# A NEW SPECIES OF BEESONIA WITH LARVAL POLYMORPHISM, INDUCING A STEM GALL ON SHOREA CURTISII IN SINGAPORE

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A NEW SPECIES OF BEESONIA WITH LARVAL POLYMORPHISM, INDUCING A STEM GALL ON SHOREA CURTISII IN SINGAPORE [HOMOPTERA: COCCOIDEA: BEESONIIDAE]

By Sadao Takagi

Abstract


Beesonia shoreae, sp. nov., inducing a hypertrophied stem gall on Shorea curtisii [Dipterocarpaceae] in Singapore, is described on the basis of larval forms purported to belong to 4 ontogenetic courses. The view is adopted that the larval polymorphism is associated with exploitation of more than a single feeding site provided by the gall's structure. The 5 known species of the Beesoniidae induce galls on dipterocarps or oaks—a combination of host plants unexpectable from the viewpoint of plant phylogeny.

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INTRODUCTION

The family Beesoniidae is a small isolated group of the Coccoidea, comprising 4 named species assigned to 2 genera, Beesonia and Mangalorea (Raman and Takagi, 1992). Beardsley (1971) mentioned that an undescribed species of Beesonia had been collected in Singapore on Shorea pauciflora. He did not describe it, because the specimens were ‘inadequate for proper diagnosis’. The host plant was later emended by Anthony (1974a; 1974b) to S. curtisii. All these species induce galls on their host plants.

In July, 1992, I stayed in Singapore for a short time. At that time Dr D.H. Murphy, University of Singapore, showed me galls on Shorea curtisii. Furthermore, he gave me some galls he had collected. A number of larval forms were mounted from the galls thus available. The view is adopted that they belong to a single species of Beesonia, mainly because the larval polymorphism is partly explainable by the presence of more than a single feeding site provided by the gall's structure. However, the mounted specimens are not complete with instars and forms, and only a limited number of them are adequate for description. Moreover, I have been puzzled how to interpret one of the observed forms.

A series of forms collected over 1 or 2 generations of the coccoid may be necessary for a complete understanding of the polymorphism, but I have had no opportunity to stay in Singapore for a longer time since then. I have, however, identified the female larvae. In this sex the species is similar to Beesonia napiformis and B. brevipes, but is easily distinguishable from the latter two in the 1st instar. I, therefore, describe the species, with emphasis on its larval polymorphism.

Acknowledgements. I am deeply thankful to Dr D.H. Murphy for his help in various ways during my stay in Singapore and for giving me valuable material. Photographs taken by him are published in this paper (Figs. 1 and 2).

I express my gratitude to Dr Hsuan Keng, University of Singapore, who helped me in various ways and identified host plants of coccoids I collected in the Bukit Timah Nature Reserve.

I am grateful to the National Parks Board, Singapore, for permission for making collection in the Bukit Timah Nature Reserve.

Dr A. Raman, Entomology Research Institute, Loyola College, Madras, India, reviewed the manuscript, and made many suggestions for improving it.

Dr Khoo Soo Ghee, Forest Research Institute of Malaysia, Kepong, Kuala Lumpur, Malaysia, read through the manuscript and suggested another possible interpretation of the polymorphism.

DESCRIPTION

Beesonia shoreae, sp. nov.

Material. Collected on Bukit Timah (165 m), Singapore, on saplings of Shorea curtisii [Dipterocarpaceae] growing on the ridge near the summit of the hill. The galled part of the stem is spindle-shaped (Fig. 1), with the female coccoid living in a pit within the swollen part (Fig. 2) (for further description, see Anthony, 1974b). Name-bearing specimen [holotype] : 1st instar larva, Form IA, deposited in the collection of the Laboratory of Systematic Entomology, Hokkaido University.

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**Diagnosis.** Because our knowledge as to the instars and forms in *Beesonia* is still incomplete or even confused, only the 1st instar females should be compared here. *Beesonia napiformis* and *B. brevipes* are parthenogenetic, and their 1st instar females can be readily recognized. A similar larval form occurring in *B. dipterocarpi* is identified as the 1st instar female (Takagi, 1987). The 1st instar female of *B. shoreae*, termed Form IA (Fig. 3) in this paper, agrees with them in the general pattern of characters. (But the same form is also the 1st instar in one of the supposed male ontogenetic courses as will be shown later.) Thus it clearly shows that the species belongs to *Beesonia*. It is easily distinguished from the corresponding forms of the other species of the family in the dorsal setae, which are mostly dilated apically. The hind tarsus is 2.3-2.5 times as long as the tibia. (The other forms of the 1st instar, IC and ID, are quite peculiar in the legs and dorsal setae, and the species may also be easily recognized by these forms.)

