

INSECT PARASITES OF THE WINTER MOTH,
OPEROPHTERA BRUMATA (L.)
(*LEPIDOPTERA* : *GEOMETRIDAE*) IN WESTERN EUROPE

By

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Introduction.

The winter moth, *Operophtera brumata* (L.), an economically important defoliator of fruit and deciduous forest trees in most of western Europe, was introduced into Nova Scotia, Canada a number of years ago and was first discovered there in 1949. Because native insect parasites were not preventing heavy defoliation in Canada each year, the advisability of establishing European parasites was investigated. Only limited information on these was found in the literature; therefore, large numbers of winter moth were reared in Europe and Canada from larvae and, to a lesser extent, eggs and pupae collected in Europe from 1952 to the end of 1956. These rearings provided much new information on the natural control of *O. brumata* in Europe, as well as colonies of several parasite species that were later liberated in Nova Scotia. A list of all known winter moth parasites in Europe, both of species recorded in the present study and compiled from the literature, and information on the life-history and distribution of the former, is given in the present paper.

Mr. J. H. McLEOD and Dr H. E. WELCH, Entomology Laboratory, Belleville, Ontario, were actively associated with this project: the former directed all investigations in Europe in 1956 and the latter was similarly engaged in 1954 and collaborated with the author in Europe in 1955. The author wishes to thank both officers for permission to include results of their respective studies in the present publication, and for helpful suggestions in the preparation of the latter. Dr. K. LEIUS, Entomology Laboratory, Belleville, kindly prepared the German Summary. Dr. H. C. COPPEL arranged for collections at Kiel and Versailles in 1952. Dr. W. KOLLMER, now of the Fisheries Laboratory, Walvis Bay, South-west Africa, was responsible for much of the collection, rearing, and shipments from Germany in 1955 and 1956.

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Materials and Methods

Winter moths were collected in various localities in western Europe (fig. 1) to see whether there were important local differences in the composition and incidence of the parasite fauna. Collections were made both from localities where the moth was scarce and from where it caused complete defoliation. Eggs were collected only at Oldenburg and reared there and at Darmstadt. Larvae were collected mostly as fourth and fifth instars in all localities except Kranichstein and Visingsö, from fruit or deciduous forest trees. The caterpillars were beaten from the foliage, collected by hand, or trapped after they had matured and dropped to the ground. They were dissected or reared until they pupated. Pupae were collected from the soil beneath oaks at Kranichstein and Kullaberg. These pupae, as well as all host pupae and immature parasites reared in Europe, were either dissected or shipped by air to Belleville. They were shipped in clean, slightly moistened sawdust in sealed tins packed in sealed cardboard or wooden boxes; between alternate layers of corrugated cardboard and cellulose padding in sealed wooden boxes; or in closed plastic bags that were enclosed in sealed wooden or cardboard boxes. Adult parasites were shipped in wooden boxes of the type described by Delucchi (1958).

The total number of hosts and parasites shipped to Belleville during the study was 182,414; the yearly totals were: 1952, 981; 1953, 943; 1954, 7,578; 1955, 50,879; 1956, 122,033. The numbers from each locality, with the years



FIG. 1. — Winter moth collection and study localities in western Europe.

of collection indicated in brackets, were as follows: Assen 27 (1955); Bingen 9 (1954), 200 (1955); Braunsfels 407 (1954); Bruchsal 713 (1955); Dannenfels 184 (1954); Durbach 20 (1954); Frankfurt 17,517 (1955), 12,650 (1956); Hasselt 4,912 (1955); Heidelberg 1,030 (1955), 480 (1956); Herznach 333 (1953); Holten 137 (1955); Kiel 31 (1952); Kullaberg 10,538 (1956); Luscherz 3,200 (1954); Mingolsheim 2,283 (1955); Oberflockenbach 1,382 (1954); Oberkirch 460 (1956); Oland 10,111 (1956); Oldenburg 3,164 (1955), 10,594 (1956); Oostmalle 3,940 (1955); Reuver 562 (1955); Schorndorf 1,746 (1954); Simpelveld 184 (1955); Versailles 263 (1952), 610 (1953), 7,463 (1955), 75,600 (1956); Vianen 694 (1955); Visingso 1,600 (1956); Wytham 687 (1952), 3,053 (1955); Zunsweier 630 (1954).

Most of the shipments were received at Belleville during June or early July. In nature the moths emerge late in the autumn, and the parasites emerge either in the summer or in the following spring; therefore, the material was held in quarantine for almost a year in conditions that resembled as closely as possible conditions encountered in nature, to obtain emergence of all species of contained parasites. When received at Belleville hosts and parasites were placed in slightly-damp, sterilized sand or vermiculite at 15-18 °C. and maintained in this condition until mid-October. The temperature was then reduced to 6.5 °C. and moths emerged from late October until early January. All host cocoons that contained immature parasites, and all naked, immature parasites were stored at either 2 °C. or -4.5 °C. from mid-January until approximately May 10; if held at 6.5 °C. during this interval many parasites would have emerged in mid-April and died before effective liberation in Nova Scotia. The environmental temperature was raised to 6.5 °C. for about a week on about May 10, then to 18 °C. for parasite emergence. Cocoons were kept damp by adding water to the vermiculite, as otherwise a large proportion of the parasite adults died just before emerging.

