britain.

Keys to the Genera and Species.

Detailed Descriptions of the Stages in the Life Cycle of *Chermes* (*Gillettea*) *cooleyi* Gillette.

Records of seasonal Stages in the Life History of *Chermes cooleyi* in Britain.

Date.	Locality.	Stages.	Remarks.
1920 Nov.	Swinley, Berks., Midhurst, Sussex	Winter larvæ, colonici on Douglas fir.	
Dec.	Kew; Bagley Wood.	Winter larvæ, colonici on Douglas fir.	
1921 Jan.	Kew; Bagley Wood.	Winter larvæ, colonici on Douglas fir.	
Feb. 15th	Laboratory, Kew.	Winter larvæ in 2nd stage.	No change in the open.
March 3rd	Laboratory, Kew.	Stem mothers, colonici Brood 1.	A few eggs laid. No change in the open.
10th	Laboratory, Kew.	Stem mothers, Eggs, colonici Brood 1.	No change in the open.
15th	In outside cages, Kew.	Winter larvæ, 2nd stage.	Development just commencing in the open.
17th	New Forest, Hants.	Winter larvæ, 2nd stage.	Development just commencing.
18–20th	New Forest. ...	Winter larvæ, 2nd stage.	Development becoming general.
25th	In outside cages, Kew.	Winter larvæ, 2nd and 3rd stages.	Majority still in 2nd stage.
31st	In outside cages, Kew.	Stem mothers of colonici Brood 1.	First eggs laid in the open.
April 4th	In outside cages, Kew.	Winter larvæ, 2nd and 3rd stages. Stem mothers, colonici Brood 1.	Egg-laying general.
19th	Alice Holt, Hants	Stem mothers, colonici Brood 1.	Egg-laying well advanced.
26th	In outside cages, Kew.	Stem mothers, colonici Brood 1. Eggs. Young.	Hatching begun.
26th	Material from Murthly, Perthshire.	Stem mothers. Eggs.	

Date.	Locality.	Stages.	Remarks.
1921 May 2nd	In outside cages, Kew.	Stem mothers. Eggs. Young.	Young hatching freely. Majority of winter forms mature.
3rd–5th	In outside cages, Kew. Watford, Herts.	Stem mothers. Eggs. Young.	Young commencing to feed.
9th	In outside cages, Kew.	Stem mothers. Eggs. Young.	Young in 2nd stage. Large number of eggs still to hatch.
14th	Watford, Herts. ...	Stem mothers. Eggs. Young.	Young in 2nd stage.
23rd	Forest of Dean, Glos.	Stem mothers. Eggs. Young, 1st, 2nd, 3rd and 4th stages.	First appearance of nymphs.
24th	In outside cages, Kew.	Stem mothers. Eggs. Young, all stages. Nymphs.	
25th	Watford, Herts. ...	Stem mothers. Young, all stages. Nymphs. Sexuparæ.	Sexupara just moulted. Few eggs of stem mothers still unhatched.
28th	Watford, Herts. ...	Stem mothers. Young. Nymphs. Sexuparæ. Stem mothers of the 1st summer brood.	Dimorphic nature of the spring brood now evident. Stem mothers of 1st summer brood on Douglas fir mature.
30th	Watford, Herts. ...	Same stages as above.	Sexuparæ increasing in numbers. Summer stem mothers also common.
June 1st	Bagley Wood, Oxford.	Nymphs. Sexuparæ.	Larvæ of colonici Summer Brood 1 mostly in 2nd and 3rd stages. Only a few nymphs and sexuparæ.
3rd	In outside cages, Kew. Laboratory, Kew.	Sexuparæ	Sexuparæ settling on the Sitka spruce in numbers.
6th	Dunster, Somerset	Sexuparæ. Stem mothers. 1st summer brood of colonici.	Sexuparæ egg-laying on Sitka spruce. Stem mothers egg-laying on Douglas fir.
12th	In outside cages, Kew.	Sexuparæ. Stem mothers. Summer Brood 1. Eggs.	Young of sexuparæ emerging. Stem mothers laying eggs.
18th	In outside cages, Kew.	Same stages as above.	Young of sexuparæ in 2nd stage.
22nd	In outside cages, Kew.	Sexuparæ. Eggs. Young. Stem mothers. Eggs. Young.	Eggs laid by stem mothers on Douglas fir, hatching.

Date.	Locality.	Stages.	Remarks.
June 30th	Midhurst, Sussex...	Sexuparæ. Eggs. Young. Stem mothers. Eggs. Young.	Sexuparæ young in 2nd stage. Larvæ hatching from eggs laid by stem mothers are assuming the winter form. Twigs tenanted by these, marked at Watford on the 22.6.21.
July 6th	In outside cages, Kew.	Sexuales. Males...	First male sexuales found at Kew.
10th	Watford, Herts. ...	Young of Summer Brood 2.	Marked twigs show larvæ have now become true winter forms.
12th	Midhurst, Sussex...	Sexuparæ. Eggs. Young. Mature males.	Eight males found to-day.
13th	In outside cages, Kew.	Sexuales. Female. Several males also found.	
15th	Midhurst, Sussex...	Sexuales. Males.	Several more males found. Many immature larvæ found dead and shrivelled on the needles.
August 4th	Midhurst, Sussex...	Young of Summer Brood 2 on Douglas fir.	Males of the sexuales now scarce.
5th	Watford, Herts....	Young of Summer Brood 2 on Douglas fir.	No change in the larvæ on the marked twigs. Sexuparæ all gone.
16th	Dawyck, Peebles...	Stem mothers of Summer Brood I. Eggs. Few young on Douglas fir.	Eggs and a few larvæ. Sexuparæ rare.
24th	Dunkeld, Perthshire.	Stem mothers. Summer Brood I. Few young. Eggs.	Few larvæ (winter form.)
25th	Murthly, Perthshire.	Stem mothers. Summer Brood I. Eggs. Few young.	
26th	Dunkeld, Perthshire.	Same stages as above.	
October 23rd	Watford, Herts. ...	Young. Summer Brood 2.	Young on marked twigs unchanged.
Nov. 24th	Watford, Herts. ...	Young. Summer Brood 2.	Young on marked twigs unchanged. These larvæ are true winter forms which become stem mothers in early spring.

Keys to the Genera and Species.

The following keys are translated from Dr. Carl Börner's, *Monographie über die Chermiden*, published in 1908. Acknowledgments are due to Dr. Appel, the Director of the Biologischen Reichsanstalt für Land- und Forstwirtschaft, and also to Dr. Börner himself, for permission to publish these and to illustrate them with figures from his text.

The keys have been somewhat modified from the original, and include only the British species of the genera *Chermes*, *Gillettea*, and *Cnaphalodes*. The two remaining genera of the family, which have representatives in Britain, namely *Pineus*, and *Dreyfusia*, have been included in the generic key, but are not dealt with in further detail at present.

The genus *Gillettea*, not dealt with by Börner, has been inserted in the keys. All the principal stages of *Gillettea cooleyi*, some of which have not yet been found in Britain, have been included, in the event of their possible appearance in this country.

With regard to the paired species, *Chermes abietis* Kalt., and *Chermes viridis* Ratz.; *Cnaphalodes lapponicus* Chol., and *Cnaphalodes strobilobius* Kalt., Cholodkovsky's latest work has been followed, and these species have been treated as distinct, although as will be seen in the keys, no satisfactory characters appear to exist in certain stages of the life history by which they can be separated.

The keys are divided into the following sections:—

(1). MORPHOLOGICAL KEYS.

(A). General key to the different normal stages of the whole group.

(B). Key to the genera.

(C). Key to the first stage larvæ of the genera *Chermes*, *Gillettea* and *Cnaphalodes*.

(D). Key to the stem mothers or fundatrices of the above genera.

(E). Key to the winged forms of the above genera.

(2). BIOLOGICAL KEYS.

(A). On the spruce.

(B). On the Douglas fir.

(C). On the larch.

Full illustrations of the terms used in the text are given in the reproduction of Dr. Börner's figures, and also in the original drawings made for this bulletin.

MORPHOLOGICAL KEYS.

(A). General Key to the Different Normal Stages of the Whole Group.

1. Lice wingless, without wing pads, and with 3 simple eyes on each side of the head 2*

1a. Lice with two pairs of wing pads, of which the larger are in front, attached to the mesothorax, the smaller behind the metathorax, and covered over in dorsal and side view. In front of the lateral simple eyes, lie several small facetted eyes, spaced relatively far apart, and hardly rounded in front. Antennal whip 1-jointed.

* The numbers in the right-hand margin of the keys refer to the succeeding section before which the same number is placed. Where subdivision of the individual numbers is necessary in the left-hand margin, the symbols a., b., etc., are placed after the numeral. *e.g.*, 1a., 1b., etc.

The Nymphal Stage.

1b. Lice with two pairs of delicate wings, the front pair larger than the hind pair. 3 simple eyes present, in addition to the typical lateral compound eyes. The central one lies near the antennal bases, the lateral ones near the compound eyes. Antennal whip normally 3-jointed.

The Winged Stages.

