

Pre-imaginal stages of the blowfly *Protocalliphora falcozi* in nests of the tree sparrow (*Passer montanus*)

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This paper offers the initial description of the first instar larva of *Protocalliphora falcozi* Séguy, 1928 (Diptera: Calliphoridae) and redescription of the second and third instar larvae and puparium, as well as distinction between *P. falcozi* and its relative *P. azurea* Fallén (Diptera: Calliphoridae). The material was sampled in the National Nature Reserve Šúr (SW Slovakia) from nests of the tree sparrow (*Passer montanus*), which has not previously been classified as a host of *P. falcozi*. Knowledge of diagnostically relevant characteristics to determine bird blowfly larvae and puparia will undoubtedly contribute to the current accepted phylogeny and classification of the genus *Protocalliphora*.

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1. Introduction

Bird blowflies (*Protocalliphora* Hough spp.) belong to the family of Calliphoridae (subfamily Chrysomyinae) together with some other genera (*Chloroprocta* Wulp, *Chrysomya* Robineau-Desvoidy, *Chrysopyrellia* Séguy, *Cochliomyia* Townsend, *Compsomyiops* Townsend, *Hemilucilia* Brauer, *Paralucilia* Brauer & Bergenstamm, *Phormia* Robinneau-Desvoidy, *Protophormiata* Grunin, *Protophormia* Townsend and *Trypocalliphora* Peus). Their larvae are blood sucking parasites on altricial nestlings. 15 species of *Protocalliphora* and 1 of *Trypocalliphora* have been recorded from the Palaearct (Schumann 1986, Kurahashi 1993), 10 from Europe (Rognes 2004), and 29 species from the Nearctic region,

including *P. rognesi* and *T. braueri* which have Holarctic distribution (Sabrosky *et al.* 1989, Whitworth 2003a, b).

Very little data has been published on the identification of pre-imaginal stages of this genus. When third instars are available, they should be allowed to pupate for easier identification. However, empty puparia are usually the only evidence of larvae in birds' nests.

Various determination keys from the Palaearctic region have been published to identify *Protocalliphora* larvae, and these are predominantly for third instar larvae, which possess more diagnostic characters than the first and second instar larvae: *Protocalliphora azurea* (Engel 1920, Rohdendorf 1957, Iwasa & Hori 1990), *P. falcozi* (Séguy 1941, Zumpt 1965, Lehrer 1972),

P. maruyamensis (Iwasa & Hori 1990) and *P. rognesi* (Engel 1920). Sabrosky *et al.* (1989) provided the key for identification of third instar larvae of 16 species in the Nearctic region. Older references include descriptions of third instars of *P. avium* (Coutant 1915, Dobrosky 1925) and *P. metallica* (Hall 1948).

Second instar larvae were described for *Protocalliphora avium* (Coutant 1915) from the Nearctic region and *P. azurea* (Draber-Moňko 2002), *P. falcozi* (Zumpt 1965), *P. maruyamensis* (Iwasa & Hori 1990), *P. rognesi* (Draber-Moňko 2002) from the Palaearctic region. The only paper concerning description of the first instar larvae was published by Iwasa & Hori (1990) for *P. maruyamensis*.

Puparia of *Protocalliphora azurea*, *P. falcozi*, *P. rognesi* and *Trypocalliphora braueri* were described by Cais *et al.* (2001), and Whitworth (2003a) published his key for the determination of puparia of 27 species in the Nearctic region. *P. falcozi* has been recorded only from the Palaearct, and mainly as adults (Gregor & Povolný 1959, Peus 1960, Lehrer 1972, Mihályi 1979, Rognes 1997). *P. falcozi* has been reported as a parasite on *Parus major* (Gregor & Povolný 1959, Lehrer 1972), *Parus palustris* (Szpila 1999, Wesolowski 2001), *Parus caeruleus* (Rognes 1997), *Ficedula albicollis* (Gregor & Povolný 1959, Lehrer 1972) and *Phoenicurus phoenicurus* (Gregor & Povolný 1959, Lehrer 1972). The tree sparrow (*Passer montanus*) was declared to be an exclusive host of *Protocalliphora azurea* (Rognes 1991).