Egg Parasites.

Research on species that attack winter moth eggs was made only during the winter of 1954-1955 at Oldenburg and Darmstadt, Germany. Branches approximately 30 centimetres long on which winter moth eggs had recently been laid were cut from the tops of apple trees near Oldenburg in early December. Some branches were brought into the laboratory, and larvae hatched from 97.1 per cent of the 933 eggs on them; the remainder of the eggs were infertile or were damaged in handling. The other branches were hung in apple trees in orchards adjacent to oak forests at both Oldenburg and Darmstadt. A proportion of the branches in each locality was brought into the laboratory on December 31, February 28, March 31, and April 30, and the eggs removed, counted, and reared to determine the presence and time of parasitism in both localities. Larvae hatched from 85.7 per cent of the 468 eggs tested at Darmstadt and from 83.9 per cent of the 3,114 eggs at Oldenburg. As no parasites emerged, it was concluded that egg parasitism in the infested apple orchards at Oldenburg and Darmstadt was negligible.

The only egg parasite of winter moth recorded in the literature is *Telenomus nitidulus* THOMS. (*Hymenoptera: Scelionidae*) (SCHREINER, 1916). MOKRZECKI and BRAGINA (1916) experimentally bred *Trichogramma semblidis* (AUR.), and HASE (1925), who synonymized *T. semblidis* and *T. evanescens* WESTW., listed the latter species as a winter moth parasite on the basis of their studies. This is, of course,

no indication that *T. evanescens* naturally attacks *O. brumata*; in fact, *T. evanescens* and *T. semblidis* are now considered distinct (MUESEBECK, KROMBEIN, and TOWNES, 1951).

Larval Parasites.

Records from the present investigation and from the literature of species that attack winter moth larvae are arranged alphabetically below. The European range of each species recorded in the present study is indicated partially by positive records but its absence from any locality is not necessarily indicated by negative records because small numbers of winter moth from many localities were reared and because some collections were of host instars that are usually not attacked by certain parasite species.

Hymenoptera: Braconidae

Apanteles albipennis (NEES). — Listed as a winter moth parasite by THIEM (1922) and SILVESTRI (1941) on the basis of studies by earlier investigators.

Apanteles ater (RATZ.). — Listed as a winter moth parasite by THIEM (1922) and SILVESTRI (1941) on the basis of studies by earlier investigators. However, WILKINSON (1945) doubted that *A. ater* parasitizes winter moth because, though the original description was of specimens reared from a host on apple believed to be *O. brumata*, the parasite has since been reared from various species, not including winter moth, that also infest apple trees.

Apanteles carbonarius (WESM.). — Listed as a winter moth parasite by THIEM (1922), WILKINSON (1940*b*), and SILVESTRI (1941), on the basis of studies made by earlier investigators.

Apanteles difficilis (NEES). — WAGNER (1929) recorded this species as a winter moth parasite in northern Germany.

Apanteles fulvipes (HAL.). — Listed as a winter moth parasite by SILVESTRI (1941) on the basis of rearings made by earlier investigators. The species is now known as *A. liparidis* (BOUCHÉ) (WILKINSON, 1945).

Apanteles immunis (HAL.). — MARSHALL (1888), THIEM (1922), and SILVESTRI (1941) recorded this species as a winter moth parasite on the basis of work by earlier investigators.

Apanteles jucundus MARSH. — This braconid was reared during the present study from winter moth larvae collected on fruit and orchard trees at Dannenfels, Durbach, Frankfurt, Heidelberg, Mingolsheim,

and Oberflockenbach. This is its first record as a parasite of *O. brumata*. It occurs in Britain (MARSHALL, 1888) and probably in other western European countries. The larva is a solitary endoparasite that, when mature, spins a yellow cocoon on the leaf or branch. The adult emerges about two weeks later. Presumably the adult attacks other species in summer. Adults of an undetermined *Mesochorus* sp. and of *Haplaspis nanus* (GRAV.) (*Hymenoptera: Ichneumonidae*) were reared from cocoons of *A. jucundus* that had been reared in captivity from field-collected winter moth larvae; therefore, the adults of both hyperparasite species must have oviposited in or on developing larvae of *O. brumata*. Females of *H. nanus* may also attack cocoons of *A. jucundus*, because they parasitize cocoons of *A. rubecula* MARSH. in England (RICHARDS, 1940).

