Descriptions of flea larvae (Siphonaptera: Hystrichopsyllidae, Ctenophthalmidae, Leptopsyllidae) of the specific parasites of the mountain beaver (Rodentia: Aplodontidae) in North America

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Abstract—The larvae of the four species of primary flea parasites of the mountain beaver, *Aplodontia rufa* (Rafinesque), are described and illustrated for the first time, and a key to their identification is provided. The larva of *Hystrichopsylla schefferi* Chapin is very large, with a total body length of more than 10 mm in the late third instar. Its mandible, with a series of marginal teeth along a scoop-shaped tip, is characteristic of members of the formerly recognized subgenus *Hystroceras*. The larvae of *Paratyphloceras oregonensis* Ewing and *Trichopsylloides oregonensis* Ewing are very similar to one another, but the former is much larger, with a total body length of about 8 mm in the late third instar, compared with 5 mm for the latter. These two species can also be separated in all instars on the basis of the setation on the abdominal segments. The larva of *Dolichopsyllus stylosus* (Baker) is extraordinary. The mandible bears two enormous, tusklike setae on a swollen base, the hypopharynx is a spiny, trilobed structure without setae, and there are five processes on the labial palps instead of the four typical in other species.

Résumé—On trouvera ici la première description des larves de quatre espèces de puces parasites primaires du castor de montagne, *Aplodontia rufa* (Rafinesque), ainsi que des illustrations et un clef d'identification des espèces. La larve *d'Hystrichopsylla schefferi* Chapin est très grande et elle atteint plus de 10 mm de longueur vers la fin de son troisième stade. Sa mandibule, qui porte une série de dents marginales à son extrémité en forme de cuiller, est caractéristique des membres de l'ancien sous-genre *Hystroceras*, maintenant non reconnu. Les larves de *Paratyphloceras oregonensis* Ewing et de *Trichopsylloides oregonensis* Ewing sont très semblables, mais la première est beaucoup plus grande avec une longueur totale de 8 mm vers la fin du troisième stade, alors que la seconde atteint seulement 5 mm. Les deux espèces se distinguent aussi à tous les stades par la pilosité de leurs segments abdominaux. La larve de *Dolichopsylla stylosus* (Baker) est remarquable. La mandibule porte deux soies énormes en forme de crocs fixées sur une base enflée, l'hypopharynx forme une structure trilobée, épineuse, mais glabre et les palpes labiaux portent cinq diverticules au lieu des quatre habituels chez les autres espèces.

[Traduit par la Rédaction]

Introduction

The mountain beaver, *Aplodontia rufa* (Rafinesque) (Rodentia: Aplodontidae), is one of the most primitive of extant rodents (Godin 1964). It has attracted the attention of mammalogists since its early discovery. It occurs as seven recognizable subspecies limited in distribution to

Received 8 September 2006. Accepted 20 February 2007.

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https://doi.org/10.4039/n06-072 Published online by Cambridge University Press

the Pacific northwest from southernmost British Columbia to northern California (Carraway and Verts 1993).

This extraordinary mammal is the primary host for a very interesting assemblage of fleas. This assemblage includes three species, each of which belongs to a monotypic genus: *Paratyphloceras oregonensis* Ewing, 1940, *Trichopsylloides oregonensis* Ewing, 1938 (both Ctenophthalmidae), and *Dolichopsyllus stylosus* (Baker, 1904) (Leptopsyllidae). In addition, the mountain beaver is also the host for the largest species of flea known, *Hystrichopsylla schefferi* Chapin, 1919 (Hystrichopsyllidae).

The opportunity to examine larvae of all four primary flea parasites of the mountain beaver arose when Don Gettinger (Department of Biology, University of Central Arkansas, Conway, Arkansas) conducted a research project to study the inhabitants of mountain beaver nests, and he kindly donated flea larvae for study. Since the larvae of these species were previously unknown, the objectives of this paper are to describe them and to provide a key to separate the species. There are a number of species of fleas that have been recorded as accidental on *A. rufa* (see Hubbard 1947; Holland 1985; Lewis *et al.* 1988). This is very likely the result of other species of small mammals invading the burrows of the mountain beaver or perhaps the mountain beaver entering the nests of other mammals, resulting in accidental transfer, rather than the result of such mammals introducing a breeding population of their fleas into mountain beaver nests. In the nests collected during this study, no adults of species other than the four primary parasites were found. Therefore, no other species are included in the key, but care should be exercised when using our key to identify flea larvae from *A. rufa* nests, and recourse must be made to the descriptions as well.

Materials and methods

Nests were excavated with extreme care and painstaking effort by Don Gettinger to reach the nest ball of *A. rufa*. Each nest ball was processed in a Berlese funnel and extracts were sorted under a stereomicroscope. All adult and larval fleas were preserved and stored in 70% ethanol; some adults and most larvae were sent to R.L.C. Pilgrim, who treated them as follows.

First-instar larvae (L_I), characterized by the presence of an egg burster on the head capsule, were found to be separable into four distinct groups; slide-mounted specimens of each group were analysed for specific characters. Samples of remaining later instars were then slide-mounted and classified into the same four groups based on the now well-established principle that setation patterns and numbers are similar throughout the life of a larva. A few pharate specimens provided unequivocal evidence of second (L_{II}) and third (L_{III}) instars, while fat-filled prepupal L_{III}, either before cocoon formation or in early cocoon occupation, were invaluable in categorizing that stadium. Unfortunately, no later cocoon stages were found, so developing adults were not available for identification.

Since larvae of the four species of mountain beaver fleas were unknown, the initial task was to determine which of the four larval groups belonged to which species. It was deduced that there were no stragglers which, at the very least, should have been represented by a small number of specimens; since no adult fleas of species other than *H. schefferi*, *P. oregonensis*, *T. oregonensis*, and *D. stylosus* were collected in nest samples, this seemed a reasonable deduction. It was further assumed that the four different larvae corresponded to these four specific fleas of the mountain beaver.

