V.—*Researches upon the Larch Chermes* (Cnaphalodes strobilobius, Kalt.), *and their Bearing upon the Evolution of the Chermesinæ in General.*

By Edward R. Speyer, *M.A.* (*Oxon.*), *F.E.S.*

Communicated by Prof. G. C. Bourne, *F.R.S.*

(Received January 27, 1922—Read February 15, 1923.)

[Plates 7 and 8.]

Contents.

	Page.
1. Introductory	111
2. The Biology of *Cnaphalodes strobilobius*, Kalt.	114
3. Numerical Research upon the Parthenogenetic Generations	120
4. Special Summary	129
5. Theoretical Considerations upon the Evolution of the *Chermesinæ* in General	131
6. General Summary	137
Appendix	138
Literature referred to in the Text	146

1. Introductory.

The research which comprises the subject-matter of this paper was carried out at Oxford University in 1913 and 1914, and again over a period of three years from 1919 to 1921. During the former time observations were made mostly in the field, but the necessity of studying this Insect in isolated cultures obtained from a definite source soon became apparent, and not long after such cultures were started, in 1919, was it realised that they were of service in throwing light upon the evolution of the very peculiar sub-family of insects known as the *Chermesinæ*. Insects falling into the Order *Homoptera* comprise a number of well-marked families, of which the *Aphidæ* are perhaps the most important. Of this large and varied family we need only mention two sub-families, the *Phylloxerinæ* and *Chermesinæ*, which both have certain peculiarities in common with Aphids generally, in so far as they exhibit an alternation of a sexual generation with a sequence of asexual parthenogenetic generations. In the two sub-families the sexual individuals (male and female) are always wingless, and the parthenogenetic individuals may be winged or wingless, but that generation which produces the sexual forms is always winged. All the individuals are oviparous.

Phylloxerinæ live upon Phanerogam plants, while the *Chermesinæ* are confined entirely to Conifers. In addition to the alternation of generations referred to above, a second complication arises in the two sub-families, the members of which, throughout their life-cycles, show a marked tendency to produce offspring unlike the parent, but, in the very considerable literature which exists, it does not appear to have been remarked that in each case the parent shows a tendency to produce offspring similar in certain biological and structural characters to the grandparent.

Further, in many forms, at two definite periods in the life-cycle, a migration takes place, by means of two winged generations, in the *Phylloxerinæ* from root to leaf of the host-plant and back, in the *Chermesinæ* from one species of Conifer to another and back.

Finally, the wingless parthenogenetic generation which is produced from the fertile egg causes a *gall* to form from the plant-tissues in the immediate vicinity in which the insect sucks by means of its proboscis.*

In the *Chermesinæ* this gall appears only upon some species of Spruce (*Picea*), on which the preceding sexual and the following parthenogenetic migrant generations are developed. The Spruce is therefore known as the Definitive Host-plant, and the Conifer to which the winged generation migrates, there to start a succession of strictly parthenogenetic generations, is called the Intermediate Host-plant, upon which no gall is produced.†

The biological resemblances in the series of parthenogenetic generations arising on the Definitive Host-plant, on the one hand, and the Intermediate Host-plant, on the other, have given rise to the term "*Parallel Series*" (of DREYFUS), with which the terms "*Paracycly*" of MARCHAL (4) and "*Polycycly*" of BÖRNER (1) are synonymous.

As it is now to be demonstrated, however, that in the *Chermesinæ* there is a definite, though sometimes a masked, alternation of *form* in successive generations, irrespective of the plant upon which the life-cycle, or portions of that life-cycle, exist, these terms of necessity lose their significance, and cannot be used as an interpretation of the stages in cyclic evolution.

It will be explained also that the comparatively few surviving species in which no migration from one plant to another takes place (and in which, coincidently, reproduction is entirely parthenogenetic) present landmarks in the evolution of the species with intensely complex life-cycles and a sexual generation; these have previously been regarded as forms which have become confined to a single host-plant, through degeneracy involving a loss of a portion of the cycle upon one or other of the host-plants. To bring matters of classification to as rapid a conclusion as possible, it will be sufficient to state that, so far, twelve species of *Chermesinæ* have been described from Europe, these being segregated in no less than seven genera, no one of which includes more than three members of true specific rank.

As the various species will be referred to later, the seven genera, with their species, definitive and intermediate host-plants, are here tabulated:—

* For the relation between Gall- and Cone-structure see A. H. CHURCH, 'Botanical Memoirs No. 9,' Oxford University Press, 1920, p. 27.

† An attempt at a gall is, however, made by *Dreyfusia piceæ* RATZ., on *Abies pectinata* and *Abies nobilis*, see BÖRNER (1), pp. 220, 221.

Chermesinæ. European Genera and Species.

Genus.	Species.	Definitive Host-plant.	Intermediate host-plant.
Pineus, SCHIMER . . .	pini, LINNÆUS	Picea excelsa . . Picea orientalis .	Pinus sylvestris.
	strobi,* HARTIG	Picea nigra . .	Pinus strobus.
Cnaphalodes, MACQUART	strobilobius, KALTENBACH . .	Picea excelsa . .	Larix europæa.
	lapponicus, CHOLODKOVSKY .	Picea excelsa . .	None.
Cholodkovskya, BÖRNER .	viridana, CHOLODKOVSKY . .	None	Larix europæa.
Chermes, LINNAEUS . .	viridis, RATZBURG	Picea excelsa . .	Larix europæa.
	abietis, LINNÆUS	Picea excelsa . .	None.
	occidentalis, CHOLODKOVSKY .	Picea excelsa . .	Larix europæa. Larix siberica.
Gillettea, BÖRNER . . .	cooleyi,* GILLETTE	None†	Pseudotsuga douglasi.
Dreyfusia, BÖRNER . .	nüsslini, BÖRNER	Picea orientalis .	Abies pectinata.
	piceæ, RATZBURG	None	Abies nordmanniana. Abies nobilis.
Aphrastasia, BÖRNER . .	pectinatæ, CHOLODKOVSKY . .	Picea excelsa . .	Abies sibirica.

* Imported from North America. † Picea pungens in North America.

Partly through incomplete information concerning the sexual forms, and partly owing to lack of knowledge concerning the life-histories, there has been great confusion in distinguishing varieties from true species. Thus *Pineus strobi*, HARTIG, and *Pineus sibiricus*, CHOLODKOVSKY, are probably western and eastern races of *Pineus pini*, L., respectively.

BÖRNER (1) has, on quite insufficient evidence, enrolled *Cnaphalodes strobilobius*, KALT., and *Cnaphalodes lapponicus*, CHOL., as a single species, and has done the same with *Chermes viridis*, CHOL., and *Chermes abietis*, L. The work of CHOLODKOVSKY (5) and STEVEN (6) points to the parthenogenetic species being entirely distinct, specifically, from those with two host-plants, and PHILIPTSCHENKO (7) has shown, through statistical measurements of the antennæ of *Chermes viridis*, CHOL., and *Chermes abietis*, L., that these two species must be regarded as different.

The Genus *Pineus* is distinct from all others: *Gillettea* and *Dreyfusia* (including *Aphrastasia*) are characteristic, but show affinities with *Chermes*, while *Cholodkovskya* has characters in common with *Cnaphalodes* and *Pineus*.

Chermes and *Cnaphalodes* are distinguished morphologically by differences which would be more appropriate in separating two closely allied species, the same applying to *Dreyfusia* and *Aphrastasia*.

However, to avoid confusion we will retain the genera which have been established, though a reduction to at most five would not seem out of place.

It is remarkable that the genera fall into a natural series in relation to their intermediate host-plants. All species which have migratory generations confine themselves to a species of *Picea* as the definitive host-plant. As intermediate host-plants the genus *Pineus* chooses a species of *Pinus*, *Cnaphalodes*, *Cholodkovskya* and *Chermes* a *Larix*, *Gillettea* a *Pseudotsuga*, *Dreyfusia* and *Aphrastasia* a species of *Abies*.

The same is true, as far as our knowledge goes, of North American species of *Cnaphalodes*, *Chermes*, *Pineus* and *Dreyfusia*. A species of *Pineus* is also recorded from New Zealand on a *Pinus*, and of *Dreyfusia* from India upon *Picea morinda* and *Abies webbiana*.

2. The Biology of *Cnaphalodes strobilobius*, Kalt.

It is now proposed to give a short account of the life-cycle of *Cnaphalodes strobilobius*, Kalt., avoiding all but essential detail. (Figs. 1–17.)

Starting from the Sexual Generation on *Picea excelsa*, the female *Sexualis*, after impregnation, lays a single yellow egg in July. The larva which hatches from the egg in August fixes upon a weak spruce-bud, is provided with wax-glands from which a white wax is secreted, and rests, without further development, until the following April. This is the first-stage larva of the Fundatrix (fig. 2). The insect becomes adult after 3 ecdyses in May, gradually converting the spruce-bud into a Gall.

The adult *Fundatrix* (fig. 8) is wingless, bronze-green in colour, and has numerous wax-glands, which cover the brownish-green eggs with a thick wad of loose wax. The number of eggs laid by the Fundatrix reaches 200. Larvæ hatch from these, secrete a small amount of wax from their sparse dorsal glands, and creep into chambers formed by the swollen bases of the deformed leaves. These are the first-stage larvæ of the *Gallicola migrans* (fig. 3). The chambers of the gall now close, and the contained larvæ, sucking within, reach a nymph-stage after 3 ecdyses. The gall-chambers open in June (fig. 13), the nymphs creep out on to the spruce needles, and, after a 4th ecdysis, are the adult *Gallicolæ migrantes*.

The *Gallicola migrans* (fig. 9), of a reddish colour, is winged, and provided with sparse wax-glands. After flying from the spruce and settling upon the leaves of *Larix europœa*, a maximum of 40 (usually 20) dark brownish-green eggs are laid under a little wax (fig. 14). At the end of June the eggs hatch to larvæ. These are the first-stage larvæ of the *Sistentes* (fig. 4).* They are entirely devoid of dorsal wax-glands, and, after sucking upon the leaves for a short time, retire beneath the bark-scales of the Larch twigs. Like the Fundatrix larva, they remain undeveloped until the following spring, when each attaches itself at the base of an opening bud, which is not affected abnormally, undergoes 3 ecdyses, and becomes the adult *Sistens*.

The *Sistens* (fig. 10) is wingless and of a bronze-green colour; the dorsal wax-glands being limited to a very small area, little wax is secreted over the bronze-green eggs (fig. 15), which are laid, over a considerable period of time, to the number of 200. The eggs hatch in about 10 days to larvæ devoid of dorsal wax-

* Steven (6) has given the name *Colonici* to this and the subsequent generations on Larch. This term is omitted here as being unnecessary and somewhat confusing in the light of what is to follow.

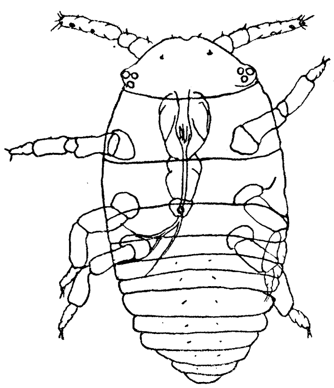


FIG. 1.—Sexualis.

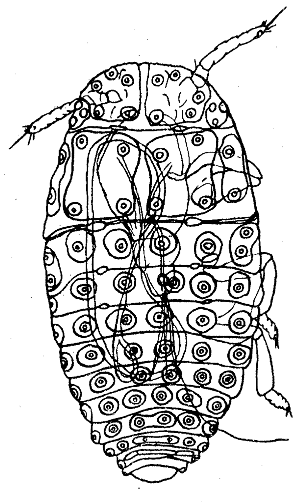


FIG. 2.—Fundatrix.

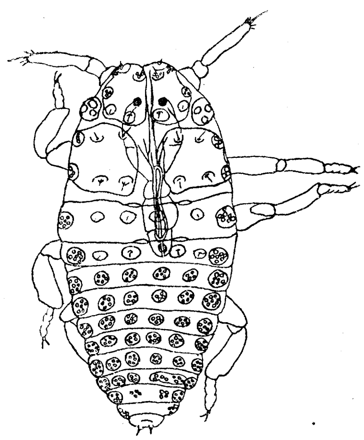


FIG. 3.—Gallicola migrans.

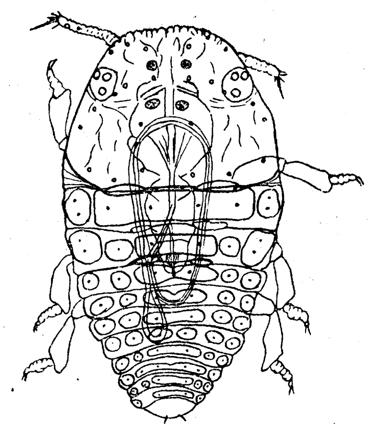


FIG. 4.—Sistens.

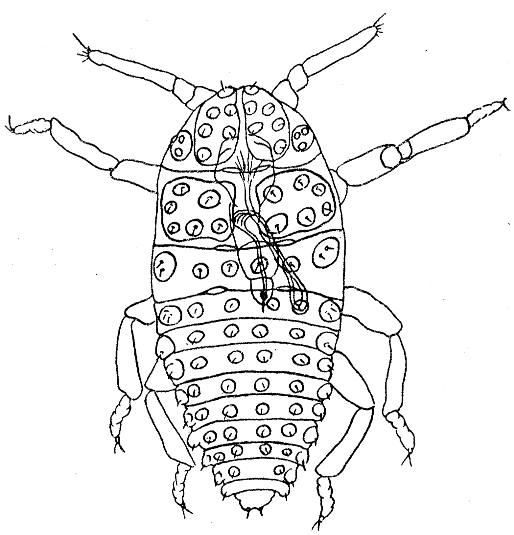


FIG. 5.—Progrediens.

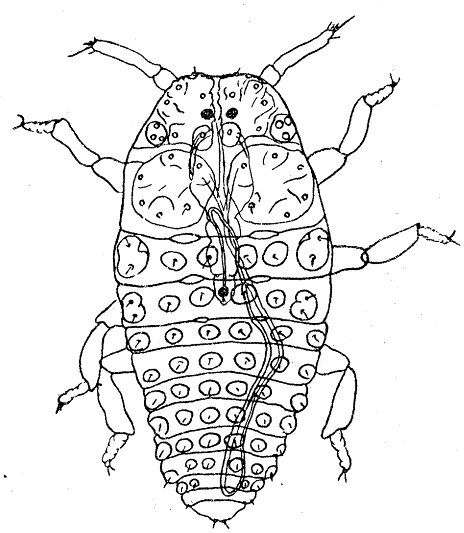


FIG. 6.—Intermediate between Sistens and Progrediens.

Cnaphalodes strobilobius, KALT. (First-stage Larvæ × 150; drawn from cleared preparations.)

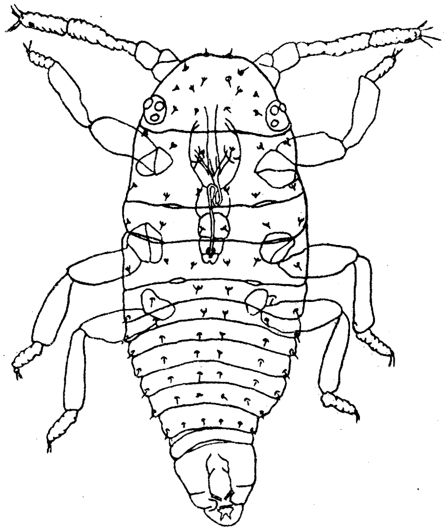


FIG. 7.—Male sexualis × 150, drawn from a cleared preparation.

