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The relationship between feeding mode and morphology in *Cheilosia* larvae (Diptera, Syrphidae)

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Third stage larvae of seven species of *Cheilosia* are described. The morphology of each species is analysed in relation to feeding mode. A variety of features are identified that appear to be uniquely related to fungal-feeding, leaf-mining, stem/root tunnelling and sap/cambium feeding. An important factor influencing larval morphology appears to be the solidity of the food. A relationship between morphology and feeding mode should be useful in analysing the larval stages of other *Cheilosia* species, the majority of which are unknown.

KEYWORDS: Larva, Morphology, Feeding mode, *Cheilosia*.

In the Palaearctic region *Cheilosia* is one of the largest syrphid genera (F. C. Thompson, pers. comm.) with many common species (Stubbs and Falk, 1983; Torp, 1984). However, larval stages are very poorly known (Smith, 1979). The few reared species have phytophagous larvae, mostly tunnelling in stems and roots of higher plants (Smith, 1979). Other feeding modes include leaf-miners (Hövemeyer, 1987; Rotheray, 1988 b), feeders in the fruiting bodies of fungi (Wallace and Lavallee, 1973; Smith, 1979) and cambium and sap feeders on pines (Burke, 1905; Tragardh, 1923).

A comparative study of the larvae of three tunnelling and one leaf-mining *Cheilosia* species showed that a variety of morphological and behavioural features could be correlated with these two feeding modes (Rotheray, 1988 b). To further investigate these relationships the larval stages of the following six European and one North American species are compared which completes analysis of all the currently known larval feeding modes in this genus: *Cheilosia canicularis* (Panzer), and *C. variablis* (Panzer) which tunnel their food-plants; *C. fasciata* Schiner & Egger which is a leaf-mining species; *C. longula* (Zetterstedt) and *C. scutellata* (Fallén) both of which feed in the fruiting bodies of fungi; *C. pagana* (Meigen) which is associated with decaying roots and finally, *C. alaskensis* Hunter which is a Nearctic species feeding on the sap and cambium of pines.

Previous descriptions of the larval stages of some of these species Dušek (1962) for *C. canicularis* and *C. variablis*; Dušek & Laška (1962) for *C. fasciata;* Burke (1905) for *C. alaskensis*) were found to lack most of the details necessary for such a comparison. They are redescribed here.

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Descriptions of the third (=final) stage larva

Cheilosia canicularis (Panzer)

Length 15–19 mm, width 5–7 mm; oval in cross-section; thorax narrower than abdomen; white to pale brown; integument with short, dark, backwardly directed vestiture or pubescence, pubescence mostly absent from the dorsal and lateral margins of abdominal segments 6–8 which are clear and shining; pubescence less dense on the thorax; one large and two smaller pairs of mouth-hooks (Fig. 1); no setal fringe surrounding mouth-hooks; mandibular lobes reduced and smooth; prothorax with a broad, sclerotised, square-shaped region (the dorsal plate, Rotheray (1988 a)) between the anterior spiracles; chaetotaxy: prothorax 11 pairs of sensilla (sensu Hartley, 1961), mesothorax 9 pairs, metathorax 9 pairs, abdominal segments 1–7 ten pairs, anal segment 7 pairs; anal segment with three pairs of small lappets, middle pair inconspicuous; grasping organ (Rotheray, 1988 b) absent; anal segment with sensilla pair 6 separated from 7 by an integumental fold; posterior respiratory process (prp) (Fig. 2): length 1·2 mm; width 0·9 mm; dark reddish brown; basal third smooth and matt, rest shining and wrinkled from base to tip; wide medial groove dorsally and ventrally in the apical half; spiracular plates divided by a groove; variable number of spiracular slits (18–24); margin of each spiracular plate with up to 4 groups of interspiracular setae (Fig. 3). Description based on four larvae.