One larva was very distinct, with greatly enlarged mandibular setae (Figs. 40, 51). It was also the only one of the four larvae that possessed characters diagnostic for the Ceratophylloidea, having the campaniform sensillum medial to seta a_1 on the *D* plate on abdominal segments (Ab) 1–5 (Fig. 44) and lacking a dorsal campaniform sensillum on Ab 10 (Fig. 46). This larva was therefore identified as *D. stylosus*, since this species is the only ceratophylloid specific to the mountain beaver. One larva was by far the largest of the four, even in the first instar, and thus could logically be assigned to *H. schefferi* on the basis of size alone; further, its egg tooth (Figs. 16, 50) was similar to that of other *Hystrichopsylla* larvae. The arrangement of multiple teeth at the scoop-shaped tip of its mandible agreed fully with that in all other known taxa of the former subgenus *Hystroceras* (in contrast to the mandible in the formerly recognized subgenus *Hystrichopsylla* (*Hystrichopsylla*), where there is only one apical tooth (Pilgrim 1992*b*)). The remaining two

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groups shared characters such as an elongated head capsule (Figs. 21, 22) and distinctive mandibles (Fig. 25), which together are diagnostic of other genera of Rhadinopsyllinae: Rhadinopsyllini. These groups were separated from each other by the great difference in size of their otherwise very similar first instars; because adult *P. oregonensis* are much larger than adult *T. oregonensis*, this suggested a basis for identification of the two taxa. Eventually, it was found that all instars of *P. oregonensis* are larger than even L_{III} of *T. oregonensis*; small but significant differences in setation and the labium, as described below, were consistent for all instars.

Specimens were examined using phase-contrast microscopy at magnifications of up to approximately 800×. All descriptions are based on slide-mounted larvae prepared as described by Pilgrim (1992*a*). Some interpretive detail was obtained from scanning electron microscopy, for which the preparation of larvae was described by Pilgrim (1992*a*). Terminology is that in Pilgrim (1988, 1991) and Pilgrim and Galloway (2000, 2003). Comparisons between specimens were made using a Zeiss comparison bridge. Voucher specimens have been deposited in the R.L.C. Pilgrim collection (Museum of New Zealand, Wellington), the J.B. Wallis Museum of Entomology (Department of Entomology, University of Manitoba, Winnipeg, Manitoba, Canada), and the Canadian National Collection of Insects (CNC, Agriculture and Agri-Food Canada, Ottawa, Ontario, Canada).

Descriptions of larvae, unless otherwise stated, are for one half of the body only and are for L_{II} and L_{III}, though these instars are not always separable (Elbel 1951; Moser *et al.* 1991). Patterns and numbers of setae in L_I are essentially identical to those in $L_{II–III}$, but setae in L_I are proportionately shorter and more slender. The rationale for determination of larval instars and for acceptability of material for study was discussed by Pilgrim and Galloway (2000).

The higher classification of Lewis (1998) is followed here.

Key to larvae of the four species of primary flea parasites of the mountain beaver

1. Mandible with two enormously enlarged, tusklike setae on a conspicuously swollen base (Fig. 40). Abdomen: *V* plates on Ab 1–7 each with 3 *v* setae (Fig. 45); Ab 10 (Fig. 46) without anterodorsal sensillum (*a–d*); anal comb with total of 6 setae in a single row. L_I: egg tooth a short, triangular ridge on a paddle-shaped egg burster plate (Fig. 19) . . . . . *Dolichopsyllus stylosus* (Leptopsyllidae)
— Mandible with 3 or 4 acicular setae, base not swollen. Abdomen: Ab 1–7, *V* plates each with 2 *v* setae (Fig. 13); Ab 10 (Fig. 14) with anterodorsal sensillum (*a-d*); anal comb with a total of 10–16 setae in a single row. L_I: egg tooth either a long, low crest on an almost quadrangular egg burster plate (Fig. 16) or a small conical peg on a depressed plate (Figs. 17, 18) 2
2. Head wider than long; mandible (Fig. 5) stout, straight, almost cylindrical, with approximately 10–12 marginal teeth on a scoop-shaped tip, base with four setae, one long, one short, two minute (rarely with three setae). Abdomen: Ab 1–9, *D* plates each with three or four *d* setae, *V* plates each with two *v* setae. L_I: egg tooth a long, low crest on an almost quadrangular egg burster plate (Fig. 16) . . . . . *Hystrichopsylla schefferi* (Hystrichopsyllidae)
— Head longer than wide; mandible (Fig. 25) strongly curved with a prominent apical tooth and 5–10 low cusps on inwardly expanded margin, base with three setae (one long, two short). Abdomen: Ab 1–7 (Figs. 30, 31), *D* plates each with two *d* setae, *V* plates each with 2 *v* setae; Ab 8–9, *V* plates each with one *v* seta. L_I: egg tooth a small conical peg on a slender, depressed egg burster plate (Figs. 17, 18) 3
3. Larvae large, middorsal head length* of L_I–L_{III} approximately 480–730 µm. Hypopharynx and labial palps as in Fig. 28. Abdomen: Ab 1–7, *D* plates each with two *d* setae; Ab 8–9, *D* plates each with three *d* setae; Ab 1–6, d_2 more than half the length of d_1. . . . . *Paratyphloceras oregonensis* (Ctenophthalmidae)
— Larvae small, middorsal head length* of L_I–L_{III} approximately 260–380 µm. Hypopharynx and labial palps as in Fig. 29. Abdomen: Ab 1–8, *D* plates each with two *d* setae; Ab 9, *D* plate with three *d* setae (Fig. 34); Ab 1–6, d_2 less than half the length of d_1 . . . . . *Trichopsylloides oregonensis* (Ctenophthalmidae)

*Measured from clypeolabral suture to hind margin of head capsule.

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Family Hystrichopsyllidae Tiraboschi, 1904

Subfamily Hystrichopsyllinae Tiraboschi, 1904

Hystrichopsylla schefferi Chapin, 1919

(Figs. 1–9, 12–16, 48–50)

Material examined

UNITED STATES. Oregon: Lincoln Co., 4.8 km south of Burnt Woods, 16.xii.1981, *ex* nest of *Aplodontia rufa*, D. Gettinger, two L_I, 4 $L_{II–III}$, plus one L_{II} from which pharate L_{III} was extracted (+4♂♂, 4♀♀); 12.iv.1981, *ex* nest of *A. rufa*, D. Gettinger, one L_I; 18.iv.1981, *ex* nest of *A. rufa*, D. Gettinger, one L_I, 11 $L_{II–III}$. Benton Co., 6.4 km south, 4.8 km west of Blodgett, 20.v.1981, *ex* nest of *A. rufa*, D. Gettinger, one L_I. **Washington:** Grays Harbor Co., 32 km north of Montesano, 25.v.1966, *ex A. rufa* nest, three L_I (BRC-L-89-06, tube No. 2).