2. Antenna 3-jointed, more or less elongate. Or secondarily 2-jointed, when it may be shortened or flattened out into a hairy disc 3

2a. Antenna 4-jointed. Whip 2-jointed, scaly. Lice of two sexes.

The Sexual Stage.

3. Antenna 3-jointed, with a relatively long, slender, and more or less distinctly scaly whip joint, whose terminal bristle is at least ⅛ the length of the joint. The second joint of the tarsus of the middle and hind legs, bears two long knobbed hairs on the dorsal surface. The tarsi of the front legs bear only one.

The First Stage Larva.

3a. Antenna 2- or 3-jointed. Elongate or flattened. Second joint of the tarsus without the knobbed hairs present in No. 3 ... 4

4. Lice without a genital aperture.

The Second and Third Stage Larvæ.

4a. Lice with a genital aperture opening on the eighth abdominal segment, and the typical genitalia.

The Stem Mother Stage.

(B). Key to the Genera.

1. Sixth abdominal segment without spiracles. Larva of the *fundatrix vera* on spruce bears chitinous plates on the dorsal surface, the larva of the *fundatrix spuria* on pine does not. Sexupara nymphs with the head and prothoracic plates, fused on either side of the middle line (Plate VII., Fig. 7).

Tribe Pineini. Genus *Pineus* Shimer. Emend. C. B. 1907.

1a. Sixth abdominal segment with spiracles. Sexupara nymphs with the head and prothoracic plates separated (Plate IX., Fig. 3).

Tribe Chermesini. 2

2. The head and prothoracic plates of the winter larvæ of the colonici on larch, fused together into a single homogeneous shield (Plate VIII., Fig. 6). The dorsal plates of the fundatrix young larva on spruce, bear one central, double-outlined gland facet (Plate VIII., Fig. 8).

Genus *Cnaphalodes* Macquart Emend. Amyot-Serville 1843. C. B. 1907.

2a. The head and prothoracic plates of the winter larvæ of the colonici on larch and Douglas fir, not fused together into a single shield. Pleural gland facets are present on the thorax and the first six abdominal segments. The dorsal plates on the head and thorax of the colonici stem mother remain isolated (Plate VIII., Fig. 13) 3

3. The thoracic plates of the winter larva on spruce, bear three to five double-outlined round gland facets, and one small central spine (Plate IX., Fig. 7b). Colour greenish or ochreous yellow. All the colonici young larvæ develop into sexuparæ.

Genus *Chermes* (*s. str.*). Börner.

3a. The thoracic plates of the winter larvæ on spruce bear many rounded or polygonal, double-outlined gland facets, and one or more central spines (Plate VII., Fig. 3). In the winter larva of the colonici on the Douglas fir there are four groups of 4-gland facets each on the thorax, each group with a central spine. Colour dark brown. Brood developing from the first spring stem mother on the Douglas fir is dimorphic, developing partly into winged sexuparæ, and partly into wingless summer generations on the Douglas fir.

Genus *Gilletea*. Börner.

4. Colonici young larvæ without pleural gland facets on the thorax, and the first 6 abdominal segments (Plate VIII., Fig. 11). The dorsal plates on the head and prothorax of the colonici stem mother, fused into a multipartite shield (Plate VII., Fig. 1.)

Genus *Dreyfusia*. Börner.

(C). THE FIRST STAGE LARVÆ.

1. With dorsal wax glands 4
1a. Without dorsal wax glands 2
2. Without any apparent definite wax glands. Integument weakly chitinised. Head and prothoracic plates divided 3
2a. Ventral wax glands present at the bases of the antennæ, subcoxæ and nearly always also upon the first ventral segment of the abdomen. (Not always easily seen in the latter place.) Head and prothorax covered by a single plate (Plate VIII., Fig. 6).

Cnaphalodes strobilobius. Winter larva. (Colonici sistens,* larch.)

3. Dorsal surface with rounded, more or less convex, wart-like areas, distributed in the same alignment as the plate spines (Plate VIII., Fig. 9). Colour black.

Cnaphalodes strobilobius. (Sexupara larva, larch.)

3a. Dorsal surface smooth, without wart-like areas. Colour light brown to sulphur yellow.

Chermes viridis. (Sexupara larva, larch.)

4. Dorsal surface bears strongly chitinised plates 5
4a. Dorsal surface bears delicate plates, or these may be lacking, the integument being quite smooth 10
5. Vertical plates fused into a single piece, only occasionally emarginate or notched upon the sides 6
6. Spinal, pleural, and marginal plates present 7
7. Individual wax gland areas composed of similar facets 8
7a. Individual wax gland areas composed of a central sunken facet, with a small central spine, surrounded by a circle of smaller facets (Plate IX., Fig. 7*a*). Head and prothoracic plates fused.

Cnaphalodes strobilobius, Cnaphalodes lapponicus. Young larva. (Fundatrix vera, spruce.)

8. Individual wax gland areas with three to five facets grouped round the plate spine (Plate IX., Fig. 7*b*). Plates almost or entirely smooth. Lice with a short curly wool covering 9

* In some species two types of development are known to exist in this generation, namely, *colonici sistentes* and *colonici progredientes*. The former are characterised by having a more strongly chitinised integument in the first larval stage, and as a rule spend some considerable time in this condition before proceeding to further development, passing through three moults to the adult stage. The latter, on the other hand, show a weakly chitinised integument in the first larval stage, and as a rule develop immediately, passing through four moults to the adult stage.

8a. Individual wax gland areas with many circular or polygonal facets, grouped round the central spines. Plate VII., Fig. 3.
Gillettea cooleyi. Young larva. (Fundatrix vera, spruce.)

8b. Wax gland areas of the marginal plates with many rounded or polygonal facets. On the dorsal plates there are never more than three to five gland-facets with large lumina, closely grouped round a central spine. Plate V, Fig. 3.
Gillettea cooleyi. Young Larva. (Fundatrix spuria, Douglas fir.)

9. Dorsal plates of the prothorax fused into a single transverse plate (Plate VII., Fig. 4).
Chermes viridis. Young larva. (Colonici sistens, larch.)

9a. Dorsal plates of the prothorax normally separated into two quadrangular central plates, and two small rather narrow side plates (Plate VII., Fig. 5).
Chermes abietis, Chermes viridis. Young larva. (Fundatrix, spruce.)

10. Marginal plates clearer on the abdominal region than on the head and thorax. Spinal, pleural and marginal plates present, the two former often fused (Plate VIII., Fig. 10) 11

11. Terminal bristle of the antennal whip about $\frac{1}{8}$ the length of the joint. Colour reddish brown turning to violet as a result of the presence of waxy powder (Plate IX., Fig. 2*b*).
Cnaphalodes strobilobius, Cnaphalodes lapponicus. Young larva. (Gallicola, spruce.)

11a. Terminal bristle of the antennal joint more than $\frac{1}{3}$ the length of the joint (Plate IX., Fig. 2*a*). Colour light green to sulphur yellow.
Chermes abietis, Chermes viridis. Young larva. (Gallicola, spruce.)

(D). The Stem Mothers.

1. Abdominal segment 6 with distinct spiracles, which are set in typical small plate areas. Abdominal segments 8 and 9 (or at least segment 8) with wax glands. Head and prothorax with separate plates 2

2. Head, prothorax, and abdominal segments 1–5 without wax gland areas on the dorsum. The plates of the segments up to abdominal segment 3, show a more or less strongly raised and wrinkled surface (Plate VII., Fig. 2). Colour copper or bronze. The abdomen shows very little wool on the dorsum and sides.
Cnaphalodes strobilobius. (Colonici sistens, larch.)

2a. Head, prothorax, and abdominal segments 1–5 with wax gland areas on the dorsum 3

3. Gland areas large, with numerous, sharply defined, separated facets 5

3a. Gland areas large, with numerous, sharply defined, more closely contiguous facets 4

4. Facets of the gland areas numerous, approximately uniform in size over the whole area (Plate II., Fig. 2).
Gillettea cooleyi. (Fundatrix vera, spruce.) Unknown in Britain.

4a. Facets of the gland areas numerous. The central facets distinctly larger than those on the outer margins (Plate IV., Fig. 1).
Gillettea cooleyi. (Fundatrix spuria, Douglas fir.)

4b. Gland facets smaller. The spinal and pleural glands have a smaller number of facets which are at least partially fused. Colour yellowish green to dark green 7

5. Gland facets large (Plate IX., Fig. 9). Few in number. The plates distinctly raised and wrinkled. Lice black, covered with thick, coarse, white wool.
Cnaphalodes strobilobius. (Colonici progrediens, larch.)

5a. Gland facets smaller, relatively more numerous. Plates flat or only very slightly raised 6

6. Wax gland areas with a very large number of facets, the largest of which are in the centre of the plate, these being considerably larger than those surrounding them (Plate IX., Fig. 8). Head with three large vertical gland plates (Plate IX., Fig. 5). Colour greenish or yellowish green, with long flowing wax threads.
Cnaphalodes strobilobius, Cnaphalodes lapponicus. (Fundatrix vera, spruce.)

