Portevinia maculata (Fal.) : last instar larva and puparium, with notes on the relationship between this hoverfly and its larval host-plant, *Allium ursinum* (*Diptera, Syrphidae*)

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Résumé. — La larve et la pupe du Syrphide phytophage *Portevinia maculata* (Fal.) sont décrits et figurées. Il est établi que l'hôte de la larve est *Allium ursinum*. Les relations évolutives entre cette plante et *P. maculata* sont discutées. Les relations phylogénétiques du genre *Portevinia* sont examinées et le bien fondé de ce genre est confirmé.

Summary. — The larva and puparium of *Portevinia maculata* (Fal.) are described and figured. It is verified that the larval food-plant of *P. maculata* is *Allium ursinum*. Consumption of *A. ursinum* bulbs by *P. maculata* larvae is detailed. The larval morphology of *P. maculata* is used to argue that the genus *Portevinia* is well-founded. It is also concluded that a close co-evolutionary relationship may exist between *P. maculata* and *A. ursinum*.

Key words. — *Diptera, Syrphidae, Portevinia*, phylogenetic relationships, larva, puparia, morphology, biology.

INTRODUCTION

The syrphid genus *Portevinia*, named after the French Dipterist Portevin, was erected for the European species *P. maculata* (Fal.). *P. maculata* was previously regarded as a species of *Cheilosia*. In the paper in which Goffe (1944) introduces the name *Portevinia* he also defines the genus. More recently, Thompson (1980) has claimed that two other Palaearctic *Cheilosia* species (*C. altaica* Stack. and *C. dispar* Hervé-Bazin) should also be consigned to *Portevinia*. The genus is unknown outside the Palaearctic.

In recent literature on European Syrphidae it has more than once been suggested that the larval foodplant of *Portevinia maculata* is *Allium ursinum* (L.), because the adults of this insect are hardly ever found away from the immediate vicinity of this plant. However, the larva of *P. maculata* has never been described and the only information so far published upon its biology is largely erroneous (e.g. in Stubbs and Falk, 1983, where the statement is made,

and wrongly attributed to myself, that *P. maculata* larvae «live in the underground portion of the leaf bases of *A. ursinum*, being fully grown in August»).

The present text describes the last instar larva of *P. maculata*, based upon specimens collected live in mid-winter from their mines in *Allium ursinum* bulbs. Observations are made on larval biology and features of the possible co-evolutionary relationship existing between *P. maculata* and *A. ursinum* are explored. The status of the genus *Portevinia* is also discussed, in the light of the morphological and biological data now available.

LARVAL BIOLOGY OF P. MACULATA

The larvae which form the basis of this article were collected in January, 1980 from deciduous woodland in Co. Wicklow, Ireland, at a locality (Knocksink Wd.) where adults of *P. maculata* had been noted repeatedly in and around stands of *Allium ursinum*. Discovery of the larvae proved remarkably easy. Moss, dead leaves and other woodland floor debris were scraped away from the surface of a trackside bank, exposing the tips of clumps of growing *Allium* bulbs. The *Allium* bulbs were dug up and discoloured bulbs with holes in them were encountered almost immediately. These discoloured bulbs were opened up on-site and one containing a syrphid larva was come across straight away. All of the *Allium* bulbs from three separate plots each of 30 × 30 cm were then removed and placed in polythene bags for examination later. Examination of these bulbs revealed that the *Portevinia* larvae, and larval damage, were almost confined to the larger bulbs. Two larvae were also found free in the soil where the bulbs were dug up, at the time of bulb collection.

The numbers of larvae, damaged bulbs and undamaged bulbs collected were as follows :

Larvae	Bulbs collected	Undamaged bulbs collected	Damaged bulbs collected	Bulbs consumed, Jan. 4/March 31
16	234	118	116	30

Tiny *Collembola* were found in damaged bulbs empty of larvae, as were one small slug and two small Isopods. There was thus no indication that bulb damage was occurring on any scale due to any agency other than the *Portevinia* larvae. It has therefore been presumed here that all the bulbs damaged to a significant extent were damaged by *Portevinia*. At the time of collection the *Portevinia* larvae were evidently in their last instar and measured on average 7 mm long and 2 mm in width. To judge from the condition of the bulbs collected, up to this stage the form of damage to bulbs was usually a loose spiral tunneled in the flesh of the bulb, beginning and ending on its side. The growing shoot was frequently attacked and killed, but in bulbs attacked some time previously secondary growing shoots were developing — whether these could give rise to healthy plants, despite the reduced food reserve of the bulb, has not been ascertained.

Larvae were placed with undamaged *A. ursinum* bulbs in small (3" × 1 $\frac{1}{2}$" × $\frac{3}{4}$") plastic containers, in the dark (exposure to light caused larvae to leave bulbs and wander), in a warm room. A layer of absorbent paper in the bottom of each container moistened with tap water

served to keep a high humidity within. One of the larvae was kept in the same conditions as the others but with bulbs of *A. triquetrum* L., instead of *A. ursinum*.