Description

Second- and third-instar larvae (L_{II} and L_{III})

Head (Figs. 1, 2, 48, 49). Setation: there are normally 17 acicular setae on each half of the head capsule, as follows. Three parietals (*par.*): outer parietal long, reaching approximately mid-length of Th I; inner parietal short, reaching approximately halfway to hind margin; middle parietal minute, not reaching alveoli of other parietals. Two minute occipitals: anterior occipital (*a.occ.*) on capsule, posterior occipital (*p.occ.*) at margin of head capsule, often hidden by overlapping prothorax. Frontal seta (*fr.*) of moderate length, reaching about half the distance to alveoli of parietal setae. Inter-antennal seta (*i-ant.*) minute. Two clypeal setae: medial one (*m.cl.*) approximately equal in length to basal diameter of antennal shaft; lateral one (*l.cl.*) slightly longer than *m.cl.* Postantennal seta (*p-ant.*) minute. Two genal setae: posterior one (*p.gen.*) long, slender, about as long as outermost *par.*; anterior one (*a.gen.*) short, slender, reaching alveolus of *p.gen*. Subgenal seta (*s-gen.*) of moderate length, slender, not reaching posterior margin of head capsule. Postclypeal seta (*p-cl.*) minute. Postmandibular seta (*p-man.*) long, slender, nearly reaching alveolus of *s-gen*. Postmaxillary seta (*p-max.*) minute. Paragular seta (*pa-gul.*) long, slender, reaching posterior margin of head capsule. In addition, there are three cervical microsetae (*cer.*) immediately posterior to the ventrolateral margin of the head capsule. Sensillation: there are normally 19 campaniform sensilla on each half of the head capsule; positions are slightly variable but typically as in Figures 1 and 2. **Labrum (Figs. 3, 4, 48):** a broadly semioval, anteriorly projecting lobe. Dorsal surface reticulated anteriorly; each half with one long seta, three short setae, two small and one large basiconic sensilla, and one campaniform sensillum. There is one large campaniform sensillum(?) (rarely two) medially on the dorsal surface. Densely covered anteriorly with a strip of short spines, which in some preparations may appear to extend to ventral surface. Ventral surface with a narrow band of short spines posteriorly; each half with one short seta, one medial basiconic sensillum, and a cluster of three small basiconic sensilla mid-laterally, and one campaniform sensillum. **Mandible (Figs. 5, 48, 49):** tapering slightly to an obliquely truncated scoop-like tip, the concavity with 10–12 marginal teeth; usually four setae basally (rarely three), the longest relatively stout, about equal in length to basal width of mandible, one seta short and stout, and one or two minute; one sensillum distal to cluster of setae. **Maxilla (Figs. 6, 7):** with a long medial apodeme directed posteriorly. Cardo: ventrally with one long and one short seta and two campaniform sensilla; one campaniform sensillum on the incomplete sclerotized ring between cardo and stipes; a moderately reticulate area posterolaterally. Stipes: produced anterolaterally as a palpifer, a squat prominence, dorsally sclerotized, bearing the palp; the anterior tip of the stipes is swollen into a mala, a blunt lobe partly surrounding the base of the palpifer. Dorsal face with a median patch of spines extending to cover the mala and reaching on to the ventral face; a dense patch of long spines on the anteromedial margin. This patch is particularly prominent in L_{III}, but corresponding spines in L_I are short; one campaniform sensillum among the short spines. Ventral face with one minute seta; four basiconic sensilla on the mala among the marginal spines. Maxillary palp of two cylindrical segments; basal segment with a minute seta and a campaniform sensillum ventrally; distal segment truncate, with four minute, terminal basiconic sensilla; small

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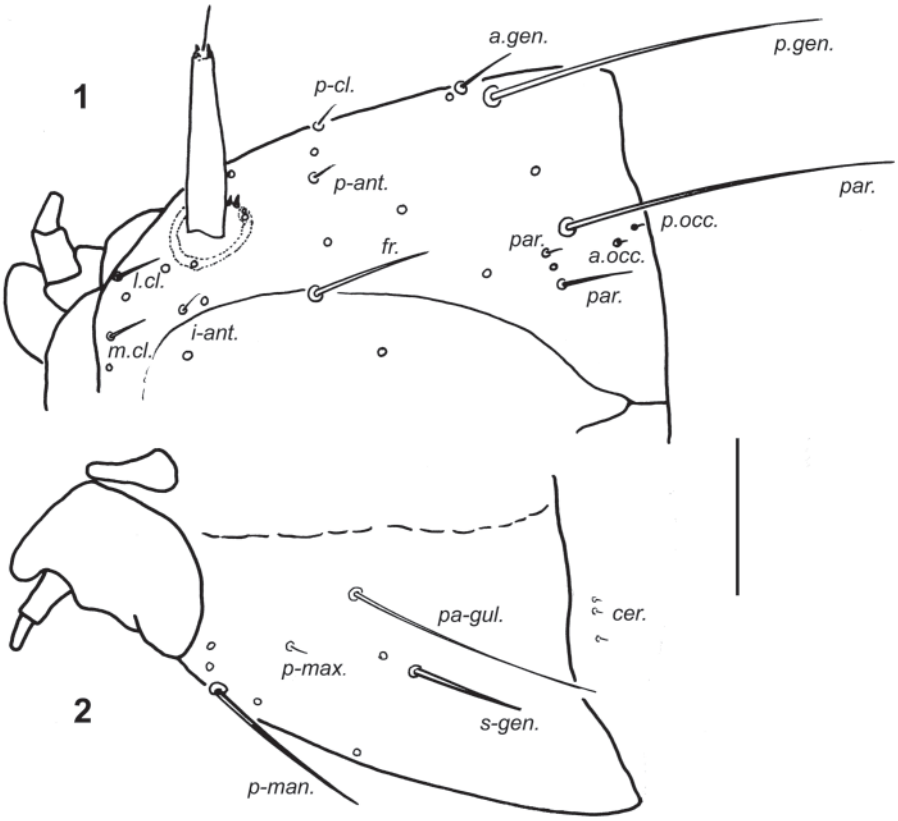
Figs. 1–2. *Hystrichopsylla schefferi*: 1, dorsal view of head, right half; 2, ventral view of head, right half. Setae: *a.gen*., anterior genal; *a.occ*., anterior occipital; *cer*., cervicals (n = 3); *fr*., frontal; *i-ant*., inter-antennal; *l.cl*., lateral clypeal; *m.cl*., medial clypeal; *p-ant*., postantennal; *p-cl*., postclypeal; *p-man*., postmandibular; *p-max*., postmaxillary; *p.gen*., posterior genal; *p.occ*., posterior occipital; *pa-gul*., paragular; *par*., parietals (n = 3); *s-gen*., subgenal. Scale bar = 0.2 mm.