7. Wax gland areas small (Plate VIII., Fig. 13). Lice with a somewhat loose, bluish-white woolly covering.
Chermes viridis. (Colonici sistens, larch.)

7a. Lice concealed under a thick wax blanket.
Chermes abietis, Chermes viridis. (Fundatrix vera, spruce.)

(E). The Winged Forms.

1. Abdominal segment 6 with well marked spiracles. Abdominal segment 8, or both 8 and 9 with wax gland areas. Head and prothoracic wax gland areas, with the outer margin of the individual facets mostly entire. The facets may be contiguous and partially fused but they are not totally fused 2

1a. Head and prothoracic wax gland areas, or the latter only, if those on the head are absent, have the outer margins of at least some of the gland facets totally fused, and therefore indistinct. If the facets are distinct, they are polygonally grouped, and clearly margined 5

2. The antennal sensoria, especially on the terminal joint, broad ... 3

2a. The antennal sensoria on all joints, but especially on the terminal joint are narrow and wedge-shaped 2b

2b. Facets of the wax gland areas smaller on the whole than in 2c (Fig. 11, p. 42). The joints of the antennal whip elongate (Plate III., Fig. *c*.).
Gillettea cooleyi. (Gallicola migrans, Douglas fir.) Unknown in Britain.

2c. Facets of the wax gland areas larger on the whole than in 2b (Fig. 12, p. 42). The joints of the antennal whip are short and stout (Plate III., Fig. *b*).
Gillettea cooleyi. (Sexupara, Sitka spruce.)

3. The wax gland areas have large, well marked facets with clear lumina, and secrete much wax 4

3a. The wax gland areas, especially on the head and prothorax, have small facets with obscure lumina, which are often no clearer than the surrounding non-porous chitin. They secrete no wax. Abdominal tergites 1–4 always without pleural wax gland areas.
Cnaphalodes strobilobius. (Gallicola migrans, larch.)

4. Abdominal segments 1–4 without pleural plates and wax gland areas, or at most with only 1–2 small gland facets in the soft integument. The spinal and pleural gland areas of the fifth and 6th abdominal segments remain separated (Plate IX., Fig. 1*a*).
Cnaphalodes strobilobius. (Sexupara, spruce.)

4a. Abdominal segments 1–4 with small facetted pleural plates. On segments 5 and 6, the spinal and pleural plates may fuse, or the spinal plates themselves and the glands facets belonging to them may fuse (Plate IX., Fig. 1*b*).

Cnaphalodes lapponicus. (Gallicola non migrans, spruce.)

5. Yellowish brown to greenish brown in colour. The whip joint of the antennæ with coarse scales, and the joint clearly widened at the sensorium, which is usually somewhat broader than the joint itself. Spinal wax gland area on the mesothorax absent... 6

6. Head without wax gland areas 7

6a. Head with the usual two pairs of vertical wax gland areas. The central area of the prothorax with two small gland areas on the posterior margin (Plate VIII., Fig. 12). Colour a dull green at first, becoming brownish green later.

Chermes viridis. (Sexupara, spruce.)

7. Colour green at first, later the head and thorax are dark brown to black, and the abdomen greenish. The first joint of the antennal whip is longer than the second.

Chermes viridis. (Gallicola migrans, larch.)

7a. Colour ochreous yellow at first, later darkening as in No. 7. The first joint of the antennal whip is shorter than the second.

Chermes abietis. (Gallicola non migrans, spruce.)

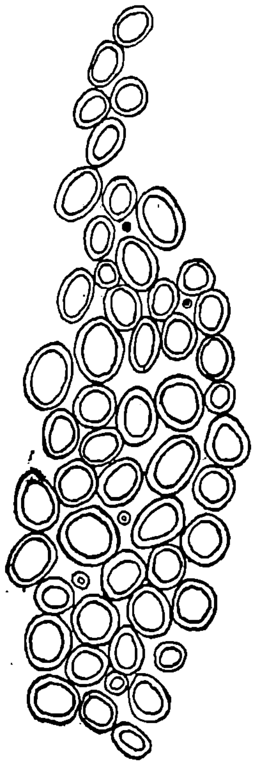

Fig. 11.

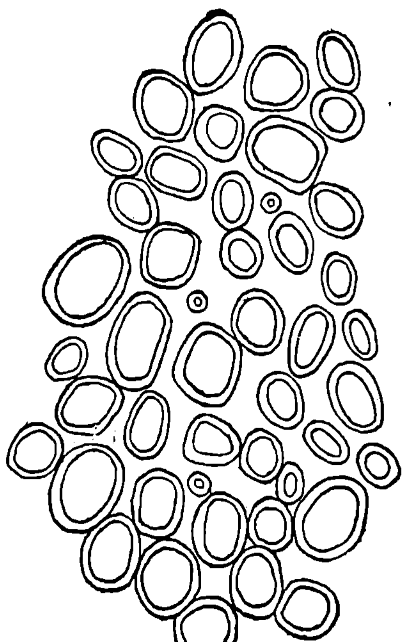

Fig. 12.

FIG. 11. *C. cooleyi.* Gallicola Migrans. Group of gland facets from first abdominal segment. x 345 (original).

FIG. 12. *C. cooleyi.* Sexupara. Group of gland facets from first abdominal segment. x 345 (original).

BIOLOGICAL KEYS.

(A). On the Spruce.

1. On the bark 2
1a. On the needles (winged forms and their descendants) 10
2. On the spring shoots, which are transformed into galls 6
2a. On the bark of last year's shoots, on the winter buds, or at the base of the buds, during the autumn, winter and early spring. Fundatrices (stem mothers) 3
3. On the bud itself 5
3a. At the base of the bud, or on the stem at some distance away ... 4
4. Usually at the base of the bud, but may be located at a little distance from it. In winter the lice have a short, thread-like covering of greyish wool. When fully developed they are yellowish green to dark green in colour, and secrete much wool. Eggs yellow to green. On *Picea excelsa*, *P. alba*, *P. sitchensis*, etc.

   Chermes abietis, *Chermes viridis*.

4a. Usually located at a little distance fom the bud. The lice are dark brown to black in colour, and secrete much wool. Eggs light brown. On *Picea Engelmanni*, *P. pungens* and *P. sitchensis*. Unknown in Britain.

   Gillettea cooleyi.

5. Winter form blackish in colour, with short, stiff, erect wax threads. The mature fundatrix varies in colour from yellowish green to brownish green. The wool is secreted in long strands. Eggs brownish green, powdered with white.

   Cnaphalodes strobilobius, *Cnaphalodes lapponicus*.

6. Galls elongate... 7
6a. Galls shorter and thicker 8
7. Galls elongate, usually encircling the shoot, and almost always involving the terminal bud. Scales compact. Colour light green to dark purple. On *Picea Engelmanni*, *P. pungens* and *P. sitchensis*.

   Gillettea cooleyi.

8. Galls with large scales. The margins of the cell mouths (at least in *Picea alba*, *excelsa*, and *orientalis*) thickly hairy. The upper sides of the gall scales also more or less hairy. Scales bright coloured, light or dark green, with the margins of the cell mouths green or reddish. Usually with a tuft of needles, or a portion of the shoot growing beyond. Usually on one side of the shoot only, but sometimes almost encircling it. The gall may also be terminal with no growing shoot beyond, but this condition is rare.

   Chermes abietis, *Chermes viridis*.

8a. Galls with smaller scales. The upper sides of the scales bare as a rule, but minute hairs (papillæ) may be present, these are only visible under a high magnification, Needles considerably metamorphosed 9
9. Galls yellowish to green in colour, and covered with a waxy bloom. The cell margins rosy red. Usually terminal in position, with a tuft of needles beyond, but they may also be found at the base of the shoot, which continues to grow beyond them. General form globular, encircling the shoot. Often, many small, brownish coloured larvæ are found located upon the outside of the gall. These secrete some wool at first, but eventually die off in the month of July.

   Cnaphalodes strobilobius, *Cnaphalodes lapponicus*.

10. On the needles of both young and old shoots. Winged forms (Sexuparæ). They appear from the middle of May to the end of June, and give rise to Sexuales 11

10a. On the needles of both young and old shoots. Winged forms (Gallicolæ non Migrantes). They appear from the end of July to the end of October, and give rise to winter larvæ 13

11. Winged forms more often on the older needles 12

12. Eggs dark yellow or reddish. Sexuales male olive green, female orange red.

Cnaphalodes strobilobius.

12a. Eggs greenish yellow, Sexuales yellow.

Chermes viridis.

12b. Eggs reddish brown, Sexuales bright red.

Gillettea cooleyi.

13. Winged forms secrete short, fine, bluish white wool. Eggs light reddish brown.

Cnaphalodes lapponicus.

13a. Winged forms have a transverse woolly band of the shape —▁— on the hind margin of the prothorax, and the first abdominal tergite. Very little wool secreted from the abdomen. Eggs yellowish or greenish in colour.

Chermes abietis.

(B). ON THE DOUGLAS FIR.