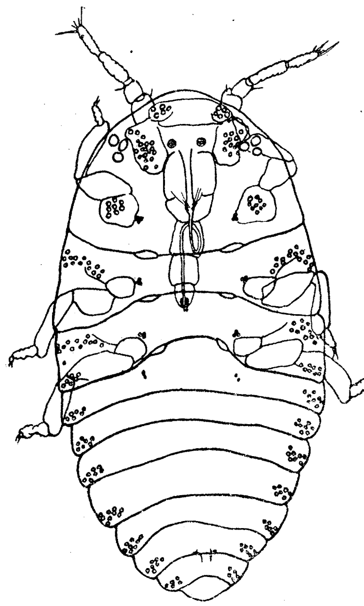


FIG. 7A. — Female sexualis × 150, drawn from a cleared preparation.

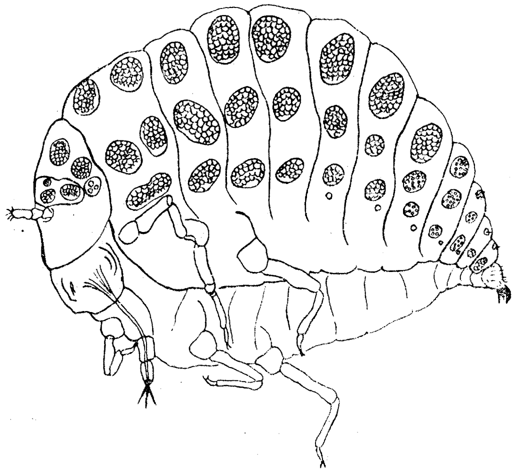


FIG. 8.—Fundatrix adult × 50, side view, drawn from a cleared preparation.

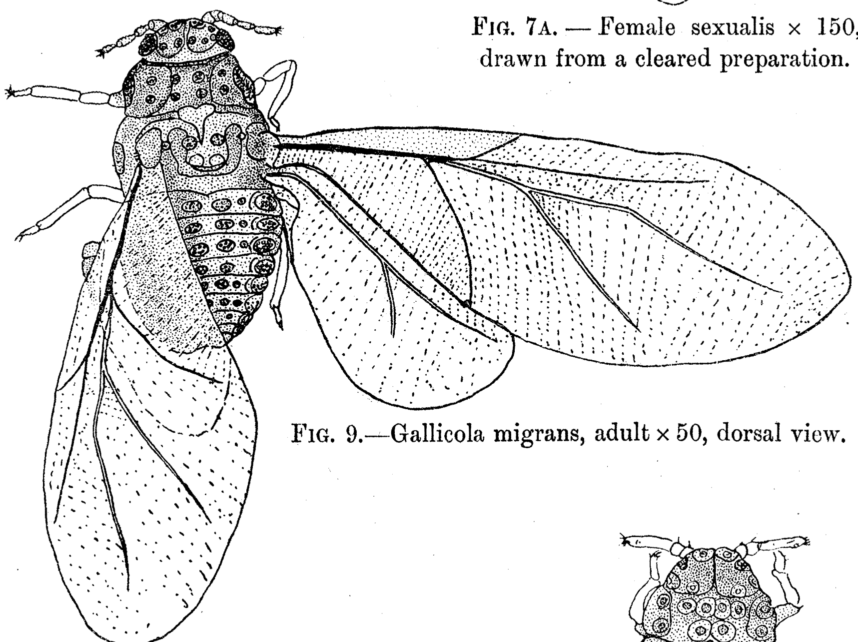


FIG. 9.—Gallicola migrans, adult × 50, dorsal view.

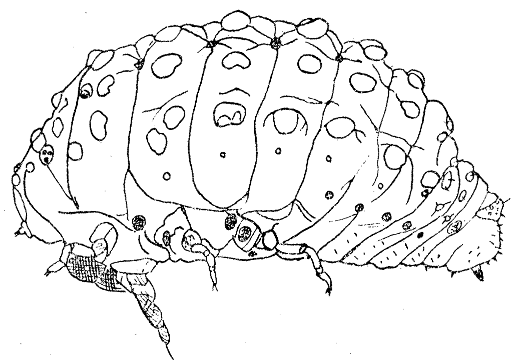


FIG. 10.—Sistens. Side view after BÖRNER. × 50.

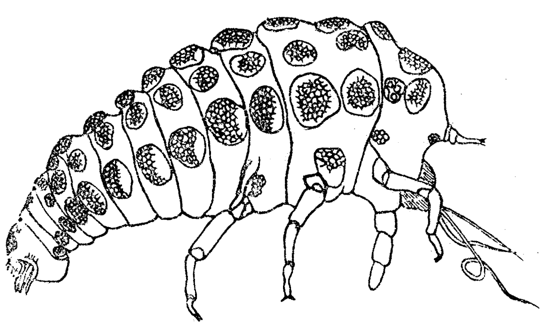


FIG. 11.—Progrediens adult × 50, side view, drawn from a cleared preparation.

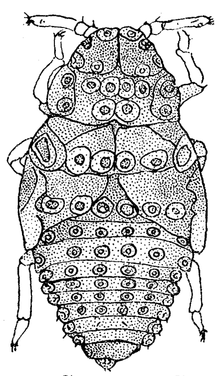


FIG. 12.—Sexupara, Stage IV (Nymph), dorsal view. × 50.

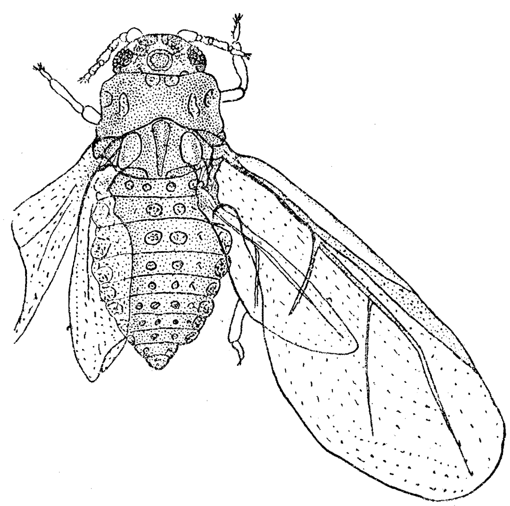


FIG. 12A.—Sexupara, dorsal view. × 50.

FIGS. 7–9.—Adult Stages on Picea Excelsa. FIGS. 10–12A.—Adult and Nymph Stages upon Larix europæa. × 50.

Cnaphalodes strobilobius, KALT. (Adult and Nymphal Stages.)

glands, but immediately distinguishable from the first-stage Sistens larva. These are the first-stage larvæ of the *Progrediens* and *Sexupara*. They suck upon the underside of the Larch leaves and develop forthwith during May and June. After 2 ecdyses the larvæ become differentiated, the large majority attaining a stout form, but a few remaining slender.

The stout forms moult a third time, and begin to secrete wax from their copious glands, but do not become adult until a 4th ecdysis is completed. These are the adult *Progredientes*.

The *Progrediens* (fig. 11) is wingless and of a black colour, and lays 20–50* (but usually not more than 30) brown eggs under a large secretion of wax (fig. 16). These eggs hatch exclusively to larvæ of the *Sistens* type. They rest till the following spring, and their fate will be traced later.

To return to the few individuals—offspring of the first *Sistens* generation—which remain slender after the 2nd ecdysis, these become nymphs (fig. 12) after a 3rd and adult after a fourth moult. They are the *Sexuparæ*.

The *Sexupara* (fig. 12*a*) is winged, and much resembles the Gallicola migrans, which, however, has fewer wax-glands than the former. After sucking upon the Larch leaves for a considerable time, the Sexupara flies to the old leaves of a Spruce, where not more than twelve eggs of a yellow colour are laid, under a considerable wax covering (fig. 17). The eggs hatch in June and July to first-stage larvæ of the *Sexuales* (fig. 1). Though the Sexuales of *Cnaphalodes strobilobius* have been known since 1887, information available upon their structure and development is of the sparsest, and they do not appear to have been figured in any paper in Chermes literature. A few details can be given here from material collected and studied at Oxford in June, 1920.

As the Sexuparæ actually bred in culture would not lay eggs when transferred from Larch to Spruce, owing, apparently, to actual flight of some duration being essential to oviposition, it was found necessary to study the insects after they had made their migration naturally. The eggs laid by them hatched in about ten days to first-stage larvæ. As far as can be judged, these larvæ are all similar in external structure; they are of a yellow colour, 0·5 mm. in length and 0·24 mm. in greatest breadth (fig. 1). Unlike the larvæ of all the other generations, they are entirely devoid of gland-structures, and the hairs upon the front, the sides of the abdominal segments, and the sterna, are so short as to be hardly discernible even under high magnification.

Again, instead of creeping away from the batch of eggs, they remain under the wool and wings of their parent, in which situation they undergo their entire metamorphosis (fig. 17). All attempts to induce the larvæ to develop away from their parent proved unsuccessful, and the number of ecdyses was not possible of

* The highest number observed is 97, but this is exceptional; great variation occurs in the number of eggs laid by parthenogenetic females, in other groups of Homoptera.

determination by direct observation. STEVEN (6) records that both sexes moult four times at intervals of five to seven days.

From the material examined, it would appear that the sexes become differentiated already in the second stage—*i.e.*, after the first moult, but the distinction lies only in the length of the hairs, which, longer in the male than the female, are still very short in both sexes. As the moults succeed each other, the antennæ become much elongated, and while the hairs of the male lengthen, those of the female disappear. The adult male (fig. 7) measures 0·60 mm. in length and 0·24 mm. in greatest breadth, so that the growth from the hatching of the egg is entirely one of length. The proboscis is well developed and the stylets are short. The character of the antennæ and disposition of the hairs are shown in fig. 7. The adult female (fig. 7*a*) measures 0·7 mm. in length and 0·4 mm. in greatest breadth. The segments of the head, thorax and abdomen are dorsally provided with diffuse glands, not raised upon chitin plates; at the bases of the coxæ and on the sternum of the first abdominal segment are a pair of small glands. The antennæ have four joints, but are shorter than those of the male.

It is remarkable that the sexual forms seem to show no distinctive character in common with any of the parthenogenetic generations; they are very small in size; the three-facetted eyes, which are larval in character, are common to all the wingless adults, while the antennæ approach distantly those of the winged forms, but retain the larval sense organs. It is important that the Sexuparæ seem to be either entirely male- or entirely female-producing, though further observation is desirable upon this point. After copulation, the female lays one yellow egg, which hatches to the Fundatrix, and the cycle begins again.

Summing up the chief characteristics of the main portion of the cycle, the following synopsis gives the sequence of generations:—

On *Picea excelsa*.

Fundatrix . . .	1st stage larva (derived from fertile egg) resting form. Dorsal wax-glands developed. Proboscis-stylets long for piercing bark.
	Adult in 4th stage. Wingless. Dorsal wax-glands profuse. Productivity high.*
Gallicola migrans.	1st stage larva develops forthwith. Dorsal wax-glands present. Proboscis stylets short for sucking within the gall.
	Adult in 5th stage. Winged. Dorsal wax-glands few. Productivity low. Migrates to *Larix europæa*.

* All the parthenogenetic forms lay eggs which are supported upon long stalks.

On *Larix europæa.*

Sistens	1st stage larva resting form. Dorsal wax-glands absent. Proboscis stylets long for piercing bark. Adult in 4th stage. Wingless. Dorsal wax-glands very few. Productivity high.
Progrediens . . .	1st stage larva develops forthwith. Dorsal wax-glands absent. Proboscis-stylets short for leaf-sucking. Adult in 5th stage. Wingless. Dorsal wax-glands profuse. Productivity low.
Sexupara . . .	1st and 2nd stage larva identical with those of *Progrediens.* Adult in 5th stage. Winged. Dorsal wax-glands fairly developed. Productivity low. Migrates to *Picea excelsa.*

On *Picea excelsa.*

Sexuales	1st stage larva develops forthwith under cover of the Sexupara. Wax-glands entirely absent. Proboscis-stylets short for leaf-sucking. Adult, both male and female, in 5th stage. Wingless. Dorsal wax-glands absent in male. Feebly developed in female. Productivity very low. The single fertile egg gives rise to the Fundatrix.

The *Progrediens* is by no means the least interesting of the parthenogenetic generations, for it is the only type of wingless adult which undergoes four ecdyses; being a sister-form, and a clear dimorphism of the *Sexupara,* we must regard the Progrediens as potentially a winged form, a conclusion which has an important bearing upon the evolution of the cycle, for we have no evidence that the truly wingless adults have been derived, through selection, from types which were once provided with wings.

It will be readily seen that, as far as the parthenogenetic generations are concerned, there is a most striking *alternation of form,* a winged, leaf-feeding, lowly-productive type being succeeded by a wingless, stem-feeding, highly-productive type. When the sexual generation is reached, however, this alternation breaks down in a singular manner. On the analogy of the *Progrediens,* the Sexuales must be regarded as potentially winged; they are lowly-productive and are leaf-feeders, yet they follow the *Sexupara* generation, which in these respects has similar characters. Between the *Sexuales* and the *Fundatrix,* on the other hand, there is a complete alternation, so that the sexual generation must certainly be regarded as the essential starting-point from which the alternation arises, while the Sexupara marks the termination of that alternation.

It is the Sexual generation, then, which is the crux of the whole life-cycle, a fact which, for other reasons, was recognised by BLOCHMANN in 1887, and which, we think very wrongly, was discarded by BÖRNER in 1908.

The wool-like wax which is secreted from special glands is adaptive to protecting the eggs and in some cases the first-stage larva, not from cold, but from excessive heat or light rays. The production of this wax is, however, irregular, for it is produced in great quantity by the Fundatrix, yet the Sistens, which oviposites at the same time of year, secretes very little. It has been found that if the eggs laid by the Progredientes or Sexuparæ have the wax removed and are exposed to bright light, quite a large percentage fail to hatch, while if kept under similar conditions in dim light, larvæ emerge from at least 95 per cent.

The presence or absence of wax-glands, then, is in the nature of a superficial adaptation, the importance of which must not be overrated from an evolutionary standpoint.

3. *Numerical Research upon the Parthenogenetic Generations.*

1. *The Sexupara.*

It will be remembered that the *Gallicola migrans* flying from the Spruce, lays, upon Larch leaves, eggs which hatch exclusively to larvæ of the *Sistens* type, and that these Sistentes, after a resting period in the first stage, lay eggs which hatch exclusively to larvæ of the *Progrediens* type, but that in the 3rd stage of metamorphosis, a few of them become differentiated and develop to the winged *Sexupara*, while the majority develop to the wingless, but potentially winged, *Progrediens.*

In 1920, it was observed that very few Sexuparæ were present on Larch-plants of 1–3 years of age in nurseries, while great numbers of these winged forms could be collected from trees 15 years of age in the immediate vicinity.

Reasons for such differences have been ascribed to seasonal variation and to difference in food obtained by the developing larvæ, but as both winged and wingless forms will arise as offspring of the same parent, and after feeding side by side on the same leaf this explanation becomes obviously doubtful.