The only rearing record for this species is that of Dušek (1962) who obtained larvae from *Petasites albus* (L.) Gaertner, *Petasites hybridus* (L.) Gaertner, Meyer & Scherbius and *Petasites kablikianus* Tausch ex Berchtold (Compositae). Eggs are laid on the upper parts of leaf petioles and larvae tunnel down into the roots. Overwintering takes place in the plant with the front end of the puparium projecting through the surface of the root (Dušek, 1962). For this study larvae were collected by A. E. Stubbs on 25 Sept. 1987 from roots and stems of *P. hybridus* at Plitivice, Yugoslavia. Identification was confirmed by rearing some larvae through to the adult stage. The larva of *C. canicularis* can be distinguished from other larvae by the form of the prp and the lack of pubescence on abdominal segments 6–8. However, in Japan, *Cheilosia yesonica* Matsumura is known from *Petasites japonicus* Mik (Asayama *et al.*, 1972). The larva of this latter species has not been studied by me.

Cheilosia variablis (Panzer)

Length 9–12 mm, width 3–3·5 mm; oval in cross-section; thorax narrower than abdomen; white to creamy-white or pale brown; integument with a dense covering of upright, tapering, sclerotised pubescence that curves back from the base; pubescence only slightly less dense and shorter on the ventral surface; pubescence absent from the dorsal surface of abdominal segment 8 (the anal segment) and very short on the thorax and ventral surface of abdominal segment 1; one large and two smaller pairs of mouth-hooks (Fig. 4); no setal fringe surrounding mouth-hooks; mandibular lobes reduced; prothorax with a broad, sclerotised, lightly striated, square-shaped dorsal plate between the anterior spiracles; chaetotaxy: prothorax with 11 pairs of sensilla, mesothorax and metathorax 9 pairs, abdominal segments 1–7 ten pairs, anal segment 7 pairs; anal segment with three pairs of almost equal sized lappets; grasping organ absent; anal segment with sensilla pair 6 separated from 7 by an integumental fold; prp (Fig. 5): length 0·8 mm; width 0·45 mm; dark brown and tapering apically; basal 0·25 clear and matt above this a deep constriction then lightly nodulate with apical 0·25

FIGS 1–11. Third stage larvae of *Cheilosia* species. 1–3 *Cheilosia canicularis*, 1, mouth-hooks, lateral view; 2, posterior respiratory process (prp), anterior view, length 1·2 mm; 3, prp, dorsal view. 4–6 *Cheilosia variablis*, 4, mouth-hooks, lateral view; 5, prp, anterior view, length 0·8 mm; 6, prp, dorsal view. 7–10 *Cheilosia fasciata*, 7, mouth-hooks, lateral view; 8, prp, anterior view, length 0·64 mm; 9, prp, dorsal view; 10, anal segment, ventral view, a = anus, e = reversible sacs, 3–7 = sensilla pair numbers (sensilla are counted from the mid-point of the dorsal surface of each segment which accounts for the apparent lack of sequence in numbering). 11, *Cheilosia longula*, abdominal segment 7 and anal segment, lateral view, 1–5 = sensilla pair numbers.

striate; four pairs of crescent-shaped spiracular slits (Fig. 6); spiracular plates level with 3 pairs of spine-like processes along the margins. Description based on 3 larvae and 2 puparia.

The larva of *C. variablis* was first mentioned by Zetterstedt (1843) but no biological or morphological details were provided. Kaltenbach (1874) records *C. variablis* in stems of *Carduus nutans* L., *Carduus acanthoides* L. (= *Carduus crispus* L.) and *Cirsium lanceolatum* L. (= *Cirsium vulgare* (Savi) Tenore) (Compositae). He states that larvae first bore into the buds and then tunnel down the main stem with the result that the main stem ceases growing and the plant responds by producing a mass of basal stems. The identification of the fly is probably incorrect as these foodplant records have not been repeated (see below). Furthermore, the feeding pattern is similar to that of *Cheilosia grossa* (Fallén), a species known to feed in *Carduus* and *Cirsium* thistles (Rotheray, 1988 a).

Brischke (1880) found larvae of *Cheilosia gigantea* Zetterstedt making cavities in roots of *Scrophularia nodusa* L. (Scrophulariaceae). Larvae were found in August and adults emerged in March of the following year. Dušek (1962) doubts this identification and considers the true identity of the *Cheilosia* species recorded by Brische (1880) to be *C. variablis*. In the British Isles the only rearing record of *C. variablis* is that of Fryer (1915) who found numerous larvae in the roots of *S. nodosa* plants.

