THE SIREX WOOD-WASPS AND THEIR IMPORTANCE IN FORESTRY.

BY

R. N. CHRYSTAL, Hon. M.A. (Oxon.), B.Sc. (For.) (Edin.).

(PLATES IX–XI.)

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(PLATES IX–XI.)

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Introduction.

This paper on the biology and forest relations of certain British wood-wasps or "horntails" (Hymenoptera, SIRICIDAE), which is based upon some studies recently carried out at Oxford (1926–27), was originally inspired by the recent accounts that have appeared concerning the destructive activities of one of the steel-blue species in New Zealand. There the wood-wasps are causing considerable anxiety on account of their attacks on *Pinus radiata*, and quite recently the New Zealand Government approached the Imperial Bureau of Entomology with a request that their newly established parasite laboratory at Farnham Royal, Bucks., might take up the study of the wood-wasp parasites, with a view to their collection and exportation to New Zealand. I have had the pleasure of co-operating with the Bureau in this work and this paper is intended to serve as an introduction to a later publication on the parasites of the woodwasps, which will be published subsequent to the completion of certain investigations now proceeding. A preliminary paper on the parasites of the wood-wasps has already been published (Bull. Ent. Res., xix, pp. 67–77).

The objectives in the present work have been threefold : to review the literature of the SIRICIDAE up to date ; to present the results of some recent studies made by myself on the biology and forest relations of two British species ; and, lastly, to touch briefly on the *Sirex* problem in New Zealand, with particular reference to the question of control measures. I should like at this point to acknowledge my indebtedness to Dr. J. G. Myers, of the Imperial Bureau of Entomology, for helpful criticism ; to Dr. James Waterston, of the British Museum (Natural History), who has kindly contributed some systematic notes on the British wood-wasps, which are published here by kind permission of the Trustees of the British Museum ; to the President and Fellows of Magdalen College, Oxford, for their kindness in granting access to the wood at Tubney, near Oxford, where most of the work has been carried out ; and to Mr. H. S. Hanson, of South Molton, North Devon, who has helped materially with specimens and personal records from that district.

Systematic Notes on British Wood-wasps.*

While the determination of any of the *Sirex* species occurring in Britain seldom presents special difficulties, their tabulation is by no means easy owing to the

* By Dr. James Waterston.

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notorious instability of the available characters. Particularly is this the case with the neuration. Thus, *S. gigas* occasionally shows a first transverse brachial vein completely or imperfectly developed. British *S. noctilio* apparently have this vein incomplete, but in continental examples it may be fully developed. The neuration

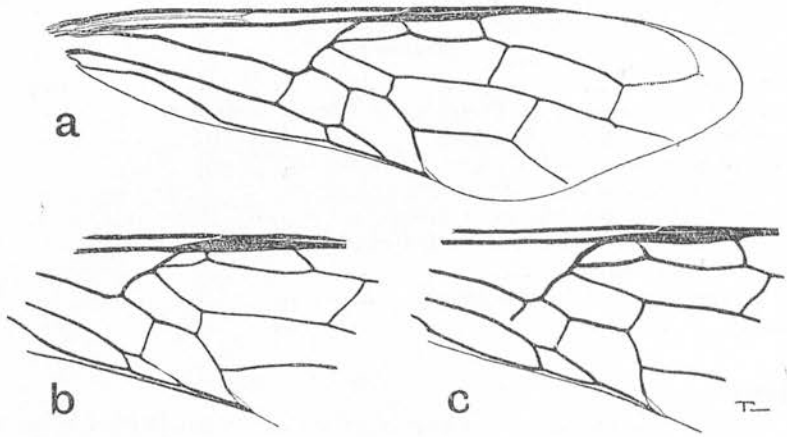


Fig. 1. Neuration of forewing: *a, Sirex cyaneus; b, S. gigas; c, S. noctilio.*

of *S. cyaneus* appears to be more constant, but (though rarely) it is not invariably to be relied upon.

The ♂ genitalia, at least in larger examples, can be drawn out in fresh specimens and studied in this way. The outer lobe (squamula) of the stipes appears to be

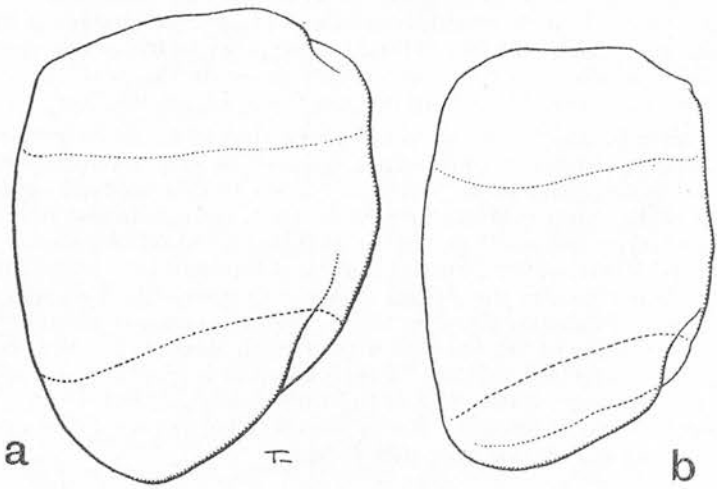


Fig. 2. Genitalia—apical appendage (squamula) of stipes: *a, Sirex noctilio; b, S. cy neus.*

narrower and straighter ventrally in *cyaneus* than in *noctilio*, and there are other differences in the apparatus seen from below.

As regards the synonymy of *Sirex* I have followed Bradley (1913) (*vide infra*).

Curtis (1829) designates *S. juvencus*, L., as the genotype. His figure and description apply to *S. noctilio*, Fab. Fortunately, however, this in no way alters the application of the name.

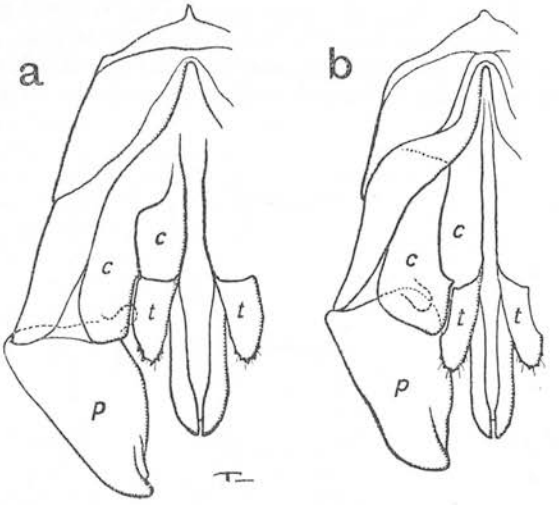


Fig. 3 Genitalia—from below: *a*, *S. noctilio*; *b*, *S. cyaneus*. (Lettering corresponds to that in Boulangé's monograph.)§

Normal examples of the four wood-wasps now occurring in Britain may be separated by the following key.

1. Head with a conspicuous yellow spot on the temples behind each eye; vertex *broadly black* separating the spots widely. Forewings with *one* transverse brachial nervure (fig. 1, *b*) ... ... *gigas*, L.
   Head immaculate; *two* transverse brachial nervures (fig. 1, *a*, *c*) 2
2. Females 3
   Males 5
3. Projecting portion of the ovipositor sheath, seen from above, nearly as long as tergites ix+x; first transverse brachial nervure complete *cyaneus*, F.
   Projection of sheath never much longer than tergite x; first transverse brachial nervure usually incomplete 4
4. Antennae wholly infuscated or black; cornus sub-equilateral; impression on tergite ix distinctly transverse; sheath distinctly shorter than tergite x *noctilio*, F.
   Antennae with scape (whole or part), pedicel and 3–5 normal funicular joints clear testaceous or ferruginous; cornus elongate triangular; impression variable, never distinctly transverse; sheath and tergite x subequal *juvencus*, L.
5. Apex of abdomen from the 8th segment black with (more or less) submetallic reflections; all femora darkened, and in the hind legs black except narrowly at apex; first transverse brachial nervure generally incomplete *noctilio*, F.
   Apex of abdomen and all femora ferruginous (the contrast between femur and tibia striking in the hind leg) 6
6. Antennae basally rufescent or pale; 1st transverse brachial nervure incomplete *juvencus*, L.
   Antennae entirely infuscated or black; 1st transverse brachial nervure complete *cyaneus*, F.

§ Boulangé, Mém. Trav. Facultés catholiques Lille, xxviii, 1924.

Sirex (*Urocerus*) *gigas*, L.

This, our only representative of the subgenus *Urocerus*, is a conspicuous yellow and black species, which is easily recognised. The large black spot (about as wide as two-thirds of the vertex) separating the paler ones on the temples distinguishes this species in both sexes from others found in the Palaearctic Region, e.g., *augur*, Kl., *fantoma*, F., *cedrorum*, Sm., *japonicus*, Sm., *xanthus*, Cam., in which there is at most a narrow darker line extending backwards behind the anterior ocellus, and hardly

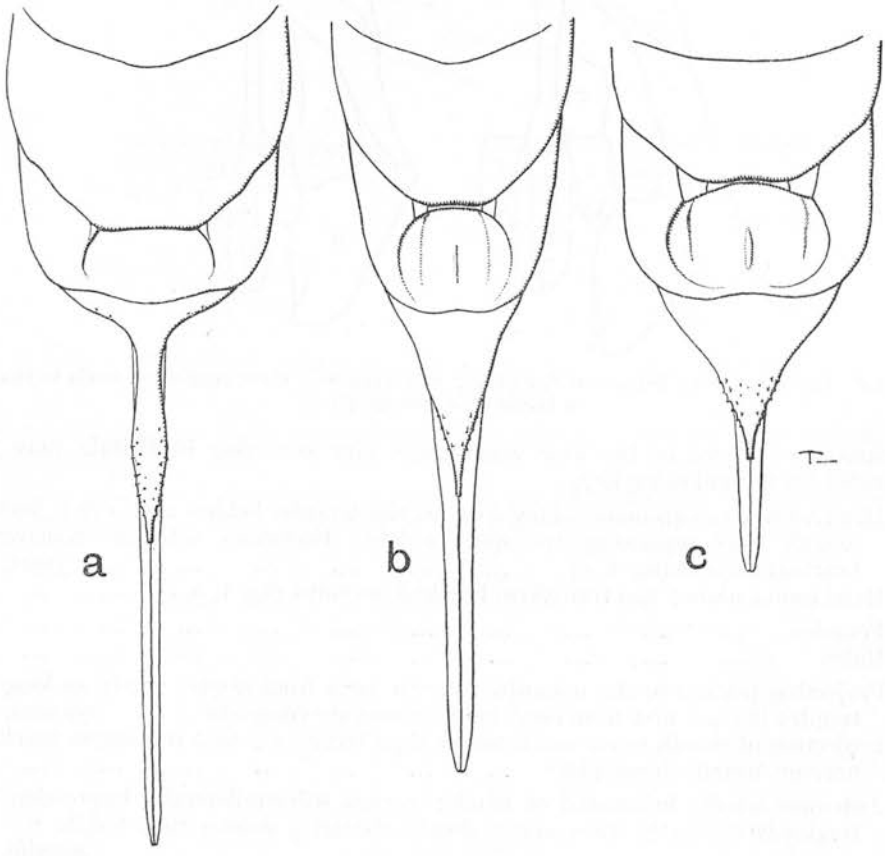


Fig. 4. Abdominal segments viii–x, dorsal view: *a*, *S. gigas*; *b*, *S. cyaneus*; *c*, *S. noctilio*.

wider than this organ. Confusion, however, may arise between *U. gigas*, L., *U. flavicornis*, F. (♂, ♀) and *U. albicornis*, F. (♀) (both North American). The first two may be separated as follows :—

U. gigas.

♂. Scape variable (black, black and yellow, or yellow) ; flagellum yellow, as is also tergite vii. Tergite ii infuscated, as a rule, only along anterior edge, and not to beyond one-half posteriorly.

U. flavicornis.

♂. Scape black ; flagellum basally ferruginous, and distally infuscated (*i.e.*, from 6th–8th joint to apex, which may be black). Tergite vii black ; tergite ii more extensively infuscated, pale mainly at sides.

♀. Tergite viii entirely yellow; tergite ix infuscated basally (sometimes only at sides), pale (yellow) broadly towards apex; tergite x wholly yellow.

♀. Tergite viii yellow only on basal third, black beyond; tergite ix wholly black; tergite x black, only the spike yellow.

According to Professor J. C. Bradley (J. Ent. & Zool. v, p. 19, 1913) the males of *U. albicornis* and *U. flavicornis* are indistinguishable.

In the British Museum are two males (Hudson's Bay) placed under *albicornis*, F., by the late F. D. Morice. These can be separated from *flavicornis*, F., by the more elongate hind tarsus, in which the first joint is slender, nearly seven times as long as wide, whereas in *albicornis* (Nova Scotia) this joint is barely five times as long as broad. In ♀ *albicornis* the abdomen is wholly black save for a pale spot at the side on tergite viii. Both of these North American species have occurred in England in the London District, and their captures have resulted in regrettable additions to synonymy; *U. albicornis*, F., was thus re-described as *Sirex stephensi*, Kirby 1882, and *U. flavicornis*, F., as *Sirex bizonatus*, Steph. 1835. The type of *U. stephensi* and cotypes (?) of *U. bizonatus* are still extant in the British Museum. *U. augur*, Kl., is also reported to have occurred in Britain, but I have seen no example so taken.

Sirex noctilio, F.

In the male this species is recognisable at once by the colour of the legs, antennae and abdomen (apex), as well as by the usually imperfect first transverse brachial nervure. The first two, and part of the third tergites are dark, and more or less metallic. The darkening of tergite iii may reach back to two-thirds, but it is generally incomplete laterally. In the female the abdomen is stout and broad, parallel-sided to the end of the 9th segment, and rather abruptly pointed on the 10th tergite.

The general surface of tergites ii–viii is dull blackish, and remains so however the insect is turned. Tergite i, beyond the usual large punctures, is smooth and shining, especially along the posterior margin.

Sirex cyaneus, F.

♂. Abundantly distinct from *S. noctilio*, F., but separable from ♂ *S. juvencus* sometimes only by the colour of the antennae; tergites i and ii wholly, iii on disc, and iv (a basal spot or spots) blue-black.

♀. The abdomen is more slender and tapers gradually from the middle of the 8th segment. The impression on tergite ix is subcircular, and at its bottom clearly longer than broad. The general surface of tergites ii–viii is dark blue from above, and distinctly coerulescent from other angles. Tergite i, beyond the usual large punctures, is faintly scaly reticulate and hence not brilliantly shining on the posterior half.

Sirex juvencus, L.

♂. See note under *cyaneus*, F.

♀. Distinguished by the incomplete transverse nervure, and the basally rufescent antennae. In the abdomen rather mo e like *cyaneus* than *noctilio*, but the ovipositor is slightly shorter than in the former, and the cornus a trifle narrower than in the latter.

The colour of the forewings, in the specimens of *juvencus* in the British Museum, is noticeably darker on rather more than the apical half, *i.e.*, from the level of the first cubital cell. In *noctilio* and *cyaneus* the wings are sub-hyaline and more or less broadly infuscated along the outer margins.

Status of the Species discussed.

Only in the case of *S. juvencus*, L., can any doubt arise as to the application of the name or the status of the insects determined by the above key. The name must

be used to designate a blue-black *Sirex* with the antennae basally rufescent, and Evans (Scottish Naturalist, p. 176, 1922) has pointed out that the male of *S. noctilio* may show this character—probably owing to immaturity. Evans' specimens had the apex of the abdomen dark and were found in galleries in timber, with ♀♀ clearly *noctilio*.

The ♂ of *S. cyaneus* (*i.e.*, reared with normal females of that species) may show on both wings an incomplete first transverse brachial nervure, and if the pale colour of the antennae basally can be due to immaturity, such a specimen would be indistinguishable from *S. juvencus* ♂.

The ♀ of *S. juvencus* is much more definable than the ♂. The ovipositor is relatively longer than in *noctilio*, and shorter than in *cyaneus*. The cornus, too, seems to be intermediate in shape, but I have not seen enough material to offer a decided opinion. In discussing these blue-black wood-wasps I have quite deliberately avoided using the longitudinal impression on the vertex, and the rugulosity of the saw-sheath as characters. They seem to me too variable to be relied upon. The tarsal characters noted by Thomson require further elucidation, and have not been dealt with here.

Status as British Insects.

U. gigas, *S. noctilio* and *S. cyaneus* are at the present day thoroughly established in Britain, but the position of *S. juvencus* is more doubtful. Examples of all four taken by J. F. Stephens are still extant in the British Museum.

No one, however, has yet collected and critically analysed the records of *Sirex* taken in England, though such a work might throw interesting light on the progress of the invader *S. cyaneus*. Since the War *U. gigas* and *S. cyaneus* have frequently been sent to the writer for determination, while true *S. noctilio* appears to be less common. *S. juvencus* has been received only twice, on each occasion probably as an importation.

Mr. Evans' notes on the wood-wasps (*Sirex*) in Scotland, already referred to, give an admirable summary of the subject. *U. gigas* was first recorded as a Scottish insect in 1813, and has now been reported from thirty of the Watsonian counties and vice-counties. It is absent, indeed, only in the extreme north and certain of the islands.

"Blue-black" wood-wasps have been known for fifty years in Scotland, and have now been noted in fourteen of the Watsonian areas. In nine (probably ten) of these *S. cyaneus* has been identified, and in two *S. noctilio*. In one county (Linlithgow) the latter species has been definitely proved to be established.

General Review of Sirex Literature.

Continental.—The important continental literature on the biology and forest relations of the SIRICIDAE dates from the beginning of the 19th century, and the earliest papers are of German origin. J. M. Bechstein was one of the pioneer workers and devoted a section of his "Forstinsektologie," published at Gotha in 1818, to the family, in which he gave a general account of the morphology and biology of *S. gigas* and *S. juvencus*, his work being chiefly remarkable for the statements made as to the predatory habits of the adults, which will be discussed later on. Bechstein's work together with that of other contemporary observers was summarised by Ratzeburg in 1844 in his great work "Die Forstinsekten," which contains a detailed description of the morphology and biology of the two species mentioned above, and also discusses at some length the forest relations of the species with special reference to their appearance in forests that have been severely damaged by defoliating insects. This work must be regarded as the principal source from which many subsequent writers derived much of their material. After Ratzeburg's time the next important contribution to the literature was Hartig's "Die Familien der Blatt-und Holzwespen," which appeared in 1860. In the section of this book that deals with the SIRICIDAE, Hartig

gives a very complete account of the larval life of *S. juvencus*, which includes some valuable observations on the characteristics of its larval tunnels and the nature of the frass. He also deals with the question of *Sirex* as an enemy of green trees and compares its status as a primary pest with that of the bark-beetles, which he regards as being immeasurably more important. Describing the life of the adults in detail he criticises at some length Bechstein's statement that they prey on other insects and cites the observations of other writers on the same subject. He concludes his account of the family with a complete systematic review. Taschenberg's textbook, "Forstwirtschaftliche Insektenkunde," followed Hartig's work in 1874, and in this a useful review of the family is given, chiefly based on the work of previous writers, some of whose errors are repeated. He deals almost entirely with *S. juvencus*, giving only a very brief account of *S. gigas*. André's book, "Species des Hyménoptères d'Europe et d'Algerie," followed Taschenberg in 1879, and in this a small section is devoted to the family. The biological notes on the species, which largely follow Bechstein's work, contain numerous errors and do not give any data regarding host trees. A long list of insect parasites is given without any data referable to their occurrence, and this was apparently drawn upon by Rudow in 1919, who quotes a similar list, without however furnishing any further details. In 1881 there appeared a paper by Wachtl entitled "Die Stahlblau Fichten- und violette Kiefernholzwespe *S. juvencus* Linne und *S. noctilio* Fabr.", in which he gave a complete morphological comparison of these species in the form of parallel keys, and also dealt briefly with their biology and distribution.

Eight years later, in 1889, Herman Borries, a Danish entomologist, published a paper on the "Occurrence and Distribution of Insect Pests in the Danish Conifer Forests." A section of this paper is devoted to the SIRICIDAE and gives a brief account of the distribution of *Sirex* in Denmark, together with some biological observations, some of the most valuable of which are those concerning the pairing habits.

In the year 1895 there appeared Judeich & Nitsche's "Forstinsektenkunde," which was published as the 8th edition of Ratzeburg's "Die Waldverderber und ihre Feinde." In this book a very complete review of the SIRICIDAE is given, covering not only the systematic side of the subject but also dealing in full detail with the biological aspect. The references to previous workers are very complete, and this work forms an indispensable guide to all literature published up to that time.

From 1895 up to the present day the most important continental works on the subject are Enslin's monograph "Die Blatt-und Holzwespen," in Vol. iii of Schröder's "Insekten Mitteleuropas," Stuttgart, 1914, and Scheidter's recent paper on the biology of *S. augur* and *S. gigas* in Bavaria published in 1923. Enslin's work contains a useful introduction to the biology of the Tenthredinoidea as a whole, and gives well illustrated systematic keys to the families and a comprehensive bibliography of the literature on the group. Scheidter's paper is valuable for its biological detail and includes several hitherto unrecorded observations on the oviposition of *S. gigas*, which will be dealt with subsequently in a comparison of the habits of this species with those of *S. cyaneus*.

British Literature.—The earliest reference to *Sirex* in Britain that I have been able to find occurs in Martyn's edition of Moses Harris' "Exposition of British Insects," London, 1792. The wood-wasp referred to, which is described and figured together with its larva under the name of *S. torvus*, is one of the steel-blue species and bears a strong resemblance in the length of its ovipositor to *S. cyaneus*. It is interesting to note that, discussing the identity of the species, Harris has grave doubts as to its being synonymous with *S. juvencus*, L. The larva is noted as living in dead wood.

Donovan (Natural History of British Insects, xi, London, 1806) records *S. juvencus* as having been taken in a London dwelling-house. He describes the species as a wood borer, but gives no further details. The figure of the insect, which is excellently reproduced on a full-page plate, is almost certainly that of *S. cyaneus*. Curtis (British

Entomology, vi, London, 1829) refers to two species of *Sirex*, *S. gigas* and *S. juvencus*. He records *gigas* from Norwich, Wilts, Kent, Berks, and near London ; and *juvencus* from fir (?) groves in Norfolk, Suffolk, Hants and Yorkshire. Some interesting biological details are given by him in respect of material received from the Hon. Chas. Harris, of Heron Court, Gloucestershire. This was obtained from some fir (? pine) trees that had suffered severely from heat and drought during the summers of 1825 and 1826. The adult wood-wasps were taken only in dead trees and eight males are recorded as emerging simultaneously. These, he relates, proved to be strong on the wing, and when released immediately rose to a considerable height. This, as we shall see, probably bears out a statement by Borries on the habit of the males at pairing time. Large numbers of males, he continues, were found during the same year (1826) flying round the towers of York Minster. These, he says, were probably seeking females, which were issuing from timbers used in supporting the roof. Shuckard (Magazine of Natural History, 1837) records *S. cyaneus* (*duplex*) from black spruce (*Picea nigra*) in Cambridgeshire, emerging at the end of May and early June. He gives no biological details, however. Three years later, in 1840, Westwood published his Introduction to the Modern Classification of Insects, in Vol. ii of which he devotes a small section to the morphology of *S. juvencus*, dealing especially with the structure of its ovipositor. He quotes an interesting record of the occurrence of this species from Bewdley Forest, Worcestershire, communicated by Mr. Raddon. During the first part of the season (1836) the proportion of females to males was only 1 in 12, while during the latter part, *i.e.*, the last 2 to 3 weeks, only females appeared. The wood-wasps continued to emerge until the end of November.

In 1882 W. F. Kirby's list of the Hymenoptera in the British Museum appeared, and in this *S. cyaneus* is recorded as having been taken by Stephens, Shuckard and Lubbock. Lubbock's specimens were bred from larch, but otherwise no record of host trees is given. From 1887 up to the present day the most important contributions to the literature include the following works :—Cameron's "Monograph of the British Phytophagous Hymenoptera," which is entirely systematic ; Morice's "Help Notes towards the Determination of British Tenthredinoidea," also systematic ; and the works of Miss Ormerod (Manual of Injurious Insects and Methods of Prevention, pp. 256–260, 1890), MacDougall (1907) and William Evans (1922).

Evans' paper is the most comprehensive account of the SIRICIDAE that has so far appeared in this country. He gives a complete historical account of the records of *Sirex* in Scotland, which is supplemented by statistical details. His biological notes, which will be discussed more fully later on, are also most valuable.

American Literature.—The American literature on the SIRICIDAE attacking conifers is, practically speaking, apart from systematic papers by Bradley and others, confined to brief records of their occurrence. Felt in his "Insects of Park and Woodland Trees," 1905, refers briefly to two species, *Sirex* (*Urocerus*) *albicornis*, F., and *Sirex* (*Paururus*) *cyaneus*, F., but the majority of other writers are content with simple records of their capture and locality. No really comprehensive account of the biology of any American species attacking conifers has appeared as yet.

Biology of S. cyaneus and S. gigas in Britain.

The major portion of the biological work has been carried out on *S. cyaneus*, this species being the only one present in the larch wood at Tubney where most of the field work was done.

Flight Period and Habits of the Adults.

The flight period of the two species overlaps to a considerable extent. *S. gigas* appears earlier and is found on the wing from June onwards until the autumn. My own records of the flight of this species during 1927 do not extend beyond 9th September, but Evans records their appearance in the South of Scotland in early October.

S. cyaneus appears as a rule towards the end of July or even later, according to the season. In 1927, for example, the flight did not become general until mid-August and the last adult was seen on 23rd September. I have no record of its appearance in flight as late as October, although Evans records finding the insect flying as late as 6th October. The flight period for both species is at its height from July to September, and this is in general agreement with the observations of Continental workers such as Hartig, Taschenberg and others. All the adults that emerged at Tubney developed, to the best of my knowledge, from larvae that had pupated some 5 weeks previously. Cases are known, however, of the insects wintering in the adult stage, and I have recently seen examples of this in both species from silver fir logs at South Molton, North Devon. I have never found *S. cyaneus* overwintering in the larch at Tubney, nor do I consider that it is by any means a common occurrence, as it seems probable that adults remaining thus in the wood over winter might be exposed to the grave danger of fungus attack, due to over-moist conditions. Further reference to the finding of emerging adults covered with fungus mycelium is made on page 000. The adults fly in bright sunlight and when in flight make a noisy buzzing sound, which has been well described by the German writers by the word "schwirren," the onomatopoeic significance of which must instantly strike anyone who has heard the insect when in flight. Bechstein, describing the flight habits, says of *S. gigas*: "The wood-wasp flies in the warm months of July and August, when pairing takes place, and the adults live by preying on other weaker insects, for example, flies"; and in another place, referring to *S. juvencus*, he writes: "This insect preys on other insects upon which it feeds." This view of the *Sirex* adult as a predator is not peculiar to Bechstein; Hartig also quotes the observations of an old writer, Jordens by name, who recorded the wood-wasps as predacious on the adults of the nun moth (*Lymantria monacha*), which he said were captured on the wing. Another writer, Thiersch, is also quoted by him to the same effect, viz. :—"The wasps not only feed on the sap of trees, *e.g.*, silver fir, etc., but also on small insects which they catch on the bark of trees and also in flight." The predatory habit is also referred to by Taschenberg, who states that the adult wood-wasps capture now and again small insects in flight, in a similar fashion to the large sawflies of the genus *Tenthredo*.

Hartig views the above statements with grave doubt and regards the evidence upon which they are based as being insufficient. With the latter view I am inclined to agree, and certainly no record of predatory habits on the part of the wood-wasps has been made by myself, nor can I find any mention of it in the British literature. The females are much the most commonly observed either on the wing, or at rest upon the bark of trees. This indicates a marked preponderance of females over males, and Scheidter observes in this connection that in a catch of several hundred adults of *S. augur* only 10 were males, and of *S. noctilio* only in one case was the majority of a catch composed of males, this having been probably made at a time when the males were just emerging and were easily caught. My own records of *S. cyaneus* also show a marked excess of females over males, the proportion being almost 2 : 1 over a period of two years, and recent figures from North Devon indicate a similar state of affairs.

During the flight period in Tubney Wood males were seen on only three occasions, once resting on the bark of a tree about 6 feet from the ground, and twice flying at a considerable height. Apropos of this, Borries quotes an observation made by Drewsen at Strandmöllen in Denmark, that wood-wasps pair in the tree-tops, after which the females descend to the lower levels for egg-laying. In the work at Tubney this summer pairing was never observed in the open, although it occurred in the cages on two occasions. The observation quoted above offers a reasonable explanation of the failure both to find adults pairing in the open, and also to observe many males in flight.

Oviposition.

Oviposition proceeds with great vigour in warm and sunny weather, but the wasps also show some activity on cloudy days and even when rain is falling. In very wet weather it is more usual, however, to find them sheltering in bark crevices. Hartig observed that the adult females of *S. juvencus* swarmed at sundown, and Scheidter also states that the females of *S. augur* and *S. noctilio* oviposited only in the late afternoon. I have found no evidence of time selection in either *gigas* or *cyaneus*, *e.g.*, *gigas* was found ovipositing in the middle of the day, while *cyaneus*, commencing about 10 a.m., would continue throughout the day until the early evening, in some cases without any marked interval of rest. Oviposition was observed in both species, in *S. gigas* on 8th July, and in *S. cyaneus* on many occasions from August until late September. *S. gigas* was found ovipositing in a sawmill where there was a considerable quantity of larch and pine logs and sawn timber. The insect selected a small freshly

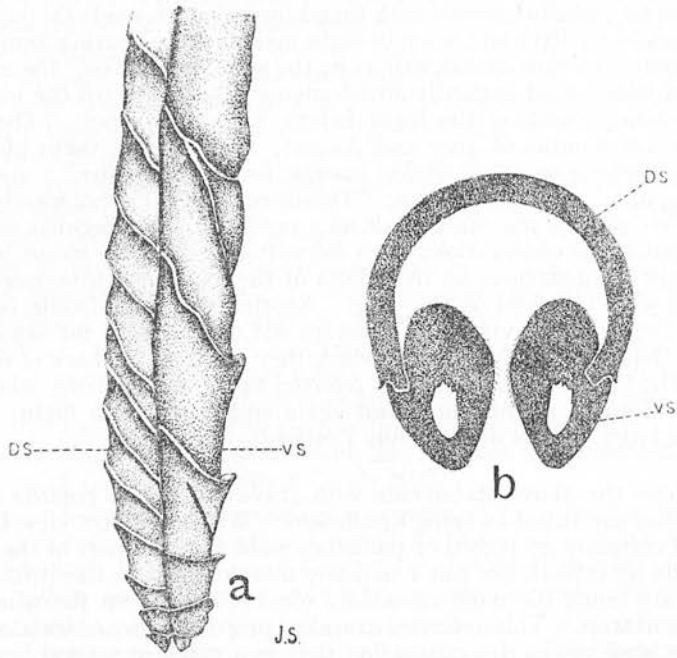


Fig. 5. Ovipositor of *S. cyaneus*: *a*, apex, showing the serrated setae, ×35; *b*, transverse section, showing the ventral valves (v.s.) slightly separated from one another, ×70. d.s. = dorsal seta, v.s. = ventral seta.

cut larch log and began its task at 11.25 a.m., boring three oviposition tunnels in the course of half an hour, each operation lasting 8–9 minutes. Two of these tunnels, on subsequent examination, failed to reveal any sign of eggs, and it was thought at first that these had been overlooked. It was discovered later, however, that the insect frequently makes trial borings, sometimes of considerable depth, in which, for some reason or another, she fails to oviposit.

Before boring commences, a close examination of the bark is made with the antennae, this operation being followed by further preliminary testing with the ovipositor and sheath, which may be withdrawn several times before a favourable spot is found. Having chosen the place of oviposition the insect raises herself upon the two outer valves that form the sheath of the ovipositor. Once she is firmly established in the desired place, the latter are released and spring back to their original horizontal

position, exposing the thin flexible tube-like ovipositor which the insect proceeds to insert into the wood with a rapid sawing movement of the toothed setae, the whole operation being accompanied by rhythmical movements of the abdomen.

It is at this point that the first egg is laid at the bottom of the tunnel. Subsequently the ovipositor is gradually withdrawn, coming to rest several times during the process. From the position of the eggs in the tunnel, lying as they do one above the other, it seems very probable that each halting place of the ovipositor represents the deposition of another egg. The halting of the ovipositor while being withdrawn is not, however, to be confused with the sawing action of the organ while the oviposition tunnel is still in course of construction.

The ovipositor (fig. 5) in transverse section can be divided into 3 parts, a dorsal valve, representing the fused inner gonapophyses of segment 9, and two ventral valves developed from the gonapophyses of segment 8.

The outer dorsal portion of each ventral valve is deeply grooved to enable the flanged portion of the dorsal valve to fit closely into it. The egg tube is formed by the

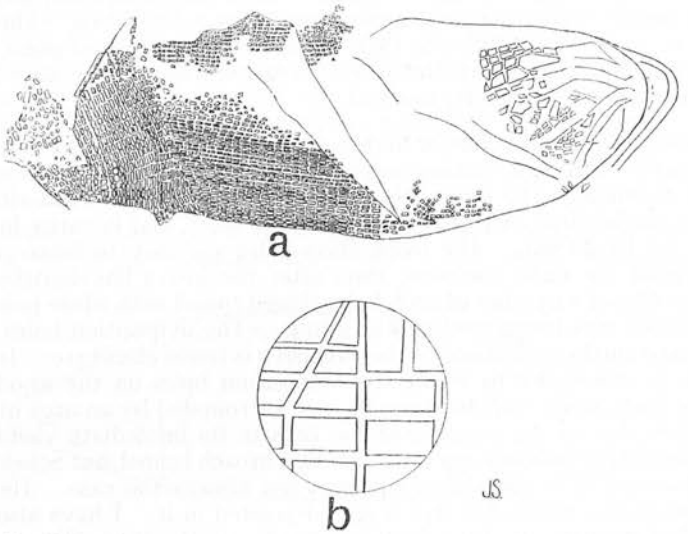


Fig. 6. Egg of *S. cyaneus: a*, sheath, × 60; small portion of sheath, × 225.

union of these valves, and if the ovipositor of an adult be examined at the time of egg laying the tube will be found full of eggs which are passing down into the oviposition tunnel. The diameter of the egg tube when empty is 0·27 mm., and on comparing this with the average diameter of the eggs which pass down it, it was found that these measured 0·36 mm. at their widest part, consequently exceeding the diameter of the egg tube by 0·09 mm. This difference in diameter is fairly constant, and the question arises as to how the egg passes down the tube into the oviposition tunnel. This is probably effected by a slight flattening out of the egg as it passes down the tube, proof of which has been found in eggs dissected out of the tube, and further the fact that the egg tube is oval in shape rather than circular confirms this ; moreover a lubricant fluid also assists the eggs in their passage down the tube. This fluid has been observed exuding from the tip of the ovipositor of *S. cyaneus* during the discharge of the eggs. Further, it has been found in all cases that the eggs are surrounded in the oviposition tunnel by a white glistening sheath of a glutinous nature.

This sheath coats the tunnel walls and also the eggs, from which it is extremely difficult to remove it. Under the microscope it always breaks up into a constant pattern (fig. 6) which somewhat resembles crystalline structure.

I found no trace of any such covering on the eggs that were still lying in the egg tubes, and therefore conclude that this substance is a glandular secretion, which, passing down the oviduct into the ovipositor, acts as a lubricant for the passage of the eggs. Burmeister (Manual of Entomology, p. 190, pl. xxvii, fig. 10) describes and figures a glandular appendage in the female reproductive organs of *S. gigas*, which he calls the gum gland. This, he says, contains a white glutinous liquid that covers the eggs and fastens them to " objects." He does not, however, figure the nature of this covering, so I am unable to compare my findings with his. Lastly, the eggs are assisted in their passage down the tube by the opening out of the two ventral valves, which increases the diameter of the tube. The actual occurrence of this can be seen when oviposition is in progress, as the eggs are sometimes visible passing down the tube through the slit formed by the opening out of the two ventral valves. The inner margins of these are covered with closely placed hairs, and it is possible that when they separate from one another the hairs act as a protection against the entry of foreign bodies, e.g., wood frass, etc., which might block up the egg tube. Close observation of oviposition is a simple matter, as the insect, completely absorbed in her task, allows one to follow her movements even with a hand lens. The oviposition habits of *S. cyaneus* do not differ in their essentials from those of *gigas*, but several instances were recorded in which the operation lasted from half an hour to one hour. These long periods are, however, unusual.

The oviposition tunnel is circular and in diameter measures slightly more than the greatest diameter of the egg, leaving ample room for the swelling of the egg when the young larva develops. The oviposition tunnel penetrates the wood either at right angles to the longitudinal axis of the stem, or at a slant, and it varies in depth from 6–7 mm. up to 18–20 mm. The oviposition holes are easy to locate with a little practice, even on the bark, for some time after the insect has departed. Plate ix shows the location of a number of such holes ringed round with white paint on a larch at Tubney, which was frequented by the adults. The oviposition holes on this tree were legion, and further reference to their density is made elsewhere. In the case of fresh trees it is still easier to locate the oviposition holes on the wood surface by removing the bark, when each hole can be seen surrounded by an area of discoloured tissue, which is due to the necrosis of the cells in its immediate vicinity. It was formerly believed that only one egg was deposited in each tunnel, but Scheidter recently showed in the case of *S. gigas* that this was not always the case. He figures one tunnel of this species which has had 6 eggs deposited in it. I have also found with *S. cyaneus* that one egg to a tunnel is the exception rather than the rule. Three to four eggs to a tunnel is quite a common number, and in some cases I have found as many as six or seven.