Apanteles juniperatae (BOUCHÉ). — MARSHALL (1888) and THIEM (1922) on the basis of studies by earlier investigators, and DELUCCHI (1953) recorded this species as a winter moth parasite.

Apanteles praepotens (HAL.). — WILKINSON (1940a) recorded this species as a parasite of winter moth in Britain and Germany.

Apanteles sessilis (ILL.). — Listed by BOURDIN (1922) and SILVESTRI (1941) as a winter moth parasite, on the basis of earlier studies by other investigators.

Apanteles sp. — One female was reared from a winter moth larva collected at Kiel.

Meteorus abscissus THOMS. — SILVESTRI (1941) listed this species on the basis of studies by earlier investigators.

Meteorus ictericus (NEES). — Reared by REICHERT (1933) from winter moth in Germany. MARSHALL (1891), THIEM (1922), and SILVESTRI (1941) also list it on the basis of earlier studies by other investigators.

Meteorus lionotus THOMS. — Reared by HADERSOLD (1938) from winter moth in northern Germany.

Meteorus pallidus (NEES). — Reared by FEYTAUD (1928) in south-western France. MARSHALL (1891), THIEM (1922), and SILVESTRI (1941) list it on the basis of investigations by earlier workers.

Meteorus pulchricornis (WESM.). — Reared by HADERSOLD (1938) in northern Germany. MARSHALL (1891), MORLEY (1914), and THIEM (1922) also list it on the basis of studies by earlier investigators.

Meteorus scutellator (NEES). — Reared by HADERSOLD (1938) in northern Germany.

Meteorus versicolor (WESM.). — Reared by HADERSOLD (1938) in northern Germany.

Meteorus sp. — One male was reared in the present study from a winter moth larva collected at Kiel.

Rogas testaceus (SPIN.). — Reared from winter moth collected on hazel at Oland. Though recorded previously from this species only in England (VARLEY and GRADWELL, 1958), it is widely distributed in Europe and Asia and may, therefore, be an incidental parasite of *O. brumata* over a large area. One parasite larva pupated inside the empty fifth-instar host, and the parasite adult emerged through a hole that it made on the ventral side of the caterpillar near its posterior end. Details of the parasite's life-history in India were published by MUZZAFER AHMAD (1944). One female of *Astiphromma strenuum* (HOLMG.) (*Hymenoptera: Ichneumonidae*) was reared in July from a pupa of *R. testaceus* from Oland.

Hymenoptera: Ichneumonidae

Agrypon flaveolatum (GRAV.). — Recorded as a parasite of *O. brumata* by MORLEY (1914) and HADERSOLD (1938); the latter author referred to it as *A. septentrionale* (HOLMG.), which was synonymized with *A. flaveolatum* by KLOET and HINCKS (1945). It was recorded in the present study in all collections from Sweden, France, Belgium and England, at Bingen, Frankfurt, Mingolsheim, Oberflockenbach, Oldenburg, and Schorndorf in Germany, and at Holten and Simpelveld in Holland. It also occurs in northern Switzerland (WIESMANN, 1944).

There is one generation each year. Adults emerge in spring and oviposit in winter moth larvae on the foliage. The latter pupate and the parasite larvae mature in autumn and pupate within transparent cocoons inside the empty winter moth pupae. Only one parasite matures in each host. Winter moth larvae are attacked on both orchard and forest trees.

Apechthis rufata (GMEL.). — One male emerged from a winter moth cocoon collected several weeks earlier as a larva on cherry at Zunsweier. This is the first record of parasitism of this host by this ichneumonid.

Aptesis abdominalator (GRAV.). — MR. J. F. PERKINS, who identified specimens of this species, believes it to be the same as *Microcryptus brumatae*, which was first described by SILVESTRI (1941) from specimens reared from winter moth collected in southern Italy. Therefore the name *brumatae*, which was also used by ARDÖ (1956) for specimens reared from *O. brumata* at Kullaberg, is a synonym of *abdominator*.

There is one generation each year; adults emerged in the spring of 1957 from winter moth cocoons collected in June, 1956, in the ground at Kullaberg and from cocoons reared from larvae collected

in May, 1956, at Versailles and exposed in the collection locality for several days after cocoons had formed. Dissections showed that the hosts were killed as mature larvae soon after cocoon formation. No adults of *A. abdominalis* emerged from winter moth cocoons reared from larvae and not exposed to subsequent parasitism; therefore, the parasite adults apparently find host cocoons in the soil and lay on the larvae inside them, and the parasites develop and spin cocoons inside those of the host. One parasite matured in each host. The occurrence of *A. abdominalis* in Sweden, France, and Italy indicates that it may be a parasite of winter moth in most of western Europe.

Campoplexis (= *Sagaritis*) *zonata* (GRAV.). — Reared by FEY-
taud (1928) from winter moth in southwestern France.