**Forms observed**

**Synopsis.** Larval forms belonging to the 1st to 3rd instars have been mounted from the material, and their sequences in ontogenetic development have been traced by the association of the 2nd or 3rd instar with the exuvial cast of the preceding instar. Four sequences of forms have been found, indicating 4 disjunct ontogenetic courses (Table 1). Form IA (Fig. 3), IIA (Fig. 8) and IIIA in Sequence 1 agree well with the 1st to 3rd instar females of *B. napiformis* and *B. brevipes* in their general characters. The 4th instar in this sequence is the adult female (IVA), which is entirely enclosed within the skin of the 3rd instar. In some other cases observed, Form IA is succeeded by another form of the 2nd instar, IIB, thus representing Sequence 2. Form IIB is quite different from IIA and substantially agrees with IID (Fig. 6), which is preceded by ID (Fig. 5) in Sequence 4. Form ID is strikingly different from IA in having thick legs and ill-developed body setae. The other form of the 1st instar, IC, is intermediate between IA and ID, being similar to IA in having well-developed dorsal setae and to ID in having strong legs (Fig. 4); it is, however, peculiar in the claws which are directed downwards.

**Form IA** (Fig. 3). Similar to the 1st instar female of *B. napiformis*: newly hatched larva elongate fusiform; segmentation distinct dorsally; prothorax occupying a large portion of thorax; metathorax and 1st to 6th abdominal segments

<table>
<thead>
<tr>
<th>Table 1. Forms observed and their ontogenetic sequences.</th>
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<tr>
<td>Sequence</td>
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<tr>
<td>of forms</td>
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<td>-------------</td>
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<tr>
<td>S1</td>
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<td>S4</td>
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Exuviation in Instar I. a: rupturing at anterior end of swollen head; p: rupturing at posterior end of body. (Note that the 1st instar larvae in Sequence 1 and 2, both belonging to Form IA, differ in the position of the exuvial rupture.)
each with a sclerotized transverse band dorsally; 7th and succeeding segments united to form a sclerotized area dorsally on posterior extremity of body. Some other features—arrangement of setae, anal plate and setae complex, ducts, antennae, legs, and marginal spinous setae—also nearly as in \textit{B. napiformis}. Dorsal derm with circular or oblong patches on prothorax. Most of dorsal setae strongly developed; elongate, flattened and apically dilated, ending in a truncate apex, except for the following setae, which are spinous: submedian setae on 2nd to 6th abdominal segments and submarginal ones on the 2nd and the 5th to 7th, the submarginal seta on the 7th much longer than the other spinous setae. Anal plate quadrate, with 4 flattened setae, accompanied laterally by a pair of setae each arising from a triangular plate, which bears 3 translucent spots. Ducts broad, shaped like a geminate pore at inner end, 4 on each side, occurring on head and thoracic segments. Antennae apparently 3-jointed, the 3rd joint longer than basal joints united, with several transverse sutures, and with a flattened seta subbasally. Tarsi rather slender, about 6 times as long as wide; in the hind leg, the tarsus is 52-56 $\mu$m long and 2.3–2.5 times as long as the tibia. Tibia+tarsus somewhat longer than trochanter+femur; claws with a denticle on plantar surface. Caudal setae exceeding body length.

\textit{Form IC} (Fig. 4). Newly hatched larva oblong; segmentation distinct dorsally on thorax and abdomen and also ventrally on abdomen; derm of thorax granulate extensively on both surfaces, with circular patches dorsally; derm of abdomen sclerotized, with spinules, on both surfaces. Many of dorsal setae strong, elongate, flattened, tending to be broadened towards apex, ending in a truncate apex, and frayed on sides (the following dorsal setae are not strongly developed: marginal or submarginal ones on head and thorax; submedian and submarginal or marginal ones on 2nd, 5th and 6th abdominal segments). There is no quadrate anal plate, but the derm above the anus is plicate in an arch; 4 setae around anus, elongate, flattened, apically truncate, accompanied laterally by a pair of much shorter, flattened setae. No spinous marginal setae ventrally (the supposed corresponding setae remain small and short in the submarginal zone). Ducts as in Form IA. Third joint of antenna less developed than in IA, without transverse suture. Legs strong; tarsi and tibiae thickened, hind tarsus about 3 times as long as wide, about 30 $\mu$m long and 1.5 times as long as tibia. Tibia+tarsus nearly as long as trochanter+femur; claws robust, directed downwards, making a right angle with tarsus. Caudal setae much shorter than body.