The total capacity of egg-laying varies considerably in different species. Scheidter, for example, found by dissection of the ovaries in *S. augur* an average of over 1,000 eggs, whereas in *S. noctilio* the average was only 400. Dissection of the egg tubes in large females of *S. cyaneus* taken at Tubney in September 1926 gave 300–400 on the average.

It is a common occurrence to find adults that have died while egg laying still fixed to the tree with the ovipositor buried in the wood. Two reasons can be assigned for this : First, the insect often chooses a place for oviposition where the sap flow is too strong, with the result that once the ovipositor is inserted she is unable to withdraw it, the moist condition of the wood causing the fibres to close in and hold it fast. Three or four dissections of adults that were found in this position were made during the summer, and in all cases the state of the egg tube showed that oviposition was at its height. Secondly, however, it is possible that some of the insects that were caught in this manner are those which, having come to an end of their egg-laying, are exhausted by their labours and thus perish in the completion of their task.

The egg (fig. 7) in both species is fusiform and translucent. It measures 1·25 to 1·5 mm. in length, is markedly constricted at one end and rather broadly rounded at the other. No definite pattern can be traced on the surface of the chorion. The eggs are deposited right up to the tunnel opening.

The incubation period is, so far as I have been able to calculate from my observations this summer (1927), 3 to 4 weeks. The young larva is completely developed before it leaves the egg (fig. 7), out of which it bites its way with the mandibles.

The first young larva found this summer on 29th August had already begun boring its own tunnel This larva measured 2 mm. in length and was one of the earliest hatched of the season, as three days later, on 1st September more young larvae were found which were still lying in the oviposition tunnel, not having begun to bore on their own account. Eggs were found up to 22nd October, and young larvae just leaving their egg-shells up to 8th November. The height of the oviposition period I take to be from the middle of August to the middle of September, and calculating 4 weeks as a maximum for the incubation period, I conclude that young larvae should still be found in the oviposition tunnels until early in November. The records which have been taken agree very closely with this estimate. On dissecting some oviposition tunnels of *S. cyaneus* recently (February 1928), two larvae were found lying in them not yet free from their egg-shells. This indicates that in the case of eggs laid late in the season, the incubation period may be much longer than usual. I have found only two cases of this so far.

The young Larva.

The morphology of the mature larva of *S. gigas* and *S. juvencus* has been described by Ratzeburg, Hartig, Cameron and others, and Yuasa, in his " Classification of the

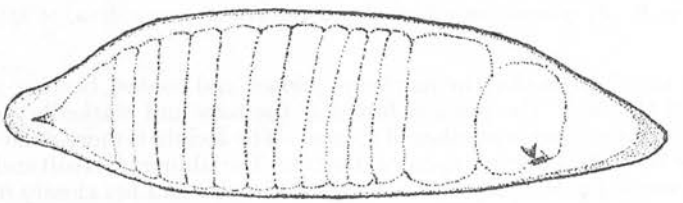


Fig. 7. *S. cyaneus*: egg with young larva *in situ*, × 60.

Larvae of the Tenthredinoidea," has described the larva of *Tremex columba*, Jurine, as a type of the family. The following notes refer to the first larval stage of *S. cyaneus* found in the oviposition tunnels at Tubney.

The first stage larva still under the cover of the eggshell is pale white and translucent, only the strongly chitinous mandibles and terminal spine showing dark brown in colour. The larva on hatching measures 1–25 mm. in length and has a uniformly cylindrical body which tapers somewhat towards the anal end. The body surface, examined superficially, appears smooth and shining, but on closer examination it is found to be covered with minute spines which are placed in regular rows on every segment. These spines, which hardly rise above the surface of the integument, do not seem sufficiently well developed to afford the larva much aid in locomotion. The head, which (as in the later stages) is markedly overhung by the prothoracic segment, is dome-shaped, smooth and shining, and directed ventrally.

The antennae (fig. 8, *b*), which are apparently two-jointed, have a truncate terminal joint armed with a number of blunt spines. In the mature larva the antennae are three-jointed and have their terminal joint markedly pointed. The mouth-parts (fig. 8) are well developed and exhibit the following characters: The

labrum (*a*) is markedly asymmetrical, a characteristic which is developed to an even greater degree in the later stages. On its front margin there are several rows of spinous processes, giving it a markedly roughened appearance. This is in contrast to the labrum of the mature larva in which the front margin is entire and heavily chitinized. The two mandibles also differ markedly from one another; the right mandible (*d*), which lies above the left when at rest, is somewhat quadrate in shape and bears a large lobe on its inner side and four blunt teeth on its outer margin; in the left mandible (*c*) the inner lobe is much less strongly developed and the outer margin is provided with only three teeth.

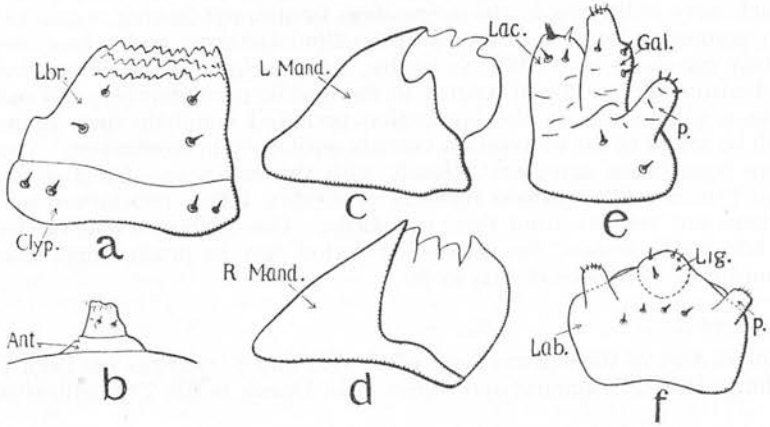


Fig. 8. *S. cyaneus:* mouth-parts and antenna of young larva, × 225.

The maxillae (*e*) are fleshy, the palpi one-jointed and conical, bearing a number of blunt setae at the tip. The galea is broad at the base and markedly constricted at the tip, on which there are a number of spines. The lacinia is more dome-shaped and bears at least three well-marked spines at the tip. The labium (*f*) is soft and fleshy with well marked single-jointed palpi. The ligula is circular and fits closely into the deep emargination of the mentum. Mamma-like thoracic legs are already well developed, and each bears a prominent terminal spine. The spiracles number nine pairs, of which the prothoracic pair are much larger than the rest. They are markedly circular in form and in this respect differ from the later stages, in which they are oval. The terminal abdominal segment is hollowed out in a deep depression on the tergum, at the apex of which are borne two short blunt tubercles. Beyond these lies the chitinous terminal spine, which in the first stage larva is markedly shorter than in the later stages.

The function of the terminal spine has always been considered to be concerned with the packing of the boring dust by the larva in its tunnel. After watching several larvae working in their burrows I have come to the conclusion that it also serves the larva as a terminal support, being driven into the sides of the tunnel for this purpose.

The young larva constructs its tunnel at right angles to the oviposition tunnel and continues to bore in this direction for a short distance before it turns inwards towards the heartwood. Many studies were made of these tunnels and text-fig. 9 shows some typical examples that were drawn as they appeared on 27th–29th September 1927.

Figure 9, *a* shows a sloping egg tunnel at the commencement of which, just below the wood surface, a larva has hatched, and is commencing to bore along the sap wood. In figure *b* the tunnel is vertical, and contains three larvae, all of which have begun

their tunnels ; and in figures *c* and *d* some newly hatched larvae are seen still lying in the oviposition tunnel, only one having begun to bore. All these figures are drawn from freshly dissected specimens and represent the varying conditions which one may expect to find in the oviposition tunnels during September and October. The study of the oviposition and young larval tunnels has been found to be of great importance in the study of the Cynipid *Ibalia*, and will be referred to again in the paper on that parasite.

The larva tunnels in the outer sapwood for the first part of its life. When it has grown to a length of 8–9 mm. it turns inwards towards the heartwood, usually following a more or less vertical direction, either upwards or downwards. As it proceeds on its way the tunnel behind is closely packed with frass, and at intervals in this the cast larval skins are to be found tightly wedged between the frass layers. Moulting begins very early in larval life, the first moult in two cases being found in

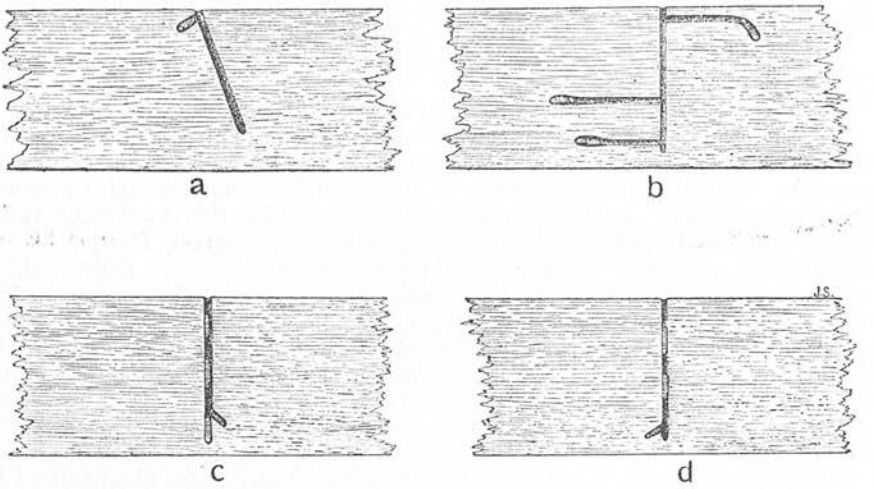


Fig. 9. *S. cyaneus:* oviposition tunnels and young larval galleries.

the frass of the oviposition tunnel itself ; and in another instance the indications were that, in the early stages at least, moulting occurs at short intervals. Recent examinations of the tunnels of very young larvae have shown that 3–4 moults take place at intervals of 1·8 mm. between each.

Direction and Length of the Larval Tunnels.

Generally speaking, the larva tunnels right to the heartwood and then curves round, returning towards the wood surface in preparation for pupation and the emergence of the adult. The variation in direction of the tunnel is, however, considerable, according to the nature of the wood. Thus larvae of *S. gigas* working in silver fir wood that was rough and knotty were often found coming up quite close to the surface in the course of their borings, in order, apparently, to avoid passing through a knotty area, the tunnel subsequently returning to the heartwood. It is, on the other hand, surprising how often one finds the larvae boring through the hardest wood. The larvae of *S. cyaneus*, when present in badly cankered larch stems, often pass straight through the worst cankered places, where the wood is very hard and resinous and consequently difficult to penetrate. Usually, however, such places are avoided, the direction of the tunnel often being abruptly altered so as to skirt around the outside of the cankered area. There are many records in the literature of *Sirex* adults

boring through coverings of lead sheeting, sometimes of considerable thickness. While this is certainly remarkable when one considers the unfamiliar nature of the medium through which the insect finds its way, the actual difficulty of boring through lead cannot, one imagines, be very much greater than that experienced by the larvae in hard and resinous wood.

Hartig records that he has found tunnels of *S. juvencus* 2–2½ feet long. The longest tunnels I have any records of are those of *S. gigas* in silver fir from South Molton, North Devon, which were measured by Mr. H. S. Hanson and reached a length of only 15 inches. In a larch log of 7 inches diameter, from which some quite large specimens of *S. cyaneus* had emerged, seven tunnels were dissected out and measured giving the following results : 6·2, 6·8, 8·4, 8·7, 10, 10·2, 10·1 inches ; while in another log only 4 inches in diameter one tunnel totalled 8 inches ; 10 inches to 1 foot is a fair estimate of the maximum length of the tunnels of *S. cyaneus* in larch at Tubney. The tunnels of *S. gigas* are probably longer on the average ; certainly on the basis of a few specimens it would appear so, but the data on this point are at present insufficient.

Pupation.

J. H. Fabre, in an essay entitled " The Problem of the Sirex," has described how in *S. augur* the larva, when full-grown, lies lengthwise in the tree not far from the centre of the trunk. In this position metamorphosis takes place and the adult insect, on emerging, is faced with the problem of cutting its way out through the wood in which it lies a prisoner. In the vertical plane in which it lies this is a difficult task for the heavily armoured adult, which is incapable of bending the body freely. The task is accomplished, according to Fabre, by the construction of an exit gallery which is the wide arc of a circle, whose lower extremity is connected with the larval tunnel, and whose upper extremity is prolonged in a straight line, which ends at the surface with a perpendicular or slightly oblique incidence. The wide connecting arc, which enables the insect to adjust its position gradually, is a curve which Fabre has shown approximates as nearly as possible to the circumference of a circle, and the construction of which is a constant feature of the species even over lengths that sometimes exceed four inches. These remarkable observations by the great French naturalist have not been duplicated in the case of *S. cyaneus*. Many pupal chambers of that species have been examined, and in nearly every case the pupal cell was so constructed that the adult was afforded a perfectly straight forward passage to the outside, whether it chose to proceed in an oblique or horizontal direction. Further, with reference to Fabre's statement as to the difficulty that would be experienced by an adult turning round a sharp-angled tunnel, several pupal cells of *S. cyaneus* have been found that show the cells lying parallel to the wood surface, the exit hole being at right angles, an indication that the adults emerging from them must have been able to bend their bodies considerably in order to emerge successfully (fig. 10).

S. cyaneus pupae were found from the end of June onwards, and the depth of wood in which they lie varies considerably. The average depth is from three-quarters to half-an-inch, but in many cases, especially in male pupae, the pupal cell lies less than a quarter of an inch from the exterior. This apparent difference in the depth at which male and female pupae are found may be compared with some observations made by a Russian worker, N. K. Stark, in a recent paper on " The Distribution of the Sexes of some Longicorn Larvae in Trees." This author working on the longhorn beetles, *Callidium sanguineum*, L. and *Saperda scalaris*, L., in old oak wood, found that the larvae and pupae which occurred at different depths were not of the same sex. The females invariably occurred in the deeper galleries and fed longer than the males, which were usually superficial feeders. The author suggests that the same distribution of the sexes may apply to *Acanthocinus aedilis*, L., another longicorn borer in pine, and to *Pissodes pini*, L., a common weevil enemy of young

pine plantations. I have good reason to believe that the distribution of the pupae in *S. cyaneus* shows the same peculiarity, which, as the author suggests, is due to variation in the length of the larval tunnel.

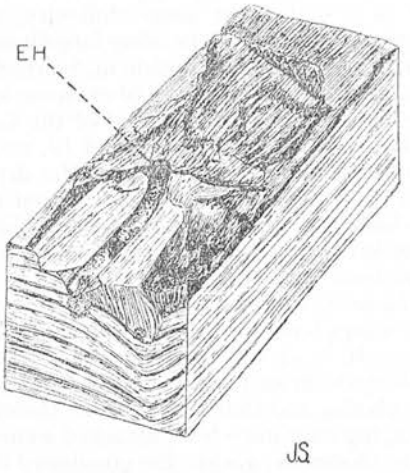


Fig. 10. *S. cyaneus:* abnormal pupal cell. EH=exit hole.

Larvae have been found ready for pupation in tunnels that were only separated from the exterior by a thin layer of bark; but such cases are unusual. Scheidter found pupae of *S. augur* 4¾ inches from the wood surface. The pupae of *S. cyaneus* when lying too deep in the wood often perish *in situ*, either in the pupal stage or as adults. For example, while examining silver fir logs for *S. gigas* material recently, I was struck by the numbers of adults that were found dead in their tunnels, sometimes in the pupal chamber, sometimes on their way to the outside. These adults were nearly always covered with fungus, but whether this fungus was the cause of death or an after-growth, I do not know; but I imagine that the death of the pupae and likewise that of the adult is due to some organism whose attack is induced by change of moisture conditions in the wood. The duration of the pupal stage in *S cyaneus* varies from 5–6 weeks.

Length of the Life-cycle in Siricidae.

The minimum period estimated by most writers for the Siricid life-cycle is two years, and with this my observations on *S. cyaneus* agree. Estimating the average duration of the egg stage at 4 weeks and the pupal period at 6 weeks, this leaves 21 months for the larval stages. From observations recently made on larvae which have hatched from eggs laid in September 1927, it would appear that up to the end of the first six months of their life the larvae reach a length of only 2–4 mm. These larvae, starting to grow in the spring, probably finish up their first year one-third to half grown. At this rate of development the approximate distribution of the stages in a two-year life-cycle would be as follows:—

Year.	Month.	Stage.
1926	August–mid-September ...	Adults ovipositing
	Mid-September–October ...	Eggs; young larvae
	October–December ...	Larvae (small, 1·2 mm.)
1927	January June	Larvae (small to 1/3 grown)
	July–December	Larvae (1/3–1/2)
1928	January–July	Larvae (1/2–full grown)
	July	Pupae
	August	Adults

Study of the relative sizes of larvae found living in the same tree at different periods of the year has shown that it is always possible to find both large and small forms at one and the same time, and this certainly suggests a possible two-year cycle. To obtain an exact figure is a matter of some difficulty, as it is fairly obvious that the period must vary considerably, depending largely upon the various factors, physical and chemical, which operate both inside and outside the wood of the tree. I do not think that we may expect to find cases of extreme length of life-cycle in the SIRICIDAE, such as have been quite often recorded of the Cerambycid wood borers, whose adults have been known to emerge from wood 17, and even 40, years after it had been converted into furniture. In these cases the dry nature of the medium has prolonged a life-cycle that normally would have been completed in 3–4 years. Dry wood conditions, no doubt, do prolong the life-cycle of SIRICIDAE to some extent, and cases have been recorded of wood-wasps emerging from the wood of a building $2\frac{1}{2}$ years after its completion. Shuckard also quotes an instance of *S. cyaneus* (*duplex*) emerging from the joists of the floor of a dwelling-house that had been built over three years. Wood-wasps have also been recorded as emerging from furniture long after its completion. It is as well to remember, however, in attempting to estimate the length of life-cycle in such cases, that wood-wasps will oviposit readily in sawn timber beams or planks, and that it is possible therefore that the wood from which the insects are emerging may have been attacked somewhat later than calculation allowed for. There is, moreover, always the possibility that in the case of timber in buildings, moisture conditions may be more favourable to a slight prolongation of the life-cycle, and, further, that the insects living in a protected environment may not perish *in situ* so readily as they do when living in logs lying exposed in the open. Under natural conditions in the forest, prolonged periods are not to be expected, and in the case of *S. cyaneus* an average period of $2\frac{1}{2}$ years may be estimated, with a possible maximum of 3 years. In cases where the adults are found overwintering in the wood, this, of course, at once lengthens the cycle by at least 6–9 months, as adults found in the wood in November are not likely to emerge before June or July of the following year.

Host Trees.

Nearly all authors have attempted in the past to assign preferential host trees to each species of *Sirex*. Thus *S. noctilio* was considered to be mainly a pine insect, which sometimes attacked silver fir and very occasionally spruce. *S. gigas* was generally regarded as chiefly an enemy of spruce, but was also recorded on silver fir, pine and larch ; Borries records it as a serious enemy of 120-year-old larch in Denmark.

Leisewitz in 1898 published a list of the European SIRICIDAE, arranged according to their host trees, and shows quite clearly that no such preferential host selection really occurs in nature. Scheidter sums up the evidence on this point in the following passages : " From this discussion the main fact emerges that neither *gigas* nor *juvencus* can be said to prefer one host tree to another. They will choose that one which is peculiar to, or most abundant in, the particular district where they occur . . . and therefore I do not think that we can designate these species as monophagous, since they are bound to no one particular species of host tree." " On the other hand," he continues, " *S. gigas* and *S. augur* are attracted to the largest trees, while *noctilio* and *juvencus* prefer trees in the pole stage." This he attributes to the fact that the two first-named species, having longer ovipositors, can penetrate the thicker bark of the larger trees more easily, while the last two, with their shorter ovipositors, are more or less confined to younger trees. From an examination of records in the literature the same conclusions appear to apply to *S. gigas* and *S. cyaneus* in this country. Evans records the two species from both pine and silver fir in Scotland, and I have records of the two species in Scots pine, silver fir, larch and spruce in Devon. In Tubney Wood *S. cyaneus* is the only species breeding in larch, to which it confines itself, leaving the Scots pine untouched. Adults of *S. gigas* were sometimes found

during the flight season in and around the wood, but it was ascertained that they were breeding in some old spruce and silver fir trees about half a mile distant. I have not found *S. gigas* averse from attacking young stems in the pole stage, having seen it ovipositing in larch poles at Tubney and also in Devon. I think, however, that there is something to be said in favour of its preference for older trees, though one might remark at the same time that *S. cyaneus* also appears to be quite capable of attacking these. The size of tree attacked may, in some cases, be no guide at all. *S. cyaneus*, for instance, is often found in the tops of larch trees not more than 3 inches in diameter.

Variation in Size of Adults.

Great variation was found in the size of the adults of *S. cyaneus* both bred from larch in cages and also taken in the open at Tubney. This phenomenon is well known in the SIRICIDAE, and Bischoff (Biologie der Hymenopteren, p. 22) alludes to it in the following passage: "In the phytophagous forms, the wood-boring SIRICIDAE are especially notable for the extreme variability in size that they exhibit, a characteristic which they share with many other wood-boring insects, and which in the case of the dwarf forms must be due to poor nourishment. In close relationship with the development of the host larvae, stands also that of the parasites, a phenomenon that is especially noticeable in those members of such groups as the PIMPLINAE which parasitise wood-borers." Evans refers to this great variation in size of the adults and gives the following figures for *S. gigas* and *S. cyaneus* respectively :—

S. gigas—large adults (measured from the front of the head to the end of Segment 8), 38, 36, 35 mm. ; small adults, 24, 18 mm.

S. cyaneus—large adults (measured as above), 30 mm. ; small adults, 16 mm.

I have also collected some figures of the variation in size of both sexes of *S. cyaneus* taken in Tubney during the past two years. Using the same method of measurement as Mr. Evans, I got the following results :—

Sex.	*Small.*	*Large.*
Male	10 mm.	18, 20 mm.
Female	10, 13, 15 mm. ...	17, 17, 22, 22, 23, 24, 24, 24, 24, 24 mm.

I have also found that this variation in size occurs in both *Rhyssa* and *Ibalia*. It is especially noticeable in the former parasite and will be further discussed in the paper dealing with that species.

Of the general truth of the statement that variation in size is related to conditions of nourishment, there can be no serious doubt. The exact nature of these conditions is, however, most difficult to ascertain. For instance, one may breed dwarf forms of both sexes of *S. cyaneus* in logs of 8 inches diameter, as well as in those which are only 3–4 inches, and conversely large adults can be bred from quite small stems. Two factors probably come into the question: the chemical constituents of the wood at different stages of decay, and its moisture content. Of the first, little or nothing is known, and one can only suggest the possibility that when wood reaches a certain stage of decay there is not enough nourishment left of the right kind to enable the insects to attain their normal size. As regards the second factor, moisture content, this must also play some part, although it is at the moment very ill-defined. I have noticed, however, that from logs kept in cages over a long period and allowed to become too dry, very small adults of both sexes were reared. Similarly in the case of trees cut in the open, I believe that smaller trees will produce undersized adults in a shorter period than larger trees, for the reason that the drying out process is much more rapid in the one than in the other.

Dr. J. Waterston has given me the following note in respect of variation in the size of adult wood-wasps in the British Museum collection.

Sirex gigas ranges in length from 12 to 40 mm. according to Enslin. The British Museum, however, possesses a magnificent ♀ of 51 mm. with an expanse of 68 mm. An average-sized female (expanse 50 mm.) is 38 mm. long. A male with the same expanse is somewhat shorter (32 mm.).

S. noctilio is only a little inferior to *S. gigas* in size. The body of the female is relatively slightly shorter. The largest examples in the British Museum measure: ♂, length 34 mm., expanse 58 mm.; ♀, length 38 mm., expanse 56 mm.

In *S. cyaneus* the body of the female is longer than in *S. noctilio*: ♂, length 31 mm., expanse 51 mm.; ♀, length 43 mm., expanse 56 mm.

No large examples of *S. juvencus* have been examined. The measurements of the largest ♀ are, length 26 mm., expanse 40 mm.

The Forest Relations of the Siricidae.

One of the most fundamental principles that research in forest entomology, especially during recent years, has laid down, is that for the proper understanding of the biology of an insect something more than a mere catalogue of entomological data is required. It is now realised that the insect *per se* is only one factor in the vast biological complex of the forest, and that if we would really understand its biology and seek to control its activities, we must take account of many factors and base our conclusions on a conception of the whole. This principle holds good in the case of *Sirex*, and I now propose to consider the problem in relation to the following questions: (*a*) do the SIRICIDAE attack healthy trees? ; and (*b*) if they do not, what are the factors concerned that render the host tree more susceptible to attack?

All Continental workers, including the earliest writers, are agreed upon one point, namely, that where wood-wasps are present trees which are in a sickly condition, from whatever cause, or which are suppressed by other trees, are liable to attack. Thus Bechstein says that subsequent to the devastation of large areas by the nun moth (*Lymantria monacha*) or bark-beetles (SCOLYTIDAE), wood-wasps may become abundant, and he quotes in support of this statement the records of such outbreaks in the Thuringerwald in 1778, 1787, 1797 and 1804. Ratzeburg also shares this view and quotes instances from Brandenburg in 1835, 1836 and 1843, and a later outbreak in East Prussia in 1850.

In all these cases the wood-wasps played a secondary rôle, causing technical damage to timber, and this we may consider as well established. The evidence on the primary status of wood-wasps as pests is, however, far from unanimous. Balzereit is one of the early workers quoted by Ratzeburg who considers that wood-wasps are sometimes primary and capable of attacking healthy trees. Of spruce, for example, he writes, "penetrated as they are by thousands of bore holes, they have the resin running down their trunks in streams on hot days and soon die as a result." Ratzeburg criticising this sentence says: "I can hardly believe that the latter (the wood-wasps) are to be considered as primary enemies, and that the flow of resin on the tree-trunks, as well as the discolouration which appears in the sapwood in the neighbourhood of the oviposition holes, is to be laid entirely to their charge . . . the cause appearing to me to be more likely due to the activity of bark-beetles in the cambial region." Ratzeburg admits, however, that when present in great numbers, it is possible that wood-wasps do attack and kill healthy trees under certain conditions.

Hartig, writing some years later, discusses the ability of *Sirex* to attack green trees in the following passage: "So much is certain, that the damage by the wood-wasp larvae does not produce such serious after-effects as do the tunnels of those beetle larvae that mine between the bark and the wood. The innermost bark layer and the sapwood region is the location of the sap flow and the place where all further stem growth occurs, so that damage to the organic tissues functioning here must exert an influence on the whole plant. In comparison with this, the damage done by

the wood-wasp larvae in the wood itself is only limited in effect and almost without any influence on the general health of the tree . . . We may conclude, therefore, that when a tree is attacked by wood-wasp larvae and dies in a short time, this tree was already sickly from another cause, which, apart from insect injury, would have ultimately caused its death."

In another place he also says that he has observed spruce trees which, although very unhealthy and attacked by wood-wasps, nevertheless continued to maintain a precarious existence for a long time. This last observation is supported by von Hagen, who found in Silesia that trees attacked over a 7-year period, while suffering considerably in loss of increment, were in no case killed outright.

These views are shared by the later writers, and Scheidter, the most recent of these, says that in the Bavarian Frankenwald the importance of wood-wasps is entirely technical, in which rôle, however, they are often serious. The American literature on SIRICIDAE contains practically no references to their forest relations. Felt mentions one species *S.* (*Urocerus*) *albicornis*, F., as attacking spruce (*Picea*), hemlock (*Tsuga*) and silver fir (*Abies*) in the eastern States and Canada, and says that while reports of considerable injuries to coniferous trees in the north-west territories have been received, comparatively little damage is usually done by the insect in the United States. I had occasion to observe this species in Eastern Canada (Ontario) during the autumn of 1919 on a visit to a stand of Balsam fir (*A. balsamea*) and made a few notes upon it during a brief stay. The area in question was quite a small one and the trees averaged 45–50 years of age. They had suffered considerably from wind damage and other troubles, fungus root rot among the number. At the time of my visit a heavy thinning was in progress, the stand having been marked as a sample plot, and there was a good deal of felled timber about in piles and also strewn singly on the ground. Large numbers of adults were flying at the time, and I endeavoured to ascertain what type of tree was most favoured by them for oviposition purposes. The choice available was considerable: green, healthy trees, vigorous as regards height growth and diameter increment ; obviously sickly trees, still green but dying rapidly ; and felled logs and branches, both green and dry. In the short time at my disposal, detailed observations were out of the question, but I was led to the conclusion that of the three types mentioned, the insects avoided the green and vigorous stems, but frequently attacked dying trees, not always successfully, on account of the strong resin flow in which the ovipositing adults were sometimes caught. Felled logs were most favoured of all, and it appeared likely that if fallen trees were present the insects would prefer these to standing trees in the majority of cases. It was with this idea in my mind that the experiments at Tubney Wood about to be described, were arranged.

Field Studies in Tubney Wood, Oxford.

The wood in which the field work has been carried out forms a small part of a mixed plantation of Scots pine and larch planted in about equal proportions. The area was planted in 1891–92 and the portion of wood in which observations were made is low-lying, quite a considerable part of it being very swampy. On my first visit to the wood, a superficial survey indicated this part as being the most likely to yield *Sirex* trees in numbers, so marked was the difference between the condition of the trees on it as compared with those on the drier portions.

The larch are in the pole stage and vary from 3 inches up to about 9 inches D.B.H., the average height being about 35–40 feet. The proportion of dead trees varies slightly, being greatest in the wetter parts. Apart from dead trees there are all gradations of green trees from healthy full-crowned trees to sickly poles that have less than one-fifth of their crown remaining. Through the kindness of Mr. W. R. Day, Mycologist to the Imperial Forestry Institute, I was able to make a survey of the wood in company with him to collect data on the following points : (1) the general

condition of the larch and its relation to soil conditions, silvicultural treatment, etc.; (2) the presence of root fungi as antecedent to, or contemporary with, the *Sirex* attack.

These two points were considered apart from the insect question. During this survey the root systems of a dozen trees were examined, both standing and wind-blown stems being chosen. The first general conclusion which was arrived at was that the swampy nature of the ground over a large part of the area resulted in the tree roots being under water for many months of the year. The soil in these parts is light sand on top with stiff sandy clay below, which holds the water. The result is that the root system of the majority of the larch is extremely poor with consequent poor crown production, a state of matters that neglect of thinnings has increased. Two root fungi were looked for, *Armillaria mellea*, the honey fungus, and *Fomes annosus*. On a previous preliminary survey it was thought that one or both these fungi might be prevalent, causing primary injury. After searching both in the field and in the laboratory, however, no sign of the rhizomorphs of *A. mellea* or of the mycelium of *Fomes* could be traced. Slight indications of attempted penetration of *Armillaria* in times past were found, but nothing extensive. On the other hand extensive root rot was present, the tap-roots of many trees being completely destroyed. This was entirely due to the waterlogged condition of the soil. Further proof of bad soil conditions was shown by the lack of fresh root development in the deeper roots, most of the new rootlets coming from the superficial parts. Further, although thinnings had as a rule been entirely neglected, even where the trees had opened out naturally and had been given a chance to grow, they had remained at a standstill, a fact that can only be explained by the soil conditions, which are inhibiting proper root action and development. This cessation of growth is well shown by a study of the wood rings, and dates back for at least 10 years. A further indication of bad soil conditions was found in the number of trees suffering from larch canker (*Dasycypha calycina*), which is a common symptom on areas of poor soil. An earlier survey gave a total of 50 per cent. of the trees as suffering from canker in some degree or other, most of the worst cases being in the wettest parts. The Scots pine, in contra-distinction to the larch, is healthy, apart from a few windfalls here and there on the exposed south-western side.

Primarily then, the area is manifestly unsuitable for the larch, which is going back in health as a result. It now remains to show what part the insects play.

In the first place, it was found, more than once, that many trees which were obviously in a dying condition, that is, they had lost from a third to half their crown, showed no sign of insect damage at all. Apart from *Sirex*, the most obvious insect borer present was the larch longhorn borer (*Tetropium gabrieli*, Weise), a very common species in larch woods. *Tetropium* was found in some cases preceding *Sirex*, but quite as often the attack of the two insects coincided. Thus on 18th October 1927, a young larva of *Tetropium* was found just commencing its burrow in the bark of a tree in which *Sirex* had oviposited during the summer. *Tetropium* very often attacks trees which are half dead and have lost half their normal crown. *Sirex*, on the other hand, as a rule allows the tree to go much further before eggs are laid. I could find no sign of the presence of bark-beetles in numbers in the trees, previous to attack by *Tetropium* and *Sirex*, nor were there any signs on the needles of defoliating insects that could have played any part in bringing the trees to their present state.

During the summer, when the flight period of the *Sirex* approached, plans were made for ascertaining by experiment what type of tree would be most favoured by them for oviposition, and how far gone in decay the wood of a tree might be before it became unsuitable as a dwelling place for the larvae. The preliminary survey had shown that wood-wasp larvae were to be found in trees which were quite bare of foliage, but of which the wood, although sound, was fairly dry. It was also known, and has been observed by previous writers, that very much decayed wood is quite

unsuitable for wood-wasps. The methods now used were two in number, and included trap stems and direct observations over long periods of the selection of standing trees by the adults.

Six trap trees were selected in the first instance, three of which were wind-blown trees with full-grown crowns and had their roots half-buried in the ground, while of the other three, two had less than half their foliage remaining and the third was quite dead. These trees were closely watched throughout the season, and the results obtained from them brought out one point quite clearly, namely, that of the three wind-blown trees, two were evidently still much too green to attract the wood-wasps for oviposition, while when placed on the third they would oviposit, but did not seem to be particularly attracted to it when left to their own devices. Of the other three, the dead tree was quite unattractive and the last two only moderately so. The adults seemed to be much more attracted to standing trees, and it was from these that the best positive records were obtained. Here again the insects were never found either upon trees with full green crowns or upon trees quite bare of foliage, the favourite type of tree being one that still retained a small part, a quarter or less, of its foliage. On such trees the insects settled and oviposited freely, and marked preference was even shown for particular trees, one of which is shown in Plate ix. This tree was from the 19th August onwards constantly visited by wood-wasps, the egg-laying operations of more than 20 adults being studied on it over a period lasting until late in September. Large numbers of oviposition holes were found on this tree, and the position of a number of these was marked by placing white rings round them, which are clearly visible in the accompanying photograph. The density of the oviposition holes was considerable in places, no fewer than six being found in one square foot of bark. This density was surpassed by a later record, a photograph of which appears in Plate xi, fig. 3, showing six oviposition tunnels lying within one half-inch square. All these holes contained larvae and eggs, but in many other cases trial borings that did not contain eggs were quite often found. Even so, however, the density of egg-laying must have been considerable. In this connection Evans, writing of *S. cyaneus* on silver fir, records that on a stem 15-feet long by 3½ feet diameter the total *Sirex* population, judging from the number of flight holes, must have numbered close on 500. In logs which contain large numbers of larvae it is remarkable how comparatively seldom one finds the tunnels running into one another. This does, of course, occur, and in rare cases tunnels can be found crossing each other at right angles. Trees of all sizes, ranging from 4 to 10 inches in diameter at breast height, were selected by the adults and oviposition extended from within 6 inches of the soil level up to the top.

The experiments at Tubney Wood have been supplemented by other observations, notably in North Devon, where, through the kindness of Mr. H. S. Hanson I was enabled to visit, in January 1928, a number of woods where *Sirex* occurs. Both *S. gigas* and *S. cyaneus* are plentiful in this part of the country and attack Scots pine, larch, spruce and silver fir. The best example of *Sirex* attack as a secondary pest was found in a silver fir wood near South Molton, North Devon, where trees over 40 feet high were dying in patches as a result of root rot caused by *Fomes annosus*, the *Sirex* appearing only on those trees in which the root rot was fairly well advanced. Some larch woods visited also showed that *Sirex* was a sure indicator of unfavourable conditions, although the cause of the trouble sometimes necessitated careful search. In one or two cases wind-blown trees were found attacked, but usually only after they had been down a little time. The above experiments and observations on standing trees susceptible to *Sirex* attack bring out the following points clearly :—

(1) That standing trees with full or half-green crowns are quite unsuitable for oviposition.

(2) That the tree has to be quite badly diseased before conditions favourable to *Sirex* appear.

(3) That the choice of trees suitable for oviposition is restricted and possibly lies between certain limits of moisture content which are at present unknown.

It is impossible at the moment to explain why cut logs are suitable for oviposition almost at once, while wind-blown trees, which still have their crowns and roots intact but are exposed to the drying influence of sun and wind, should be apparently unsuitable for a season at any rate. Recognition of standing trees suitable for oviposition is therefore difficult, but during this last season considerable help was obtained from a study of the Cynipid parasite (*Ibalia*) during its flight period. The females of this parasite on more than one occasion picked out fresh *Sirex* trees for us, the last time being late in October long after the *Sirex* had disappeared. The trees favoured by *Ibalia* all closely resembled one another in the state of the crown, of which only a quarter to a fifth remained.