1. On the needles, mostly on the undersurface. Lice dark brown to black in colour. Little or no wool upon the dorsal surface of the body, but a white fringe surrounding the body margin. The stem mothers of the colonici sistentes appear in early spring as balls of white wool, under which light brown, powdered eggs are laid. The first spring brood is dimorphic, the nymphal forms and the winged migrants appearing from the end of May onwards. The stem mothers of the colonici Summer brood are found ovipositing on the new shoots of the fir at this time, they secrete much wool.

Gillettea cooleyi.

1a. On the needles, winged forms. They commence to settle upon the Douglas fir from the end of June onwards. They are dark reddish brown in colour, and secrete much wool. Unknown in Britain.

Gillettea cooleyi.

(C). ON THE LARCH.

1. On the bark, up to the needle bases 2

1a. On the needles 5

2. On the brown or yellow bark of shoots one year old and upwards 3

2a. On the soft green bark of the young shoots 4

3. On older bark, usually of the main stem and older branches, but rarely extending to the shoots of last year. Lice greenish in colour, with white waxy down. They are more conspicuous at the end of winter, and in the early spring.

Chermes viridis. (Colonici sistens.)

3a. Chiefly upon the bark of last year's shoots, but also extending to older shoots, usually near the buds, or even at their base. Lice naked (without wool) upon the dorsal surface, and only showing a trace of wool ventrally. A large number of eggs are laid in April and May.

Cnaphalodes strobilobius. (Colonici sistens.)

4. Black, wingless lice, naked or rarely covered with white flecks of wool. The stem mothers lay brown, powdered eggs, under a thick woolly covering, from the end of May to the autumn. Brood dimorphic, partly developing into winged migrants in May.

Cnaphalodes strobilobius. (Colonici progrediens.) (Sexupara).

5. Lice greenish or yellowish in colour. Without a thick waxy coat, only slightly powdered. These forms always develop into nymphs and winged migrants, from the end of May to the end of June.

Chermes viridis. (Sexupara.)

5a. Winged migrants with eggs 6

6. Dark red brown to black in colour. No wool on the head and thorax. Eggs brown, powdered. These forms appear from early July onwards.

Cnaphalodes strobilobius. (Gallicola migrans.)

6a. Abdomen greenish in colour, head and thorax darker. Lateral and posterior margins of the prothorax with very short white wax threads. Eggs green, scarcely powdered. These forms appear from the end of July onwards.

Chermes viridis. (Gallicola migrans.)

The following descriptions of the different stages in the five generations of the life-cycle of *Chermes cooleyi* are partly original and partly based on Gillette. The taxonomic characters used are those of Börner (1908), and the terms employed in describing the plates, wax pores, and other structures used in classification, are illustrated in the text-figures and plates.

GENERATION I.—FIRST STAGE LARVA OF THE FUNDATRIX VERA.*

PRIMARY HOST, *Picea* (PLATE VII, FIG. 3).

General Description.

Elongate-oval in shape, 0·6 mm. long, 0·3 mm. broad. The body almost black, sparsely covered by a greyish white wool, which radiates in stout cylindrical threads from the wax pores along the body margins, and rises in a white crest along the middle line (Gillette). This form is to be found during the winter and early spring, located in the bark crevices, with the setæ deeply sunk in the tissues.

Detailed Structure.

The distribution of the chitinous plates and the wax glands on the dorsal surface, is as follows: The head bears two triangular plates, separated at the middle line (these are the "vertical plates" or "Scheitelplatten," of Börner). On these plates, three areas of wax pores are present as follows: On the front margin, on the side margin, and on the interior hind margin bordering the middle line. Each of these glands is composed of 15 to 30 rounded or polygonal, double-margined facets with rge lumina. One or more small plate spines are present lying between the facets.

The prothorax bears one quadrangular plate, and one elongate-oval marginal plate, on each side of the middle line. The centralplates show four glands, comprising 15 to 20 facets, similar in size and structure to those of the head. The usual plate spines are present.

In speaking of the glands on the prothorax and the following segments, Börner has employed the terms, *spinal, pleural* and *marginal.* Spinal

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* So far unknown in Britain. Described from notes made in Stanley Park, Vancouver, and from a figure of the larva publ shed by Börn r (Zool. Anz. 34. p. 506, 1909).

glands are those lying nearest to the middle line, pleural, those lying immediately outside them ; and marginal glands, as their name denotes, those outlining the body margin itself. Thus in the prothorax of the *C. cooleyi* larva, there are two spinal, two pleural, and one marginal gland on each side. The above terms also apply to the chitinous plates.

The meso- and metathorax bear one spinal, one pleural and one marginal gland on each side. The plates are round or oval in shape, and bear ten to twenty-five facets similar to those already described, in addition to the usual plate spines.

On the abdomen, segments 1 to 4 show one spinal, one pleural and one marginal plate on each side. The gland facets vary in number from 8 to 15, and are similar in structure to those already described. On segments 5 to 7 the spinal and pleural plates may fuse, and one marginal plate occurs on each side. On segment 8 only the marginal plate is distinct, and on segment 9, no distinct plate occurs, but a few gland facets are present, as well as numerous terminal spines.

On the ventral surface, there are glands at the bases of the antennæ, and on the middle sub-coxæ. The antennæ, legs, and rostrum or beak, do not exhibit any characters useful in classification.

GENERATION I.—MATURE STEM MOTHER OR FUNDATRIX VERA.*

PRIMARY HOST, *Picea* (PLATE II., FIGS. 1, 2).

General Description.

" Fully grown examples measure 1 to 1·5 mm. in length, by 0·8 to 1·2 mm. in width. The colour is a dark rusty-brown, and the entire dorsal surface is mottled with dark spots, representing the wax glands, which occur upon all the segments but the last " (Gillette).

Detailed Structure.

The Dorsal Surface.—On the anterior margin of the head, the glands are continuous. On the hind margin there is one spinal, one pleural, and one marginal gland on each side.

All three segments of the thorax bear one spinal, one pleural, and one marginal gland on each side.

On the abdomen, segments 1 to 4 bear glands similar to those on the thorax. Segments 5 and 6 have the spinal plates fused, with one pleural and marginal plate on each side. On segment 7 the spinal and pleural plates tend to fuse, the marginal plates remaining distinct. On segment 8 only spinal and marginal plates are present, and on segment 9 no definite plates occur, but numerous spines are present.

The lumina of the gland facets are small, the facets being uniform in size, and contiguous.

The Ventral Surface.—Glands are present at the bases of the antennæ and middle sub-coxæ.

The antennæ are about 0·14 mm. long, and have the first two joints short and stout, and of about equal length. The third or terminal joint is the antennal whip, " *Fühlergeissel* " (Börner), and is about twice as long as joints 1 and 2 combined, and bears two tactile hairs or spines at the tip (Gillette).

The rostrum is elongate and narrow, and the stylets are longer than the body. Compare with the Fundatrix Spuria.

GENERATION. II.—WINGED MIGRANT TO THE DOUGLAS FIR, GALLICOLA MIGRANS.* PRIMARY HOST, *Picea.*

General Description.

" The winged female is bright shining rufous at first, but by the time the wings are spread, the eyes are black, and a few hours later the head and mesothorax are black also. The other parts of the body gradually

* So far unknown in Britain.

become darker, the abdomen retaining the rusty colour longest. In about an hour after the pupal skin is shed, the white secretion begins to show over the wax glands, and the insect soon flies away. The size varies between 1·5 and 2 mm." (Gillette).

Detailed Description.

The anterior margin of the head bears two large transverse glands, which almost fuse in the middle line. On the hind margin there are two long, narrow glands, which may or may not fuse in the centre.

On the prothorax the spinal and pleural glands fuse together into a narrow transverse band on the hind margin. Marginal glands are present and occupy the entire breadth of the segment, they may fuse with the pleural glands. Two round spinal glands are present on the hind margin of the mesothorax, and two elongate-oval spinal glands are present on the metathorax.

On the abdomen, segments 1 and 2 bear no pleural plates, segment, 3 to 7 bear spinal, pleural and marginal plates; on segment 8 only marginal plates are present and segment 9 bears no distinct plates.

The arrangement of the plates is variable, the smaller ones being often wanting, and the larger ones fused together. The above description, however, covers the usual types found.

The gland facets are double-margined and placed close together. Careful comparison with those of the winged sexupara, has shown that their lumina are on the average smaller. Figs. 11 and 12, p. 42. show the comparative sizes of the gland facets in the two forms.

The fore wing is about 1½ times as long as the body. The costal nerve is yellow. Two discoidal veins and one stigmal vein are present. The hind wings are about equal in length to the body, and bear one discoidal vein.

The antennae are 5-jointed. Joints 1 and 2 are short, stout, and subequal in length. Joints 3 to 5, compose the antennal whip. Joint 3 is stouter and more conical than the two following. Joints 4 and 5 are long and narrow and not specially enlarged at the distal end in the region of the transverse sensoria, which are present on all three joints of the whip. The sensoria are narrow, and less than one quarter of the length of the joint (Plate III., Fig. *c*).

GENERATION III.—FIRST STAGE LARVA OF THE FUNDATRIX SPURIA.