For this study larvae of *C. variablis* were obtained from *S. nodosa* and *Scrophularia auriculata* L. (*aquatica* auctt.) plants at Bedford Purlieus, Northamptonshire in September 1985 and 1987 by A. E. Stubbs who kindly forwarded the following notes. Most larvae were found in the nodular rhizome of *S. nodusa* plants. These swollen rhizomes were hollowed out by the larva. In places where the rhizomes of several plants grew close together and were touching, larvae tunnelled across from one to the other. In small plants larvae tunnelled up into the main stem after the rhizome had been hollowed out. These observations suggest that the rhizome is the initial feeding site and that when small rhizomes are attacked, extra food is obtained by tunnelling up the stem to complete larval development. However, in *S. auriculata* plants two larvae were located in the stems but this plant lacks a nodular rhizome. Adult flies emerged from late April to mid May in the year following collection. The larva of *C. variablis* can be distinguished from other larvae by the form of the prp.

Cheilosia fasciata Schiner and Egger

Length 8–10 mm, width 2·5–3·5 mm; subcylindrical in cross-section; thorax narrower than abdomen; abdomen truncate posteriorly; white to creamy-white, hind gut obscured by white adipose tissue; integument with a dense covering of long (up to 0·8 mm) upright, tapering pubescence the tips of which are directed posteriorly; pubescence shorter on the thorax and ventral surface of the abdomen; lateral margins of the mesothorax and metathorax with some dark, sclerotised spicules; 6 pairs of mouth-hooks (Fig. 7); mouth-hooks surrounded dorsally and laterally by a fringe of setae; mandibular lobes reduced; prothorax without a sclerotised dorsal plate between the anterior spiracles; sensilla with 2–3 apical setae; chaetotaxy: prothorax with 11 pairs of sensilla, mesothorax and metathorax 9 pairs, abdominal segments 1–7 ten pairs, anal segment 7 pairs; anal segment with one pair of large lappets; grasping organ present, consisting of a pair of eversible sacs immediately behind the anus with a large, projecting integumental fold either side of the anus and sensilla 6 not separated from 7

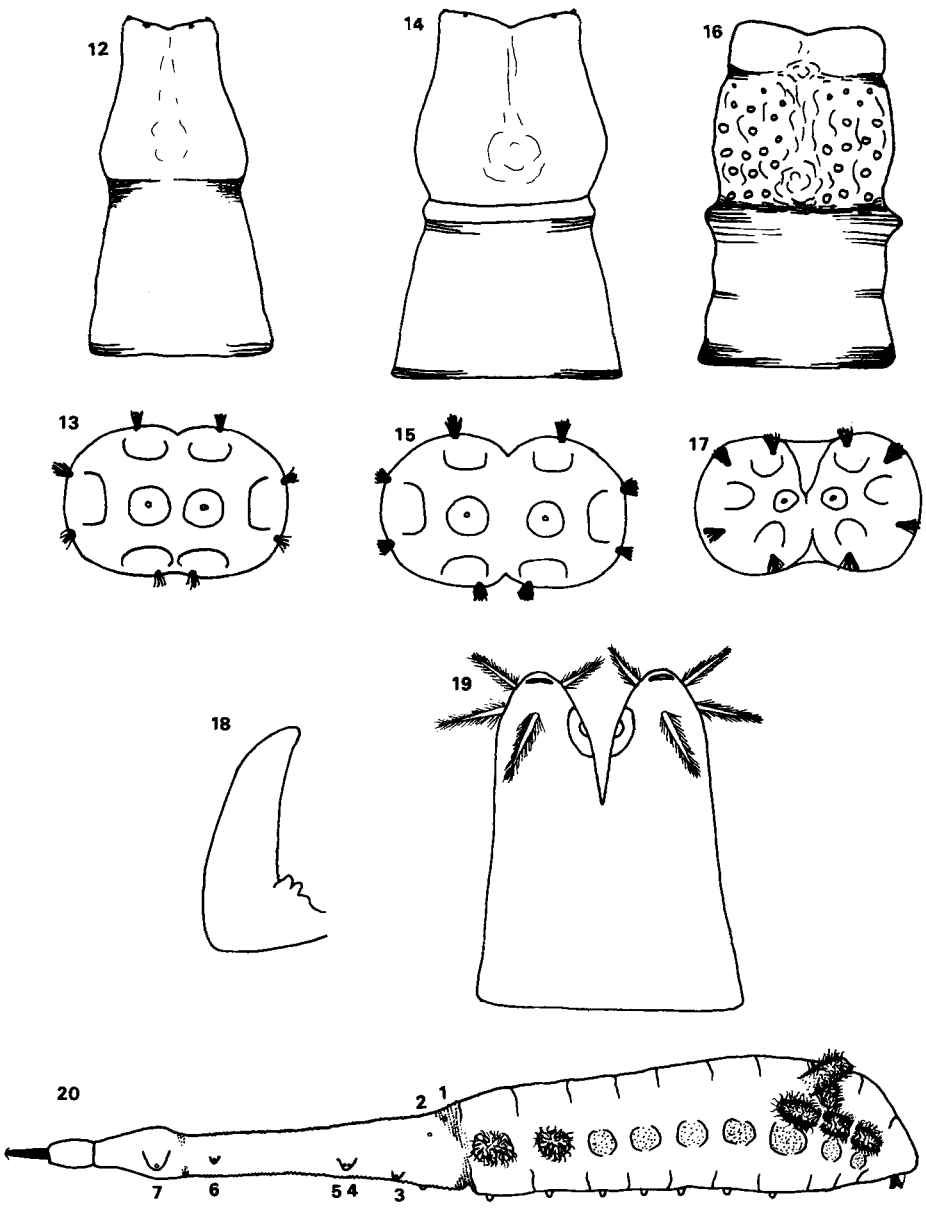
(Fig. 10); prp (Fig. 8): length 0·64 mm; width at base 0·48 mm; width at tip 0·36 mm; basal 0·25–0·33 clear and matt, beyond this to tip nodulate, shining and tapering towards the tip; spiracular plates with slight inward slope; 3 pairs of elongate and narrow spiracular slits (Fig. 9). Description based on 6 larvae.