spinules evident on the area of articulation between the segments. **Hypopharynx (Fig. 8):** an elongated lobe projecting between the maxillae; tip deflected ventrally, with a pair of long, slender setae. **Labial palp (Fig. 8):** very short, cylindrical, with four processes, three short and one approximately 2 times as long. **Antenna (Fig. 9):** shaft elongated and cylindrical, gradually tapering from base to tip; sense organ located approximately one-fifth of shaft length from the tip, appearing to include two internal chambers; axial seta less than one-quarter length of antennal shaft; a corona of four basiconic sensilla. Antennal mound lightly convex, covered with polygonal platelets especially peripherally; a subsurficial sclerite partly surrounds the base of the shaft. Antennal mound papillae α_1, β_1, α_2, β_2, and α_3, together with sensilla γ and δ, subtend about 150° along lateral margin of antennal mound; the five papillae stand in a gap in the sclerite; α_1–α_3 short, conical, sometimes with a short terminal filament, β_1–β_2 much shorter than α_1–α_3; sensilla γ, δ, and ϵ situated on sclerite, ϵ on medial side of mound.

Thorax (Figs. 12, 13). Th I: dorsal plate, *D*, covering much of dorsal surface and reaching over sides of segment. Spiracle at an indentation at posterolateral edge of *D*. Setation and sensillation: anterior row of five slender setae: a_1, a_2, a_3, and a_5 short, a_4 approximately 2 times as long and stout, a_1–a_3 on *D*, a_4 and a_5 on separate small platelets. Posterior row: *D* with three long, slender setae, d_1, d_2, and d_3; ventrolateral plate, *VL*, with one long seta, *vl*, reaching to mid-length of Th II; ventral plate, *V*, small, with one short, slender seta, *v*, slightly longer than a_5. One ventral microseta anterior to *VL*. *D* with two sensilla in each of dorsal and ventral rows, medial of a_1, a_2 and d_1, d_2. With a

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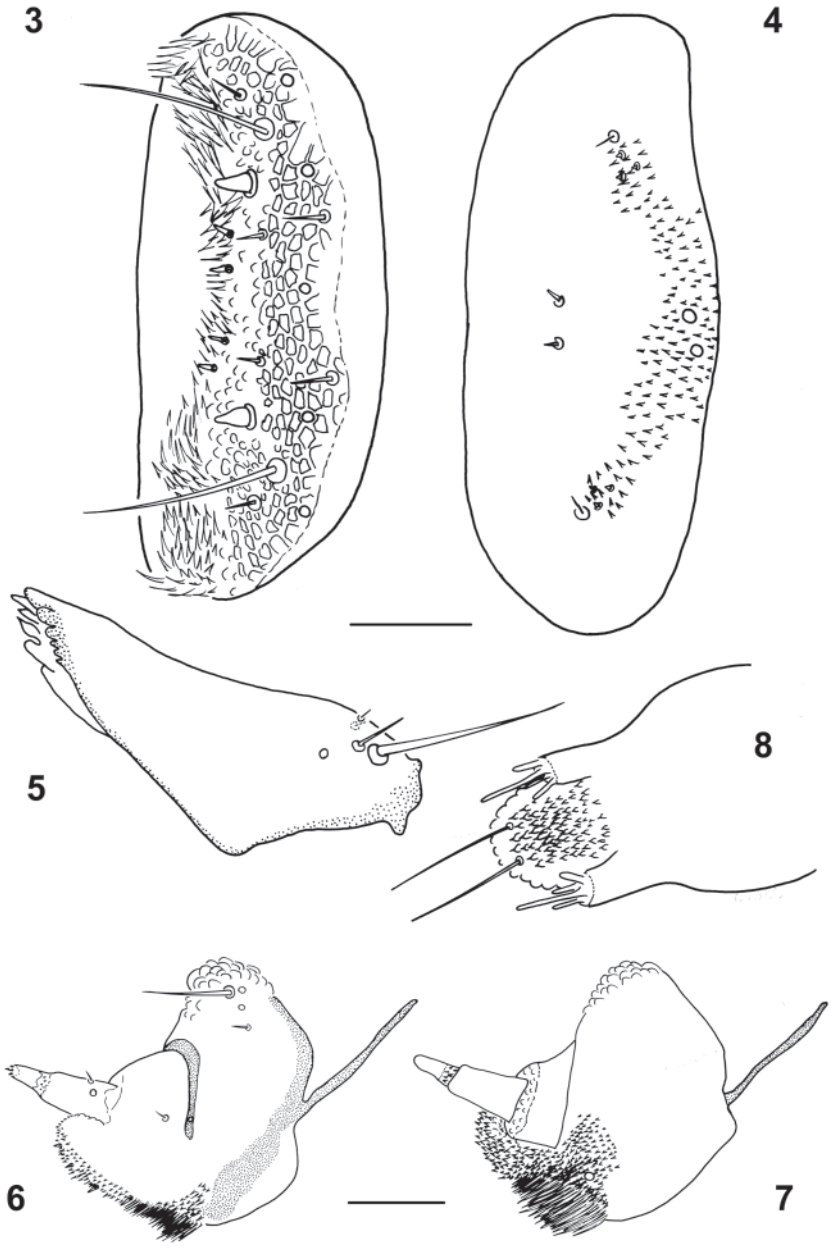
Figs. 3–8. *Hystrichopsylla schefferi*: 3, labrum, dorsal surface; 4, labrum, ventral surface; 5, mandible; 6, left maxilla, ventral view; 7, right maxilla, dorsal view; 8, hypopharynx and labial palps, ventral view. Scale bars = 0.05 mm (Figs. 3–5, 8) and 0.1 mm (Figs. 6, 7).



