On the biology of *Loewia foeda* (Meigen) (Diptera: Tachinidae)

Figure 1. *Loewia foeda*, live female (Karmøy, Norway).

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Introduction

Parasitization of non-insect arthropods in Tachinidae is rare and only four species have been documented as chilopod parasitoids: *Eloceria delecta* (Meigen) (Giard 1893a, 1893b; Herting 1960), *Loewia foeda* (Meigen) (Thompson 1915) and *Loewia* sp. (Cerretti & Tschorsnig 2010) from the Palaearctic Region, and *Chromatocera harrisi* (Reinhard) (Reinhard 1935, O'Hara 2002) from the Nearctic Region.

The genus *Loewia* Egger is mostly Palaearctic in distribution, with the presence of one Holarctic species (*L. foeda*) in the Nearctic Region (Wood & Wheeler 1972) possibly due to an introduction. Centipede hosts have been recorded from two of the 17 currently known species of *Loewia* (see Cerretti *et al*. 2014): *L. foeda* reared from *Lithobius* sp. (Thompson 1915), and a species of *Loewia* that is probably *L. brevifrons* (Rondani) reared from *Eupolybothrus fasciatus* (Newport) (Cerretti & Tschorsnig 2010, Cerretti *et al*. 2014). It is likely, however, that all species of *Loewia* are parasitoids of chilopods.

There are two important works on *L. foeda*: Thompson (1915) with descriptions and figures of the three larval instars and Wood & Wheeler (1972) that reviews the taxonomic history, describes and illustrates the adult, and briefly discusses its life history.

Presented below are the results of field observations of *L. foeda* (Fig. 1) in Norway and experiments and dissections that show that *L. foeda* practices direct larviposition. The puparium is described for the first time.

Material and methods

Field observations were made at various locations in Karmøy (Slettavatnet and Grodvatnet) in western Norway.

For the larviposition experiments a five deciliter glass jar was used, with a cover of elastic fabric held in place with a rubber band. Larviposition was filmed with a compact camera placed on top of the jar with the lens protruding through a hole cut in the fabric. After a couple of hours the host was checked for signs of parasitization and the video analyzed. Females used for these experiments were collected near Slettavatnet on 12.viii.2013 (while host-searching) and 18.viii.2013 (while feeding).

Females used for dissections were from Slettavatnet (Karmøy) and Finnvik (Suldal) in western Norway (leg. H. Haraldseide; several specimens hand-netted in the field), and Köln in Germany (leg. J. Wehlitz-Franzen; five specimens collected in Malaise traps, July–August 1989). Nine females in total were dissected.

Puparia were found under moss and bark, but most often in the transition zone between rotting wood/bark and soil. Host centipedes were not found but several puparia had centipede segments stuck to them, so the puparia were almost certainly those of *Loewia foeda*. These puparia fit the description of the third larval instar given by Thompson (1915) and also closely match the puparium of a *L. foeda* female housed in Staatliches Museum für Naturkunde (Stuttgart) (from Slovakia, reared in 1966 but without host information). The puparium of *L. foeda* was unknown to Herting (1960) and Ziegler (1998) and they cited Thompson (1915).

The host, *Lithobius forficatus* (Linnaeus), was identified by the first author using Andersson *et al*. (2005).

Field observations

Adults have been recorded in Norway from the beginning of July to the end of August, with single specimens as late as the end of September. They are uncommonly observed, but this is probably due more to their unimpressive habitus and lifestyle than to their rareness. They visit flowers of Daucaceae (*Angelica sylvestris* L., *Heracleum sphondylium* L.) but are most often seen resting on stones or foliage (cf. observations of *L. crassipes* (Mesnil) in Turkey by Bystrowski 2011). Host-searching can typically be observed as follows: the female scuttles energetically and seemingly somewhat systematically over the substrate and disappears under stones, bark and into other crevices where the host is to be expected, only to reappear seconds later and continue. Once an area is searched it flies a short distance and continues.

