

The larval stages and metamorphosis of *Lebia* (*Poecilothais*) *bifenestrata* A. Morawitz, 1862 (Coleoptera: Carabidae)

Личиночные стадии и метаморфоз *Lebia* (*Poecilothais*) *bifenestrata* A. Morawitz, 1862 (Coleoptera: Carabidae)

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КЛЮЧЕВЫЕ СЛОВА. Личинки, описание, хетотаксия, гиперметаморфоз, Lebiini, Brachinini.

ABSTRACT. The type of development and the larval stages of *Lebia* (*Poecilothais*) *bifenestrata* A. Morawitz, 1862 are described and discussed. Because the larvae of *L. bifenestrata* feed on leaf beetle pupae, have two instars and hypermetamorphosis, their development generally agrees with that of other known *Lebia*. However, they show some evolutionarily primitive features such as only a few apical sensilla on palpomere 2 in the first instar larva, as well as a mobile tarsus and a bidentate nasale in the second instar larva. The features of larval chaetotaxy allow for the Lebiini and Brachinini to be considered as related groups.

РЕЗЮМЕ. Изучено развитие и описаны личиночные стадии *Lebia* (*Poecilothais*) *bifenestrata* A. Morawitz, 1862. В общих чертах развитие данного вида аналогично развитию других видов *Lebia*, для которых характерно питание куколками листоедов, два личиночных возраста и гиперметаморфоз. Однако личинки *L. bifenestrata* обладают признаками, которые можно считать примитивными: небольшое число сенсилл на вершине 2 пальпомера у личинки I возраста, а также подвижная лапка и двузубое назале у личинки II возраста. Особенности хетотаксии личинок позволяют считать трибы Lebiini и Brachinini родственными группами.

Introduction

Only three groups of ground beetles are currently known to develop as parasitoids: the tribe Peleciini,

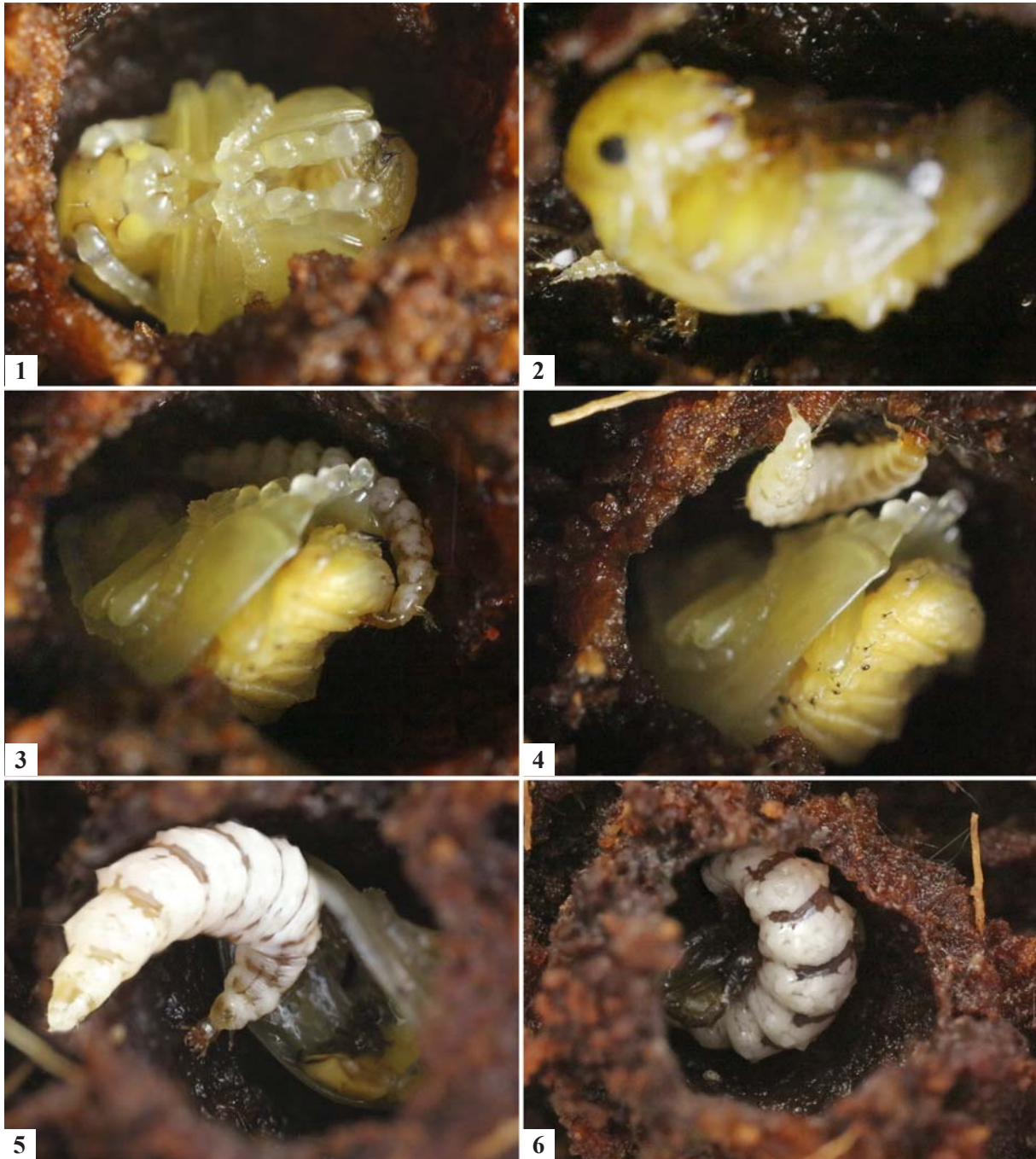
genus *Lebia* Latreille, 1802, and some closely related genera within the subtribe Lebiina, as well as members of the subfamily Brachininae. The biology of Peleciini is poorly studied. According to the available information, their larvae feed on centipedes [Salt, 1928; Liebherr, Ball, 1990]. Brachininae show a wide range of hosts representing various families of Coleoptera [Erwin, 1967; Juliano, 1984, 1985; Hovorka, 1996; Saska, Honek, 2004; Makarov, Bokhovko, 2005; Matalin, Makarov, 2014] or mole crickets (Orthoptera: Grillotalpidae) [Frank et al., 2009; Weed, Frank, 2005]. The larvae of *Lebia* feed exclusively on leaf beetle pupae [Silvestri, 1904; Lindroth, 1954; Capogreco, 1989; Weber et al., 2006]. Adults of the subgenus *Poecilothais* Maindron, 1905 feed mainly on species of the genera *Pyrrhalta* Joannis, 1865 and *Xanthogaleruca* Laboussiere, 1934, to a lesser extent on species of the genus *Gonioctena* Chevrolat, 1843 [summarized by Habu, 1967].

Since Silvestri [1904], three larval “instars” have been distinguished in *Lebia*. However, “instars” Ia and Ib differ only in size and actually represent the first instar larva at the beginning and at the end of the feeding period [Capogreco, 1989]. Thus, the larval development in all hitherto studied *Lebia* species passes only one moult [Silvestri, 1904; Lindroth, 1954; Capogreco, 1989; Weber et al., 2006]. According to Capogreco [1989], we distinguish two instars for the larvae of *Lebia*. Due to well-developed legs and sensory organs, the first instar larva finds a leaf beetle pupa or prepupa inside a soil chamber as a host. After finding the host, the larva starts feeding,

greatly increasing in size, to moult thereafter. The second instar larva shows shortened appendages, it does not feed, to eventually pupate in the host's chamber. Such a lifestyle makes both finding and studying the preimaginal stages of *Lebia* significantly complicated, accounting for the larvae of *Lebia* having been much less studied than those of other genera of Carabidae. At present, larval morphology has been described in detail only for *Lebia (Lebia)*

scapularis (Geoffroy, 1785) and *Lebia (Lebia) viridis* Say, 1823, while the chaetotaxy has been studied only in the latter species. No larvae of the subgenus *Poecilothais* have been described yet.

The present paper provides the first description of the preimaginal stages of *Lebia (Poecilothais) bifenestrata* A. Morawitz, 1862, morphological features and the metamorphosis of parasitoid ground beetles being discussed as well.



Figs 1–6. First instar larva of *L. bifenestrata* and its host: 1 — pupa of *P. annulicornis* in pupal chamber; 2 — larva before feeding; 3 — larva during feeding; 4 — larva restoring a destroyed wall of pupal chamber; 5–6 — larva at the end of the feeding period.