small group of two minute supplementary setae (*s*), approximately 20 µm long, and two sensilla slightly posterolateral of *VL*. **Th II–III:** *D* limited to dorsal surface; dorsolateral plate, *DL*, present. No spiracles. Setation and sensillation: anterior-row setae longer than on Th I; a_1 reaching halfway to d_1 alveolus, a_2–a_5 diminishingly short and slender, slightly longer and stouter on Th III, a_3 on *DL*. Posterior row: d_1, d_2, *dl*, and *vl* long and slender; *v* short and stout, slightly longer than a_5. Microsetae (µ, Figs. 12, 13): an irregular row of six towards the anterior margin of each segment. *D* with one sensillum in anterior row, anteromedial of a_1; two sensilla in

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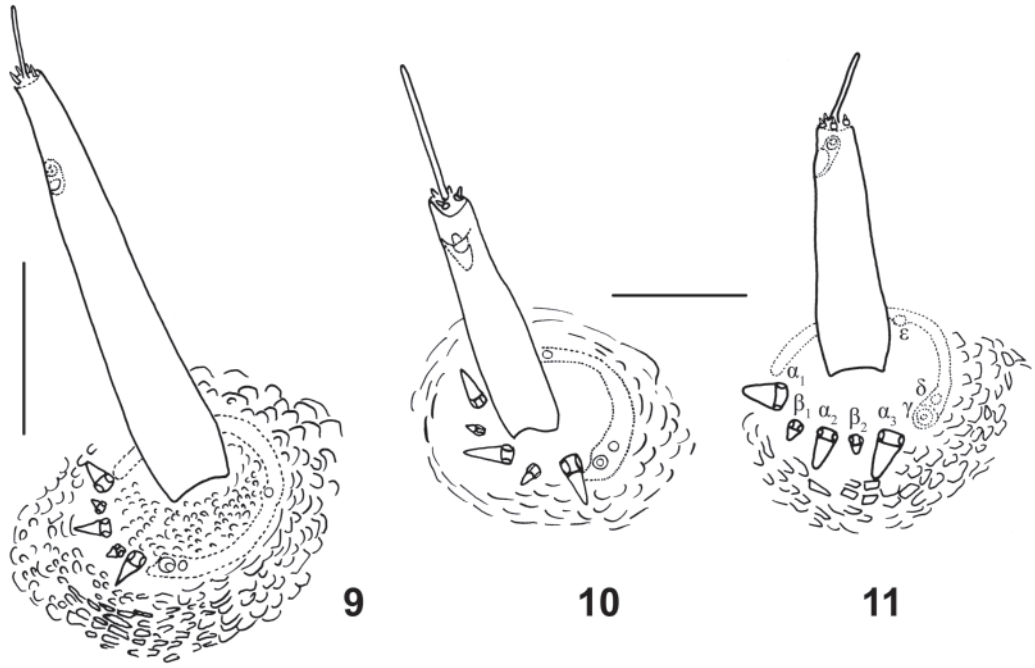
Figs. 9–11. Antennae: 9, *Hystrichopsylla schefferi*; 10, *Paratyphloceras oregonensis*; 11, *Dolichopsyllus stylosus*. α_1–α_3, papillae; β_1 and β_2, papillae; γ, sensillum; δ and ϵ, sensilla-like structures. Scale bars = 0.1 mm (Fig. 9) and 0.05 mm (Figs. 10, 11).



posterior row as for Th I. With a small group of two minute supplementary setae and two sensilla slightly posterolateral of *VL*.

Abdomen (Figs. 12–15). Ab 1–7: *D* narrower than on Th II–III, almost quadrangular but with an expansion at posterolateral corner, accommodating setae d_3–d_5 in relevant segments. Spiracle present near anteromedial margin of *DL* on each segment. Setation and sensillation: anterior row of six slender setae; a_1 reaching halfway to d_1, a_2–a_6 diminishing in length; a_1 on *D*; a_2 on *DL* anteroventral to spiracle; a_3 anteroventral to a_2; a_4 anterolateral to *VL*; a_5 and a_6 on separate small platelets; a_5 between *VL* and *V*; a_6 slightly anteromedial to *V*. Setae a_2–a_4 form a distinct triangle. Posterior row: *D* usually with three (Ab 1–3) or four (Ab 4–7) long *d* setae (range 3–5, often asymmetrical), all reaching at least well onto following segment; *dl* and *vl* also long and slender, nearly as long as *d* setae; v_1 long and slender, v_2 one-half to two-thirds length of v_1. Microsetae: an irregular row of five along anterior margin of each segment (Figs. 12, 13). Sensilla as in Th II–III in general position, irrespective of number of *d* setae. **Ab 8:** *D* as on Ab 1–7. Spiracle as on Ab 1–7. Setation and sensillation: anterior row: a_1–a_6 slender, relative lengths and positions as on Ab 1–7 but a_2 anterodorsal to spiracle. Posterior row: *D* with four (occasionally three or five, unilaterally) very long *d* setae; *dl* and *vl* long and slender; v_1 long, slender, reaching *V* on Ab 9, v_2 one-half to two-thirds length of v_1. Microsetae as on Ab 1–7. Sensilla as on Ab 1–7. **Ab 9:** *D* as on Ab 1–8. No spiracle. Setation and sensillation: anterior row of five short, slender setae; relative positions of a_1 and a_2 as on Ab 1–8, a_3 between *DL* and *VL*, a_4 between *VL* and *V*, a_5 medial of *V*. Posterior row: *D* with four (rarely two or five, unilaterally) *d* setae; *d* and *dl* setae very long and stout, often reaching to tip of anal strut; *vl* long and stout, reaching nearly to base of strut; v_1 reaching well onto Ab 10, v_2 one-half to two-thirds as long as v_1. Three microsetae towards anterior margin of segment; one dorsal, approximately in front of a_1, two ventral, approximately in front of a_4, a_5. Sensilla as on Ab 1–8. **Ab 10 (Figs. 14, 15):** with two well-sclerotized dorsolateral plates, which almost meet middorsally, and a single median ventral plate. No spiracle. Setation and sensillation: two stout upper ventrolateral setae (*v-l*) on each dorsolateral plate, variable in length, reaching at least to