This paper aims to describe the first instar and to re-describe the second and third instar and puparium of *P. falcozi* since all available relevant published data has been insufficient and too generally diagnostic for the whole genus. Here, we emphasize the characteristics to distinguish the pre-imaginal stages of *P. falcozi* and *P. azurea*, since they belong to the most common species found in nests of cavernicolous nesters in central Europe.

2. Material and methods

Sampling of the material was conducted in the National Nature Reserve Šúr situated in SW

Slovakia on the SE fringe of the Malé Karpaty Mts. (48° 42' N, 17° 16' E). The conservatory area is formed by rare alder wetlands in a flooded terrain depression combined with thermophilous oak woods. The collected specimens belong to first instar larvae (11), second instar larvae (17), third instar larvae (32) and puparia (20), and were all obtained directly from nestlings or nest material during the 1st–3rd broods of the tree sparrow. The material was sampled in the periods of May 20–June 26, 2006 and May 2–June 27, 2007. Some of the larvae were kept to develop to puparia and to adults, and this allowed species determination according to Draber-Moňko (2004). The pre-imaginal stages were identified from nests where only specimens of *P. falcozi* adults occurred. Mixed infestation by *P. falcozi* and *P. azurea* appeared only twice during our research, and in these cases the pre-imaginal stages were thus not identified. The puparia of *Protocalliphora azurea* were obtained from nests of *Parus major* in the Botanic Gardens in Bratislava.

Larvae were killed by soaking in hot water (to avoid deformation) and they were stored in 76% alcohol. Larvae and puparia were mounted in Canada balsam. A digital Leica DFC195 camera mounted on a Leica DM 1000 stereomicroscope was used for microphotography. Samples for SEM analysis were dehydrated in graded alcohol, subjected to the critical drying point of CO₂ (CPD 030, BAL-TEC, BG PRÜFZERT). Specimens were mounted on carbon stubs and coated with a layer of gold in an ion sputtering apparatus (SCD 050, BALZERS, Lichtenstein). SEM pictures were taken using a JXA 840 A (JEOL, Japan) scanning microscope.

The study material is deposited at the Department of Zoology, Faculty of Natural Sciences, Comenius University.

3. Terminology

With their tapering anterior and truncated posterior ends *Protocalliphora* larvae generally do not much differ from other genera of Calliphoridae. Their body consists of 12 segments, pseudo-cephalon, 3 thoracic segments (T I–T III), 7 abdominal segments (A I–A VII) and the anal division, completely covered with spines. The T I an-

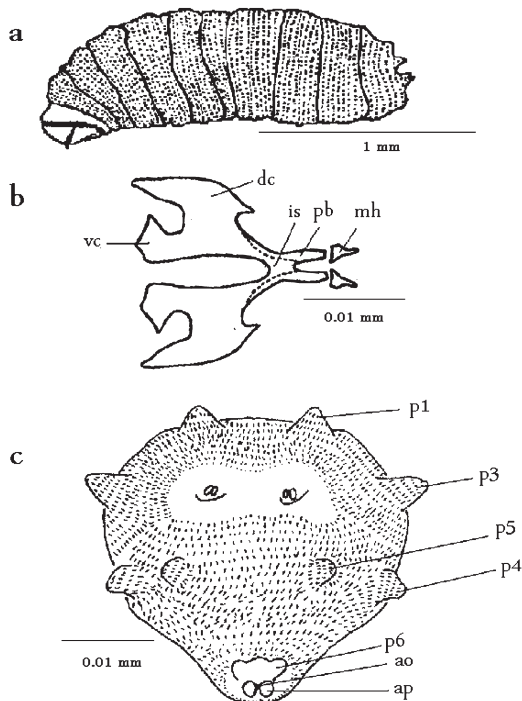


Fig. 1. First instar of *Protocalliphora falcozi*. – a. Whole body, lateral view. – b. Cephaloskeleton, ventral view; dc: dorsal cornua, is: intermediate sclerite, mh: mouthhooks, pb: parastomal bar, vc: ventral cornua. – c. Posterior spiracular region; ao: anal opening, ap: anal papillae, p1: dorsal papillae, p3: supralateral papillae, p4: infralateral papillae, p5: subventral papillae, p6: ventral papillae.

terior spinose band is exceptional, since it is modified to a crown of setae (prothoracic fringe), which most likely adheres the larva to the host during blood-sucking. Each abdominal segment has normally three distinct ventral spinal bands – ventral bands bounded by 8 ventral pads (Fig. 1).