Campoplex (= *Omorgus*) *mutabilis* (HOLMG.). — One male emerged in July from a winter moth cocoon that was reared from a caterpillar collected on oak at Kullaberg approximately a month earlier. Previously, *C. mutabilis* was reared from winter moth in England by BROOKS and BROWN (1936). It has been recorded frequently from various hosts throughout most of Europe and may, therefore, be an incidental parasite of *O. brumata* throughout most of its range.

Cratichneumon culex (MULL.). — One male emerged in July from a winter moth cocoon collected in the soil beneath oak trees at Kullaberg shortly after winter moth larvae matured. This is the first record of winter moth parasitism by this ichneumonid. The time of attack and the host stage attacked are unknown.

Cratichneumon (= *Ichneumon*) *fabricator* (FAB.). — Listed by THIEM (1922) and SILVESTRI (1941) on the basis of studies by earlier investigators.

Cryptus poecilopus RDW. — Reared from winter moth by earlier investigators, according to THIEM (1922) and SILVESTRI (1941). The correct identity of this species is unknown.

Dusona (= *Campoplex*) *pugillator* (L.). — MORLEY (1914), THIEM (1922) and SILVESTRI (1941) listed this species as a winter moth parasite on the basis of studies by other, earlier investigators; however, MORLEY doubted the accuracy of the earlier records.

Ephialtes pictipes (GRAV.). — Three specimens that were reared from *O. brumata* that originated on fruit trees at Schorndorf constitute the first record of winter moth parasitism by this ichneumonid. Parasite eggs were laid on host caterpillars, and larvae that hatched from them developed externally and spun silken, transparent cocoons on the foliage. Parasite adults emerged seven to 10 days later. No other host records for this species are known.

Eulimneria crassifemur (THOMS.). — One female was reared

from a winter moth cocoon from Versailles. Previously it was not known that this species attacked *O. brumata*, though it is polyphagous and is widely distributed in Europe and Asia. THOMPSON and PARKER (1935) described its morphology and stated that there are one or two generations each year, depending on the locality; in the present investigation, evidence for one generation on winter moth at Versailles was provided by the one parasite specimen that emerged in spring from a host cocoon that formed the previous summer.

Eulimneria rufifemur (THOMS.). — Several adults of this ichneumonid emerged from winter moth that originated on fruit and forest trees at Frankfurt, Zunsweier, and Reuver. This is the first time that *E. rufifemur* was reared from this host, though it is recorded in the literature from other hosts throughout most of western Europe and Britain. The larva is an endoparasite; when mature it emerges from the caterpillar and spins a cocoon inside that of the host. The adult parasite emerges two or three weeks later and probably parasitizes other species during the summer or autumn.

Gelis (Pezomachus) audax (FORST.). — THIEM (1922), MEIER (1927) and SILVESTRI (1941) list this species on the basis of studies by earlier investigators. Its correct identity is unknown.

Hemiteles areator (PANZ.). — HADERSOLD (1938) suggested that this species parasitizes winter moth because a cocoon of the parasite was found on an apple tree that was infested with winter moth. However, REICHERT (1933) reported *H. areator* as a hyperparasite of winter moth through *Meteorus ictericus* (NEES). More definite evidence for parasitism of *O. brumata* by *H. areator* obviously is required. *H. areator* has been reared from numerous other species of braconids and ichneumonids.

Horogenes (= Dioctes) exareolata (RATZ.). — One female of this species, that has also been included in the genus *Angitia*, emerged in July from a winter moth cocoon that had been reared from a larva collected on hazel at Oland several weeks earlier. Previously, this ichneumonid was reared from *O. brumata* collected on apple in Ireland (BEIRNE, 1942).

Limmerium spectabile RDW. — The correct identity of this species, which was listed by THIEM (1922) and SILVESTRI (1941) on the basis of studies by earlier investigators, is unknown.

Lissonota biguttata HOLMG. (= *femorata* HOLMG.) — This species, previously recorded from winter moth by VARLEY and GRADWELL (1958), was reared in the present study from larvae collected on forest and fruit trees at Hasselt, Wytham, Versailles, Braunfels, Frankfurt, Oldenburg, and Zunsweier. No other published information on its distribution or hosts was found. The larva of *L. biguttata* matures

after the host larva has spun its cocoon, and forms a light brown, translucent cocoon inside that of the host. The adult parasite emerges two or three weeks later and probably produces a second generation on other species.

Mesochorus confusus HOLMG. and *Mesochorus crassimanus* HOLMG. — Listed as winter moth parasites by MORLEY and RAIT-SMITH (1933). It is probable that neither parasitizes winter moth, because the ichneumonid portion of the publication is based on MORLEY (1914) who recorded *M. confusus* and *M. crassimanus* as hyperparasites of winter moth through *Phobocampe crassiuscula* (GRAV.) and *Meteorus pulchricornis* (WESM.), respectively.