Рис. 1–6. Личинка I возраста *L. bifenestrata* и её прокормитель: 1 — куколка *P. annulicornis* в камере; 2 — личинка перед началом питания; 3 — личинка в процессе питания; 4 — личинка заклеивает разрушенную стенку камеры; 5–6 — личинка в конце питания.

Material and methods

Collecting and rearing

In the last third of May 2015, live adults of *L. bifenestrata* were collected in a floodplain forest in the valley of Kedrovaya River, Khasansky District, Primorsky Krai, Russia (43°05'58"N 131°33'20"E). The beetles were active in daytime and found highly abundant on the leaves of *Viburnum sargentii* Koehne, 1899 together with feeding larvae of *Pyrrhalta annulicornis* Baly, 1874 (Coleoptera, Chrysomelidae). Subsequently, both the adults of *L. bifenestrata* and the larvae of *P. annulicornis* were transferred to the laboratory in Moscow, Russia. From early June to mid-July, they were maintained under long-day conditions (LD) (16:8) at 22–24°C and 75–80% humidity in plastic cages, each

2.4 litres in capacity (10x14x10 cm), with coconut chips and live stems of *Viburnum opulus* (Linné, 1753) serving as a substrate. Adult *L. bifenestrata* were fed with pieces of larvae of *Zophobas morio* Fabricius, 1776 (Coleoptera: Tenebrionidae), as well as of small insects, mostly aphids. After three weeks of cultivation, the substrate was examined every two days and larvae of *L. bifenestrata*, as well as pupal chambers of *P. annulicornis* were collected. All pupal chambers of the leaf beetle found were dissected and their infestation with ground beetle larvae was checked.

The larvae of *L. bifenestrata* were preserved in 70% alcohol, altogether two larvae of the first instar and four larvae of the second instar being mounted on slides using the Euparal (D~1.05) medium. The larvae, both in alcohol and in slides, and adults are deposited in the collec-



Figs 7–12. Adults of *L. bifenestrata*: 7–9 — parental generation; 10–12 — daughter generation.

Рис. 7–12. Имаго *L. bifenestrata*: 7–9 — родительское поколение; 10–12 — дочернее поколение.

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Imaging and larval descriptions

Slides of the larvae were examined under a Zeiss Axio Scope.A1 microscope and photographed with a Canon EOS 5D Mark III camera with a Canon MP-E 65 mm macro lens. The extended focus technique was applied, and photographs were stacked using Zerene Stacker software. The measurements were taken using an ocular-micrometer mounted on a Leica M165C stereo microscope.

The nomenclature of the primary setae and pores follows Bousquet and Goulet [1984] with modifications [Makarov 1996], while the numeration of the secondary setae is after Bousquet [1985].

Results

Features of behaviour and development

The first instar larva of *L. bifenestrata* enters the pupal chamber of *P. annulicornis* and seals the inlet. Thus, the infested chambers do not differ in appearance from the uninfested ones. At first, the larva moves freely in the chamber and finds a place to attach to the host (Fig. 2). Most often, it begins feeding from the lateral parts of the abdomen. It is noteworthy that the sclerotization of the integument in these parts of the pupa does not differ from the adjacent abdominal and dorsal parts. The matter can be assumed to lie in the curvature of the surface. Due to the relatively small mandibles (Fig. 15), the larva is unable to capture the parts of the host pupa that show a large curvature radius.

The first instar larva feeds almost continuously. During two or three days, it eats the host's pupa almost entirely, leaving only fragments of the thoracic cuticle. When disturbed, the larvae stopped feeding and moved around the chamber to hide behind the remains of the pupa. From time to time, the larva tried to close the hole in the wall of the pupal chamber that was made and utilized for observations. The larva thereby used an adhesive substance secreted by the glands of the 10th abdominal segment. After four or five days, the first instar larvae moulted into the second instar, which did not feed, but, remaining in the chamber, gradually underwent the metamorphosis. The development of the second instar larva lasted from 7 to 9 days, *vs.* only 6–8 days for the pupa. Interestingly, the beetles hatched under laboratory conditions differed significantly from the specimens of the parental generation both in their larger size (TL = 5.64 mm [CI = 5.48–5.80 mm], n=5 *vs.* TL = 4.79 mm [CI = 4.64–4.94 mm], n=10; p<0,001), and a better developed light elytral pattern (Figs 10–12, *vs.* Figs 7–9).

Description of the first instar larva Figs 13–28.

Habitus. Larva campodeiform, mobile, with a large head, well developed legs and sensory appendages.

Colour. Head and mandibles yellow-brown, other appendages pale yellow. Thoracic tergites yellow-grey, pleur-

ites yellowish, poorly pigmented, sternites unpigmented, indistinguishable from the surrounding cuticle. Legs, apart from yellow-brown claws, pale yellow. Abdominal tergites and pleurites slightly lighter than thoracic ones, sternites barely pigmented. Urogomphi light, with slightly darkened apices. Pygidium pale yellow.

Microsculpture. Head, prothorax, pleurites, sternites, and most of appendages without any microsculpture; anterior part of metanotum, as well as abdominal tergites I–VIII each with short transverse rows of 3–8 microspines. Tergite IX without microsculpture, basal portion of pseudosegments of urogomphi with a coarse meshed sculpture (Fig. 26). Ventrolateral surface of tarsi with several individual spines (Fig. 30).

Head virtually quadrate, with unexpanded temples, sharply narrow before occiput (Fig. 15). Frontal sutures strongly curved inward near dorsal tentorial pits; epicranial groove short, approximately half the diameter of first antennomere. Frontal sclerite weakly delated in basal portion, with two large egg teeth on each side, evenly narrowed anteriorly from front mandibular condyle to rounded angles of paraclypeus. Nasale strongly protruding forward, with a smooth, rounded, anterior margin (Figs 14–15). Parietal sclerite with neither carinae nor grooves; eye tubercles weakly protruding, with four (3+1) simple eyes, eyes of anterior row 1.5–2.0 times as large as the eye of posterior row. Antennae 4-segmented, with a disproportionately large third antennomere (Fig. 15); 1st antennomere virtually quadrate, weakly narrowed towards apex; 2nd antennomere ca 1.5 times shorter than first one; 3rd antennomere barely longer than first and second combined, evenly expanded distally, with a large, conical, sensory appendage; 4th antennomere suboval, approximately same length as first one. Mandibles quite long, weakly curved, similar in length to parietale; cutting margin of terebra a thin plate, not serrate; retinaculum very small and triangular, placed basally; penicillus short, not reaching retinaculum (Fig. 15). Maxillae short, with a large smooth cardo and wide stipes (length/wide = 1.6–1.7); lacinia absent; galea 2-segmented; 1st galeomere short, virtually quadrate; 2nd galeomere narrow and long, 3 times longer than the first one, with apex half the length of apical palpomere. Palps 4-segmented, approximately as long as stipes; first three palpomeres virtually equal length, 4th palpomere long and narrow, with a conical apex (Fig. 19). Mentum oblong, poorly expanded forwards, 1.3 times as long as wide; ligula entirely reduced; palps 2-segmented, shorter than mentum; basal palpomere short, transverse; apical palpomere almost 2 times longer than basal one, with a rounded apex (Figs 17–18).