Once the eggs are laid and the larvae have started work, they can continue to bore in the wood even when it has apparently dried out considerably, or when the tissues have become permeated with fungus mycelium. Thus I have found silver fir logs, the wood of which was full of fungus, with large numbers of *Sirex* boring in them. Once these larvae have matured, however, and the adults have emerged, such logs are no longer suitable for the raising of another generation. The logs by this time have reached a stage of decay at which the wood becomes soft and crumbly, and such conditions are quite unsuited to the young stages.

I should like at this point to refer to an important paper just published by Buchner entitled " Holznahrung und Symbiose," which may be described as an extended survey of the symbiotic relationships existing between wood-boring insects and fungous or bacterial symbionts. Most of the new work deals with the bark and wood-boring Coleoptera, but some remarkable new observations on *Sirex* are also described, and it is these that I should like to discuss here.

Buchner has found that the SIRICIDAE have living in association with them symbiotic fungi. These are carried by the adults in two pear-shaped glands lying at the base of the ovipositor, which contain countless numbers of strap-shaped *Oidia* of a Basidiomycete, which he states are conveyed at oviposition into the egg-tunnel. There, it appears, they develop, the mycelium ramifying through the surrounding tissues, and when the larva hatches the fungus-filled wood is taken into the alimentary tract. This Buchner suggests may represent a totally new variation of *Ambrosia* culture, in that the insect does not use the fungus itself as food, but depends on its containing an enzyme, which, acting upon the wood particles in the alimentary tract, brings them into a digestible form. These fungi, he says, are only found in the wood-boring SIRICIDAE, being absent in the parasitic ORYSSINI. He states that the *Oidia* are still present in the glands of dried museum specimens.

With a view to testing these conclusions an examination was made of an adult *S. cyaneus* that had been preserved in spirit for some months. After some difficulty, the glands described by Buchner were isolated and mounted, after treatment with cotton blue. They were found, as Buchner states, full of fungus bodies, which strongly resembled the *Oidia* as described and figured by him. Examination of the oviposition tunnel and the young larval tunnels was then made, and a number of sections stained in different ways were prepared. These showed quite clearly that the tissue in the immediate neighbourhood of the oviposition tunnel and young larval gallery was thoroughly permeated by the hyphae of a Basidiomycete fungus, and it was interesting to note that the hyphae were particularly dense in the region where the young larva was feeding. Buchner has not himself investigated the further developments of the fungus in the oviposition tunnel, larval gallery and surrounding wood, but concerning these he writes : " It must be that the oviposition tunnels are filled with eggs and fungus alternately and that by the time the larvae have hatched the wood in their immediate neighbourhood has been thoroughly penetrated by fungus

mycelium." The proof of this statement was found in many sections cut from the oviposition tunnels of *S. cyaneus*, and, further, in one section of an oviposition tunnel, the eggs in which had perished, the gelatinous egg-covering which lines the tunnel wall was permeated by numerous hyphae, affording clear proof that the fungus precedes the hatching of the larvae in beginning operations upon the wood.

Buchner's work has opened up a totally new line of enquiry, which should throw a flood of light upon the problem of the food requirements of wood-wasp larvae. The results of his future work will be awaited with interest, and meanwhile we also intend to investigate the question in the case of *S. cyaneus*, especially as regards the identity of the fungus itself, and its behaviour in the alimentary tract. That we have in this case, as Buchner says, an important example of symbiosis before us, there cannot, in my opinion, be much doubt.

Status of Sirex as a Forest Pest in Britain.

This can be considered from two aspects: (1) the relation of *Sirex* to the living tree; and (2) its importance as a timber pest. As regards the first of these, we must consider the *Sirex* as indicators of pathological conditions rather than as prime factors in their production. This rôle, as we have seen, they share with such longhorn wood-borers as *Tetropium* in larch woods, and they may in one sense be looked upon as beneficial, in that they call the forester's attention to the need for further enquiry into the underlying causes of ill-health. The recognition by foresters of the close connection getween the prevalence of such pests as *Sirex* and the health of a stand is one which will become increasingly important in this country as our coniferous areas, now in the young stage, approach maturity.

From the timber point of view the importance of *Sirex* has never loomed large in this country. Definite records of losses due to their work are almost non-existent. Miss Ormerod records *S. juvencus* (? *cyaneus*) as causing damage to 70-year-old silver fir in Cumberland in 1889, but in this case only some 40 trees were involved, the total loss being about £40.

It is unfortunate that no statistics are forthcoming concerning the losses in home-grown timber due to *Sirex*, as it is possible that such figures, if available, would show the wood-wasps to be more important than is generally realised. This would apply more especially to timber stored in yards and warehouses. In a recent conversation with a small timber dealer in the west country, I was informed that the proportion of logs rendered worthless as the result of *Sirex* borings was in many cases by no means negligible. This is probably quite often the case, but one has always to remember the possibility that the wood has been previously weakened by fungi, and thus rendered worthless quite apart from the work of *Sirex*.

Natural Enemies of Sirex.

Woodpeckers are said to destroy the larvae of *Sirex*. Scheidter regards them as being their principal natural enemies and cites woodpecker marks as useful indications of infestation. Evans also records that in Scotland, the Great Spotted Woodpecker, *Dendrocopus major*, L., attacks both *gigas* and *cyaneus* indiscriminately. Woodpecker work is much in evidence on the larch at Tubney and after examining many trees both here and in other localities, I have come to the conclusion that it is the larvae of the larch longhorn, feeding between the bark and wood, which they seek out, rather than those of *Sirex*. A good deal of the woodpecker work does not appear to me to penetrate sufficiently deep into the wood to capture the *Sirex* grubs.

Wishing to obtain further information on this point, I have examined some of the literature dealing with the food of woodpeckers, especially such results as are based on stomach analyses. I have selected the work of Collinge in this country, Rörig and von Vietinghoff von Riesch in Germany, and Beal in the United States. In all

cases the records of *Sirex* grubs in the stomachs of woodpeckers are conspicuous by their rarity. Collinge, for example, reports on 91 specimens, of which *D. major*, L., numbered five, *D. minor*, L., eight, and *Gecinus viridis*, L., 78. He estimates the percentage of insect food at 75, and gives a list of bark-beetles, weevils, longhorn beetles, LUCANIDAE and wood-boring Lepidoptera, but does not mention *Sirex*. The records of Von Riesch and Rörig tell practically the same story; and in the important monograph by Beal on the food of woodpeckers in the United States, which contains a mass of detail based on stomach analyses, *Sirex* grubs are never considered. That *Sirex* grubs are sometimes sought out by woodpeckers is undoubtedly true, but I do not believe that they are a primary object of search, and certainly the records quoted above would seem to support this view.

Mention has already been made of the frequency with which in certain localities one finds *Sirex* adults apparently killed by fungi while on their way out of the wood. Nothing is known, so far as I am aware, of the cause of this or whether it is sufficiently widespread to be of much importance. The insect parasites, *Rhyssa persuasoria*, L., and *Ibalia leucospoides*, Hochenw., have already been mentioned in the introduction to this paper and have been dealt with in a separate paper (Bull. Ent. Res., xix, p. 67, 1928).

Sirex in Australia and New Zealand.

The presence of *Sirex* in Australia and New Zealand has been known for a number of years. In Australia Levick reported in 1926 the occurrence of *S. gigas* imported in "white deal" from Danzig, which had been used in buildings, but states that there is no evidence that the insect has become established in Australia. The danger of its occurrence was, however, sufficiently realised by the authorities to cause them to list *Sirex* as an injurious pest under the Vegetation and Vine Diseases Act of 1915, which empowered quarantine officers to seize and burn all timber found to be infested. In New Zealand the situation is more serious. One of the steel-blue species, the exact identity of which is uncertain, although it has been provisionally determined as *S. juvencus*, has been present in that country for some years. Mr. David Miller, the Government Entomologist, who has watched its progress during the last few years, refers to its work in his recent bulletin on Forest and Timber Insects in New Zealand. He states that the original home of the insect was on the east coast of the North Island, but adds that by the year 1925 it became evident that its range had considerably extended.

The chief host tree is *Pinus radiata* (*insignis*), of which it attacks not only felled stems, but also living trees. It is also known to attack native species, having been found boring in weather boards of the New Zealand conifer rimu (*Dacrydium cupressinum*). Dr. R. J. Tillyard, of the Cawthorn Institute, Nelson, New Zealand, has also described the activities of the insect in a recent newspaper article entitled: "The Giant Horntail," which appeared in the "Nelson Evening Mail" of 9th February 1927. In this article Dr. Tillyard records his opinion that the insect was introduced into New Zealand from North America in Oregon lumber and gives two other localities, viz., Feilding and Marlborough provinces, as being infested. He regards the climatic conditions of New Zealand as being very suitable to the insect and dwells especially upon the large size which they may attain under the favourable climatic conditions of their new home. In a recent paper on the "Ancestry of the Order Hymenoptera" he discusses the feeding habits of the wood-wasps in New Zealand and states that they have taken to burrowing in the sapwood of the pine (p. 308). This cannot be regarded as a sign of any radical change in the habits of the insect, consequent upon their establishment in New Zealand. It has already been shown that in Europe and elsewhere wood-wasp larvae spend quite a considerable portion of their life burrowing in the sapwood layers. In America, he says, wood-wasps are kept in check by the severe winter conditions, and he also instances the

power exercised by the parasites *Rhyssa* and *Ibalia* in both Europe and America as a check upon their increase. Further he states that in New Zealand standing green trees are attacked quite as often as fallen stems, and advocates the establishment of mixed plantations as one means of mitigating the severity of attack.

Sufficient evidence has already been adduced to show that under European, and so far as we know American, conditions wood-wasps are not, as a rule, considered to be primary enemies, in that they do not usually attack healthy trees, and it is this aspect of the problem in New Zealand which requires the most careful study. Two possibilities suggest themselves; either that under the climatic conditions of New Zealand the insect has so changed its habits as to become a primary pest, in which case the seriousness of the problem can hardly be over-estimated; or that there is some underlying cause which predisposes the pine to their attack, the nature of which is so far unknown. Dr. Tillyard's theory that intense cold plays a considerable part in the control of *Sirex* in America is hardly tenable in view of the fact that these insects are quite as abundant in the coniferous forests of the colder regions of the continent as they are in the warmer climate of the western seaboard.

So far as the control exercised by parasites is concerned, their presence, no doubt, does act to some extent as a check on the increase of the insect to abnormal proportions. At the same time it must be realised that, parasites notwithstanding, *Sirex* play an important part in Europe and America, not as primary pests, but as members of the vast army of insects which attack fallen timber and render it unfit for structural purposes. This would certainly not be the case were the parasites as effective as Dr. Tillyard would have us believe.

While I do not wish to under-estimate the important part played by the parasites in control, for I think their introduction into New Zealand could not fail to be a very important step, yet I consider that for the complete solution of the problem attention should be directed to another aspect of the question which concerns the forester.

It is said, for instance, that the insect is attacking healthy trees. What do we understand by the term "healthy tree"? It is well known to foresters that the determination of a tree as being in perfect health is often extremely difficult, especially where exotic species are concerned. Plantations of such species often maintain an outwardly healthy appearance for a number of years, while in reality their condition may be far from satisfactory. This may be due to unsuitable soil, exposure, and similar factors, or as we have already shown, to fungus disease, the presence of which is often unsuspected until other more obvious agents of destruction follow in its wake. *Sirex*, as we have seen, is one of the commonest of these "after-effects," and therefore I would submit that one of the most urgent needs at the present time in dealing with this problem in New Zealand is a thorough study of the conditions, silvicultural and otherwise, under which *Pinus radiata* is being grown, as I feel confident that it is there that the real cause of the trouble will be found.*

Summary.

(1) A complete review of the classification and status of the Siricid wood-wasps occurring in Britain is given in this paper.

(2) The biology of *S. cyaneus*, F., which has been studied at Tubney Wood, Oxford, during the past two years, is described, together with supplementary notes on *S. gigas*, L.

* Since the above was written a paper has appeared by Mr. A. C. Clark, Christchurch College, Canterbury, New Zealand, "The Infestation of *Sirex juvencus* in Canterbury" (Te Kura Naghere, no. 2, pp. 10-16, December 1927). I received this paper too late for inclusion in my own work but it has been reviewed in the Rev. App. Ent. XVI, p. 221, 1928. Mr. Clark's work on *Sirex juvencus* is the first attempt at a thorough study of the insect in relation to forest conditions in New Zealand, and some of his conclusions bear out the truth of what has been said above to a remarkable degree.

(3) A study of the forest relations of *S. cyaneus* at Tubney has shown that this species cannot be considered a primary enemy of healthy green trees. Trees which are favoured by *Sirex* are usually markedly unhealthy from one cause or another. At Tubney unsuitable soil conditions were the principal factors.

(4) *Sirex* and *Tetropium gabrieli*, Weise, the larch longicorn beetle, may occur almost simultaneously as indicators of pathological conditions in larch woods.

(5) In North Devon *Fomes annosus*, a root fungus, was the predisposing factor in the case of silver fir attacked by *Sirex*.

(6) Both *S. cyaneus* and *S. gigas* may occur in the same tree. This was found to be the case at South Molton, North Devon, in silver fir. *S. gigas* appears to prefer larger trees, and it is not present in the larch at Tubney Wood, which is in the pole stage.

(7) The primary object of the work was to acquire a knowledge of the parasites of *Sirex*, *Rhyssa persuasoria*, L., and *Ibalia leucospoides*, Hochenw. Both parasites were studied at Tubney, and have already been dealt with (Bull. Ent. Res. xix p. 67, 1928).

(8) It is considered probable that the results obtained in the above study will throw some light on the *Sirex* problem in New Zealand. Emphasis is therefore laid upon the importance of studying the silvicultural conditions in relation to *Sirex* attack.

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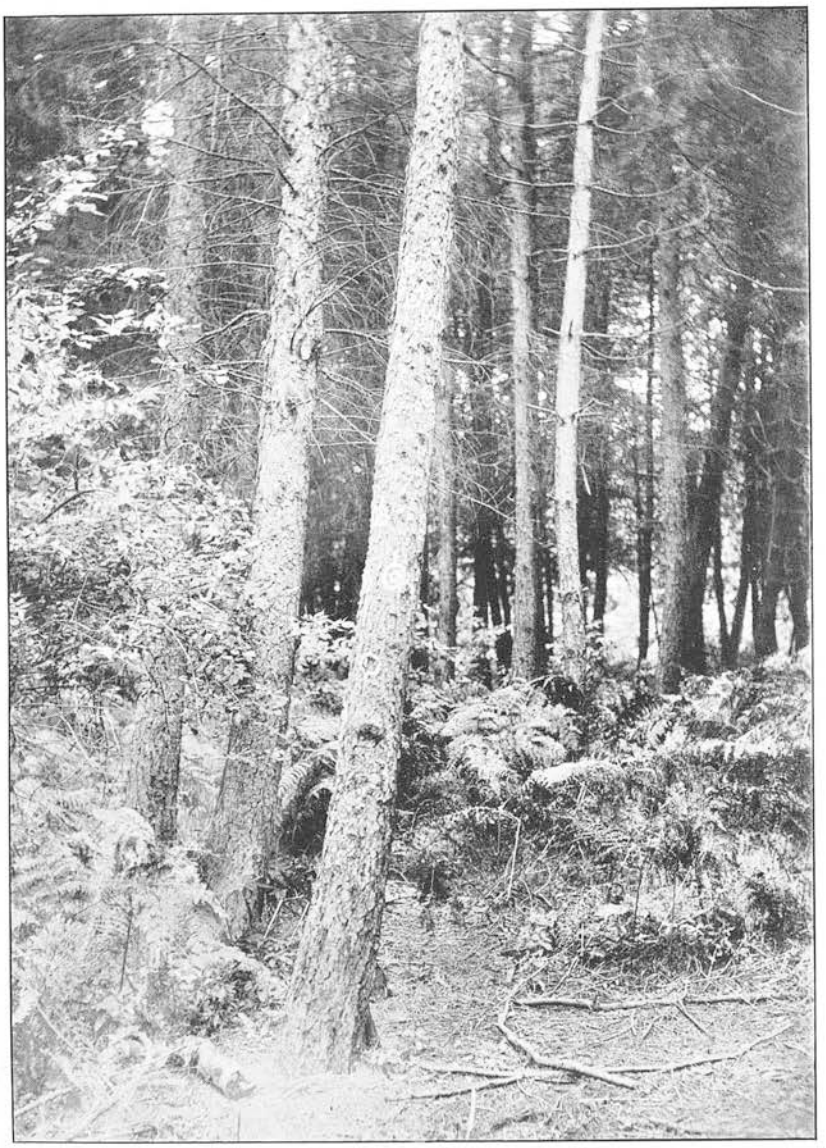
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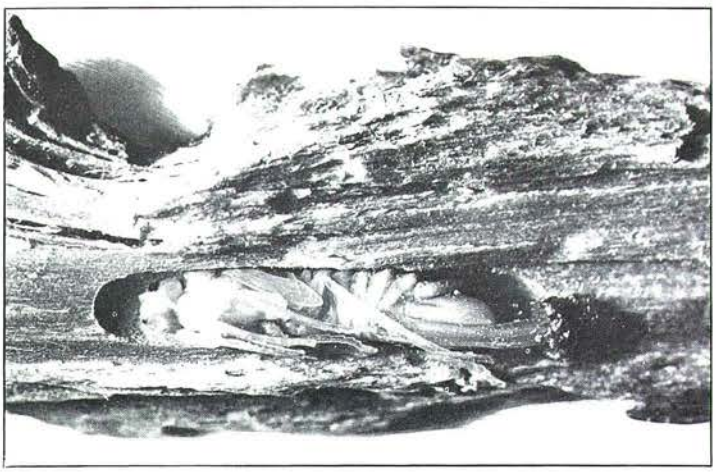
Sirex tree in Tubney Wood; a favourite haunt of the adults during August and September; the white rings indicate where females oviposited.

Explanation of Plate X.

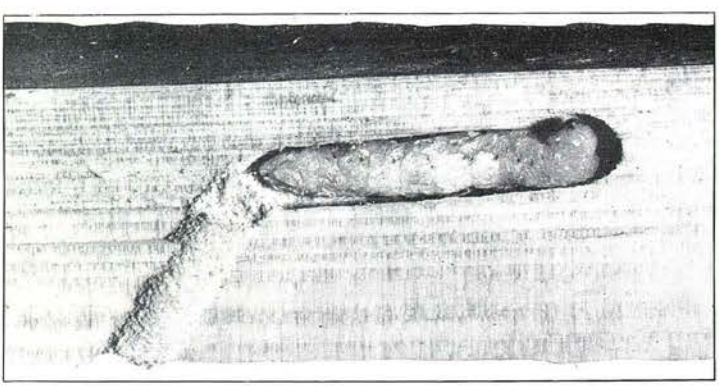
Fig. 1. Pupa of *Sirex cyaneus*, Tubney Wood, July 1927. The eyes have already darkened and the last larval skin is still attached to the ovipositor sheath.

Fig. 2. *Sirex* lava in a small log of silver fir burrowing in the superficial layers of the wood, although nearly full-grown; this may occur quite often in small logs that are full of larvae.

Fig. 3. Egg of *Sirex gigas* lying in the oviposition tunne.



1



2



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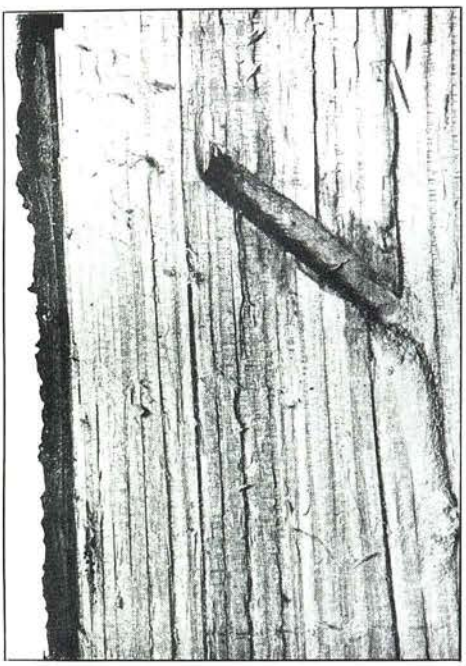
Explanation of Plate XI.

Fig. 1 Pupal chamber of *Sirex cyaneus* in larch, showing the average depth at which it is found in the wood.

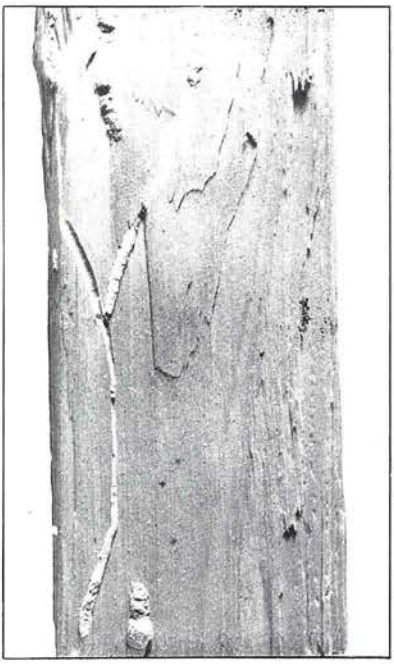
Fig. 2. Tunnels of young *Sirex* larvae in the sapwood of silver fir. The oviposition tunnel from which the two larval tunnels arise can be distinctly seen. Note also the vertical direction of the tunnels made by the larvae in the earliest stages.

Fig. 3 Inner surface of larch bark showing six oviposition holes of *S. cyaneus* within half a square inch; each tunnel contained young larvae.

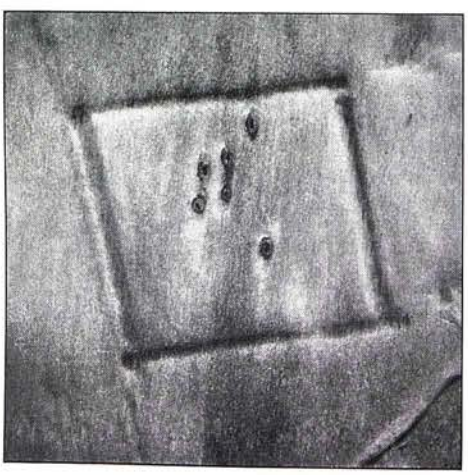
Fig. 4. Exit holes of *Sirex gigas* in silver fir. (Specimen from Mr. H. S. Hanson, North Devon.)



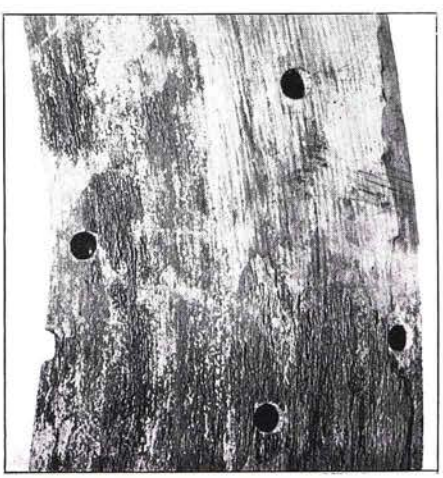
1



2



3



4

STUDIES OF THE SIREX PARASITES

Part I.

The Biology and Post-embryonic Development of Ibalia leucospoides Hochenw. (Hymenoptera-Cynipidae)

by

R.N. Chrystal, Hon.M.A.(Oxon), B.Sc.(Forestry) (Edin.)



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Introduction. The biological studies of Ibalia leucospoides Hochenw., the Cynipoid parasite of the Sirex woodwasp, S. cyaneus Fabr. which are described in this paper represent one portion of a comprehensive study of the woodwasps and their parasites which has been carried out during the past three years. The work, which was begun in 1926, was carried on for some time in co-operation with the Imperial Bureau of Entomology, Parasite Laboratory at Farnham Royal, Bucks. Several papers describing various phases of the work have already appeared, viz. a paper by myself on the biology of Sirex cyaneus, Fabr. a joint preliminary paper on the parasites of the woodwasps, written in conjunction with Dr. J. G. Myers; and a third paper by Dr. Myers dealing with the results of the biological studies of Rhyssa persuasoria L. which were carried out by him at Farnham during the season of 1928.

It is my intention, in the present paper to deal solely with Ibalia leucospoides Hochenw., and to give as complete an account of its biology and post-embryonic development as possible, with special reference to the studies which have been made by myself at Oxford during the past three seasons. For the completion of the work a further paper on the Ichneumonid parasite of the woodwasps, Rhyssa persuasoria L. will be necessary, and this it is hoped will be completed as soon as sufficient material is available for the completion of the morphological studies.

Apart from the immediate practical object for which the parasite work was undertaken, namely, to endeavour to supply Sirex parasites in quantity for export to New Zealand; biological studies of the woodwasp parasites provided a field of research the scope of which was considerable. Study of the literature showed that practically nothing was known about the habits of Ibalia, while in the case of Rhyssa, a

considerable amount of biological work still remained to be done, especially on the oviposition habits and larval life, concerning which much of the matter contained in the literature was vague and contradictory. This is partly understandable having regard to the difficulties attendant on such studies which as I have found in the present work, can be successfully conducted only provided there is unlimited material at one's disposal and an ample margin of time over which to check results.

In this respect, the conditions under which these studies were made, have been favourable, especially from the point of view of field work, for which several very suitable woodland areas were available. I am much indebted to all those who so kindly aided me either by sending material for study or by affording me access to places where such material was to be found.

On the Origin of the Parasitic Hymenoptera.

The problem of the origin of the parasitic Hymenoptera is one which lies at the very root of the subject of this paper, as it has for a long time been the considered opinion of the best authorities (Handlirsch, Brues, Tillyard)(55.56) and this group has arisen from a Siricoid stem. Handlirsch, quoted by Brues (1910) sought to derive the first parasitic forms possessing a long ovipositor, from Pseudosiricidae which no longer laid their eggs in wood, but the eggs of woodboring beetles (e.g. contemporary Buprestidae). He cites the Ephialtitidae as being possibly descended from such a primitive stock. Brues, while finding difficulty in accepting this theory in detail, admits that considering the common occurrence of Siricoid forms in Jurassic deposits, and taking this fact in conjunction with the primitive morphological

characters of the recent Siricidae and allied families, we have good grounds for regarding these forms as allied to the ancestors of the higher Hymenoptera.

In a later paper (12) Brues considers that the prevalent view of the Siricidae as the oldest Hymenoptera, may be somewhat premature, as the lower Tertiary strata, especially the lower Oligocene show very diversified Hymenopterous types. He is more inclined to regard the Siricidae as the remnant or offshoot of a group from which the parasite Hymenoptera arose, and he cites the Oryssidae, which family Burke (14) has recently shown are ectoparasitic on Buprestid beetles. He regards this family as the most primitive of the parasitic group.

The parasitic habit, according to Brues, appears for the first time in the Clistrogastra section of the Order. This Sub-order includes the great super-families Ichneumonidea, Chalcidoidea, Serphoidea and Cynipoidea. Further, in the most primitive families of the parasitic Hymenoptera, the parasitic connection is confined to wood-boring insects. Thus in his own words - "Oryssidae, the most generalized group of Evaniidae, the more primitive Braconidae, many of the structurally primitive Ichneumonidae, and the Capitoniidae, are restricted to hosts having such habits."

This he considers, points to the fact that "such close linkages in habit are not easily changed, and that we may find therefore that similarity of host habit is an important factor in determining what insects may be attacked." In a further discussion on this interrelation between taxonomy and habit, the same author writes - "A general survey of habits in the parasitic Hymenoptera shows that certain taxonomic groups of hosts are commonly attacked by discrete groups of closely

related parasites. It is natural that such combinations should impel our attention, as they may be fitted with the least effort into a classified scheme, and furthermore, their mere recurrence is sufficient to indicate that they are not due merely to chance." In support of these remarks he gives the following table:-

	Parasites	Hosts to which they are restricted.
Family:	Alysiidae	Dipterous larvae.
	Trigonalidae	Vespidae.
Sub-families	Evaniinae	Cockroaches and their Oothecae.
	Ichneutinae	Sawfly larvae.

(Here I should also place on the findings of the present work -

	Ibaliinae	Woodwasp larvae.
Genera	Polygnotus	Cecidomyiid larvae
	Coccophagus	Soft scales.

In a second paper entitled "Observations on Woodboring Insects, their parasites and other associated insects" (13) Brues again stresses the point that the most primitive groups of both the parasitic and phytophagous Hymenoptera are definitely associated with a woody flora, and in support of this statement he cites the following examples.

Parasite Forms.

Ichneumonidae	...	Rhyssini
Braconidae	...	Spathiinae
		Hormiinae
		Helconinae

These groups are the smaller and more primitive ones of the above families and are parasitic on woodboring species. Of the phytophagous groups he cites the Siricidae, on which family I have already quoted his conclusions above. Dealing with the question of habits in relation to parasitism, Brues

comments on the difficulties which occasionally confront the parasite in attaining its host, concluding that a secluded habitat such as that of any woodborer, must act as a powerful factor in restricting the kind of parasite which can attack certain types of host. Thus woodborers can usually be reached only by species, possessing long ovipositors. This is fully borne out when we think of the Rhyssa and Ephialtes type of parasite.

In the general outline of their life cycle, Brues observes that all these are, generally speaking, very uniform. Oviposition may take place during the egg, larval or pupal stages, the egg being laid either outside or inside the body of the host. "In some cases the young larva exhibits great modifications in body form, and when these are of a transitory nature, disappearing almost entirely after one or two ecdyses, we get a transition stage to several very clearly defined cases of hypermetamorphosis."

Here he cites his own researches, and those of Wheeler and Smith (51) on the active free-living 1st stage larva found in the Chalcidoid families Eucharidae and Perilampidae, the first named by Wheeler the Planidium or "Diminutive Wanderer" on account of its remarkable roving habits. This larva, Brues observes, is quite comparable morphologically, and otherwise, to the Triungulin type of the Meloidae and the Strepsiptera.

With the above conclusions in mind, we may now briefly consider what contributory evidence the following study of the Ibalia parasite will have to offer us. In the first place, if we consider that Brues is correct in considering that close linkages in habit between host and parasite are not easily changed and therefore presumably of ancient origin;

then the record of Ibalia shows quite clearly that the association between it and the Sirex woodwasp is of very long standing. The fossil record of the Ibaliinae affords as we shall see, evidence of their antiquity, and further the remarkable manner in which the parasite has adjusted its oviposition habit to fit in with that of the host, provides us with new data which very strongly support this hypothesis. This complete adjustment of habit on the part of the parasite to the ways of the host is one of its most remarkable features, and in this respect I consider it surpasses the Rhyssini which although admittedly attached to wood boring species, do not exhibit that close linkage in habit to the same degree.

Turning, in the second place, to the larval life, we shall find in the Ibaliinae another example of that remarkable hypermetamorphosis of which Brues has given examples. The primary larval stage in Ibalia although not of such a dramatic type as that of the Planidium, is at the same time unique in the superfamily Cynipoidea and is undoubtedly the relic of bygone days when its ancestors led a more active life, and had to wander in search of their food. Finally, the primary larval type adds further confirmatory evidence of the correctness of the view that the Ibaliinae must be regarded as a distinct, and possibly aberrant type of the Cynipoidae.

The Super-family Cynipoidea.

The Cynipoidea are divided into two great groups, Cynipidae Phytophagae, comprising the sub-family Cynipinae, which includes the gall-making species and their inquilines, and the Cynipidae Zoophagae which contains the parasitic sub-families. The latter alone concern us here. They are divided into nine sub-families in all, but of these only six

are represented in Europe (Kieffer and Dalla Torre, 1910). For the separation of these sub-families the following table by Kieffer, which forms part of his excellent review of the super-families - (Die Gallwespen (Cynipoidea) Mitteleuropas. Schröder, Insekten Mitteleuropas, Band III, 1914) will be found useful.

Cynipidae Zoophagae.

Table of Sub-families (After Kieffer).

1. The second tarsal joint of the hind leg bearing on the outer margin a styloid process. Cubital vein arising from the anterior half of the basal vein.

Sub-family Ibaliinae.

The second tarsal joint of the hind leg without a styloid process. The cubital vein, when present, arising from the base or before the middle of the basal vein.

2.

2. Dorsal surface of the scutellum with a cup-shaped raised area. Antennae eleven to sixteen jointed. Usually fifteen jointed in the male and thirteen jointed in the female.

Sub-family Eucoilinae.

Dorsal surface of the scutellum without the cup-shaped raised area. Male antennae fourteen jointed. Female antennae thirteen jointed.

3.

3. The second abdominal tergite about half the length of the abdomen, seldom less, in which case the cubital vein arises from the middle of the basal vein. Body without sculpture. The third, fourth, fifth, or sixth antennal joint of the male often excavated.

Sub-family Charipinae.

The second abdominal tergite less than half the length of the abdomen. At the most, only the third joint of the male antenna excavated. Cubital vein either absent or arising from the base of the basal vein.

4.

4. The second abdominal tergite very small, tongue-shaped.

Sub-family Aspicerinae.

The second abdominal tergite not tongue-shaped

5.

5. Abdomen markedly petiolate. Second tergite markedly longer than the third.

Sub-family Anacharitinae.

Abdomen sessile. Second tergite markedly shorter than the third.

Sub-family Figitinae.

The first thing which strikes one after a general review of the above sub-families is the marked difference in size which separates the Ibaliinae from the rest. While we find the range of size in the Ibaliinae varying from six to seventeen mm., in all the other sub-families the average size is much smaller, the range extending from 0. 75-6 mm. Morphologically, the Ibaliinae appear to approach the Figitinae most closely, and this point was recognised by Hartig in 1840, when he included them as a tribe of the Figitinae. Later writers however, Thomson, Ashmead, etc., raised them to sub-family rank, and Brues' palaeontological studies in 1910 lend support to this view. These are contained in a paper on the parasitic Hymenoptera of the Tertiary of Florissant, Colorado (11), in which he described a new genus Protoibalia, the type of which he named P.connexiva. This remarkable fossil, which he figures in this paper,

combines the characters of Ibalia and certain true Cynipoids. The region of Florissant is very rich in fossil parasitic Hymenoptera, and Brues records that one hundred and twenty five species have been described from that locality, as against sixty three from the rest of the world. Of these one hundred and twenty five species, only three are Cynipoidea, and it is certainly remarkable that an example of the Ibaliinae should be one of them. The deposits are of Miocene age. Study of the larval morphology has also shown that the Ibaliinae are probably a more primitive Cynipoid type than any other yet described. No other entomophagous Cynipoid is associated in the same way with the wood boring host; the Figitinae and Euccoilinae being chiefly parasitic upon Diptera, the Anacharitinae on Hemerobiid larvae, and the Charipinae on Aphids and Coccids.

Sub-family Ibaliinae, Ashm.

1862. Fam. Ibaliidae. C.G.Thomson.
Öfv. Ak. Förh. Vol. 18, p. 397.

1869. Fam. Ibalioidae. A. Förster.
Ver. Ges. Wien. Vol. 19, Abh. p. 329.

1877. Sub-Fam. Ibaliinae. C.G.Thomson.
Opusc. Ent., Vol. 8, p. 778.

1886. Sub-Fam. Ibaliinae. Ashmead,
Trans. Amer. Ent. Soc., Vol. 13, p. 60.

1890. Sub-Fam. Ibalina. P. Cameron.
Monogr. Brit. Phyt. Hym. Vol. 3, p. 156.

Description. (After Kieffer and Dalla Torre)

"Forewings with two completely closed, and a third distally opened cubital cell. Cubital veim entire, arising from the anterior half of the basal vein. Radial cell very elongate and closed. Areola lying opposite the root of the Radial cell. Second tarsal joint of the hind legs furnished with a styloid process on the outer margin. Abdomen almost sessile. Tergites two to five in the female sub-equal, the sixth

tergite being the largest.

Distribution - Europe, Asia, America.

1 Genus, 13 species.

Genus Ibalia, Latr.

1798. Ophion (Part) J.C.Fabricius.
Ent. Syst. Suppl. p. 210, 235.

1802. Ibalia. Latreille,
Hist. Crust. Ins. Vol. III, p. 306.

1806. Sagaris. Panzer,
Krit. Revis. Vol. II, p. 91.

Six European and Asiatic species of the Genus are recorded by Kieffer and Dalla Torre. Of these only four belong to Europe proper, I.drewseni Borries, Denmark and Piedmont. I.schirmeri Kieff., Berlin. I.leucospoides (cultellator) Hochenw., Europe, Asia Minor and I.arcuata D.Torre and Kieffer, Italy, Germany, England.

Schulz (49) in a recent paper (1912) on the sub-family considers I.schirmeri and leucospoides synonymous and has grave doubts of the validity of Borries' species, Drewseni. I can give no record in the British literature of the species arcuata which is recorded by Dalla Torre and Kieffer from England, and in this paper I shall therefore confine myself to I.leucospoides Hochenw. the only British species of which I have any personal knowledge.

Ibalia leucospoides, Hochenw.
- Synonymy -

Ichneumon leucospoides, Hochenw. Schrift. Berlin. Ges.naturf. Fr. VI, 1785, p. 345, ♀; T.8, F.5 and 6.

Ichneumon cultellator, Fabricius, Entom. System. II, 1793, p. 167, No. 142, ♀.

Ophion cultellator Fabricius, Suppl. Entom. System. 1798, p. 239, No. 20, ♀.

Ophion cultellator Panzer, Faun. Insect. German. VI, 1799, p. 72, T. 6 ♀.

Ibalia cultellator Latreille, Hist. nat. Crust. & Insect, III. 1802, p. 306.