It is, in fact, practically certain that the differentiation of the two forms takes place during maturation of the ova within the parent, and that the external difference does not become apparent until the 3rd stage is reached.

An attempt was made to obtain exact figures of the proportions of winged to wingless individuals by infecting isolated Larch plants with definite numbers of larvæ hatching from the eggs of a single Sistens in each case, but through the transference of the larvæ from the plant of their origin to another, such large numbers failed to develop that the experiment proved unreliable.

In 1921, a count of the Sexuparæ from two plants of the same age, growing under similar conditions, was taken. The figures can only be approximate, but they are considered representative.

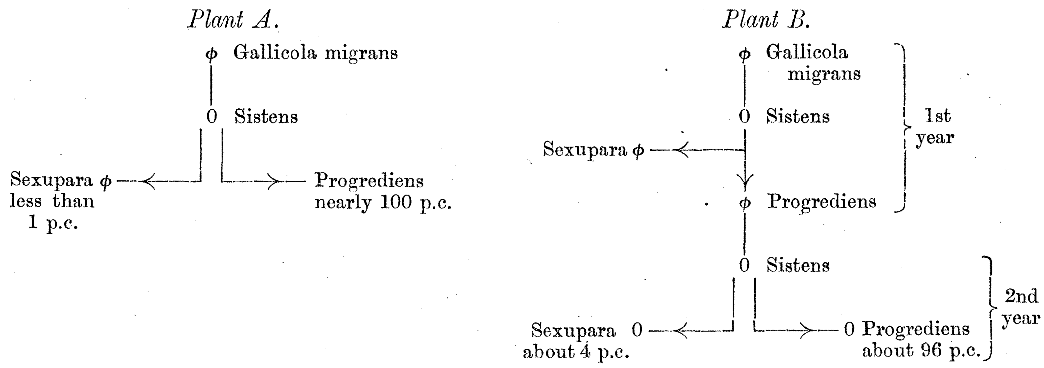
Plant A was infected with *Gallicolæ migrantes* from Spruce in June, 1920. About 20 Sistentes oviposited in March and April, 1921, each laying an average of 100 eggs, so that the total larvæ of the Progrediens type was in the region of 2000; 17 *Sexuparæ* developing from these were collected from May 21–25, which gives a proportion of considerably under 1 per cent.

Plant B was infected with *Gallicolæ migrantes* from Spruce in June, 1919; 10 Sistentes oviposited in March and April, 1921, laying an average of 100 eggs, so that the total larvæ of the Progrediens type was in the region of 1000; 40 *Sexuparæ* developing from these were collected from May 20–29, giving a proportion of about 4 per cent.

Judging, then, from the large numbers of winged forms which appear on older trees, where the parthenogenetic generations have been developing for numbers of years, we can conclude that the *Sexuparæ* appear first in very small numbers, and increase from year to year at the expense of the Progredientes. How far this process goes we are unable to judge, but it is very improbable that the Sistentes ever produce larvæ which develop exclusively to winged forms.

The Sexuparæ appear only in the first generation of Progredientes each year, and are never produced by subsequent Progrediens generations.

The results of the observations are here given in tabular form :—



2. *The Progrediens.* (See Appendix II, p. 139.)

From Plant A above, and from a second plant similarly infected with Gallicolæ in 1920, the eggs of the *Progredientes* were collected between May 23 and July 7, 1921. From the 24 egg-clusters with an average of 24 eggs, 315 larvæ were hatched; these were all of the *Sistens* type,* and will not become adult until 1922.

On several plants, including *Plant B*, similarly infected with Gallicolæ, but in 1919, no larvæ other than *Sistentes* were observed to hatch from the eggs laid by Progredientes in 1920. The *Progredientes* of the 1st year, therefore, give rise entirely to *Sistentes*, in conformity with the alternation of form.

In 1921, however, the *Progredientes* on *Plant B*, derived from the *Sistentes* of the

* CHOLODKOVSKY (5) has obtained similar results.

2nd year, behaved differently, though they developed under conditions similar to the *Sistentes* of the 1st year upon *Plant A*.

From *Plant B*, between May 23 and July 7, 1921, 15 egg-clusters with an average of 10 eggs each hatched to 93 larvæ of the *Sistens* type and 10 larvæ of the *Progrediens* type, so that here, for the first time, the alternation of form is broken, the *Progrediens* parent giving rise to a few *Progrediens* larvæ amongst a majority of *Sistentes*.

The greatest number of Progredientes larvæ obtained from a single egg-cluster was 3, while some clusters gave entirely larvæ of the *Sistens* type, as in the first year.

The *Progredientes* larvæ developed and their eggs were collected between June 28 and August 17, 1921; 42 egg-clusters, with an average of 5 eggs each, hatched to 124 larvæ entirely of the *Sistens* type, thus restoring the alternation.

No difference in the structure of these Sistentes and Progredientes was discernible as compared with those forms as produced in earlier generations, and measurements taken of the size and length of the antennal joints and hairs, and also of the proboscis and legs, showed no divergence out of the ordinary range of variability. A few of the Progrediens offspring, however, showed intermediate characters between the Sistens larva and the Progrediens larva (fig. 6), and these will be referred to later. One difference, however, was observed, in the *Progredientes* of the second generation, in that some of them reached maturity already in the 4th stage.*

From two other plants infected with a mixture of the two generations of second year *Sistentes* 30 egg-clusters, with an average of 15 eggs each, laid by the *Progredientes* immediately derived from the former, and collected from May 28–July 18, 1921, hatched to 211 *Sistentes* and 50 *Progredientes*, the latter including a few intermediate forms, thus giving about 25 per cent. *Progredientes*. These *Progredientes*, from which 40 egg-clusters, averaging 5 eggs in each, were collected between July 7 and August 4, produced, again, entirely *Sistentes*, the actual number obtained being 124.

The results of these experiments are, for convenience, tabulated, so that they may be compared with each other (see p. 123).

To obtain information as to the subsequent progress of the Progrediens generations, reference to field observation is necessary.

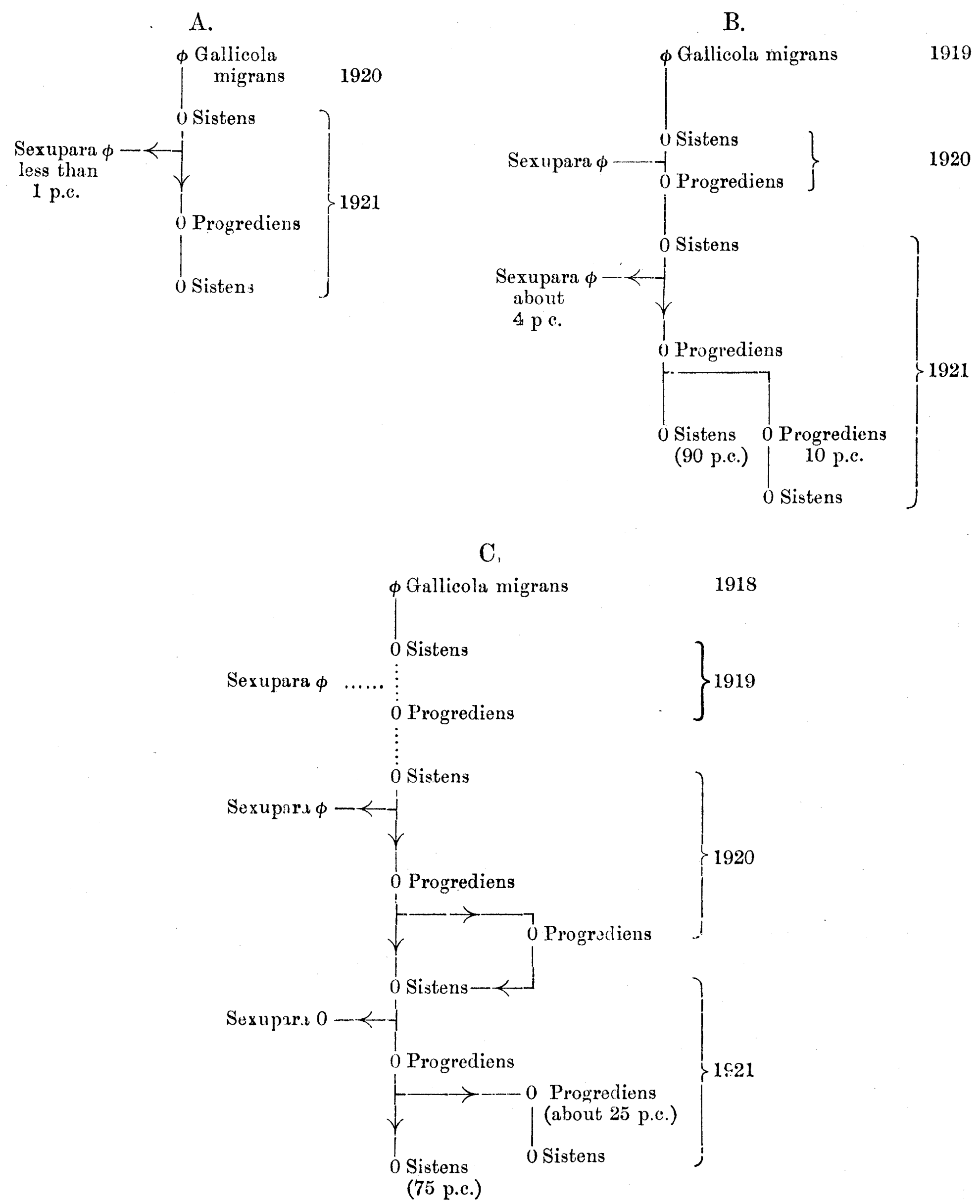
It is essential to recognise that Progredientes taken from trees in nature belong to mixed generations, for the Gallicolæ from Spruce make an annual visit to the Larch, and each year an ever-increasing number of Sistentes, derived directly or indirectly from them, come into existence.

A general census of larvæ hatching from eggs laid by Progredientes will, however, give a clue to the procedure if the age of the trees from which they are collected is noted.

As examples, a count of the offspring of the first Progrediens generation of 1913,

* STEVEN (6) has referred to this.

upon a tree of about 10 years of age, gave a proportion of 60 per cent. Sistentes and 40 per cent. Progredientes. A similar record, but from a much older tree, in 1914, gave 25 per cent. Sistentes and 75 per cent. Progredientes. Upon young trees, in October, 1919, the *last* Progrediens generation of the year gave rise to 12 per cent. Sistentes and 88 per cent. Progredientes (the count involving nearly 400 individuals).



Finally, upon 15 year-old trees, during October, November, and December, the last Progrediens generation of the year produced 6 per cent. Sistentes and 94 per cent. Progredientes.

Before drawing conclusions which point strongly to the fact that the Progredientes gradually eliminate the Sistentes the further removed they become in their parentage from the Gallicola migrans, we append a brief note upon a parallel elimination in the case of the *Sistens*.

3. *The Sistens.* (See Appendix I, p. 138.)

It has been pointed out that the *Gallicola migrans* gives rise only to *Sistentes*, and these latter only to larvæ of the *Progrediens* type.

This sequence must be continued for a number of years from the Sistentes which are derived from the first Progrediens generation of each year. In February, 1914, 1672 eggs, laid by Sistentes of various origins upon a Larch tree, of about 10 years of age, hatched exclusively to larvæ of the *Progrediens* type. In April and May, 1920, 1842 eggs, laid by Sistentes on plants of not more than 3 years' age, produced entirely larvæ of the Progrediens type, and similar results obtained on the same plants in 1921.

It is well-known that a great majority of the Sistentes perish during the resting period (see STEVEN [6]), but this applies less to individuals arising from the Gallicolæ and Progredientes of the first annual generation than to those arising from the later Progrediens generations.

However, in May, 1919, some Sistentes, collected from a tree of at least 40 years old, produced both larvæ of the *Progrediens* and the *Sistens* type, as follows :—

Eggs collected.	Eggs hatched.	Progrediens larvæ.	Eggs hatched.	Sistens larvæ.	Total.
May 17, 1919	May 18–25	70	May 23–31	38	108
	May 21–26	19	May 18–31	139	158
	May 21–25	7	May 18–27	81	88
	Total	96		258	354

Four other egg-clusters produced 329 larvæ, entirely of the *Progrediens* type. STEVEN (6) has obtained egg-clusters from Sistentes which hatched entirely to larvæ of the *Sistens* type.

Conclusions upon the Numerical Research.

Most striking is the fact that in all three types of parthenogenetic forms upon the Larch—namely, Sexupara, Progrediens and Sistens—one type increases, as generation after generation is produced, at the expense of one or other, or even both of the two others.

First we see the Sexupara arising in very small numbers, and gradually increasing from year to year in the first annual generation produced by the Sistens. Then the Progrediens type makes its appearance in small numbers amongst the offspring of the parent Progrediens, which should, in accordance with the established alternation of form, give rise only to Sistentes, and subsequently increases at the expense of the Sistens type.

Lastly, the Sistens type, after a great number of generations, makes its appearance amongst the offspring of the parent Sistens, which should give rise only to the Progrediens-Sexupara type, which it finally eliminates.

Now the Sexupara is clearly a true dimorphism of the Progrediens, and, owing to BÖRNER'S observation that a single individual Sistens will give rise to larvæ of the Sistens and Progrediens type, both he and MARCHAL (4) uphold that the Progrediens is also a dimorphism of the Sistens, the latter even going so far as to suggest that the dimorphism in this case has arisen by mutation. From the facts which research upon isolated stocks of known origin have brought to light, we cannot hold the view of those authors who laid no stress upon the clear existence of an alternation of form in the successive generations of the main cycle upon both host-plants.

In the case of *Cnaphalodes strobilobius*, it has been demonstrated that a regular alternation of form is pursued in successive generations until the third year of parthenogenetic reproduction upon the Larch. At this point the Progrediens gives rise to a small number of Progredientes amongst a majority of Sistentes. This is a clear divergence from the normal procedure of reproduction, and does not constitute a true dimorphism in the Sistens and Progrediens types.