The pseudocephalon has antennae, maxillary palpus and mouthhooks. The cephaloskeleton is composed of basal and intermediate sclerites and mouthhooks. Intermediate sclerite of each instar proceeds to the basal sclerite which consists of dorsal and ventral cornua. Paired labial sclerites are situated between the mouthhooks and the median beam of the intermediate sclerite. A labrum and accessory sclerite are absent.

The anal division has anal papillae and 7 distinct pairs of papillae (dorsal, subdorsal, supralateral, supraventral, infralateral, subventral and ventral papillae), but these are not distinct on all

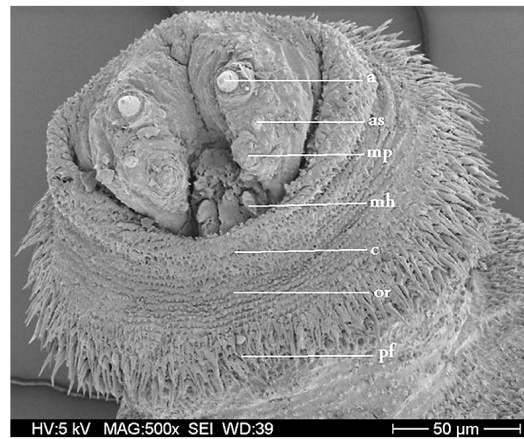


Fig. 2. SEM of anterior end of body of the first instar of *Protocalliphora falcozi*, ventral view; a: antenna, as: additional sense organ, c: cirri, or: oral ridges, pf: prothoracic fringe, mh: mouthhooks, mp: maxillary palpus.

instars. The posterior spiracle region is divided into a hyperspiracular region (above the posterior spiracles), a mesospiracular region (between the posterior spiracles) and a hypospiracular region (under the posterior spiracles).

Apart from a well-sclerotized and darkened cuticle, the puparium also differs from larvae, having a less distinct prothoracic fringe which is inverted during pupation and also poorly distinguishable papillae. Externally the puparia have varyingly developed cuticular folds (close to the posterior spiracles) and cuticular ridges (dorsally and ventrally on each segment), and these are not visible on larval instars. The terminology used for the description of pre-imaginal stages was that of Courtney *et al.* (2000) and Whitworth (2003a).

4. Descriptions of larvae and puparium

4.1. First instar larva

The body length is 0.9–2.25 mm ($n=4$). Spines of each segment are only just visible and lack distinct difference in their shape and size. The prothoracic fringe is very short compared to that in other instars (Fig. 1a), and the ventral pads are clearly distinguishable on each abdominal segment. Three ventral bands are distinct and unin-

Table 1. Second instar larval characters of *Protocalliphora falcozi* and *P. azurea*.

	Reference	Length (mm) min–max mean ± S.D. (n)	Number of lobes of anterior spiracles (n)
<i>P. falcozi</i>	Present study	1.6–5.6* 3.65 ± 1.36 (13)	8 (10)
<i>P. azurea</i>	Draber-Moňko (1996)	6.0–6.5–	6–7 (occasionally 8)

* Fully developed second instar larvae, the only difference was in length.

rupted. Anterior spiracles are absent.

Each lobe of the pseudocephalon bears antenna, maxillary palpus (cluster of several sensilla) and accessory sensillum. On the surface of the pseudocephalon there are numerous cirri and oral ridges, while the labial lobe and ventral organ are absent or indiscernible (Fig. 2).

Cephaloskeleton is small, mouthhooks are more strongly sclerotized than the other parts. The intermediate sclerite is elongated (when compared to the second and third instars), and the dorsal cornua is longer than the ventral one (Fig.

3a, 3b). The parastomal bar is fused with the intermediate sclerite (their border is marked by a dashed line, Fig. 1b).