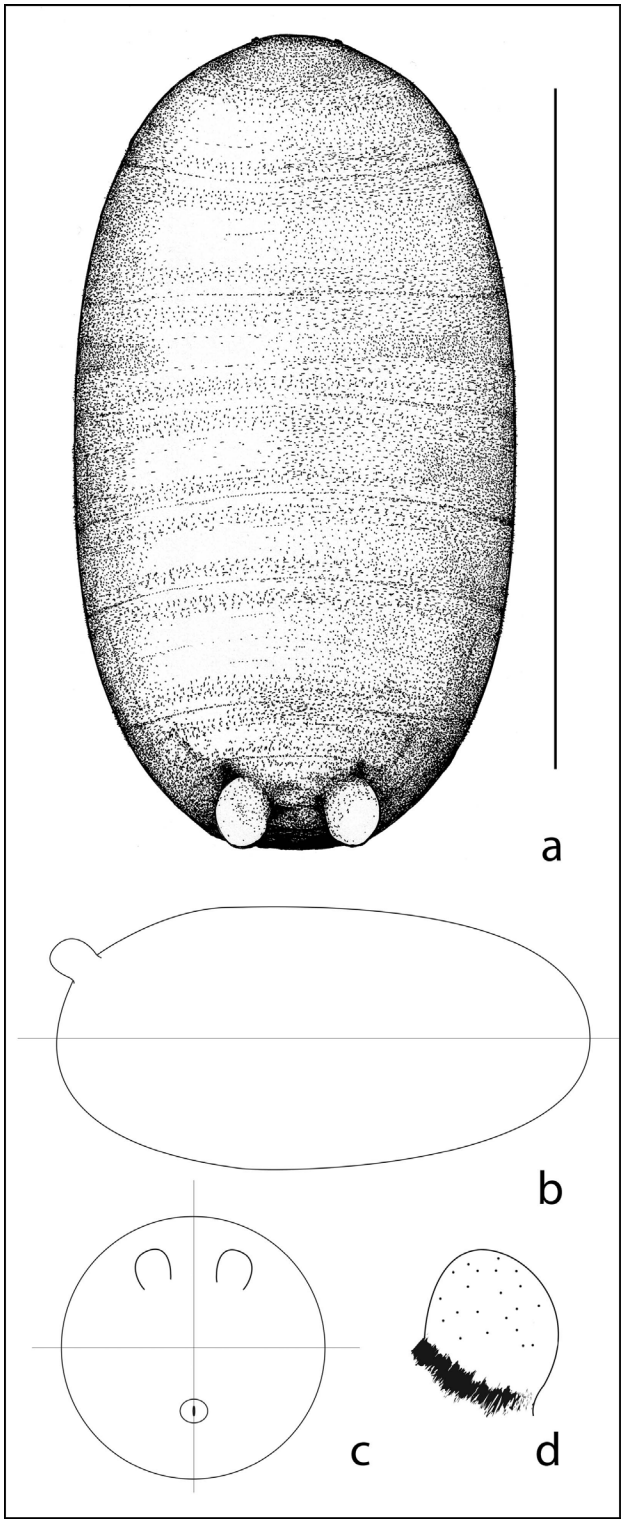

Figure 2. *Loewia foeda*, puparium. **a**. Dorsal view. **b**. Lateral view. **c**. Posterior view**. d**. Right posterior spiracle. Scale bar for (a): 5.0 mm.

Puparium

Eight puparia were examined. They are 6.0–6.5 mm long and 3.0 mm wide, reddish-brown to black, cylindrical and blunt, sometimes slightly widening posteriorly, occasionally a little bit dorsoventrally compressed. Surface texture smooth and dull with transverse striations, segmental divisions usually clearly visible. Complete bands of minute spines present dorsally and ventrally (Fig. 2a,b,c). Lateral muscle scars sometimes well defined. Anterior spiracles small, black, with 4–6 circular openings which are asymmetrical in position and number. Posterior spiracles shiny, large, well separated, knob-like, globular and protruding (almost stalked), situated posterodorsally; no spiracular slits are visible, but scattered punctures are shining through the smooth surface (Fig. 2d). Anal plate situated posteroventrally, circular to slightly oval, sometimes poorly defined and opening slit-like.

Of the eight puparia collected during the winter of 2012/2013, three showed signs of hymenopteran hyperparasitization and one contained a dead ichneumonoid larva/prepupa.