Ophion cultellator Walckenaer, Faun. Paris. II, 1802, p. 74, No. 10, ♀.

Banchus cultellator Fabricius. Syst. Piez. 1804, p. 127, No. 4. ♀.

Ibalia cultellator Latreille, Hist. nat. Crust. & Insect, XIII. 1805, p. 205, ♀; T. 100, F. 5.

Sagaris cultellator Panzer, Krit. Revis. II, 1806, p. 91.

Cynips cultellator Jurine, Nouv. meth. class. Hymen. 1807, p. 286, ♀♂.

Ibalia cultellator Illiger, Magaz. f. Insectenk. VI, 1807, p. 192.

Ibalia cultellator Latreille. Gen. Crust. & Insect. IV, 1809, p. 17.

Diplolepis Ibalia Lamarck, Hist. nat. anim. s. vert. IV, 1817, p. 163, No. 8, ♀.

Ichneumon cultellator Thunberg, Bull. acad. sc. St. Petersbourg, VIII, 1822, p. 265, ♀.

Ibalia cultellator Curtis, Brit. Entom. I, 1824, p. 22; T. 22.

Ichneumon cultellator Thunberg, Mem. acad. sc. St. Petersbourg, IX, 1824, p. 320, ♀.

Ibalia cultellator Ronscolombe, Ann. sc. nat. XXVI, 1832, p. 184, No. 1, ♀. ♂.

Ibalia cultellator Westwood, Magaz. of Nat. Hist. VI, 1833, p. 494, nota.

Diplolepis Ibalia Lamarck, Hist. nat. anim. s.vert. Ed. 2a, IV, 1835, p. 373, No. 8, ♀.

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Ibalia cultellator Westwood, Introd. mod. Classif. Insect., II, 1840 Synops. p. 55.

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Cynips (Ibalia) cultellator Blanchard, Cuvier: Regn. anim. Ed. 3a. Insect. II, 1849; T. 113, F. 1.

Banchus cultellator Dumeril, Mem. acad. sc. Paris XXXI, 1860, p. 897, No. 4.

Ibalia cultellator Giraud, Verh. zool. bot. Ges. Wien, X. 1860, p. 175, No. 1, ♀ ♂.

Ibalia cultellator Thomson, Öfvers, Svensk. Vet. Akad. Förh. XVIII. 1861, p. 406, No. 1. ♀ ♂.

Ibalia cultellator Taschenberg, Hymen. Deutschland. 1866. p. 123, ♀ ♂

Ibalia cultellator Cameron, Monogr. Brit. Phytoph. Hymen. III, 1890, p. 260, No. 1, ♀ ♂; T. 14, F. 14.

Description of the species. The following description of the species, partly based on that of Dalla Torre and Kieffer (1910) has been enlarged to some extent, with special reference to the secondary sexual characters and the structure of the abdomen concerning the details of which I find myself in disagreement with the illustrations given by these authors.

Ibalia leucospoides Hochenw.

Adult female - (Plate 1.) Head Black, vertical region from the ocelli to the inner margin of the eyes obliquely striated; the posterior third of the same region along the margin of the eyes punctate and glossy. Occiput strongly concave. Genae emarginate. Frontal region rugosely striated with a well-marked shallow excavation in the centre, the edges of which are distinctly margined. Antenna fossae bordered by parallel ridges. The antennae almost as long as the abdomen, thirteen-jointed, third joint not markedly longer than the fourth. Terminal joint about one-quarter as long as the succeeding joint, and one-and a half times longer than broad. The apical portion of this joint broadly rounded in the female (Text-Fig. 3.). Terminal joints, three and four, sub-equal and markedly shorter than the succeeding joints.

Thorax. Black, at least twice as long as broad, the dorsal surface not markedly rounded. Pronotum raised and incised in the centre of the front margin. Mesonotum oval, with three distinct longitudinal furrows running the whole of its length, and two similar, less conspicuous lateral furrows, terminating about half way up the segment. Dorsal surface of the segment rugosely striated in a transverse direction. Scutellum sharply separated by a transverse furrow, and showing at its base two large smooth foveae with margined sides. The edges of the scutellum margined, the apex deeply

emarginate. Dorsal surface of the median segment divided into two halves by a distinct longitudinal carina. Wings smoky-grey, not markedly hairy, not fringed. Legs black, the tibia and tarsi sometimes inclining to deep mahogany. Hind coxae placed wide apart, strongly developed, with a distinct blunt tooth-like prominence on their outer margins. Hind femora well developed, somewhat curved and pointed at both ends. Hind tarsi five-jointed, the first joint twice as long as the four succeeding joints together. Claws simple, pulvilli absent, empodium pad-like, sub-triangular. Head, thorax, and legs covered with a fine grey pubescence.

Abdomen. (Text. Fig. 1.) Dorsal aspect blade-like; in lateral view the outline of the posterior segments markedly rectangular. Petiole black, very short, remainder of the absomen mahogany in colour, very dark on the dorsal surface becoming lighter ventrally. Tergites two to five sub-equal; tergite six, the largest, almost as long as three, four and five together. The visible portion of tergite seven triangular in shape. This segment bears a large, distinct, spiracle, lying ventrally.

Abdominal sternites two to six much reduced in size and confined to the basal portion of the sternal region. They are overlapped by tergite two and half of tergite three. Sternite seven (Hypopygium) very long and triangular in outline. This sternite is overlapped by tergite three (part), tergites four, five, and part of six (Dalla Torre and Kieffer use the word "pflugscharförmig" - ("ploughshare-like") to describe the shape of this segment). Further details of its structure will be considered when we come to consider the question of

oviposition, and the structure of the ovipositor.

Length. Small females 7.5 to 9.0 mm.

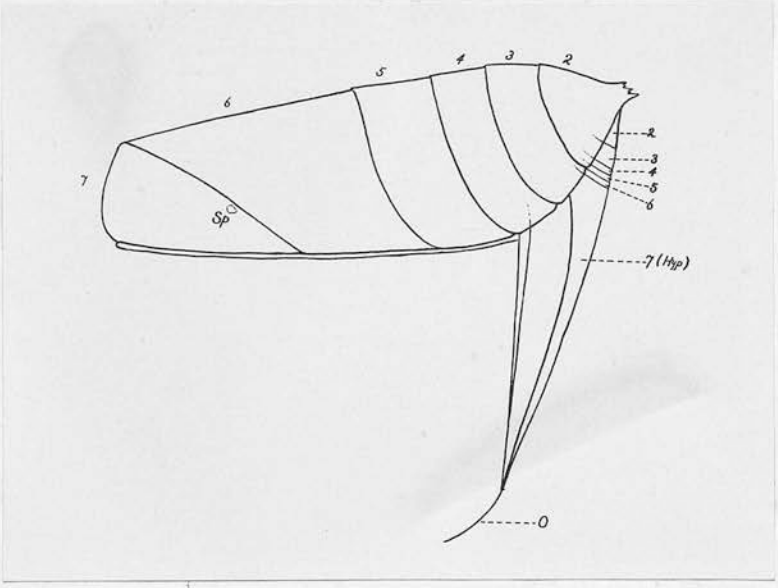
Large females 12.5 to 14.1 mm.

Male. The chief points of difference in the male insect are as follows:- Antennae fifteen jointed, third joint with a sinuous excavation on the outer side. Of the terminal joints the apical one is elongate and pointed, being slightly shorter than the next three which are elongate and sub-equal (Text Fig. 3.).

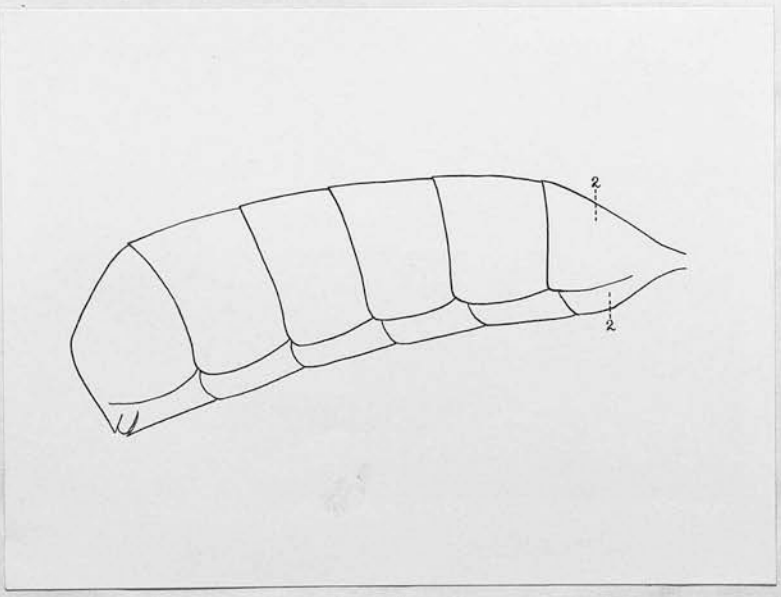
Abdomen. In dorsal view, the blade-like character of the abdomen is as marked in the male as in the female. In lateral view, the dorsal outline is however quite different being regularly crescentic with the hind portion much less markedly angulate (Text. Fig. 2.). Tergite two, triangular, dorsally slightly longer than tergites three, four and five which are sub-equal. Tergite six slightly longer than the preceding tergites, but not nearly so long as the sixth tergite in the female. Tergite seven sub-rectangular, spiracle distinct. The posterior two-thirds of the segment with a sparse covering of fine, grey hairs. Abdominal sternites two to six not reduced as in the female. All the sternites closely overlapped by the tergites. Sternite two the shortest and sternite seven, the longest.

Length. Large male 10 to 12 mm.

Small male 6.5 to 7.5 mm.



Text-Fig.1. Ibalia leucospoides Hochenw.
Female abdomen. The segments are numbered 2-7 respectively. x 11.
Hyp. ... Hypopygium.
Sp. ... Spiracle.
O. .. .. Ovipositor.



Text-Fig.2. Ibalia leucospoides Hochenw.
Male abdomen. x 8.

Historical Review of the literature on the biology of the Ibaliinae in Europe and N. America.

Europe. The earliest note of any sort on the habits of Ibalia which I have been able to trace in the European literature, is that of Latreille in his Histoire Naturelle des Crustacées et des Insectes, T. 13, p. 197 and pp. 205-6. Paris 1802.

Writing of I.cultellator (leucospoides) he records on p. 197, "qu'il depose ses oeufs dans le bois", and on pp. 205-6 "J'ai trouvé ces insectes dans les environs de Brive, dans un bois de vieux charmes, voltigeant autour de ces arbres, au moi de mai." No reference is made to the presence of Sirex in the vicinity and the author evidently did not realise the connection of Ibalia with the woodwasp. The occurrence of adults in May is interesting, and suggests either that Ibalia was parasitising S.gigas which as a rule flies earlier in the year than cyaneus; or that it was parasitic on one of these species of the genus which attack broadleaved trees on the Continent, but which do not occur in Britain. In the British literature, the first reference of note is that of Curtis (20) in his British Entomology, Vol. III, plate 22, London, 1840. The plate, which shows the adult male in colour and some smaller drawings of the adult morphology, is excellent. The figures of the male and female are by far the most accurate ones I have seen, though the details of the morphology of the female abdomen are somewhat incorrect.

Curtis recognises the insect as a Cynipid, and refers it to the family Diplolepidae Latr. He records finding a male flying in a garden at Bungay in Suffolk and quotes Latreille's note, which I have already cited. He is quite unaware of the parasitic habits of the insect and supposes it to be a gall-maker like the rest of the family. These

observations of Curtis were quoted in the same year (1840) by Westwood in his Introduction to the Modern Classification of Insects (59). Westwood describes the genus Ibalia as "curious and exceedingly rare". Blanchard (7) in 1841 also records I.cultellator from France and Germany. He states that it is found in the spring, but is very rare. Nineteen years later in the year 1860 we find the parasitic habits of the genus being suspected for the first time. That year a French entomologist, Dr. Giraud, published his "Enumération des Figitides de l'Autriche". (30) and referring to I.cultellator he writes:-

"Je l'ai capture pendant le mois d'aôut à Salzbourg, dans un chantier du bois de pin. Monsieur Kollar et mon ami Monsieur Tschek, m'ont l'assuré l'avoir pris aussi, dans les mêmes conditions, et à la même époque dans la Basse-Autriche. Il est trés vraisemblable, que sa larve vit parasite de quelque grand coléoptère."

At the same time as this note was published by Giraud, Reinhard in his "Die Figitiden der Mittlern Europa" (47) referred to Ibalia in the following footnote, which I quote in full from the original paper. "Die Vermuthung, das Ibalia cultellator Fabr., auch zu den parasitischen Gallwespen gehört, gewinnt sehr an Gewicht durch eine Beobachtung des Herrn von Heyden in Frankfurt am Main, der sie in grosser Zahl mit S.juvencus aus Kiefern-holz erzogen hat. Sie flogen Ende Juni und Anfang Juli aus." This is the first reference to von Heyden's observation which I have traced and I have been unable to find any published account written by von Heyden himself.

Reinhard's note soon attracted the attention of Taschenberg who published a further note on the habits of the species the next year (1861) (52). This contains

some interesting observations upon the relative proportions of the sexes, of which the males were apparently the greater.

"In dieser Zeitschrift (Berlin Ent. Zeit. IV. 205) ist angegeben, dass dieses schöne Thier wahrscheinlich in Sirex juvencus parasitisch leben möge. Meine diesjährigen Erfahrungen bestätigen diese Vermuthung. Am 12. September, in den sonnigen Nachmittagsstunden umflogen diese Thiere eine abgestorbene Kiefer (P.sylvestris) und spazierten gemächlich mit erhoben Flugeln an den Stamme, welcher bis über 8 Fuss seiner Höhe der Rinde beraubt war, hier und noch weiter oben umher. Einiger Male sassen ihrer zwei übereinander die ich nach meiner Gewohnheit auf eine Nadel brachte,in der Voraussetzung Männchen und Weibchen sicher bei einander zu haben. Um keine Zeit zu verlieren und eine möglichst reiche Erndte zu halten, liess ich mich auf nähere Betrachtung zunächst nicht weiter ein. Der Stamm war mit zahlreichen Fluglöchern versehen, welche alle, vom Umfange eines groben Schrotkorns, in schräger Richtung nach unten verliefen. Aus einem sah die Vorderseite eines Kopfes hervor, ich vermuthete dahinter einen Sirex juvencus ♂, brachte aber bald durch einige Nachhülfe ein stattliches ♀ der Ibalia heraus. Jetzt überzeugte ich mich, dass die auf einander sitzenden Exemplare nur Männchen gewesen waren. Sie überwogen der Zahl nach bedeutend; denn bei der auch an den folgenden Tagen fortgesetzten Jagd erbeutete ich an noch andern ähnlich Stellen von diesem mehr trägen Insekt zu 20 Mannchen nur 4 Weibchen. Beide Geschlechter sind in Curtis Br.Entom 22 abgebildet und beschrieben. Das Weibchen ist auch von Westwood kurz charakterisirt und der Hinterleib desselben abgebildet."

By the year 1881, the supposition that the insect was a parasite had reached the textbooks and we find Altum (2)

referring to the genus thus:- "Nur eine Art, cultellator (leucospoides) unser grösster Cynipide, welcher in Holzinsekten (man vermuthet S.juvencus oder auch Holzkafer) schmarotzt." Ten years later (1891) Herman Borries in his paper "Om Slaegten Ibalia" (On the Genus Ibalia) (8) contributed a more detailed account of the habits of the insect than any which had appeared hitherto. I propose to consider this paper in some detail, because it is the only contribution to the literature which gives any really trustworthy data on the biology of Ibalia. Borries' observations, although very incomplete, lead one so far on the way to a solution of the problems surrounding the insect's habits, that it was by using the few hints which he was able to give us, that we obtained the first clues upon which all our subsequent biological work at Tubney wood and elsewhere was built up.

After some preliminary notes on the genus, Borries states that the old idea that Ibalia parasitises the larvae of woodboring beetles originated from the insects having been captured singly in timber yards.

Apparently unaware of von Heyden's observations quoted above, he cites Taschenberg as the first observer to find Ibalia in numbers in the forest itself, and he quotes the note to which I have already referred. Taschenberg's views were later confirmed, according to Borries, by Drewson in Denmark, who bred Ibalia repeatedly from logs which contained S.juvencus and S.noctilio. To these records Borries himself adds the following account of the species, which I have translated in full from the original paper:-

"In some logs attacked by S.juvencus which Herr Skovrider Fritz had lying in a breeding cage, and from which Rhyssa persuasoria L. had previously emerged, a few specimens of an

Ibalia were found still lying in their pupal chambers." (This proved to be a new species which was described by the author as I.Drewseni Borr.). "In the frass lay two cast larval skins, one of Sirex and the other of Ibalia, the latter having small tridentate mandibles with awl-shaped points. I conjecture from this that the Ibalia larva is an internal parasite, but have no confirmatory evidence."

"When Ibalia lays eggs in August, usually only one year old Sirex larvae are found lying in the superficial wood layers, and she must therefore oviposit in these, since the older larvae (two years old and more) lie deeper in the wood. The galleries of the young larvae are not far from the wood surface and are running in such a direction that the Ibalia' ovipositor (15 to 22 mm. long) can easily reach them. "Sirex larvae parasitised by Ibalia appear to change the normal direction of their tunnels, as instead of attacking the heartwood, the larva turns about and confines itself to the outer portion of the sapwood, steadily approaching the outside in a more or less slanting direction, ending close under the surface (3 to 5 mm.) and nearly parallel to it. The egg or larva of the parasite appears to be carried by the host larva for a couple of inches or more along its tunnel. The pupal chamber which is cut off from the rest of the tunnel by a wall of boring dust, was 15 to 17 mm. long by 3.5 mm. broad." In contrast to the methods employed by Ibalia the author cites the habits of Rhyssa persuasoria L. which he says begins to oviposit in May, and with its 40 to 50 mm. long ovipositor can reach the full grown Sirex larvae a month or two before they pupate. He states that he nearly always found Rhyssa 15 to 25 mm. from the wood surface, usually in that portion of the Sirex tunnel which is directed towards the wood surface.

The vital observation in this paper is that referring to the superficial position of parasitised larvae. The value of this as an indication of parasitism will be made fully apparent in the subsequent account of the insect's habits as studied during the present work. Six years after the appearance of Borries' paper, an account of the biology of Ibalia was published in Vol. VII of André's great work "Les Hyménoptères d'Europe et d'Algérie." (3).

Here the larvae are recorded as being "toutes parasites de larves de Coléoptères et d'Hyménoptères lignicoles" Latreille's observations, and the writings of Giraud, and Reinhard, are cited, but those of Taschenberg and Borries are, for some reason, omitted. Dalla Torre's statement that Ibalia is parasitic on S.gigas L. is regarded by André as probably erroneous.

Some account of the North American species is also given by André. These I shall deal with later.

In 1899, Dominique (25) gave, in a systematic paper on the sub-family, some biological notes, which are however chiefly compiled from sources already cited. This author states that for his own part, he can only tentatively connect the insect with S.noctilio, which was very common in the locality where the Ibalia were found. In 1902 Dalla Torre and Kieffer's monograph of the genera of the family Cynipidae appeared as Fascicules nine and ten of Wytsman's Genera Insectorum (24). This work does not contain any biological data. In the following year (1903) Schirmer (50) published a short paper entitled "I.cultellator Latr. und I.schirmeri Kieff. Schmarotzer bei S.juvencus L." In this paper he records the capture of both species near Berlin in 1895, but states that since that time he has seldom seen them, thereby concluding that they are very rare. In 1902 he

found I.schirmeri in numbers on piled pine logs. He saw adults of both sexes walking along the logs, noted pairing, of which however, he gives no details, and remarks that their gait is such that no net is necessary for their capture. This last remark suggests that the insect was very intent on oviposition and did not concern itself with his presence in her proximity. In that year the flight of the Sirex (S.juvencus) adults lasted till well into October and the Ibalia flight period probably also extended over the same period, or perhaps longer. This author thinks that the Ibalia parasitises the full-grown larvae, but has no evidence to offer in support of this theory. Subsequent references to Ibalia in the European literature can be briefly dealt with, as they contain nothing of biological interest. Morley in 1908, in Vol. III, of his "British Ichneumons", p. 29, gives the following footnote: "I may perhaps be pardoned a note on this parasitic Cynipid, which is so conspicuous and yet so rare that Cameron describing it in 1890 (Phytophagous Hymenoptera III, p. 261) believed it had not been found in Britain since the time of Curtis. Marshall (E.M.M. 1895, p. 27) records two specimens of Ibalia cultellator taken in March 1888 at Hartlepool where S.noctilio was unusually common."

" Late in 1900 Mr. E.Saunders sent me a specimen captured, I believe, in Scotland by Col. Yerbury that year. Last year (1907) I received a female from Mr. Denison Roebuck, taken by Mr. H.H.Corbett at Doncaster in 1905 and Mr. A.H.Hamm has just presented me with another specimen taken by him at Tubney near Oxford in 1907" (31). The most recent record of the insect's capture in this country is that of Mr. G.A. Crawshay who collected eighteen specimens near Leighton-Buzzard and Guildford, Surrey, one of which is labelled "Ex S.gigas". This collection is now in the British Museum. Finally, Hubault [redacted] in his paper on Insect damage to the

coniferous plantations of the Alsatian Vosges, records finding a male Ibalia on a heap of green firewood much visited by Sirex. He gives no details of the insect's habits.

American literature.

The American references to the Ibaliinae are hardly more numerous than the European. The American species range from Canada, Pennsylvania, Colorado, and Nevada to California, Georgia and Mexico. Provancher in Vol. II of his "Petite Faune Entomologique du Canada (1883)" (46) refers to I.maculipennis, Norton in these words : "Nous avons frequemment rencontré cet insecte en compagnie des Braconides, sur les troncs de sapins morts, cherchant sans douts a déposer ses oeufs dans le corps de larves lignivores, dont la moulée révêlait la presence."

The same species is referred to by Harrington (32) (1881) as possibly parasitic on Tremex columba L., Xiphydria albicornis Harr. and Dicerca divaricata (Coleoptera. Buprestidae). Harrington also records finding S.(Urocerus) cyaneus Fabr. and I.ensiger Norton on Vancouver Island. (Canadian Entomologist, XXIX, pp. 16-21), Packard on p. 383 of the "5th Report of the U.S.Entomological Commission, Forest Insects," (45) quotes Norton (Can. Ent. 1887, p. 85) on I.maculipennis, both sexes of which he found on the bark of old sugar maples, and reckoned as a possible parasite of Oryssus sayi which was present in the tree. This conclusion, was, however, based on no evidence, and as we now know Oryssus to be itself a parasite of Buprestid beetles, it may be presumed that the maple was also attacked by a Tremex, which insect the Ibalia was probably parasitising. Felt (27), refers to Packard's note and records I.maculipennis from Ploughkeepsie N.Y. ovipositing on hickory infested by the Buprestid, Dicerca obscura var. lurida Fabr. and a

species of Tremex. He records L.leucospoides as a rare parasite on Tremex and suggests that I.maculipennis has similar habits. He adds a short description of the species and figures the same.

In 1922 there appeared a more detailed account of the habits of I.maculipennis than any which had hitherto appeared. The author of this paper, Lewis H.Weld (58) found the species working on some dead Hickory trees near Evanston, Illinois, on the north branch of the Chicago river, and the observations recorded in his paper extend over six seasons, from June 22nd 1913, to June 12th 1919. The section of the paper devoted to Ibalia is sufficiently considerable to call for detailed criticism and may be dealt with in two parts:- (a) The field studies made by the author on the biology of the insect and (b) His studies on the variability in size of the adults. During the whole period of his field observations the author took two hundred and twenty one females and one hundred and sixty four males of this species, which gives one some idea of the amount of material with which he had to work.

In the flight season, he states, the adults were readily disturbed when sunning themselves on the bark of the dead trees, but the females, when ovipositing could easily be picked off the stem by hand. He records finding as many as twenty three adults on a stem at one time. He discusses the oviposition habits of the insect, in the following passage:- "the knife-like abdomen is thrust deeply into a crack in the outer bark, and several attempts were made by clipping off the ovipositor, and then boring a series of holes around the area and removing the block of wood, to trace its further course into the wood. It does not seem to be driven into the solid wood, but into a hole probably made by a 'horntail' (woodwasp) the summer before, which has become

plugged up by a growth of sterile mycelium. When the horntail egg hatches, the larva eats a straight course towards the centre of the tree, and one which had penetrated three to five mm. into the wood, measured 1.2 mm. in length. As they advance, they moult frequently and four to five larval skins were found in the first inch."

"It is into this plug that the Ibalia ovipositor is thrust, and when the egg hatches the larva probably crawls along until it overtakes the horntail larva ... How large the horntail larva has become, and how far it has penetrated into the wood, when attacked, is not known."

Of course, having failed to discover the oviposition tunnel of the woodwasp, the author was bound to go far astray in the rest of his findings.

It is, however, remarkable to find him crediting the larva of the parasite with the ability of moving towards its host in the tunnel. This is clearly impossible for two reasons, the first being, that the larva is legless and not sufficiently well equipped with ambulatory spines to enable it to proceed along the tunnel; and the second, the presence of closely packed frass in the tunnel, which provides a barrier the mandibles of the parasite larva could not possibly remove.

The author records finding mature larvae of Ibalia, fifty mm. deep in the wood. Some of these he figures and of them he writes:- "Seven Ibalia larvae were also found, 13.8 to 20 mm. long, apparently full-grown, not near a horntail larva in any case, but in burrows they had evidently made for themselves." Close examination of the author's figures of these larvae coupled with study of the text leads one to suspect that the author has here mistaken the larvae of a Megarhyssa for those of the Ibalia. The larvae figured

are distinctly Pimpline in type, and the depth at which they were found in the wood distinctly suggests that they belonged to that group. Ibalia pupae were also recovered but at what depth, the author does not say. The dates of emergence of the adults in the U.S.A. is given as June 1st in Pennsylvania and up to July 21st in Maine, the majority being taken in June. These records were taken from labels on museum specimens which the author studied. The second part of this note deals with the range in size of the adults which in the male varied from 9.2 - 15.7 mm. and in the female from 9.2 - 17 mm; the females being always somewhat larger than the males and also more variable in size. This variability was not, however, greater than in a gall-making Cynipid, and the author concludes that Ibalia's tendency to dwarfism must be considered not as being due to lack of food, but as "an expression of the normal tendency of the species to depart from the type." The most recent American reference which I have been able to find is that of Essig (26), in his "Insects of Western North America", New York, 1926. Here he records I. ensiger as having been found ovipositing in Monterey Cypress and Monterey pine which were infested by the larvae of Sirex areolatus Cresson, and S. behrensi Cresson, on the Campus of the University of California, November 25th and 26th, 1922.

The insect was found in this case by Mr. Stanley E. Flanders who published the following short note upon it in the Journal of Economic Entomology (28).

I.ensiger on Monterey Cypress.

"The burning of Hearst Hall on the Campus of the University of California, in June 1922, caused the death of a number of trees, among them three Monterey Cypress. On November 25th 1922, I found eleven specimens of S.behrensi Cresson and

two specimens of S.areolatus Cresson on the trunks of these trees. All but one were rigid in death, with their ovipositors embedded in the wood. One, S.areolatus, was moving slowly over the bark. No indication of larval work was found. Roaming over the tree trunks, or with their ovipositors inserted in them, I found twenty one females of the species I.ensiger. The ease with which they removed their ovipositors when disturbed, leads one to believe that they used the holes made by the Siricidae.

Those of the Siricidae that failed to remove their ovipositors, stood guard over their young, protecting them from the Ibaliidae."

Here we have another example of a shrewd guess insufficiently followed up by observation to confirm its accuracy. Apart from the last sentence, with which I disagree, the death of the Sirex being due in all probability to exhaustion and quite unconnected with the presence of Ibalia; the record is an extremely interesting and valuable one. The Western species is here associated with woodwasps of the steel-blue group, and I note also that the date of oviposition corresponds with my own records at Tubney, where I have found the insect at work as late as October 19th. The climatic conditions of Western California no doubt favour the insect, and enable it to extend the oviposition period up to a later period of the year than would be possible in this country.

Studies on the Biology and Morphology of Ibalia leucospoides Hochenw (Oxford 1927 - 1929).

Notes on the distribution of Ibalia in Britain.

The field studies on the biology of Sirex cyaneus in Tubney wood showed that after some practice it was possible to select with a fair degree of accuracy, the type of tree which contained woodwasp larvae. This question I have

already fully discussed on pages 239-242 of my paper on the "Sirex woodwasps and their Importance in Forestry", and its importance lies in the fact that on the recognition of trees which are likely to be attacked by the adults, the success of field observations depends. Generally speaking, it was found that trees which while still green, had less than one-third of their crown remaining, were the most likely to be selected by the insect for oviposition. Using this as a guide it then becomes possible in any Sirex area toselect those trees in which it is highly probable that oviposition has recently taken place, and which will therefore contain eggs and young larvae. This last form of selection is all important when one is dealing with the Ibalia parasite as a study of its life history will show. To facilitate the field work on Ibalia, therefore, the following points were stressed in seeking for suitable material:-

(1) Trees which show signs of recent oviposition by the woodwasp, i.e. which contain fresh oviposition tunnels; are extremely likely to harbour suitable material for the early stages of the parasite.

(2) The full-grown larvae of the parasite may also be found in trees similar to the above, but those which also show a number of tiny exit holes connecting with a short superficial Sirex tunnel in the wood are even more promising. Logs which have dried out to some extent, may contain a few mature larvae, but they are less favourable.

(3) Sometimes one meets with larch logs which have the wood surface so scored by the tunnels of the larch longhorn beetle (Tetropium) that the Sirex oviposition holes are recognised with difficulty. Such logs should always be searched for the parasite as they come under the same category as those in Section 1.

(4) In the flight season (August - October) a close watch on likely Sirex-trees will nearly always result in the discovery of the parasite at work, if it be present in the locality.

Such, briefly, were the 'rough and ready' field notes which served our purpose when in 1928 an effort was made to find out how extensively Ibalia occured throughout the south of England. My first visit was to South Molton, North Devon, where through the kindness of Mr.H.S.Hanson, I was able to do a considerable amount of field work. Here Ibalia was found in January, 1928 in spruce, an adult lying dead in its tunnel, while in July of the same year, when investigating some likely larch logs near there, I found the full-grown larvae. Since that time, I understand, Mr.Hanson has found the species in small numbers.

In May 1928 through the kindness of Mr.H.R.Munro, forester to the Hon. R.A.R.Plunkett-Ernle Erle Drax, C.B., D.S.O., of Charborough Park, Wareham, Dorset, I received some specimens of Sirex cyaneus and two specimens of Ibalia. This discovery enabled me to select a small area of larch in Bere Wood near Bere Regis, Dorset, where Mr.Munro, acting on my instructions, marked a few trees. I visited the area in August and found both Sirex and Ibalia busily ovipositing on the trees, and since then on examining some selected logs which were afterwards sent to Oxford, I have been able to recover a large number of the parasite larvae in various stages. Similar accounts could be written of the discovery of the insect at Wangford Warren, Brandon, Suffolk, and Holkham Park, Norfolk in both of which places the larvae and adults of the parasite have been secured in numbers. Further, the chance finding of Sirex in some Deodar (Cedrus deodara) logs in the Forest of Dean in July, 1928 enabled Dr.Myers

who was then at the Imperial Bureau of Entomology, Parasite Laboratory, Farnham Royal, to recover the parasite from a new locality, and also a new host tree.

I have dwelt at some length on this question to show that the discovery of Ibalia in such numbers is not entirely due to "luck" but is really governed by the success or failure of carefully planned field studies. In a recent review of the joint paper (Nature, Vol. 122, p. 665, October 27th, 1928) on the Sirex parasites published by Dr. Myers and myself last year, this element of luck in finding the parasite was stressed to some extent. While this is certainly partially true, my own field studies and the records obtained by the Parasite Laboratory of its collections of Sirex parasites collected for them by Mr. H.S. Hanson in Devon, show quite clearly that systematic methods of collection and observation play a large part in producing the best results. In this connection, I may add, that when the Imperial Bureau of Entomology first began to consider seriously the question of the technique to be employed in collecting large numbers of the larvae of the Sirex parasites, it was on my advice that the region of North Devon was chosen and Mr. Hanson given charge of the work. Preliminary surveys of chosen woods had convinced us that the only feasible method of obtaining the desired material in large quantities was to collect together in certain definite parts of the wood, dumps of selected logs which would attract the woodwasps and their parasites from all quarters.

As it happened, by far the greater number of parasite larvae obtained in Devon were those of Rhyssa persuasoria L., the numbers of Ibalia being relatively small. The principle is, however, similar in both cases and the success of the work, which I understand from Mr. Hanson, has been considerable, is chiefly due to the method of work employed. The account

of this work which has been prepared by Mr. Hanson, and which will, I understand, be published shortly, should contain some data of great interest and value. My studies of the distribution of Ibalia in Britain have so far been confined to the South. I have no personal records of its occurrence in the North. Under certain conditions, however, which are discussed on p. 102 I believe that the insect will be found as widely spread as its Sirex host.

Flight period of the adults. The first adult Ibalia which I obtained was bred from a pupa taken in Tubney wood, and emerged in a cage at the laboratory on August 15th, 1927. On August 24th, nine days later, the first adult was seen in the wood. This was a large female which was found ovipositing on a dying larch at 3 o'clock in the afternoon. From this time onwards right up to October 16th, of that year (1927) adults were found fairly regularly in the open at Tubney while a few were bred from larch wood in the laboratory. (See Table App. I). In 1928, the first adult was seen at Tubney on August 30th, but it is certain that they had begun to emerge some time before this, and the late record is due to the fact that so much work was entailed in the laboratory studies, that regular observation at Tubney was impossible. Owing to my receiving a quantity of larch material from other parts of the country, notably Norfolk and Dorset, we were able to carry out a lot of breeding work in the laboratory during 1928, the first adult, a female, emerging on July 20th.

The adults are most active on the wing in sunny weather, but they do fly on dull and windy days. In wet weather they seek shelter under the bark scales, and four adults were found in these shelters on a wet, windy day in September (1928). With the advent of colder nights in late September and October, the insect no doubt escapes death for some weeks by sheltering

in bark crevices. Thus during the autumn of 1928, severe night frosts on September 30th, and October 1st were thought to have killed off all the adults which up till then had been busily ovipositing in the larch at Tubney. For some days not a single adult was seen, but a fortnight later two large females reappeared and continued ovipositing as actively as before. The latest record of Ibalia emerging after the end of October, occurred in December 1928 when a large female emerged from some Brandon, Suffolk, logs, which were stored in a cage at 18, Museum Road. When kept in cages at the laboratory, they feed greedily on honey and water or split raisins, but I have never seen them visit flowers in the open for the purpose of obtaining nectar. As a rule, when I have studied them, thay have either kept to the larch in which they were ovipositing, or if they have flown away, it was usually only a few yards off to the foliage of elder bushes, on which they rested for a short time.

Proportion of the sexes. A table showing the relative numbers of both sexes of Ibalia which have been captured or bred during the past three years is given in the appendix. In the laboratory, the males generally emerged first and this I find also quite commonly in both Sirex and Rhyssa. Of the two sexes, the table shows the females to be predominant but under natural conditions the excess of females over males is probably not so great as the figures would lead us to suppose. Only two males have been captured in the open. One of these was caught on an outdoor cage in Tubney wood during the summer of 1927, and the other was taken at Brandon, Suffolk, walking about on a larch log on October 1st, 1928, quite near the spot where a female was found just under the bark ready to emerge. [x]

This single observation of the male Ibalia apparently hovering around the vicinity of a tunnel from which the female

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[x] See Appendix 3 for further notes on this paragraph and the next.

was about to emerge is interesting in view of similar observations which have been made by Gade, Champlain and Barlow in North American species of Megarhyssa. These are quoted by Dr. Myers in his last paper on Further Biological Notes on Rhyssa and Ibalia, parasitising S.cyaneus Fabr. Bull. Ent. Res., Vol. XIX, pt. 3, p. 317. Gade (Bull. Brooklyn Ent. Soc. VII. pp. 103-104, 1884) found in Megarhyssa lunator that the males congregated in numbers round a tree trunk at a spot where a female was found just below the wood surface ready to emerge. Champlain (Ent. News Philadelphia, XXXII, p. 241, 1921) also found in M. atrata Fabr. that the males assemble at points where the females are about to emerge. He also showed that in one case at least, the male was able to effect pairing by thrusting the abdomen through a hole which had been gnawed either by the enclosed female or the male attempting to force a way in. Dr. Myers was unable to find any indication of similar behaviour on the part of Rhyssa, but this observation of the behaviour of a male Ibalia suggests that future attention to the point may show that the habit of awaiting the emergence of the females also prevails in this species.

Pairing. Oviposition habits, and the attraction of the adults to Sirex infested trees. (Plate 2, and Plate 4 Fig. 1).

