

**The biology of *Ibalia drewseni* Borries (Hymenoptera : Ibalidae), a parasite of siricid woodwasps**

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SYNOPSIS

An account is given of the life history of *Ibalia drewseni*, an internal parasite of siricid woodwasps. The immature stages are described, and a key is given for the separation of the adults from those of *I. leucospoides*. The distribution of the species is discussed.

INTRODUCTION

DALLA TORRE & KIEFFER (1910) listed four species of *Ibalia* in western Europe (*drewseni* Borries, *schirmeri* Kieffer, *leucospoides* (Hochenwarth) and *arcuata* Dalla Torre and Kieffer) and two species in eastern Siberia (*suprunenkoi* Jacobson, and *jakowlewi* Jacobson). They considered *cultellator* Latreille a synonym of *arcuata*. Weld (1952) concluded that *arcuata* is a synonym of *leucospoides*, and Bischoff (1953) considered *schirmeri* a synonym of *drewseni*. Of the four species of *Ibalia* in North America, *ensiger* Norton is possibly conspecific with *leucospoides* (G. J. Kerrich, *personal communication*). Schulz (1912) inclined to the view that *leucospoides* was the sole European species.

During extensive surveys, involving the collection of siricid-infested timber in Europe, Turkey and Morocco, only *leucospoides* and *drewseni* have been encountered, although dark forms of *leucospoides* are common, particularly in south-western Europe and Morocco.

The biology of *leucospoides* was studied by Chrystal (1930), and Madden (1968) has described the role of siricid fungal symbionts as host indicators for *leucospoides*. No account of the biology or parasitic status of *drewseni* has been published, although Borries (1891) recorded its association with Siricids in Denmark.

MATERIALS AND METHODS

Siricid-infested timber was collected in 130 localities in Europe (England, Scotland, Ireland, Norway, Sweden, Germany, France, Switzerland, Belgium, Holland, Spain, Portugal, Italy, Yugoslavia, Bulgaria, Czechoslovakia, and Hungary), Turkey and Morocco, and kept under outdoor conditions at Silwood Park. *I. drewseni* was obtained from 18 localities in Europe and 4 localities in Turkey. The females were mated after emergence and stored at 5° C. in gauze-covered observation cages (30 × 30 × 30 cm.). They were supplied with water, and honey containing 1 per cent. protein hydrolysate. For rearing studies, *Pinus sylvestris* L. logs (19–25 cm. long, 10–16 cm. diameter) were offered to females of *Sirex noctilio* (F.), *S. juvenis* (L.), *S. cyaneus* (F.), *Xeris spectrum* (L.) and *Urocerus gigas* (L.), which all oviposited readily. The culture logs were exposed to *drewseni* females about two weeks later, when the eggs of the Siricids had begun to hatch. The behaviour of the females on the culture logs was studied, and the timber was dissected at intervals to obtain the immature stages of the parasite. The parasite was reared at 25° C., and observations on behaviour were made at room temperatures (21 ± 4° C.) and humidities (65 ± 5 per cent. R.H.) under ordinary laboratory lighting. Longevity of adults was studied at 25° C.

The immature stages were described from fresh specimens, and details were obtained from whole mounts or head capsules mounted from 70 per cent. ethanol in lacto-phenol after lightly staining in van Gieson's picro-fuchsin.

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METHODS

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In studies on the females' reactions to fungal attractants, the symbiotic fungus from *S. juvencus* was cultured on potato dextrose agar at 24°C., and samples of fungus-impregnated medium were put into 1 cm. diameter cavities drilled in 12 mm.-thick Perspex sheets. Each sheet was covered with 1 mm.-thick card, a pin-prick being made through the card into each cavity. Such a bioassay sheet was separated from another sheet of Perspex by 2 cm.-wide wooden blocks to form a shallow observation box. Antennal palpations and ovipositor probes down the pin holes into the cavities were recorded.

LIFE HISTORY

Adult *drewseni* emerge from mid-May until mid-June (Table I) in contrast with *leucospoides*, which begins to emerge some days or even weeks after the beginning of the siricid flight period and continues after the Siricids cease to emerge (fig. 1). Emergence of *drewseni* may continue for two or three seasons.

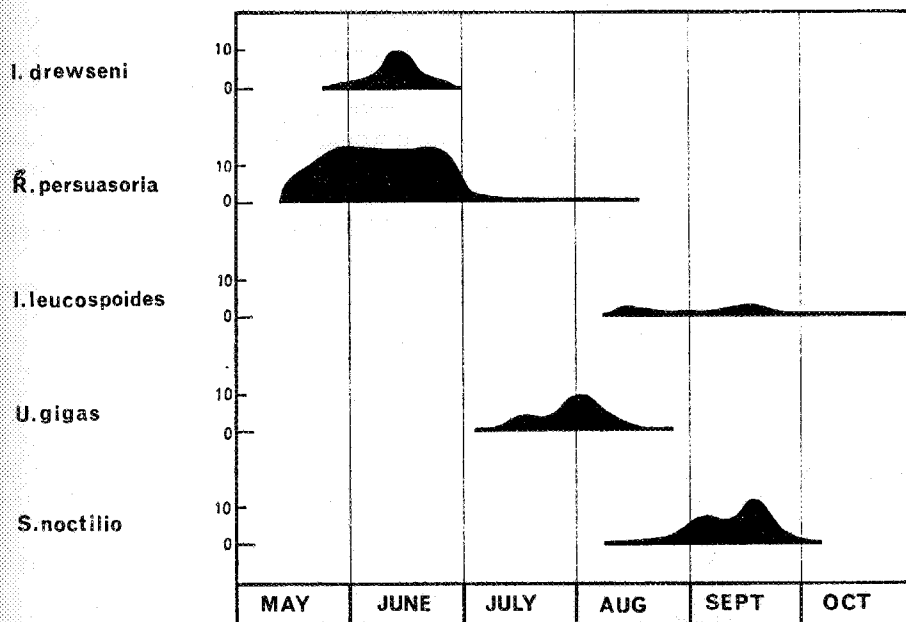


FIG. 1.—Emergence of *I. drewseni* and associated insects from Thetford Chase, Norfolk (1965).