The foodplant of this species is *Allium ursinum* L. (Liliaceae) (Beling, 1988; Dušek & Laška, 1962; Nielsen, 1979). The ecology of *C. fasciata* was investigated by Hövemeyer (1987) from whose study the following details were obtained. The larva is a solitary leaf-miner and is able to start a new mine in a fresh leaf if the old one is mined out. There is usually one generation per annum and overwintering takes place in the leaf litter within the puparium. For this study larvae were kindly forwarded by K. Hövemeyer who collected them from *A. ursinum* leaf mines on 3 June 1987 at Gottingen Wald, 7 km east of Gottingen, W. Germany. The larva of *C. fasciata* can be distinguished from other larvae by the form of the prp and anal segment. It most closely resembles *Cheilosia semifasciata* Becker, another leaf-mining species (Rotheray, 1988 b). *C. fasciata* can be separated from this latter species by the tip of the prp being more than half as wide as the base of the prp (0·36/0·48 mm). In *C. semifasciata* the tip is half as wide as the base (0·20/0·40 mm).

Cheilosia longula (Zetterstedt)

Length: 7–9 mm, width: 1·5–3 mm; oval in cross-section; white to pale brown; thorax narrower than abdomen; anal segment tapering, more so ventrally than dorsally, to a point behind the final integumental fold which circumvents the anal segment, the rest of the anal segment is parallel sided, the overall effect is a slightly extended and narrow tipped anal segment (Fig. 11); larva coated completely in pale yellowish pubescence which is shorter on the thorax; pubescence with backwardly directed tips and in two sizes: on dorsal margins of integumental folds it is short, dense and lightly sclerotised, in crevices and between integumental folds it is less dense, longer and more heavily sclerotised; one pair of poorly developed mouth-hooks and mandibular lobes large with prominent ridges; setal fringe present; prothorax large and without dorsal plate; chaetotaxy: prothorax with 11 pairs of sensilla, mesothorax and metathorax 9 pairs, abdominal segments 1–7 ten pairs, anal segment 7 pairs; first two pairs of lappets on anal segment small and inconspicuous, third pair larger and in a dorso-ventral position on the final, parallel-sided section of the anal segment; grasping organ absent; anal segment with sensilla pair 7 separated from 6; prp (Fig. 12): length 0·60 mm; width at tip 0·20 mm; pale brown and tapering; basal half matt to mid-point constriction, beyond this to tip shiny; groove from mid-point constriction separating the two spiracular plates usually absent; 3 pairs of spiracular slits, four groups of interspiracular setae (Fig. 13). Description based on 8 larvae.