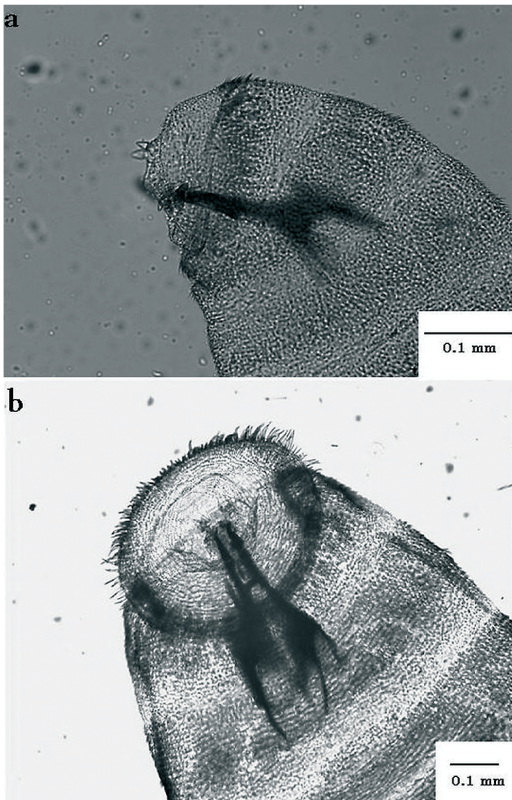


Fig. 3. Cephaloskeleton of first instar of *Protocalliphora falcozi*. – a. Lateral view. – b. Ventral view.

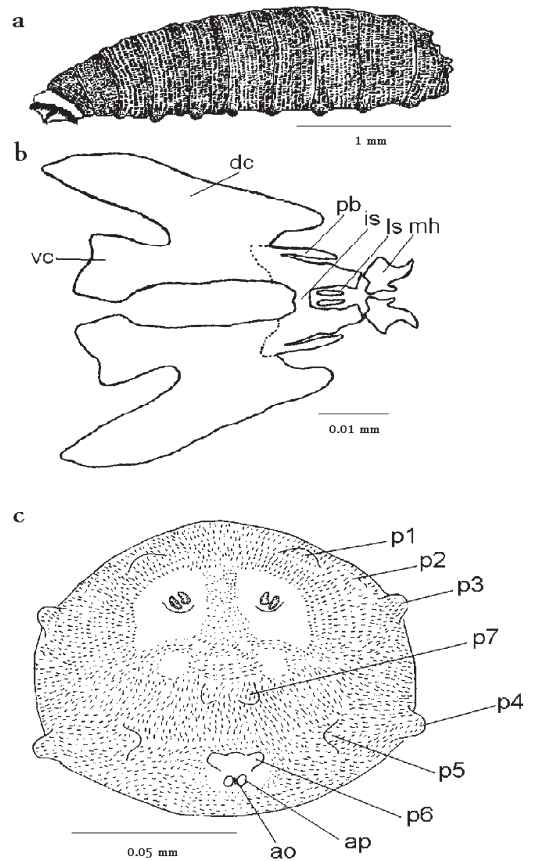


Fig. 4. Second instar of *Protocalliphora falcozi*. – a. Whole body, lateral view. – b. Cephaloskeleton, ventral view: dc: dorsal cornua, is: intermediate sclerite, ls: labial sclerites, mh: mouthhooks, pb: parastomal bar, vc: ventral cornua. – c. Posterior spiracular region; ao: anal opening, ap: anal papillae, p1: dorsal papillae, p2: subdorsal papillae, p3: supralateral papillae, p4: infralateral papillae, p5: subventral papillae, p6: ventral papillae, p7: supraventral papillae.



Fig. 5. SEM of anterior end of body of the second instar of *Protocalliphora falcozi*.

They have anal papillae and only 5 pairs of tiny papillae (dorsal, supralateral, infralateral, subventral and ventral) developed on the anal division, with the supralateral, infralateral, subventral, ventral and anal papillae clearly distinguishable. The anal papillae are rounded and the anal opening is situated slightly anterior to the anal papillae. The posterior spiracles are small and bilobed (without a gap between two forming slits) and they are poorly sclerotized. The peritreme is incomplete, with an absent spiracular scar (button). Spines in the mesospiracular region are also absent (Fig. 1c).