The adults mate readily in the observations cage, both before and during oviposition. The male mounts the female from behind while she is resting, walking or drilling, and strokes her antennae with his own in a rowing action. Responsive females, generally 0-3 days old, lower the hypopygial sternite, while the male puts the tip of its gaster at the base of the hypopygium. Precopulatory behaviour usually lasts for less than a minute but once continued for seven minutes. Copulation occupied 1.7 minutes (range 0.3-2.9, n = 10). Multiple mating by both sexes is common, and frequently several males attempt to mate with one female simultaneously. Often one male succeeds in pairing while the remainder continue antennal stimulation.

Newly-emerged females of *drewseni* have many mature eggs in the ovaries (mean 110, range 42-175, n = 9), and oviposition begins on the day of emergence. When offered siricid-infested logs, females walk over the bark exploring with their antennae, which were lowered rhythmically so that the distal 2-3 segments touched the bark. Usually the antennae were raised and lowered alternately, but sometimes they were raised and lowered together. During exploratory behaviour, the abdomen is often

rhythmically raised and lowered. At siricid oviposition shafts the female stops and explores the hole with the antennae (Plate I, fig. 1), which are often inserted down the shaft for about half of their length. Antennal palpation occupied 10–46 seconds. If sufficiently stimulated, the female withdraws the antennae and lowers the gaster at right angles to the body with the ovipositor slightly exposed at the tip (Plate I, fig. 2). The gaster is brought up between the legs until the tip of the ovipositor locates the hole (Plate I, fig. 3), and the ovipositor passes down the shaft from its coiled-up position in the gaster, which is raised (Plate I, fig. 4). The ovipositor valvulae are serrated at the tip, enabling the female to drill down shafts that are wholly or partially blocked with bore-dust or other obstructions. The mean maximum breadth of the ovipositor was 0.07 mm. (range 0.05–0.09 mm.,  $n = 10$ ) compared with 0.32 mm. (range 0.23–0.35 mm.,  $n = 10$ ) in *S. noctilio*. The duration of drilling by *drewseni* was variable, depending on the depth of the drill and the numbers of siricid eggs (Table II). Probes of less than two minutes' duration were recorded down the short (1–2 mm.) trial drills or probes of the Siricids in which no eggs are found.

*I. drewseni* oviposits in the haemocoel of mature host embryos, or first, second and third instar larvae. Parasitised hosts have, on the cuticle surrounding the oviposition puncture, a ring of black scar-tissue, which is lost during the succeeding moult. *I. drewseni* is able to parasitise host larvae even when they have tunnelled from the oviposition shaft into the surrounding wood. One parasitised third instar host had a 1.5 mm. long frass-filled tunnel at right angles to the drill shaft, which was

TABLE I.—Emergence of *I. drewseni* and associated insects from three European localities

Country	Locality	Host tree	Species	Number		Emergence period
				♂	♀	
ENGLAND	Thetford Chase, Norfolk.	<i>Larix decidua</i>	<i>I. drewseni</i>	12	11	26 May–25 June
			<i>R. persuasoria</i>	64	34	11 May–11 Aug.
		<i>Pinus sylvestris</i>	<i>I. leucospoides</i>	6	8	10 Aug.–27 Oct.
			<i>S. noctilio</i>	20	13	12 Aug.–29 Sept.
			<i>U. gigas</i>	28	2	7 July–16 Aug.
SWITZERLAND	Ablandschen Valley, Jaun.	<i>Picea abies</i>	<i>I. drewseni</i>	16	6	21 May–10 June
			<i>R. persuasoria</i>	43	5	2 May–12 June
			<i>M. emarginatoria</i>	32	24	16 May–5 June
			<i>X. spectrum</i>	30	22	11 June–15 July
			<i>S. juvencus</i>	189	81	2 July–12 Aug.
FRANCE	Le Boreon, Alpes Maritimes.	<i>Picea abies</i>	<i>I. drewseni</i>	25	12	21 May–1 June
			<i>R. persuasoria</i>	133	42	12 April–17 July
			<i>M. emarginatoria</i>	15	26	21 May–15 June
			<i>I. leucospoides</i>	4	7	11 Aug.–19 Aug.
			<i>Ps. sternata</i>	8	7	16 May–1 June
			<i>X. spectrum</i>	9	7	25 June–17 July
			<i>S. juvencus</i>	768	199	13 July–11 Sept.
			<i>S. cyaneus</i>	3	1	23 July–23 Sept.
			<i>U. gigas</i>	1	1	3 July–24 July
<i>U. augur</i>	7	6	18 July–20 July			

TABLE II.—Duration of ovipositor probing by *I. drewseni* down the oviposition shafts of siricid species (10 observations per species)

Siricid species	Depth of oviposition shaft (mm.)	Number of siricid eggs per shaft	Duration of ovipositor probe by <i>I. drewseni</i> (minutes)
<i>S. noctilio</i>	5.2 (1–8)	0–3	5 (3–9)
<i>S. cyaneus</i>	5.7 (1–10)	0–4	11 (5–23)
<i>S. juvencus</i>	5.0 (1–18)	0–4	16 (8–36)
<i>U. gigas</i>	9.2 (2–16)	0–8	48 (41–58)