\textit{Form ID} (Fig. 5). Newly hatched larva elongate ovoid; segmentation indistinct except for posterior abdominal segments, where the derm is sclerotized, with spinules, on both surfaces. Submarginal dorsal setae on meso- and metathorax and 1st, 3rd and 4th abdominal segments somewhat thickened and blunt apically; submedian seta on 7th abdominal segment elongate and blunt, and submarginal seta on the segment thickened and spinous. There is no quadrate anal plate; anus surrounded by 6 flattened and blunt setae each arising from a plate bearing 3 translucent spots. No spinous marginal setae ventrally (the supposed corresponding setae are small and short). Ducts small, but positioned as in IA and IC. Third antennal joint short, without transverse sutures. Legs remarkably thickened; hind tarsus about 1.4 times as long as wide, about 20 $\mu$m long, only a little longer than tibia. Tibia+tarsus about as long as femur; claws robust, but not directed downwards. Caudal setae much shorter than body.
Form IIA (Fig. 8, right). Agrees with 2nd instar females of *B. napiformis* and *B. brevipes* in general body structure. Anal setae slightly narrowing towards apex, ending in a truncate apex, thus differing from the acuminate ones in *B. napiformis* and the narrowly rectangular ones in *B. brevipes*. Other features are not compared here, because no adequate specimens are available.

Form IIB. Substantially agrees with Form IID, differing from the latter mainly in the following characters: the segment bearing the anal plate is thickly sclerotized; antennae 2-jointed, the basal joint represented by a slender ring; tarsi as long as tibiae.

Form IID (Fig. 6). Body elongate oblong; membranous; segmentation suggested by sutures on abdomen. Derm with 3 kinds of pores: 5-locular disc pores strewn over dorsal surface, and also on ventral surface but fewer; slender ducts scattered except on a broad median area of ventral surface of thorax and abdomen, each opened in a pore as large as a 5-locular disc pore; larger pores are restricted to the dorsal surface and mostly to the submedian region, each having a sclerotized circular structure just interiorly (so that the pore must lead to a short duct). Anus situated dorsally, opened in a round plate, which bears 6 flattened, apically truncated setae. Antenna represented by an elongate, irregularly conical process with thick and slender setae. Legs well developed; tarsi slender, somewhat longer than tibiae; in the hind leg, the tarsus is 4-5 times as long as wide, 46-54 μm long, and about 1.2 times as long as the tibia; claws rather slender, with a pointed process applied to basal half of plantar margin and with a small denticle subapically on plantar surface.

Form IIIA. Similar to the 3rd instar females of *B. napiformis* and *B. brevipes* so far as based on the available specimens, which are, however, generally not good in condition.

Exuviation in 1st instar larvae

As the Form IA larva develops, the head becomes a large rounded mass; at exuviation the swollen head ruptures from the anterior end in the larva of Sequence 1 (Fig. 7, left), but in that of Sequence 2 the derm is thickly sclerotized throughout and split from the posterior end of the body up to the thorax. In Form IC, too, the head grows anteriorly, and exuviation takes place at its anterior end (Fig. 7, right). In Form ID the whole body grows stout, and the posterior part of the body is split along the margin for the emergence of the 2nd instar larva (Fig. 8, left).

Sequences of forms

Interpretations

Sequence 1. As stated in Diagnosis, the larval forms of this sequence agree in their general body structures with the 1st to 3rd instar larvae of the parthenogenetic species *Beesonnia napiformis* and *B. brevipes*, and I have no doubt that they are female larvae. They occur in pits formed on the stems. In the pit the insect directs its posterior extremity outwards (Fig. 2), and exuviation at the anterior end of the body in the 1st instar forces the 2nd instar larva to remain within the growing gall. In fact, the 2nd and 3rd instar larvae are legless. The exuvial cast of the 2nd instar remains around the posterior part of the body of the full-grown 3rd instar female.
The adult female is entirely enclosed within the skin of the 3rd instar, and its occurrence is indicated, in mounted specimens, by the presence of another set of mouthparts within the skin of the 3rd instar, and sometimes also by the presence of embryonic larvae. It is assumed to be wholly membranous and extremely simplified in structure as in *B. napiformis* and *B. brevipes*.