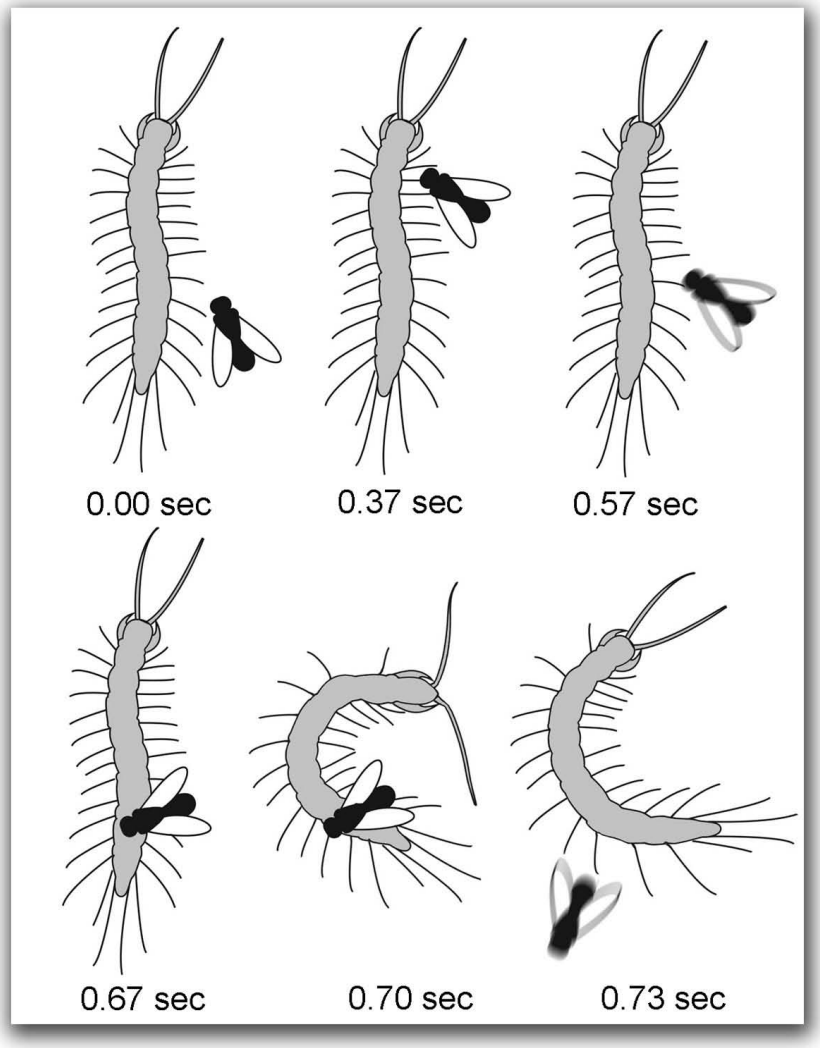

Figure 3. Typical attack of a female *Loewia foeda* on *Lithobius forficatus*, schematically.

Experiments on larviposition

The first author made experiments to determine what type of oviposition strategy is used by *L. foeda*. One female fly at a time was placed in a jar together with a single centipede (later identified as *L. forficatus*). The experiment was done twice. In the first experiment, a previously host-searching female was used. The second experiment used a female caught while it was feeding on a flower of *Angelica sylvestris*. After two hours the results were the same, but the second female showed much less interest in the centipede and the attacks were less frequent. It should be noted that in the second experiment a semi-teneral centipede was used and this might have had a secondary effect.

In the first 10 minutes the first female made contact with the centipede six times (first contact after two minutes). The second female made contact only once (first contact after 30 seconds).

The attacks were extremely fast (Fig. 3). The fly runs up on the side of the centipede or lands directly on it and clings on to its dorsolateral surface. The centipede reacts violently and twitches; in doing so the fly flies off, leaving the centipede in an agitated state, jerking both its head and tail while fleeing.

Whenever the fly came too near the head of the centipede, it retreated and flew off. *Loewia* nearly always attacked when the centipede was still, only very rarely making contact with a moving centipede.

Immediately after both trials several first instars were observed on the hosts' posterior two-thirds: recumbent larvae were observed on the lateral soft membranous area and erect larvae were visible on the ventral sclerotized parts of the segments. Counts of the larvae deposited on the host were not possible due to the difficulty in handling the live centipede.