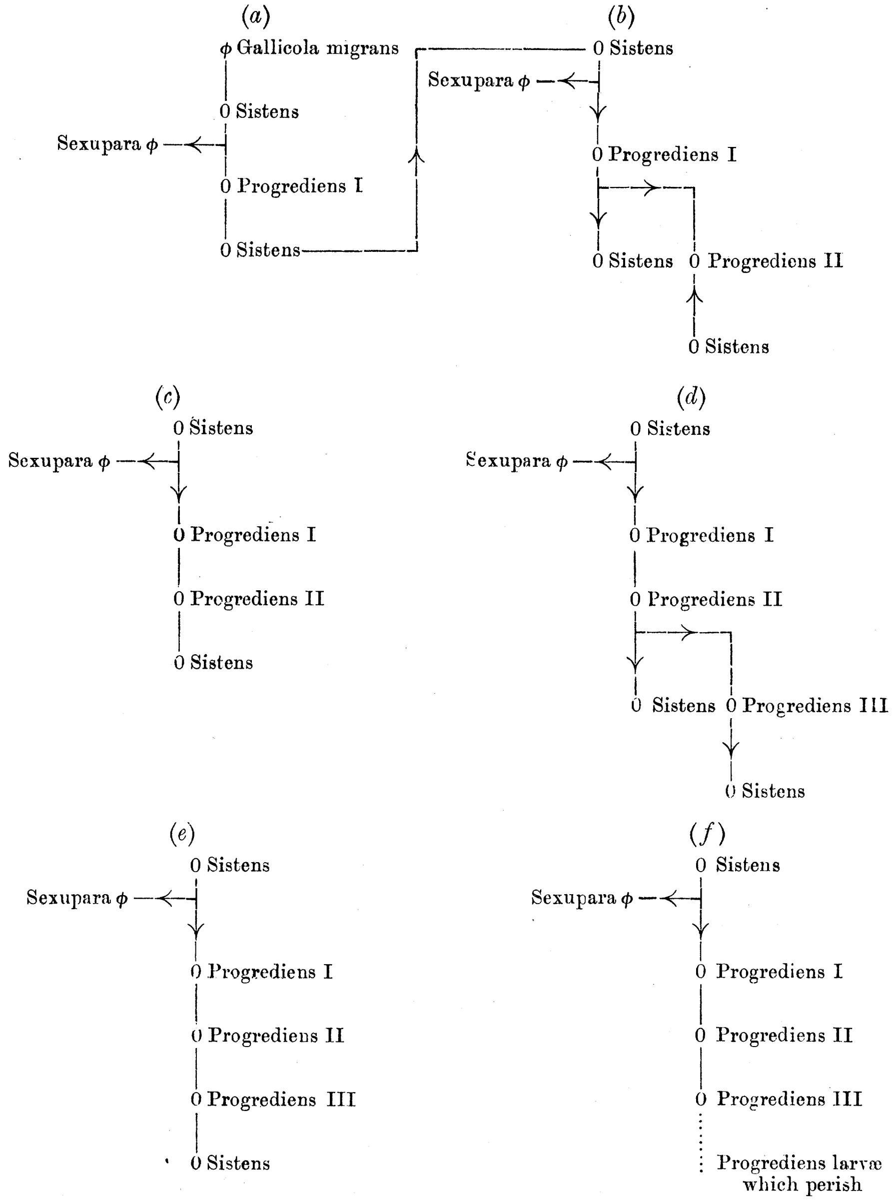
The abnormally-produced Progredientes, indeed, rectify the divergence, by giving rise exclusively to Sistentes.

In the following (fourth) year the figures show that the abnormality is intensified in the first Progrediens generation, though a return to the normal is again effected in the second generation.

From the recorded observations of various authors and from those given above, it seems practically certain that divergence from the normal alternation of form increases still further, and leads to an entire elimination of the Sistens type from the offspring of the first Progrediens generation. A second complete generation of Progredientes is thus constituted, this last producing offspring of the Sistens type. Later, by the same process, these latter Sistentes are again replaced by Progredientes, so that finally a succession of Progrediens generations results, running through the summer and autumn, until the offspring of the third generation perish with the leaf-fall.

To make this clear a series of diagrams (*a–f*) is set out to show the course of elimination of the Sistens type, and the resulting constitution of successive Progrediens generations.

It is noteworthy that both CHOLODKOVSKY and NÜSSLIN have bred through a sequence of generations comparable with diagram (*e*) (see MARCHAL [4], pp. 177 and 178) :—



Elimination of the Progrediens and Sexupara by the Sistens will take place concurrently with this, but sufficient information is as yet not forthcoming to include this in the scheme.

The gradual increase of the Sexupara over the Progrediens in the first generation of each year is not strictly comparable with the elimination processes which occur between Sistens and Progrediens, for the Sexupara is a true dimorphism of the Progrediens. It has been suggested by various authors that the proportions of the various types to each other are determined by climatic or other environmental causes; no clear proof of this has been put forward, but we have strong evidence to show that climate plays little if any part in determining or influencing the proportions of one type to another. That referring to the Sexupara and the first annual Progrediens generation has already been detailed, but observations upon the last Progrediens generation collected from Larches in 1913 may be added.

Progredientes larvæ taken from trees of about 15 years of age were kept on young plants in a warmed glass-house in September, 1913, and allowed to mature and oviposit under these conditions during November and December.

Of 103 eggs deposited by 7 adults, 89 hatched to larvæ of the Progrediens type, and none to larvæ of the Sistens type. One egg-cluster of 24 eggs was subjected to frost after being laid, and 53 days passed before the last larva had hatched, but all the larvæ were of the Progrediens type.

As compared with this, of 122 eggs deposited by six adults under natural conditions, 87 hatched to larvæ of the Progrediens type, and 9 to larvæ of the Sistens type; of these three egg-clusters, comprising in all 62 eggs, hatched exclusively to larvæ of the Progrediens type, and 100 per cent. of the eggs produced larvæ. Two clusters were brought into a warm temperature after being laid, and hatched entirely to Progredientes. Keeping in mind that the eggs belonged to generations of mixed origin, the small number of Sistentes amongst the larvæ produced under natural conditions is not considered sufficient to show that a warm temperature was the cause of their appearance amongst a great majority of Progredientes. Further, if climatic conditions had any marked influence in determining the proportions, a majority of Sistens larvæ, which pass through a resting period till the spring, should be expected, rather than a majority of Progrediens larvæ which perish.

We must conclude, from observations upon the proportions of Sexupara to Progredientes in the first summer generation of each year, and of Progredientes to Sistentes in subsequent generations, that environmental conditions are factors which play little, if any, part in the determination of those proportions.

Hence it is only open to us to postulate that there exists a definite mechanism which governs the normal alternation of form in successive generations. At a certain period in the life-cycle on the intermediate host-plant, this mechanism appears to break down, and though at first there is a recovery, later the failure in this mechanism results in the parent producing offspring similar to itself.

No doubt this mechanism lies in the maturation processes of the ova, and may be governed by the actual manner in which the chromosomes divide.

Sections of various stages have been prepared, but the difficulty in interpretation of the cytology is such that it would be very inadvisable to draw conclusions from the material examined.* Whatever the cytological conditions may be, it is clear that the

* In his account of the 'Biology of Dreyfusia nüsslini, B,' MARCHAL ((4) p. 180, figs. 10 and 11) gives figures of the second and fourth stages of the Progrediens. He states, beneath these figures, that during development from the second to the fourth stage, the number of ovarioles becomes reduced from four to two or three, on each side of the gut. We consider that this process has no bearing upon phenomena which may occur in the Progrediens generations of Cnaphalodes strobilobius, KALT., for in Dreyfusia

disturbance in the alternating mechanism tends to bring the parthenogenetic generations on the intermediate host-plant to an end. For it seems that the same processes which work in the elimination of Sistentes from the Progrediens generations, also cause the Progredientes to disappear from the Sistens generations, and it has been pointed out that when Progredientes are produced late in the year, they perish, and that few, if any, Sistentes arising from later summer generations survive the resting period. It must be added that several attempts have been made to induce these Sistentes to mature, but in every case the insects have died in the first larval stage.

However, this failure is not necessarily adverse to the survival of the species, for the Sexuparæ, year by year, and in increasing numbers up to a certain point, are flying to the Definitive Host-plant, there to set the main cycle in motion again. Through the failing mechanism, however, vast numbers of Sistentes and Progredientes die, but these, being incapable of migration, would, in a few years, become overcrowded, to the extinction of themselves and the Sexuparæ and so of the species, if they were allowed to survive.

Finally, in holding to the view that the winged Sexupara is a dimorphism of the Progrediens, we see no reason to suppose that the former has arisen by a process other than by Natural Selection.

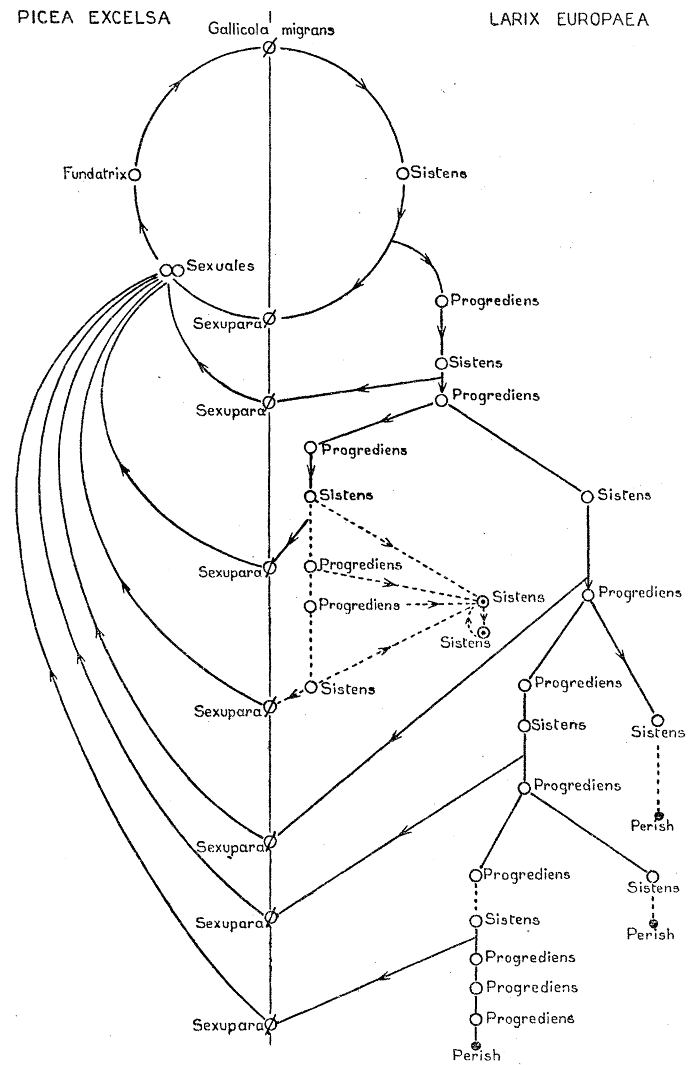
Intermediate Forms.

Larvæ showing characteristics of both the Progrediens and the Sistens have been obtained in small numbers already amongst the offspring of the first Progrediens generation of the second year, and they continue to appear whenever the Progrediens produces both Progrediens and Sistens larvæ (see fig. 6).

They vary in their intensity from the Progrediens towards the Sistens type; the proboscis stylets are always longer than in the typical Progrediens and so bear towards the Sistens type; but the arrangement of the separate rounded plates on the dorsal surface of the abdominal segments (which are characteristic of the Progrediens larva) remains constant. The characters of the head and prothorax tend towards the Sistens larva.

BÖRNER (2) has figured one of these intermediates as the Sistens larva of "? Cnaphalodes lapponicus (CHOL.)," a species which is confined to the Spruce only, and to which these forms and BÖRNER's figure have no relation. Though it is probable that they do not reach maturity, the intermediates have some significance, as they probably show a tendency towards a restoration of the alternation of form, which is attained in the subsequent generation. They have been included in the figures given as Progredientes, and their numbers are not sufficiently great to affect the proportions materially.

nüsslini the Progrediens gives rise to a number of Sistentes which pass through a resting stage, and at the same time a number of Sistentes which develop forthwith (termed Hiemo- and Aestivosistens respectively). Here we suggest that the production of the two forms is determined by the amount of nutriment in the ova.



Approximate Scheme of the Life-Cycle of *Cnaphalodes strobilobius*, KALT.
The dotted lines indicate the nature of the generations eventually reached after a long period of parthenogenetic reproduction.

4. SPECIAL SUMMARY.

The following points, which do not appear to have been brought out in the work of previous authors, will serve to summarize the chief characteristics in the biology of *Cnaphalodes strobilobius*, KALT. :—

A. *The Life-cycle in General.*

1. An *Alternation of Form* in successive generations upon the two host-plants (*Picea excelsa* and *Larix europæa*) is the normal course of biological development. This alternation relates to: (*a*) The presence and absence of wings; (*b*) low and high productivity; (*c*) adaptation to leaf- and stem-feeding. The offspring, therefore, resemble the grandparent in these characters.

2. The alternation is terminated by the winged *Sexupara* generation, in giving rise to the Sexual individuals, which are considered as potentially winged forms.

3. The *Sexuales* start the alternation in giving rise to the *Fundatrix*. The mature male and female, though retaining general characters common to larval stages of parthenogenetic generations, differ morphologically from the individuals of all other generations. They approach roughly, however, the adults of the winged generations in the structure of their antennæ.

B. *The Parthenogenetic Generations upon the Larch.*

1. The wingless *Sistens*, produced by the winged *Gallicola migrans*, gives rise, *in the first year*, to *Progredientes*, which are held to be potentially winged forms, and to a very small number of winged *Sexuparæ*, which represent a true dimorphism of the Progrediens.

The Progredientes give rise entirely to Sistentes, in conformity with a true alternation of form.

2. *In the second year*, these Sistentes give rise again to Progredientes and Sexuparæ, but there is an increase in proportion of the latter to the former, as compared with the first year, irrespective of environmental conditions. The Progredientes produce, amongst a majority of Sistentes, a small number of Progredientes. The appearance of the latter is interpreted as a *failure in the mechanism* which effects a normal alternation of form. The second generation of Progredientes thus constituted restores that alternation in producing a pure generation of Sistentes.

3. *In subsequent years* the proportion of Sexuparæ to Progredientes increases further. Through intensification of failure in the alternating mechanism, the Sistentes are gradually eliminated from the generations arising from the Progredientes, so that finally a succession of Progrediens generations results, the Sistens being replaced entirely by the Progrediens type.

4. After a number of years the Sistens, through a similar process, fails to produce a pure generation of Progredientes and Sexuparæ, and gives rise also to a number of Sistentes. This results, finally, in a total elimination of the Sexupara-Progrediens generation, and Sistens produces Sistens.

5. Through this elimination of one type by another, the wingless parthenogenetic generations on the Larch come to an end.

6. Individuals intermediate in structure between Sistens and Progrediens show an effort to return to a normal alternation of form.

7. Though both Sistens and Progrediens types are produced by a single individual Sistens or Progrediens, these forms cannot be regarded as a dimorphism of one another, as held by Börner and Marchal, owing to the special circumstances attendant upon their origin.

THEORETICAL CONSIDERATIONS UPON THE EVOLUTION OF THE *Chermesinæ* IN GENERAL.

Taking the life-cycle of *Cnaphalodes strobilobius*, KALT., as an example, it is now proposed to compare with it the cycles of such other Chermesinæ as are now well known, and to conclude with an attempt to trace their evolution with the help of the processes which have been observed to take place.

1. The Genus *Chermes*.

The cycle of *Chermes viridis*, RATZ., resembles closely that of *Cnaphalodes strobilobius*, but the Progrediens generation is entirely absent. The *Sistens* produces only the *Sexupara* upon Larch as the intermediate host-plant, together with *Sistentes* similar to the parent. The cycle upon the Spruce as the definitive host-plant resembles biologically that of *Cn. strobilobius*.

Chermes abietis, L., is a parthenogenetic species, with no sexual generation, living entirely upon the Spruce without migration. The winged forms produced by the Fundatrix are termed *Gallicolæ non-migrantes*, and their eggs, laid upon the Spruce, give rise to the *Fundatrix*. There is thus a simple alternation of a winged with a wingless generation. Both Fundatrix and Gallicola non-migrans differ structurally from the corresponding generations of *Chermes viridis*, RATZ.