**Sequence 2.** So far as represented by the available exuvial casts, the 1st instar larva in this sequence cannot be distinguished from that in Sequence 1 (ontogenetic course of female) except for the wholly sclerotized derm and the position of the exuvial rupture. On the other hand, the 2nd instar form (IIB) almost agrees with that in Sequence 4 (IID). I became aware of the presence of Sequence 2 only when examining mounted specimens, and, therefore, I am not sure whether the specimens were taken from any particular site of the gall. It is noteworthy that the exuvial rupture in the 1st instar takes place not in the swollen head but around the posterior margin of the body as in Form ID, the 1st instar larva in Sequence 4. The 2nd instar larvae thus produced have well-developed legs in both these sequences (S2 and S4). The view is adopted that both the sequences represent ontogenetic courses of the male (see Discussion below).

**Sequence 3.** Only the 1st instar (IC) is known, though the enlarged and ruptured heads of several full-grown larvae indicate the production of the succeeding instar. In Form IC the legs are thickened and the claws are directed downwards, suggesting some peculiar behaviour, but, because no larva of the succeeding instar has been identified, any interpretation as to the form may be a mere assumption.

**Sequence 4.** The 1st and 2nd instar forms in this sequence are remarkably different from those in the female ontogenetic course (S1), and the 2nd instar form (IID) is similar to the ‘intermediate male instar’ of *Mangalorea hopeae*. I am inclined, therefore, to believe that they are male larvae. (As stated above, Form IA and IIB in Sequence 2 are also interpreted as male larvae, Form IIB substantially agreeing with IID). The 1st instar larva (ID) occurs between layers in the bark of the hypertrophied twig. Many individuals of this form were found crowded together in the bark, each of them being set in a pinhole, about 0.2 mm in diameter, formed in the inner layer of the bark, with the head held in the bottom of the pinhole (Figs. 9-12). (This pinhole is much smaller than the female's pit, which is narrow at the opening, but much broadened internally, attaining over 1.25 mm in diameter.) Exuviation occurs around the posterior end of the body, suggesting that the 2nd instar larva thus produced is liberated from the pinhole. The robust legs and the poorly developed dorsal setae of Form ID may be adaptive for creeping between the bark layers, which, in the hypertrophied twig, may be loosened to make a thin interspace between. In the 2nd instar form (IID) the legs are slender, but show no trace of reduction. The larvae of this form must move to somewhere else, otherwise their legs should have been atrophied as in the case of the *Mangalorea hopeae* intermediate instar male. According to Anthony (1974b), eventually ‘the plant tissues necrotize, become brown, and the whole twig on which the gall occurs dries out’. The tissues thus go on to change after the completion of the gall, and I wonder if the interspace in the bark would grow larger so that the 2nd instar males, though having only slender legs, could easily move in the bark. In any case the males must escape from within the bark during the larval stage or at the adult stage eventually to meet the adult females imprisoned in the pits. It is supposed above that the 1st
instar larvae of Form ID require for their settlement a relaxation of the bark tissues and that the crawlers creep into the bark interspace caused by the parasitism of their mother. If this is the case, the stem gall should harbour 2 generations (mother and sons) of the coccoid. (The female crawlers should disperse to induce new galls.)