*Ibalia drewseni*

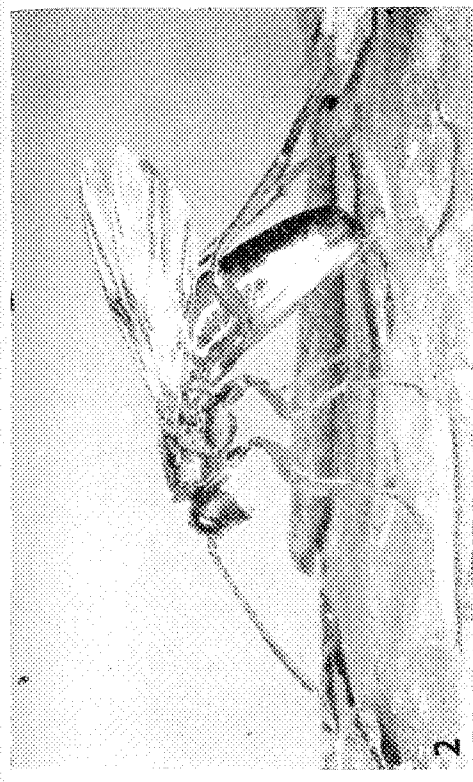
oviposition shafts the female stops (fig. 1), which are often inserted down to the depth of the palpation occupied 10-46 seconds. The antennae and lowers the gaster slightly exposed at the tip (Plate I, fig. 3) until the tip of the ovipositor passes down the shaft from its tip (Plate I, fig. 4). The ovipositor is used to drill down shafts that are not free of obstructions. The mean maximum length of shafts is 0.09 mm., n = 10) compared with *I. cincta*. The duration of drilling by the drill and the numbers of siricid eggs found in the shafts in which no eggs are found. The first, second or third instar host embryos, or first, second or third instar host embryos, which is lost during the succeeding stages, are even when they have tunnelled through the wood. One parasitised third instar host embryo, which was

*I. drewseni* in three European localities

Species	Number		Emergence period
	♂	♀	
<i>I. drewseni</i>	12	11	26 May-25 June
<i>I. asioria</i>	64	34	11 May-11 Aug.
<i>I. noides</i>	6	8	10 Aug.-27 Oct.
<i>I. asioria</i>	28	2	7 July-16 Aug.
<i>I. drewseni</i>	16	6	21 May-10 June
<i>I. asioria</i>	43	5	2 May-12 June
<i>I. ginatoria</i>	32	24	16 May-5 June
<i>I. sum</i>	30	22	11 June-15 July
<i>I. us</i>	189	81	2 July-12 Aug.
<i>I. drewseni</i>	25	12	21 May-1 June
<i>I. asioria</i>	133	42	12 April-17 July
<i>I. ginatoria</i>	15	26	21 May-15 June
<i>I. noides</i>	4	7	11 Aug.-19 Aug.
<i>I. ta</i>	8	7	16 May-1 June
<i>I. sum</i>	9	7	25 June-17 July
<i>I. us</i>	768	199	13 July-11 Sept.
<i>I. us</i>	3	1	23 July-23 Sept.
<i>I. us</i>	1	1	3 July-24 July
<i>I. us</i>	7	6	18 July-20 July

*I. drewseni* down the oviposition shafts (minutes)

Number of eggs	Duration of ovipositor probe by <i>I. drewseni</i> (minutes)
5	(3-9)
11	(5-23)
16	(8-36)
48	(41-58)



Oviposition by *I. drewseni*

FIG. 2.—Ovipositor tip being manoeuvred towards shaft entrance.  
FIG. 4.—During oviposition, abdomen returned to normal position.

FIG. 1.—Female palpating over a siricid oviposition shaft.  
FIG. 3.—Ovipositor passing down into shaft.

3.0 mm. deep. The mean length of the extended ovipositor of *drewseni* was 16.0 mm. (range, 12.0-21.5 mm.,  $n = 11$ ). Normally one egg is deposited in the host, but three embryos were found in one, and two eggs were common.

The *drewseni* embryo develops within the embryonic membrane, from which develops a conspicuous trophamnion composed of large, polygonal cells. After 15 days, the first instar larva emerges from the trophamnion (fig. 2b). The trophamnion undergoes no further change, and remains within the host throughout larval development. The first two larval instars each last 8-10 days. The second instar exuviae and particularly the mandibles are often attached to the cuticle of third instar larvae. The advanced third instar parasite emerges from the host larva when the latter is mature and moults into the final, fourth instar 45-50 days after oviposition. Pupation takes place within 20 days, and adults begin to emerge 104 days after oviposition. Longevity of adult *drewseni* at 25° C. was 37 days (range 10-43,  $n = 10$ ).