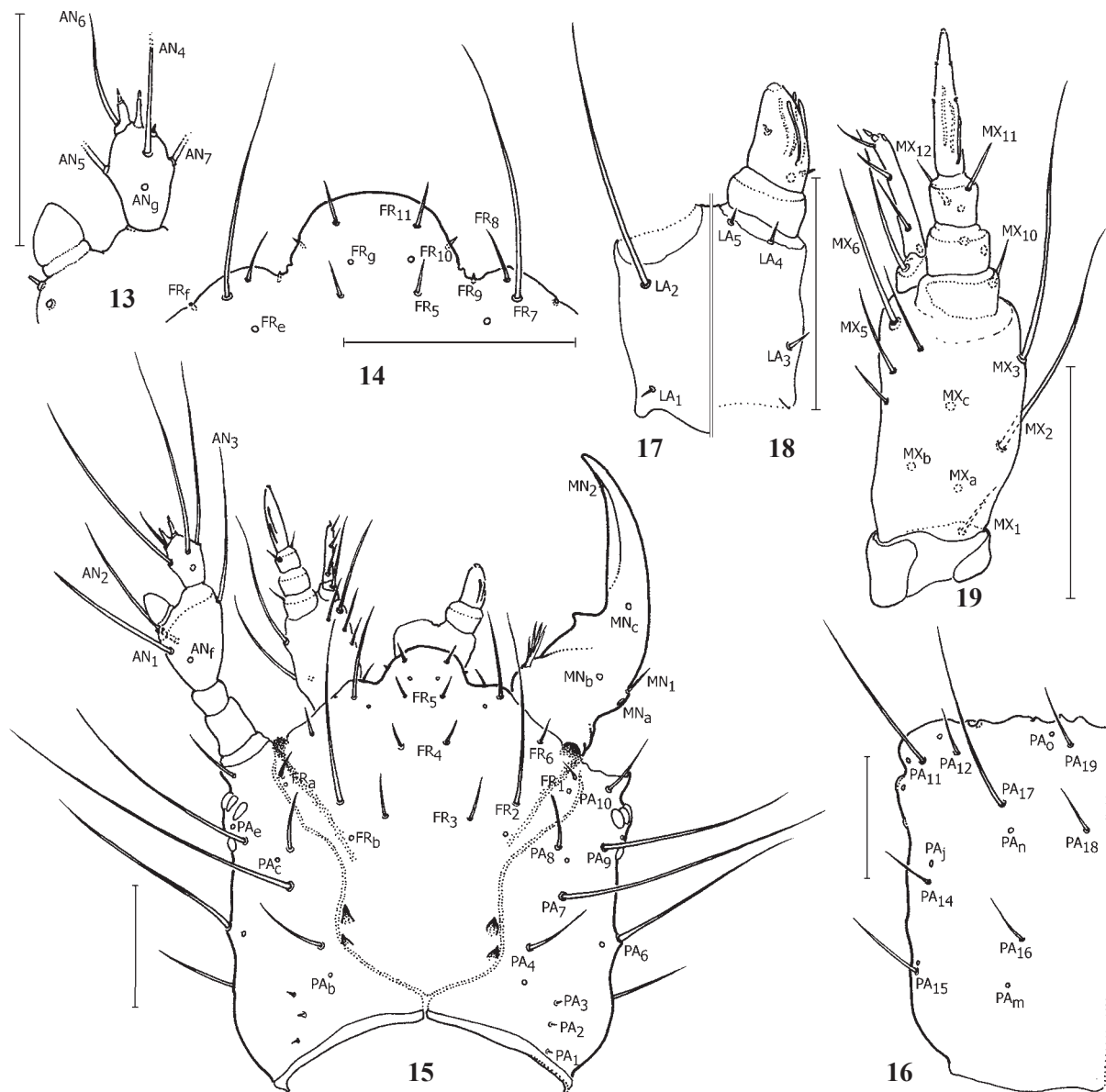
Thoracic segments moderately wide; tergites well-sclerotized, slightly narrower than head. Pronotum transverse, with rounded sides and a weak lateral carina, 1.4 times wider than long (Fig. 20). Meso- and metanotum shorter, with a well-developed anterior carina and a slight lateral one, 2.5 times wider than long (Fig. 22). Prosternum well-sclerotized, transverse and roundly triangular (Fig. 21). Episternum and epimeron of pro-, meso- and metathorax well-sclerotized, with strongly pigmented areas of apodeme attachment (Figs 21–23). Pleurites of meso- and metathorax oval; sternites poorly-sclerotized, with hardly distinguishable boundaries (Fig. 23). Legs long, forelegs slightly shorter than hind ones (Fig. 29). Coxae large, conical; trochanter relatively long, 0.4 times as long as coxa and 0.75 times as long as femur; femur and tibia quite wide (0.65–0.71 times as long), slightly delated distally; tarsus narrow, strongly narrowed towards apex, slightly shorter than femur and distinctly shorter than tibia; claws separated from pretarsus by a membrane, unequal in length, anterior claw 3.5 times as long as posterior one (Fig. 30).

Abdomen. Tergites I–VIII small, sharply transverse, poorly-sclerotized, with a weak anterior carina visible only in medial part; lateral carina undeveloped; lateral sides each with a distinct impression (Fig. 24). Epi- and hypopleurites rounded, with sclerotizations as on tergites; sternites very weakly sclerotized. Mesosternum transverse, trapezoidal; inner poststernites small and narrow; outer ones rounded and visibly convex (Fig. 25). Urogomphi relatively long, 4-segmented, with an unclear border of basal segment; all segments, especially distal ones, clavate, expanded towards apex (Fig. 26). Pygidium conical, approximately two times longer than IXth abdominal segment, clearly narrowed to the apex.

Chaetotaxy. Chaetome of first instar larva generally very similar to the typical one, with a minimal number of secondary setae.

Frontale with a virtually complete set of sensilla except only for FR₆; FR₂ and FR₇ much longer, while other setae much shorter; pairs of mesosetae FR₃–FR₅ arranged in parallel rows from middle of sclerite to nasale; pairs FR₈–FR₉ and FR₁₀–FR₁₁ containing one microseta (FR₉ and FR₁₀) and one mesoseta (FR₈ and FR₁₁) (Fig. 14). Parietale with macrosetae PA₇ and PA₈ on dorsal surface, PA₆ on lateral and PA₁₁ and PA₁₇ on ventral ones; PA₅ and PA₁₃, as well as PA_a, PA_d, PA_h and PA_g absent (Fig. 16).

Antennae with macrosetae AN₁–AN₅, AN₇ and a typical



Figs 13–19. First instar larva of *L. bifenestrata*: 13 — apex of antenna; 14 — anterior margin of frontale; 15 — head, dorsal view (left mandible, right antenna and right maxilla not shown); 16 — left half of parietale, ventral view; 17 — mentum, ventral view; 18 — labium, dorsal view; 19 — right maxilla, dorsal view. Scale bars: 0.1 mm.

Рис. 13–19. Личинка I возраста *L. bifenestrata*: 13 — верхина антенны; 14 — передний край фронтале; 15 — голова, сверху (левая мандибула, правые антенна и максилла не показаны); 16 — левая половина париегального склерита, снизу; 17 — подбородок, снизу; 18 — нижняя губа, сверху; 19 — правая максилла, сверху. Масштаб: 0,1 мм.

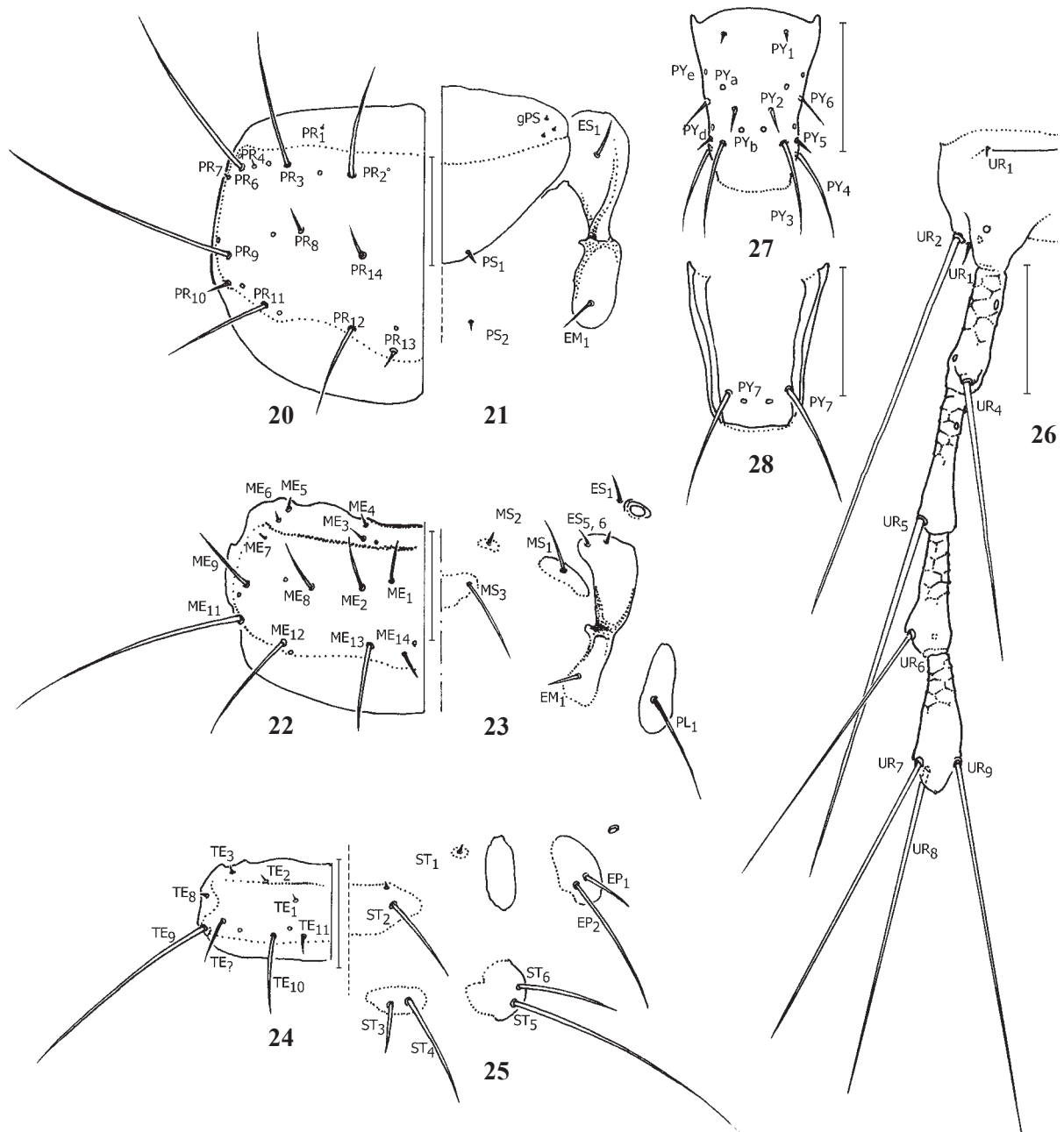
set of sensilla (Figs 13, 15); AN₆ quite long, same in length as apical antennomere, its base coupled with base of apical sensilla; 3rd antennomere with placoid and bell-shaped sensilla near sensory appendage (Fig. 13).