Netelia (= *Paniscus*) *virgatus* (FOURC.). — Listed by MORLEY and RAIT-SMITH (1933) as a winter moth parasite; however, this record is based on the fact that STENTON (1910) experimentally induced oviposition by *N. virgatus* on *O. brumata*.

Netelia (= *Parabatus*) *latungula* (THOMS). — This species also occurs in north-eastern United States and the adjacent areas of Canada (TOWNES, 1938). Adults emerged from winter moth collected at Oberflockenbach, and cocoons were found inside winter moth cocoons from Versailles, Frankfurt, Oldenburg, Simpeld, Kullaberg, and Oland. HADERSOLD (1938) reared *N. latungula* from *O. brumata* in northern Germany. In the present study parasite adults emerged in spring from winter moth cocoons reared from larvae collected in the previous summer; therefore, the parasite attacks larvae of the winter moth and has one generation each year.

Phobocampe bicingulata (GRAV.). — HADERSOLD (1938) reared this species in northern Germany.

Phobocampe crassiuscula (GRAV.). — This ichneumonid was reared from winter moth that had been collected on forest and orchard trees at Wytham, Bruchsal, Dannenfels, Durbach, Frankfurt, Heidelberg, Mingolsheim, Oberflockenbach, Kullaberg, and Oland. Previously, it was recorded as a winter moth parasite by MORLEY (1914) in Britain. Parasite larvae develop in winter moth larvae, emerge when the latter are nearly mature, and spin cocoons on the foliage. The parasite adults emerge about three weeks later. These adults probably produce a second generation on other host species in summer or early autumn. The hibernation site of the parasite is unknown. *Mesochorus confusus* HOLMG. (*Hymenoptera: Ichneumonidae*) parasitized *P. crassiuscula* in England (MORLEY, 1914). In the present investigation adults determined as *Mesochorus* sp. (*Hymenoptera: Ichneumonidae*) and *Dibrachys cavus* (WLKR.) (*Hymenoptera: Pteromalidae*) emerged in summer from cocoons of *P. crassiuscula* that originated as larvae at Frankfurt, Oland, and Kullaberg, and at Frankfurt, respectively. The life-histories of the two parasite species

were not studied in detail: both apparently oviposit in or on winter moth larvae, because the cocoons of *P. crassiuscula* from which they emerged were reared in the laboratory from field-collected host larvae.

Phobocampe uncinata (GRAV.). — BIGNELL (1898) reared this species from winter moth in England, and THIEM (1922) and SILVESTRI (1941) listed it on the basis of studies by earlier investigators.

Phygadeuon brumatae RDW. — The correct identity of this species, which was listed by THIEM (1922) and SILVESTRI (1941) on the basis of studies by other investigators, is unknown.

Pimpla contemplator (MULL.). — Three adults of this species emerged in June from cocoons of *O. brumata* at Wytham. This is the first record of winter moth parasitism by this species. The host stage parasitized is unknown because the hosts, though collected as mature larvae, were exposed in the collection locality for approximately a week after they had pupated.

Hymenoptera: Eulophidae

Eulophus larvarum (L.). — This eulophid, that has been referred commonly to both the genera *Comedo* and *Cratotrechus*, was reared in the present study from winter moth larvae collected on fruit and forest trees at Bruchsal, Dannenfels, Frankfurt, Heidelberg, Kiel, Oberflockenbach, and Oland. Previously it was recorded as a parasite of *O. brumata* in northern Germany (HADERSOLD, 1939) and in southern Italy (SILVESTRI, 1941). It is also known in Britain (KLOET and HINCKS, 1945) and France (CHEVALIER, 1930) and may, therefore, be an occasional parasite of winter moth in most of western Europe.

Larvae of *E. larvarum* are ectoparasites; from three to six develop gregariously and pupate on the foliage near the posterior end of the shrivelled last-instar host. Parasite adults emerge between one and two weeks later and probably produce a second generation on other host species. Details of the morphology and life-history were described by SILVESTRI (1941).

Diptera: Phoridae

Megaselia rufipes (MG.). — Several adults emerged in July from winter moth cocoons that had been reared from caterpillars collected on fruit and forest trees at Braunfels, Dannenfels, and Frankfurt. This is the first record from winter moth, though it was recorded previously from various Lepidoptera, Hymenoptera, and Coleoptera in Europe and Britain. Details of the life-history in Germany were published by NIKLAS (1957).

Diptera: Tachinidae

Blepharomyia amplicornis (ZETT.). — Reared by SILVESTRI (1941) from winter moth collected in central Italy.