A parallel case is found in *Cnaphalodes lapponicus*, CHOL., which is similarly confined to the Spruce with but two parthenogenetic alternating generations. This species differs in slight but constant characters from *Cn. strobilobius*, KALT.

2. The Genus *Dreyfusia*.

PAUL MARCHAL (4) has thrown much light upon the cycles of *Dreyfusia nüsslini*, B., and *piceæ*, RATZ. In the former species the Fundatrix generation on *Picea orientalis* is structurally identical with the Sistens generation upon *Abies pectinata*. The *Fundatrix* gives rise to a majority of *Gallicolæ migrantes* and a very few winged forms, which do not migrate, and produce larvæ which fail to reach maturity. The Gallicolæ produce *Sistentes* (called Hiemosistentes), which rest in the first larval stage. These Sistentes produce *Sexuparæ* and *Progredientes* (differentiated in the 3rd stage) and a form similar in structure to the *Hiemosistens*, but developing forthwith, and known as the *Aestivosistens*. The Progredientes produce *Aestivosistentes*, and the latter, irrespective of their origin from the *Hiemosistens* or *Progrediens*, give rise again to *Hiemosistentes*.

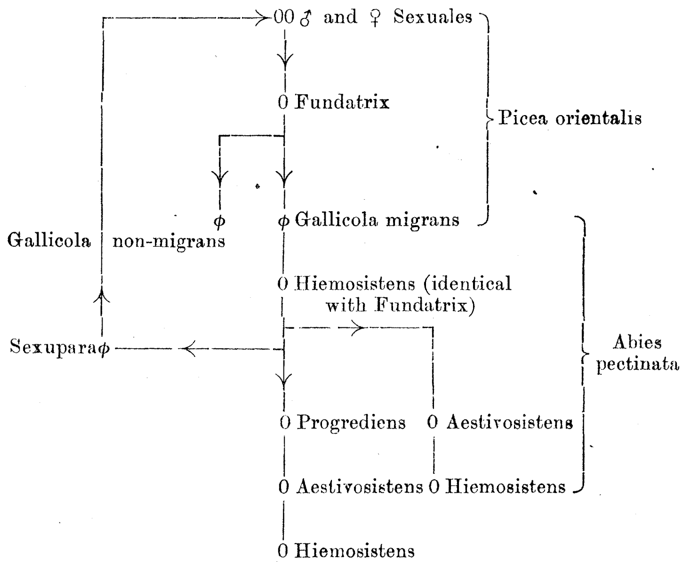
The *Sexuales* are produced normally by the *Sexupara*.

Structurally, *Dreyfusia piceæ*, RATZ., differs little from *D. nüsslini*, B., but the cycle is a parthenogenetic one upon *Abies nordmanniana*. Here the *Hiemosistens* gives rise to the *Aestivosistens*, the *Progrediens*, and a winged form called by MARCHAL the *Exsul alata*, but which we prefer to call the *Progrediens alata*, for it behaves similarly to the *Progrediens* in producing *Aestivosistentes* without migrating.

The *Aestivosistentes* arising from both types of *Progredientes* produce *Hiemosistentes*; but those arising from the *Hiemosistens* produce a second mixed generation of *Hiemo-* and *Aestivosistentes;* the latter again give *Hiemosistentes.*

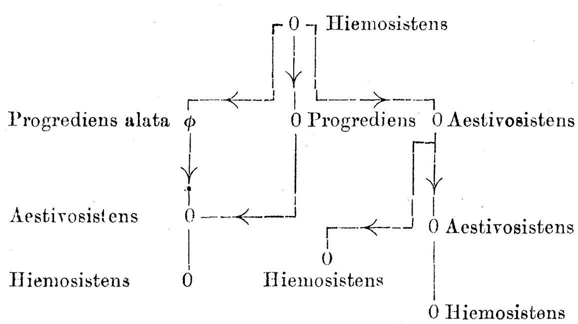
The cycle of these two interesting species may be represented as follows:—

Dreyfusia nüsslini, BÖRNER.



Dreyfusia piceæ, RATZ.

Abies nordmanniana.



3. The Genus *Pineus*.

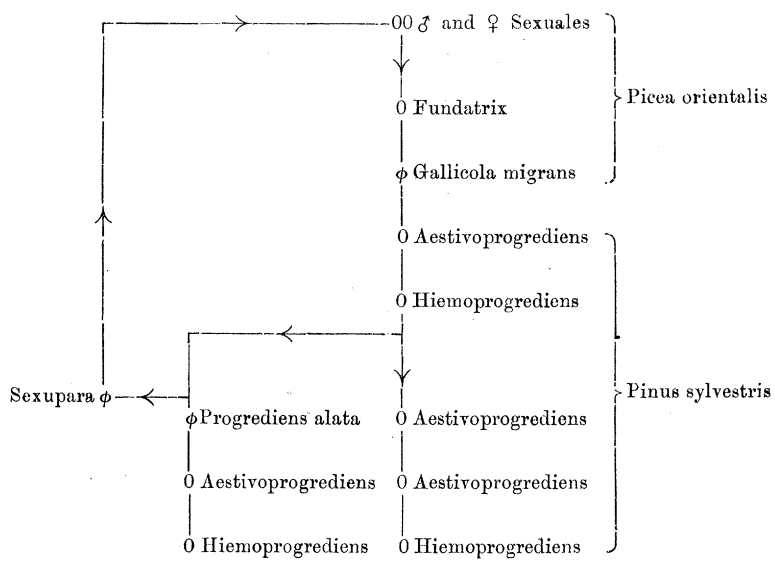
It is to PAUL MARCHAL (4) again to whom we owe a detailed knowledge of the only European species, *Pineus pini*, L. There are two distinct races of this species, which he names respectively the "*Oriental*" and the "*Indigenous*." In the "Oriental" race, the cycle upon the Definitive host—*Picea orientalis*—consists of Male and Female *Sexuales*, the *Fundatrix*, and the *Gallicola migrans*. The Gallicola migrates to *Pinus sylvestris*, where apterous individuals, reaching maturity in the

5th stage of metamorphosis are produced. The latter develops forthwith in late summer and gives rise to another generation, the individuals of which are similar in structure, but enter a resting period in the 3rd or 4th stage of metamorphosis, becoming adult in the 5th stage in the following spring. MARCHAL has recognised that both these forms are really of the *Progrediens* type, and not of the *Sistens* type found in most other *Chermesinæ*. We will call the two generations "*Aestivo-progrediens*" and "*Hiemoprogrediens*" respectively. The Hiemoprogrediens gives rise to winged Sexuparæ, which migrate back to the *Spruce*, to *Progredientes alatæ*, which remain on the Scots Pine and are differentiated from the *Sexupara* in the 4th stage (nymph) of metamorphosis, and, lastly, to Aestivoprogredientes, which are differentiated from both the foregoing in the 3rd stage.

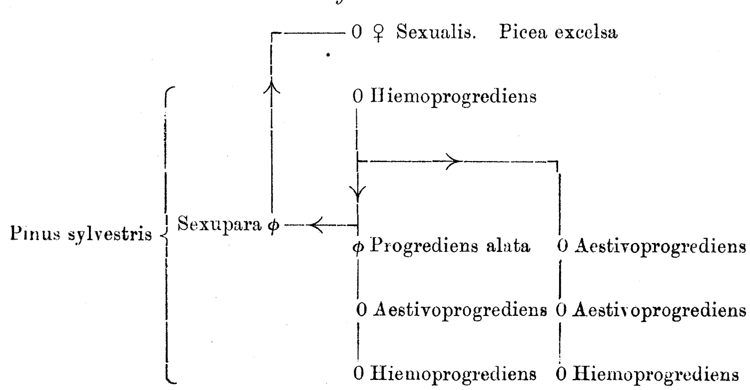
The *Aestivoprogredientes* give a second generation of the same form, which produces *Hiemoprogredientes*. The *Progredientes alatæ* do the same.

Pineus pini, L.

Oriental Race.



Indigenous Race.



The cycle of the *Indigenous Race* is confined to Scots Pine, and is similar to that of the Oriental Race upon the Intermediate Host-plant. There is, however, a migration by the *Sexupara* to *Spruce*, but on the latter plant the Sexupara is capable of producing only the female *Sexualis*, which, in the absence of the male, is entirely unproductive, causing the cycle upon the definitive host-plant to be abortive. The two cycles, which are parallel to the two species of *Dreyfusia*, are represented on p. 23.

MARCHAL expressly states that, though both races are present in France, they remain distinct biologically, and that the Indigenous race will not complete the cycle on the Definitive host even if Picea orientalis is present in the neighbourhood.

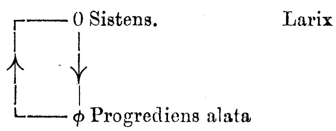
STEVEN (6*a*) points out that both races exist in Great Britain, and that *Dreyfusia nüsslini* and *piceæ* occur similarly.

The cycle of *Pineus strobi*, HTG., is, according to MARCHAL, similar to that of the Indigenous race of *P. pini*, but takes place upon the Weymouth Pine, with an abortive Sexualis generation upon *Picea nigra*.

4. *The Genus* Cholodkovskya.

The only species known, *Ch. viridana*, CHOL., found in Russia upon Larch, has a purely parthenogenetic cycle of two generations only. From BÖRNER's description and figures of the larval forms (BÖRNER [3]) we have no hesitation in considering that they represent a *Sistens* and a *Progrediens alata* generation, alternating—thus :—

Cholodkovskya viridana, CH.



This species is of great importance from an evolutionary standpoint.

Not enough is yet known of the life-histories of the genera *Gillettea* and *Aphrastasia* to warrant their inclusion here.

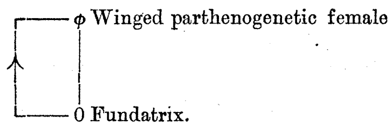
Having now reviewed the main characteristics of the life-cycles of the *Chermesinæ*, it is necessary to add a few important observations which have been made by PAUL MARCHAL (4). In *Dreyfusia nüsslini*, B., he observed that occasionally a *Gallicola migrans*, issuing from the gall, remained upon the definitive host-plant instead of migrating, and that these non-migrants laid eggs, the larvæ from which failed to develop. He adds that some galls tended to produce more sedentary forms, but that the migrants were always in the majority. Out of 40 galls he obtained only 3 non-migrant forms.

Under the heading of *Polymorphism in Chermes*, he points out, after an allusion to BÖRNER's discovery of the so-called "dimorphism" in the *Sistens* and *Progrediens* forms, that the *Progrediens* is closely related to a winged form, a theory which is in full accordance with what we have suggested for the Progrediens type in *Cnaphalodes.*

In writing of "Differentiation in Sexuality," in relation to *Pineus pini*, however, MARCHAL's arguments do not seem consistent. He says, "Productivity is attenuated through the succeeding generations (migrantes and exsules)*, and in the spring appear the Sexuparæ, which constitute a means of return to sexuality." Now in no known Chermesine is the productivity attenuated through the succeeding generations, for the *Sistens* type, in all genera and species, if not quite so highly productive as the Fundatrix, is certainly much more so than the *Gallicola migrans*, the generation which preceded it. In *Dreyfusia nüsslini*, B., again, the *Sistens* and *Fundatrix* are identical in structure and productivity upon MARCHAL's own showing. The productivity thus alternates in successive generations as far as the main cycle is concerned.

With the main facts in hand, it appears that the cycle of *Chermesinæ* is explicable only upon the lines now to be laid out.

In the first place, we must assume that the primitive insects from which the Chermesinæ sprang lived upon some species of *Spruce*, were winged, and of both sexes. In the second, that parthenogenesis set in early by the production of a primitive *Fundatrix*, which again produced the winged Sexuales, thus starting an alternation of form. Next, that the male Sexualis dropped out, making parthenogenesis complete, and giving an alternating cycle, thus :—



The winged female is what we now know as the *Gallicola non-migrans*, and this type of cycle has been preserved in *Chermes abietis*, L., and *Cnaphalodes lapponicus*, CHOL., species now much modified and specialised by selection.

Migration appeared, and perhaps by the progressive increase of migratory over sedentary winged forms, combined with adaptive selection, the cycle was transferred to those Conifers which now constitute the Intermediate Host-plants. Here the winged form continued to produce the wingless *Fundatrix*, and by processes of selection in a different environment from the original host-plant, from which the progressing species are now represented as entirely cut off, they became respectively what we now identify as the *Progrediens alata* and the *Sistens*. A species which has remained in this stage of evolution is *Cholodkovskya viridana*. It is probable that here already the wingless *Progrediens* became differentiated from the *Progrediens alata*. Last of all, the *Sexupara* was differentiated from the latter, and returning to the definitive host-plant by a series of adaptations similar to those in the first migration, gave rise to a female which was impotent in absence of the male sex. This stage in evolution has been preserved in *Dreyfusia piceæ*. The female, and the male, which we think were evolved later, are individuals which give evidence of

* Exsules = parthenogenetic generations upon the intermediate host-plant.

their novelty in having few characteristics in common with any other phase in the cycle, and probably show no characters in common with the original sexual forms, which, we submit, are represented most closely by the winged forms now existing.

With the return to sexuality, however, and with the processes and mechanism of alternation of form imprinted in the germ-plasm, it is not difficult to assume that the successful stages were recapitulated in such species in which sexual forms now exist, resulting in a reappearance of the Fundatrix and Gallicola generations, and a linking up of the separate cycles upon the two host-plants. The observations of P. MARCHAL upon sedentary winged forms amongst the migrants of *Dreyfusia nüsslini*, B., supply evidence in favour of this theory.

What has been termed "*Polymorphy*" in the *Chermesinæ* has merely arisen through the action of Natural Selection upon a simple alternating cycle, first in one, and then in a second, and different, environment, with a final recapitulation of the original cycle, through the reappearance of long-lost sexuality. CHOLODKOVSKY recognised the relation of the *Sistens* type to the *Fundatrix*, when he applied the term "*Fundatrix spuria*" to the former, and MARCHAL has shown that the Sistens and Fundatrix of *Dreyfusia nüsslini*, B., are actually identical in structure.

During the process of evolution, however, profound changes have taken place in the various cycles, no doubt through progressive failure in the alternating mechanism. In *Chermes viridis*, CHOL., the Progrediens generations have been entirely eliminated, and it seems that the Sexupara is now eliminating those Sistentes which have appeared out of their turn in the alternation, and which perhaps replaced the Progredientes earlier. In *Cnaphalodes strobilobius* it is the *Progrediens alata* which has been replaced by the Sexupara. The species of the genera *Pineus* and *Dreyfusia* have arisen from an early stock in evolution, so that the elimination process has had time to advance still further, and has been combined with the appearance, in *D. nüsslini* and *D. piceæ*, of *Æstivosistentes*, which have no larval resting period, and in *Pineus pini*, of Hiemoprogredientes, which go through a resting period. Further, in the latter species, probably the most ancient of all known Chermesinæ, the failure in the alternation of form has been thrown back to such an extent that the Sistens type has been entirely eliminated, and even the winged Gallicola is capable only of producing a Progrediens type.

There is a curious and striking parallel in the divergence of the ancient genera Pineus and Dreyfusia, with the divergence of the more recent genera Chermes and Cnaphalodes. The two former have reached what appears to be a complete stability, this being true also of the monocyclic species, whilst the two latter are still in a state of change, so far as their biology is concerned.