SECONDARY HOST, *Pseudotsuga* (PLATE V., FIG 3).

General Description.

Elongate-oval, 0·4 mm. in length, 0·25 mm. in breadth. Colour, dark brown to black. The white wool is most prominent round the body margins, forming a fringe. Wool on the dorsum sparse. The body is heavily chitinised, the thoracic plates appearing smooth and shining.

Detailed Description.

The head bears two triangular " vertical plates," separated at the middle line. Each of these bears the following wax glands : Two marginal areas on the front and side margins of the head respectively, each composed of numerous, polygonal, double margined facets ; and within these, three smaller glands each composed of 4 facets, two of which are situated behind the marginal areas, and the third at the base of the inner margin of the plate.

The central portion of the prothorax bears a rectangular plate on each side of the middle line, and an oval-shaped marginal plate.

On the central plates there are at each corner groups of 4 to 5 gland facets, arranged round a central spine, the individual facets being similar in structure to those on the head. The two inner groups of facets correspond to the spinal glands of the succeeding segments, and the two outer groups to the pleural glands.

The marginal plates bear many gland facets, which are similar in size and structure to those on the plates of the head.

The meso- and metathoracic segments each bear one spinal, one pleural, and one marginal plate on either side. The gland facets of the spinal and pleural plates are grouped as in the head and prothorax, and vary in number from 3 to 5. The facets of the marginal plates are numerous and similar in structure to those of the preceding segments.

On segments 1 to 5 of the abdomen there are spinal, pleural, and marginal plates on each side, with gland facets similar to those already described; on segment 6 the spinal plates are fused in the centre, the pleural and marginal plates being distinct. This segment bears three pairs of dorsal hairs or spines on each side, which are not always easily seen. On segment 7 the spinal and pleural plates fuse, the marginal plates remaining distinct; on segment 8 only the spinal plates and marginal plates remain, the former bearing 2 spines; segment 9 bears a single plate upon which the gland facets are indistinct. Two spines are present.

On the ventral surface of the head there are two large groups of oval shaped gland facets, lying just below the antennal bases.

Two smaller groups of similar shaped facets, occur on the sub-coxæ of the middle pair of legs.

The antennæ are three-jointed, the antennal whip being more than twice as long as joints 1 and 2 combined. This joint is irregularly scaly, bears a group of small sensoria on the under surface near the tip, and also four terminal spines.

Generation III.—Larva of the Fundatrix Spuria. Stages 2 and 3. Secondary Host, *Pseudotsuga* (Plate IX., Figs. 4, 6).

The second stage larva is 0·5 mm. in length, light brown in colour and shows very little trace of wool. The well-defined chitinous plates of the first stage larva, have all disappeared in this stage, and are replaced by thin plates, arranged as shown in the accompanying figure. No definite gland facets are visible. The whip joint of the antenna is much reduced in length, and shows no well-marked transverse scales as in the first stage larva.

The third stage larva is 0·6 mm. in length, rather darker brown in colour, and shows an increasing amount of wool. The chitinous plates are more evident, and the large polygonal facets of the wax gland areas begin to appear in this stage.

The antennæ show a further reduction in length of the whip joint, which is smooth and without scales.

Generation III.—Mature Stem Mother, or Fundatrix Spuria. Secondary Host, *Pseudotsuga* (Plate IV.).

General Description.

Roundish oval in shape. Dark rusty brown to black. 0·8 to 1·2 mm. in length by 0·6 to 0·9 mm. in breadth.

Detailed Description.

On the front margin of the head, four glands are present and two in the centre of the hind margin.

The gland facets are polygonal in shape, with large lumina, the facets in the centre of the plate being markedly larger than those on the outside This applies to all the glands as far as abdominal segment 3.

On the prothorax there are two spinal, two pleural plates, and one marginal plate on each side; and on the meso- and metathoracic segments one spinal, one pleural, and one marginal plate on each side.

On segments 1 and 2 of the abdomen the number of plates is similar to the thorax. The central gland facets begin to lose their distinct outline in the spinal region of segment 3. On segments 3 to 6 the number of plates is similar to the thorax. The facets become less distinctly outlined, until in segments 5 and 6 they disappear altogether. On segment 7 the spinal glands are fused and the pleural and marginal glands distinct. On segment 8 only spinal and marginal glands are present, and on segment 9, there are no glands, but numerous spines occur.

Two large wax glands are present on the ventral surface at the bases of the antennæ, and two very small areas on the sub-coxæ of the middle pair of legs. The rostrum is short and stout, and the stylets are shorter than the body.

Generation IV.—Winged Sexupara. Secondary Host, *Pseudotsuga* (Plate III).

General Description.

Length 1·75 to 2 mm. Head black, powdered with white. The eyes shining black, the antennæ dark brown. The prothorax and mesothorax dark brown with wool on the sides and hind margin and the metathorax dark brown, with wool in the centre and on the sides.

Tne abdomen and legs dark brown. The wings are slightly smoky and as long as the body. The venation of the fore wing is normal, and the hind wing shows a faint transverse vein.

Detailed Description.

Two large glandular plates reaching the border of the compound eyes are present on the front margin of the head, and there are two small glands on the hind margin.

On the prothorax there are two small glands in the centre of the front margin. One marginal gland on either side, and two larger and more elongate glands on the hind margin. There are two circular gland areas on the hind margin of the mesothorax on either side of the middle line, and on the metathorax there are two elongate-oval glands on the hind margin.

Marginal glands are present on all the segments of the abdomen. The pleural glands are very small on segments 1 and 2, larger on segments 3 to 6, and thereafter smaller. They are absent on segment 9. The spinal plates are present on segments 1 to 7, and are not fused. Segment 8 bears no spinal plate and segment 9 bears numerous setæ and spines.

The gland facets are double margined and contiguous. Their lumina are distinctly larger than those of the winged gallicola, and this character seems to be constant. (Fig. 12, p. 42.)

The antennæ are 5-jointed, joints 1 and 2 short, stout, sub-equal in length. Joints 3 to 5, the antennal whip, are also rather short and stoutly built, usually tapering at the base. The sensoria are narrow and wedge shaped, and the scales of the joints are coarse. In comparison with the antennæ of the gallicola, the short and stout build of the whip joints (Plate III., Fig. *b*) is in marked contrast to the longer, narrower and more tapering whip-joints of that form (Plate III., Fig. *c*).

Generation V.—Sexuales or Sexual Generation. Primary Host, *Picea.*

The Male.—General Description (Plate V., Figs. 1, 2).

Bright red in colour, eyes black, 0·6 mm. long, elongate-oval in shape, the body tapering markedly towards the hind end. Body mostly smooth, no wool present.

Detailed Description.

No definite glands can be seen, the body segments have, however, rows of well-marked spines which are disposed in approximately the same alignment as the plates in the other forms. The antennæ are about $\frac{1}{3}$ of the length of the body, and are four-jointed. Joints 1 and 2 are short, stout and sub-equal in length, joint 3, the first joint of the antennal whip is more than 1½ times as long as 1 and 2 and is very scaly. Joint 4 is somewhat shorter than 3, and bears four long spines at the tip, with a group of sensoria somewhat below the tip itself. The legs are long and rather slender. The rostrum is stout and the very short rostral stylets are characteristic of this generation.

The Female.—General Description (Plate VI.).

Reddish in colour, but not so bright as the male; the eyes black, composed of three facets; 0·4 mm. long, roundish oval in shape, the body not markedly pointed towards the hind end.