4.2. Second instar larva

The body length is given in Table 1. Spines of each segment and prothoracic fringe are distinct (Fig. 4a). On T II–A VII the central spines are slightly longer than the marginal ones. Ventral pads are easily distinguishable on each abdominal segment, and there are three distinct and uninterrupted ventral bands. Anterior spiracles are present, number of developed lobes is given in Table 1.

Each lobe of the pseudocephalon bears antenna and maxillary palpus, with an accessory

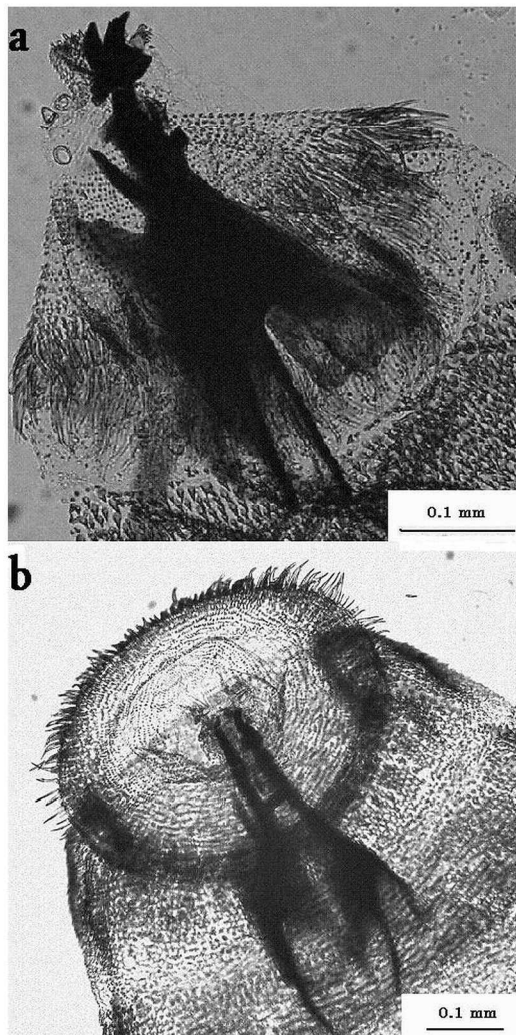


Fig. 6. Cephaloskeleton of second instar of *Protocalliphora falcozi*. – a. Lateral view. – b. Ventral view.

sensillum indiscernible or absent. Numerous cirri and oral ridges occur on the surface of the pseudocephalon. The labial lobe and ventral organ are absent or indiscernible (Fig. 5).

The cephaloskeleton is stout, mouthhooks are more strongly sclerotized than the other parts. The parastomal bar is not fused with intermediate sclerite, and the dorsal cornua is longer than the ventral one (Fig. 4b, 6a, 6b).

Anal papillae and all 7 pairs of papillae are developed on the anal division, including distinct supralateral, infralateral, subventral and ventral papillae. The subdorsal papilla is poorly developed, and anal papillae are rounded, while the

Table 2. Third instar larval characters of *Protocalliphora falcozi* and *P. azurea*

	Reference	Length (mm) min–max mean \pm S.D. (n)	Number of lobes of anterior spiracles (n)
<i>P. falcozi</i>	This study	4.3–10.4* 7.98 \pm 1.91 (15)	8–11 (15)
	Zumt (1965)	12–13–	5–7 (occasionally 10)
<i>P. azurea</i>	Draber- Moňko (2004)	13–15–	8
	Iwasa & Hori (1990)	13–15–	5–10

* Fully developed second instar larvae, the only difference was in length.

anal opening is situated slightly anterior to the anal papillae. Posterior spiracles have 2 slits with a distinct gap between them. The peritreme is incomplete but more sclerotized in comparison with the first instar. A spiracular scar (button) is developed although it is not clearly distinguishable, and spines are developed in the meso-spiracular region (Fig. 4c).

4.3. Third instar larva

The body length is given in Table 2. Spines of each segment and prothoracic fringe are distinct (Fig. 7a). On T II–A VII central spines are slightly longer than the marginal ones. Ventral pads are easily distinguishable on each abdominal segment, and there are three distinct and uninterrupted ventral bands. Anterior spiracles are present, number of developed lobes is given in Table 2.