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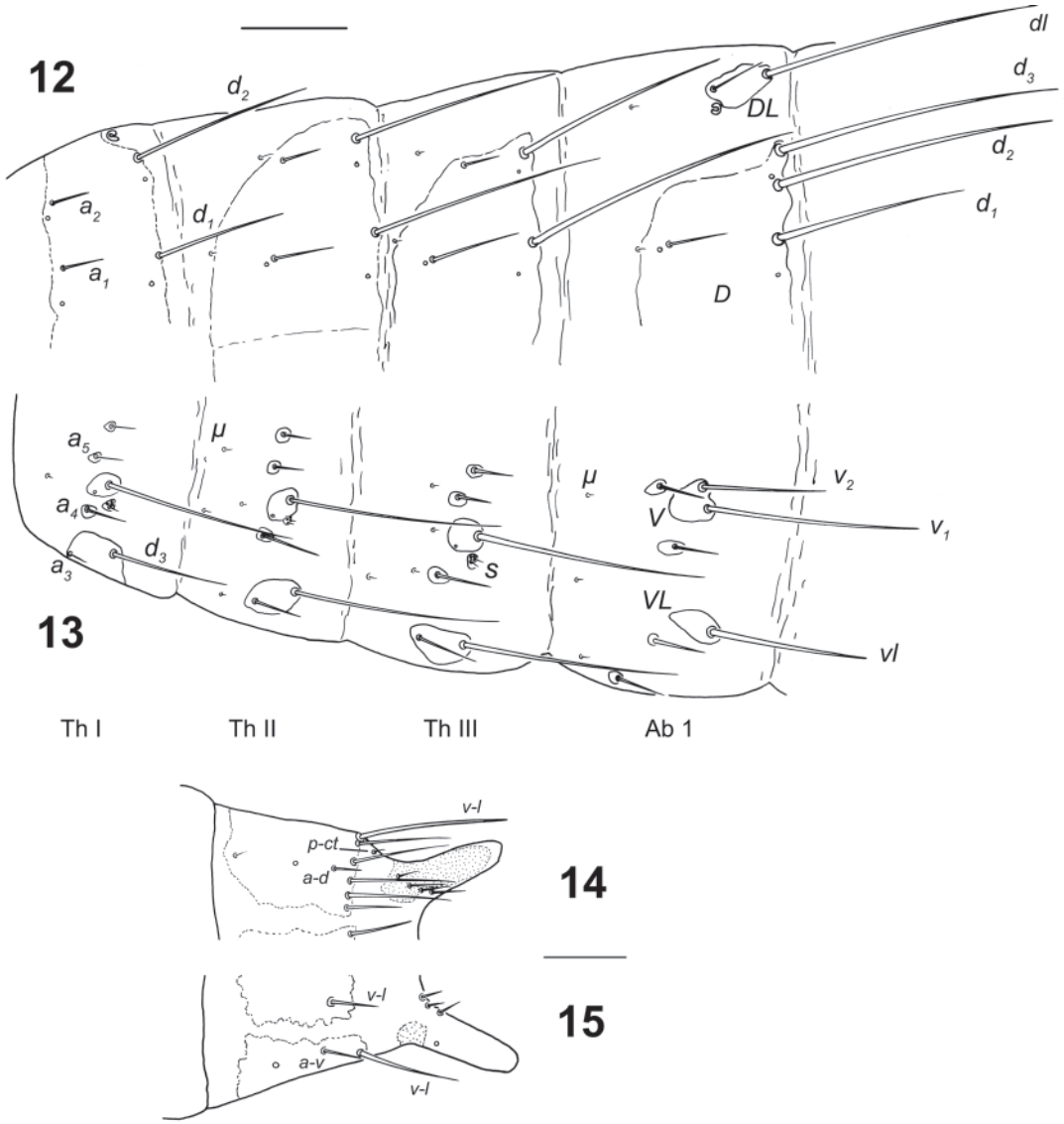
Figs. 12–15. *Hystrichopsylla schefferi*, thoracic segments (Th I–III) and first abdominal segment (Ab 1): 12, dorsal view, right half; 13, ventral view, right half. *D*, dorsal plate; *DL*, dorsolateral plate; *VL*, ventrolateral plate; *V*, ventral plate. Setae: a_1–a_5, anterior row; d_1–d_3, dorsal; *dl*, dorsolateral; *vl*, ventrolateral; v_1 and v_2, ventral; μ, microseta; *s*, supplementary setae. Tenth abdominal segment: 14, dorsal view; 15, ventral view. Setae: *a-v*, anteroventral; *p-ct*, post-ctenidial; *v-l*, ventrolateral. Scale bars = 0.3 mm (Figs. 12, 13) and 0.2 mm (Figs. 14, 15).



base of anal strut but not beyond the tip; the third *v-l* seta on the ventral plate much shorter, not reaching base of anal strut; one microseta on anterior margin of dorsolateral plate; anteroventral seta (*a-v*) on dorsolateral plate not always reaching alveolus of upper *v-l*; anterodorsal seta (*a-d*) on dorsolateral plate short; post-ctenidial seta (*p-ct*) minute, just behind lateral portion of anal comb. Anal comb a single row of 5–6 short setae on each half. Two sensilla, one anterior to *a-v*, one anterior to *a-d*. **Anal strut and anal mound:** strut less than half the length of Ab 10, fingerlike, bluntly rounded at tip, slightly curved ventrally; dorsal surface with a strip of sclerotized cuticle, widest and most heavily sclerotized at the base,