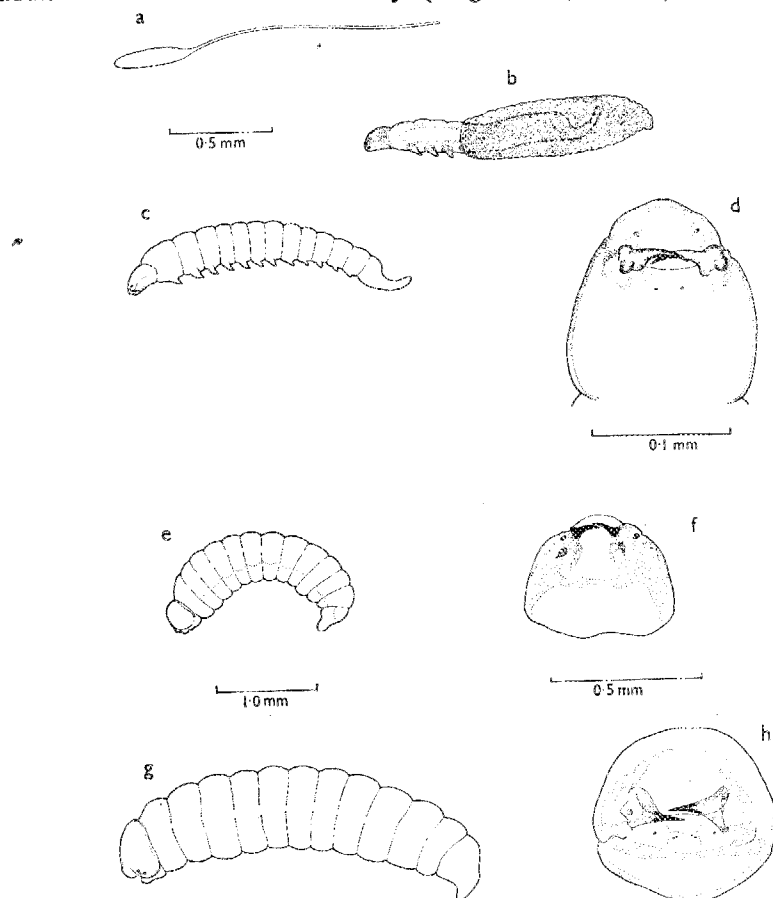


FIG. 2.—Immature stages of *I. drewseni*: (a) egg; (b) first instar larva emerging from trophamnion; (c) first instar larva; (d) head capsule of first instar larva; (e) second instar larva; (g) third instar larva; (h) head capsule of third instar larva.

#### HOST DETECTION STUDIES

Because *drewseni* emergence takes place in May and June, and the hosts emerge considerably later when few, if any, *drewseni* would be living, the parasite probably responds to siricid oviposition shafts of the previous year. Siricid oviposition shafts aged 1-2 days stimulated no drilling response but shafts made 12, 25, 34, 46, 149 and 161 days previously elicited oviposition behaviour. Successful parasitism was recorded in 46 day-old cultures, when most hosts were in the third or fourth instar with galleries

of 2–10 mm. separating them from the oviposition shaft. The highest level of parasitism (6 of 21 hosts) was recorded when *I. drewseni* was offered culture logs containing first instar larvae and advanced embryos (aged 9–14 days) of *S. noctilio*. Parasitism was recorded in the following species under laboratory conditions: *S. noctilio*, *S. juvencus*, *S. cyaneus* and *U. gigas*. Antennal palpation and drilling down oviposition shafts of *X. spectrum* were also recorded.

The emergence of *I. drewseni* coincides with that of *Rhyssa persuasoria* (L.), an ichneumonid ectoparasite of siricid larvae, and it was possible that *drewseni* behaved as a facultative cleptoparasite, utilising the drill shafts of *R. persuasoria* to gain access to the host. Although the two parasites were maintained together on siricid culture logs and a wide age-range of *persuasoria* drill shafts was offered, there was no evidence of cleptoparasitic behaviour.

Bioassay of fungal symbiont cultures aged 2 weeks, 4, 6, 8 and 10 months since inoculation resulted in antennal palping activity and ovipositor probing in response to all samples (Table III). No palpations or probes were made down holes into empty (control) cavities.

TABLE III.—Response of *I. drewseni* to cultures of symbiotic fungus

Age of fungus	Number of	
	palpations	drills
2 weeks . . . . .	13	3
4 months . . . . .	6	1
6 months . . . . .	6	2
8 months . . . . .	2	1
10 months . . . . .	2	2
Total . . . . .	29	9

#### DESCRIPTION OF THE IMMATURE STAGES

##### *Egg* (fig. 2a)

Acuminate, with hymenopteriform egg-body; length of egg body, 0.25–0.45 mm. (mean 0.34 mm.); width, 0.8–0.13 mm. (mean 0.10 mm.); long thin pedicel, 1.00–2.35 mm. (mean 1.41 mm.) ( $n = 10$ ). Chorion smooth, milky-white.

##### *First instar larva* (fig. 2b, c, d)

Length, 0.86–1.4 mm. (mean 1.06 mm.); width, 0.12–0.25 mm. (mean 0.16 mm.) ( $n = 6$ ). Composed of head and 13 body-segments. Colour creamy-white, semitransparent, shape fusiform with marked prolongation of terminal segment into an elevated tail. Body segments 1–12 each bear a pair of conspicuous pseudopodia, broad at base, more or less pointed distally; pseudopodia become progressively smaller towards caudal end. Head (fig. 2a) with well sclerotised falcate mandibles; pair of well developed sensorial pits in clypeal region; one or more pairs of ill-defined sensoria in labial region.

##### *Second instar larva* (fig. 2e, f)

Length, 2.1–2.4 mm. (mean 2.25 mm.); width 0.5–0.8 mm. (mean 0.65 mm.) ( $n = 4$ ). Shape fusiform, markedly arched dorsally, composed of head and 13 body-segments with reduced caudal tail on terminal segment. Pseudopodia wholly lacking. Colour creamy-white, slightly transparent, cuticle smooth without setae or papillae. Head with well sclerotised, falcate mandibles, which are relatively smaller and less robust than in the first instar.

##### *Third instar larva* (fig. 2g, h)

Length 3.5–4.4 mm. (mean 3.85 mm.); width 0.8–1.4 mm. (mean 1.10 mm.) ( $n = 4$ ). Similar to second instar except: caudal tail much reduced; mandibles not falcate, with straight blade, more than twice as long as those of second instar; well developed sensoria present in labial region.