Chaetotaxy of mandibles entirely corresponding to the typical one (Fig. 15).

Maxillae with sets of setae and sensilla typical of *Lebia* larvae. Stipes, including gMX₃, without numerous secondary setae, with very long MX₂ and MX₃ on lateral surface, and a

thick and long MX₆ instead of a lacinia; galea with additional setae, 1st galeomere very small, MX₇ absent, while MX₈ unusually long and reaching the apex of galea; apical galeomere with a row of three setae; MX₁₀ and MX₁₁ quite long, not shorter than diameter of 3rd palpomere; apical palpomere with three long (about half as joint length) finger-shaped sensilla (Fig. 19).

Mentum with a single macroseta LA₂, other setae very short; LA₃ single; LA₆ and LA₇ absent; 2nd palpomere with four finger-shaped sensilla (Fig. 18).



Figs 20–28. First instar larva of *L. bifenestrata*: 20 — pronotum, left half; 21 — prothorax, left half; 22 — mesonotum, left half; 23 — mesothorax, left half; 24 — abdominal tergite IV, left half; 25 — sternites and pleurites of abdominal segment IV, left half; 26 — abdominal tergite IX and left urogomph; 27 — abdominal segment X, dorsal view; 28 — abdominal segment X, ventral view. Scale bars: 0.1 mm.

Рис. 20–28. Личинка I возраста *L. bifenestrata*: 20 — переднеспинка, левая половина; 21 — переднегрудь, левая половина; 22 — среднеспинка, левая половина; 23 — среднегрудь, левая половина; 24 — тергит IV сегмента брюшка, левая половина; 25 — стерниты и плевриты IV сегмента брюшка, левая половина; 26 — тергит IX сегмента брюшка и левая уругомфа; 27 — X сегмент, сверху; 28 — X сегмент, снизу. Масштаб: 0,1 мм.

Tergite of prothorax with long macrosetae PR_2 , PR_3 , PR_6 , PR_9 , PR_{11} and PR_{12} arranged in a perimeter, discal setae PR_8 and PR_{14} 3 or 4 times shorter; microsetae PR_5 at anterior angles, while PR_4 , PR_6 and PR_8 entirely reduced. Ventral surface of prothorax without additional setae; microsetae ES_2 – ES_4 absent from anterior angles of episternum (Fig. 21). Chaetotaxy of meso- and metanotum very similar to typical, with mesosetae ME_1 , ME_2 , ME_8 and ME_9 in anterior row, and microsetae ME_{11} – ME_{13} , as well as mesoseta ME_{14} in posterior row (Fig. 22). Pleurites with a very long PL_1 ; episternum and epimeron with typical setae; sternites with macroseta MS_3 ; mesoseta MS_1 displaced to coxal base; MS_2 as a microseta, while MS_4 absent (Fig. 23).

Legs without additional setae; coxae with a complete set of setae, among them CO_6 very long, while CO_7 – CO_9 much shorter; trochanter with an ordinary chaetome, TR_4 very long, TR_8 same in length as apical setae; apical FE_2 and FE_3 much longer than opposite FE_4 and FE_5 ; TI_1 very long, not shorter than tibia, in apical group TI_2 – TI_4 much longer than opposite TI_5 – TI_7 (Fig. 29). Tarsus with a relatively long TA_1 in basal half; apex, except for spiniform TA_2 and TA_7 , only, with TA_4 and TA_5 ; TA_3 and TA_6 replaced by short conical outgrowths; UN_1 and UN_2 very short (Fig. 30).

Chaetome of abdominal tergites with an appreciable reduction of setae in anterior row — TE_1 very small, TE_6 and TE_7 , reduced; setae TE_9 and TE_{10} clearly recognized in posterior row, mesoseta of an unclear homology placed near TE_9 (Fig. 24). Pleurites with typical setae, EP_2 very long; sternites with a standard composition of setae, but poststernites with unusually long ST_4 and, especially, ST_5 (Fig. 25).

Urogomphi with a complete set of macrosetae, most of which only half as long as urogomphi; UR_9 same in length as UR_7 and UR_8 (Fig. 26).

Segment X with typical setae, only apical PY_3 , PY_4 and PY_7 , relatively long, not shorter than diameter of segment X; PY_6 about same in length as PY_2 (Figs 27–28).

Description of the second instar larva

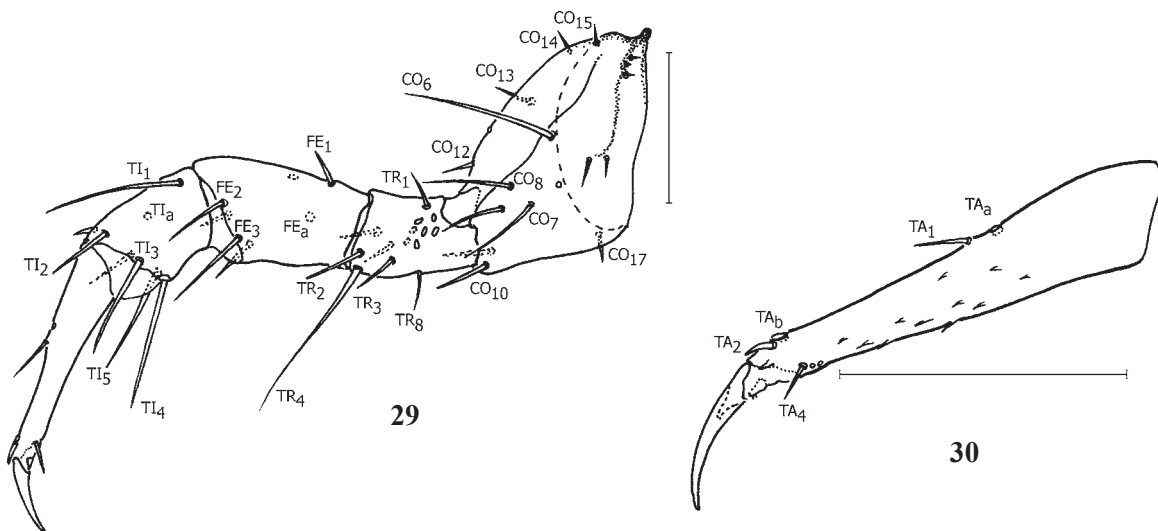
Figs 31–57.

Habitus. Inactive physogastric larvae with shortened appendages and partially reduced sense organs.

Microsculpture. Anterior part of frontal sclerite with distinct transverse rows of spines; mandibles both with small individual teeth and rows of teeth, especially strong near retinaculum; stipes and mentum with only individual teeth. Cuticle of thorax and abdomen covered with long spines, sparser on sclerites and legs.