Each lobe of the pseudocephalon bears antenna and maxillary palpus, with the accessory sensillum indiscernible or absent. On the surface of the pseudocephalon there are numerous cirri and oral ridges, and the labial lobe and ventral organ are also indiscernible or absent (Fig. 8). The cephaloskeleton is thick, with the mouthhooks more sclerotized than other parts. The parastomal bar is not fused with the intermediate sclerite and the dorsal cornua is longer than the ventral one (Fig. 7b, 9a, 9b).

The anal papillae and all 7 pairs of papillae are developed on the anal division, including distinct supralateral, infralateral, subventral and ventral papillae. The subdorsal papilla is poorly developed, while the anal papillae are rounded with the anal opening situated slightly anterior to the anal papillae. There are posterior spiracles with 3 slits,

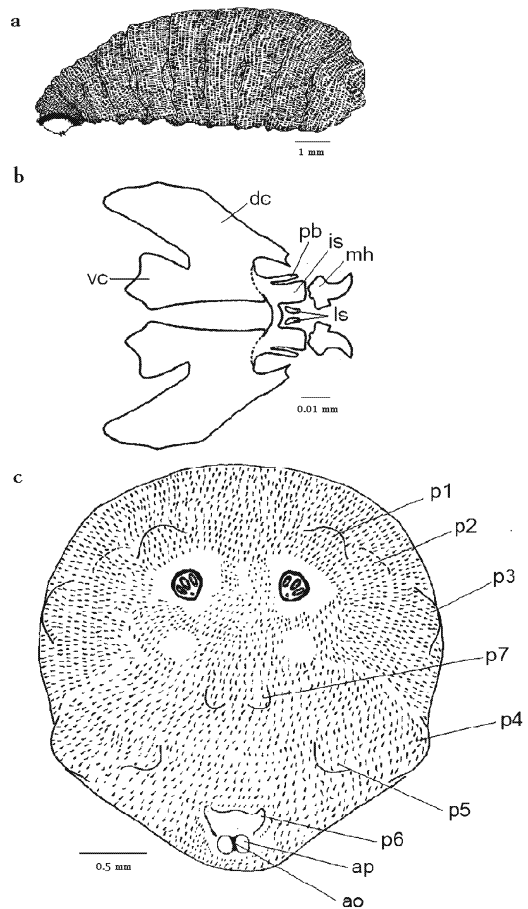


Fig. 7. Third instar of *Protocalliphora falcozi* – a. Whole body, lateral view. – b. Cephaloskeleton, ventral view; dc: dorsal cornua, is: intermediate sclerite, ls: labial sclerites, mh: mouthhooks, vc: ventral cornua. – c. Posterior spiracular region; ao: anal opening, ap: anal papillae, p1: dorsal papillae, p2: subdorsal papillae, p3: supralateral papillae, p4: infralateral papillae, p5: subventral papillae, p6: ventral papillae, p7: supraventral papillae.

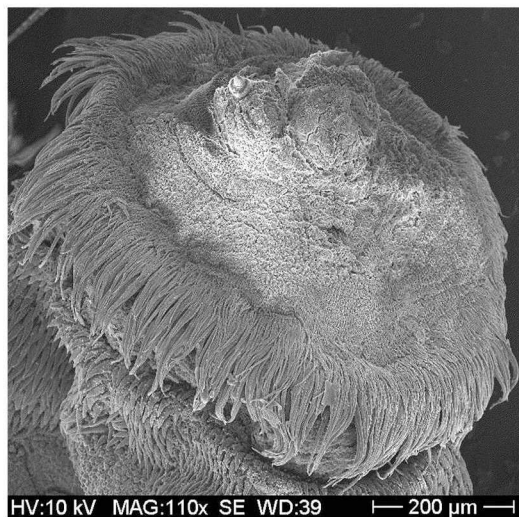


Fig. 8. SEM of anterior end of the third instar of *Protocalliphora falcozi*.

with a distinct gap between them. The peritreme is complete and a spiracular scar (button) is developed but seldom easily distinguishable. There are also mesospiracular spines (Fig. 7c).