Blondelia nigripes (FALL.). — This tachinid, often referred to as *Lydella nigripes*, was reared from winter moth collected on forest trees at Frankfurt. It was not recorded previously from this host but is polyphagous and widely distributed in Europe and Britain and may be an incidental winter moth parasite throughout most of its range. DOWDEN (1933) published details of its life-history and morphology. In the present study parasite larvae emerged from winter moth cocoons and formed puparia from which adults emerged about two weeks later. There is presumably another generation on other host species.

Ctenophorocera (= *Pales* = *Neopales* = *Nilea*) *pavida* (MG.). — Reared from winter moth in Italy by SILVESTRI (1941).

Cyzenis albicans (FALL.). — This species was first described as *Tachina albicans* (FALLEN, 1810) and subsequently included in both the genera *Cyzenis* (ROBINEAU-DESVOIDY, 1863) and *Monochaeta* (BRAUER and BERGENSTAMM, 1889). It has also been referred to as *leucophaea* MEIG., *schistacea* MEIG., and *perturbans* ZETT. It was reared from winter moth collected in all localities except Dannenfels, Durbach, Kiel, Kranichstein, Oberkirch, Assen, Simpelveld, and Vianen where the collections were small or included mostly early-instar caterpillars that are parasitized less frequently by this tachinid; in addition, *C. albicans* has been taken in central Sweden (LUNDBECK, 1927) and as far south as Lausanne, Switzerland (SPEYER, 1940). The southern limit of its distribution is unknown though SILVESTRI (1941) did not rear it from several thousand winter moth collected in central and southern Italy and Sicily. In Britain *C. albicans* is known from Somerset in the south to Golspie on the coast of Sutherland in the north (FORDHAM, 1935). Recorded hosts are all geometrids: (*O. brumata*; *Triphosa dubitata* (L.) (LUNDBECK, 1927); and *Eupithecia pimpinellata* (HBN.) (VAN EMDEN, 1954); and, experimentally, *Ope-rophtera fagata* (SCHARF.) (VARLEY and GRADWELL, 1958).

There is one parasite generation each year. Adults emerge in spring at about the time that winter moth larvae hatch, and live for three to five weeks. LUNDBECK (1927) recorded adults at the beginning of September in Denmark, but as none survived after early July in the present study and as there is no published record of a second generation, this record is doubtful. The onset of adult emergence is affected by temperature, and, according to SPEYER (1940), also by intrinsic factors, because puparia from several localities reared in the same environment yielded adults at times corresponding to

the natural times of winter moth larval hatch in those localities. Males and females usually are present in equal proportions. Mating occurs 3 to 4 hours after emergence at temperatures between at least 7.8 °C and 22.8 °C.; usually it lasted between 15 and 25 minutes but occasionally exceeded 40 minutes. Each male can fertilize several females. At 18 °C. males fed only water lived three to four weeks and females four to five weeks. In nature both sexes probably feed: DAY (1948) recorded adults on flowers of hawthorn (*Crataegus oxyacantha* L.) and wood spurge (*Euphorbia amygdaloides* L.), and VARLEY and GRADWELL (1958) observed feeding on the sap flux from leaves damaged by feeding caterpillars. Effect of natural food on the fecundity and longevity is unknown, though in tests females that ate honey and water lived no longer than those fed only water. Preoviposition period of mated females fed honey and water at 18 °C. was usually between 12 and 15 days and occasionally over three weeks. The microtype eggs are laid on the foliage or flowers of the host plants. Five females laid up to 688 eggs each in 12 days or less; the maximum per female in a 24 hour period was 307, and one specimen laid 270 in three hours and 10 minutes. As in other microtype-laying species of tachinids, potential fecundity probably depends on the size of the female, with which the number of ovarioles in each ovary is correlated (BESS, 1936).

Adults of *C. albicans* oviposit on many different plants. Parasitized winter moth larvae were collected on foliage of apple, pear, cherry, plum, linden, elm, oak, hornbeam, and hazel; in addition BAER (1921) observed adults of this parasite on willow and blueberry, which are occasionally infested by winter moth. *C. albicans* also parasitizes *Triphosa dubitata* (L.) and *Eupithecia pimpinellata* (HBN.) which eat the foliage of blackthorn (*Prunus spinosa* L.) and buckthorn (*Rhamnus* sp.), and the flowers of several Umbelliferae and Compositae, respectively (MEYRICK, 1927). Most of the eggs of *C. albicans* are laid on the underside of the leaf; this was observed also with *Leschenaultia exul* TNS. (Diptera: Tachinidae) by BESS (1936) who recorded relatively more mortality among eggs on the upper surface, probably because of higher temperatures caused by direct exposure to sunlight.

Eggs are fully developed before they are laid. Over eighty per cent of those deposited on a caged tree in nature were viable three weeks later, and others held at 1 °C.-2 °C. and relative humidities between 90 and 100 per cent lived about eight weeks. Though they can be ingested by any larval instar of *O. brumata*, most eggs are eaten by the fifth-stage caterpillars that consume a greater leaf surface than earlier instars.