Head rounded, subquadrate, weakly narrowed towards base; epicranial groove longer than antennomere 1 (Fig. 31). Frontal sclerite narrow, 1.8 times longer than wide, evenly tapered before mandibular condyles; frontal sutures weakly curved near tentorial pits; paraclypeus distinctly rounded; nasale moderately protruding, with two large teeth (Fig. 32). Parietal sclerite with convex sides, both eye tubercles and simple eyes absent; carinae and grooves undeveloped. Antennae very short, 3-segmented, far from reaching the outer angles of paraclypeus; 1st antennomere very short and wide, annular; 2nd antennomere (coupled together with 2nd and 3rd true antennomeres) conical, as long as wide, with a small sensory appendage near apex; apical antennomere oval, approximately 0.8 times as long as previous one (Fig. 34). Mandibles triangular, distinctly narrowed in distal half, half as long as parietal sclerite; terebra with small teeth; retinaculum quite long, with apex sharply directed forward; penicillus relatively short (Fig. 33). Maxillae short, with a wide cardo and massive stipes narrowed towards apex; lacinia absent; galea 2-segmented, with partly accreted galeomeres; 1st galeomere short, transverse, 2nd galeomere 3.5 times as long as 1st, regularly narrowed towards apex (Fig. 38). **Labrum** with an elongated mentum and short 2-segmented palps (Figs 41–42); mentum 1.7 times as long as wide; ligula absent; palpi about half as long as mentum, 1st palpomeres wide and transverse; apical palpomeres conical, regularly narrowed towards apex (Fig. 43).

Thoracic segments with slightly sclerotized tergites and pleurites; sternites, except for prosternum, with invisible borders. Pronotum transverse, without any carinae, 1.6–2.0 times as long as wide; pre- and post-tergite without visible borders (Fig. 44). Meso- and metanotum with a well-developed anterior margin and a clearly visible pigmented stripe in area of fragma (Fig. 46). Pleurites slightly pigmented only in apodeme area (Fig. 47). **Legs** short and stout, trochanter,



Figs 29–30. First instar larva of *L. bifenestrata*: 29 — middle leg, frontal view; 30 — tarsus, frontal view. Scale bars: 0.1 mm.

Рис. 29–30. Личинка I возраста *L. bifenestrata*: 29 — средняя нога, спереди; 30 — лапка, спереди. Масштаб: 0,1 мм.

femur and tibia accreted in a conical structure, approximately as half as long as leg (Fig. 48); coxae short and wide, tarsus very short, conical, almost triangular in profile; claws accreted both with each other and with pretarsus into a short conical section with two hooks near apex (Figs 49–50).

Abdominal segments wide and transverse, with poorly marked borders of sclerites (Figs 51–53); hypopleurites and outer poststernites clearly protruding as bulging tubercles; 1st abdominal segment with unusually large and clearly bordered hypopleurites (Fig. 53). Urogomphi absent, replaced by a group of setae (Fig. 54). Segment X short and conical (Figs 56–57).

Chaetotaxy. Second instar larva, as the first instar, showing most of primary sensilla and only a small number of secondary ones.

Frontale with not only FR₇ and FR₁₁ rather long, but also FR₁; discal FR₃–FR₅ relatively longer than in first instar larva (Fig. 31); FR₉ at anterior margin very small, while FR₁₀ and FR₁₁ approximately same in length (Fig. 32). Due to expansion of temporal area, topology of setae on parietale significantly changed. On dorsal surface, FR₈ and FR₇ removed from FR₉, and FR₄ removed from FR₁–FR₃; all macrosetae

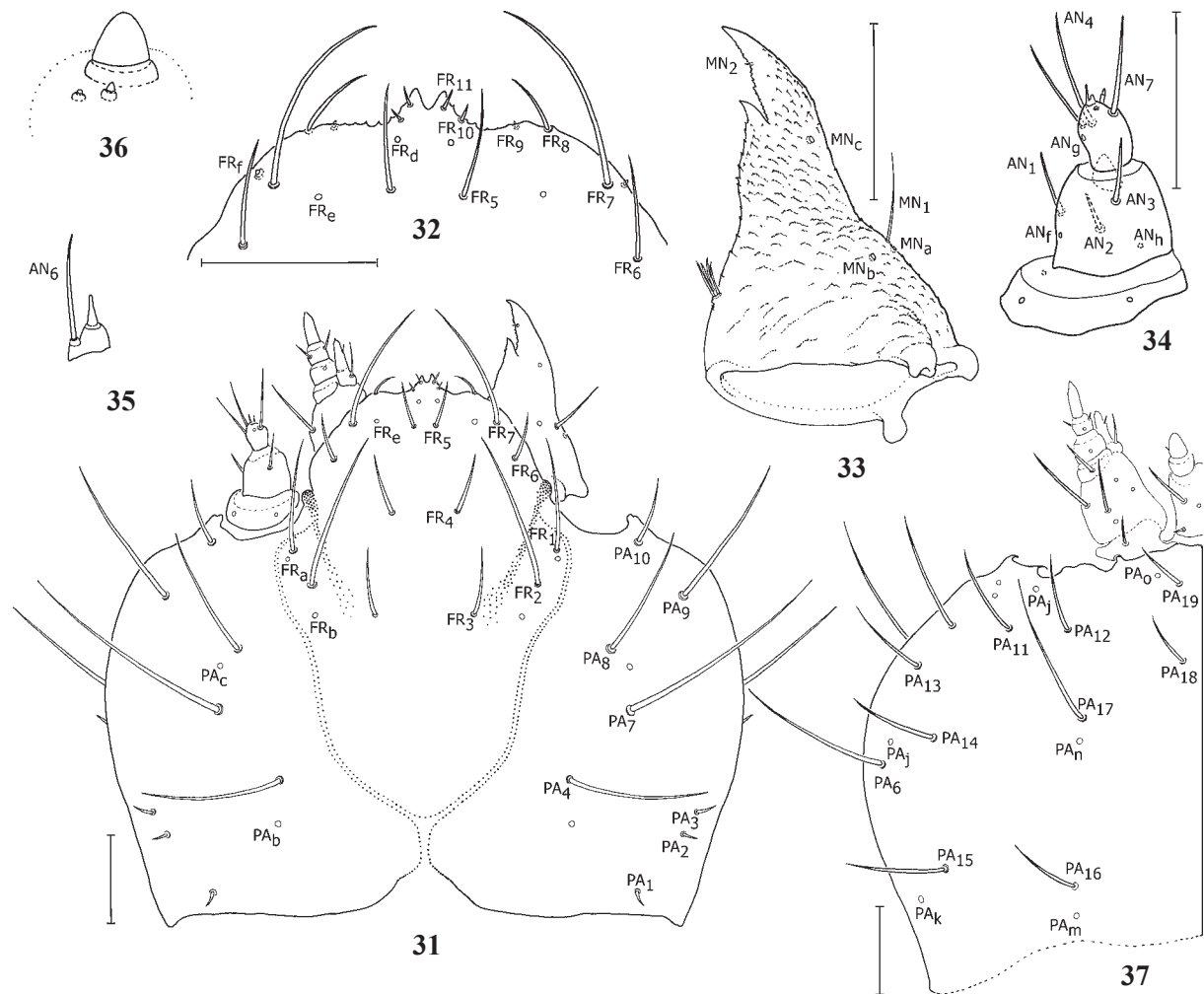
just about same in length; ventrolateral surface covered with setae of different length (Fig. 37).

Antennal setae much shorter than in first instar larva (Fig. 34); however, apical complex of sensilla, its structure and position of AN₆ retaining all features (Figs 35–36). Stipes with shortened MX₄–MX₆ equal in length (Fig. 38); 2nd galeomere with shorter additional setae (Fig. 40); apical palpomeres of maxillae with four finger-shaped sensilla (Fig. 39). Chaetotaxy of labium same as in first instar larva (Figs 41–42), but apical palpomeres with only two finger-shaped sensilla (Fig. 43).

Weakly sclerotized thoracic segments with the same set of setae as in first instar larva, except for much longer PR₆, PR₈ and PR₁₄; as a result, differences in setal length in second instar larva generally less pronounced.

Chaetome of abdominal tergites similarly modified, but hypopleurites with a group of two or three macrosetae, poststernites with much longer setae, while outer posttergites with two additional macrosetae (Fig. 52).

Despite the fusion of several leg sections, their sensilla retaining their relative positions, with borders of individual



Figs 31–37. Second instar larva of *L. bifenestrata*: 31 — head, dorsal view; 32 — nasale, dorsal view; 33 — right mandible, dorsal view; 34 — left antenna, dorsal view; 35 — apical sensilla of 4th antennomere; 36 — apical sensilla of 3rd antennomere; 37 — left half of head, ventral view. Scale bars: 0.1 mm.

Рис. 31–37. Личинка II возраста *L. bifenestrata*: 31 — голова, сверху; 32 — назале, сверху; 33 — правая мандибула, сверху; 34 — левая антенна, сверху; 35 — сенсиллы на вершине четвертого членика антенн; 36 — сенсиллы на вершине третьего членика антенн; 37 — левая половина головы, снизу. Масштаб: 0,1 мм.

segments being well-visible. Generally, chaetome in both instars very similar, except for much longer CO_6 and TR_8 , as well as a much shorter TA_1 in second instar larva (Fig. 48).