Discussion

In the Coccoidea remarkable sexual dimorphism in the larval stage is rather unusual (in spite of the grossly different adult male and female). In many species, the sexes of the 1st instar larvae, and especially of crawlers, are indistinguishable. This is a reason why I regard Sequence 2 as belonging to the male. In this sequence the 1st instar cannot be distinguished from that in the female ontogenetic course (S1) in external characters, but definitely differs from the latter in exuviation. Sequence 4 is interpreted as representing another ontogenetic course of the male, with the 1st instar form (ID) quite different from, but the 2nd instar form (IID) substantially agreeing with, the corresponding form (IA or IIB) in Sequence 2. The other 1st instar form, IC, agrees with the 1st instar female in the way of exuviation, but there is no definite evidence to show that it belongs to the female. Polyphenism — ‘the existence of environmentally cued alternative phenotypes in a population’ (West-Eberhard, 1989) — is well known in some insect groups with cyclic parthenogenesis, but, so far as I am aware, polymorphism (in the broad sense) in larvae of the same instar feeding on the same gall is quite extraordinary. Beardsley (1984) in his revision of gall-inducing coccoids gives no account of larval polymorphism. However, it may not be inconceivable that occasionally a gall insect would exploit more than a single feeding site provided by the structure of the gall. In fact, Mangalorea hopeae males occur among spinous processes grown on the outer surface of the spherical gall induced and inhabited by a female (probably their mother) (Raman and Takagi, 1992). In the hypertrophied stem gall induced by B. shoreae the bark tissues, assumed to be loosened due to the gall’s growth, afford to the coccoid an extra site to feed on. I am muchinclined to the view that exploitation of this site would have resulted in the appearance of the robust-legged form of the 1st instar male (ID) and its succeeding instars, giving rise to a new ontogenetic course of the male (S4). The original course (S2) persists, and another form of the 1st instar (IC) indicates another course of ontogeny.

The B. dipterocarpi larvae are also supposed to be polymorphic (Takagi, 1987), and not all of the polymorphic forms are comparable to those of B. shoreae. The galls are quite different between these species, and it is natural to suppose an intimate association between the gall structure and the inhabiting polymorphic forms.

BEESONIIDAE: DISTRIBUTION AND HOST ASSOCIATION

Five species are now known in the family Beesoniidae (Tables 2 and 3). Three of them are associated with dipterocarps in Southeast Asia and South Asia, and the other two occur on oaks in warm temperate eastern Asia. I once supposed that B. napiformis and B. brevipes are not congeneric with B. dipterocarpi, but failed to find any distinct difference of generic value between their 1st instar females (Takagi, 1987). B. shoreae is similar to B. napiformis and B. brevipes in gall formation and to
Table 2. Beesoniidae: a list of genera and species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Host plant</th>
<th>Gall site</th>
<th>Locality</th>
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<tbody>
<tr>
<td><em>M. hopeae</em> Takagi, 1992</td>
<td>Hopea</td>
<td>Bud*</td>
<td>South India</td>
</tr>
<tr>
<td><em>B. dipterocarpi</em> Green, 1926</td>
<td>Dipterocarpus</td>
<td>Bud*</td>
<td>Burma</td>
</tr>
<tr>
<td><em>B. shoreae</em>, sp. nov.</td>
<td>Shorea</td>
<td>Stem</td>
<td>Singapore</td>
</tr>
<tr>
<td><em>B. napiformis</em> (Kuwana, 1914)</td>
<td>Oaks**</td>
<td>Stem</td>
<td>Nepal, China, Korea, Japan</td>
</tr>
<tr>
<td><em>B. brevipes</em> Takagi, 1987</td>
<td>Oaks***</td>
<td>Stem</td>
<td>Nepal, Japan</td>
</tr>
</tbody>
</table>

* Vegetative axillary bud.
** *Quercus, Lithocarpus and Castanopsis.*
*** *Quercus* in Nepal. *Beesonia sp.* in Takagi (1987), occurring on *Castanopsis* in Japan, is tentatively referred to *B. brevipes.*

*B. dipterocarpi* in host association, supporting the view that all these species belong to the same genus.

Because the family is now known from all of the 3 main regions of dipterocarp forests in Asia (western part of southern India and Sri Lanka; Indochina, northern India and lowland Nepal; and the botanical region Malesia), further forms are expected to occur in the vast dipterocarp zone (for possible beesonidi galls from Thailand and Sri Lanka, see Raman and Takagi, 1992, p. 30; also see Jenkins and Mabberley, 1994, who found many echinate galls on herbarium specimens of dipterocarps from Asia and Africa; further, Anthony, 1980, recorded many galls from Asian dipterocarps). The distribution of the family, therefore, may be supposed to cover the tropical dipterocarp zone and the warm temperate oak zone of Asia. This pattern of geographical distribution is common to many other groups of organisms. However, the dipterocarp-oak combination in host association is hardly expected from the viewpoint of plant phylogeny. Nevertheless, it finds other examples in leaf-mining microlepidopterous genera *Monocercops* and *Chrysocercops* (Kumata, 1989; 1992). Oaks are also abundant at higher altitudes in western Malesia. The primitive diaspidine genus *Kyphosoma* was erected on the basis of 3 species occurring on montane oaks in Malaya and Sabah (Takagi, 1993). Recently, by the courtesy of
Dr. J.H. Martin, the Natural History Museum, London, I have had the opportunity to examine specimens of a *Kyphosorna* species collected by him in Brunei on 'meranti merah' (*Shorea* sp.) at 400-500 m. The meaning of the dipterocarp-oak combination is unknown. I think, however, that the combination is worthy of attention in studying phytophagous insects in eastern to southeastern Asia.