C. longula has been reared from several species of fungi within the genera *Boletus* (Buxton, 1955) and *Suillus* and *Leccinum* (Hackman and Meinander, 1979). Little is known of the habits and behaviour of the larva. I found larvae of *C. longula* in the fruiting bodies of undetermined *Boletus* fungi under *Pinus sylvestris* L. trees at Rothiemurchus Forest, Speyside and at Rannoch, Perthshire in Scotland during August and September 1988. First stage larvae were located on the underside of the cap close to the margin suggesting that female flies oviposit here. Larvae were often very numerous and, although detailed estimates were not made, up to 80 larvae were found in individual fungi and infestation rates were over 50%. No aggressive encounters were



FIGS 12–20. Third stage larvae of *Cheilosia species*. 12–13 *Cheilosia longula* 12, prp, anterior view, length 0·60 mm; 13, prp dorsal view. 14–15 *Cheilosia scutellata*, 14, prp, anterior view, length 0·64 mm; 15, prp, dorsal view. 16–17 *Cheilosia pagana*, 16, prp, anterior view, length 0·68 mm; 17, prp, dorsal view. 18–20 *Cheilosia alaskensis*, 18, mouth-hooks, lateral view; 19, prp, anterior view, length 0·40 mm; 20, third stage larva, lateral view, length 10 mm, 1–7 = sensilla pairs numbers on the anal segment.

observed between larvae. Infested fungi lost their shape and appeared as brown smudges on the ground. Searching such fungal remnants was the quickest method of locating third stage larvae. Within them, larvae are submerged completely and are not visible except when the tip of the prp is thrust out of the semi-liquid material. During September and October larvae pupate in the leaf litter and soil beneath the remains of the fungus.

Observations of feeding behaviour in the laboratory showed that third instar larvae fed intermittently during the day. To commence feeding the mouth-hooks are lifted upward and forward. This stretches the mandibular lobes and the front of the head into a three sided cavity which is pushed into the food in front of the larva. The cavity fills with food and the mouth-hooks are retracted down and backwards which closes the cavity and food enters the mouth. Several of these movements are repeated rapidly before the larva pauses and then starts the cycle again. For distinguishing the larva of *C. longula* see under the following species.

Cheilosia scutellata (Fallén)

Length: 8–10 mm, width: 2–3 mm; oval in cross-section; white to pale brown; thorax narrower than abdomen; anal segment tapering to a point behind the final integumental fold which surrounds the anal segment, the rest of the anal segment is parallel sided, the overall effect is a slightly extended and narrow tipped anal segment; larva coated completely in pale yellowish pubescence which is shorter on the thorax; pubescence with backwardly directed tips and in two sizes: on dorsal margins of integumental folds it is short, dense and lightly sclerotised, in crevices and between integumental folds it is less dense, longer and more heavily sclerotised; one pair of poorly developed mouth-hooks and mandibular lobes large with prominent ridges; setal fringe present; prothorax large and without dorsal plate; chaetotaxy: prothorax with 11 pairs of sensilla, mesothorax and metathorax 9 pairs, abdominal segments 1–7 ten pairs, anal segment 7 pairs; first two pairs of lappets on anal segment small and inconspicuous, third pair larger and in a dorso-ventral position on the final, parallel-sided section of the anal segment; grasping organ absent; anal segment with sensilla pair 7 separated from 6; prp (Fig. 14): length 0·64 mm; width at tip 0·28 mm; pale brown and tapering; basal half matt to mid-point constriction, beyond this to tip shiny; groove from mid-point constriction separating the two spiracular plates; 3 pairs of spiracular slits, four groups of interspiracular setae (Fig. 15). Description based on two larvae collected from deliquescent fungus, probably a *Boletus* species, at Freshfield, Lancs. on 5 Sept 1960 (Brindle, 1965). These specimens are in the collections of the British Museum (Natural History), London.

C. scutellata has been reared a number of times from a variety of fungi (Smith, 1979) but little is known of its habits and behaviour. The larvae of *C. longula* and *C. scutellata* can be distinguished from other larvae by the form of the prp, mouthparts and pubescence. *C. longula* can be separated from *C. scutellata* which it closely resembles, by its parallel sided prp. However, Wallace and Lavallee (1973) have reared and described the larva of *Cheilosia pallipes* Loew from the fungus *Suillus americanus* in North Carolina, USA. The larva of this species appears to closely resemble *C. longula* and *C. scutellata*, but has not been studied by me.