No pairing has been observed in the open, and it was not until the season of 1928 that I observed it in the cages. The act of pairing was preceded, in all the cases observed by a prolonged stroking by the male of the female's antennae, the male standing a little to the right of the female, who lowers the hypopygial sternite, until it lies at right angles to her body. The male organ is inserted at the base of the hypopygium, the whole operation lasting only a few minutes, (August 25th, 1928). My own observations on the pairing of Ibalia have been supplemented during the

present season (1929), by two more which Mr.H.R.Munro has sent me from Dorset. In the first of these, which is dated August 9th, Mr.Munro writes that while watching Ibalia ovipositing in a Sirex egg tunnel, he saw a male come up to her and circle round her several times. When he had approached close to her, the pair proceeded to brush one another with their antennae. The male then crawled on to the back of the female and pairing was effected, the brushing of the antennae continuing whilst pairing was in progress. The second observation was made two days later, when a male Ibalia was again observed to pair with the female whilst oviposition was in progress. The male in this case also, kept continually brushing the female's antennae with his own, but the female's antennae remained stationary. The female continued ovipositing after pairing had taken place. This habit of brushing the antennae, prior to, and during pairing, I have discussed elsewhere (p 40) and Mr.Munro's observations are in accord with my own as regards its being a feature of the pairing act.

Ibalia was found ovipositing for the first time on the afternoon of August 24th, 1927 about 3 p.m. The insect was standing quite motionless when first observed, at a height of about five feet from the ground. In this case, the seventh sternites (Hypopygium), between which the ovipositor runs, were inserted, as far as one could see, in a bark crevice, at right angles to the body; and the insect, well poised on all six legs kept raising the whole body slowly up and down in rythmical motion, the knife-like abdomen rising and falling in a vertical plane in more rapid motions. The whole operation of oviposition was closely observed soon after this. The insect first proceeds to examine the bark systematically with the antennae, which,

pointing somewhat obliquely forward search out every nook and cranny. During this tour of inspection the abdomen in continually in rapid vertical motion, a characteristic sign that the insect is on business bent, and not wandering idly over the bark. When she has found a likely spot, the antennae are suddenly directed vertically downwards, and and if at this point one follows her movements with a lens, it will be seen that the insect is inserting the terminal joints of both antennae into a Sirex oviposition tunnel. Repeated observation of the parasite's behaviour when ovipositing, has convinced me that her most important action, prior to oviposition itself, is the inspection often prolonged, of the Sirex oviposition tunnel, with the tips of both antennae.

I have often purposely disturbed the insect while she has been engaged in the task of lowering the ovipositor into the tunnel, and have always found that so far from taking immediately to flight, as one might expect, she merely retraces her steps, so to speak, and repeats her inspection of the tunnel with the antennae. Her second inpection is often as prolonged as the first, and I have even been able to induce her to repeat this operation several times, before leaving her to continue the work in peace.

The prolonged testing of the tunnel with the tips of the antennae indicated that sense organs, probably olfactory were concentrated in that region, and wishing to gain some further information as to the nature of these I examined them, both superficially and in section. The olfactory sense, which is well known to play an important rôle in the Hymenoptera as a whole, is specially keenly developed in the parasitic groups, and most writers are agreed that the olfactory organs are largely concentrated in the antennae.

Imms (Text-book of Entomology, pp. 64-65) in his general introduction to the sense organs of insects, gives an excellent general classification of the types of sensory organs of touch, taste and smell which is largely based on the work of Schenk and Berlese. This I propose to deal with in some detail, before proceeding to discuss the occurrence of the olfactory organs in the parasitic Hymenoptera with special reference to Ibalia.

The organs of touch, taste and smell, remain for the most part, according to Imms, as isolated sensillae, and their cuticular parts are to be regarded as modified setae. The following classification, which is taken from Imms, is founded upon the characters afforded by the structure of the cuticular parts. It is, however, as this author states, only approximate, as the types are often not sharply differentiated, and intermediate forms are often found.

Classification of the various types of Tactile, Olfactory and Gustatory organs found in Insects (After Imms, p. 64).

(a) Trichoid - setiform, articulated with a base which is set below the general surface of the cuticle.

(b) Basiconic - Conical, immobile, arising from the general surface of the cuticle.

(c) Styloconic - (Biarticulate type of Berlese). Differs from the basiconic sensilla in consisting of one or more pegs of the basiconic type which are elevated on a style or cone.

(d) Placoid - Consisting of a plate or membrane covering an enlarged pore canal.

(e) Coeloconic - Derived from a basiconic sensilla by the latter becoming sunk into a pit with its apex not projecting.

(f) Ampullaceous - (Flask-shaped organs of Lubbock and Forel). Derived from the coeloconic sensilla by the pit becoming prolonged deeply inwards to form a narrow canal. The latter becomes swollen at its extremity, into an ampulla which encloses a slender hair-like process.

For our present purpose we may concentrate our attention on the fourth or Placoid type of sensilla as we find that in many families of the parasitic Hymenoptera this is the predominant type present. According to Bischoff (Biol. der Hymenopteren, pp. 150-153) the Sensilla Placoidea is the only type present in the Braconidae and Cynipidae, while they are also predominant in the Chalcididae and Ichneumonidae.

The antennal joints in many of these parasitic Hymenoptera present a curiously ribbed appearance due to the presence of numerous elongate strap-shaped sensory areas or Rhinaria, which are provided with a special sensory pore covered by a transparent membrane. In some families (Chalcididae) this pore is situated in the basal half of the Rhinarium, while in others (Braconidae, Ichneumonidae, Cynipidae) it is centrally placed. In the Oryssidae, the pore stretches for the whole length of the Rhinarium. In other Hymenopterous families the Rhinaria are oval and not strap-shaped.

Seurat (48) in his "Contributions a l'étude des Hyménoptères Entomophages," pp. 32-33, quotes the work of Nägel who studied the antennal sensillae of many Hymenoptera, particularly small Braconidae. These olfactory pits, "Porenplatten," he found were quite as large in the very small species (3 mm. long) as in the larger Ichneumonida (Ophion) almost ten times their size. Seurat working on Doryctes gallicus (Braconidae) found similar pits on the antennal joints, and noted that the scape, the ring joint, and the first joint of the flagellum bore no pits. The second whip joint bore one, the sixteen joints following, three, and the last twelve joints, five. Of the shape of the Rhinaria and the position of the olfactory pits he writes "si on examine les choses dans le détail, on voit sur la

surface de chaque article des depressions allongées ou cannelures, étroites, dirigées parallèlement à la longueur de l'article, et presque aussi grandes que ce dernier. Vers le milieu de chacune de ces cannelures, une place claire, elliptique représente la fossette olfactive." This author also found similar pits on the antennae of Aphidius, Apanteles glomeratus L., and Phytodietus corvinus Grav., the latter an Ichneumonid parasite of Callidium.

These sensillae are found on the antennae of both sexes and some workers record the numbers present on the male antennae as exceeding those on the female antennae. In this connection Bischoff (5) writes - "Bezüglich der Zahl der Sensilla placoidea herrscht auch nach den Geschlechtem eine teilweise recht erhebliche Verschiedenheit, die wohl in englsten Zusammenhange mit der Wichtigkeit des betreffenden Sinnes fur das Geschlecht stehen dürfte." (Bischoff, Biol. der Hymenopteren, p. 152). Seurat also states that he considers the olfactory sense to be quite as important in the male for sexual purposes as it is in the female for oviposition.

The Antennal Sensillae in Ibalia. (Text Fig. 3).

The Rhinaria on the antennae of Ibalia are elongate and strap-shaped, with the sensory pore centrally placed. In general appearance they do not differ markedly from those of Rhyssa persuasoria ♀, as figured by Bischoff p. 151, fig. 72 (d) (after Wacker). The centrally placed sensory pore is also typical of the family Cynipidae amongst others. Each Rhinarium measures 50 to 60μ in length by 5 to 6μ in breadth. The diameter of the sensory pore is 7 to 9μ. The surface of the Rhinarium is very slightly raised above the general level of the cuticle, and this gives rise to that ribbed appearance of the antennal surface which

Seurat describes in Doryctes. The ribbing is, however, much less conspicuous in Ibalia as it is discontinuous. It is most markedly evident at the tips of the male antennae.

The shape and size of the Rhinaria do not differ in the two sexes, but there is some difference in their numbers on the terminal segments of the antennae. Comparative counts have been made of the numbers present on the last seven segments with the following results:-

Nos. of Rhinaria present (on one side only) on last seven segments of the antennae.

Joint.	Female.	Male.
Terminal	75-80	45-50
2nd.	33	58
3rd.	29	55
4th.	25	60
5th.	17	35-45
6th.	15	45-50
7th.	13	35-45.

These figures indicate that, as regards the terminal joint, the female is more richly provided with Rhinaria than the male. The broadly rounded apex of this joint in the female has doubtless something to do with this. From the second joint backwards, however, the number of Rhinaria in the female diminish while those of the male keep fairly consistently high. These figures approximate as they are, appear to me to have a certain significance. In the female it is clear that the last three to four joints are more richly provided with sensory areas than the others. These are the joints with which an inspection of the Sirex egg-tunnel is made, and it is probable therefore that the olfactory function of these sensoria is to be correlated with the task of oviposition.

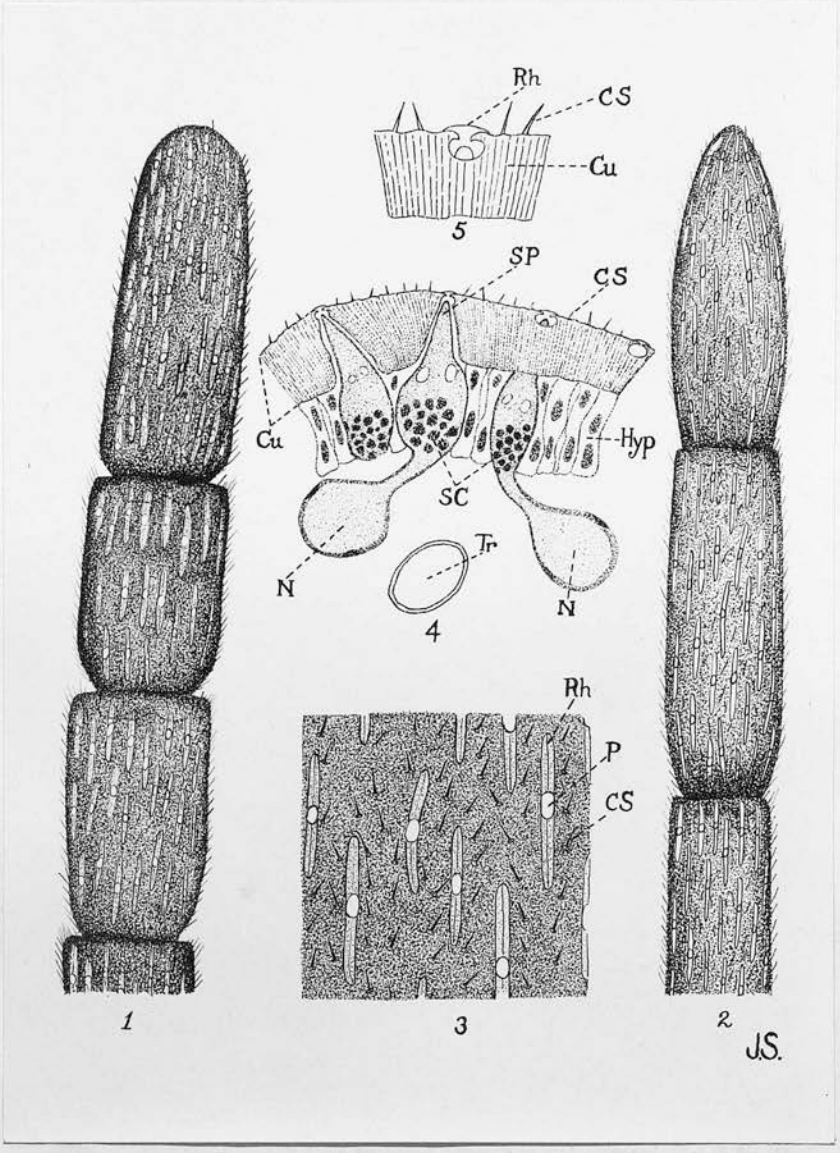
In the male, on the other hand, we find fair numbers of sensoria on all the joints, (the joints behind number seven are also well provided with them). The function of these

sensoria is probably sexual. This I conclude from observations made on two occasions of the male's actions prior to pairing. He spends considerable time stroking the antennae of the female with his own, and I have noted that for this purpose he uses the whole antennae and not just the terminal portion. It is during this operation that I believe the olfactory function of the antennae comes into play, although no doubt other occasions also arise when it is employed. (See pp 33-34).

Transverse sections made in the region of the terminal joints show a typical example of the placoidal type of sensilla (Text fig. 3). The cuticular region which is fairly thick bears large numbers of cuticular spines which do not originate from sensory cells. At regular intervals in the cuticular wall luminae appear, the openings into which are covered by a thin membrane, below which two cuticular processes project, covering as it were, the opening into the chamber. Into this pore canal the placoid sensilla runs, bearing at its core a nerve fibre ending in a multinucleate sensory cell (s.c. at the base; which in turn leads to an antennal nerve. The tissue lying in between each sensory area consists entirely of columnar hypodermal cells with large, ovoid nuclei (Text Fig.3)

Returning to the question of oviposition, it will be convenient to recapitulate briefly at this point, what I have already written (17 pp. 228-230), about the oviposition of S.cyaneus, so that the reader can grasp the full significance of the parasite's actions. The Sirex oviposition tunnel is circular, and enters the wood either vertically or obliquely, penetrating the wood to a depth of seventeen to twenty mm. In this tunnel a number of eggs varying from two to three up to six to seven are laid, and each egg is covered with a mucilaginous coat of a peculiar and constant pattern. The eggs, which are fusiform, lie in the tunnel, one above the other, and the tunnel is often so full that the topmost egg projects slightly beyond the wood surface.

It is into such a tunnel that the ovipositor is now inserted, and it is of interest to note at this point that its diameter is almost exactly one-quarter that of the oviposition tunnel, so that there is ample scope for free movement when once inserted. Once satisfied by inspection of the hole with the antennae that all is well, the insect then bends the abdomen



Text-Fig.3. Ibalia leucospoides Hochenw.
Studies of the antennae.

1. Terminal joints of the female antenna. x 37.
2. Terminal joints of the male antenna. x 37.
3. Enlarged portion of the antennal surface. x 168.
   C.S. .. Cuticular spine; P. .. Sensory Pore;
   Rh. ... Rhinarium.
4. Transverse section of the female antenna. x 168.
   Cu. .. Cuticle; Hyp. .. Hypodermis; C.S. .. Cuticular spine; S.P. .. Sensory Pore; S.C. .. Sense Cells; N. ... Nerve; Tr. ... Trachea.
5. Enlarged drawing of the sensory pore.
   Rh. .. Rhinarium; other letters as in Fig.5.

at right angles to the rest of her body, and releases the hypopygium, the apical portion of which is actually inserted into the tunnel as the ovipositor itself is lowered down. Sometimes the insect experiences considerable difficulty in finding the tunnel entrance with her ovipositor, and on several occasions I have observed her turn herself completely round and commence the inspection of the hole with her antennae all over again. This she may do more than once before she is satisfied, and the operation of inserting the ovipositor begins in earnest.

The duration of oviposition varies very greatly. Periods as short as ten minutes were recorded, but these would seem, and in some cases were definitely proved to be, failures. Much longer periods varying from twenty minutes up to one hour and forty-five minutes are more usual. The insect's activity is prodigious. One of the first females studied, remained on the same tree from 11.20 a.m. till 5 p.m. ovipositing practically all the time, and I have records of other cases of continuous activity during the best part of the day until a late hour. The absorption of the insect in her work is complete. Not only is she quite undisturbed by rapid movements in her vicinity but once she has really started, one can watch her movements with a hand lens and she remains quite undisturbed. In the laboratory, one can carry the log on which she is working, up and downstairs, without causing her the least alarm. One of the most striking examples of the insect's devotion to her work was afforded me one day at Tubney, when after watching a large specimen at work on a tree, from which she did not seem to be gaining much satisfaction, I placed her in a box, and carried her rapidly over to another tree some distance away, which I knew contained many fresh oviposition tunnels. On this tree I released her

and was delighted to see her get down to business at once, so much so, that in the course of two hours she parasitised the occupants of five Sirex oviposition tunnels, which I removed at once for later study.

The extreme docility of many of these Hymenopterous parasites and the great ease with which they can be handled has been remarked upon by more than one observer. Cushman (22), p. 232, writing on Calliephialtes refers to the great ease with which adult females could be handled and photographed while ovipositing. The material on which the insect was ovipositing was often carried from the insectary to a greenhouse, some twenty feet away, placed before the camera and photographed several times, without the insect being in any way disturbed or attempting to fly away.

The discovery that Ibalia reaches the host in the oviposition tunnel led amongst other things, to the further discovery that the insect herself was the best guide one could have to Sirex-infested trees, on which no visible sign of the insect's presence (i.e. exit holes) could be traced. Three such trees were located in Tubney by this means, one in the early part of October 1927, and two during the season of 1928.

From observationsmade during 1927 and 1928, it would appear that the parasite, once she has selected a tree keeps fairly closely to it, and does not wander farther afield. Two cases have been noted of adults which by reason of some peculiarity, in one case the insect had lost a leg, were easily recognised again, being found day after day working upon the same tree on which they were originally seen. The parasite was seen working at all heights, from the base of the tree to the top.

Reproductive Organs and Ovipositor. (Plate 3).

The structure of the reproductive organs and ovipositor in the Cynipoidae has been studied by a number of workers of whom the following may be mentioned:- Hartig in 1840, Alder (1) and Beijerinck in 1887, and Fruhauf (29) who recently published a very detailed account of these organs in two gall-making species, Biorhiza aptera Bosc; and Rhodites rosae L., In the parasitic species, James has described the reproductive system in Figites anthomyiarum Bouche.

If we examine the chitinous portions of the reproductive apparatus of a gall-making species such as Dryophanta, figured by Cameron (British Phytophagous Hymenoptera. Vol. 3) (Plate 3. Fig. 6.) the following main parts can be readily distinguished :- (a) The anal or anterior plates (A. P.) which are broad at the base and narrowed at their apices where they are fused together and enclose the terminal portion of the alimentary tract. (b) The Sheath or Posterior plates which lie below these and are somewhat similar in structure to the anal plates but remain free at their apices, and enclose the ovipositor when at rest. (c) The so-called Triangular Plate which lies at the base of the two pairs of plates, and to the apical portion of which are fused the "boring bristles" (Stechborsten) of the ovipositor, while one of its basal angles is joined to the anal plates, and the other to the sheath plates. (d) At the base of the sheath plates there is a semicylindrical piece of chitin through which the "boring bristles" pass, and where they join up with the basal ventral-valve of the ovipositor, in the grooves of which they run.

If, now, we take a species such as Figites, which has a longer ovipositor than Dryophanta, we find that in order

to accomodate within the abdomen the greater length of ovipositor, the basal portions have been, twisted round, as it were, through part of a circle, the basal attachment, (b) now lying above the apical portion of the ovipositor. (Plate 3. Fig. 7.). This development reaches its most extreme condition in the case of Ibalia, where, in order to bring the greater part of the ovipositor within the abdomen, the basal portion has now described a semicircle, while the anal and sheath plates have correspondingly increased considerably in length. (Plate 3. Fig. 1.).

The Ovipositor - When not in use, as already stated, the ovipositor is almost completely concealed within the body. The insect's first action, when oviposition is about to take place, is, as we have seen, to lower the elongate seventh abdominal sternites (Hypopygium), which fall downwards like a knife blade, and within the V-shaped cavity of which the ovipositor lies. If we trace the ovipositor backwards, we find that, entering the body at the base of the abdomen, it passes along the dorsum, curls sharply round the apical region, and returns along the ventral side to its point of origin. It is, in fact, coiled up within the abdomen like a watch spring. As it lies within the abdomen we find that it is completely enclosed in a thin membranous sack, the walls of which are highly muscular. This sack represents a portion of abdominal segment eight, and it acts in conjunction with the intersegmental membrane between segments seven and eight. Muscular contraction of the walls of the sack drives the ovipositor forwards, i.e. along the dorsum of the abdomen, and at the same time, downwards, i.e. down the Hypopygium, when the time comes for it to descend the tunnel of the Sirex. The action of the ovipositor can be easily studied in living specimens, by transmitted light.

In transverse section, the ovipositor shows three distinct portions. The first of these, which I have called the ventral valve, ("Schienenrinne" of the German authors,) is semicircular, and on its inner flat surface it bears two flanges which fit into corresponding grooves in the two 'boring bristles' or'bristle valves'. These three parts, thus fitted together, form a circular boring organ, down the central canal of which the egg channel passes. (Plate 3. Fig.3). The ends of the bristles are strongly toothed, and it is with these that a roughly circular hole is made in the integument of the host larva. (Plate. 3. Fig. 2.).

Reproductive Organs. - The reproductive organs in Ibalia correspond in their general structure to those of Rhodites rosae L., which were described in detail by Fruhauf in 1922; and those of Figites anthomyiarum Bouché., described by James in 1928. The ovaries are elongate and somewhat pear-shaped, and estimates of the total number of eggs which they contained were made in the case of two large females on August 6th, and September 6th, 1928. In the first of these I counted three hundred and twenty-five eggs in one ovary and two hundred and ninety in the other, six hundred and fifteen in all; and in the second, three hundred and two in one ovary, and three hundred and eighty-four in the other, six hundred and eighty-six in all. Thus the large females probably carry six hundred to seven hundred eggs as a general rule. The total number of eggs varies of course with their size. In Cynips and Biorhiza which have small eggs like those of Ibalia, Beijerinck found eight hundred eggs in the ovaries, and Fruhauf increases this number in the case of Biorhiza to one thousand. In species like Diplolepis however, where the eggs are large, their numbers, according to Kieffer, hardly reach one hundred. The eggs of Ibalia

are typical of the Cynipoidea being milky-white in colour and pedunculate. As they lie in the ovary, the sausage-shaped egg-body points towards the oviduct, which position is characteristic of all the Cynipoidea, and distinguishes them from some other parasitic Hymenoptera, such as Rhyssa, Ephialtes etc, in which the stalk of the egg is directed towards the oviduct, and is the first portion of the egg to pass into the ovipositor canal.

The prolongation of one end of the egg into an elongate stalk is directly connected with the problem of its passage down the ovipositor. In B.aptera, Fruhauf has shown (P. 691) in the following table, the relations between the length of the egg-body, the egg-stalk, and the ovipositor canal:-

B.aptera.

Length of Egg-body and Egg-stalk	470μ
" " Egg-body	94μ
" " Egg-stalk	376μ
" " Ovipositor Canal	625μ

The ratio between the length of the egg-body and the egg-stalk is therefore approximately 1 : 4, and between the total length of the egg, (Body + Stalk) and the ovipositor canal, approximately 4 : 5.

The same data computed in the case of Ibalia gave the following results:-

Ibalia leucospoides.

Length of Egg-body and Egg-stalk	1270μ
" " Egg-body	250μ
" " Egg-stalk	1020μ

This gives us a ratio of 1 : 4 between the length of the egg-stalk, and the egg-body, but when we measure the length of the ovipositor canal, we find in Ibalia that this is so much longer than in other Cynipoidea, the ratio between the total

length of the egg, and the length of the ovipositor canal, does not approach the figure 4 : 5. While the egg is passing down the ovipositor however, the stalk can, and probably does, stretch considerably, so that this ratio may be approached. Roughly speaking, then, we find that the length of the egg-stalk is proportionate to that of the ovipositor canal, and those species which have long ovipositors have longer egg-stalks than those with shorter ovipositors.

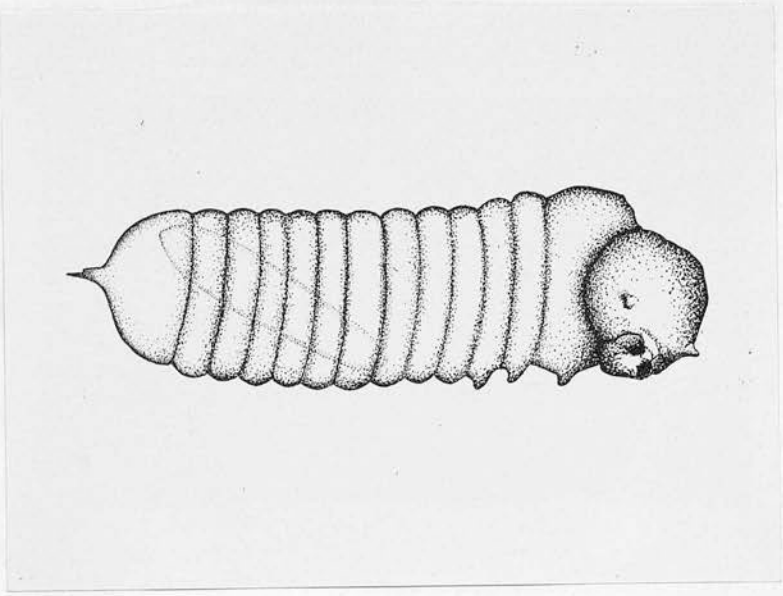
Let us now consider the measurements of the egg and ovipositor canal in cross section. In B.aptera, Fruhauf gives the maximum diameter of the egg-body as 120μ, the diameter of the stalk as 10.5μ, and the diameter of the ovipositor canal as 12μ. From these figures he calculates that the contents of the egg-body must be compressed into a space 1/10 - 1/12 of the normal, to enable them to pass through the fine canal of the ovipositor. In Ibalia, the diameter of the egg-body measures 40 - 50μ; of the stalk 6 - 8μ; and of the ovipositor canal 10μ. This means that the contents of the egg-body must be compressed into a space 1/6 - 1/8 of the normal. When oviposition takes place the liquid contents of the egg-body are forced back into the thickened free end of the egg-stalk, leaving the egg-body so reduced in size that it can easily pass down the ovipositor canal. Once it passes into the body of the host, the liquid contents flow down into it, the last portion of the egg-stalk being, according to Fruhauf's findings in B.aptera, assisted down the canal by the compressing action of powerful muscles at the base of the ovipositor. The oviducts are of moderate length and at their base they pass into two sack-like expansions of the vagina. These I have identified with the "Eileitertasche" which Fruhauf describes in Rhodites rosae, and into which he states the duct of the Receptaculum Seminis

opens. At the base of the oviducts, and opening into the "Eileitertasche" are two long, coiled glands, which are exactly similar in form and structure to the "Schlauch-formige Eileiterdrüsen" of Rhodites rosae. (Fruhauf, p. 712, Figs. 17 and 17b.). James figures similar glands to these in Figites anthomyiarum, and suggests that they may be the source of a potent secretion which the parasite injects into the host at egg-laying, thereby rendering it quiescent for a certain period. This brings us to the question as to whether these parasites paralyse their prey at the time of egg laying. Myers has shown that Sirex larvae parasitised by Rhyssa are in all probability paralysed previous to oviposition. My own studies of this parasite confirm this, as I have seen similar puncture marks in the larval integument as Dr. Myers describes.

An attempt has also been made to throw some light on the question in Ibalia, and a study of the different rate of heart beat in parasitised and non-parasitised larvae was made. (Cf. Myers, Bull. Ent. Res. 1928. p. 321). The results obtained were however, quite inconclusive, and all that one can say at present, is that the Sirex larva parasitised by Ibalia does not show that almost complete absence of movement which the larvae parasitised by Rhyssa do. Elsewhere in this paper I have cited a case of a Sirex larva which was first parasitised by Ibalia, and then parasitised by Rhyssa. This larva certainly showed a very much slower heart beat than the normal, and I have noted similar cases at other times. The differences in heart beat are not however sufficiently constant to enable one to draw a satisfactory conclusion.

The Egg Stage.

The first discovery of the Ibalia egg within the body of the Sirex larva was made by myself in August 1927, when I found the one shown in text figure 4.



Text-Fig.4. Sirex larva parasitised by Ibalia, found in larch, Tubney Wood, August, 1928. x 55.

In this case, as the figure shows, the egg was lying transversely towards the tail end of the larva, but subsequent observations have shown that it may be laid in any part of the larva's body. Parasitised larvae, mounted fresh in "Liquide de Faure", show the egg-stalk quite clearly lying in a crumpled condition within the body of the host. The function of the egg-stalk in effecting the passage of the egg contents down the ovipositor canal, has already been discussed, but other functions have also been ascribed to it, both in the Cynipoidea, and other families in which stalked eggs occur. Adler (1) and Cameron (15) both considered that the stalk served a respiratory function in some gallicolous Cynipoids, the latter observing that its length varies in proportion to the distance the eggs were laid from the source of oxygen supply in the plant. Riley, quoted by Sharp, observed that in the Cynipoids, Callirhytes clavula and Biorhiza nigra

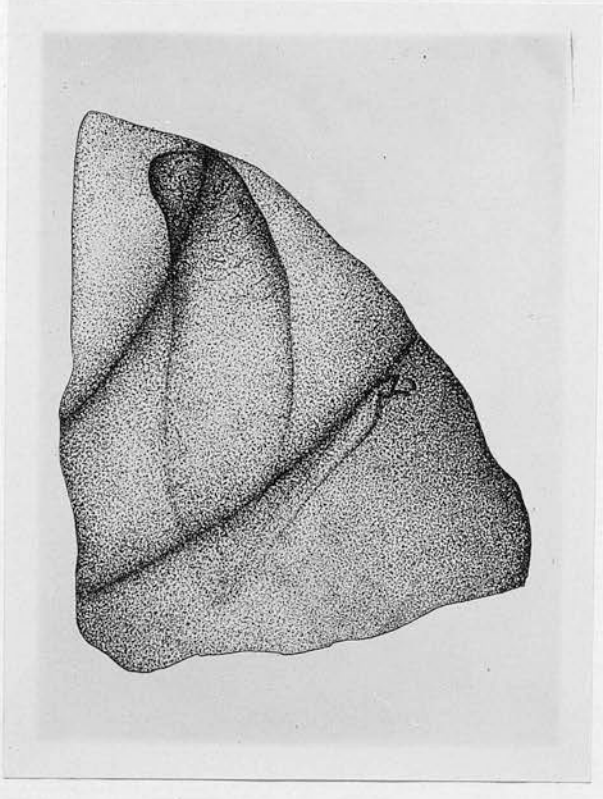
the egg-stalk alone is inserted into the plant to start with, the egg fluids collecting at the posterior end of the egg:- "The fluids are then gradually absorbed from this exposed position into the inserted portion of the egg, and by the time the leaves have formed ... the egg contents are all contained within the leaf tissue. In the Chalcids, Imms (35) has shown that the eggs of Blastothrix britannica, a parasite of Lecanium capreae, possess a peduncle which protrudes through the body wall of the host, the tip of which disappears, and thus puts the cavity of the chorion into communication with the outside air. Timberlake has also shown in Microterys, a parasite of Coccus hesperidum, that the egg is formed by two bodies connected by a hollow stalk. This stalk, together with the smaller body, projects through the body wall of the host and apparently serves for the respiration of the egg and the young larva in the early stages. Howard and Fiske also state that the eggs of Schedius kuvanae, a Chalcid parasite of the Gipsy moth protrude through the chorion of the eggs of the host in which they are deposited. In Charips victrix, the Cynipoid hyperparasite, Haviland (33) showed that the peduncle of the egg was so reduced, that its function, whether respiratory or otherwise, has been lost.

In Ibalia, the stalk of the egg appears in some cases I have examined, to be in direct communication with the outside, and in one larva I have even seen it passing outside the body. Text Figure 5 b. shows a case in which the egg-stalk leads apparently directly to the circular hole made by the ovipositor in the larval integument. I entertain some doubt however, of the egg-stalk serving as a breathing organ. In the first place, the crumpled condition in which it lies in the larva's body renders this unlikely; and secondly, the end of the stalk being thickened to receive the fluid egg contents, it would have to be broken off so as to put the egg contents in direct communication with the outside air.

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a.



b.

Text-Fig.5. (a) Sirex larva parasitised by Ibalia, showing the remains of the Sirex egg from which the larva has only recently hatched.

(b) Enlarged portion of the same larva showing the Ibalia egg and its stalk. Note the circular hole in the larval integument where the ovipositor was inserted. x 110.

In the majority of larvae examined only one egg was found, but quite a number of cases have been recorded by Dr. Myers and myself in which two eggs occurred. These observations have been confirmed since by the discovery of two first-stage larvae in the same host, and during the past year cases have occurred where three or more parasite larvae were found in the host. This question of super-numerary larvae I have dealt with in more detail elsewhere (p.), but here it raises one interesting point. The female, prior to oviposition, inspects the egg tunnel with her antennae, and from what we have already noted of the structure of these, it would appear that the terminal joints are the seat of the sensory pits, presumably olfactory, which guide the insect to her victims. Does the female then, out of sheer prodigality, lay several eggs in the same larva, or is the same larva parasitised by different females, or by the same female at different times? Both the last alternatives are possible, as in some hosts the Ibalia larvae found were at different stages, indicating that oviposition might have taken place on more than one occasion. On the other hand we know that in the case of Rhyssa, the same female will lay two to three eggs on the larva's body at one and the same time, and I have also observed that Ibalia, once she has used an oviposition tunnel, frequently crosses and recrosses it seeking for other tunnels in which to oviposit. It would seem therefore, that she recognises those tunnels which she has already visited, and it is possible that she leaves some odour behind her by which other females are also furnished with this information. If this were so, the discovery of several eggs in one larva points to the activity of the female laying several at the same time as Rhyssa sometimes does.

The eggs of the parasite which are laid earliest, contain advanced embryos in three to four weeks. These are still covered by the egg shell and underneath that the embryonic membrane. Thus on September 29th,* a number of Sirex larvae were dissected out from a tunnel in which Ibalia had oviposited about a month before. These all showed the mature embryo lying in its egg shell. Again on October 27th, four Sirex larvae placed as shown in text figure 6, were taken from a tunnel in which Ibalia had oviposited on August 31st, a period of eight weeks and two days. Advanced embryos of Ibalia were seen in three out of the four. On the other hand, on October 29th, a tunnel was opened, which Ibalia had visited seventeen days before. The Sirex larva was found still unhatched, and inside it an Ibalia egg. Similar observations made on November 1st, showed another Ibalia egg lying in a Sirex larva, after twenty days had elapsed since the parasite oviposited. Finally, on December 12th, 1927, another Ibalia egg was found in a Sirex larva, two months after the last adult was seen. As it lies in the body of the host, the shape of the egg does not differ materially from what it was when lying in the oviduct. Comparative measurements of the host and the parasite's egg-body are as follows;-

	Length.	Breadth.
1st stage Sirex larva.	1.6 mm.	0.38 mm.
Sirex egg.	1.48 mm.	0.53 mm.
Ibalia egg-body.	0.32 mm.	0.08 mm.

Miss Jackson (38) and other writers, have shown to what enormous proportions the eggs of many of the endoparasitic Hymenoptera may attain in the body of the host after oviposition. Miss Jackson quotes instances of this from Wardle's work (1914) on the Stephanid, Hypamblis, Henneguy (1892) on the Chalcid Smicra (Chalcis) and Marchal (1906) on the Proctotrypid

* 1927.

Platygaster. In her own work on D.rutilus a Braconid parasite of the Coleopteron, Sitona lineata L., she states that the cubic contents of the egg during development increased over one thousand-two-hundred times. A figure approaching this is also quoted by Oglobin in his work on another species of Dinocampus (D.coccinellae) a parasite of Coccinellid beetleswhere the egg was found to enlarge one thousand times.

The ovarian egg in Ibalia varies in length from 0.23 to 0.4 mm. and 0.04 to 0.05 mm. in width. This measurement is not easy to obtain as it is often difficult to define exactly where the egg-body ends, and the stalk begins and the above figures represent the mean of a number of measurements. Eggs measured just after oviposition in the body of the host do not differ in length (0.25 to 0.32), but increase very slightly (0.08 mm) in width. As the embryo develops, the length does not increase much at first (0.38) but there is a marked expansion (2-4 times) in width. The advanced embryo's which are found in the Sirex larva from October onwards show a marked increase in both dimensions as the following figures will show.

Advanced Embryos.

Length. mm.	Breadth. mm.
0.82	0.16
1.7	0.34
0.67	0.12
0.84	0.14
0.9	0.2

These figures showing an increase varying from three to eight times in both dimensions, indicate that the increase in cubic capacity of the egg is considerable.

One of the most interesting results which have been obtained from the present studies has been the discovery of the oviposition habit of Ibalia. The insect has now been observed for two seasons both in the field and also in the laboratory, and so far she has never been seen to attempt oviposition in any place other than the Sirex egg tunnel. This definitely rules out any possibility that the insect is also a parasite of wood boring Coleoptera, as some authors have previously considered possible. In the south of England the oviposition period may be taken as extending from the latter half of August to mid-October, that is the same period as S.cyaneus is also in flight, and probably some S.gigas as well.

The question now arises as to whether or not Ibalia is a parasite of both these species in Britain? So far, in my own work, at Tubney and elsewhere, I have only been able to connect the insect with S.cyaneus, and Crawshay's specimens in the British Museum, although labelled "ex S.gigas." do not help us much, as we know that gigas and cyaneus often occur together in the same log, and we have no proof that cyaneus was absent in this case. Further, while I have on several occasions seen gigas busily ovipositing in larch in the woodyard at Bagley wood near Oxford, I have never yet found Ibalia in that neighbourhood, and indeed, the time of the year (June, July,) is rather early, in my experience, to find the insect in flight. On the other hand, it is difficult to suggest any good reason why Ibalia should not attack gigas as well as cyaneus, but in the absence of direct evidence, the question must, for the moment remain unanswered.* During the oviposition period, the Sirex egg tunnels may contain freshly laid eggs, larvae in the egg shell ready to hatch, and 1st stage larvae either

* See Appendix 4.