Regardless of the complete reduction of urogomphi, the set of their sensilla generally preserved. Tergite IX with reliably identifiable UR_1 – UR_3 , but six macrosetae directly on urogomphi replaced by three microsetae of unclear homology (Fig. 54).

Segment X with the same set of setae as in first instar larva, but PY_6 approximately 2 times longer (Figs 56, 57).

Diagnosis. The larva of *L. bifenestrata* is well distinguished from the other known larvae of *Lebia* by a small sensorial plate with only several sensilla at the apex of the 2nd labial palpomere, as well as by a bifurcated nasale in the second instar larva. Moreover, it differs from the larvae of *L. cyanocephala* and *L. scapularis* by a very short 1st galeomere, while from the larva of *L. viridis* by a long FR_3 and equally long MX_{11} and MX_{12} (in *L. viridis*, MX_{12} approximately twice as long as MX_{11}).

Diagnosis of the genus *Lebia* based on larval features

The currently known larvae of *Lebia* belong to different subgenera and have been described with a varying degree of accuracy. Therefore, comparing them correctly and creating a diagnosis of the genus are extremely difficult. Nevertheless, as the larva of *L. bifenestrata* described above has some features shared with all known larvae of *Lebia*, they can be taken as characteristic of this genus as a whole: ligula, as well as LA_6 and LA_7 , completely reduced; gLA_3 absent; gMX with only one or two setae; 2nd galeomere with one or two additional setae and only half to third as long as maxillary palps; posterior row of eyes with a single simple eye; tarsus with unequal claws, TA_3 and TA_6 replaced by spines; TE_7 absent; UR_7 not shorter than neighbouring UR_7 and UR_8 .

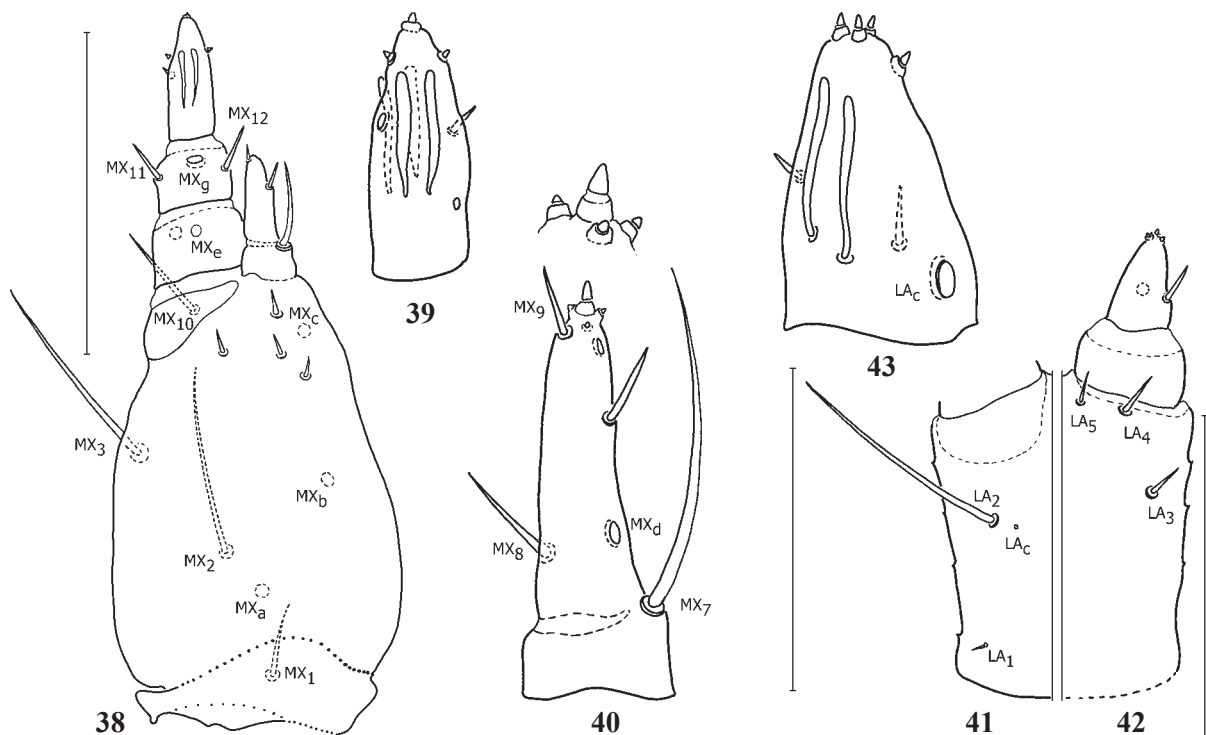
Discussion

Features of biology

The number of larval stages and the duration of development in *L. bifenestrata* generally agree with the information presented by previous authors [Silvestri, 1904; Chaboussou, 1939; Lindroth, 1954; Capogreco, 1989]. However, there are two aspects of interest.

The usage by the larva of *L. bifenestrata* of a special secret for the reconstruction of the walls of their host's pupal chamber is the first of them. Silvestri [1904: 71] observed earlier how a full-grown first instar larva builds a special cocoon before moulting. To do this, the larva used the secretion of modified Malpighian tubules, the proximal part of which was thickened and had its own muscles [Silvestri, 1904: 80]. However, other *Lebia* larvae complete their development in the host's pupal chamber without building a special cocoon [Chaboussou, 1939; Lindroth, 1954; Capogreco, 1989]. Thus, an intermediate condition seems to be observed in *L. bifenestrata*. In this case, the larva is capable of producing a secret, but its use is very limited, only confined to the reparation of walls in the host's pupal chamber.

The significant differences observed adults in parental and daughter generations, both in size and coloration, is the second interesting aspect of our study. The