Cheilosia pagana (Meigen)

Length: 9–10 mm, width: 2–3 mm; subcylindrical in cross section; thorax and anal segment tapering; creamy-white; integument with short backwardly directed pale

pubescence; pubescence slightly shorter and less dense on the ventral surface and on the thorax; pubescence on the dorsal surface of abdominal segments 5–7 longer and more upright; one pair of poorly developed mouth-hooks; mandibular lobes large with prominent ridges; setal fringe present; prothorax large and lacking a dorsal plate; anterior margin of the dorsal surface of prothorax with short, thick sclerotised spicules; chaetotaxy: prothorax with 11 pairs of sensilla, mesothorax and metathorax 9 pairs, abdominal segments 1–7 ten pairs, anal segment 7 pairs; anal segment with three pairs of well developed lappets of which the posterior pair is the largest; grasping organ absent and anal segment with sensilla 7 partially separated from sensilla 6; prp (Fig. 16): length 0·68 mm; width at tip 0·32 mm; pale brown; basal half matt and lightly striate, midpoint constriction then shiny and nodulate to tip; constriction close to tip; spiracular plates sloping inward, 3 pairs of spiracular slits; margin of each spiracular plate with 4 groups of setae (Fig. 17). Description based on one larva and one puparium.

The only rearing record for this species is five larvae from decaying roots of *Anthriscus sylvestris* L. Hoffm. Umbelliferae on 1 Oct 1978 at Horsendon Hill, Middlesex (Stubbs, 1980) on which material the above description is based. The larva of *C. pagana* can be distinguished from other larvae by the form of the prp and the mouthparts.

Cheilosia alaskensis Hunter

Length: head to anus 9–12 mm, anus to tip of prp 4–6 mm, width: 2–4 mm; subcylindrical in cross-section; creamy-white; integument with varied pubescence: thorax and abdominal segments 1 to 5 with bands and groups of short, sclerotised, backwardly directed spicules, these bands becoming wider towards the head and completely coating the anterior fold of the prothorax, the bands are situated on the anterior margins of raised bars and ridges; on abdominal segments 6–8 spicules absent instead there are isolated amounts of longer, yellowish pubescence, areas between pubescence are clear and generally shining; the overall effect is a concentration of sclerotised spicules on the anterior part of the body; one large and three somewhat spatulate mouth-hooks (Fig. 18); spicule band above the mouth-hooks; mandibular lobes reduced; dorsal plate on prothorax nodulated; chaetotaxy: prothorax with 11 pairs of sensilla, mesothorax and metathorax 9 pairs, abdominal segments 1–7 ten pairs, anal segment 7 pairs; dorso-lateral ridges on the mesothorax, metathorax and the first abdominal segment comprising slightly projecting bars centred on sensilla pair 3 and coated with long yellowish pubescence (Fig. 20); a pair of large projections on abdominal segment 1 comprising at the tip, sensilla pairs 1, 2 and the cuticular patches through which the pupal horns are projected (Hartley, 1961), the lateral margins of these projections also coated in yellowish pubescence; the ventral surface of the metathorax and abdominal segments 1–7 with a pair of projections bearing sensilla pair 9; anal segment extended into a long tail which forms a sheath for the breathing tube (Fig. 20); sensilla pairs 3, 4/5, 6 and 7 borne on four pairs of fleshy, lateral projections of the sheath; the tube and sheath are retractible to the fleshy projection bearing sensilla pair 7; grasping organ absent; prp (Fig. 19): length 0·4 mm; width 0·2 mm; uniformly reddish-brown; smooth and shining; spiracular plates elongate with four groups of interspiracular setae; three pairs of spiracular slits. Description based on six larvae.