Examination of the activities of the collected larvae proved that at this point in their development they were demolishing a far greater proportion of each bulb they attacked then would have been concluded from the damaged bulbs collected in the field. Normally, only one larva entered each bulb, but once there it continued to consume the bulb tissues until there was nothing left but the tough outer skin of the bulb. There was no doubt that the larvae were successfully attacking unblemished, healthy bulbs and consuming the bulb tissue itself, rather than acting as saprophages feeding upon decaying bulb tissue, or on fungi, etc. which might have caused bulbs to rot.

Keeping the larvae in a warm room almost indubitably speeded up their development because they had all pupated by the middle of March, at which point the first adult (a male) hatched : in Ireland the normal flight period of *P. maculata* is from the third week in May to the end of June. The time interval between puparium formation and emergence of the adult was in each case approximately three weeks. Prior to pupariation each larva left the bulb in which it had been feeding, to pupate free in the container, unattached to any surface. The larva fed upon *A. triquetrum* developed at the same rate as the other larvae, pupated normally and produced an apparently normal adult fly.

LARVAL MORPHOLOGY (MATURE, FINAL-INSTAR LARVA).

Length : 8-9 mm., width (max.) 2.5-3.0 mm.
Description : more or less cylindrical, with a flattened ventral surface, uniformly off-white in colour ; tapering anteriorly, abruptly truncated posteriorly, the body terminating in an almost flat disc of tissue, into which the last abdominal segment is incorporated (see fig. 1-3). General body surface covered in minute, close-set, recurved spinules of rather uniform size, except on the terminal disc of the abdomen, from which they are absent. Terminal disc smooth and featureless, except for posterior spiracular process.
Head : antenno-maxillae well developed, visible as a pair of tubular processes each side of the mid-line, at the anteroventral extremity of the larva ; dorsal lip (sensu HARTLEY, 1961) a simple membranous flap ; tips of large, heavily sclerotised mouth-hooks prominent externally ; ventral pocket beneath mouth not apparent.
Thorax : tapering, posteriorly nearly the same width as the abdomen ; anterior fold of the prothorax (sensu HARTLEY, 1961) complete ; lateral lobes of the prothorax evident beside the mouth, but not prominent ; prothoracic, spiracular processes weakly sclerotised, simple tubes, short and narrow, placed dorso-laterally and carried part-concealed in pockets in the body-surface ; thoracic segmental setae distributed as on abdominal segments, except that only 1 pair of dorso-lateral setae could be detected on each segment ; prolegs absent on thorax.
Abdomen : seven segments detectable (from segmental setae) ventrally, six dorsally ; primordia of pupal spiracles obvious on dorsal surface of abdominal segment 1 ; seventh abdominal segment modified to form, with eighth segment, the disc of tissue terminating the abdomen posteriorly ; posterior spiracular process sessile, 3-4 × as wide as long, brightly shining, black, its spiracular disc almost flat, with a mirror-like surface shine, the spiracular slits four per side, each a simple horse-shoe shape with its ends pointing toward the periphery of the disc (see fig. 4) ; 2 pairs of dorso-lateral, 3 pairs of ventro-lateral and 2 pairs of ventral segmental setae carried by each segment (except seg. 7, where the dorso-lateral setae cannot be detected), those of segment 8 forming part of the fringe of setae rimming the terminal disc of the abdomen ; segmental setae decreasing in length and strength towards the anterior end of the larva ; prolegs (and their associated crochets) and lappets absent from abdominal segments.
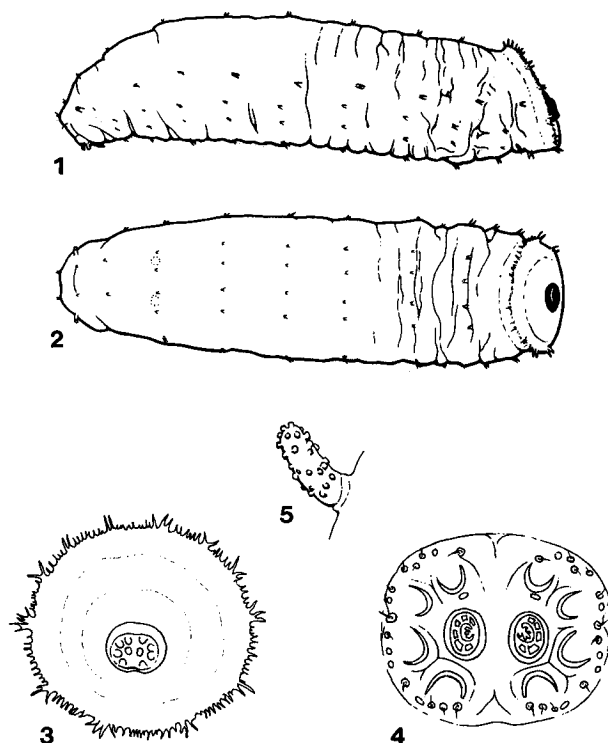
Fig. 1-5 : *Portevinia maculata* (FAL.). — 1 : larva, lateral view ; — 2 : larva, dorsal view ; — 3 : larva, terminal disc of abdomen showing fringe of setae and posterior spiracular process ; — 4 : larva, spiracular disc of posterior spiracular process showing horse-shoe shaped spiracular slits ; — 5 : puparial horn.