Larvae of *C. albicans* probably hatch only in the host mesenteron, as in dissections only unhatched parasite eggs were found in the foregut, whereas both unhatched eggs and empty chorions were found

in the midgut. Freshly-hatched larvae make a hole in the wall of the host's alimentary canal, immediately enter the body cavity and, often within an hour after ingestion, locate and enter the wall of the salivary gland. Here the parasite feeds until the host pupates. Feeding causes swelling of the host gland but does not close the salivary duct or affect formation of the cocoon. After the host pupates the first-instar larva makes a respiratory funnel that opens to the exterior on the ventral side of the pupa near the thoracic-abdominal junction, and feeds with its posterior spiracles inserted in this funnel until only the empty pupal case remains. When mature the parasite larva withdraws its spiracles from the funnel, reverses itself, and forms a puparium inside the empty host pupa. Only one parasite matures in each host pupa.

Because they are laid on the foliage, eggs of *C. albicans* are eaten by larvae of all defoliators that are associated with *O. brumata*; however the only associated species in which the parasite larva is known to mature is *T. dubitata*. The commoner species of *Lepidoptera* associated with winter moth, such as *Tortrix viridana* L. (*Tortricidae*) and *Erannis defoliaria* (CLERCK.) (*Geometridae*), may be physiologically unsuitable as hosts. Tests showed that no parasites developed in larvae of *Alsophila pometaria* (HARR.) (*Geometridae*), which is the most abundant defoliator associated with *O. brumata* in Canada, or in larvae of *Trichoplusia ni* (HBN.) (*Noctuidae*), *Pieris rapae* (L.) (*Pieridae*), *Anagasta kühniella* (ZELL.) (*Pyralidae*), and *Malacosoma americanum* (F.) (*Lasiocampidae*); but the parasite developed and pupated in *Rhyacionia buoliana* (SCHIFF.) (*Olethreutidae*) and *Galleria mellonella* (L.) (*Pyralidae*), neither of which is a natural host.

The larval stage usually lasts three to four weeks at 18 °C. Duration of the first instar varies considerably because there is no moulting until after the host has pupated. Duration of the second instar averages three to four days and that of the third nine to 10 days. Pupation follows formation of the puparium by a week or less. The parasite pupa soon enters diapause and does not develop further until the following spring.

The only insect parasite of *C. albicans* recorded was *Perilampus ruficornis* (FAB.) (*Hymenoptera: Perilampidae*) which was found at Bruchsal, Oberflockenbach, and Luscherz. It emerged also from puparia of *Lypha dubia* (FALL.) from Oland and may, therefore, attack both tachinid species throughout most of western Europe. *P. ruficornis* overwintered as the adult and emerged in spring from puparia reared from winter moth collected as larvae in the previous spring and summer. Apparently the perilampid enters the winter moth larva and, eventually, the enclosed larva of *C. albicans*, but does not kill the tachinid until after the puparium has formed. STEFFAN (1952)

reported that it attacks several other tachinid and hymenopterous parasites of Lepidoptera.

Adults of *C. albicans* are also attacked by the fungus *Entomophthora muscae* (F.) FRES. Approximately 1,600 flies that had been collected at Visingso and shipped by air to Belleville in five wooden boxes died en route or within 48 hours of arrival. The high mortality is at least partially attributed to the unusually high parasite population density in the boxes that facilitated spread of the fungus. No information was obtained on its incidence in natural populations of *C. albicans*.

Lypha dubia (FALL). — This tachinid was reared from winter moth collected in all localities except Wytham, Bingen, Durbach, Kiel, Kranichstein, Oberkirch, and the five localities in Holland. Previously it was reared from winter moth in the U.S.S.R. (SCHREINER, 1916) and is known to occur from northern Scandinavia (LUNDBECK, 1927) to at least as far south as northern Italy (BONGINI, 1921). There is one generation each year. Adults emerge in spring from the soil and, according to LUNDBECK (1927), lay eggs that soon hatch on the foliage near the larvae of their host. Winter moth in both orchards and forests are attacked. One parasite larva matures in each host, emerges after the latter has spun a cocoon, and forms a puparium in the soil either inside or outside the host cocoon. Parasitism of *L. dubia* by *Perilampus ruficornis* (FAB.) (*Hymenoptera: Perilampidae*) was recorded at Oland.

Masicera flavicans GOUREAU. — The correct identity of this species, which was listed by BOURDIN (1922), is unknown.