In conclusion, it may be remarked that the researches carried out have perhaps given some clue as to how the complex cycles of some Aphids arose, and may have thrown some small light upon a very specialised process of evolution. We have purposely refrained from comparisons and analogies with other insects and animals in which alternation of parthenogenesis and sexuality, as well as alternation of form, are exhibited. It seems possible, from what has been said, that the life-cycles of other Aphids, which appear more simple than those of Chermesinæ, have really been evolved from complex alternating cycles, by processes analogous to those to which we have alluded. Further afield it would be dangerous to speculate, but there is doubtless a wide scope for research on similar lines in other Phyla of Animals, and perhaps even in Plants.

6. General Summary.

On pp. 129 and 130, a summary upon the Biology of *Cnaphalodes strobilobius*, Kalt., has been given; it seems desirable to repeat, in a shortened form, such points as are applicable to the *Chermesinæ* in general, adding to them some general conclusions, upon the theoretical portion of this paper.

1. An Alternation of Form is the normal course of biological development in all Chermesinæ.

2. This alternation breaks down at a certain point in the life-cycle of *Cnaphalodes strobilobius*, Kalt., the numerical proportions of one form to another produced in the same generation showing the period at which failure in the alternating mechanism takes place.

In certain other genera, the failure of this alternating mechanism has been thrown back to, and established in, the main cycle upon the intermediate host-plant.

3. The *Progrediens* type of *Cnaphalodes strobilobius*, Kalt., is potentially a winged form, and is not a true dimorphism of the Sistens type. This applies also to all Chermesinæ in which either or both of these types occur.

4. The *Sexuales* are different morphologically from all other generations. They are held to be a new production in evolution.

The winged parthenogenetic generations at present in existence are representative of the original sexual forms which were lost early in evolution.

5. Species which are purely parthenogenetic have ceased to develop from an evolutionary point of view, and show the probable course of evolution in the various genera.

6. Migration from one species of Conifer to another is responsible for a duplication in the series of form-alternating, parthenogenetic generations; the series upon one Conifer has become morphologically different from that on the other through the action of Natural Selection in two different environments.

7. In existing species with two host-plants, that portion of the cycle which now takes place upon the definitive host-plant has arisen through a stimulus given by a recent return to sexuality, this accounting for the linking up of the two cycles and a duplication of the series of parthenogenetic generations.

8. Under these circumstances the theories of "Parallel Series" and "Polymorphy" become obsolete.

Appendix.

In dealing with the numerical proportions of the various parthenogenetic generations of *Cnaphalodes strobilobius*, Kalt., upon the Larch, we have given the summary of figures obtained, but it may serve a useful purpose to give more exact details of the way in which these figures were obtained.

With regard to the plants upon which the insects were bred, these were young trees of 2 years of age, taken from a nursery at Bagley Wood, near Oxford, in the summer of 1919. The plants were fumigated with Hydrocyanic Acid gas so as to sterilise them completely, and then placed in pots, and protected from re-infestation with muslin cages.

I.

Winged *Gallicolæ* were placed upon the plants, or a whole gall, just before emergence, so that each plant became infected by the offspring of a single parent *Fundatrix*. In April, 1920, the *Sistentes* became adult, and the eggs were taken at intervals from each individual so as to obtain as nearly as possible a full number.

The eggs hatched as follows:—

1920.

Egg-cluster.	Eggs laid.	Hatched.	Progredientes.	Totals.
No. 1	April 1–15	April 16–May 4	140	
	April 15–20	April 28–May 7	11	
	April 20–30	May 11–May 18	37	
	May 1–7	May 15–22	33	
	May 7–10	May 21–24	7	228
No. 2	April 1–12	April 16–May 4	112	
	April 12–20	April 29–May 6	49	161
No. 3	April 1–12	April 16–May 4	124	
	April 12–20	April 25–May 12	73	197
No. 4	April 1–12	April 23–May 1	40	40
No. 5	April 1–12	April 20–May 2	72	72
No. 6	April 1–12	April 19–April 30	55	
	April 12–20	April 29–May 8	66	121
No. 7	April 1–12	April 16–May 1	101	101
No. 8	April 16–28	April 29–May 16	183	183
			Total Progredientes	1103
			Sistentes	0

From other plants similarly infected 769 additional eggs all hatched to larvæ of the *Progrediens* type, the last egg hatching on June 1.

Numbers of these Progredientes were transferred to uninfected plants, where very few developed to the winged Sexupara form. In June and July the adult *Progredientes* laid eggs which hatched entirely to larvæ of the *Sistens* type. These became adult in the spring of 1921, and again laid eggs which hatched to larvæ of the *Progrediens* type, the last egg hatching on June 7.

In the meantime, clean plants had been infected with *Gallicolæ* in June, 1920, and one plant which had been potted in 1919, but not fumigated, and which had been naturally infected in 1918, was kept secure from re-infection during 1919 and 1920. Thus three stocks, belonging to three different years, were obtained, breeding under similar conditions.

On the unfumigated plant, however, *Sistentes* produced by two generations of *Progredientes* were present in 1921. They laid eggs which hatched to larvæ of the *Progrediens* type, but these developed to a greater proportion of winged Sexupara forms than on the plants holding the 2nd year *Sistentes*, but the exact proportions could, unfortunately, not be determined.

II.

In taking the proportions of *Progredientes* to *Sistentes* produced by the Progrediens generations of the first, second and third years, it was found almost impossible to take the eggs as they were laid; whole egg-clusters were therefore removed from each plant at suitable intervals, so that a complete succession of eggs could be obtained through each generation. There was some overlapping in the generations, but close observation prevented any serious error.

Plants A and A_1 had upon them Sistentes of the 1st year in the spring of 1921. Plant B had Sistentes of the 2nd year in the spring of 1921. Plants C and C_1 had a mixture of two generations of the 3rd year in the spring of 1921.

On C_1 Progredientes had been placed in 1920; it is possible, but not certain, that the 1921 Sistentes here represent the offspring of the 2nd Progrediens generation in 1920.

1921. *Progredientes.* First Year. Generation I.

Tree No.	Eggs collected.	Eggs hatched.	Sistentes.	Eggs hatched.	Progredientes.	Total.	No. of egg-cases.
A	May 23	May 24–June 7	16	—	0	16	17
		May 25–June 8	19	—	0	19	19
		May 28–June 8	15	—	0	15	15
	May 28	May 29–June 11	23	—	0	23	25
		May 31–June 11	13	—	0	13	13
		June 2–June 11	10	—	0	10	10
	June 9	June 10–June 22	6	—	0	6	6
		June 10–June 22	16	—	0	16	42
		June 10–June 22	11	—	0	11	11
		June 11–June 22	33	—	0	33	33
		June 11–June 22	8	—	0	8	21
		June 14–June 22	5	—	0	5	14
	July 7	July 7–July 15	14	—	0	14	97
		July 11–July 14	6	—	0	6	18
		July 12–July 14	2	—	0	2	13
A_1	May 28	May 31–June 11	26	—	0	26	26
		May 31–June 10	16	—	0	16	16
		June 2–June 10	14	—	0	14	14
	June 9	June 11–June 20	17	—	0	17	40
		June 11–June 20	7	—	0	7	12
		June 11–June 22	21	—	0	21	45
		June 11–June 18	4	—	0	4	13
		June 12–June 20	10	—	0	10	25
		June 15–June 17	3	—	0	3	19
Totals	(Period) 45 days	(Period) 52 days	315	—	0	315	564

Lineage.

ϕ Gallicola migrans from Spruce. June, 1920.

0 Sistentes. Adult, April, 1921–

Sexupara less than 1 per cent. ϕ — 0 *Progredientes.* Adult, May 1–June 8, 1921.

● Eggs.

0 *Sistentes* larvæ, 100 per cent.

Result: All eggs laid by the Progredientes, derived from the Sistentes produced directly from the Gallicola migrans, hatch to the *Sistens* form.

1921. *Progredientes.* Second Year. Generation I.

Tree No.	Eggs collected.	Eggs hatched.	Sistentes.	Eggs hatched.	Progredientes.	Total.	No. of egg-cases.
B	May 23	May 25–June 8	11	—	0	11	11
		May 26–June 8	10	May 28 May 29	2	12	12
		May 28–June 8	7	May 28	1	8	8
	May 28	May 29–June 10	7	—	0	7	16
		May 31–June 10	8	—	0	8	10
		May 31–June 9	14	May 31	1	15	18
	June 9	June 11–June 22	2	—	0	2	12
		June 12–June 23	6	—	0	6	6
		June 16–June 22	5	June 13 June 17	3	8	14
		June 15	1	—	0	1	3
		June 15–June 20	4	—	0	4	7
		June 16–June 22	3	June 22	1	4	4
	June 28	June 30–July 11	8	July 2	1	9	12
		July 5–July 7	4	July 6	1	5	7
	July 7	July 13–July 16	3	—	0	3	14
Totals	(Period) 45 days	(Period) 47 days	93	(Period) 36 days	10	103	154

Lineage

♀ Gallicola migrans from Spruce, June, 1919.

↓

0 Sistentes, adult, April, 1920.

Sexupara less than 1 per cent. ♀ ←

↓

0 Progredientes, adult, May, 1920.

↓

0 Sistentes, adult, April, 1921. Hatching of eggs lasted till June 7.

Sexupara about 4 per cent. ♀ ←

↓

0 *Progredientes,* adult, May 10–June 20, 1921.

↓

● Eggs.

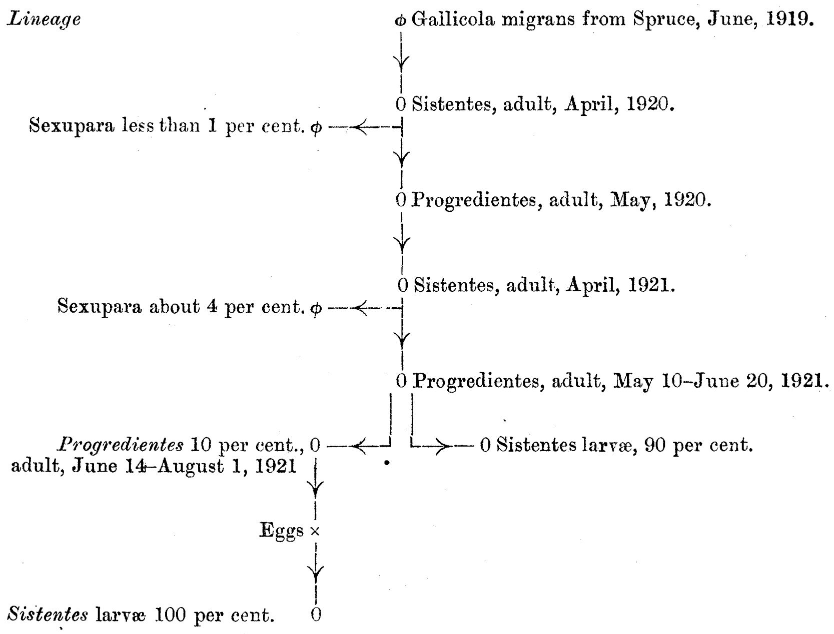
Progredientes larvæ, 10 per cent. 0 ← → 0 *Sistentes* larvæ 90 per cent.

Result: Eggs laid by Progredientes hatching from the second year Sistentes produce 90 per cent. Sistentes larvæ and 10 per cent. Progredientes larvæ.

1921. *Progredientes.* Second Year. Generation II.

Tree No.	Eggs collected.	Eggs hatched.	Sistentes.	Progredientes.	Total.	No. of egg-cases.
B	June 28	June 30–July 7	6	0	6	6
		July 7	1	0	1	1
		July 7–July 11	4	0	4	4
		July 11	1	0	1	1
	July 7	July 11–July 13	6	0	6	6
		July 11–July 14	3	0	3	3
		July 11–July 13	2	0	2	2
		July 11–July 15	6	0	6	6
		July 11–July 14	5	0	5	5
		July 11	1	0	1	2
		July 13–July 15	4	0	4	4
	July 18	July 20–July 25	4	0	4	7
		July 21–July 25	4	0	4	4
		July 21–July 25	4	0	4	4
		July 21–July 25	5	0	5	5
		July 21–July 25	2	0	2	6
		July 21	1	0	1	6
		July 21	2	0	2	7
		July 21–July 22	2	0	2	8
		July 21–July 25	7	0	7	9
		July 18–July 25	7	0	7	13
		July 24	1	0	1	2
		July 25	3	0	3	3
	August 4	August 8–August 11	3	0	3	4
		August 8–August 17	5	0	5	6
		August 8	1	0	1	6
		August 8–August 17	3	0	3	5
		August 8–August 11	4	0	4	4
		August 8–August 17	5	0	5	5
		August 8–August 17	3	0	3	5
		August 8–August 17	3	0	3	3
		August 8–August 12	2	0	2	3
		August 9–August 17	2	0	2	4
		August 9	1	0	1	2
		August 9–August 12	2	0	2	5
		August 10	1	0	1	2
		August 10–August 17	3	0	3	7
		August 11	1	0	1	3
		August 11	1	0	1	8
		August 11	1	0	1	3
		August 17	1	0	1	5
		August 17	1	0	1	5
Totals	(Period) 37 days	(Period) 49 days	124	0	124	199

1921. *Progredientes.* Second Year. Generation II.—*continued.*



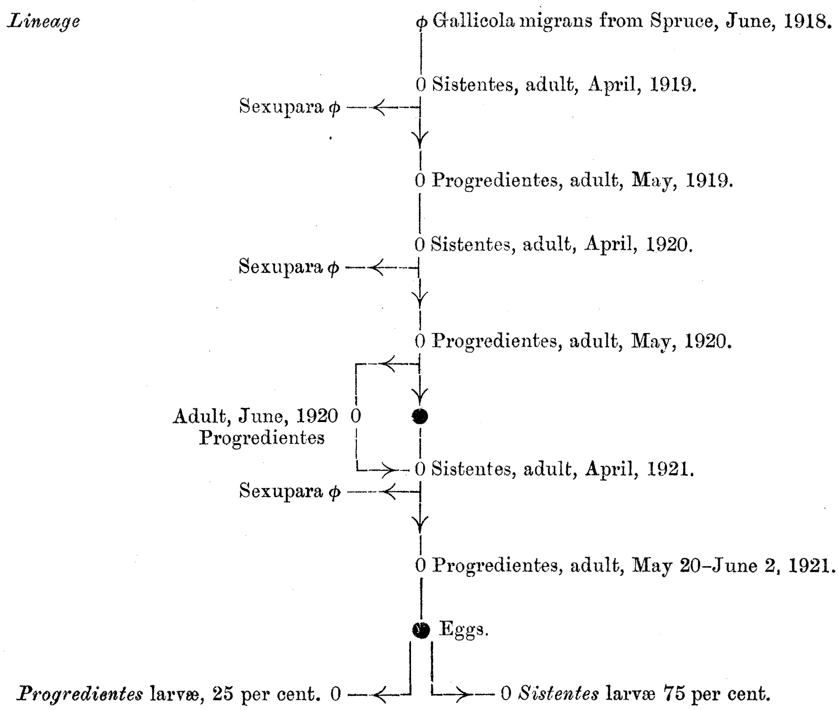
Result: Eggs laid by the second generation of Progredientes in the second year produce only Sistentes larvæ.

1921. *Progredientes.* Third Year. Generation I.