##### *Fourth instar larva* (fig. 3)

Length 9.2–10.5 mm. (mean 9.90 mm.); width 2.6–4.5 mm. (mean 3.70 mm.) ( $n = 5$ ). Shape similar to third instar except: head much retracted into thoracic region; caudal tail absent. Colour creamy-white, not transparent. Pairs of well-developed disc-like pleural swellings on body segments 2–11. Spiracles (fig. 3c) present on body segments 2–11; spiracle on first abdominal segment much reduced (fig. 3d); spiracle on eighth abdominal segment vestigial; atrium globose with sclerotised

n shaft. The highest level of para-  
*seni* was offered culture logs cons-  
 s (aged 9-14 days) of *S. noctilio*.  
 s under laboratory conditions: *S.*  
 es under palpation and drilling down  
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 maintained together on siricid culture  
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weeks, 4, 6, 8 and 10 months since  
 and ovipositor probing in response  
 robes were made down holes into

*Cultures of symbiotic fungus*

Number of	drills
ants	3
	1
	2
	1
	2
	9

**IMMATURE STAGES**

egg body, 0.25-0.45 mm. (mean 0.34 mm.);  
 1.00-2.35 mm. (mean 1.41 mm.) (n = 10).

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 site, semitransparent, shape fusiform with  
 tail. Body segments 1-12 each bear a pair  
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 ) with well sclerotised falcate mandibles;  
 e or more pairs of ill-defined sensoria in

mm. (mean 0.65 mm.) (n = 4). Shape  
 d 13 body-segments with reduced caudal  
 Colour creamy-white, slightly transparent,  
 l sclerotised, falcate mandibles, which are

mm. (mean 1.10 mm.) (n = 4). Similar  
 bles not falcate, with straight blade, more  
 d sensoria present in labial region.

5 mm. (mean 3.70 mm.) (n = 5). Shape  
 oracic region; caudal tail absent. Colour  
 sc-like pleural swellings on body segments  
 spiracle on first abdominal segment much  
 vestigial; atrium globose with sclerotised

annulation, leading directly into well defined closing apparatus. Larval cuticle smooth except pleural discs which bear small pointed papillae. Head (fig. 3b) with well developed, sclerotised tridentate mandibles; disc-like antennal pits each with pair of small sensoria; silk press well-defined, sclerotised; clypeus with lobed ventral margin; labrum emarginate ventrally, half-covering mandibles, bearing 7-8 pairs of sensoria; maxillary areas each with one rudimentary palp bearing 4 small sensoria; labial area with pair of rudimentary palps each with 3-4 small sensoria; ventral margins of labrum, maxillae and labium with minute papillae.

*Comparisons with the immature stages of I. leucospoides*

The immature stages of *drewseni* are very similar to those of *leucospoides*. The eggs appear identical. The first instar larva of *drewseni* can be distinguished from that of *leucospoides* by the pseudopodia, which are considerably larger and more fleshy, and also more conspicuous on abdominal segments 7-9, in *leucospoides*. The caudal tail of *drewseni* tends to be more pronounced and relatively larger. The trophamnia are very similar. Second instars of *drewseni* have a relatively smaller head but are otherwise similar. The third instar larvae of both species are indistinguishable.

The final instar larvae are readily distinguished, because the first abdominal spiracle of *drewseni* is considerably reduced (fig. 3a), and the atria of the remaining spiracles are markedly globose with a narrow stalk, compared with the relatively undifferentiated atrium and stalk of *leucospoides* (fig. 3e).