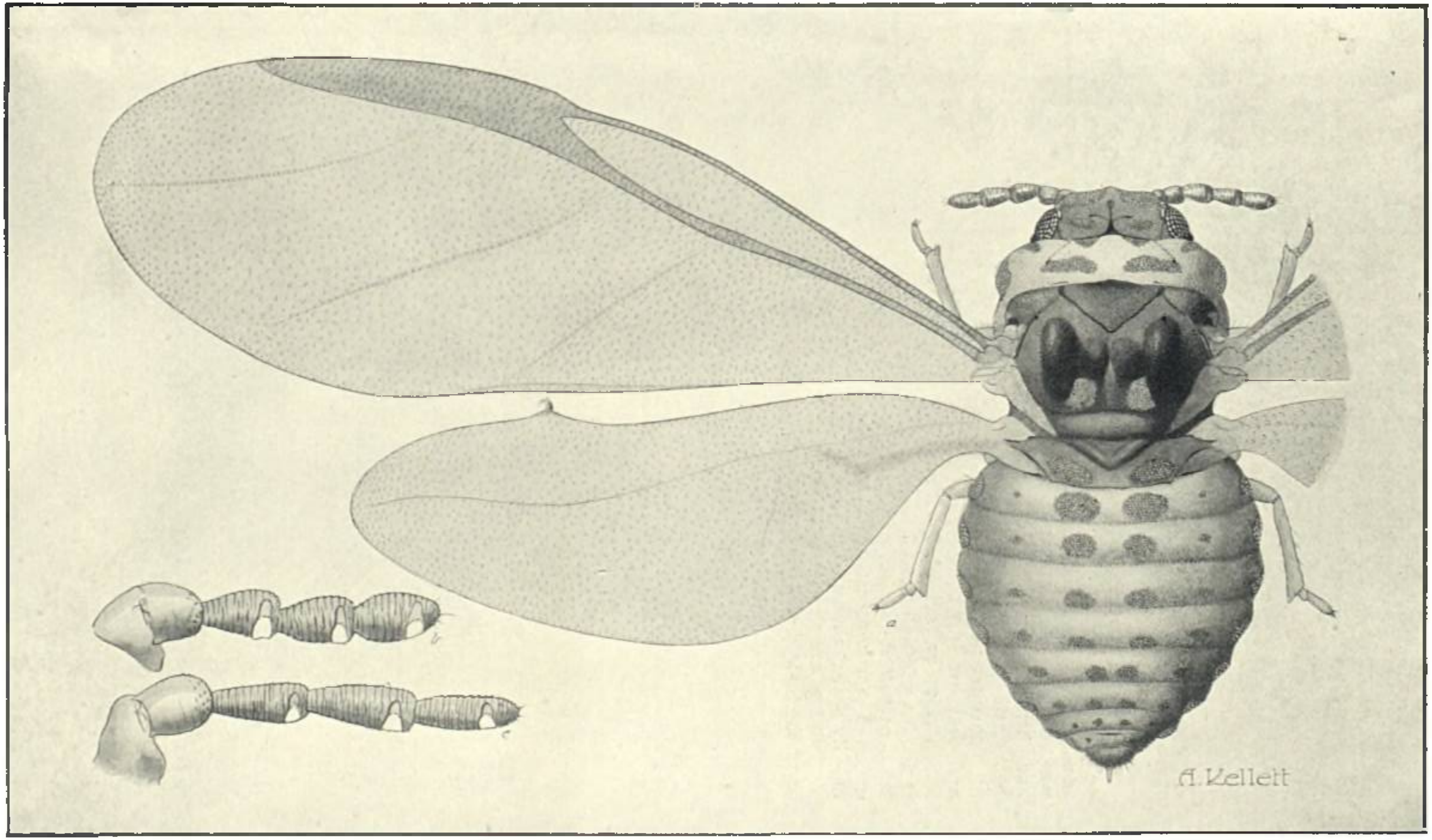
Detailed Description.

In contrast to the male form, definite wax gland areas can be located on all the segments of the female. Of these the marginal areas are the most distinct, and from those occurring on the front margin of the head, wax threads were observed to proceed. The gland facets are round, and rather indistinct, their arrangement on the spinal and pleural areas being still rather obscure.

The antennæ are four-jointed rather more than ¼ the length of the body, and they are less conspicuous than those of the male. Joints 1 and 2 are short, stout, and sub-equal in length; joint 3, the first joint of the whip, is about twice as long as 1 and 2 combined, and joint 4, the terminal joint, is about half the length of joint 3, and bears five terminal bristles and a group of four sensoria just behind the tip. The joints of the whip are less heavily scaled than in the male.

The legs are shorter than those of the male, the rostrum is stout and, as in the male, bears very short stylets.

PLATE III.



a. C. cooleyi Gillette. Winged sexupara. x 60 (original). *b.* Antenna of winged sexupara. x **240** (original).
c. Antenna of winged gallicola. x 210 (original).

[*To face p.* 50.

PLATE IV.

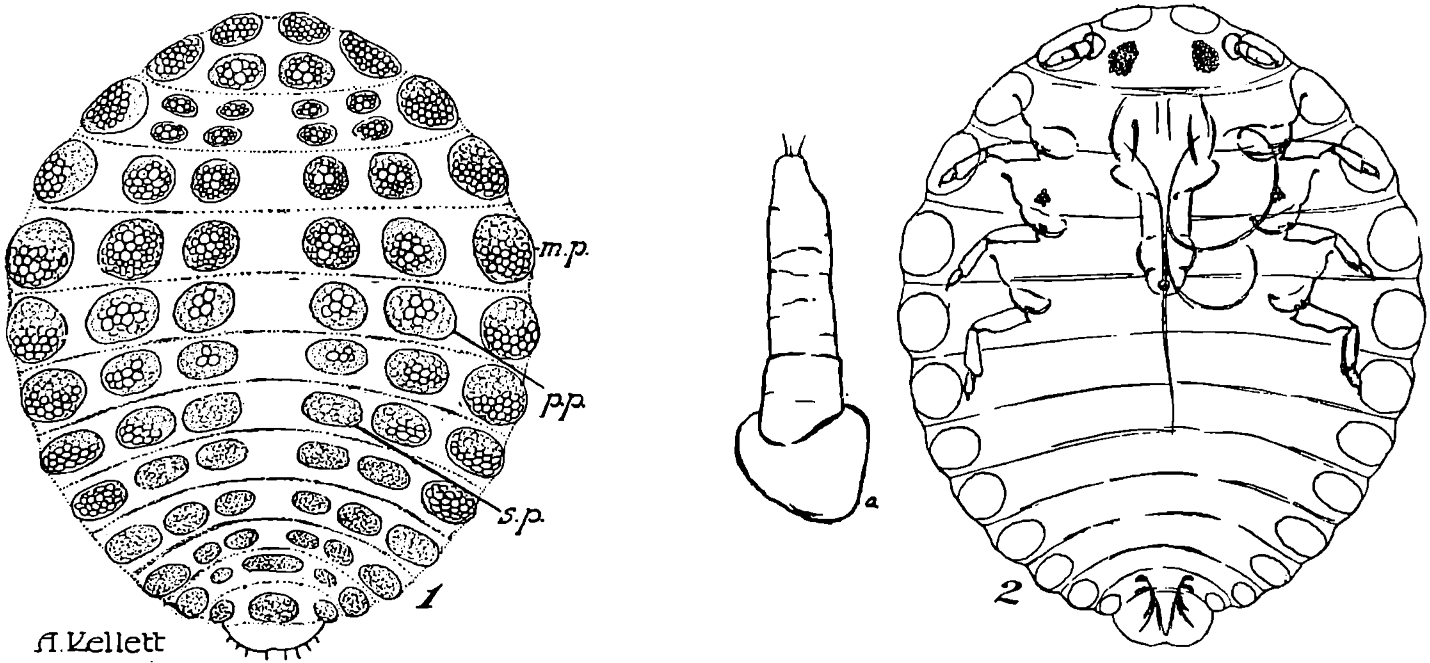
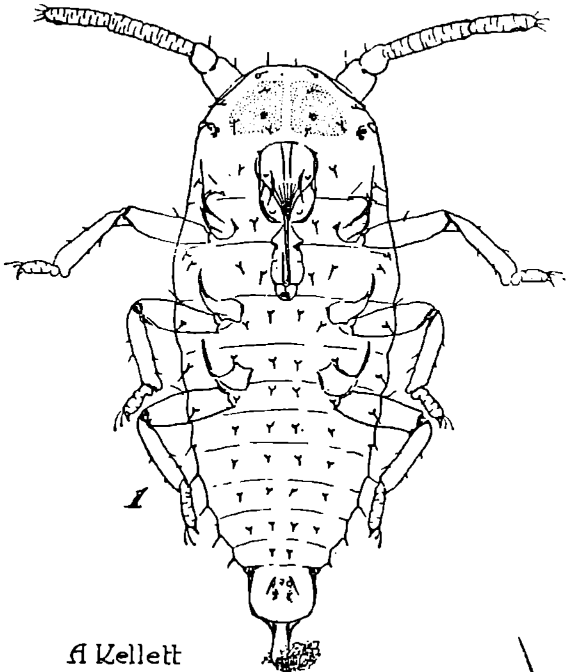
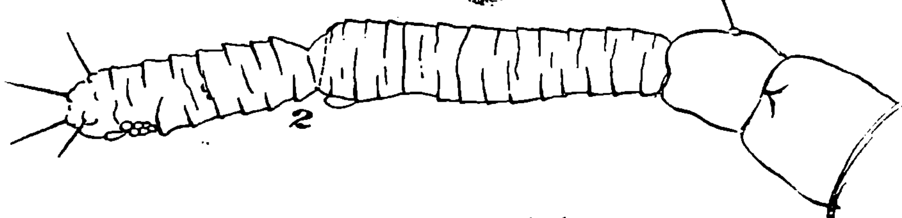


FIG. 1. Mature stem mother, fundatrix spuria of *C. cooleyi* on Douglas fir.. Dorsal aspect. x 80 (original). s.p. = spinal plate, p.p. = pleural plate, m.p. = marginal plate.
FIG. 2. The same, ventral aspect. x 80 (original). a = antenna.

PLATE V.