Tree No.	Eggs collected.	Eggs hatched.	Sistentes.	Eggs hatched.	Progredientes.	Total.	No. of egg-cases.
C_1	May 28	May 31–June 8	6	May 31–June 8	3	9	18
		May 31–June 11	6	—	0	6	10
		June 2–June 10	6	—	0	6	13
C	June 9	June 11–June 22	7	June 10–June 17	3	10	10
C_1		June 17–June 22	4	June 10–June 22	6	10	37
		June 10–June 20	3	—	0	3	6
C		June 11–June 22	6	—	0	6	10
		June 12–June 15	3	June 20	1	4	7
		June 12–June 16	2	—	0	2	7
C_1		June 17–June 22	3	June 16	1	4	14
C		June 20	1	—	0	1	1
C_1	June 28	June 28–July 11	14	June 30–July 11	4	18	24
		June 30–July 11	6	June 29–July 11	12	18	21
C	July 7	July 8–July 13	3	—	0	3	6
		July 8–July 13	4	—	0	4	9
		July 8–July 12	4	July 8	1	5	9
		July 8–July 15	9	—	0	9	15
		July 8–July 14	11	—	0	11	18
		July 8–July 16	17	July 8–July 12	4	21	22
		July 8–July 14	9	July 8–July 12	7	16	27
		July 8–July 16	19	July 8–July 11	2	21	30
		July 8–July 14	11	July 8–July 12	3	14	34
		July 8–July 16	21	July 15	1	22	32
		July 8–July 15	15	July 11	1	16	36

1921. *Progredientes.* Third Year. Generation I.—*continued.*

Tree No.	Eggs collected.	Eggs hatched.	Sistentes.	Eggs hatched.	Progredientes.	Total.	No. of egg-cases.
C	July 18	July 19–July 25	3	—	0	3	29
		July 19–July 25	3	—	0	3	31
		July 19–July 21	2	July 19	1	3	30
		July 19–July 22	4	—	0	4	20
		July 25	1	—	0	1	15
		July 19–July 25	8	—	0	8	27
Total	(Period) 51 days	(Period) 56 days	211	(Period) 50 days	50	261	458

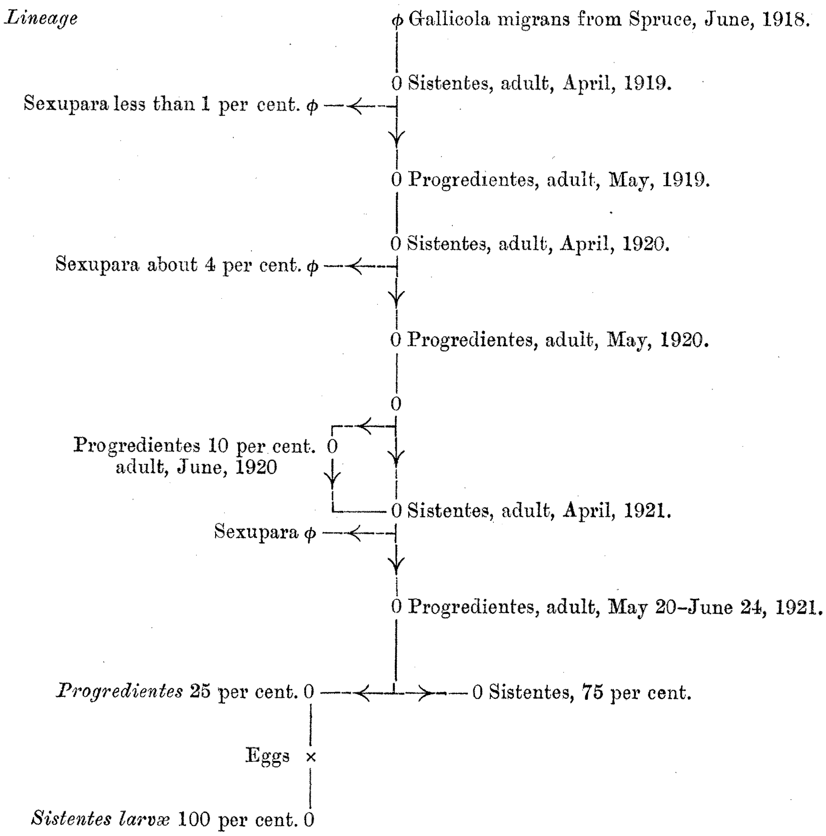


Result: Eggs laid by Progredientes hatching from the third year Sistentes produce 75 per cent. Sistentes and 25 per cent. Progredientes larvæ.

1921. *Progredientes.* Third Year. Generation II.

Tree No.	Eggs collected.	Eggs hatched.	Sistentes.	Progredientes.	Total.	No. of egg-cases.
C	July 7	July 7–July 13	12	0	12	15
	July 18	July 19–July 25	10	0	10	10
		July 19–July 25	6	0	6	13
		July 19–July 21	6	0	6	9
		July 19–July 24	12	0	12	17
		July 22–July 25	4	0	4	4
		July 21–July 22	2	0	2	2
C_1		July 24	1	0	1	1
	August 4	August 8–August 12	2	0	2	2
		August 8–August 17	4	0	4	6
C	30 egg-clusters.	August 8–August 18	65	0	65	157
Total	(Period) 28 days	(Period) 42 days	124	0	124	236

Lineage



Result: Eggs laid by the second generation Progredientes in the third year produce only Sistentes larvæ

LITERATURE REFERRED TO IN THE TEXT.

(1) Börner, C. "Eine monographische Studie über die Chermiden," 'Arb. Kais. Biol. Anst. f. Land-u.-Forstwirtschaft,' Berlin, 1908, pp. 81–317.

(2) *Idem.* "Über Chermesiden," 'Zool. Anzeiger,' vol. 34, No. 18–19, VII, pp. 554–557, 1909.

(3) *Idem.* *Ibid.*, 'Zool. Anzeiger,' vol. 34, No. 16–17, VI, pp. 498–511, 1909.

(4) Marchal, P. "Contribution à l'étude de la Biologie des Chermes," 'Annales des Sciences naturelles, Zoologie,' vol. 18, pp. 153–385, 1913.

(5) Cholodkovsky, N. A. "Chermes injurious to Conifers," 'Dept. of Agric. Central Board of Land Administration and Agriculture,' Petrograd, 1915.

(6) Steven, H. M. "Contribution to the knowledge of the Family *Chermesidæ*," 'Proc. Roy. Soc. Edinburgh,' vol. 37, Part III, No. 2, 1917, pp. 356–381.

(6*a*) *Idem.* "Chermesidæ in relation to British Forestry," 'Trans. Roy. Scott. Arboricultural Society,' vol. 31, Part II, 1917, pp. 131–155.

(7) Philiptschenko, I. "Les espèces biologiques du Chermes, et leur différentiation statistique," 'Journ. Russe de Zool.,' vol. 1, Part II, pp. 261–285, 1916.

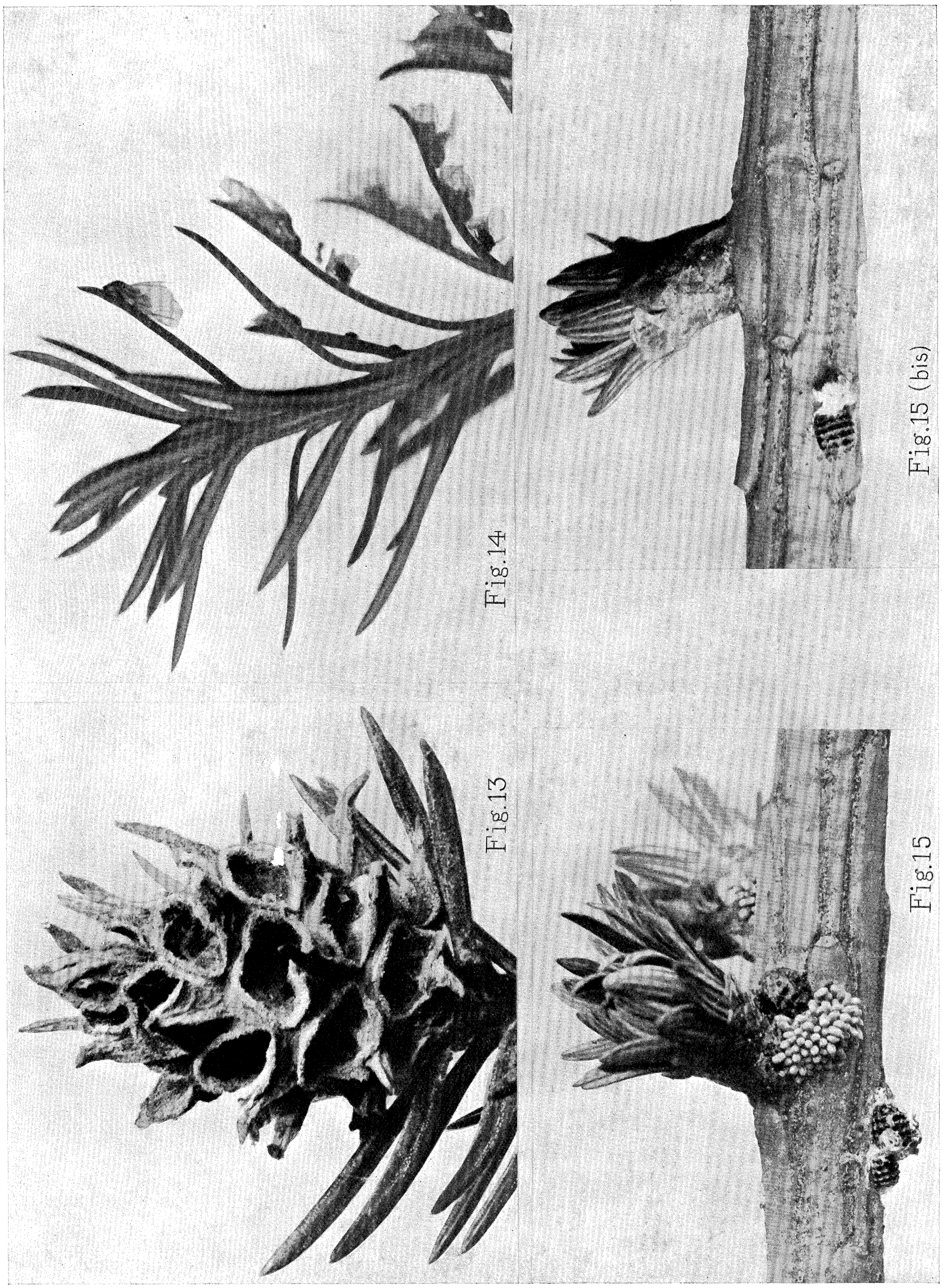


FIG. 13.—Opened gall upon Picea excelsa. × 8.

FIG. 14.—Gallicolæ migrantes laying eggs on Larix europæa. × 8.

FIG. 15 and FIG. 15 (*bis*).—Sistentes laying eggs on Larix europæa. × 8.