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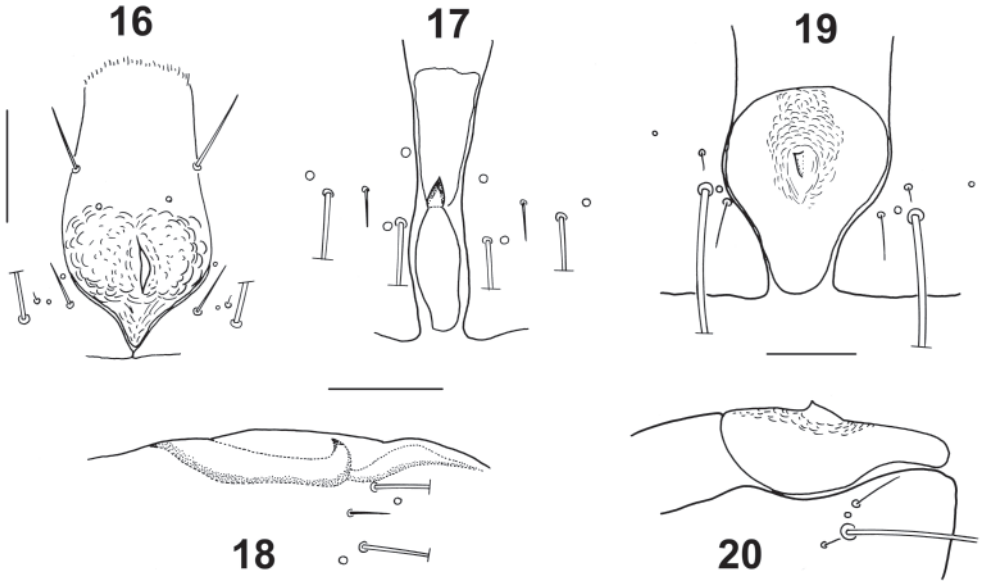
Figs. 16–20. Egg bursters of first-instar larvae, dorsal and lateral views: 16, *Hystrichopsylla schefferi* (dorsal); 17, *Paratyphloceras oregonensis* (dorsal); 18, *P. oregonensis* (lateral); 19, *Dolichopsyllus stylosus* (dorsal); 20, *D. stylosus* (lateral). Scale bars = 0.02 mm (Fig. 16), 0.01 mm (Figs. 17, 18), and 0.05 mm (Figs. 19, 20).



extending around to ventral surface; dorsally densely provided with spine-tipped pustules; a sensillum on ventral surface. Anal mound with a row of 6–8 short setae.

First-instar larva (L_I)

As $L_{II–III}$ except as follows. **Maxilla:** patch of spines on stipes much less prominent, spines shorter. **Egg burster (Figs. 16, 50):** approximately one-third the length of head capsule, with a distinct posteriorly directed extension almost reaching posterior margin of head capsule; a knifelike, convex egg tooth located in middle of egg burster plate; coronal suture very short. **Antenna:** shaft nearly uniform in diameter, only slightly swollen basally, shorter than in later instars, but axial seta approximately one-third length of shaft.

Remarks

Hystrichopsylla schefferi is a remarkable flea on the basis of its large size, a third-instar larva reaching 10 mm or more in total body length. This is the first description of the larva of a member of the former subgenus *Hystroceras* (subgenera of *Hystrichopsylla* were synonymized by Smit (1975)). Pilgrim (1992*b*) mentioned briefly that species in the Palaearctic subgenus *Hystrichopsylla* are distinct from those in the Nearctic and eastern Palaearctic subgenus *Hystroceras*, especially in the nature of their mandibles. The mandible of *H.* (*Hystrichopsylla*) *talpae* (Curtis), for example, is shorter and tapers to a blunt apical tooth (see illustrations in Oudemans 1913; Cotton 1970); other observed subspecies of *H.* (*H.*) *talpae*, namely *orientalis* and *alpina*, conform to this pattern (R.L.C. Pilgrim, unpublished data). The form of the mandible in *H.* (*Hystroceras*) *schefferi*, with its numerous sharp, apical teeth, is found also in *H.* (*Hystroceras*) *microti* Scalon, subspecies of *H.* (*Hystroceras*) *dippiei* Rothschild, and *H.* (*Hystroceras*) *occidentalis occidentalis* Holland (R.L.C. Pilgrim, unpublished data).

Hystrichopsylla schefferi is unusual, further, in having three or four (occasionally five) *d* setae on Ab 1–9. No other species of *Hystrichopsylla* s.l. we have seen (*e.g.*, *Hystrichopsylla* (*Hystroceras*) *dippiei*) has more than three *d* setae on Ab 1–9; more commonly there are only two *d* setae on Ab 1–8 and three *d* setae on Ab 9 only (*e.g.*, *Hystrichopsylla* (*Hystrichopsylla*) *talpae* subsp., *H.* (*Hystroceras*) *microti*, and *H.* (*Hystroceras*) *o. occidentalis*). We also note that, in specimens before us, there appear to be only 19 campaniform sensilla on each half of the head, a condition shared among the *Hystrichopsylla* spp. we have seen. Most flea larvae typically

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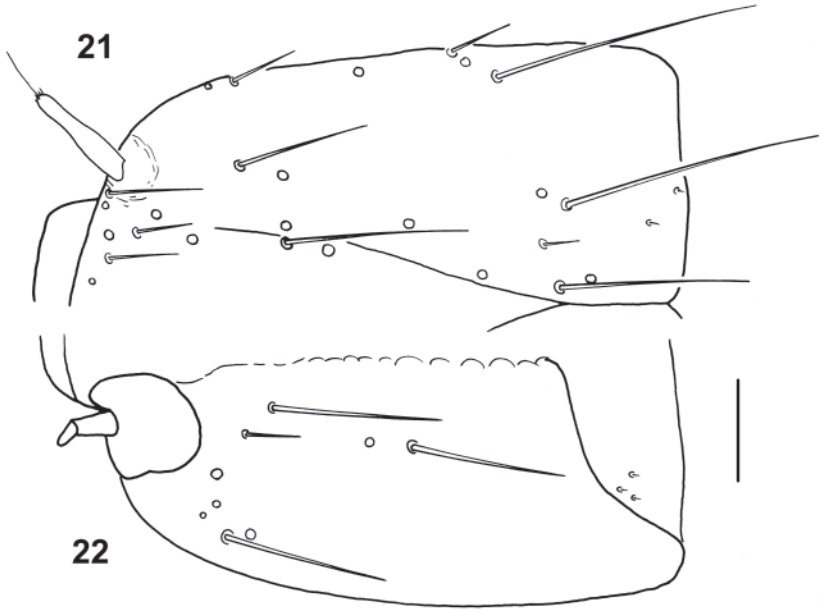
Figs. 21–22. *Paratyphloceras oregonensis*: 21, dorsal view of head, right half; 22, ventral view of head, right half. Scale bar = 0.1 mm.



have 20 per half (for example, see Pilgrim and Galloway 2000, 2003). In these species, there is a cluster of three sensilla, often arranged in a triangle, near *p-man*. In *Hystrichopsylla* spp., there are usually only two sensilla in this position.