**POSTSCRIPT**

When I visited Singapore in 1992 and learned from Dr. Murphy how to find *Beesonia* galls on *Shorea curtisii*, I realized that this type of galls could be easily overlooked. Since I had not been trained in collecting insect galls, I must have often overlooked in my Malaysia trips not only such galls but also conspicuous galls appearing like buds or fruits. In addition, in the family Diaspididae, my main-interest group, gall-inducers are few, relative to the size of the family (Beardsley, 1984). Moreover, in general, my search for coccoids in the tropical rain forest was largely limited to seedlings and saplings (needless to say, the crown was far from accessible except for occasional fallen trees). All this is another reason why I believe that there must be not a few unknown beesoniids in the dipterocarp forest. Various types of galls may be induced by them, offering them opportunities to develop peculiar ways of life and polymorphism. My study on *B. shoreae* is incomplete, but I hope that my report on its larval polymorphism will caution future workers in this family against introducing careless confusion. I myself did not expect to find as many as 4 forms of the 1st instar from the inconspicuous stem gall of *B. shoreae*. *B. dipterocarpi*, inducing a conspicuous type of gall, is also polymorphic in the larval stage, and Green (1926; 1928), being unaware of the polymorphism, confused instars and forms in describing the species. His confusion has not yet been cleared.

The interpretation adopted in this paper for the larval polymorphism of *Beesonia shoreae* may not be the only possible one. Dr. Khoo attempted to reinterpret Form IC, ID and IID and their ontogenetic sequences, and suggested to me a more complicated pattern of polymorphism.

In concluding this paper, I would like to cite a passage from Dr. Raman's review of the manuscript: 'Although not a very good comparison, I have seen larvae of (a) gall-inducing thrips, (b) inquilinous thrips, and (c) predatory thrips occurring at the same time in a gall. This should not mean that your observations can be misleading. I am only cautioning about a potential problem that can arise later on.'

**REFERENCES**


Correction to earlier paper

In an earlier paper published in this journal a certain error crept in, which may be corrected.

Fig. 1. Stem galls. Courtesy: Dr D.H. Murphy.

Fig. 2. Second (left) and 3rd (right) instar female *in situ*, part of the stem removed. The 3rd instar female, dark in colour, is situated deep in the pit, with the exuvial cast of the 2nd instar remaining near the opening of the pit. Courtesy: Dr D.H. Murphy.
Fig. 3. First instar larva, Form IA. Scale: 0.1 mm.
Fig. 4. First instar larva, Form IC, with head starting to expand anteriorly. Scale: 0.1 mm.
Fig. 5. First instar larva, Form ID, with head starting to grow. Scale: 0.1 mm.
Fig. 6. Second instar larva, Form IID. A: dorsal surface; B: ventral surface; C: antenna, ventral surface; D: hind tibia, tarsus and claw, ventral surface; E: anal plate; F: ducts; G: short duct; H: 5-locular disc pore. Scales: 0.1 mm (AB); 50 μm (CDE); 10 μm (FGH).
Fig. 7. First instar exuvial casts. Left: Form IA (female); right: Form IC. Scales: 0.1 mm.
Fig. 8. Left: exuvial cast of Form ID. Right: 2nd instar female, Form IIA, posterior end of body. Scales: 0.1 mm.
Fig. 9. Part of a galled stem split longitudinally, showing a row of pinholes. p: pinholes in vertical section; b: bark; w: wood. (The outer layer of the bark, above the row of pinholes in the picture, was ripped off, and the 2nd instar larvae and their exuvial casts were removed from the pinholes.)

Fig. 10. Pinholes in vertical section magnified.
Fig. 11. Surface of inner layer of bark, showing openings of pinholes and part of the wall of a female pit (f).

Fig. 12. Openings of pinholes magnified. Some pinholes with 2nd instar larvae (Form IID) exposing their posterior ends. (The larval bodies are shrunken probably owing to a certain process in preparing the material for scanning electron microscopy. It is unknown how much the structures in the bark have been modified by the process.)