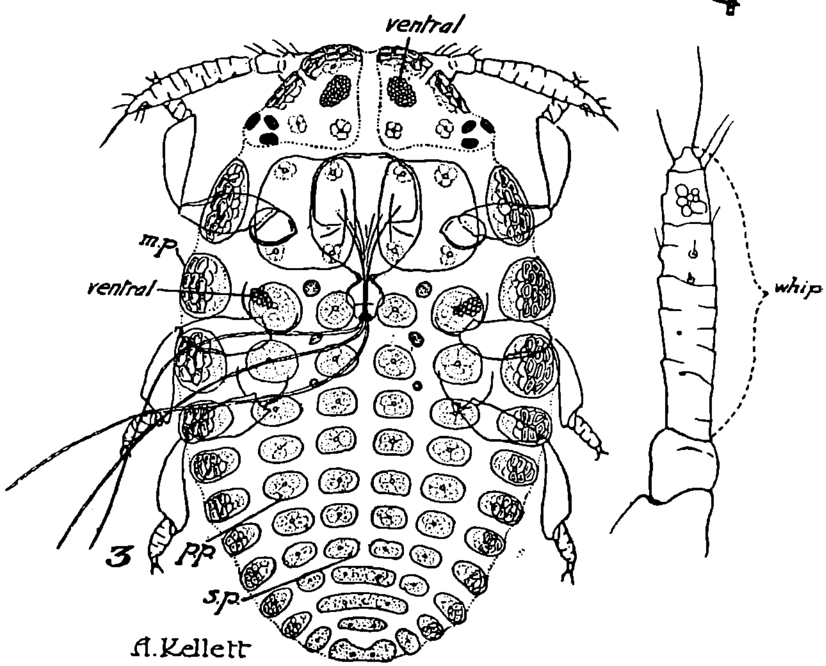


FIG. 1. *C. cooleyi* Gillette, adult male. x 135 (original).
FIG. 2. Antenna of adult male. **x 500** (approx.) (original).
FIG. 3. *C. cooleyi* Gillette, first stage winter larva on Douglas fir. **x 165** (original). s.p. = spinal plate, p.p. = pleural plate, m.p. = marginal plate.

PLATE VI.

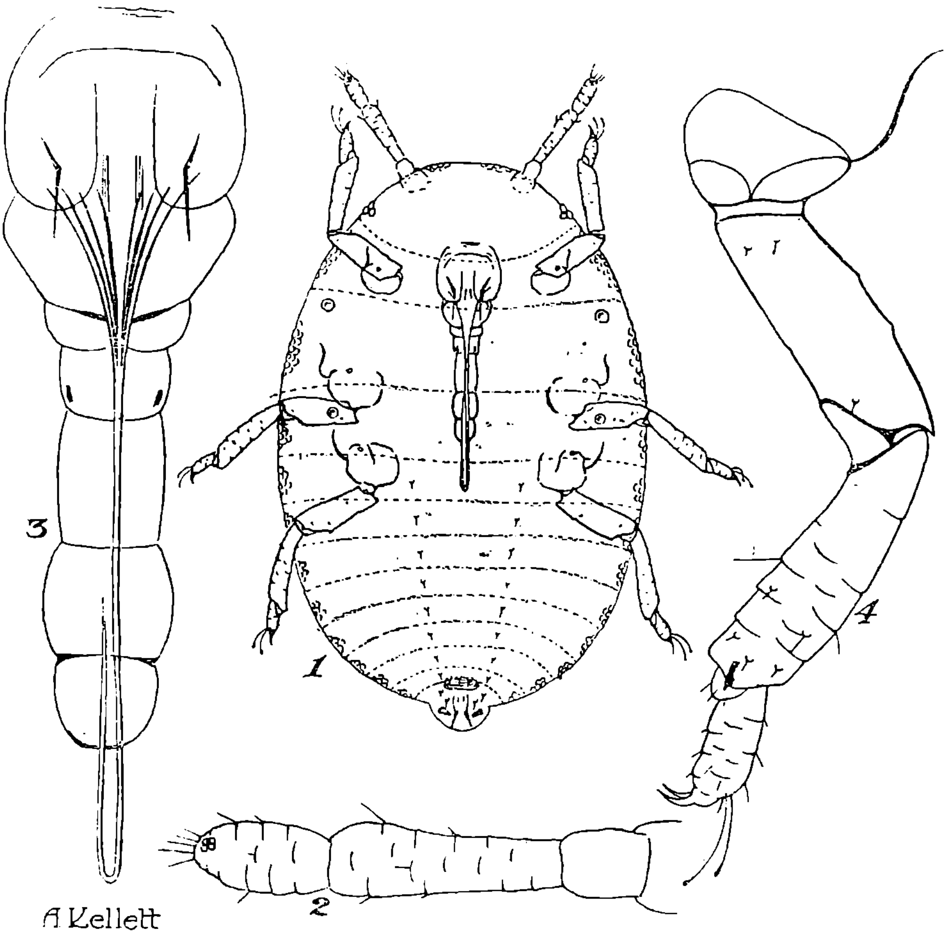


FIG. 1. *C. cooleyi* Gillette, adult female. x 172 (original).
FIG. 2. Antenna of the same. x 500 (approx.) (original).
FIG. 3. Rostrum. x 500 (approx.) (original).
FIG. 4. Leg. x 500 (approx.) (original).

PLATE VII.

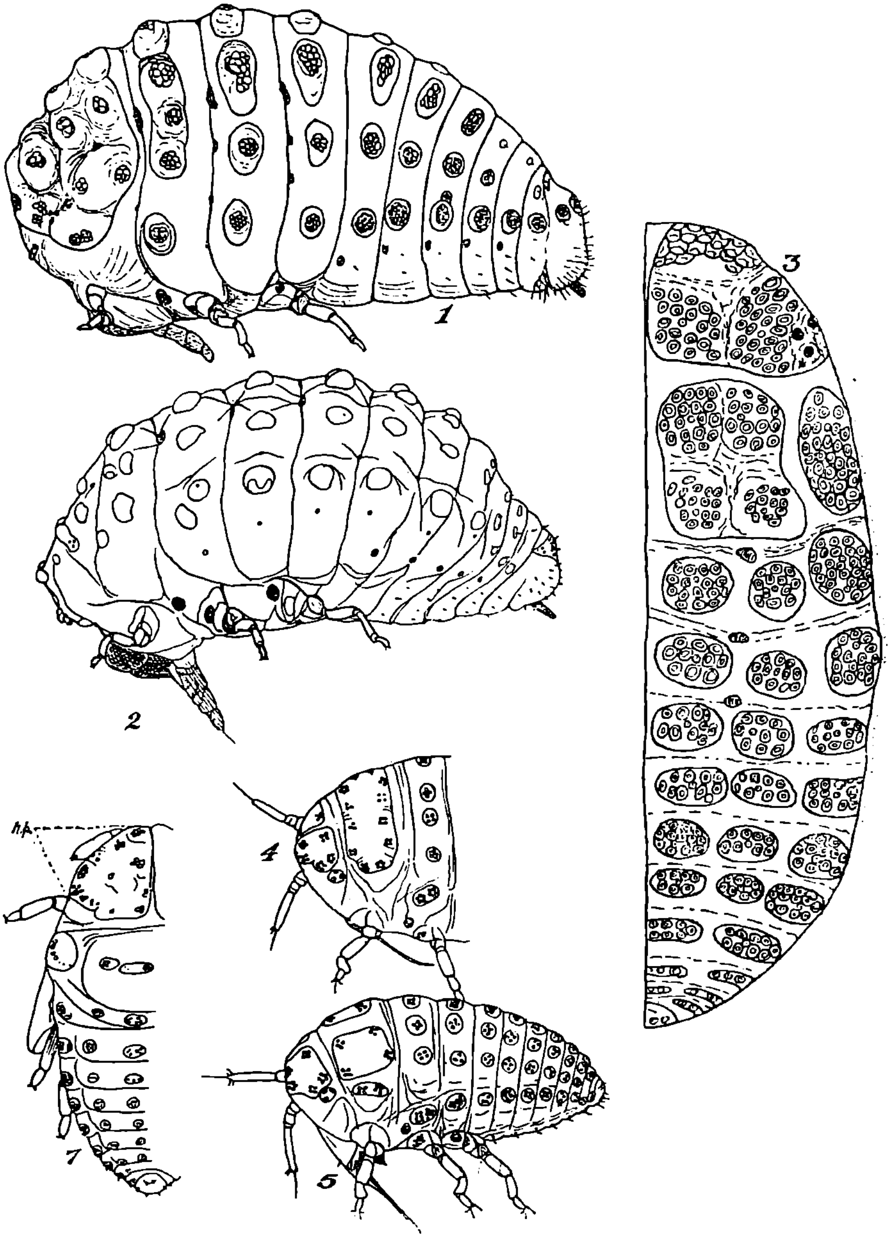


FIG. 1. *Dreyfusia*, colonici stem mother. Side view. x 50 (after Börner).

FIG. 2. *Cnaphalodes strobilobius*, colonici stem mother. Side view. x 30 (after Börner).

FIG. 3. *C. cooleyi*, young larva of fundatrix on spruce showing pore plates of left side. x 170 (redrawn from Börner).

FIG. 4. *C. viridis*, young larva of colonici on larch. x 57 (after Börner).

FIG. 5. *C. viridis* and *abietis*, young larva of fundatrix on spruce. x 57 (after Börner).