Phorocera obscura (FALL.). — This species has also been referred to as *P. vernalis* R.-D. and *P. caesifrons* MACQ. It was reared from winter moth from Oostmalle, Versailles, Frankfurt, Heidelberg, Oberflockenbach, Schorndorf, Zunsweier, Kullaberg, Oland, and Luscherz in the present study, and recorded from southern Italy by SILVESTRI (1941). There is one generation each year. Adults emerge in spring and lay macrotype eggs on late-instar winter moth caterpillars. The parasite larva matures after the host has spun a cocoon, emerges usually from the host pupa and occasionally from the mature larva, and forms a puparium external to or, occasionally, inside the host cocoon. One or, less often, two tachinid larvae mature in each winter moth. Details of the life-history and morphology were published by SILVESTRI (1941). The species attacks *O. brumata* in both deciduous forests and orchards.

Phryxe longicauda WAINW. — This species was reared from winter moth collected on forest trees at Versailles and Frankfurt. Previously, it was recorded from the same host on cherry at Herznach, Switzerland (DELUCCHI, 1953). *P. longicauda* was separated from

P. vulgaris (FALL.) in Britain by WAINWRIGHT (1940); thus, earlier records of winter moth parasitism by *P. vulgaris* (BAER, 1921; LUNDBECK, 1927) may refer to *P. longicauda*. Mature larvae of *P. longicauda* leave the host cocoon and form puparia in the soil, and adults that emerge from the latter several weeks later probably produce a second generation on an alternate host.

Phryxe nemea (MG.). — Recorded by PSCHORN-WALCHER and HERTING (1955) in northern Switzerland.

Phryxe vulgaris (FALL.) — Listed by BAER (1921) and LUNDBECK (1927). It may not, however, be a winter moth parasite because *Phryxe longicauda* was separated from it by WAINWRIGHT (1940), and several investigations, including the present one, showed that *P. longicauda* parasitizes winter moth.

Smidtia conspersa (MG.). — Several adults of *S. conspersa* (= *Epicamponera conspersa*) emerged from winter moth collected on forest trees at Versailles and Oberflockenbach. This is the first record of winter moth parasitism by *S. conspersa*; however, it is distributed from southern Sweden to at least as far south as France (LUNDBECK, 1927) and may occasionally parasitize *O. brumata* throughout this range. There is one generation each year. The puparium is formed inside the winter moth soon after the latter pupates, and the adult emerges in the following spring.

Zenillia libatrix (PANZ.). — *Z. libatrix* was reared from *O. brumata* collected from fruit and forest trees at Braunfels, Kranichstein, and Schorndorf. It was not reared previously from winter moth, though it is polyphagous and widely distributed in Europe and Britain and probably is an incidental parasite of *O. brumata* over a large area. Details of the morphology and life-history were published by DOWDEN (1934). The female lays microtype eggs on the foliage, the puparium is formed inside the winter moth pupa, and the adult emerges in summer and probably attacks other host species.

Pupal Parasites.

Winter moth cocoons were collected at Kranichstein in July — August and November — December, 1954, and at Kullaberg in June, 1956; and cocoons reared from larvae collected at Versailles in 1956 and at Wytham in 1952, 1953, and 1955 were temporarily exposed in their respective localities. With the exception of *C. culex* at Kullaberg and *P. contemptator* at Wytham, which may have been pupal parasites, the only species reared were those that are known to parasitize winter moth larvae and mature inside the cocoon. More information on pupal parasites might be obtained from collections of pupae at intervals during the entire pupal period.

The only pupal parasite recorded in the literature is the ichneumonid *Pimpla turionellae* (L.) (= *P. examinator* (FAB.). It was reared by HADERSOLD (1938) from a cocoon collected on an apple tree that was infested by winter moth; in this case, its host it not known accurately. SILVESTRI (1941) reared *P. turionellae* from winter moth pupae collected in the soil, and experimentally observed parasitism of winter moth pupae by this species.

SUMMARY

Sixty-three species of insect parasites of the winter moth, *Operophtera brumata* (L.) (*Lepidoptera: Geometridae*), including 26 reared in the present investigation and 37 recorded only in the literature, are listed. Eleven of those reared in the present study are new parasite records for winter moth. Thirteen of the records from the literature are questionable because in each case the identity of either the parasite or host is uncertain. Notes on distribution and life-history are given for species reared in the present study.

ZUSAMMENFASSUNG

In vorliegender Untersuchung wurden insgesamt 63 Insekten als Parasiten des Frostspanner, *Operophtera brumata* (L.), behandelt. Von diesen sind 37 Arten nur aus der Literatur bekannt. Die übrigen 26 Arten wurden aus dem gesammelten Material gezüchtet. Von letzteren waren 11 Arten bis jetzt noch nicht als Parasiten der Frostspanner bekannt. 13 in der Literatur genannte Arten sind mit einem Fragezeichen zu versehen, weil die Bestimmung der Parasiten-Arten oder des Wirtes zweifelhaft erscheint. Bemerkungen über die Biologie und Verbreitung der von uns gezüchteten Arten werden gegeben.

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