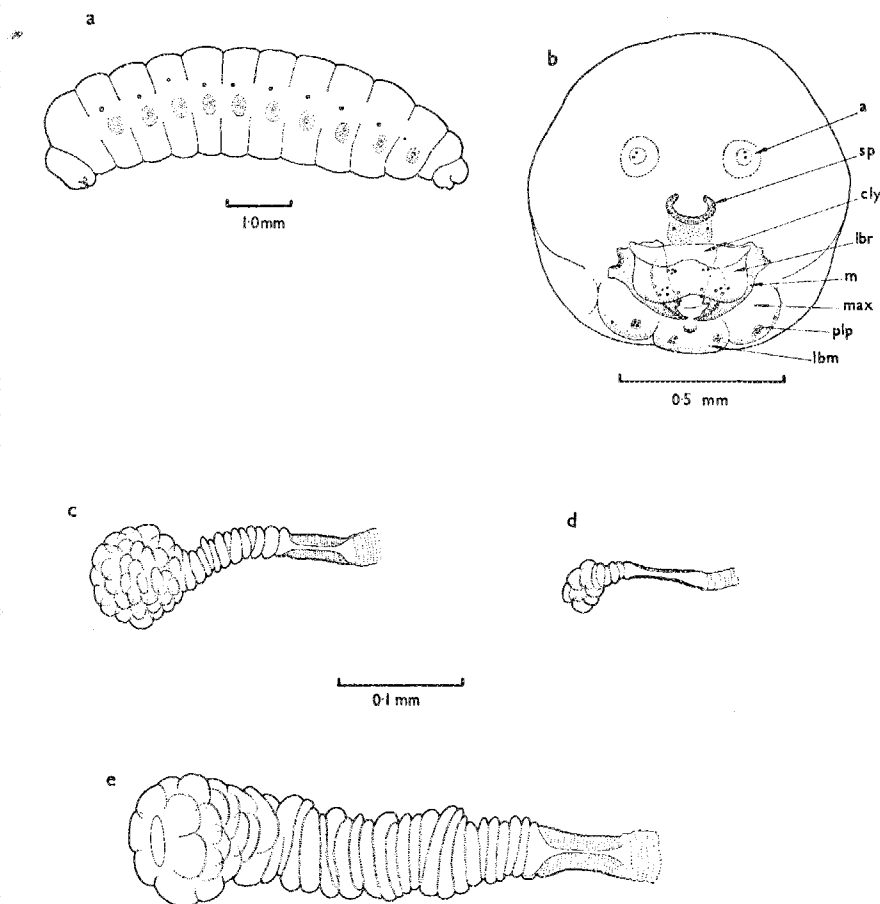


FIG. 3.—Final instar larvae of *Ibalia* species. (a-d) *I. drewseni*: (a) final instar larva; (b) head capsule of final instar larva; (c) mesothoracic spiracle; (d) first abdominal spiracle. (e) *I. leucospoides*, mesothoracic spiracle. a, antenna; cly, clypeus; lbr, labium; lbr, labrum; m, mandible; max, maxilla; plp, palp; sp, silk press.

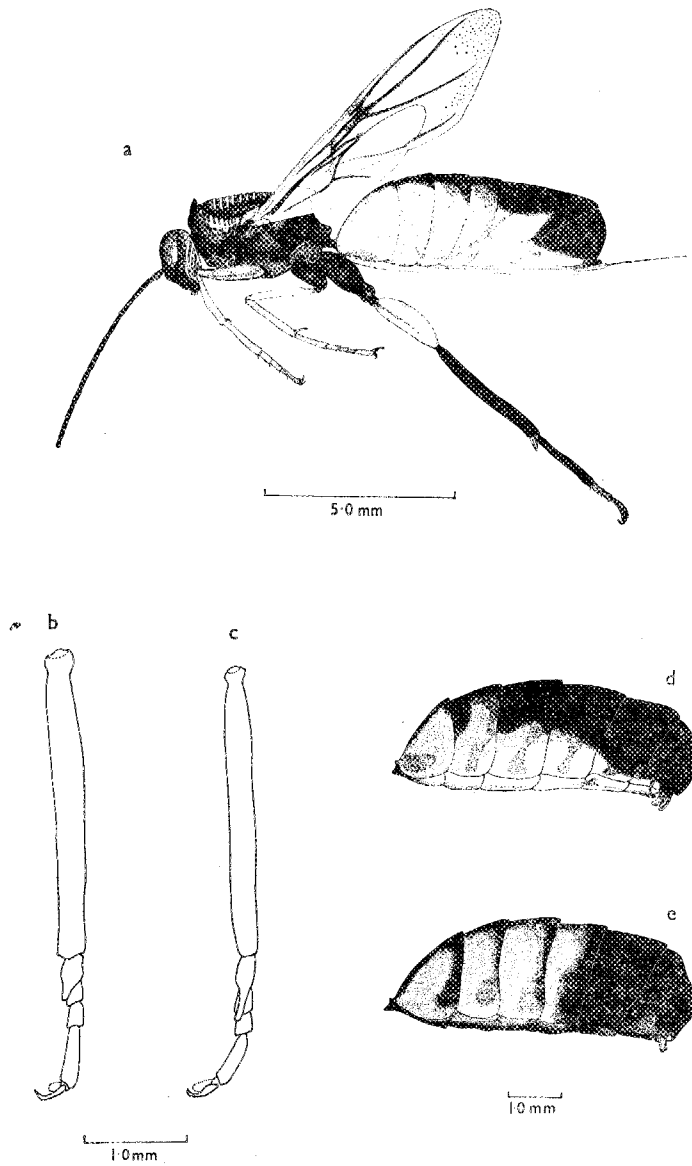


FIG. 4.—(a) *I. drewseni*, female. (b) Metathoracic tarsus of *I. drewseni*. (c) Metathoracic tarsus of *I. leucospoides*. (d) *I. drewseni*, male gaster. (e) *I. leucospoides*, male gaster.

KEY TO ADULTS OF *drewseni* AND *leucospoides*

Femur, tibia, tarsus of pro- and mesothoracic legs reddish-brown. Metathoracic legs except femur, and sometimes (? often) tibia and distal segments of tarsus in part, black. Sides of pronotum less strongly and extensively rugose, with short transverse rugae above, less strongly rugose below. Prolongation of second metathoracic tarsal segment almost or just reaching apex of third segment (fig. 4b). Gaster mainly black dorsally, red below with large amber-coloured translucent area (fig. 4a, d). Propodeum without pair of distinct teeth. Length: female, 11–14 mm.; male, 7–11 mm. . . . . *drewseni* Borries



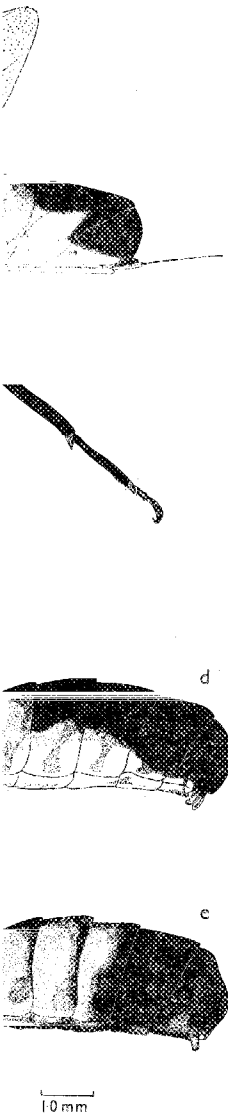
Legs  
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*I. drew*  
altitudes  
from which  
ENGLAND  
SWITZERL  
1643 m., T  
50 m.; Sw  
377 m., B  
Eger 650  
1100 m.; T  
Sogut 160

*I. drew*  
(Italy), B  
Kieffer, 1  
and *S. juv*

*I. drew*  
*A. cilicic*  
*Pinus syl*  
species w  
*X. spectr*  
from the





of *I. drewseni*. (c) Metathoracic tarsus  
 e) *I. leucospoides*, male gaster.