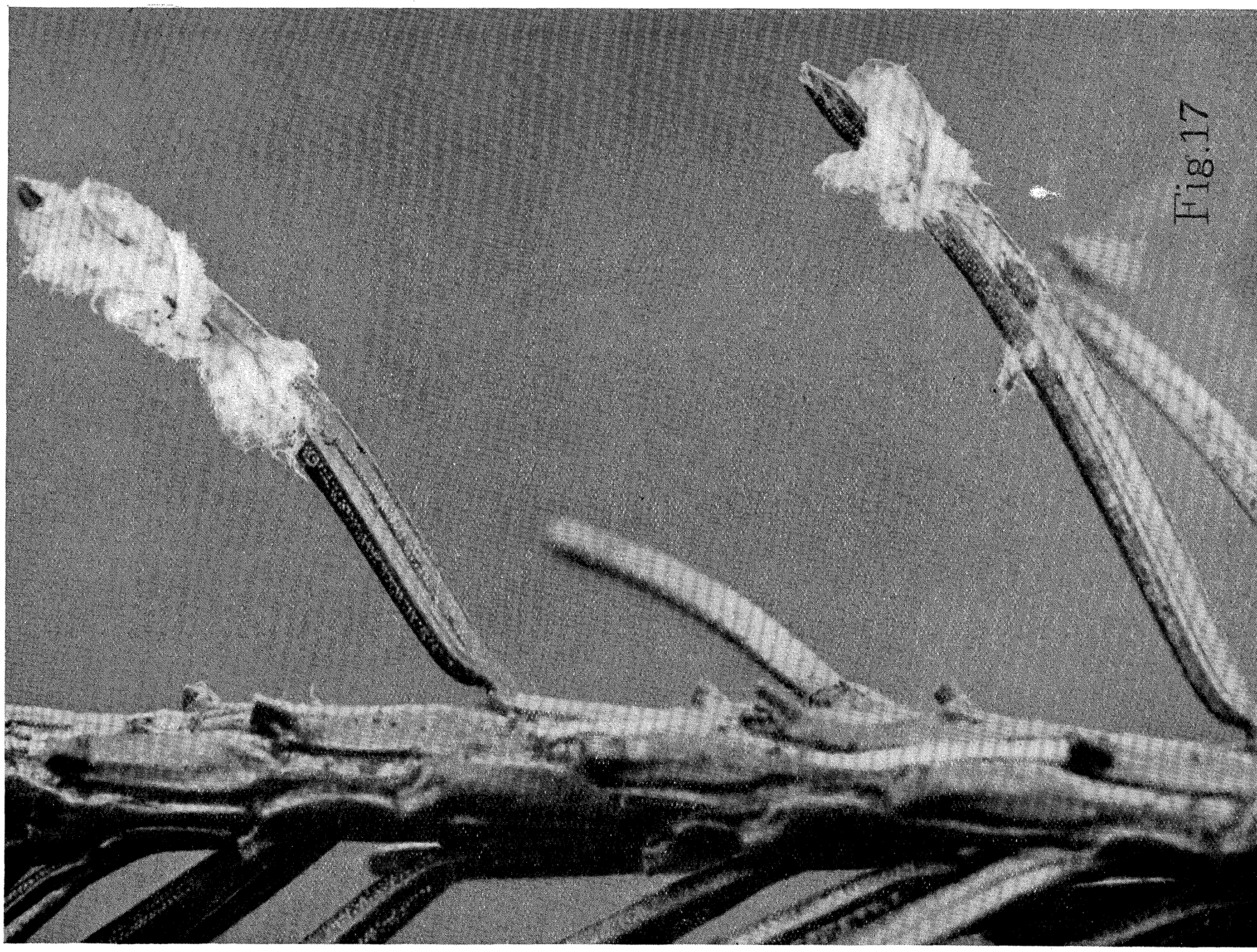
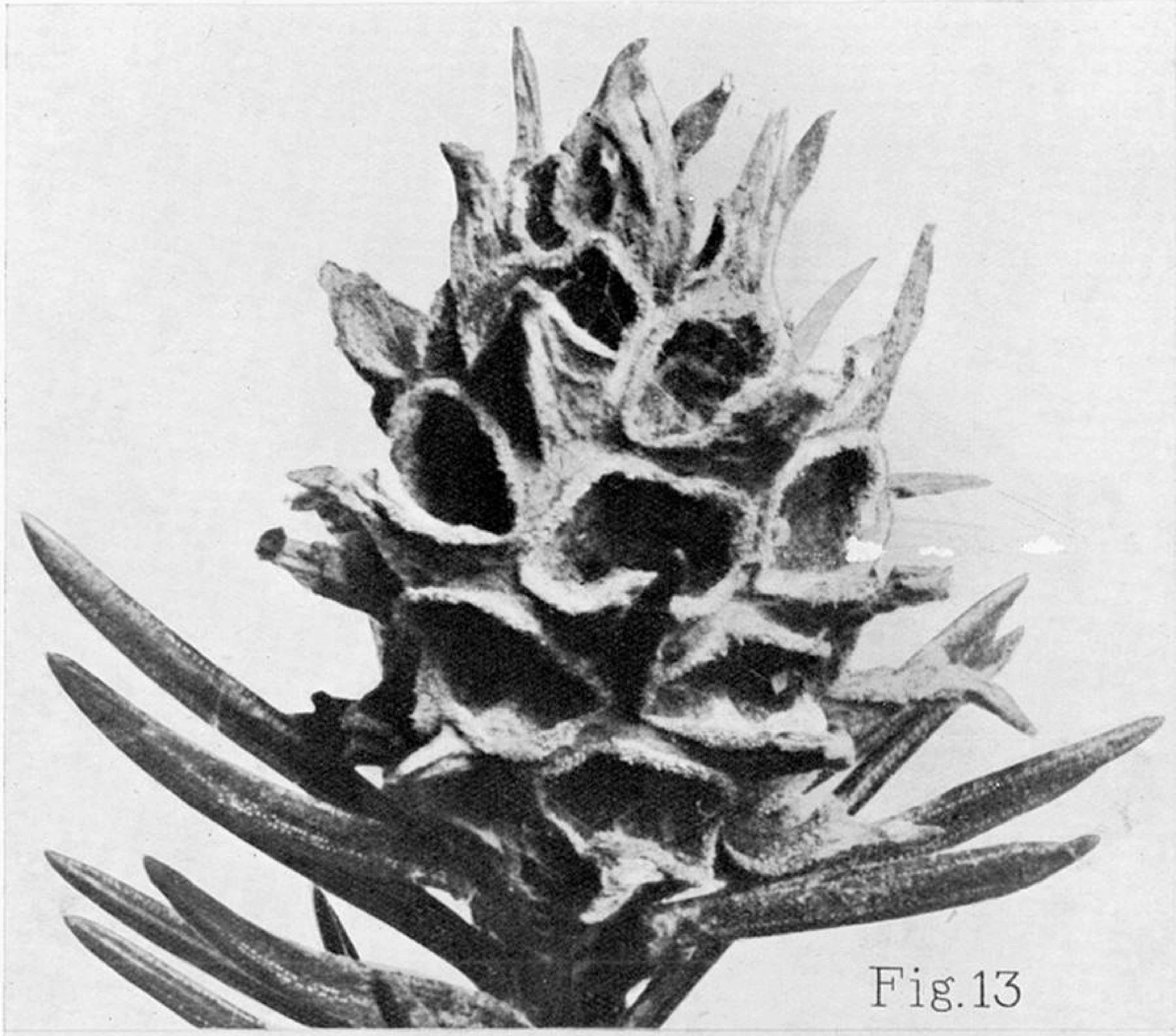
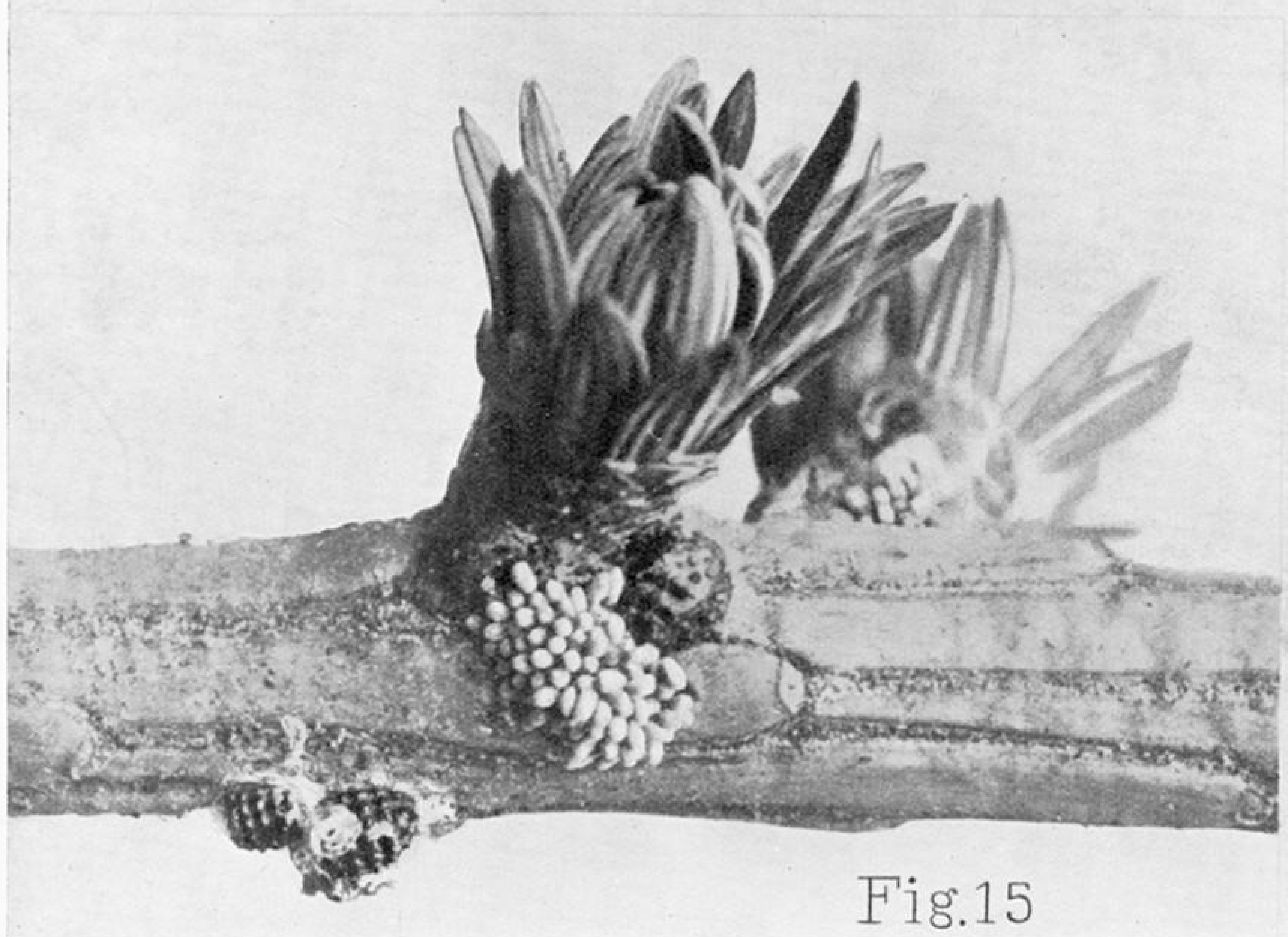


Fig. 17.—Sexuparæ upon broods of sexuales on Picea excelsa. × 8.

Fig. 16.—Progredientes laying eggs on Larix europæa. × 8.





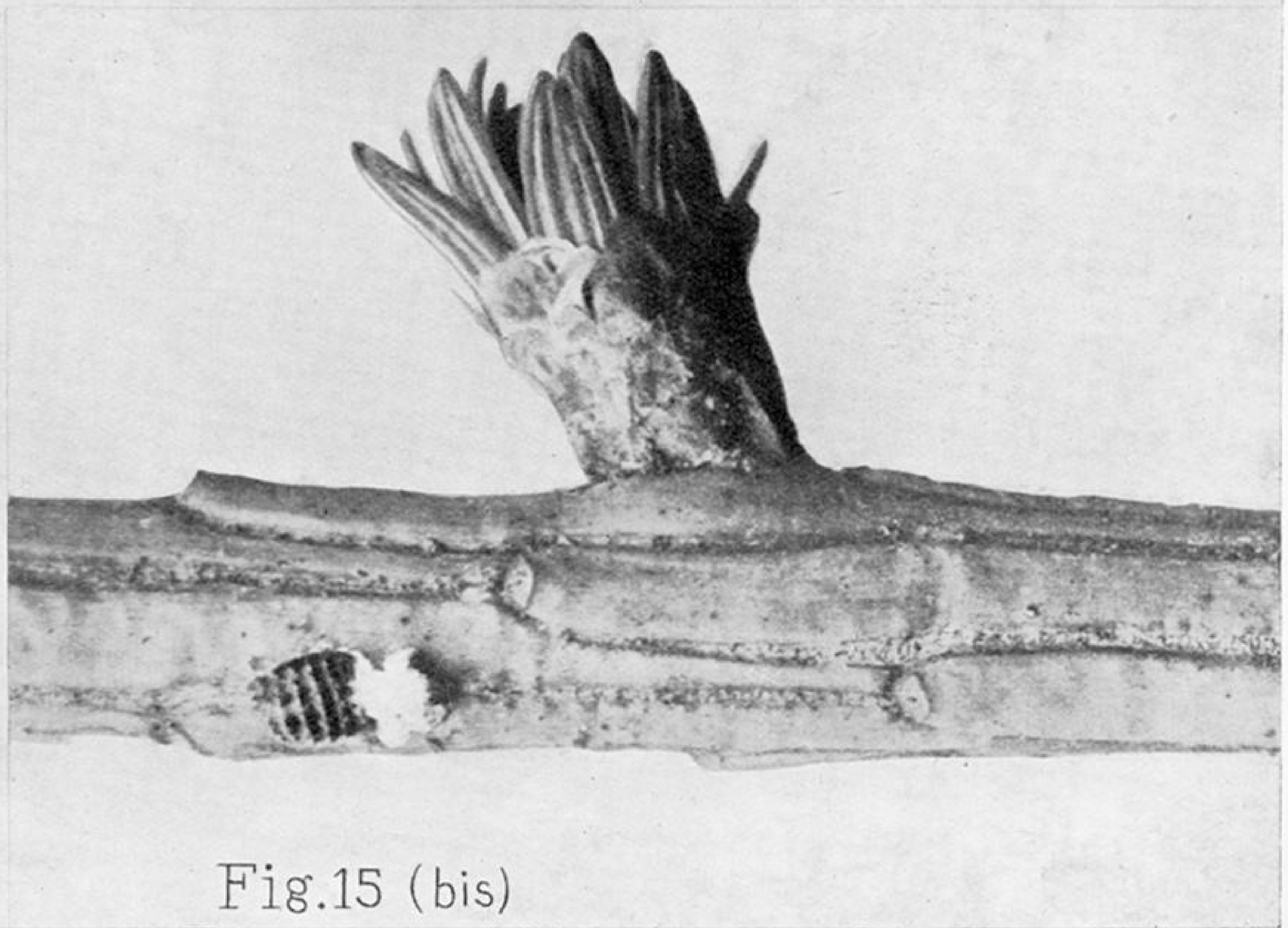


FIG. 13.—Opened gall upon Picea excelsa. × 8.

FIG. 14.—Gallicolæ migrantes laying eggs on Larix europæa. × 8.

FIG. 15 and FIG. 15 (*bis*).—Sistentes laying eggs on Larix europæa. × 8.

FIG. 16.—Progredientes laying eggs on Larix europæa. × 8.

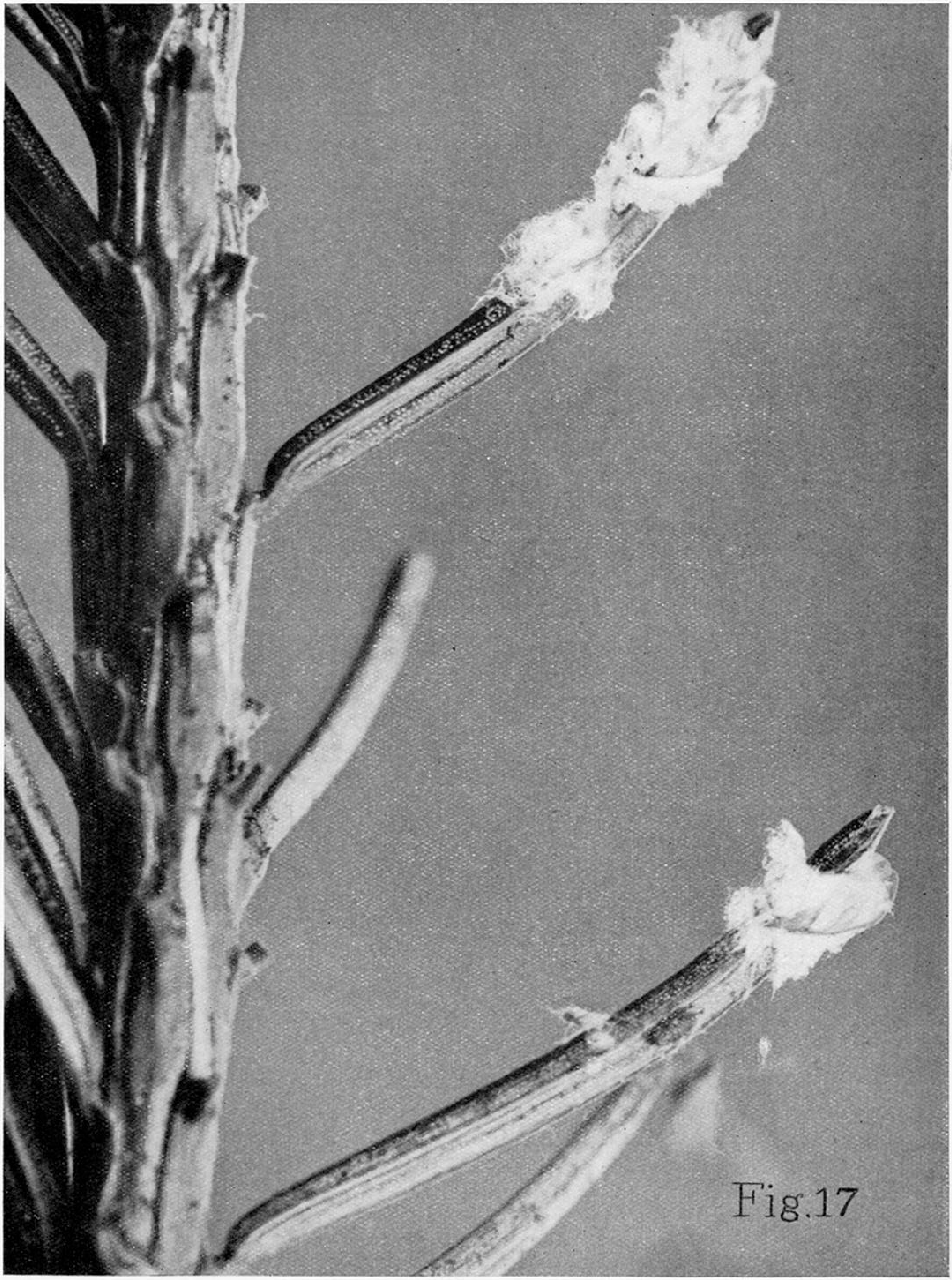


FIG. 17.—Sexuparæ upon broods of sexuales on Picea excelsa. × 8.