The feeding habits of the larva of *C. alaskensis* were studied by Burke (1905) in Washington State, U.S.A. Larvae are found in abandoned bark beetle tunnels on the

trunks of living *Tsuga heterophylla* (Rafin.) Sarg. trees (Pinaceae). Occupation of these tunnels by *Cheilosia* larvae is indicated by a small mass of dried resin on the surface of the bark. The tip of the prp sticks through the resin to the outside air. The larva scrapes an oval-shaped cavity next to the sapwood with its mouth-hooks and feeds on the sap and cambium. The larva lives surrounded by resin and the larval growth period may be longer than a year. The larva pupates in the resin mass on the outside of the bark. For this study larvae were obtained from the Smithsonian collection of syrphid larvae, currently housed at the Royal Museum of Scotland. The collection contains material collected by Burke (1905). Three additional larvae were also examined from resin masses on the bark of *Abies grandis* Lindley (Pinaceae) collected by H. L. Osborne on 5 May 1972 at Crane Creek, Latch Co. Idaho, U.S.A. These larvae are also part of the Smithsonian collection.

The larva of *C. alaskensis* can be distinguished from other larvae by the form of the anal segment with its long tail and the thorax with its dorso-lateral ridges coated in long pubescence. However, as Burke (1905) mentions, there are other similar species from bark beetle tunnels on pines, one of which has a shorter tail than *C. alaskensis*. I have examined unidentified larvae in the Smithsonian collection that may be referable to this short-tailed species. They appear to be similar to the larva of *Cheilosia morio* Zetterstedt described by Tragardh (1923). Burke (1905) also reared *Cheilosia hoodiana* Bigot from abandoned bark beetle tunnels on *Abies concolor* (Gordon) Hildebrand. I have found unidentified larvae in the Smithsonian collection that may be referrable to this species. They are similar to *C. alaskensis*, differing chiefly in the smaller amount of pubescence coating the dorso-lateral ridges. Both these groups of larvae closely resemble *C. alaskensis* in having one well developed pair of mouth-hooks, a dorsal plate, anterior concentration of spicules, dorsolateral ridges and a pair of projections on the dorsal surface of the first abdominal segment.

Discussion

The larval stages of *C. canicularis* and *C. variablis* are similar to other tunnelling species such as *C. albipila* Meigen, *C. fraterna* (Meigen) and *C. grossa* (Fallén) (Rotheray, 1988 a). All these species possess a large anterior pair of mouth-hooks with two or three smaller pairs behind, a dorsal plate, a broader than high body shape and a concentration of spicules towards the anterior end of the larva. They do not possess a well developed grasping organ and mandibular lobes or have a setal fringe around the anterior margin of the mouth. These features are interpreted as adaptations to a tunnelling mode of feeding. The mouth-hooks are probably more effective at rasping off fragments of food from the relatively compact tissues of roots and stems than the arrangement of several more equally sized mouth-hooks of the leaf-miners. The dorsal plate may help to prevent wear of the prothorax during the characteristic feeding movements of the tunnellers which involve the thorax being lifted and thrust against the tissues in front of it (Rotheray, 1988 a). The broad body shape and spicules at the front end of the body probably prevents the larva from slipping during feeding. This is achieved by frictional forces when the anterior end of the larva is pushed against the walls of its tunnel by waves of contraction initiated at the posterior end of the larva. In a tunnel this is presumably more effective than maintaining position with a grasping organ at the posterior end of the larva as in *C. semifasciata*, a leaf-mining species (Rotheray, 1988 b).

The larva of *C. fasciata* is morphologically very similar to that of *C. semifasciata*. It also has a uniform covering of long, upright spicules, a taller than broad body shape, six pairs of evenly sized mouth-hooks, a setal fringe around the mouth-hooks and a well developed grasping organ. It does not possess a dorsal plate. These features are interpreted as adaptations to a leaf-mining feeding mode (Rotheray, 1988 b). Numerous, even-sized mouth-hooks with a setal fringe are more effective at rasping the fluid-filled cells of the leaf and preventing the food from being washed away than a single large pair of mouth-hooks and lack of setal fringe characteristic of the tunnellers. The larva of *C. semifasciata* feeds by twisting only its thorax sideways. This is unusual because dipteran leaf-miners normally feed with the whole body orientated sideways (Hering, 1951). The grasping organ, taller than broad body shape and long upright pubescence help the larva maintain position when twisting its thorax to feed. It remains to be confirmed whether *C. fasciata* also feeds by twisting its thorax sideways but this is suggested by the characters it shares with *C. semifasciata*.