PUPARIAL MORPHOLOGY

Puparium : Length c. 7.00 mm ; unicolourous pale brown, except for black, shining, posterior spiracular process, shape and surface morphology very similar to that of larva, except that puparium is anteriorly more blunt-ended ; puparial horns see fig. 5 ; posterior disc and spiracular process as in larva.

DISCUSSION

A : The phylogenetic position of **Portevinia maculata**

Portevinia is segregated from *Cheilosia* by only a few insignificant features of adult morphology. It is thus worthwhile to consider whether or no the data now available about the larvae of *P. maculata* lend support to the practice of recognising *Portevinia* as a distinct genus.

According to SMITH (1979) the genus *Cheilosia* includes more than 130 described Palaearctic species and information is available about larval morphology and or biology for

approximately 30 of these species. All known *Cheilosia* larvae consume plant tissues of some sort, the genus including leaf miners, stem, bulb and root borers and fungus feeders. The larvae of one species, *C. fasciata* SCHINER & EGGER, are known to mine the leaves of *Allium ursinum*, the plant with which *P. maculata* is associated. There are few other syrphid genera with plant-feeding larvae, the only additional Palaearctic genera exhibiting this habit being (so far as is known) *Emerus* and *Merodon*. Elsewhere, *Graptomyza* species are also plant-feeding as larvae.

P. maculata larvae can easily be segregated from larvae of all syrphid tribes other than elements of the *Cheilosini* and *Eumerini*, but attempts to place *Portevinia* larvae more precisely are rendered difficult by their possession of the following combination of characters : body entirely without lappets ; posterior spiracular process wider than long ; sensilla each with more than one seta ; terminal abdominal segment modified to form a flat disc. Of these four features, the first two separate *P. maculata* larvae from all known *Cheilosia* larvae, the third distinguishes *P. maculata* larvae from those of *Merodon* and the fourth is found only in *P. maculata*. *P. maculata* larvae are also dissimilar to known *Eumerus* larvae in the first character mentioned. In the key to the larvae of syrphid genera provided by TORP (1984) the larva of *P. maculata* would run to couplet 33, which deals with the larvae of *Temnostoma* species and *Volucella inanis* (L.), none of which possesses lappets. The form of the posterior spiracular process (wider than long) and the last abdominal segment (flattened into a disc terminating the abdomen) serve to distinguish *P. maculata* larvae from the larvae of these species. Further, the clumps of chitinised, epidermal "teeth" found above the mouth in *Temnostoma* larvae are absent from *P. maculata* larvae.

The spiracular disc of the posterior spiracular process found in *P. maculata* larvae bears 4 simple, horse-shoe shaped slits on each side. Four slits per side is a rare condition in syrphid larvae (most possess 3 slits each side and some, like *Temnostoma*, have a large number of slits), known only in some *Cheilosia* (see DUSEK and LASKA, 1967) and *Merodon* (see STUCKENBERG, 1956) species. Simple horse-shoe shaped slits oriented as in *P. maculata* are equally rare, being known elsewhere only in *Ferdinandea* : (see HARTLEY, 1961). Similarities between *P. maculata* larvae and larvae of *Eumerini* could be due primarily to the demands made by a tuber/corm/bulb-inhabiting life-style, but known tuber/corm/bulb-inhabiting *Cheilosia* larvae retain the characteristic *Cheilosia* larval form. Equally, any attempt to argue for a close relationship between *P. maculata* and *Eumerini* based on larval similarities would be confounded by differences between the adults of the flies.

HEISS (1938) said "The larvae and puparia of the *Syrphidae* exhibit as much variety of form and life habits, perhaps, as can be found in any one family of the *Diptera*. Within one genus, however, with a few exceptions, the species are remarkably uniform, not only in structure, but in life habits". With the notable advances that have been made in syrphid taxonomy at generic level during the last 40 years, Heiss' statement can be seen to be even more valid today than it was in 1938, and it is apposite to consideration of the position of *Portevinia*. Viewed in the context of Heiss' statement, the larval morphology of *P. maculata* demonstrates the wisdom of segregating this species from *Cheilosia*, as a genus in its own right, while showing at the same time that there is some justification for concluding that a close phylogenetic relationship

exists between *Portevinia* and *Cheilosia*. It would also suggest that examination of their larvae could prove decisive in deciding the correct generic placing of the other *Cheilosia* species (*C. altaica* and *C. dispar*) which have been consigned to *Portevinia* latterly.