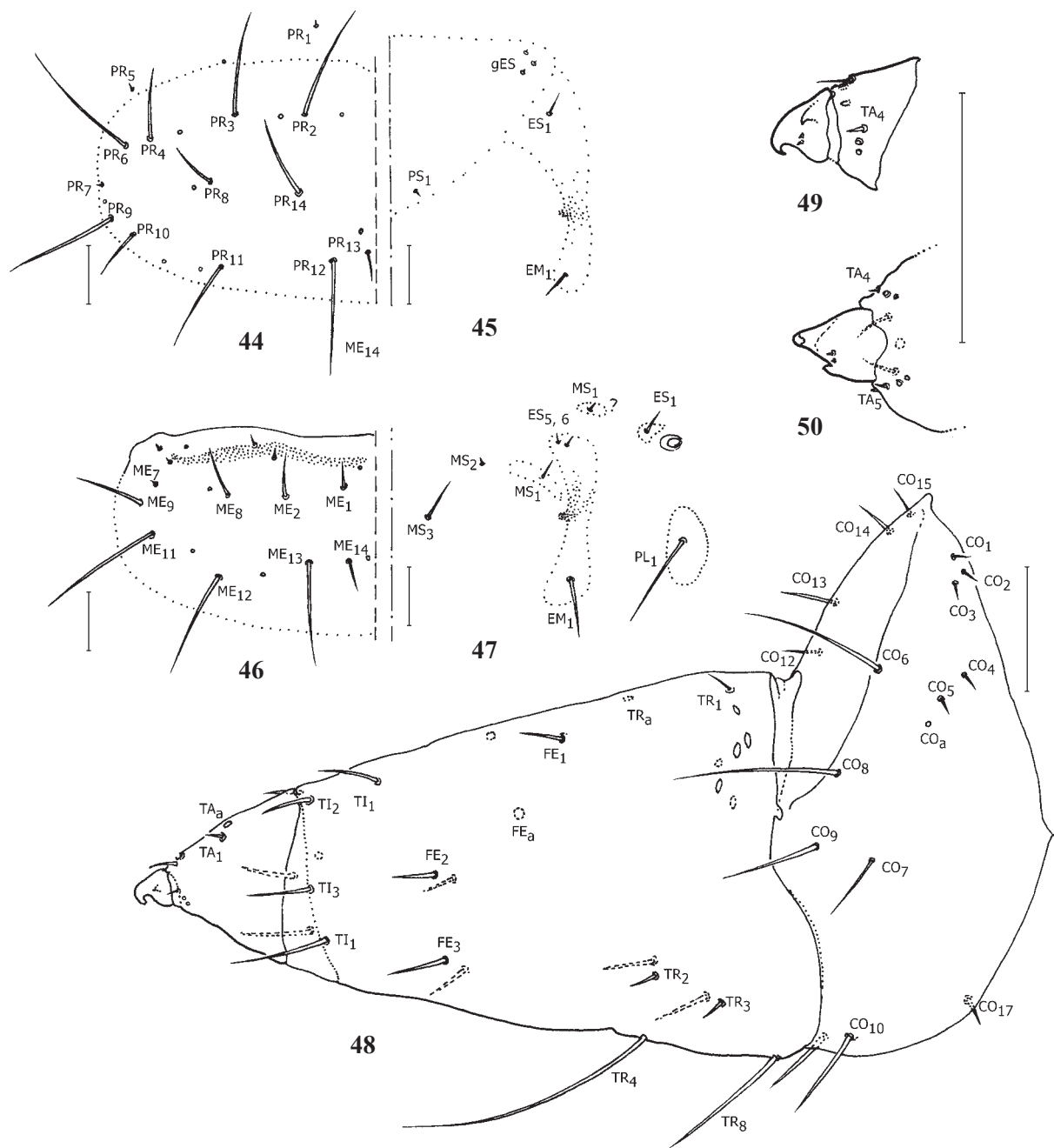


Figs 38–43. Second instar larva of *L. bifenestrata*: 38 — left maxilla, dorsal view; 39 — 4th maxillary palpomere; 40 — galea, dorsal view (apical sensilla shown above); 41 — mentum, ventral view; 42 — labium, dorsal view; 43 — 2nd labial palpomere. Scale bars: 0.1 mm.

Рис. 38–43. Личинка II возраста *L. bifenestrata*: 38 — левая максилла, сверху; 39 — четвертый членик максиллярного щупика; 40 — галей, сверху (выше показаны апикальные сенсиллы); 41 — подбородок, снизу; 42 — нижняя губа, сверху; 43 — второй членик губного щупика. Масштаб: 0,1 мм.

matter is that several forms of *L. bifenestrata* clearly different in elytral patterns have long been described earlier [see review in Habu, 1967]. The beetles of the parental generation, collected in 2015 in natural habitats, belonged to the typical form (Figs 7–9), while the descendants of the first generation hatched in the laboratory later the same year appeared to represent the form *lucescens* Bates, 1873 (Figs 10–12). Among the beetles we collected in 2016–2021 in natural habitats in the

Khasansky District, both forms were present. These forms were thereby clearly distinguished by size: the typical form was virtually smaller, while the forma *lucescens* was on average 1.0 mm larger. A distinct hiatus in the phenotypes suggests a discrete effect of some factor. Because *L. bifenestrata* can feed on leaf beetles of varying sizes and the larval development can involve various hosts, this seems to be highly probable as such factor.



Figs 44–50. Second instar larva of *L. bifenestrata*: 44 — pronotum, left half; 45 — prothorax, left half; 46 — mesonotum, left half; 47 — mesothorax, left half; 48 — middle leg, frontal view; 49 — tarsus, lateral view; 50 — tarsus, ventral view. Scale bars: 0.1 mm.

Рис. 44–50. Личинка II возраста *L. bifenestrata*: 44 — переднеспинка, левая половина; 45 — переднегрудь, левая половина; 46 — среднеспинка, левая половина; 47 — среднегрудь, левая половина; 48 — средняя нога, спереди; 49 — лапка, сбоку; 50 — лапка, снизу. Масштаб: 0,1 мм.

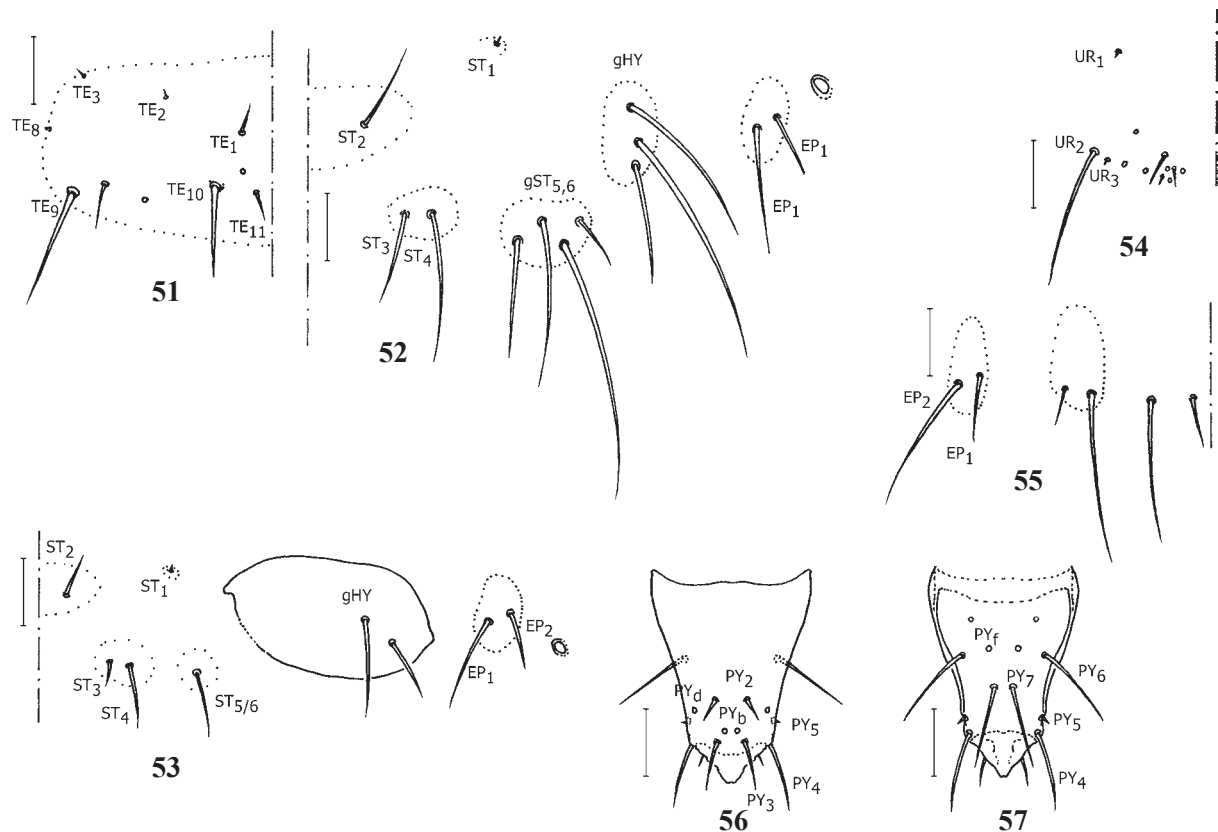
Ontogenetic changes

The sole larval moult in the ontogeny of *L. bifenestrata* is accompanied by significant morphological changes. Besides changes in the proportions, the desclerotization, the microsculpture complication of the cuticle, the reduction of eyes and urogomphi, the shortening of sensorial appendages, as well as the consolidation of leg segments are thereby observed. Similar changes have been described in other species of *Lebia* [Silvestri, 1904; Chaboussou, 1939; Lindroth, 1954; Capogreco, 1989]. Despite such cardinal transformations, the chaetome of *L. bifenestrata* retains almost all of its elements. Changes in the chaetotaxy are insignificant and mostly similar to general trends: the shortening of setae on sensitive appendages, urogomphi and legs. However, such a relative constancy/conservatism is an important feature. An increase in the number of sensory elements with an increased body size (*i.e.*, surface area) is typical of ground beetle larvae [Makarov, 1996]. In the case of *Lebia* (this actually being true for all studied species), large additional setae developed on the pleurites and sternites, upon which a non-feeding second instar larva rests inside the pupal chamber, is the only

quantitative change. A similar trend is also known in Brachinini larvae [Habu, 1986; Makarov, Bokhovko, 2005; Frank et al., 2009], although in different genera it is expressed in different ways. Thus, in the *Brachinus* Weber, 1801 chaetome of the larvae of different instars is mostly similar, and the ontogenetic changes in chaetotaxy [Makarov, Bokhovko, 2005] are virtually identical, to those in *Lebia*. In the first instar larvae of *Pheropsophus* Solier, 1833, homochaetosis is observed, *vs.* heterochaetosis in the older instar larvae characterized by an increasing number of macrosetae on the sternites and pleurites [Frank et al., 2009]. Thus, hypermetamorphosis is similarly realized in Lebiini and Brachinini.