The fungal feeders form a distinctive morphological group in relation to tunnellers and leaf-miners. They have a narrow, slightly extended anal segment with a dorsally sited prp (Fig. 11), well developed mandibular lobes with ridges, a setal fringe, poorly developed mouth-hooks, no strongly sclerotised pubescence and an oval body shape. These features are well suited for life in a semi-fluid medium. The slightly extended anal segment enables the prp to be stuck out into the air. The mouthparts are similar to those of *C. pallipes* another fungus feeder which, as pointed out by Wallace and Lavallee (1973), resemble those of *Eumerus* larvae. *Eumerus* larvae feed on the products of fungal/plant decay in bulbs (Creager and Spruijt, 1935). The cavity formed when the mandibular lobes are expanded during feeding movements is well suited to gathering the semi-liquid food into the mouth. Under such circumstances strongly developed mouth-hooks are not an advantage. The grasping organ and the pubescence are not developed as would be expected in larvae that inhabit a semi-liquid medium.

The larva of *C. pagana*, which probably also feeds on a semi-liquid diet resulting from fungal decay of roots shares many of the characters of the fungal-feeders except that it does not have an extended anal segment.

The larva of *C. alaskensis* is the most derived of all those studied here. The extended anal segment bearing the breathing tube is reminiscent of the 'rat-tailed' sheath characteristic of eristaline larvae (Hartley, 1961) from which it differs in being broader, not as retractile, having at least four pairs of prominent fleshy projections bearing sensilla at their tips and being initiated from the fold immediately behind the anus so that sensilla pairs 1–3 are situated on the sheath. In eristalines sensilla pairs 1–3 occur on a broader part of the anal segment immediately before it narrows into the sheath. The prp of *C. alaskensis* also has divergent spiracular plates unlike the eristaline prp. Moreover, the spiracular slits in *C. alaskensis* are borne on elongated spiracular plates which increase the effective length of the prp.

The larva of *C. alaskensis* is most similar to that of tunnelling *Cheilosia* larvae. Like them it has a pair of strongly developed mouth-hooks, a dorsal plate and an even more strongly developed concentration of spicules on the anterior part of the body. Unlike them however, it has dorso-lateral ridges, a pair of projections on the first abdominal segment and prominences on the ventral surface. The sapwood and cambium are the most solidified tissues fed on by any *Cheilosia* species and when feeding, the larva of *C. alaskensis* probably requires a firm grip of the upper and lower surfaces of the blotch-shaped cavity to prevent it slipping. The prominences on the ventral surface and dorso-lateral ridges increase the height of the larva and create a greater surface area

which may enhance frictional forces between the larva and the cavity walls during feeding. The solidity of the wood increases the problem of wear on the dorsal surface of the prothorax and it is more heavily protected than in other tunnelling species: the dorsal plate is nodulated and the anterior margin of the prothorax in front of it is heavily coated in pubescence.

A major preoccupation of insect larvae is feeding (Hinton, 1948). The diversity of larval characters in *Cheilosia* is likely to have been influenced by this particular need rather more than others such as a need to regulate temperature or escape from enemies. A common factor linking the various feeding modes and associated larval morphologies is the relative solidity of the food (Table 1). Recognition of these feeding mode morphological correlates may prove useful when consideration is given to the larval stages and feeding modes of other *Cheilosia* species, the majority of which are unknown.

Table 1. Diagnostic characters for the five larval feeding modes known within *Cheilosia*.

Character	Feeding mode: Fungi[1]	Plants/fungi[2]	Leaves[3]	Stems/roots[4]	Sap/cambium[5]
Body shape:					
Oval	X				
Subcyclindrical		X			X
Higher than broad			X		
Broader than high				X	
Mouth-hooks:					
Poorly developed	X	X			
Row of six evenly-sized hooks			X		
1 large and 2 or 3 small hooks				X	X
Mandibular lobes	X	X			
Setal fringe above mouth	X	X			
Pubescence:					
Weakly developed	X	X			
Upright			X		
Spicules concentrated at front end				X	X
Grasping organ			X		
Dorsal plate on prothorax				X	X
Dorso-lateral ridges					X
Extended anal segment	X				
Anal segment with tail					X
Prominences on ventral surface					X
Solidity of food increases→	semi-liquid	semi-liquid	compact	semi-solid	solid

[1] *C. longula, C. scutellata;* [2] *C. pagana;* [3] *C. fasciata, C. semifasciata;* [4] *C. albipila, C. canicularis, C. fraterna, C. grossa, C. variablis;* [5] *C. alaskensis.*

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