AND *leucospoides*

bracic legs reddish-brown.  
 etimes (? often) tibia and  
 es of pronotum less strongly  
 e rugae above, less strongly  
 etathoracic tarsal segment  
 nt (fig. 4b). Gaster mainly  
 r-coloured translucent area  
 tinct teeth. Length: female,  
 . . . . . *drewseni* Borries

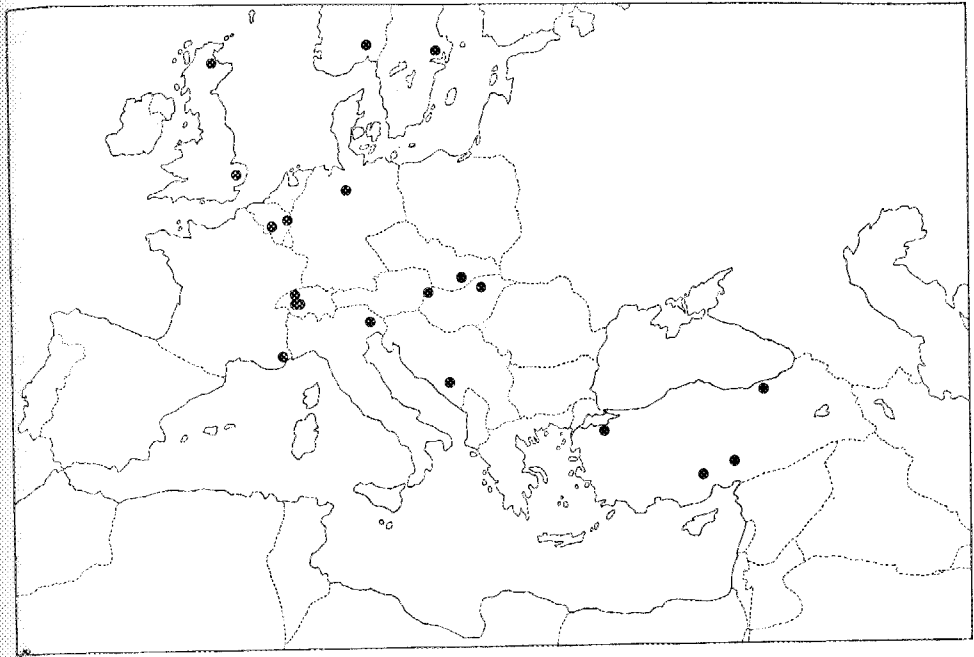


FIG. 5.—Distribution of *I. drewseni*

Legs black. Sides of pronotum strongly transversely rugose on about half of its area or more. Prolongation of second metathoracic tarsal segment normally extending distinctly beyond apex of third segment (fig. 4c). Gaster mainly red or reddish-black, not translucent (fig. 4e). Propodeum with pair of very distinct teeth. Length: female, 9–15 mm.; male, 9–14 mm. . . . . *leucospoides* (Hochenwarth)

DISTRIBUTION AND HOST RECORDS

*I. drewseni* was recorded from 18 European and 4 Turkish localities (fig. 5) at altitudes of 15–1643 metres, and was most abundant in Switzerland. Localities from which *drewseni* was recorded were:

ENGLAND: Thetford 15 m. (Norfolk); SCOTLAND: Dalroy 150 m. (Inverness-shire); SWITZERLAND: Jaun 1600 m., Lucelle 770 m., Delemont 895 m.; FRANCE: Le Boreon 1643 m., Tend 1100 m., Turini 1607 m. (Alpes Maritimes); GERMANY: Fallingbostel 50 m.; SWEDEN: Skokloster 50 m.; NORWAY: Nordmarker 130 m.; BELGIUM: Eupen 377 m., Rochefort 100 m.; ITALY: Carnia 1100 m.; HUNGARY: Sopron 250 m., Eger 650 m.; CZECHOSLOVAKIA: Banska Stiavnica 725 m.; YUGOSLAVIA: Knezina 1100 m.; TURKEY: Meryamana 1200 m. (Trabzon), Orhaneli 400 m., Namrun 1400 m., Sogut 1600 m. (Karsanti).

*I. drewseni* had been previously recorded from Copenhagen (Denmark), Piedmont (Italy), Budapest (Hungary) and Kashiho (Saghalien) (Borries, 1891; Dalla Torre & Kieffer, 1910; Yasumatsu, 1937), and previously recorded hosts were *S. noctilio* and *S. juvencus* in Denmark (Borries, 1891).

*I. drewseni* was reared from the following host-tree species: *Abies alba* Miller, *A. cilicica* (Antoine and Kotschy) Carr., *Picea abies* (L.), *P. orientalis* (L.) Link, *Pinus sylvestris*, *P. brutia* Ten. and *Larix decidua* Miller. The associated siricid species were *S. noctilio*, *S. juvencus*, *S. cyaneus*, *U. gigas*, *U. augur augur* (Klug) and *X. spectrum*. Several species of Curculionidae and Cerambycidae were also recorded from the siricid-infested material. Parasitism of Siricids by *drewseni* ranged from

less than 1 to 36 per cent., compared with 1-71 per cent. by *leucospoides* from the same localities.