FIG. 7. *Pineus strobi*, sexupara nymph. Dorsal view. h.p. = head and prothoracic shield (after Börner).

PLATE VIII.

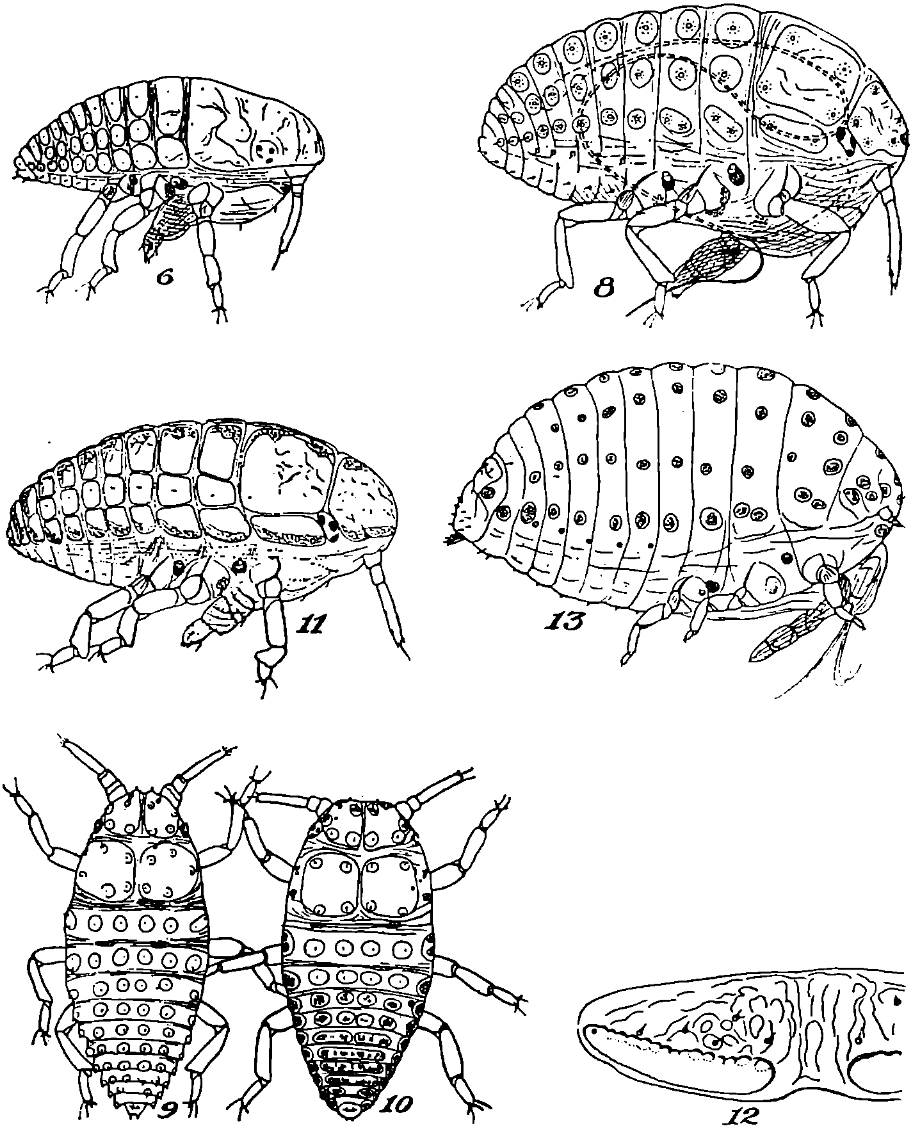


FIG. 6. *Cnaphalodes strobilobius*, young larva of colonici sistens on larch. x 86 (after Börner).

FIG. 8. *Cnaphalodes strobilobius* and *lapponicus*, young larva of fundatrix on spruce. x 86 (after Börner).

FIG. 9. *Cnaphalodes strobilobius*, young larva of colonici progrediens on larch. x 86 (after Börner).

FIG. 10. *Cnaphalodes strobilobius* and *lapponicus*, young larva of gallicola on spruce. x 86 (after Börner).

FIG. 11. *Dreyfusia*, young larva of colonici. Side view. x 100 (after Börner).

FIG. 12. *C. abietis*, gallicola, mesonotal gland area. x 173 (after Börner).

FIG. 13. *C. viridis*, stem mother of colonici on larch. Side view. x 46. (after Börner).

PLATE IX.

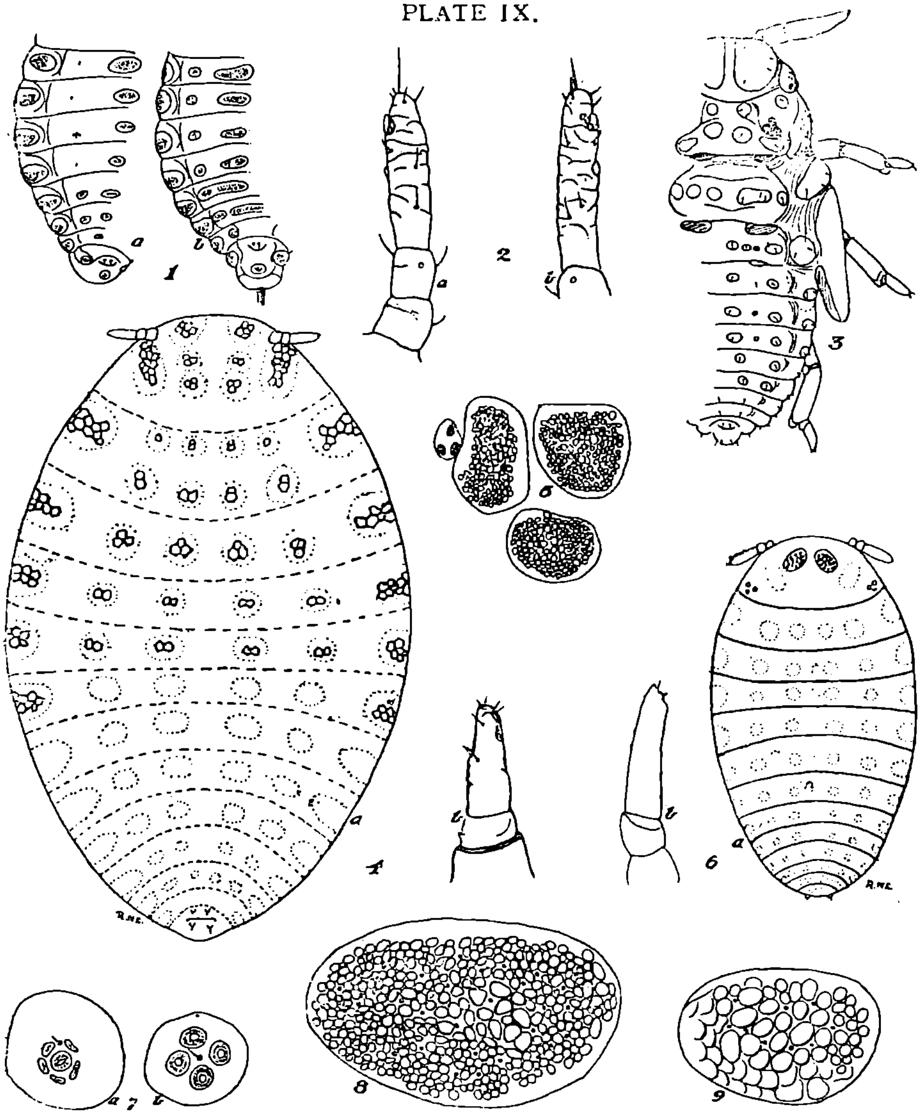


FIG. 1. Arrangement of abdominal plates in (*a*) *Cnaphalodes strobilobius* sexupara; (*b*) *Cnaphalodes lapponicus*, gallicola non migrans. x 60 (after Börner).

FIG. 2. Antennæ of gallicola young larva; (*a*) *Chermes abietis*. x 320. (*b*) *Cnaphalodes strobilobius*. x 330 (after Börner).

FIG. 3. Dreyfusia. Sexupara nymph. x 100 (after Börner).

FIG. 4. *Chermes cooleyi*; (*a*) third stage larva of fundatrix spuria on Douglas fir in spring; (*b*) antenna. x 360 (original).

FIG. 5. *Cnaphalodes strobilobius* and *lapponicus*. Vertical gland plates on head. x 98 (after Börner).

FIG. 6. (*a*) *Chermes cooleyi*, second stage larva of fundatrix spuria on Douglas fir in spring; (*b*) antenna of the same. x 365 (original).

FIG. 7. (*a*) *Cnaphalodes strobilobius* and *lapponicus*. Abdominal pleural plate. (*b*) *Chermes viridis* and *abietis*. Abdominal pleural plate. x 465 (after Börner).

FIG. 8. *Cnaphalodes strobilobius* and *lapponicus*, fundatrix vera, spruce. Marginal plate of first abdominal segment. x 200 (after Börner).

FIG. 9. *Cnaphalodes strobilobius*, fundatrix spuria, larch. Marginal plate of first abdominal segment. x 325 (after Börner).

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