4.4. Puparium

The body length is 7.11–8.34 mm (mean \pm *S.D.* = 7.95 ± 0.42 , $n = 9$), with all 3 ventral spine bands easily distinguishable. There are cuticular folds in the hypospiracular and mesospiracular region. However, there are only small ones in the hyperspiracular region. Additionally, the cuticular ridges are as distinct as the cuticular folds. The puparia found in nests were sometimes covered by nest material.

5. Discussion

Identification of pre-imaginal stages of bird blowflies according to their morphological characteristics appears indisputably more difficult than for adults. In some cases this seems almost impossible.

Lack of available data on determination of *Protocalliphora* larvae demands arduous sampling since these obligate bird parasites are necessarily connected to their host, and this is essential

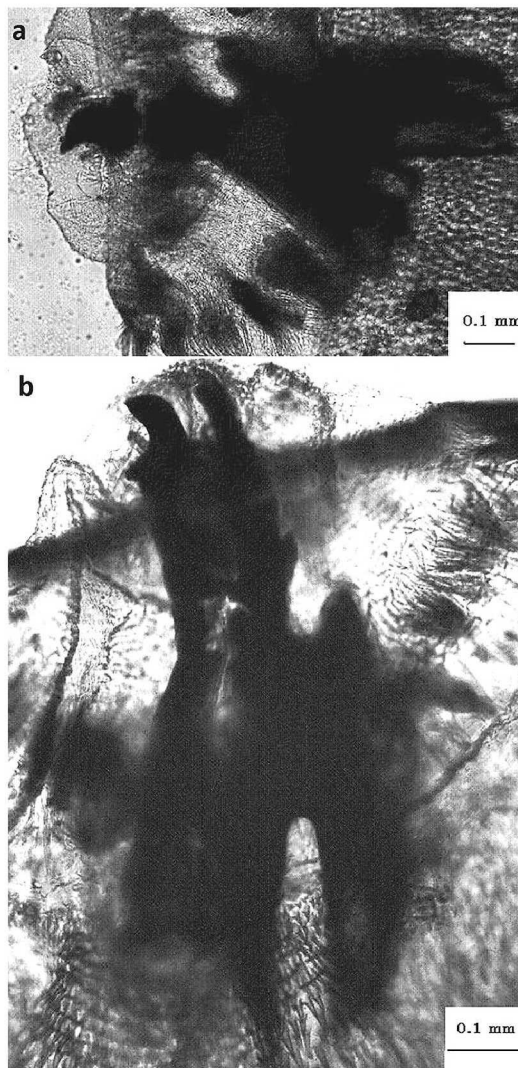


Fig. 9. Cephaloskeleton of third instar of *Protocalliphora falcozi*. – a. Lateral view. – b. Ventral view.

to complete their development successfully (Bennet & Whitworth 1991). Additionally, enough host nests with nestlings are required in order to collect sufficient material of larvae and puparia. We have not yet acquired an approach to keep larvae artificially, due to an alternative host used to nourish bird blowfly larval instars (larvae presumably cannot complete their development on presocial nestlings). Another problem occurs in obtaining eggs since females kept under artificial conditions cannot lay their eggs despite apparent mating (Bennet & Whitworth 1991). Such inadequate material results in insufficient opportunity

to compare more species in their pre-imaginal stages. Therefore, some authors described *Protocalliphora* larvae entirely according to characteristics distinctive of additional or even all genus species (e.g. Zumpt, 1965: descriptions of the second and third instars of *P. falcozi*).

Since larvae of the same instar can have varying nutrition their characteristics can vary, and this makes identification more complicated (e.g. distance between spines, prothoracic fringe diameter and the distance between posterior spiracles). Also, during food deficiency, the body length of a more advanced instar may be shorter than that of a younger one. Moreover, length often varies within the same instar due to differing food sources and conditions. Certain body parts such as the cephaloskeleton and posterior spiracles also have a surprising degree of variability in their sclerotization in the same instar.

In comparison with the Nearctic region, recent research on bird blow flies in the Palaearctic area has not been intensive enough. Larvae of *Protocalliphora distincta*, *P. isochroa*, *P. lii*, *P. peusi*, *P. nuortevai* and *P. proxima*, all Palaearctic species, have not been described. Most data already distinguishes only *Trypocalliphora* larvae from *Protocalliphora* and *Protocalliphora rognesi* from *P. azurea* and *P. falcozi*.