Hypermetamorphosis in Carabidae

The information presently accumulated allows for the variants of hypermetamorphosis observed in different groups of ground beetles to be compared. Comparing the Brachinini and the Lebiini is of particular interest, because the Brachinini still retains the status of an “enigmatic group” of Carabidae. Based on imaginal features, various authors considered Brachininae either as a separate family [Jeannel, 1941] or a subfamily of Carabidae [Lindroth, 1969]. In the latter case, the Brachininae is



Figs 51–57. Second instar larva of *L. bifenestrata*: 51 — abdominal segment IV, left half; 52 — sternites and pleurites of abdominal segment IV, left half; 53 — sternites and pleurites of abdominal segment I, left half; 54 — abdominal tergite IX and left urogomph; 55 — sternites and pleurites of abdominal segment IX, left half; 56 — abdominal segment X, dorsal view; 57 — abdominal segment X, ventral view. Scale bars: 0.1 mm.

Рис. 51–57. Личинка II возраста *L. bifenestrata*: 51 — тергит IV сегмента брюшка, левая половина; 52 — стерниты и плевриты IV сегмента брюшка, левая половина; 53 — стерниты и плевриты I сегмента брюшка, левая половина; 54 — тергит IX сегмента брюшка и левая урогомфа; 55 — стерниты и плевриты IX сегмента брюшка, левая половина; 56 — X сегмент, сверху; 57 — X сегмент, снизу. Масштаб: 0,1 мм.

phylogenetically considered as either closely related to the Paussinae [Eisner et al., 1977, 2000] or the sister group to Harpalinae [Maddison et al., 1999; Ober, 2002; Ober, Maddison, 2008]. At the same time, some authors indicated that, based on larval features, the Brachinini was closely related to the Lebiini [Makarov, Bokhovko, 2005]. New data on larval morphology presented above allow for the relationships between the Brachinini and the Lebiini to be newly discussed.

A correct discussion of the level of differences in Carabidae developing with hypermetamorphosis is only possible when comparing the variants of the same development type in other families of Coleoptera. Hypermetamorphosis among Coleoptera is quite rare to be observed, presently being known in the Micromaltidae, Eucnemidae, Rhipiceridae, Bothrideridae, Rhipiphoridae and Meloidae. Since the development of Micromaltidae and Eucnemidae is not associated with larval parasitism, they are not to be further discussed. Among the other families, both Rhipiphoridae and Meloidae are entirely represented by parasitoids, vs. only some species of Rhipiceridae and Bothrideridae developing with hypermetamorphosis. The morphological structures and chaetotaxy of the members of the above

families are usually described for the first instar larvae, while the older instars are much less studied. Nevertheless, according to the literature data [Newport, 1845, 1847; Parker, Boving, 1924] and our own observations, we can argue that moulting of Rhipiphoridae and Meloidae larvae from the first instar to the second instar is accompanied not only by shortening the appendages and changing the proportions, but also by the loss of a great number of cuticular sensilla. For example, in *Metoecus paradoxus* (Linnaeus, 1760) (Rhipiphoridae), the last instar larvae entirely lose all sensorial structures of the cuticle (our data). The differentiation of the appendages, as well as the structure of the cuticle in these larvae corresponded to the late embryo of Coleoptera [Kobayashi et al., 2013; Nikura et al., 2017], that is, hypermetamorphosis in these beetle families is based on a deep secondary desembryonization. Such a profound desembryonization is observed in neither Carabidae nor Rhipiceridae [Solervincens, 2005], nor Bothrideridae [Craighead, 1921; Dodge, 1941], because the changes of proportions and the partial reduction of appendages occur with the preservation or even a slight complication of the primary chaetome. Thus, seemingly similar variants of metamorphosis could have evolved,

Table. Morphological features and chaetotaxy of the larvae of Peleciini, Brachinini and Lebiini.
Таблица. Особенности морфологии и хетотаксии личинок Peleciini, Brachinini и Lebiini.

Feature	Peleciini	Brachinini	Lebiini (<i>Lebia</i>)	Lebiini (other)
sensory appendage of 3 rd antennomere	increased	increased	ordinary	ordinary
large sensilla on 4 th maxillary palpomere	finger-shaped	finger-shaped	absent	absent
large sensilla on 2 nd labial palpomere	finger-shaped	finger-shaped	conical	absent or finger-shaped
ligula	entirely reduced	entirely reduced	entirely reduced	present or reduced
LA ₆	ordinary	entirely reduced	entirely reduced	ordinary
gMX	3	1–2*	0–1	6–48
number of macrosetae on galeomeres	3	3–6**	3–4	1–2
FR ₈ , FR ₁₁	absent	ordinary	ordinary	ordinary
FR ₉ , FR ₁₀	absent	reduced	reduced	ordinary
PA ₅	present	present	absent	present or absent
claws	single	single or paired	paired, unequal (large and small)	paired, sometimes unequal (large and small)
TA ₃ , TA ₆	ordinary	absent in L ₁ , present in L ₂	replaced by spines	ordinary
TA ₄ , TA ₅	ordinary	absent	ordinary	ordinary
UN ₁ , UN ₂	macrosetae	macrosetae	microsetae	microsetae
TE ₇	absent	ordinary	absent	ordinary or short
urogomphi	short	short	long and segmented	short or long and segmented
UR ₉	shorter than UR ₈ and UR ₇	shorter than UR ₈ and UR ₇	equal to UR ₈ and UR ₇	shorter than UR ₈ and UR ₇

NOTES. *interpretation of MX₄ and MX₅ by Frank et al. [2009] is wrong, because these setae belong to gMX; **absent in *Pheropsophus*.

ПРИМЕЧАНИЯ. *интерпретация хет MX₄ и MX₅ в работе Frank et al. [2009] неверна, поскольку эти хеты относятся к gMX; **отсутствуют у *Pheropsophus*.

obviously repeatedly, on the basis of different changes in development.

As a result, the habitual or even structural macro-morphological similarities of larvae in the Coleoptera species that develop with hypermetamorphosis may not be regarded as a reliable evidence of phylogenetic relationships. Still an analysis of larval chaetotaxy can help us solve this problem. Because the larvae of different instars in ground beetles that develop with hypermetamorphosis differ significantly, only the larvae of the same instar are to be used separately for adequate comparisons.

First instar triungulinid-like larvae are known for three tribes of Carabidae: Peleciini, Lebiini, and Brachinini. During a short time these larvae must find an immobile or almost immobile host in the thickness of a substrate. Because vision hardly helps in this search, triungulinid-like larvae partially or completely lose their eyes, while their chemoreceptors are very well developed. The main morphological and chaetotactic differences between the larvae of these tribes are summarized in Table below.

At first glance, the similarities and differences in the larvae in the groups as presented in Table are evenly distributed and mosaic. However, this similarity has different meanings. For example, the reduction of a ligula in one case is related to the disappearance of LA_6 , while in the other cases is not. This means, the reduction of these structures must have taken place in parallel and independently.

Considering the variability of traits in the larvae of various Lebiini and the significant differences between the larvae of *Pheropsophus* and *Brachinus*, the conclusion that there are no significant differences between the triungulinid-like larvae of Brachinini and Lebiini can be made. On the contrary, Peleciini demonstrate the unity in adaptive traits, differing in essential features from both Brachinini and Lebiini, and thus contradicting the opinion of Liebherr and Ball [1990]. Due to too limited information, it is rather difficult to discuss the relationship of Peleciini based larval features. In our opinion, the structure and chaetotaxy of the nasale and labium brings Peleciini closer to Licinini.

Since the larvae of Peleciini of the older instars are known only based on an incomplete description [Salt, 1928], we cannot discuss the larval features of Lebiini and Brachinini alone. In the first instar larvae of both tribes, a mosaic combination/distribution of the similarities and differences is likewise observed. Whereas, based on some features, the larvae of *Brachinus* are more evolutionarily advanced (completely fused leg joints, very short setae of head appendages, legs, and segment X), considering some other larval traits, such as *Lebia* (a reduced number of antennomeres, reduced urogomphi). However, the larvae of different *Pheropsophus* share some structures with conditions typical of Carabidae (separate leg segments and antennomeres), combining certain other structures with evolutionarily advanced conditions (reduction of urogomphi, partial fusion of legs segments, a single claw). This actually

levels out the differences between Brachinini and Lebiini based on larval features.

Based both on our results and the literature data, the following conclusions can be made:

(a) The larvae of Brachinini that develop on the eggs of mole crickets (*Pheropsophus*) and or the pupae of different beetles (*Brachinus*, *Aptinus*) differ in many traits.

(b) The larvae of Lebiini that develop with hypermetamorphosis are equally similar to both *Brachinus* and *Pheropsophus*.

(c) The specific features of the chaetome similar in both Lebiini and Brachinini indicate that at most the Brachinini belongs to the Truncatipenne group.

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