*I. drewseni* has been sent to Tasmania, Australia, for breeding and subsequent release in the plantations of *P. radiata* D. Don infested by *S. noctilio*.

#### DISCUSSION

*I. leucospoides* and *I. drewseni* were the only species of cynipoid parasite reared from siricid-infested timber collected in Europe, Turkey and Morocco. Colour variants, e.g. the dark forms of *leucospoides* from south-west Europe, probably account for the confused state of *Ibalia* taxonomy.

*I. drewseni* has been discovered infrequently and at relatively low population levels over a wide geographical area. In its northern European range, *drewseni* occurs in temperate zone areas, where winter temperatures are low and mean annual precipitation is high. Eastern European records are from areas of continental climate, and at its southern limits in south-west France and Yugoslavia the localities are essentially alpine. *I. drewseni* was only recorded from one area (Orhaneli, Turkey) having a Mediterranean-like climate.

The life cycle of *drewseni* is similar to that of *leucospoides*, and there are only minor differences in their immature stages. The major differences in their biology are the periods of emergence and the subsequent nature of parasitism. *I. leucospoides* parasitises mature embryos and first and second instar larvae before they migrate too far into the wood from the oviposition shaft (Chrystal, 1930), and it is well synchronised with the host. By contrast, *drewseni* emerges up to four weeks before female Siricids appear, and six or more weeks before the hosts are suitable for parasitisation. Therefore *drewseni* parasitises siricid larvae produced the previous autumn. Late-emerging siricid females oviposit until mid-October, and the eggs hatch at the end of the month or later. Under winter conditions in Tasmania, eggs of *S. noctilio* took up to three months to hatch (Coutts, 1965). Siricid eggs and young larvae overwinter and many would be susceptible to *drewseni* the following spring. This was confirmed when old culture logs were offered to *drewseni* females, which were attracted to the oviposition shafts. They were able to parasitise third instar larvae even when the hosts were some millimetres from the oviposition shaft. The low numbers of *drewseni* probably reflect the number of hosts available in May and June, compared with the situation presented to *leucospoides* in the autumn.

Madden (1968) has described the responses of *leucospoides* to cultures of the fungal symbiont from *S. noctilio*, *Amylostereum* sp. The present study confirms that both *Ibalia* species are stimulated to oviposition behaviour when presented with siricid symbionts, although the response of *drewseni* was considerably less intense. It is possible that *drewseni* and *leucospoides* respond to similar attractants, but the fungal activity associated with the age of the oviposition shafts available to *drewseni* could differ, although fungal metabolism would probably be much reduced during the winter. Oviposition responses cannot be to the symbiont only, because they were released by the shafts of *X. spectrum*, which do not contain a symbiotic fungus, although air-borne fungal spores can enter the shaft and develop in the wood. Fungal mycelium was found in the oviposition shafts of *X. spectrum* five days after oviposition (*unpublished data*).

Despite the relatively low percentage parasitism of Siricids by *drewseni*, this species occupies a particular niche within the parasite complex that helps to maintain siricid populations at a comparatively low level in Europe. Its parasitism is complementary to that of *leucospoides*, which parasitises siricid embryos and larvae in the autumn, although the possibility exists that *leucospoides*-parasitised larvae could be parasitised by *drewseni* the following spring. If multiparasitism occurs, presumably only one larva would survive, because this happens when superparasitism occurs (as it commonly does) in both species.

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Although *I. drewseni* has rarely been found in areas of Europe with a typical Mediterranean climate, it has been consigned to Tasmania for further study and for possible release in pine plantations infested with *S. noctilio*, and there seems to be no reason why this species should not become established and take its place with other imported parasites in helping to control *S. noctilio* in Australia, particularly in the cooler and wetter parts of its host's range.

## SUMMARY

*Ibalia drewseni* Borries is recorded from England, Scotland, Norway, Sweden, France, Switzerland, Czechoslovakia, Turkey and Yugoslavia for the first time.

Under experimental conditions, the females seek out siricid oviposition shafts made during the preceding autumn and oviposit in the young larvae. At 25°C., embryos develop in the course of 8–10 days and are surrounded by a characteristic trophamnion. After 15 days, the first instar larvae emerge from the trophamnion. The first and second larval instars are each of 8–10 days duration. The third instar larvae emerge from the host body and enter the final instar approximately two weeks later. After the host is consumed, the larvae pupate, and adults begin to emerge 104 days after oviposition.

Females of *I. drewseni* respond positively to a wide age range of siricid oviposition shafts (14–300 days), and are able to parasitise 46-day-old third instar larvae, even when these have burrowed into the wood and have a frass-filled gallery separating them from the oviposition shaft. All siricid species offered to *drewseni* elicited oviposition behaviour. *I. drewseni* responds to cultures of the symbiotic fungus, *Amylostereum* sp., with typical antennal palpation behaviour, and probing with the ovipositor into fungus-filled cavities has been recorded.

The pseudopodia of the first instars of *I. drewseni* and *I. leucospoides* (Hochenwarth) are similar and probably typical of *Ibalia* species. The final instar larvae of the two species are readily distinguished on the basis of a reduced first abdominal spiracle in *drewseni*. *I. drewseni* and *I. leucospoides* are probably the only species of *Ibalia* in western Europe, Turkey, and North Africa, and a key for the separation of the adults is given.

I am indebted to the Commonwealth Institute of Entomology for its help in determining the adult material and to Dr. G. J. Kerrich for providing an original key for separating the *Ibalia* species. I also wish to thank Mr. Frank Wilson for his helpful criticism of the manuscript, and Mr. L. T. Woolcock for taking the photographs.

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