THE EPITHELIUM OF THE GUT AS A BARRIER AGAINST ENCAPSULATION BY BLOOD CELLS IN THREE SPECIES OF PARASITOIDS OF BUPALUS PINIARIUS (LEP., GEOMETRIDAE)

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SUMMARY

Three habitual parasites of the pine looper are generally not eliminated by the haemocytic defence reaction of their usual host, because the eggs are laid or the larvae settle behind the epithelium of the gut. This acts as a barrier against the passage of blood cells. This conclusion is supported by the observation that larvae of all three species are encapsulated during abnormally long stays in the host's body cavity. In two species this results from the parasitoid's failure to oviposit in the usual way, being either egg deposition at a less favourable site on the host's integument, or in a less suitable larval instar of the host. In the third species encapsulation results from the failure of the parasitoid's larva to enter the mid-gut due to some unknown factor(s) related to superparasitism.

INTRODUCTION

Many insect species defend themselves against the invasion of the haemocoel by parasitoids (tachinid flies and braconid and ichneumonid wasps) by the formation of a covering of blood cells and melanin laid down around the parasitoids' eggs or larvae. This process of encapsulation causes the death of the parasites involved, most probably due to asphyxiation (SALT 1970).

In spite of this, each species of insect has some habitual parasitoids against which the defence reaction is usually ineffective. These parasitoids have evolved various devices which enable them to escape encapsulation by the blood cells of their usual host. For example, the females of some wasp species coat their eggs with a substance which prevents the proper reaction of the host's blood cells, or the larva produces a substance that suppresses the immune reaction of the host (SALT 1968, NAPPI 1975). Others lay their eggs in particular organs of the host, or the larvae penetrate such organs, which are apparently inaccessible to blood cells. This way of avoiding the defence reaction is demonstrated by three species of habitual parasitoids of the larvae of the pine looper, Bupalus piniarius L. It will be shown that it is highly probable that these parasitoids use the epithelium of the host's gut as a barrier against its immuno-competent haemocytes.
OVIPOSITION AND LARVAL SETTLEMENT

Two species of flies (Diptera, Tachinidae), Eucarcelia rutilla (Will.) and Blondelia piniariae Htg. (after HERTING 1960) have been reported as parasitoids of the pine looper over large parts of the host's range (ESCHERICHI 1931, THOMPSON 1944). Also, a wasp, Poecilostictus cothurnatus (Grav.), (Hymenoptera, Ichneumonidae), although less widely distributed and less common than the tachinids, has been reared from B. piniarius at several localities in Europe (HEQUIST 1948, JÄNNER 1937, PERKINS 1959, PLOTNIKOV 1914, URBAN 1966). In the field population we have studied in the central part of the Netherlands, all three species are present annually, although the percentage of parasitization may vary considerably between years.

Several aspects of the biology of E. rutilla have been studied in considerable detail by HERREBOUT (1966, 1969). Some relevant features of its reproductive biology may be summarized as follows. The female is oviparous and attaches its eggs to the integument of the caterpillar, preferably of the segments 2, 3 and 4. During the first hours after deposition the larvae hatch by making a hole through the chorion and the integument of the host; they then enter the body cavity, and normally find their way to the wall of the fore-gut. There they settle between the single layer of flat epithelial cells and the cuticular lining of the lumen of the gut (fig. 1).

The bionomics of B. piniariae have been described by DowDEN (1933). This species is also oviparous. The egg is not laid externally, but is deposited directly into the body cavity of the host by means of a sharp piercing organ, preferably in the segments 5 to 8. The egg hatches immediately after deposition, and the active maggot enters the mid-gut, normally within a quarter of an hour, by making a hole in the epithelium, which closes soon after its passage. The maggot finally settles between the epithelium and the peritrophic membrane, where it attaches its posterior spiracles, by means of the stigmatic hooks on the last segment, to one of the host's tracheae situated on the outer surface of the gut (fig. 1).

Fig. 1. Schematic representation of the sites of oviposition (1) and of the sites of larval settlement (2) in three species of parasitoids of the host B. piniarius. For further explanation see text.