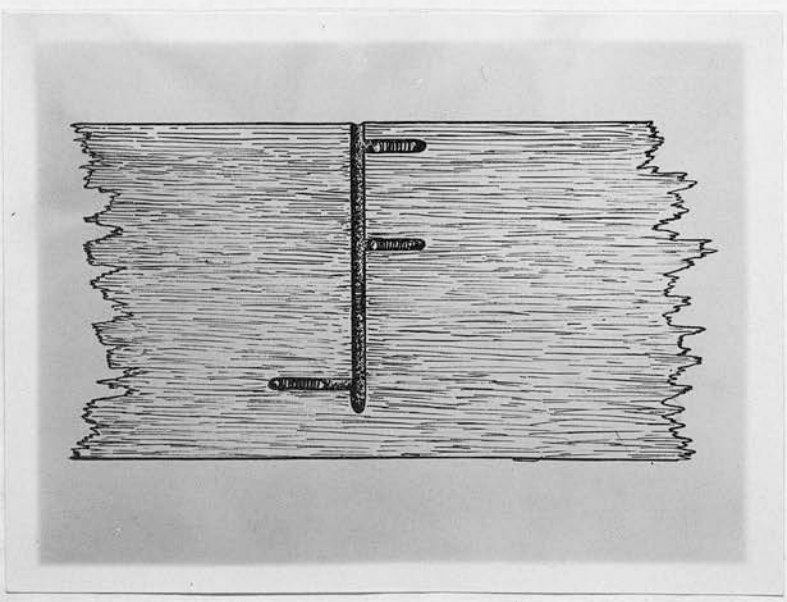
partially or completely freed from the egg shell. Ibalia will oviposit in all these stages (Plate 4. Fig. 2, Plate 6, Fig. 2.)

It has been possible to collect a fair amount of data on this question, by using the following methods. In the first stages of the work, the oviposition tunnels were removed immediately after the insect had finished her work, and taken back to the laboratory where they were dissected out and their contents mounted for study. By this method we were able to collect a good deal of information as to the state of affairs during the months of September and October, 1927. It soon became necessary, however, to mark oviposition holes which could be left 'in situ' for varying periods, and removed from time to time as occasion demanded. For this purpose strong paper labels were pinned close to the oviposition hole while the parasite was still at work, a process to which she never offered any objection, and a long series of marked holes has been obtained. From these, valuable data have been collected regarding the numbers of Sirex parasitised in any one egg tunnel, the length of the egg-stage, and percentage of parasitism.

Observations on the numbers of Sirex parasitised in each egg tunnel.

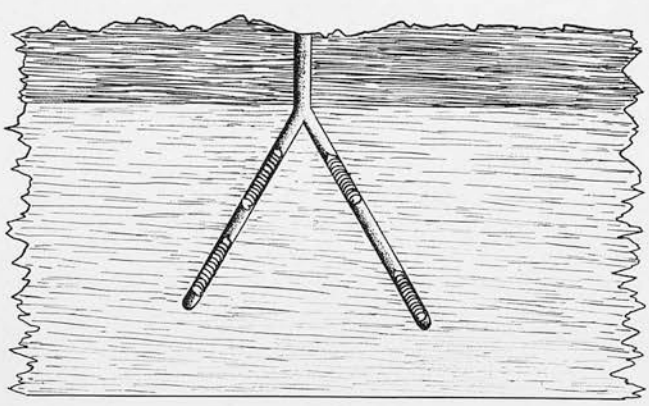
All the evidence which I have obtained up to the present shows that Ibalia always parasitises the Sirex in the egg tunnel, and never after the larva has begun to bore away from it. Indeed this must necessarily be so, since during the flight period of the adults, very few, if any, first-stage woodwasp larvae have begun to bore away from the egg tunnel. In one case I have also been able to dissect out the ovipositor of Ibalia from a Sirex egg tunnel, which had two larval tunnels leading away from it. The ovipositor was found

lying in the centre of the tunnel surrounded with boring dust and on careful examination of the side tunnels I could find no sign of the frass having been disturbed by the ovipositor of the parasite. This is the only time I have ever found the ovipositor of the parasite left sticking in the tunnel, and is in marked contrast to Rhyssa whose ovipositor is continually found stuck fast in the wood. It is evidently a rare occurrence for Ibalia to lose her life while ovipositing. The length of the ovipositor corresponds fairly closely with the depth of the Sirex egg-tunnel, which can always be searched right to the bottom. A normal egg-tunnel always contains several eggs and a number of observations were made to determine the numbers of larvae which were parasitised in the same tunnel. One of the first tunnels examined was one which had been visited by Ibalia on August 31st, 1927. The tunnel was dissected out on October 27th, 1927, and contained four Sirex larvae all of which were parasitised. Text Fig. 6, shows the position of these larvae at the time the tunnel was



Text-Fig.6. Sirex egg-tunnel containing four larvae, three of which were parasitised by Ibalia.

dissected. On March 23rd, 1928 a tunnel visited by Ibalia on August 30th, 1927, was examined. Three Sirex larvae were found in this, the larvae having begun their longitudinal tunnels which had attained a length of 1. and 1.5 mm. respectively. All three larvae were parasitised. On October 6th, 1928, I took three Sirex egg-tunnels from the cages at 18 Museum Road. The first of these contained three larvae, all parasitised and the other two, four larvae apiece, all of which were also parasitised. Some of these larvae were still lying in the egg-tunnel, but one of the larvae lying at the bottom of the tunnel had begun boring and was almost twice the size of the others. One very interesting observation was made at this time, of a single hole in the bark made by the woodwasp communicating with two egg-tunnels lying side by side in the wood. Both these tunnels contained larvae all of which were parasitised.(Text. Fig. 7.)



Text-Fig.7. Abnormal Sirex egg-tunnels in larch. The larvae in both tunnels were parasitised by Ibalia.

On November 27th, 1928, I dissected a Sirex egg-tunnel visited by Ibalia on September 19th, 1928. This tunnel contained five larvae ranging from two to five mm. in length. All the larvae were parasitised, one larvae containg two parasites. Two other tunnels of September 18th, and October 13th, 1928 were also examined at the same time and contained a full quota of parasitised larvae. Tunnels containing both parasitised and unparasitised larvae are, of course, equally common. One tunnel, marked on September 13th, 1928, was examined on January 15th, 1929, and four Sirex larvae were found in it, of which three were parasitised. The position of the parasitised larvae showed that the parasite had attacked the two uppermost larvae in the tunnel, missed the third and attacked the lowest. While all the parasitised larvae had begun their tunnels, the non-parasitised larva was still lying in the egg-tunnel.

The Trophic Membrane or Trophamnion.

The trophic membrane or trophamnion is the name given to the single layer of cells lying just below the chorion and surrounding the embryo in the eggs of many endoparasitic Hymenoptera. It has been found in representatives of all the parasitic groups and notable contributions to the study of its origin and development have been made by Silvestri in Litomastix, Henneguy in Chalcis (Smicra) clavipes and Marchal in the Platygasters. Up to the present time this layer of cells has been considered by most writers as playing an important part in the nutrition of the embryo (Imms, Text-book, p. 541). Further light has been shed on its functions however, by the recent work of Miss Dorothy Jackson, who in a recent paper on the Biology of Dinocampus rutilus Nees already cited on p. , has shown that this nutritive function may continue beyond the embryonic stage and affect the welfare

of the later instars.

The trophamnion is very conspicuous in Ibalia, and in the light of such observations as I have been able to make on it, a brief review of the work of Miss Jackson and her predecessors may be given here. Previous to Miss Jackson's work, most writers had found the embryonic membrane completely enveloping the developing embryo up to the time of eclosion. Subsequent to this, the cells of the membrane became dissociated and scattered throughout the body of the host. Miss Jackson quotes Timberlake (1911) Haviland (1926), Speyer (1925), Kauffmann (1923), Oglobin (1913), Seitner and Nötzel (1925) and Menzel (1926) as describing the process of cell dissociation in various parasitic families.

In her own work, Miss Jackson discusses the origin of the trophamnion with reference to the work of Henneguy, Marchal, Grandiori and Spencer but does not deal with this aspect of the question in Dinocampus rutilus. Her work begins at the time when the membrane is fully formed round the embryo, and the significance of her results lies rather in its subsequent function after dissociation of the cells has taken place. In Dinocampus, Miss Jackson finds that as the embryo develops, the cells of the trophamnion gradually increase in size, until after the larva ruptures the chorion and escapes into the abdomen of the host, when they become dissociated from one another and disperse throughout the body cavity of the beetle (Sitona). "At this time they assume a globular form, and become of an opaque white colour, due to the presence of fatty matter which they absorb from the body fluid of the host. As the larva grows, the cells increase in size and in their later stages they consist almost entirely of globules of a fatty nature. The cell membrane in this case becomes very much stretched and ruptures with the least pressure the fatty

contents being discharged into the body cavity of the beetle. When the Braconid larva is young as many as six hundred to seven hundred of these dissociated cells may be found in the abdomen of the host, but as the larva grows they diminish in numbers."

These cells with their ingested fatty contents constitute, according to Miss Jackson, the principal food of the larva in its later stages, and she records finding their remains in numbers within the mid-gut of the full grown larva.

This nutritive function of the dissociated cells, Miss Jackson points out, has been largely overlooked by previous writers; many of whom while recording the presence of opaque white globules in the body fluid of parasitised insects, have usually mistaken these for "disorganised fat body" of the host.

In some cases, as for example, Apanteles glomeratus, where according to Grandiori, the embryonic membrane continues to surround the larva throughout its life, Miss Jackson admits that the persistence of these cells may be of no value to the larva; but in D.rutilus the curious development and nature of these cells points in her opinion to the certainty, that they fulfil the very important and vital function of supplying the larva with food at a critical period of its life.

The Trophamnion in Ibalia. (Plate 6. Fig. 1. Plate 10. Figs. 6 and 7.)

Haviland (33) (p. 469) discussing the occurrence of a trophamnion in the Cynipoidea, states that it is absent in the Eucoilinae, and that its occurrence in Charips is the first record of its appearance in the Cynipoidea. In Ibalia, the first signs of its presence were found during the Autumn of 1928 when young Sirex larvae were being dissected

to obtain data on the precentage of parasitism, and to collect specimens of first-stage larvae of the parasite. From September onwards advanced embryos were found lying in the body-cavity of the host closely swathed in the trophamnion. I have obtained no data so far on the development of this membrane in Ibalia. The earliest stage which I have observed occurred in an egg of the parasite which contained an embryo in an early stage of development. Through the transparent chorion it was quite possible to make out the embryonic membrane, the large nuclei of the cells being clearly visible. At this stage, the cells are closely knit together and somewhat polygonal in shape, while a clear space separates the developing embryo from the trophamnion layer. My dissections of Sirex larvae have been carried out at regular periods from October, 1928 to the time of writing (September 1929) and a large number of the parasites found have been advanced embryos surrounded by the trophamnion. These are, undoubtedly, the progeny of females which laid eggs in August and September, 1928, and the length of time which elapses before the larva finally leaves the shelter of the trophamnion apparently varies from two to three months to almost a year. During the winter months these advanced embryos are found lying lengthwise, completely enclosed within the trophamnion. By this time, the embryo, which had previously shown signs of a rapid increase in size, has attained vast proportions. It is now stretched out to its fullest extent and on p.55 I have given some figures of the size which it attains at this stage.

This tremendous increase in size is a measure of the extreme elasticity of the cell membranes of the trophamnion cells. After the larva has left the trophamnion, the cells contract, and exhibit in most cases the polygonal arrangement of the earlier stages. At this advanced stage of embryonic development, the chorion, which was easily discernible in the earlier stages, has become so stretched and attenuated as to be very hard

to distinguish. Miss Jackson describes the eclosion of a larva of Dinocampus in which the act was accompanied by a violent twisting of the larva's body within the membrane. She figures (Plate 3. Fig. 1.) such a larva, whose body is bent in a semicircle within the trophamnion, from the lower side of which the chorion has become separated and appears as a fine transparent membrane. This method of eclosion I have never met with in Ibalia, the larva making its way out of the trophamnion without any marked twisting of its body. (Plate 10. Fig. 6.) The cells of the trophamnion vary greatly in size and shape. Some of the larger cells varied from 0·12 x 0·12 mm. to 0·08 x 0·12 mm., while the smaller cells measured 0·03 x 0·03 mm. to 0·03 x 0·02 mm. These measurements were taken from Trophamnia which the larva had vacated. The nuclei of the cells are very large, as can be appreciated by the following measurements of typical cells.

(1)	Cell Measurement.	Nucleus.
	·12 x ·07 mm.	·09 x ·05 mm.
	·08 x ·08	·05 x ·05
	·09 x ·07	·07 x ·04
	·08 x ·07	·05 x ·04
	·04 x ·04	·03 x ·03

During the winter months (1928-29) a number of larvae were found emerging from the trophamnion. This is always effected head first, and I have never found a larva which emerged from the trophamnion and left it broken at both ends, as Miss Jackson figures in Dinocampus. The trophamnion is left behind as a complete sack with a V-shaped opening at one end. The empty trophamnia are easily found on dissection of the host larva, and in cases where more than one parasite is present, give one a clue to the number of eggs laid in the first instance, even though some of the embryos have perished

We may now proceed to consider, in the light of Miss Jackson's work on Dinocampus, what changes are undergone by the trophamnion in Ibalia. Taking the simplest possible case first; i.e. where only one parasite larva is present in the body cavity, and this larva in its first stage. Quite a number of these have been found, and the trophamnion has in every case been found lying free, with its cellular structure clearly defined, and showing no sign of dissociation of any kind. The cells do not begin to separate from one another, and there is no marked cell division, Henneguy's discovery in Chalcis (Smicra) clavipes that the trophamnion cells disperse whilst the larva is still within, has not been duplicated in the case of Ibalia.

Clearly, then, one has to look further on in the larval development, and second stage larvae were sought for. These were fairly easily found as a number of Sirex larvae dissected about this time (January-March, 1929) contained both the first- and second-stage larva of the parasite living together, both apparently in a healthy condition. I quite expected in these cases to observe the dissociation of one trophamnion, if it occurred at all, but was disappointed in every case. The trophamnion from which the second-stage larva had come was quite unchanged in appearance from those previously studied. The results of these studies indicated that up to the second larval stage at any rate there is no marked change in the trophamnion and observations were then extended to the third stage larva.

It is, as I shall show later, towards the latter end of this stage that the host larva is destroyed and the parasite larva takes its place in the tunnel. To get the best results in this case it was again desirable to find a host larva which should contain only one parasite, and this one in the required

stage. This took a little time, but finally on March 2nd, 1929, I found the specimen I was seeking. The host larva, about 6 mm. long, was plump and healthy in appearance, and but for its characteristic place in the superficial layers of the wood with its head pointing outwards; it would have been impossible to foretell the presence of a parasite larva inside. On opening the body the internal organs also looked normal enough, the mass of fat body seemingly neither more nor less than normally seen in a healthy larva of the same size. At first the parasite larva was completely concealed by the masses of fat body, but very soon its pale glistening form emerged from the fat tissue in a mass of which its head was deeply imbedded. This larva was found, as others had been before, with the exuvium of the second-stage slowly peeling off the body. Having ascertained that only one parasite was present I proceeded to search for the trophamnion or its remains.

This I found, after some searching, buried beneath some fat tissue and on examination of it could find no sign of any change in its appearance from others which I had already seen. I have been quite unable therefore to find any change taking place in the trophamnion up to the third larval stage of the parasite. This larva at the moment of writing (March, 1929) in the third-stage would probably have emerged from its host in the course of the summer and it may be that the cells of the trophamnion would have dispersed during this period. This, however, does not seem to me very likely, and in any case one would imagine that if these cells exercised a nutritive function in the case of Ibalia, signs of activity would have appeared before the third stage, when the larva is actively growing and needs all the assistance it can get. I conclude, therefore, that in Ibalia the trophamnion cells do not play the part in the nutrition of the larva which Miss Jackson has

described in Dinocampus and I imagine that they either degenerate and disppear, just before the final destruction of the host larva, or that they are devoured by the parasite together with the remains of its host.

The Larval Stages.

First stage Larva. (Plate 10). On emerging from the trophamnion the first-stage larva is pale, milky-white in colour and semi-transparent. Its length varies from 0.6 to 2 mm. The head which is markedly flattened dorso-ventrally, is followed by thirteen body segments the last of which is produced into a prominent tail, a characteristic feature of the first-stage which becomes progressively shorter in the later stages, until in the full grown larva only the merest trace of its former existence remains.

This caudal appendage, which is a common feature in many primary parasite larvae, has been for many years the subject of much discussion, and divergent views have been held as to its function. Seurat, in 1899, described the caudate larva of Mesochorus vittator Zett. and that of another undetermined Encyrtid, of which latter he writes that the anal segment "se prolonge dorsalement par rapport a l'anus en un appendice conique qui rappelle la queue des Ichneumonides." (1899, p. 90). The latter structure is now known as the anal vesicle and is to be distinguished from the tail proper. Both these structures he regarded as locomotory in function, aiding the larva to move about inside the host. Half a century earlier (1844) Ratzeburg had found a similar structure to the latter in the Ichneumonid Anomalon circumflexum Grav. To this he attributed a respiratory rôle. In 1909 Weissenberg (Sitz. Gesell. Natur. Freunde, No.1.) put forward the theory that the tail appendage is used to some extent for storing the waste products of metabolism. Timberlake (53) discussing the tail appendage of the primary

larva of Limnerium validum Cr. states that while he found one fine tracheal branch running down into it, this was not important enough to cause one to regard the tail as a tracheal gill. "It may, however," he writes, "be considered a blood gill. There is nothing in its structure to contradict this, as it is filled with blood, and lined with hypodermal cells."

Muesebeck (1918) (42), writing of the primary larva of Meteorus versicolor is quite satisfied as to the locomotory function of the tail. His view is that, "the caudal appendage is merely a fleshy extension obviously to aid the larva in getting out of the egg, and later in locomotion. It does not have the significance of the anal vesicle in Apanteles lacteicolor, for in M. versicolor there is no need for a special respiratory device, the tracheal system being already well developed in the first-stage larva."

More recently still, Tothill (1922) (57), in a detailed paper on the parasites of the Fall Webworm (Hyphantria cunea Drury) deals with the same question (p. 71). He rejects the hypothesis that the tail has a locomotory function, and also that it may be a storage place for solid waste matter; the latter for the simple reason that the collectors of those substances, namely, the fat body and malphigian tubules do not enter the appendage.

He finds, in the case of the species Campoplex pilosulus Prov., that the internal structure of the tail is such as to warrant the conclusion that it is a highly specialized type of tracheal gill. This he describes and figures in some detail (pp. 71 and 74), Figs. 52, 53, 54, 56 and 57).

The caudate larval type is characteristic of all the primary larvae of the parasitic Cynipoidea which have been described up to date. Specially remarkable in this respect is the larva of Eucoila Keilini Kieff. which is described by Keilin and Pluvinel as having "le segment anal le plus

posterieur se prolonge pour donner une queue aussi longue que le reste du corps." James (37) also describes other primary Figitine and Eucoiline larvae which have the tail well developed. In Ibalia the tail is not nearly so long, nor does it have the spiny projections at its base, which are described by Keilin and Pluvinel as being present in Eucoila Keilini.

As none of these primary larvae show any signs of an organised tracheal system the tail cannot be regarded as a tracheal gill but that it probably serves as a blood gill is quite feasible in Ibalia at any rate, as it is always fully distended with blood. It also possesses a well marked layer of hypodermal cells with conspicuous oval-shaped nuclei. While observing larvae emerging from the trophamnion it has also occurred to me that the tail may assist at this time, and subsequently, for movement. Keilin and Pluvinel also describe the tail of the primary larva of Eucoila Keilini as having at its base "un appendice épineux qui fait saillie sur la face ventrale, et cette region semble recouverte de petites écailles chitineuses." May these not be further evidence of a locomotory function?

In lateral view, the general outline of the larva's body is slightly sinuate, as the head is usually depressed, the body curved, and the tail elevated. In surface view, the head appears distinctly broader than long, markedly constricted and truncate in front, rather less constricted behind, with the sides broadly rounded (Plate 10. fig. 3). The labial region forms a broad arch over the mouth cavity, extending well over the mandibles. The mandibles, which are very conspicuous, are best seen from the ventral side. They are remarkable both for their size and falcate form, which is much more accentuated in the first-stage than in either of the two following, in both of which the simple form is retained. Only in the final stage

do the mandibles become dentate. The condyle of each mandible articulates in a deep socket situated at one end of a stout transverse bar of chitin in the labial region. The mandibular muscles are attached to the lateral chitinous walls of the head. The surface of the head is smooth and shining and devoid of hairs or spines of any sort. I have been unable to detect any signs of antennae, but the labium bears a few circular sensoria the location of which is shown in Plate 10, figure 3. The body segments, thirteen in number, taper rapidly from the fifth segment onwards. The width of the body varies from .19 mm. in the thoracic region, .15 mm. in the centre to .06 mm. at the tail Segments one to twelve each carry a pair of long pseudopodia, which are fleshy, finger-like processes, sometimes rounded, and sometimes slightly pointed at the tips (Plate 10. Figs 1 and 2). They bear no spines of any kind. These processes constitute the most distinctive feature of the larva, and are remarkable for their length, which varies from .036 to .045 mm. or from 1/5 to 1/4 of the body width,

The occurrence of this polypodeiform larval type in the first-stage is a feature which distinguishes this larva from all other known Cynipoid larval types. Its significance I have discussed elsewhere in this paper (pp.94-96)

Internal Structure. (Plate 10. Figs 4 and 5) The greater portion of the internal anatomy of the first-stage larva is clearly visible in unstained specimens through the transparent cuticle. Preliminary studies were made of specimens mounted in salt solution and dilute glycerine, after which whole mounts were prepared, stained either with Dalafield's haematoxylin and eosin or borax carmine. The alimentary tract is much the most conspicuous of the internal structures. The fore-gut is short and has a narrow lumen, expanding in the mesothoracic region into the large sac-like mid-gut which occupies the remaining four-fifths of the body length and about two-thirds of its breadth. The epithelium of the mid-gut the cells of which stain deeply in

either haematoxylin or borax carmine, is composed of polyhedral cells, with large conspicuous circular nuclie. The mid-gut usually appears much distended and full of fluid matter. At the end of the mid-gut there is a slight constriction at the point of origin of the malphigian tubules. This is followed immediately by a marked expansion of the lumen of the hind-gut just before the anal opening is reached. The anus is dorsally placed, but has no conspicuous chitinous ring round it, such as Haviland described in the primary larva of Charips. The salivary glands are the next most prominent organs which catch the eye. Their common duct opens into the pharynx in the labial region. The glands themselves are very long almost two-thirds of the body in length. Their cells are large and the nuclei round or oval shaped. The malphigian tubules of which there are two, are much shorter and narrower than the salivary glands, they do not exceed one-third of the body in length. They are lined with brick-shaped cells with prominent nuclei and the central lumen is narrow and straight.

Nerve Cord. At this stage of larval development, the nerve cord appears as a more or less solid chain of ganglia which extend almost to the tail end of the body. The supra- and suboesophageal ganglia are but indifferently differentiated and their commissures are indistinguishable. The remaining ganglia, while showing signs of separation from one another are still closely approximated, and longitudinal connectives are absent.

In the second- and third-stage larvae the appearance of the nerve cord alters considerably, and I have found this of great assistance in separating individuals of the respective stages from one another. Before leaving the subject of the nerve cord it is interesting to note that Haviland describes the nerve cord of the second-stage larva of Charips as a broad unconstricted bar The second-stage larva of Ibalia shows a much more advanced development of the nerve cord.

Respiration is entirely cutaneous in this stage larvae, there being no sign of any organised tracheal system. I have already

referred to the possible functioning of the caudal appendage in this respect.

Second-Stage Larva. (Plate II.)

The second-stage larva measures on an average 2.5 to 3 mm. long by .7 to .8 mm. broad. It is very pale milky white in colour and glistening, the latter being due to the mucous with which the body is covered. The general form of the larva is greatly changed from that of the previous stage instar. The head, though still markedly truncate in front, has lost its flattened and elongate shape and become cylindrical, while the body, from being rather dorso-ventrally flattened has assumed a cylindrical shape, with the caudal appendage, very much reduced in length. Finally, but by no means the least important change, the pseudopodia of the previous instar have now completely disappeared. The external surface of the body is quite devoid of spines or bristles of any kind, and the cuticular covering of the head is smooth and shining, in marked contrast to the body segments which have their cuticular surface completely traversed by minute transverse furrows. The effect of this is to give the body of the larva a roughened appearance which is evident to the naked eye. In this stage and the one which follows it we witness a gradual transition from the polypodeiform to the vermiform type. It is the body segments which acquire the true vermiform shape quickest, the head not assuming its ultimate shape until the fourth instar is reached.

Internal Structure. The mandibles, as in the preceding instar are overhung by the labrum which is again raised in a prominent arch. Though they retain their falcate shape the tips have now lost the marked curves which characterised the mandibles of the first-stage larva. In whole mounts of the larva, the details of the articulation of the mandibles with the Tentorium can be easily made out, as well as the muscular attachments to

the lateral walls of the head. These points are illustrated in Plate II Fig. 5.

Alimentary Tract - This can also be seen to much better advantage in this stage. The foregut as seen from the ventral surface is broad and flattened for the first part of its course, but becomes suddenly rather constricted just before the junction with the mid-gut is reached. There is also a very clearly marked invagination of the foregut into the lumen of the mid-gut which it enters on a papilla. As in the preceding instar, the mid-gut occupies about four-fifths of the body length and two-thirds of its width. In most cases it appears fully distended with liquid food material and the polyhedral cells of its epithelium are of the same type; but with somewhat more prominent nuclei; than in the first-~~instar~~ stage larva.

The constriction beyween the mid- and hind-gut is again very marked in this ~~instar~~ stage, and the latter, which is very short, broadens out into a bulbous lumen before the anal opening is reached. The structure of the salivary glands and Malphigian tubules, which are shown in Plate II. Fig. 3., does not call for special notice. In the nerve cord, however, we note a great advance in development, the transversely-elongate supra-oesophageal ganglion being now well defined and occupying about two-thirds of the width of the head. The commissures leading to the sub-oesophageal ganglion proceed from the central portions of each half of the ganglion.

The sub-oesophageal ganglion is almost rectangular and is connected with the first thoracic ganglion by very broad connectives. This also applies to the three following ganglia, so that we may regard the first four ganglia of the nerve chain as being still very imperfectly separated from one another. From ganglion four however up to ganglion nine

the connectives are well developed, the ganglia being placed at fairly regular distances from one another. The last three ganglia of the chain (Nos. 9, 10 and 11) are again imperfectly separated from one another, numbers ten and eleven especially so.

The terminal ganglion (No. 11), has rounded sides and is elongate. It terminates on the hind margin of segment eleven. The difference between the structure of the nerve cord in the two stages chiefly lies in the length of the connectives and the value of this as a means of detecting the larval stage will be apparent if the figures of the two stages are compared.

Respiration in this stage is still carried on cutaneously, but the rudiments of the future tracheal system, which begins to function partially in the next stage; are visible in both the thoracic and abdominal region.

Third Stage Larva. (Plate 12)

The third-stage larva is pale milky white and glistening like its predecessor and measures 4.5 to 6 mm. in length by .7 to .8 mm. in width. The process of transition to the mature vermiform larval type has now advanced a stage further, and apart from the cylindrical form of the body, and further reduction of the caudal appendage, it is also marked by the change in the shape of the head. This has now become much less truncate in front and exhibits the globular form which is so characteristic of the final stage. There are also faint indications of the retraction of the head region into the first thoracic which is also a feature of the full grown larva. The surface of the head is smooth as in the previous stage, while the cuticle of the body segments has the same striated appearance as before.

The mandibles, which are still overhung by the labral arch, are altered both in size and shape in this stage.

They have now definitely lost their falcate form and are quite straight, while comparative measurements of the mandibles of both stages show that they have almost doubled in length in the latter stage instar. Of the internal organs, the nerve cord is the most noticeable as far as change in appearance is concerned. Following the sub-oesophageal ganglian there are eleven ganglia present, of which all, save the last two, are more or less widely separated by longitudinal connectives. The last ganglion which lies in segment ten gives off four nerves, two of which run out sideways, and two directly backwards to supply the terminal body segments.

The tracheal system also shows that advance in development. Two pairs of thoracic spiracles are now present on segment two and three and with careful examination it is possible to make out the longitudinal tracheae with their spiracular areas still unopened, and two transverse tracheal bands, one of which is situated in the prothoracic region, and the other in the tenth abdominal segment. The alimentary tract, salivary glands and Malphigian tubules do not exhibit any marked difference in structure from the previous stage instar, and the anal opening has now assumed a terminal position, consequent on the disappearance of the caudal appendage.

This being the penultimate larval stage it is the one in which the parasite leaves the interior of the host larva, demolishes its remains until only a shrivelled skin is left behind, and finally, settles down in the tunnel previous to entering upon the full grown larval state.

Fourth Stage Larva. (Plate 13.)

In this, the final larval-stage, the body is yellowish white and shining, averaging 10 mm. in length by 3 to 4 mm. in breadth. In dorsal view only twelve segments are visible, the head and anal segment being completely hidden. The body

is narrowed at both ends attaining its maximum width about the third abdominal segment. The longitudinal pleural folds are very marked on abdominal segments one to six. The spiracles number ten pairs of which the last is vestigial and difficult to make out. They are situated on the dorsal portion of the pleural region, just above the pleural lobes and are thus well seen in both dorsal and lateral view. They are borne on thoracic segments two and three, and abdominal segments one to eight. In side view the head is seen to be deeply sunk in the first thoracic segment while the anal segment is likewise retracted. The last trace of the caudal appendage is still visible as a short sub-triangular process attached to the anal segment. The body surface of the larva is for the most part smooth and shining, but the pleural region of segments two to eleven inclusive bears circular or oval-shaped "bosses" which are thickly studded with minute spines, each of which is borne on an elevated base. The armature of these areas stands out in marked contrast to the smooth surface of the surrounding integument. I have figured these "Pleural Bosses" on Plate 13. Figs. 5,6, and 7. The spines which cover them are cuticular in origin and from their appearance and position it is possible that they may serve a locomotory function.

In ventral view the retraction of the head into the first thoracic segment is well seen. In reality the head is directed ventrally in this instar, and the anal segment is also retracted within the penultimate segment. The anal opening, is terminal and transverse.

The Head. (Plate 13, Fig. 2.) In surface view the head exhibits the following characters. The vertex and frontal region is smooth save for two small raised bosses which lie laterally about half way between the top of the head and

the base of the labrum. Though not very large they are quite conspicuous, owing to the fact that the central region is more strongly chitinized than the outer portion. In the middle of this central portion there are two circular sensoria. Surrounding this portion is a paler region which is sparsely studded with minute papillae. These sensory areas are, without doubt, homologous with antennae, and both Keilin and Pluvinel and James described similar, but much larger, sensory areas, in Eucoila and Figites. Between these bosses lies the clypeal region, the suture between this and the labrum being quite distinct. The labrum which is membraneous and transparent, is broadly emarginate in front, and has a somewhat bilobed appearance. Most of its surface is covered with minute spines, which are longer and more conspicuous on the front margin than they are behind.

The larger of these spines usually occur singly, but in the case of the smaller ones, two are often borne on the same base. In addition to these, I have detected other, larger, spines which are borne on elevated cone-shaped bases, lying three on either side of the central depression, towards the front portion of the labrum. Behind these lie two minute sensoria on either side.

Through the transparent labrum, the powerful mandibles are distinctly visible. In this larva the mandibles are distinctly tridentate, although the second and third (i.e. posterior) teeth are much less strongly developed than the very powerful first teeth, which are heavily chitinized, slightly falcate, and sharp-pointed. In having tridentate mandibles this larva differs from other Cynipoid larvae which have been described, all of which have bidentate mandibles.

Lying between and below the mandibles, the U-shaped hypopharynx can be clearly seen, and below this the salivary duct can be traced in some well mounted specimens from the point of union of the individual salivary ducts into the common duct which opens on the floor of the mouth in the labial region. Flanking the mandibles on either side are the fleshy maxillary regions. Both the labium and maxilla bear conspicuous sensoria, which are of the same type as those in the antennal region.

Some notes on the nature of the larval food.

As I have already pointed out, I have frequently been surprised by the plump and healthy appearance of parasitised Sirex larvae. On many occasions when finding half-grown Sirex larvae near the wood surface, their healthy appearance has caused me to doubt their being parasitised, although their place and direction in a tunnel near the wood surface indicated that dissection would yeild a parasite. In nearly all cases such larvae were parasitised, and several of them contained more than one parasite larva. On dissecting these wood-wasp larvae, one is at once struck by the fact that the fat body shows no very marked diminution in volume compared with that of a non-parasitised larva of similar size, and this even when more than one parasite is present. Some diminution in volume of the fat body there must be, and Ratzeburg in 1844 showed that in some cases the fat body does decrease in volume as the parasite larva grows. Timberlake, also, working on Campoplex validus found a diminution of the fat body, but indicated that although fat cells might be occasionally swallowed by the parasite larva, the fat body was never directly attacked.

This whole question has been recently discussed in full by Tothill in his paper on the parasites of the fall web-worm (Hyphantria) and some of his conclusions may be discussed here. In Campoplex pilosulus Prov. an Ichneumonid parasite of the web-worm, Tothill considers that the disappearance of the fat body cannot be attributed to the parasite, but must be due to the action of the web-worm larva itself drawing upon the reserves stored up in the fat body to replace the loss of blood and lymph fluids sucked away by the parasite. No trace of the presence of fat cells was found in the mid-intestine of either the second or third stages of this larva, only lymph and occasional blood cells being present. The fact that the web-worm caterpillar remains alive during the first few instars of Campoplex is attributed by Tothill to the feeding habits of the parasite at this stage of its life. Observing that only the blood serum and lymph are sucked away by the parasite in these early stages, and the main tissue systems left intact, Tothill likens this material to the milk secreted by the mammal for the rearing of its young. "Its absorption by the parasite", he writes, "seems to have little more effect on the welfare of its host, than does the taking of the maternal milk by a lusty infant".

"The longevity of the host larvae," he continues, "is also enhanced by the fact that the parasite does not eliminate solid waste during the feeding stage. As in many other hymenopterous larvae that dare not soil the food supply, the hind intestine has become closed. As solid wastes cannot be voided in the ordinary way, they are stored up in the mid-intestine until the feeding period has passed. It must be remembered, however, that the liquid food of this larva is so digestible that the indigestible residue to be eliminated or stored up is exceedingly small."

In his studies of the Apanteles parasite of the same host larva, Tothill reaches similar conclusions. He rejects the views of Seurat that the chief food of the larva of A.glomeratus is fat body; and likewise that of Tower, who considered that blood and fat body formed the main diet of A.militaris. Apart from the fact that he finds no traces of fat cells in the food remains of the mid-intestine, he considers the mandibles of the larva much too small and weak to lacerate even the softened cells of the fat body. The comparative immobility of the larva would also, he considers, prevent it moving from one portion of the fat body to another, while the closed condition of the mid-intestine which is also a feature at this stage indicates that the larva utilizes the blood and lymph to avoid storing up bulky waste materials.

Some consideration of these points is of extreme interest in the case of Ibalia. Here we find, as in Campoplex and Apanteles, that until the end of the feeding period, the mid-intestine is completely shut off from the hind gut. Further, the mid-intestine in all three stages is usually distended with liquid food, and if for example the contents of the gut of a third stage larva be examined in section no definite trace of fat cells can be seen, the liquid contents being entirely composed of blood and lymph. If, then, one dissects a healthy looking Sirex larva about 7 to 8 mm. in length, and finds, as I have done on several occasions no fewer than three living Ibalia larvae living inside, one can gain a fair idea of the amount of blood and lymph which such a larva must give up to its parasites without seemingly being very much affected by the loss. The liquid nature of the food also explains how three parasites larvae are able to exist at one and the same time within the host. Only when the third-stage larva is well advanced and the larva is preparing to leave the host does a ravenous

feeding period set in, and it is doubtless at this period that the destruction of the supernumerary parasites by the victorious one takes place. The parasite larva completes the destruction of its host only after emergence. Of this I have obtained definite proof, as on more than one occasion I have found larvae leaving the host, with two thirds of the body projecting out of the body and the head embedded in the body cavity, the contents of which were still quite fresh and liquid. (Plate 8 Fig 1.) The mandibles of the larva at this stage are quite powerful enough to tear an opening in the body-wall of the host, and to encompass the destruction of any other living organism within the body, the contents of which it soon devours, leaving the empty shell behind, which is afterwards pressed backwards to the rear end of the larval cell. (Plate 8. Figs 2, and 3).

Length of the Larval Life.

Exact determination of the duration of the larval life has been attended, as one would expect in the case of a wood-boring parasite, with considerable difficulty. The following estimates of the length of the various instars have been based partly on field observations and dissections of larvae taken from marked oviposition tunnels, and partly on the records of a number of cases in which two or more parasites have been found in the same host larva. These will be considered separately.

From field observations and dissections of larvae from marked tunnels it is apparent that the duration of the egg-stage may vary from six weeks to almost a year. During most of this period the embryonic larva is lying in the trophamnion apparently ready to make its way out at any time.