B : **Portevinia maculata** and **Allium ursinum**

Allium ursinum enjoys a wide distribution in Europe, from Norway to the Pyrenees and from Ireland to Asia Minor. It intrudes into Northern Asia through Siberia to Kamschatka. *Portevinia maculata* has, so far as is known, a much more restricted range at present, being largely confined to countries on the Atlantic seabord of Europe, from southern Norway southwards to France (including the offshore islands of Great Britain and Ireland). It does extend into Europe as far as Switzerland, but is unrecorded from Poland, the USSR and Jugoslavia. Within its range, *P. maculata* can be locally abundant where *A. ursinum* occurs.

The effect of individual *P. maculata* larvae upon individual bulbs of *A. ursinum* has been described earlier in this text. It is evident that each *P. maculata* larva which reaches pupation has destroyed at least four or five otherwise healthy and viable *A. ursinum* bulbs, usually from among the largest available. If it could be assumed that all the *Portevinia* larvae present in the area searched had been found and that all the damaged bulbs collected from this area would not produce healthy *A. ursinum* plants, then each *Portevinia* larva would have effectively destroyed ten or more *A. ursinum* bulbs during its development. At the larval density recorded here (5 per 30 cm.sq.) a loss of between 25 and ·50 largish *A. ursinum* bulbs per 30 cm.sq. would be incurred each year, reducing the field density of reproductively mature bulbs to a level lower than that recorded in N. Germany by ERNST (1979).

At the field densities of larvae and bulbs recorded at the Irish site sampled, the depradations of *P. maculata* larvae must exert an influence upon the reproductive performance of the *A. ursinum* stands, and especially upon the production of daughter-bulbs as an ingredient in the plant's reproductive performance. However, ERNST (l.c.) points out that *A. ursinum* can maintain its population density even if only a small proportion of the bulbs produce seed-setting flowers each year, so even high populations of *P. maculata* larvae are unlikely to exert a *limiting* influence on the reproductive performance of *A. ursinum*.

ERNST (l.c.) comments that *A. ursinum* is unusual among deciduous woodland ground-flora species in its greater dependence upon sexual reproduction than vegetative reproduction for successful population maintenance, but offers no explanation for this unusual reproductive stratagem. The close dependence of *P. maculata* upon *A. ursinum* bulbs would be expected to lead to drammatic population fluctuations of both species, if the plant's reproductive success were largely dependent upon daughter-bulb production. Possibly, the reproductive strategy of *A. ursinum* represents a response to the continued attentions of the bulb-predator *P. maculata*. If so, while it ensures the survival of the plant, it also ensures the continued use of *A. ursinum* by *P. maculata* larvae and may well be responsible for the apparent monophagy of *P. maculata*, the fly progressively specialising in exploitation of such a suitable and dependable host.

Whether phytophagous larvae of many other syrphids are monophagous is at present unknown. Well-known bulb-feeders like *Merodon equestris* and *Eumerus* species use a number

of plants belonging to two or three different plant families as larval food sources. Polyphagy of this sort is, for the fly, an obvious safeguard against the otherwise serious consequences of local eradication of a particular plant by some abundant generation of bulb-feeding larvae. The capacity of *Eumerus* species and *M. equestris* to seriously reduce commercial crops of bulbs of plants like *Narcissus* species and *Allium* species can be seen from the accounts of HODSON (1927, 1932). Further investigation may show that *P. maculata* is not entirely monophagous, of course. The successful rearing of one larva of *P. maculata* on *A. triquetrum* bulbs alluded to earlier shows that *P. maculata* could consume bulbs of *Allium* species other than *A. ursinum*, if these were encountered by *P. maculata* larvae. But whether the female of *P. maculata* will oviposit elsewhere than in stands of *A. ursinum* also needs to be established before the likelihood of encounters in the field between *P. maculata* larvae and bulbs of other *Allium* species can be assessed (in the Irish locality upon which the present account is based, *A. ursinum* is the only *Allium* species present). Also, it is unfortunate that it is not known whether the reproductive strategy of *A. ursinum* is the same throughout the plant's geographical range, or whether it is significantly different (and more dependent upon bulb formation) at extremes of its range far removed from the present range of *P. maculata*. Equally, it could be of significance if *P. maculata* adults are important as pollinators of *A. ursinum* flowers. The adult flies certainly visit *A. ursinum* flowers. It would seem fitting if a fly whose larvae are such effective bulb predators of *A. ursinum* should prove equally effective in ensuring that the plant sets fertile seed.

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