Larvae of *P. azurea* and *P. falcozi* often interact with the same host and their hosts build similar nests or remain in nests for approximately the same period, therefore identification of their larval instars still seems doubtful. Original morphometric analysis supported by other references showed shorter second and third larval instars for *P. falcozi* than for *P. azurea*. The number of anterior spiracle lobes may be the same in both species, and hence this does not represent a reliable characteristic for identification (Tables 1 and 2). Differences in the shape of cephaloskeletons in these 2 species appear also insignificant (Draber-Moňko 2004). However, there is some degree of discrepancy in the intermediate sclerite region, including the parastomal bar. Detailed synthesis of cephaloskeletons requires additional material for analysis.

Segments of *Protocalliphora* species, which are completely covered with spines, exhibit relatively rare features for dipteran larvae. The *Trypocalliphora* larvae burrow directly into the flesh

of nestlings and spend their period in hosts, so that they do not have segments completely covered with spines, and this can play a defensive role in a host's body (also e.g. *Auchmeromyia* Brauer and Bergenstamm and the third instar of *Cordylobia* Gruenberg).

The main features of *P. falcozi* larvae include enlarged antennae, numerous cirri and oral ridges on the pseudocephalon. Enlargement of antennae and maxillary palpi in the first instars of parasitic or predatory species from the genera *Bellardia* Robineau-Desvoidy, *Onesia* Robineau-Desvoidy and *Pollenia* Robineau-Desvoidy was also observed (Szpila 2003, 2004). This phenomenon is possibly associated with a necessity for better orientation in nature. Females of *Calliphora* Robineau-Desvoidy, *Phormia* Robineau-Desvoidy and *Lucilia* Robineau-Desvoidy, which do not have enlarged antennae and maxillary palpi, lay their eggs directly onto a suitable food source, whereas parasitoids do so when actively searching for their host in soil (Szpila et al. 2008). Females of *Protocalliphora* spp. lay their eggs directly on nestlings or on nearby nest material. Even though they can lay on a suitable food source (nestlings), larvae are intermittent feeders, leaving their hosts facultatively after sucking enough blood, but they soon search for this source again.

There is a lack of detailed information concerning the anal pad of *Protocalliphora* larval instars. The anal pad, which has been described in the second instar of *P. rognesi* (Draber-Moňko 2002) is similar to that of *P. falcozi*. The position of the anal opening of the first instar of *P. falcozi* corresponds with that of *Phormia regina* (Meigen, 1826) and *Lucilia illustris* (Meigen, 1826) and this was described by Szpila et al. (2008).

There are morphological differences for identification in puparia and adults between *P. falcozi* and *P. azurea* (Cais et al. 2001, Draber-Moňko 2004). In our analyses, some additional characteristics used in determination of Nearctic species (Whitworth 2003a) have also been taken into account. The cuticle surface of fully developed puparia of *P. falcozi* is distinctly different than in *P. azurea*. On the surface they are wrapped in a hair cocoon, and this is usually absent in *P. azurea*.

We propose that data obtained in our analyses will be useful in complex phylogenetic simulations. Iwasa and Hori (1990) declared that some characteristics, which are absent in other Chrysomyinae genera, presumably corresponded with specialized blood sucking habit such as in *Protophormia*, *Phormia* and *Chrysomya*. For example, these include undeveloped tubercles at abdominal segment VIII, prothoracic fringe, relatively small mouthhooks, small posterior spiracles with a long distance between them. Except in *Protocalliphora*, obligatory haematophagy is seen only in rare forms of parasitism of Calliphoridae larvae. Morphology of bird blowfly larvae may be beneficial to comprehend the evolution of Calliphoridae when larval haematophagy originating in saprophagy is considered. However, the data offered in this paper is proposed to become essential for complex phylogenetic syntheses.

Further analysis should undisputedly lead to the elaboration of a key to identify all bird blowfly larval instars. Morphometric characteristics of the cephaloskeleton will most likely present a definitive challenge in diagnostics, whereas the number of anterior spiracle lobes and their shape and size will become secondary in species identification.

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