First-stage larvae just out of the trophamnion were found on November 27th, 1928, six weeks after the host was parasitised. On the other hand, many other parasites found on the same date

and about the same age were still enclosed within the trophamnion, although apparently fully developed. Again Sirex larvae parasitised on September 13th, 1928 contained advanced embryos within the trophamnion on January 15th 1929, four months later; while two months later still (March 13th 1929) more marked tunnels from Tubney wood were dissected, and in one larva parasitised on September 18th, 1928 six months previously, an Ibalia egg was found in which the embryo appeared to be about half developed.

Other dissections made of Sirex larvae from Dorset and Brandon logs which had to the best of my knowledge been frequented for the first time by the parasite last autumn (1928) gave similar results. In all these cases the Sirex larvae recovered were either lying in the oviposition tunnel itself or in lateral tunnels only a few millimetres long.

The duration of the following stages cannot be calculated with certainty from field observations, but I have found both stages in larvae dissected during the period June 1928 to September 1929. It is in the third-stage that the parasite leaves the host larva and the photograph (Plate 8 , fig. 1) shows the parasite in the act of leaving the body of the Sirex. This picture was taken on June 13th, 1928. Ecdysis probably takes place very soon after this and the fourth- stage larva occupies the cell of its victim from June until the following July or August, a period of thirteen months or more. That the fourth-stage is a long one is certain, as I have found such larvae lying in the cells from the month of June onwards, and I know that they pass the winter in this state.

Before proceeding to draw up in tabular form the conclusions which I have reached with regard to the length of the larval life, it is necessary for us to consider the evidence which Sirex larvae containing more than one parasite

afford us, as from these I believe we may get some further light on this difficult subject.

During the first season's (1927) work both Dr. Myers and myself found Sirex larvae which contained two parasite eggs. At that time we considered this to be a comparatively rare occurrence, but since that time, I have had the opportunity of examining a considerable amount of material from three different sources and have been able to calculate the precentage of these cases. The figures given in the following Table (A) include all the Sirex larvae dissected by myself since the start of the work in July, 1927, up to the present time(August, 1929.)

Table A.

Locality.	No. of larvae dissected.	No. with two or three parasites.	Percentage.
Brandon.	242	9	3.7
Tubney.	574	14	2.4
Dorset.	656	13	1.8
Total	1472	36	2.4

The next Table (B) gives a detailed summary of the contents of each larva and the locality from which it was taken.

Table B.

No.	Date.	Locality.	No. of Parasites.	Remarks.
1.	5.10.27	Tubney	2	Eggs.
2.	24. 8.28	Tubney	2	Eggs.
3.	17.10.28	Brandon	2	Larvae 1st-stage and 3rd-stage. Both alive.
4.	1.11.28	Tubney	3	(1st-stage larva. (alive). 2nd-stage (alive). (2nd-stage(dead). (Host larva 6-7 mm. long.
5.	1.11.28	Tubney	3	(1 advanced embryo in T.A.(alive) (1 2nd-stage(alive). 1 3rd-stage (alive). (Host larva 8 mm.long
6.	1.11.28	Tubney	2	(2 advanced embryos in T.A.(alive (Host larva 4 mm. long).
7.	6.11.28	Tubney	2	(2 advanced embryos in T.A. (alive).

Table B. continued

No.	Date.	Locality.	No. of Parasites.	Remarks.
8.	6.11.28	Tubney	3	(1 advanced embryo in T.A.(alive). (1 3rd-stage larva (alive). (1 3rd-stage larva (dead).
9.	8.11.28	Tubney	2	(1 1st-stage larva (alive) (Ecdysing). (1 3rd-stage larva (alive).
10.	10.11.28	Dorset	2	(1 1st-stage (alive). (1 3rd-stage (alive).
11.	24.11.28	Dorset	2	(1 advanced embryo in T.A. (alive). (1 1st-stage (alive). (Host larva 5 mm. long).
12.	24.11.28	Dorset	2	(2 advanced embryos in T.A.(alive). ((Host larva 3 mm. long).
13.	24.11.28	Dorset	2	(2 advanced embryos in T.A.(alive). ((Host larva 5 mm. long).
14.	24.11.28	Dorset	2	(2 advanced embryos in T.A.(alive). ((Host larva 3 mm. long).
15.	27.11.28	Tubney	2	(2 advanced embryos in T.A.(alive). ((From oviposition tunnel, marked (19.9.28.)
16.	27.11.28	Tubney	2	(1 egg embryo about half developed. (1 advanced embryo in T.A.(alive). ((From oviposition tunnel of (18.9.28.)
17.	27.11.28	Tubney	2	(1 egg embryo about half developed. (1 advanced embryo in T.A.(alive). ((From oviposition tunnel of (18.9.28).
18.	18. 1.29	Dorset	2	(2 advanced embryos in T.A. ((alive).
19.	22. 1.29	Dorset	2	(1 advanced embryo in T.A. (1 1st-stage larva (alive).
20.	22. 1.29	Dorset	2	2 advanced embryos in T.A.(alive)
21.	22. 1.29	Dorset	2	(1 advanced embryo in T.A. (1 1st-stage larva (alive).
22.	28. 1.29	Tubney	2	2 advanced embryos in T.A.
23.	2. 2.29	Brandon	2	(1 advanced embryo in T.A. (1 3rd-stage larva (alive).
24.	5. 2.29	Brandon	2	2 advanced embryos in T.A.(alive)
25.	7. 2.29	Tubney	2	2 2nd-stage larvae (alive).
26.	26. 2.29	Brandon	2	2 advanced embryos in T.A.(alive)
27.	13. 3.29	Tubney	2	2 advanced embryos in T.A.(alive)
28.	23. 4.29	Brandon	2	advanced embryos in T.A.
29.	24. 6.29	Dorset	2	(1 advanced embryo in T.A. (1 2nd-stage larva.
30.	24. 6.29	Dorset	3	2nd-stage larvae.
31.	8. 7.29	Brandon	2	(2nd-stage larva. 3rd-stage lar- (va.
32.	8. 7.29	Brandon	2	(2nd-stage larva. (3rd-stage larva.
* 33.	8. 7.29	Brandon	7	Advanced embryos. All in T.A.
34.	10. 7.29	Brandon	2	(Advanced embryo. 2nd-stage (larva.
35.	14. 7.29	Dorset	3	(1 advanced embryo. 2 2nd-stage (larvae.
36.	14. 7.29	Dorset	2	2nd-stage larvae.

*Note. This very exceptional case of superparasitism I judged worthy of record, and have illustrated it on Plate 7,

These records show that for a time at least a host larva 6-8 mm. long can support as many as three parasites. How long this state of affairs can continue is unknown, but one thing is certain, namely, that in the end, one of the larvae must prevail over the others, as I have never found more than one fourth-stage larva in a tunnel, nor do I think it possible for two such larvae to occupy the same chamber.

Sirex larvae which contain more than one parasite do not appear any different externally to others and it is only their position in the wood which gives one a clue to their being parasitised at all. Of the larvae (Nos. 4, 5 and 8) in which three parasites were found, only one had all three alive (No.5). In the other two, one of the second- or third-stage larvae was dead, the third occupant being an advanced embryo still in its trophamnion. Are we to conclude from this, that the second- or third-stage larva which remained was the stronger of the two older larvae, and that it will destroy the other occupant in due course? It seems most probable that this will be the case.

Again, what conclusions are we to draw from the above records as to the length of the larval stages? To begin with, it is quite certain that when two or three parasites are found together within the same host, all these came from eggs which were laid during the same season. The parasite is, as I have already shown, quite unable to reach her victim in any place other than the oviposition tunnel, and unless it is possible for the Sirex egg or young larva to lie in the oviposition tunnel over two seasons; a state of affairs which I have never found; no other explanation of the origin of these parasites is possible.

Let us take a few examples therefore and see to what conclusions we are led. In larva No. 5, dissected on November 1st, 1928, I found one advanced embryo in the trophamnion, one

second-stage and one, third-stage larva, all three alive. The host larva was about 8 mm. long. Presumably, therefore, the larva was parasitised not later than the autumn of 1927, thirteen months previously. This would be possible, if we allow for a long embryonic stage and first-stage, and a short second-stage. Neither of the other two cases where three parasites occurred (Nos. 4 and 8) contradict this view, one of the more advanced larvae being dead in each case.

No. 9 is an interesting case. Here the first-stage larva was ecdysing, the other larva being in the third-stage. Supposing the host to have been parasitised in the autumn of 1927, this gives us a long embryonic stage, and first-stage, and the possibility that the second-stage larva had ecdysed only a short time previously.

We may conclude from this that the transition from the embryonic stage to the first-stage is variable, i.e. the former may last from two to three months up to one year. Let us consider larva No.11, which came from a Dorset log. By all appearances this larva had been parasitised sometime during the autumn of 1928. It was dissected on November 24th, one advanced embryo in the trophamnion and one first-stage larva being found inside. A year hence, I conclude, such a larva might have yielded either an advanced embryo in the trophamnion and a third-stage larva, or larvae of the first- and third-stage.

Several larva (Nos. 15, 16, 17) were taken from tunnels marked during the autumn of 1928. A period of two months had elapsed in each case before dissection. The conditions in all three cases were on the lines of what the above calculations would lead us to expect. In the first larva there were two advanced embryos, and in the last two the embryo was only about half developed. The advanced condition in the first case indicates that the preliminary stages are shorter than in the last two.

All those larvae (Nos. 6,7,12,13,14,18,19,20,21,22,24,26,27) in which either two advanced embryos or one advanced embryo and one first-stage larva were found, were probably parasitised during the autumn of 1928. The fluctuation in the duration of the embryonic stage would account for the variation of the period at which the first-stage larvae were found. (In No. 11 possibly only one to two months after oviposition. In Nos. 19 and 21 certainly over three).

The last record which we need consider here is No. 25, a Sirex larva from Tubney wood dissected on February 7th,1929. In this larva two, second-stage larvae were found, and by the method of calculation used above, the eggs were laid sometime during the autumn of 1927. As a matter of fact, this particular larva was taken from a tree which was much frequented by Sirex and Ibalia during the season of 1927, but which was felled and brought into the laboratory early in the summer of 1928 before the adults were in flight. These larvae probably passed most of the year 1928 in the embryonic stage and first larval stage, and would have been due to pass into the third-stage sometime about April of the present year (1929).

Summary. Taking all the observations already cited above into consideration, they may be briefly summarised as follows:-

(1) Complete life cycle of Ibalia occupies a period of not less than three years.

(2) Larval stages are liable to fluctuate greatly in length, but the embryonic stage and first-larval stage, and the fourth-stage are probably longer than the two intervening stages.

(3) If the three year life cycle is based upon some such plan as is indicated in the table set out below, it should be possible to find all larval stages of the parasite in any month of the year. The indications are that this is the case.

(4) The following table represents an attempt to express in tabular form the distribution of the stages in a three-year cycle. [The black lines represent the range of variability in length of each]

Table C. Distribution of Stages in a three year Life Cycle of Ibalia leucospoides Hoch.

Year.	Jan:	Feb:	Mar:	April.	May.	June.	July.	Aug:	Sept:	Oct:	Nov:	Dec:
1927								E	E	E	E	E
											1	1
1928	E	E	E	E	E	E	E	E				
	1	1	1	1	1	1	1	1	1	1	1	1
							2	2	2	2	2	2
									3	3	3	3
1929	2	2	2									
	3	3	3	3	3	3	3	3	3			
						4	4	4	4	4	4	4
1930	4	4	4	4	4	P	P	A	A			

E. = Embryonic Stage. P = Pupa.
1,2,3,4 = Larval stage. A = Adult.

From this table we see that we may expect first-stage larva to emerge from the trophamnion as early as four months after oviposition or as late as the thirteenth month. The second-stage larva may appear as early as the twelfth month or as late as the twentieth. The third-stage larva may appear as early as the fourteenth month or as late as the twenty-fourth. The fourth-stage appears during the twenty-third or twenty-fourth month and lasts over a period of twelve months leaving a maximum period of two months for the prepupal and pupal stage.

The parasitised Sirex larva. Length and depth of tunnels.

The observations of Borries, already referred to (p 20), on the superficial nature of the tunnels of parasitised Sirex larvae led me, in the first instance, to the discovery of Ibalia

larvae in larch at Tubney during the summer of 1927. Since then a considerable number of observations have been made on the length and depth of tunnels made by parasitised Sirex larvae. The first tunnels were examined in detail on October 31st. 1927 when two were found. Both tunnels were traced from the egg-tunnel to the place where the Sirex larva was lying. Their length was 1.85 inches and both larvae were heading for the outside, one of them lying almost at right angles to the surface of the wood. Both larvae were about 12 mm. long and contained third-stage larvae of the parasite. On November 7th. 1927, another tunnel examined, measured 2.5 inches in length from the Sirex egg-tunnel to the Ibalia pupal cell in which a dead adult was lying. The greatest depth to which the tunnel penetrated the wood was .31 inches (8 mm.) while the Ibalia pupal cell was only .15 inches (4 mm.) below the surface. Eight larval skins of the Sirex were found in the tunnel, the last lying, closely packed in the frass at the end of the pupal chamber. On November 18th. 1927, a Sirex larva was found in a superficial tunnel 2.25 inches long. This larva measured 11 mm. in length and contained a third-stage Ibalia larva.

On January 10th. 1928, a full-grown larva of Ibalia was found in a Sirex tunnel 2.3 inches long, which lay at a constant depth of about .31 inches below the wood surface, and the larval chamber of which was obliquely placed leaving the future adult about .5 inch to bore to the surface. On the 12th of the same month, two more tunnels were examined. Of these, the first, was 1.5 inches long to the Ibalia pupal cell, and lay at a depth of .2 inches, and the second lying at the same depth was 1.8 inches long. Both pupal cells were obliquely placed. Other tunnels examined at about the same time measured 2.5 and 3 inches in length respectively and lay at depths of .15 inches

and .2 inches. The length of the larval cells in these two tunnels was .7 inches (18mm.) and .6 inches (15 mm.) respectively.

The majority of the tunnels of parasitised larvae conform to the types described above. This makes it possible for us to say, therefore, that when examining wood for parasitised larvae those which are found in superficial tunnels at a distance varying from one to three inches from the egg tunnel with the direction of their tunnels tending to turn outwards; such larvae are probably parasitised. There are, however, occasional exceptions to this rule, and I should like to quote two of these here. The first was a tunnel found on January 23rd, 1928 in a larch log from Tubney wood. In this log I found a full-grown Ibalia larva lying .3 inches below the surface. Tracing the tunnel back I found that it descended to a maximum depth of .8 inches the deepest which I had found up to that time. The tunnel described almost a complete circle in its course, and was finally traced to the egg-tunnel of the Sirex which lay less than an inch away from the place where the parasite larva was found. In this egg tunnel the ovipositor of the parasite was found and a figure of it is shown in Plate 5. The length of this tunnel was 7.5 inches a figure which has only been recorded once since. I have referred to this tunnel before under oviposition. The second example of an unusually long tunnel came to my notice in some larch from Brandon, Suffolk. In this case the tunnel did not descend so deeply into the wood, but its length was about the same, and the circular course of the tunnel was again very marked. This tunnel is figured on Plate. 8. Fig. 3. The length of the tunnel made by the parasitised larva is, as one would expect, in marked contrast to that made by the normal larva which as I have shown in S.cyaneus, varies from six to twelve inches.

The tendency of parasitised larvae to turn towards the wood surface is as we have seen very marked, and my numerous observations on this point amply confirm those made by Borries in 1891. Superficial examination of young Sirex larvae gives us no clue however to their condition, as the parasitised larvae are as plump and healthy looking as those which are unparasitised. There seems to be however, a marked difference in the rate of boring. Comparative measurements of tunnels made during a period of one year by parasitised and non-parasitised larvae respectively showed that the latter made tunnels 2.5 to 3.5 inches long in the time, while the former had only progressed 1.3 to 1.5 inches, about half the distance. One would very much like to know what stimulus directs the parasitised larva to the outside of the log. That this is Nature's device to ensure the safe exit of the future adult parasite can hardly be doubted, and it may be that as the destruction of the host larva proceeds, a similar instinct to turn outwards [redacted] may be aroused in it, as must actuate the normal full-grown larva when about to pupate.

On the Larval Stages of the Entomophagous Cynipoidea.

The first contribution to our knowledge of the larval stages of the entomophagous Cynipoidea was made by Bouché in 1834, (6) when he described the full-grown larva of the Figitine, F.anthomyiarum Bouché, a pupal parasite of Anthomyia (Diptera). Many years after in 1884, Handlirsch described the full-grown larva of Anacharis typica Walker, a parasite of Hemerobius nervosus Walker. These two studies laid the foundation of our knowledge of the full-grown larval type, but up to that time nothing was known concerning the younger stages. This gap in our knowledge remained unfilled until 1913, when Keilin and Pluvinel (40) published a paper on which the larval stages of the Eucoiline parasite,

E.Keilini a parasite of Pegomyia Winthemi Mg.

In this paper, these authors not only described the primary larva of a parasite Cynipoid for the first time, but added a parasitic larval type which was new to science, and which they named the Eucoiliform larva. For the purposes of comparison later on I shall quote here in part the author's original description of this remarkable form. "La larve jeune est formée de deux parties distinctes; la tête et le corps. La tête, relativement aplatie, porte sur sa face ventrale deux papilles coniques, et tout à fait a son éxtremité, la bouche .....Le corps a une forme conique; il est constitué par des segments circulaires difficiles à compter mais probablement au nombre de douze.

Les trois premiers (thoraciques) portent chacun une paire d'appendices longs et grèles, que par leur position et leur forme on peut assimiler à des pattes inarticulées, et le segment le plus posterieur se prolonge pour donner une queue aussi longue que le reste du corps. A sa base, un appendice épineux fait saillir sur la face ventrale, et cette région semble récouverte de petites écailles chitineuses.

Peut-être les autres segments portent-ils aussi chacun une paire d'appendices en tous cas peu volumineux et de faible saillie? .....L'aspect de cette larve est tout à fait étrange et elle diffère nettement de toutes celles qui ont été signalées jusqu'a present."

In 1921, the next contribution to our knowledge of these larvae appeared in Haviland's paper on Charips (Allotria) victrix, (Sub-family Charipinae) of which all the larval stages were described. In this case, the primary larva, was found to be of the caudate type, but lacked the remarkable thoracic appendages which are such a feature of Eucoila. Seven years later in 1928 there appeared a remarkable paper by James (37)

on the Cynipoid parasites of Dipterous larvae, which marked a considerable advance upon our previous knowledge, of the primary and intermediate larval stages of the group. In this paper, James described all the larval stages of Cothonaspis rapae Westwood, Figites anthomyiarum Bouché, both belonging to the sub-family Figitinae, and two species of the genus Kleidotoma of the sub-family Eucoilinae. In Cothonaspis, James found that the primary larva was definitely Eucoiliform, with the typical thoracic appendages proportionately longer than those of E.Keilini. Both species of Kleidotoma also conformed more or less to the Eucoiliform type. In Figites, however, the primary larva while inclining to the same type, appeared to emerge from the egg at a later stage in its embryonic development than any Cynipoid larva yet described. Discussing the problem which these larvae present, James writes that the early stages in his opinion, bear a modified resemblance to certain stages of development which in other insects are passed through in the egg stage; eclosion is hastened, in these parasitic larvae, according to him, by the operation of two factors; (1) the small amount of yolk present, a common feature of the egg in parasitic Hymenoptera; and (2) the favourable environment in which the egg is laid. "If then", he writes; "we adopt Imm's view, that insect larvae of different types represent arrestations of growth in any one of the three states of embryonic development, which have been classified by Berlesc as Protopod, Polypod, and Oligopod respectively, we can conclude that in these Cynipoids [redacted] eclosion takes place at or near , the protopod stage (James, p. 310, Imms pp. 178-9).

The primary larva in both Figites and Kleidotoma is protopod in type, and consequently, if James' reasoning is correct, we should expect to see this followed by a polypod stage. This, as James has shown, is what does happen, and in

his paper the "Polypodeiform" larval type is described for the first time. James concludes by suggesting that it is not at all improbable, but that a larval stage corresponding to the oligopod type may yet be found.

Comparing Haviland's work on Charips, in which the primary larva is devoid of thoracic processes, James concludes that this probably represents a stage of development prior to, or at least, at the very commencement of, the protopod stage.

The Primary larva of the Ibaliinae.

Brues, writing of the Ibaliinae, states "that while they are considered by some to be aberrant Cynipidae, they exhibit affinities with the Siricidae, and are without doubt a relic of some primitive group". The life history of Ibalia has already contributed some evidence which supports this statement and now the larval morphology may supply us with further material in its favour. In Ibalia we find a primary larval stage which is definitely "Polypodeiform". This is unique among the parasitic Cynipoidea so far as we know at present.

The 'polypodeiform' larvae described by James in the Figitinae and Eucoilinae were second-stage, not primary larvae. Furthermore, the primary larvae of Ibalia represents apparently, a much more markedly developed 'polypodeiform' stage, than those which James found in the two families mentioned above. What hypothesis can we frame which will explain this phenomenon? We must admit, in the first place, that the Ibalia larvae hatches from the egg at a later stage than do those of the Eucoilinae, etc.. We may then suggest that, in spite of this fact, the primary larva of Ibalia hatching at this stage represents a more primitive type of parasitism, in support of which view, we offer the following reasons. Firstly, the remarkably intimate relationship which exists today between Ibalia and Sirex denotes association over a very long period

of time. Secondly, we may regard Ibalia as a primitive Cynipoid, which the fossil record, such as it is, certainly warrants, and, further, we may presume it to be descended from a phytophagous stock, which evolved side by side with that of the Siricidae. Originally, then, we may suppose that the full-grown larva of Ibalia was polypodeiform, i.e. an eruciform caterpillar which wandered in search of its food, and in this view we are supported by Wheeler (60) who in his Social Insects, p. 47, advances the theory, "that the remote ancestral Terebrants sought out their prey or hosts as active larvae, since their mothers had not yet acquired the habit of laying their eggs directly in, or on the larval food."

The primary larvae of Ibalia which we find today may therefore be considered to be a relic of what was once an eruciform or active larval type. With the passage of time the mother acquired the habit of ovipositing in the host egg or larva, for which purpose an ovipositing apparatus was evolved, which exceeds in complexity that of all other members of the superfamily. This habit, once acquired, there was no further need for energetic movement on the part of the larva, and we find today that the last vestiges of this active larval type appear in the primary stage. The transition, which we find in the later larval stages from the 'polypodeiform' (eruciform) to the vermiform type follows in general agreement with the known fact, that the latter can arise from either an 'eruciform' or a 'campodeiform' primary stage.

These suppositions, then, taken together, have led me to the conclusion, that we must regard Ibalia as a primitive type, which in its adaptation to the parasitic habit has not proceeded as far as the other sub-families of the Cynipoidea. The reasons for this can never be definitely known, but it is highly probable that the conditions under which the Ibalia

parasite passes its life within the body of a slow-moving wood-boring larva, have necessitated less change in the larval morphology than was perhaps required in the case of the Eucoiline and Figitine larvae whose life cycle is so much more rapid.

The occurrence of a polypodeiform larval type in the Eucoilinae and Figitinae we must regard as an obvious link in the sequence of the larva's growth. Whether or not there are any data to be gathered here which will throw further light upon the phylogenetic relationship of these two sub-families to the Ibaliinae, is a question which we are unable to answer at the present time?

Keilin and Pluvinel have drawn attention to the fact that the biology and primary larval form of Eucoila bear some resemblance to that found by Marchal in the Platygasters. They stress the fact however that in both cases the full grown larval stages are the same, and conclude with the sentence "Il ne faut donc voir dans ces ressemblances, au fond superficielles, aucune marque de parente proche, c'est sans doute là le resultat d'une simple convergence due à un mode de vie analogue."

In the Cynipoidea, the full grown larval type is constant in its general form in both parasitic and gall-making species. The departure of the primary larval type in Ibalia from the rest of the parasitic species, is therefore a signal mark of its isolated position in the superfamily.

Pupal Stage and Emergence of the Adult.

From the begining of June onwards, the Ibalia fourth-stage larvae which are going to pupate during the current season begin to pass into the prepupal state. The first sign of change is seen in the gradual wrinkling of the previously smooth and shining larval skin, and in the head region the

compound eyes of the pupa begin to appear as patches of a pale purple colour. As development proceeds, the head of the larva, usually sunk in the prothorax, becomes protruded, and the pupa forms rapidly underneath the larval skin. The principal stages in the transition are well seen in Plate 9, which shows, from left to right:- (a) a fourth-stage larva still unchanged, (b) the same larva with the skin just beginning to wrinkle, (c) the head of the pupa now recognisable beneath the larval skin, (d) the whole body of the pupa visible beneath the larval skin, and (e) the freshly ecdysed pupa with the larval skin attached to the tail end. Normally, the larval skin is cast while the pupa is still white, but in some cases I have seen pupae advance quite far in their development with the larval skin still round them. This is, however, quite abnormal, and such pupae do not as a rule come through. The pupal stage lasts for five to six weeks and the course of development is identical in every case. About a week elapses after the larval skin shows signs of an impending change, before the prepupa is at the stage shown in Plate 9, fig. 1.d. Two days later, the pupa has cast the larval skin, and appears white and glistening except for the eyes. Colouring proceeds slowly at first, and for ten days the only noticeable change is in the eyes, which turn to dark purple. These are followed by the mandibles, and after these the whole of the head and thorax, which turn quite black in the course of a few days. The abdomen begins to darken about the third or fourth week, and assumes its normal colour very rapidly once the change has begun. The antennae and legs are the last organs to change, remaining hyaline almost to the end (Plate 9, fig.2). The hind legs always darken first. Finally the wings are withdrawn from their sheaths, expanded, and fully developed in twenty-four hours. The insect is now ready to cast the last covering of all, the pupal exuvium,

which is a very thin, close-fitting shroud, from which she extricates herself with much labour. The first sign of movement which the insect makes, is when the legs are moved sideways to break through the pupal skin. Now ready to emerge, the insect has, under normal circumstances, to cut her way out of the wood in exactly the same way as the Sirex adult does. This she does, leaving behind her a small, circular exit-hole, which except for its size, exactly resembles that of the wood-wasp.

Notes on the Percentage of Parasitism.

Dr. Myers in his studies at Farnham during the summer of 1928 estimated the percentage of parasitism by Ibalia at 5.9%, a figure which he arrived at after examining some fifty-one larvae. In my work at Oxford I have also tried to collect as many data as possible on the subject, and these are set out in tabular form in the appendix. The material from which I obtained these figures was obtained from three localities, Tubney Wood, Dorset, and Brandon, Suffolk. The earliest records (July 1927 - April 1928.) are all from Tubney wood and represent the total number of Sirex larvae which were mounted on slides during that period, and from which the first studies of the parasite larva were made. From November 1928, however, I adopted a more systematic method of collecting data by taking logs four to six feet long from each locality, as far as possible, and extracting from these the larvae which they contained. These larvae were then dissected and records of their condition kept, and in this way I have recorded the results of the dissections of some 1500 larvae during the past year. The logs were chosen entirely at random in the areas where Ibalia was known to be present, and their contents varied considerably. Some, which had lain for a long time, in places where they became too dry or the reverse, yielded large numbers of dead larvae, while from others fifty to a hundred larvae were frequently taken. The results obtained show quite clearly that of the three localities, the Dorset area was the most prolific in Ibalia, which I take to be due to the greater concentration of the Sirex-trees within a small area. They indicate also that in any area where Ibalia is common, the percentage of parasitism should reach 25- 30%. The presence of Rhyssa on the same area does, however, affect the numbers of Ibalia, and I have discussed this question on p. 102 .

This, I believe accounts for the fact that the percentage of parasitism by Ibalia is lower at Tubney than either Dorset or Brandon. Finally, but by no means the least important service which the working of this material has rendered me, was the data which it supplied on the length of the larval stages, supernumerary parasites etc, the details of which I have already discussed.

Ibalia and Rhyssa - Their interrelations - Hyperparasitism. Superparasitism.

In his last paper on these parasites Dr. Myers records finding a Rhyssa larva 8.5 mm. long feeding upon an Ibalia pupa. This is the only case of hyperparasitism of which there is any record. In our previous joint paper it was stated (p.75) that "Rhyssa does not oviposit in Sirex larvae young enough to contain Ibalia larvae at any stage, so that the risk of superparasitism is probably absent". Since then, however, I have had considerable doubt as to the accuracy of this statement, and during the seasons of 1928 and 1929 these questions of hyperparasitism and superparasitism were continually in my mind, and several rather significant observations, about to be described, led me to try and obtain more detailed evidence upon them. While working on the larch at Charborough Park in Dorset, and also at Oxford I was struck by the fact that while the logs were markedly rich in Ibalia material, they contained practically no Rhyssa. Similar conditions appeared to prevail also in the larch logs I was receiving from Brandon, Suffolk.

In Devon, on the other hand, Hanson, who worked through a vast amount of material of all kinds, during the season of 1928, gathering Rhyssa larvae for the Imperial Bureau of Entomology; found Ibalia comparatively scarce in that part of the country. In May and June, 1929, when the Rhyssa oviposition was at its height I placed a number of larch logs from Tubney

Wood and Brandon in a cage and kept close watch on the activities of Rhyssa on these. It soon became evident that the logs supplied were full of Sirex, as the Rhyssa females kept continually boring into them. It was also equally certain that judging by the short periods during which oviposition lasted, either we might expect a large percentage of ineffectual attempts at oviposition, an occurrence with which we were already familiar; or that the Sirex larvae being attacked were lying in the superficial layers of the wood.

On June 4th, I cut out a Rhyssa oviposition-site and found a Sirex larva 11 mm. long, which was lying less than an inch below the surface, and on which was fixed a first-stage Rhyssa larva 3 mm. long, and about two days old. The Sirex larva, which looked quite inactive and was certainly paralysed, gave a faint heart action of eleven beats per minute. On dissection, this larva yielded three first-stage Ibalia, all just emerging from the trophamnion.

This, my first record of superparasitism, was followed by two more on June 11th, when I found a Sirex larva with the Rhyssa egg just hatching, and inside the larva a third-stage Ibalia; and another Sirex with a second-stage Rhyssa larva feeding upon it, the Sirex containing another third-stage Ibalia. The most recent case of superparasitism which we have found occurred at the end of June. The oviposition hole of a Rhyssa marked on the 24th. of the month, was cut out on the 26th and in the wood was found a Sirex larva with the Rhyssa's egg upon it. This larva was placed in a capsule and the egg left to hatch. Within a couple of days however, an Ibalia larva emerged from the Sirex, destroyed the Rhyssa egg in so doing, and finished off its host in the usual manner. This larva, at the moment of writing (August) shows no signs of preparing to pupate this year, and will, in all probability, overwinter in the larval stage to

emerge as an adult next summer. These findings showed then, that Sirex larvae parasitised by Ibalia not only do fall victims to Rhyssa, but that they are in most cases even more vulnerable than normal larvae, by reason of their superficial location in the wood. This being so, it follows that in districts where Rhyssa is abundant, Ibalia may be expected to occur sparingly, and vice-versa, To test this, apart from the results which Mr. Hanson had already obtained in Devon, I obtained a larch tree from the Brandon area, cut it into small portions and extracted from these all the Sirex, Rhyssa and Ibalia which they contained. This task, which took ten days to accomplish, yielded some very interesting results which I have tabulated below.

Sirex, Ibalia and Rhyssa obtained from a larch tree (Brandon, Suffolk), June 11th-20th, 1929.

IBALIA			SIREX		RHYSSA	
Larvae full-grown.	Pre-pupae	Pupae	Larvae	Pupae	Pupae	Adults
140	5	39	152	68	3	7
	Total = 184		Total = 220		Total = 10	

Total = 414

Ibalia = 44.4 per cent.
Sirex = 53.1 per cent.
Rhyssa = 2.4 per cent.

The above total representing as it does the total population of a single tree, indicates that the abundance of Ibalia in the Brandon area can be correlated with the scarcity of Rhyssa in the same region.

One further observation of interest was obtained from this Brandon Log. The Sirex were practically all in the advanced larval or pupal stage; the Ibalia were in the majority of cases about to pass into the prepupal state and would have emerged this year, while the Rhyssa were also in the pupal or adult stage. Last season had evidently witnessed the emergence of quite a number of woodwasps and parasites (most of the latter, to judge by the tunnels were also Ibalia), and this season I conclude will see the last of the woodwasp-parasite population leave the tree. This uniformity of development was very striking and is comparable to similar cases which I have seen in logs from Dorset.

The above observations indicate, that if an effort is made in the future to send Ibalia as well as Rhyssa to New Zealand, it will be advisable to liberate the two parasites in different regions. The point is sufficiently interesting and important to warrant the collection of more data upon it, but from what I have already seen in the four areas where I have studied it, I imagine that the two parasites will be distributed in the manner I have indicated.

Since this was written, I have come across one case of superparasitism in larch at Tubney.

SUMMARY.

(1) This paper contains an account of studies made during the past three years, on the biology and post-embryonic development of Ibalia leucospoides Hochenw. (Hymenoptera Cynipoidea) a parasite of the Sirex wood-wasp, S.cyaneus Fabr. (Hymenoptera Siricidae.)

(2) The oviposition-habit, which is quite specialised, is one of the features of the life-history, as the parasite can only reach the host while it is still in the oviposition-tunnel.

(3) The larval stages, the morphology of which has been studied in detail, are distinctly hypermetamorphic. The primary stage is "polypodeiform", and thus differs from that of any other known Cynipoid.

(4) The duration of the larval stage is estimated at three years, and for almost two-thirds of this time the parasite remains within the body of the host-larva. Parasitised Sirex larvae hardly ever burrow deeper than the sapwood, and the length of tunnel which they make averages two to three inches, but sometimes attains a length of six to seven inches

(5) Dissections of large numbers of Sirex larvae from different localities has supplied data from which the percentage of parasitism could be estimated. These dissections have also thrown much light on the course of the larval development.

(6) The interrelations of Ibalia and Rhyssa persuasoria L, the Ichneumonid parasite of the wood-wasp have also been studied. It has been found that Sirex parasitised by Ibalia are also liable to be parasitised by Rhyssa, and for this reason it is believed that in regions where Rhyssa is abundant, Ibalia will occur sparingly. Statistics bearing on this question are given.

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Plate 1. Ibalia leucospoides Hochenw.
Adult female. x 9.

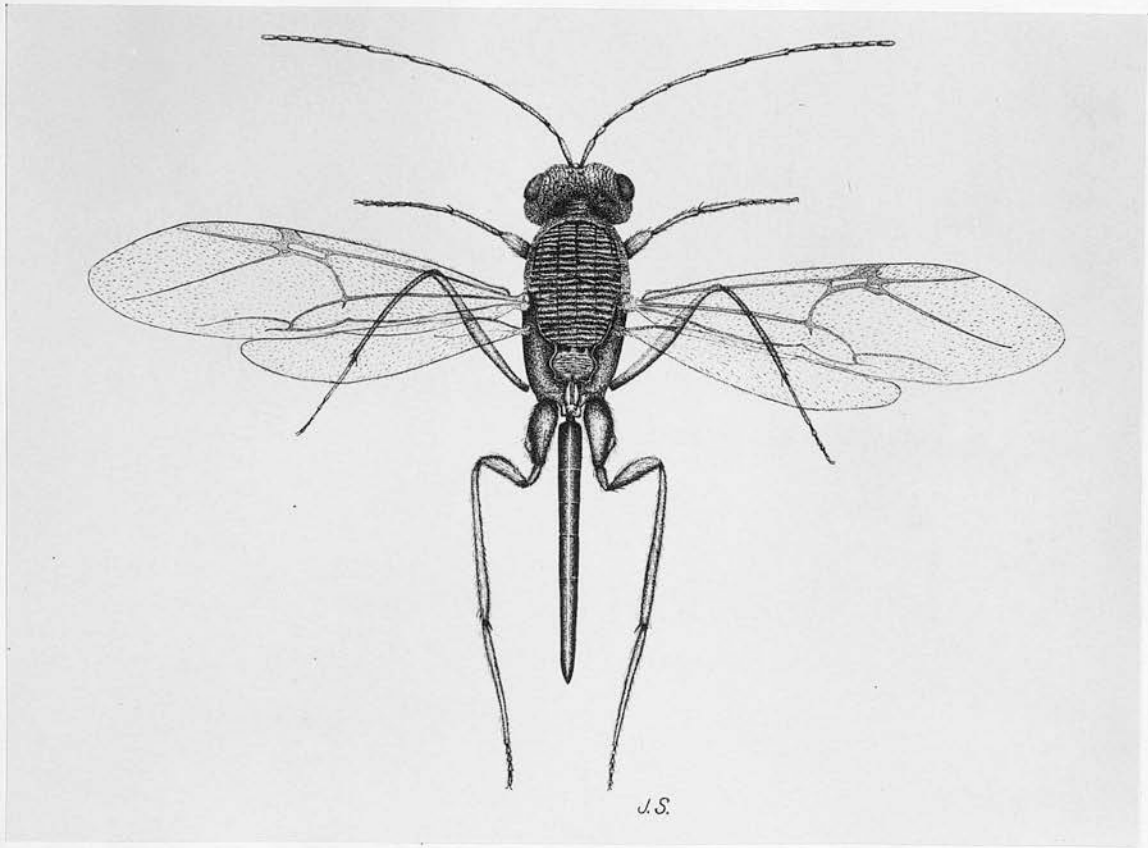

J.S.

Plate 2. Ibalia leucospoides Hochenw. Oviposition.

Drawings made from field-notes and sketches. Tubney Wood, Oxford, 1928.

Fig.1. Inspection of the bark with the antennae.

Fig.2. Inspection of the Sirex egg-tunnel with the antennae.