Dissection of gravid females

Mature and immature first instars were arranged in slightly oblique rows of 5–6 within a coiled uterus, which filled much of the abdomen. Although all nine dissected females (including the ones from the larviposition experiments) were gravid, only five contained mature first instars (Fig. 4). The larvae, especially the younger ones, were separated from each other by an extremely fine membrane, but this membrane always remained connected with the uterus when the larvae were moved with a pin. It is obvious that these membranes consist of the remains of the former eggshells which are now more or less glued together and to the uterus.

The flies of German origin used for the dissections were immediately killed in the fluid of a Malaise trap, and the Norwegian material by freezing, so it very unlikely that there was enough time for hatching of the larvae from eggshells in the uterus after the death of the female.

No evidence for internal larval nourishment was found; mature first instars (on the average approximately 0.7 mm in body length) were no larger than their immature siblings.

The two females used in the experiments were almost depleted of larvae when they were dissected: 30 mature larvae were counted in the first female and about 100 in the second female. The dissection of another female, with the uterus filling nearly the entire abdomen, yielded more than 300 larvae which were fully developed or nearly so.

Discussion

The question of larvipary versus ovolarvipary is one of definitions but also sometimes blurred by facultative responses. An ovolarviparous species might appear to be, or may sometimes be, larviparous if the larva breaks the chorion at or just before deposition. Most authors define larvipary by the presence of nutritive glands in the uterus. In Tachinidae, "larvipary" has been regarded as the misinterpretation of ovolarvipary by Wood (1987) and O'Hara (2008). Herting (1960) concluded that larvipary does not occur in Tachinidae based on the lack of evidence of nutritive glands in the uterus. Meier *et al*. (1999) defined viviparous species as those that deposit live larvae, meaning that the larvae hatch from their egg shells within the female. They further divided viviparity into larviparity and pupiparity, with the latter term reserved for species that retain a larva within the female until it forms a puparium (i.e., only Streblidae). Given this definition of larvipary, which is defined by the hatching of eggs internally rather than the nutritive nature of the uterus, *L. foeda* is in our opinion truly larviparous rather than ovolarviparous. In ovolarviparous species, mature first instars hatch from their eggs immediately after being deposited on a host or substrate, and to the casual observer this may be mistaken for larvipary.

It could be assumed that a dipteran centipede parasitoid would rather avoid direct contact with the host, which is a potentially dangerous animal to a fragile fly. The sudden direct attack, as was observed during our experiments, was therefore unexpected at first. However, there exists a plausible explanation for this behavior: an exposed centipede host, once located by a female tachinid, should be immediately attacked before it gets the chance to escape under the substrate beyond the reach of the fly. There are probably limited opportunities for larviposition and any chance must be acted upon.

Judging from the immediate success of the experiments it is believed that *Lithobius forficatus* is a natural host of *L. foeda*.

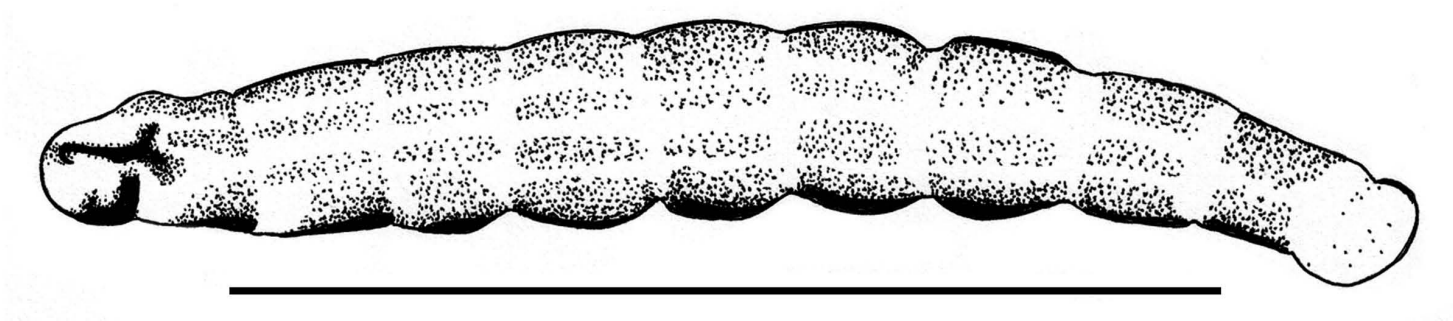

Figure 4. Mature first instar larva from the uterus. Scale bar: 0.5 mm.

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