Fig.3. The tip of the abdomen applied to the mouth of the egg tunnel preparatory to the release of the Hypopygium.

Fig.4. The Hypopygium lowered.

Fig.5. The same in closer view, showing the tip of the ovipositor about to descend the egg-tunnel. (The tip of the hypopygium will eventually be inserted into the tunnel mouth.)

Fig.6. Diagrammatic sketch of the position which the ovipositor occupies in the tunnel in relation to the host larvae.

Hyp. ... Hypopygium :

O. ... Ovipositor.

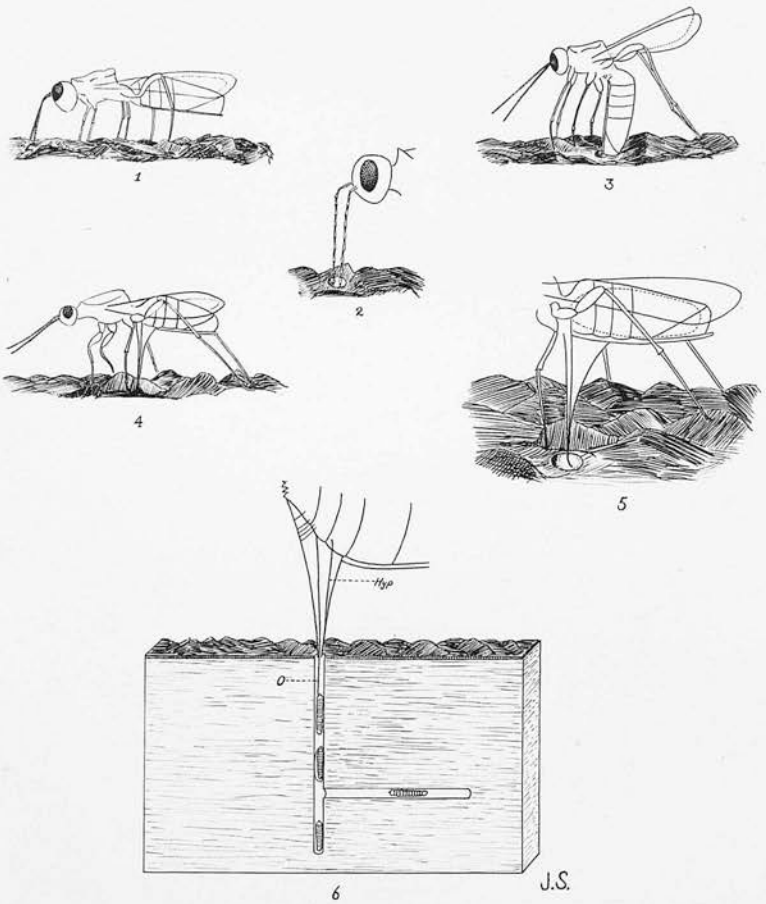

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Hyp
O
6
J.S.

Plate 3. *Ibalia leucospoides* Hochenw.
Reproductive Organs and Ovipositor.

Fig.1. Abdomen of the female with one side exposed to show the ovipositor and reproductive organs *in situ*. x 8.

T.P. ... Triangular Plate.
M.S. ... Muscular Sheath.
A.P. ... Anal Plates.
S.P. ... Sheath Plates.
Hyp. ... Hypopygium.
b. ... Base of ovipositor.
O. ... Ovipositor.

Fig.2. Apical portion of one of the "Bristle Valves" showing the toothed edge. x 112.

Fig.3. Ovipositor in transverse section showing - x 112.

VV ..... Ventral Valves.
BV ... Bristle Valves.
E.C. ... Egg Canal.

Fig.4. Ovaries (Ov.), Acid Gland (A.Gld.) and Vaginal pouches., (V.S.). x 7.

Fig.5. Ovary and Oviduct. x 41.

Fig.6. Ovipositor of *Dryophanta*. (After Cameron, British Phytophagous Hymenoptera, Vol.3, Plate 5, Fig.16.) Lettering as in Fig.1.

Fig.7. Ovipositor of *Figites*. (After Cameron, British Phytophagous Hymenoptera, Vol.3, Plate 5, Fig.20.) Lettering as in Fig.1.

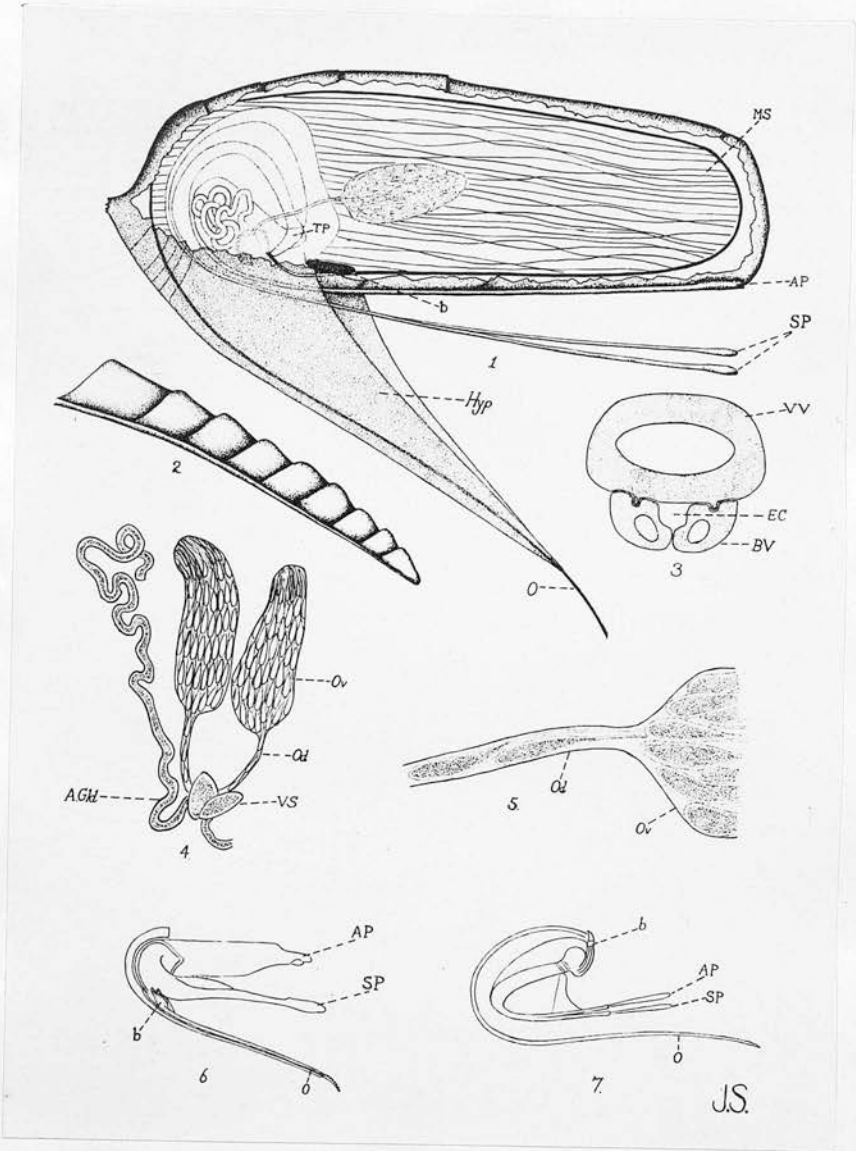

MS
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Od
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b
AP
SP
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J.S.

Plate 4. Fig.1. *Ibalia leucospoides* Hochenw. ovipositing in larch. Oxford, September, 1928. x 3.

Fig.2. *Sirex cyaneus* Fabr. First-stage larva showing the egg of Ibalia inside. x 50.



Fig. 1

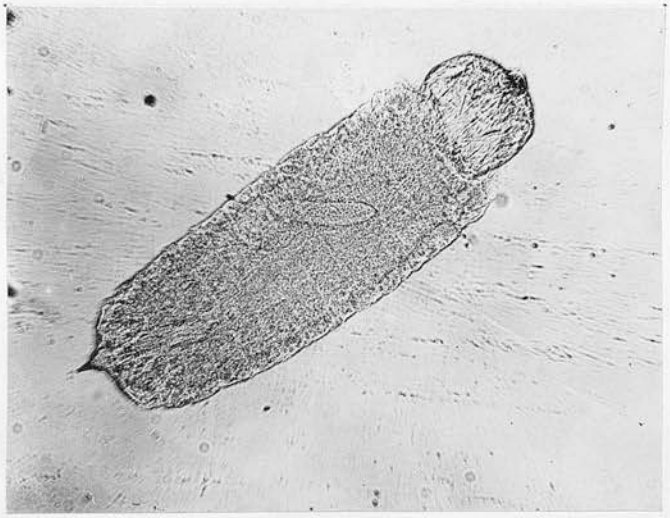


Fig. 2

Plate 5. Fig.1. Ovipositor of *Ibalia* found in a *Sirex* oviposition tunnel. x 8.

Fig.2. The *Sirex* tunnel in section, showing at the left of the picture, the commencement of a larval tunnel, at the end of which a fourth-stage larva of *Ibalia* was found. x 8.

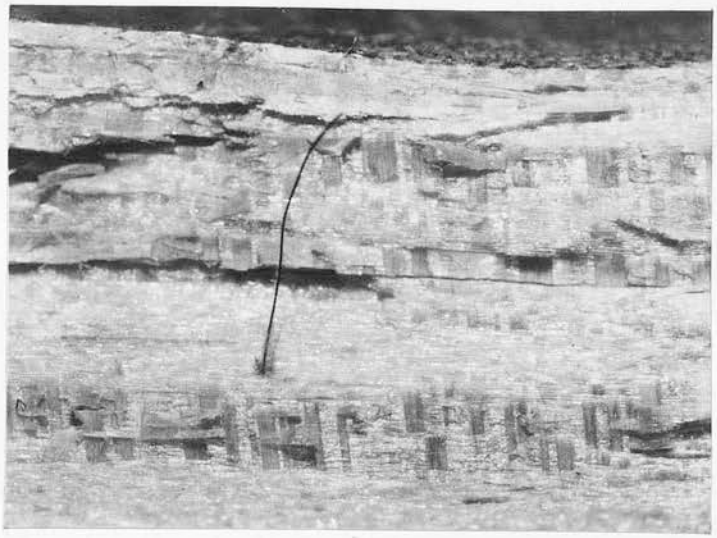


Fig. 1

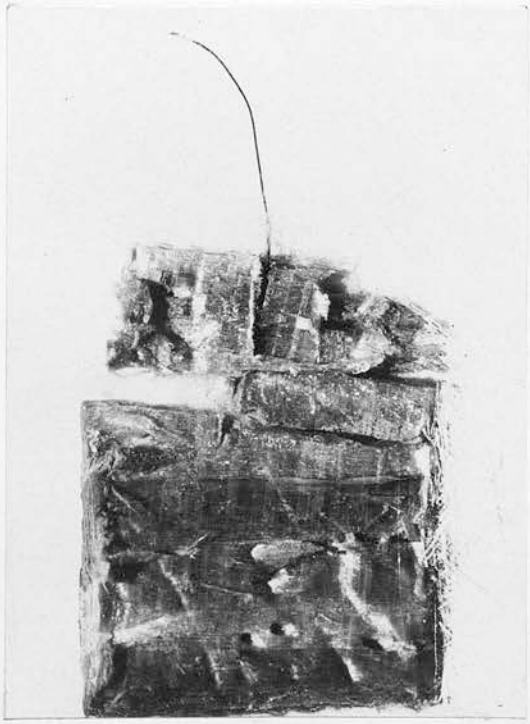


Fig. 2

Plate 6. Fig.1. Advanced embryo of *Ibalia* lying within the trophamnion.
x 150

Fig.2. *Sirex* egg containing an advanced embryo, within which was found an *Ibalia* egg, which can be seen on the right of the picture.
x 50.

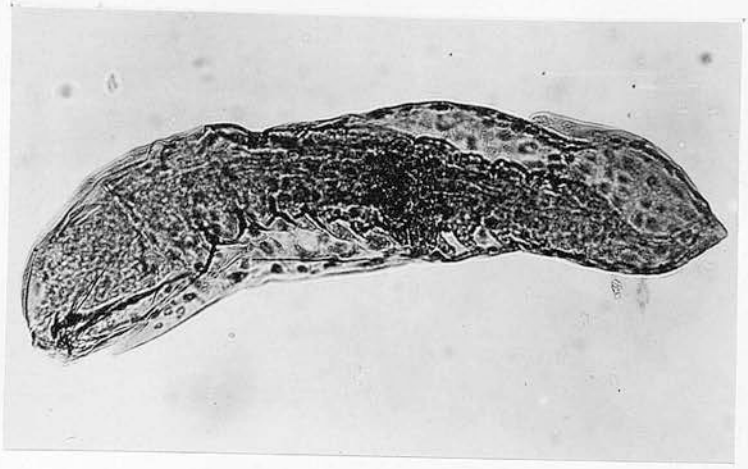


Fig. 1



Fig. 2

Plate 7. Fig.1. Seven advanced embryos of *Ibalia* which were taken from the host larva shown in Fig.2. All are within the trophamnion. Oxford, July, 1929. x 12

Fig.2. Remains of a *Sirex* larva dissected for *Ibalia*. x 12



Fig. 1

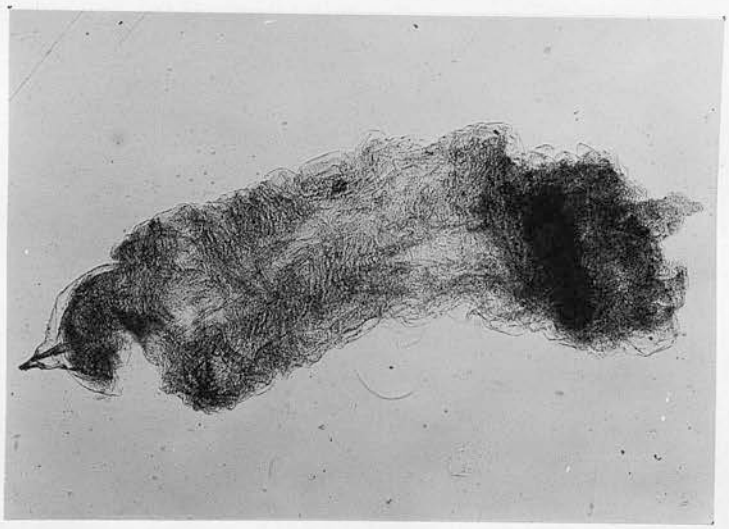


Fig. 2

Plate 8. Fig.1. *Ibalia* larva emerging from the *Sirex* host. x 3

Fig.2. *Ibalia* fourth-stage larva lying upon the remains of the *Sirex* host. x 3

Fig.3. *Ibalia* fourth-stage larva lying in its cell at the end of the *Sirex* tunnel, the beginning of which is seen at the extreme right of the picture. Nat.size.

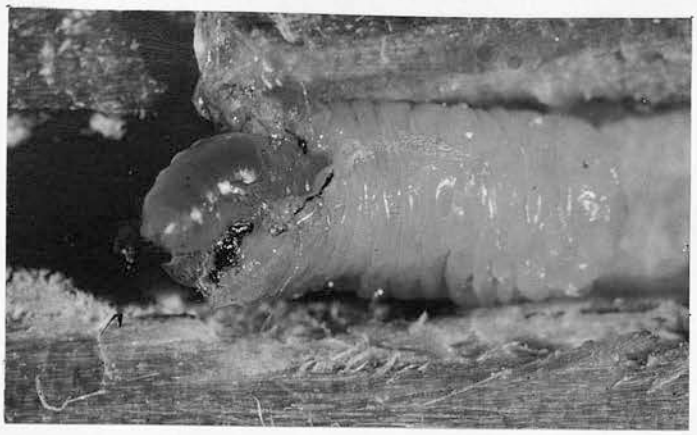


Fig. 1

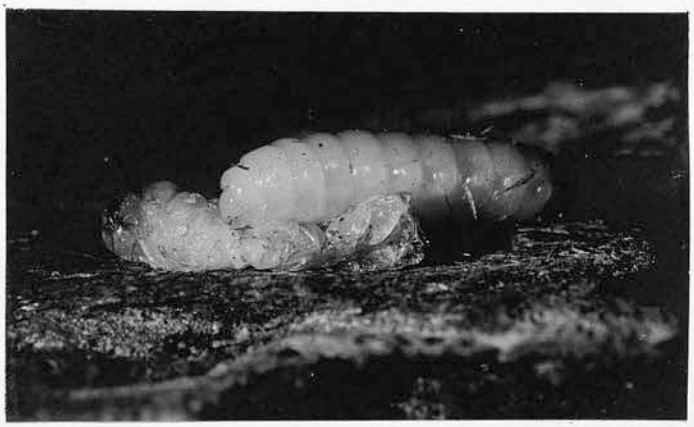


Fig. 2

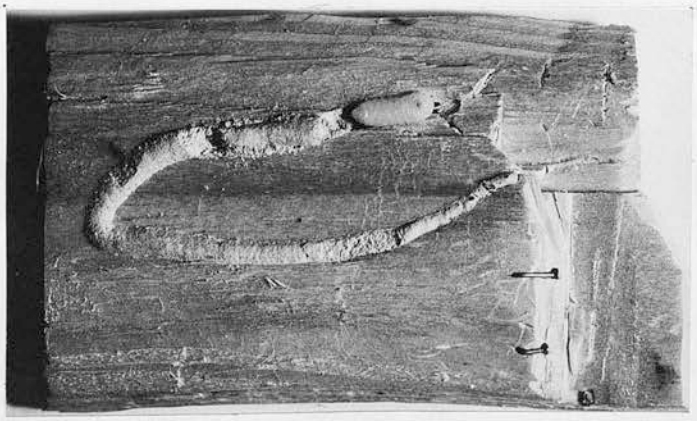


Fig. 3

Plate 9. Fig. 1. Ibalia leucospoides Hochenw. transition from larval to pupal stage. x 3

(a) Fourth-stage larva unchanged.
(b) The same, showing skin commencing to wrinkle.
(c) Prepupa, first-stage.
(d) The same, second-stage.
(e) Freshly ecdysed pupa, showing discarded larval skin.

Fig.2. Ibalia leucospoides, male pupa at an advanced stage of development. x 3.

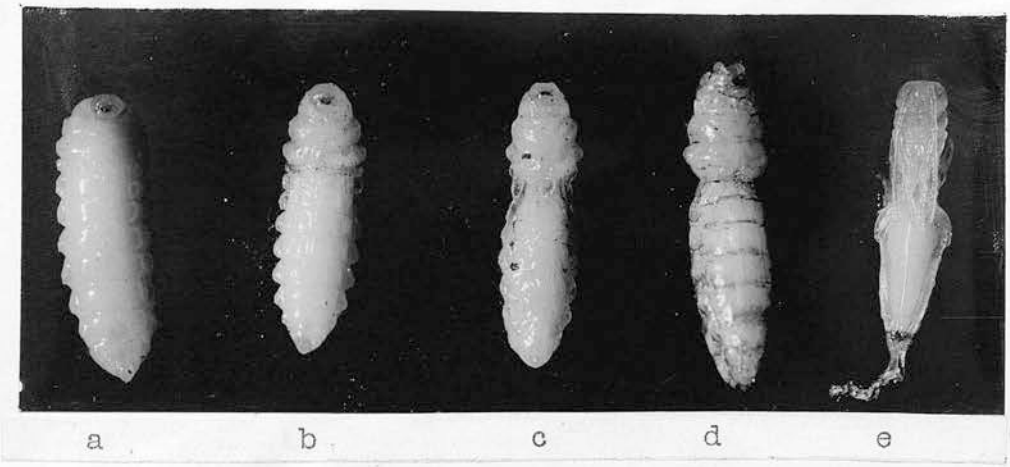


Fig. 1



Fig. 2

Plate 10. Ibalia leucospoides Hochenw.
First-stage larva.

Fig.1. Larva in side view, showing pseudopodia and caudal appendage. x 50.

Fig.2. Pseudopod. x 112.

Fig.3. Larval head, ventral view. x 50.

Fig.4. Body of the larva in long section. x 55.

F.G. ... Fore-gut.
M.G. ... Mid-gut.
H.Int... Hind Intestine.
G. ... Gonad.
Sal.Gld.... Salivary Gland.
N.C. ... Nerve Cord.
S.G. ... Supra-oesophageal ganglion.
A. ... Anus.

Fig.5. Epithelial cells of the mid-gut. x 112.

Fig.6. First-stage larva emerging from the trophamnion. x 50.

Fig.7. Shrunken condition of the trophamnion after the larva has vacated it. x 25.

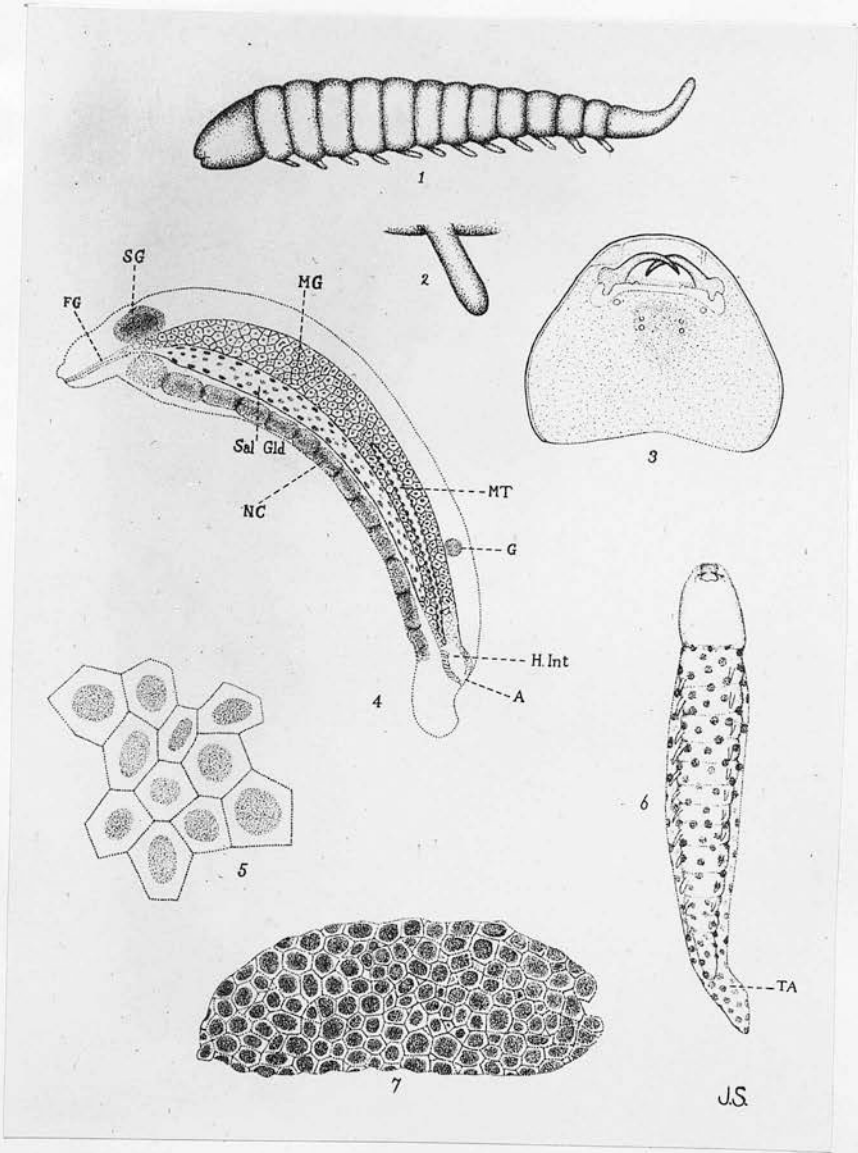

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FG
MG
Sal Gld
NC
MT
G
H.Int
A
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TA
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J.S.

Plate 11. Ibalia leucospoides Hochenw.
Second-stage larva.

Fig.1. Larva in side view. x 25

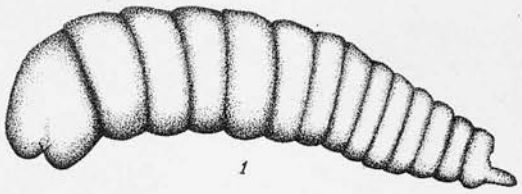
Fig.2. Larva in ventral view, showing nerve cord. x 25

Fig.3. Larva in ventral view, showing alimentary canal and appendages. x 25

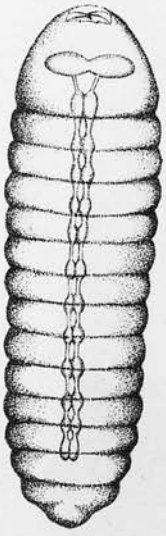
M.G. ... Mid-gut.
H.Int. . Hind Intestine.
Sal.Gld. Salivary Gland.
M.T. ... Malphigian tubules.

Fig.4. Head of the larva, ventral view showing labrum and mandibles. x 32

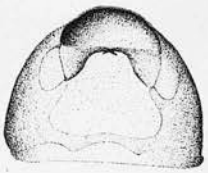
Fig.5. The same, magnified, showing the mandibles. x 50



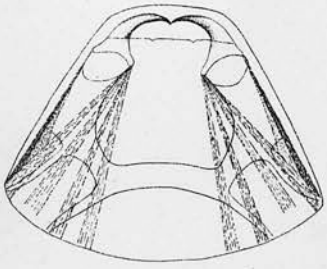
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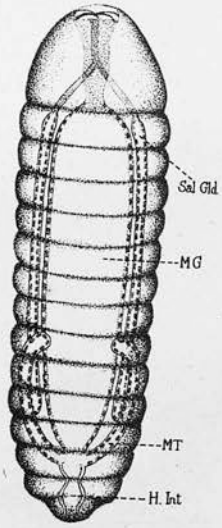
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J.S.

Plate 12. Ibalia leucospoides Hochenw.
Third-stage larva.

Fig.1. Larva in side view. x 15.

Fig.2. Larva in ventral view, showing nerve cord. x 15.

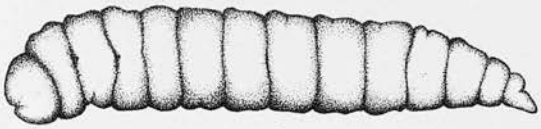
Fig.3. Larva in ventral view, showing the head and thoracic segments 1 to 3. x 25.

F.G. ... Fore-gut.
S.G. ... Salivary Gland.
Tr. ... Trachea.
Sp. ... Spiracle.
M.G. ... Mid-gut.

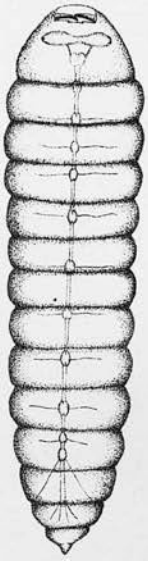
Fig.4. Enlarged view of mid-abdominal segment showing mandibles and part of the cast skin of the second-stage larva. x 25.

Fig.5. Transverse section of the larva taken in the region of the junction between the Malphigian tubules and the hind intestine, showing the closed condition of the latter in this instar. x 50.

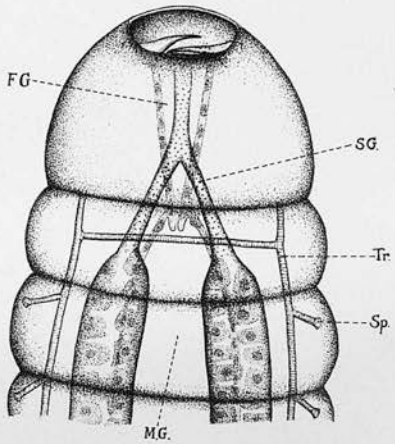
Cu.. ... Cuticle.
Hyp. ... Hypodermis.
G. ... Gonad.
H.Int... Hind Intestine.
M.T. ... Malphigian Tubules.



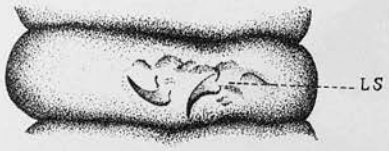
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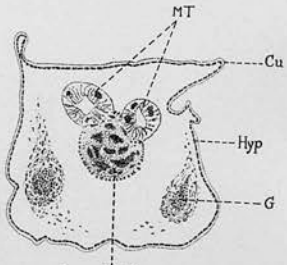
2



3



4



5

J.S.

Plate 13. *Ibalia leucospoides* Hochenw.
Fourth-stage larva.

Fig.1. Larva in side view. x 7

Fig.2. Head of the larva. x 25.

M.D. ... Mandible.
Ant. ... Antenna.
Clyp.... Clypeus.
Lbr. ... Labrum.
Hyp. ... Hypopharynx.
Mx. ... Maxilla.
Lab. ... Labium.
Sal.D. . Salivary Duct.

Fig.3. Clypeus and Labrum. x 50.

Fig.4. Mandibles. x 50.

Fig.5. Transverse section through the larval integument in the region of a "Pleural Boss". x 112.

S. ... Cuticular spine.
Cu. .. Cuticle.
Hyp... Hypodermis.
O. ... Oenocytes.
M. ... Muscles.

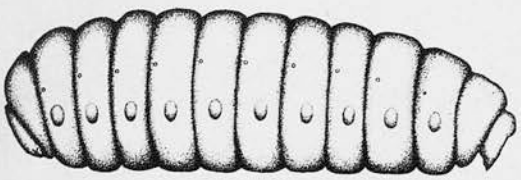
Fig.6. Transverse section through the larval integument in the region of a "Pleural Boss". x 50.

O. ... Oenocytes.
M. ... Muscles.
Other lettering as in fig.5.

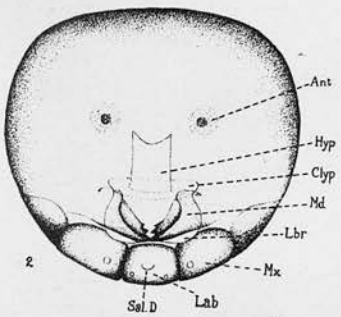
Fig.7. "Pleural Boss" in surface view.

Fig.8. Transverse section of the larva in the region of the junction between the Malphigian tubules and the hind-intestine, showing the closed condition of the latter in this instar. x 20.

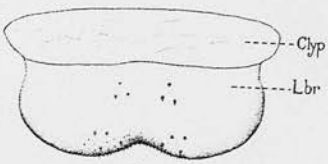
Ht. ... Heart.
Tr. ... Trachea.
H.Int.. Hind Intestine.
F. ... Fat Body.
M.T. .. Malphigian Tubules.
Sal.Gld. .. Salivary Gland.
Other lettering as in fig.6.



1


Ant
Hyp
Clyp
Md
Lbr
Mx
Sal.D
Lab

2


Clyp
Lbr

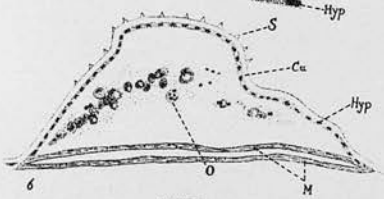
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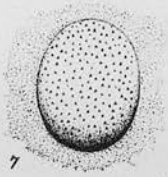
4


S
Cu
Hyp

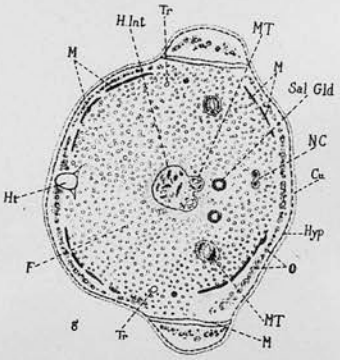
5


S
Cu
Hyp
O
M

6



7


H.Int
Tr
MT
M
M
Sal Gld
NC
Cu
Ht
Hyp
F
O
MT
Tr
M

8

J.S.

APPENDIX I.

Tables showing numbers of adults of *Ibalia leucospoides* Hochenw. taken in the field or bred in the laboratory during the period from August, 1927 to September 17th, 1929.

Year	Month	Male	Female	Locality
1927	August	1	14	Tubney and
1927	September	3	9	Museum Road
1927	October	0	7	
1928	July	0	2	Dorset
1928	August	14	39	Dorset
1928	September	2	51	Dorset and
1928	October	2	3	Tubney Wood.
1929	July	6	3	Tubney Wood and
1929	August	19	9	Museum Road.
1929	August	16	23	Dorset (Munro).
1929	September	25	30	Museum Road.
				Barton Bendish, Norfolk.
				Dorset.
		88	190	

APPENDIX II.

Tables showing the percentage of parasitism in Sirex larvae taken from larch logs from Tubney Wood, Oxford; Bere Wood, Dorset; and Brandon Suffolk; during the period July, 1927 to September, 1929.

Locality - Tubney Wood.

Date	No. of larvae examined.	Number Parasitised.	Percentage of Parasitism
July, 1927 to April, 1928.	125	30	24
November, 1928.	85	18	21
January, 1929.	89	16	17.8
February, 1929.	28	12	42
March, 1929.	6	2	33
April, 1929) May, 1929.)	21	4	19
August, 1929.	128	20	15.6
	92	17	18.4
September, 1929.	106	21	20
	155	30	19.3

Locality - Bere Wood, Dorset.

Date	No. of larvae examined	Number parasitised	Percentage of Parasitism
November, 1928.	47	20	42.5
January, 1929.	118	36	30.5
February, 1929.	55	18	32.7
March, 1929.	9	3	33.3
April, 1929.	117	37	31.6
May, 1929.	40	10	25
June, 1929.	72	43	59.7
July, 1929.	133	56	42.1
August, 1929.	65	41	63
September, 1929.	14	4	28.5

Locality - Brandon, Suffolk.

Date	No. of larvae examined	Number parasitised	Percentage of parasitism
August, 1928	6	6	100
January, 1929	7	3	42.8
February, 1929	34	13	38.2
March, 1929	43	16	37.2
April, 1929	37	6	16.2
July, 1929	67	19	28.3
August, 1929.	48	13	20

Summary.

Locality	No. of larvae examined	Number parasitised	Percentage of parasitism
Tubney Wood	835	170	20.3
Bere Wood, Dorset.	670	268	40
Brandon, Suffolk.	242	76	31
Total	1747	514	29.4

APPENDIX III.

Ibalia at Barton Bendish, Kings Lynn, Norfolk, September, 1929. Emergence of the adults. Since writing that portion of the paper which deals with the behaviour of the emerging adults (p.) I have been able to make some further observations on this question. During a recent visit to Norfolk, I came upon a very small, isolated, mixed wood, of larch, oak, ash and other species. The larch of which most of the stand was composed, were mostly poorly grown trees, 35-40 years old, and about 20-30 feet in height. Owing to the extremely isolated position of the wood I thought at first, that it was an unlikely place in which to find Sirex, but on making a search I found traces of its presence on some half-dozen dead trees. The day was bright and rather warm and about 4 p.m. I saw a male Ibalia flying around one of these trees on which it finally settled. The insect was evidently searching for something to judge by the intent manner in which it probed the bark crevices with its antennae. A few minutes later, I observed several more males flying round and settling on the stem much higher up, all acting in the same manner as the first one I had observed. Six of these males were caught and the tree was felled for further examination. Only one Sirex larva was found in the wood, but there was ample evidence that a number of fair-sized adults had recently emerged. A number of fourth-stage Ibalia larvae were lying in their superficial wood cells and two females were found busily engaged in making their way out of the wood.

On returning to the wood next day, I observed more males flying round another dead tree which was close to the spot where I had found them on the previous day. This tree was also felled, and more than half of

of the stem dissected. In it I found eight females all cutting their way out of the wood, some with their heads already visible at the surface. I also found, as on the previous day, several fourth-stage Ibalia larvae, and in addition two larvae of Rhyssa, one adult of which I caught sight of later, flying high up the stem of a dying tree nearby. There were also several male Sirex in the tree, one Sirex larvae with a third-stage Ibalia inside it, but no female Sirex.

These observations appear to me to be of the greatest interest inasmuch as they confirm those made at Brandon last year, when the male Ibalia was found searching the bark in the vicinity of an emerging female. That the approaching emergence of the females was the cause of the activity of the males round the dead trees I have not the slightest doubt, as when put into a cage together, pairing followed almost immediately. I was, unfortunately, unable to continue my observations for more than two days, but the trees are being watched by my assistant, Mr.C.C.Brooks, and once the females have emerged, they will no doubt guide us to the trees in which the Sirex females have laid their eggs. The discovery of a colony of the woodwasps and their parasites in this very small and isolated patch of woodland is another interesting feature, and it is quite probable that in most of the woodland patches which are very numerous in this part of the country, the larch when present, will, if in the proper condition, yield the woodwasp and its parasites.

I may say, in conclusion, that I am extremely indebted to Mr. G. Rutterford of Avenue Farm, Barton Bendish, for giving me permission to cut the trees and assisting in every way to facilitate my examination of their contents.

APPENDIX IV.

Ibalia leucospoides Hochenw. and *Sirex gigas* L.

In a recent letter, from Mr. H.R.Munro, Charborough Park, Dorset, writes that early in September he observed female *Sirex gigas* busily ovipositing in some trap larch logs which he had placed at my suggestion in Bere Wood, Dorset. The *Sirex* frequented the logs for some eight days and soon after the end of this period Mr.Munro observed two female *Ibalia* busily ovipositing in the same logs. It appears that there was no sign of *S. cyaneus* ovipositing in these logs during this period although the species is present in the wood. It seems likely therefore that the *Ibalia* were parasitising the eggs of *S. giga s.*