Family Ctenophthalmidae Rothschild, 1915

Subfamily Rhadinopsyllinae Wagner, 1930

Tribe Rhadinopsyllini Wagner, 1930

Paratyphloceras oregonensis Ewing, 1940

(Figs. 10, 17, 18, 21–28, 30–33)

Material examined

UNITED STATES. Oregon: Lincoln Co., 4.8 km south of Burnt Woods, 12.iv.1981, *ex A. rufa* nest, D. Gettinger, two $L_{II–III}$; 18.iv.1981, *ex A. rufa* nest, D. Gettinger, two $L_{II–III}$; 16.xii.1981, *ex A. rufa* nest, coll. D. Gettinger, four L_I plus two L_I from which pharate L_{II} were extracted. Benton Co., 6.4 km south, 4.8 km west Blodgett, 20.v.1981, *ex A. rufa* nest, coll. D. Gettinger, five L_I, five $L_{II–III}$ (+1♂, 1♀). **Washington:** Grays Harbor Co., 32 km north of Montesano, 25.v.1966, *ex A. rufa* nest, coll. unknown, CNC (BRC-L-89-06, tube No. 2), one L_I, three $L_{II–III}$.

Description

Second- and third-instar larvae (L_{II} and L_{III})

Head (Figs. 21, 22). Head capsule longer than wide, sides very lightly convex, almost parallel-sided. Setation: there are normally 17 acicular setae on each half of the head capsule, as follows. Parietals (*par.*): innermost and outermost parietal setae long, slender; outermost reaching well beyond posterior margin of head capsule, innermost about two-thirds length of outermost; middle parietal seta very short, slightly anterior to other parietals and reaching alveolus of outermost. Occipitals: anterior (*a.occ.*) and posterior (*p.occ.*) occipitals minute. Frontal seta (*fr.*) long, slender, reaching just over one-half the distance to alveolus of outermost *par.* Inter-antennal seta (*i-ant.*): length at least twice the basal diameter of antennal shaft. Clypeal setae: median (*m.cl.*) and lateral clypeal setae (*l.cl.*) slightly longer than *i-ant*. Postantennal seta (*p-ant.*) extraordinarily long, reaching base of antenna. Genal setae: posterior one (*p.gen.*) long, slender, about as long as outermost *par.*; anterior

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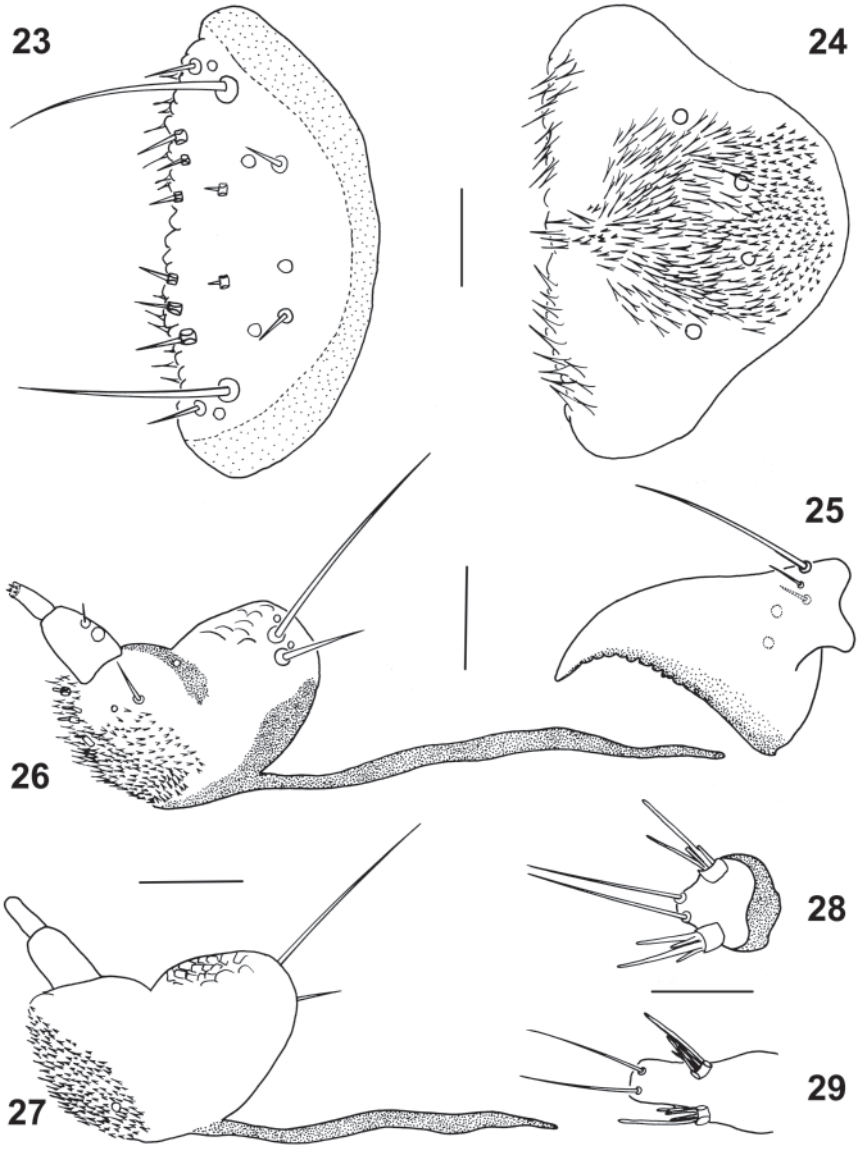
Figs. 23–29. Mouthparts of *Paratyphloceras oregonensis* and *Trichopsylloides oregonensis*. *P. oregonensis*: 23, labrum, dorsal view; 24, labrum, ventral view; 25, mandible; 26, left maxilla, ventral view; 27, right maxilla, dorsal view; 28, hypopharynx and labial palps, ventral view. *T. oregonensis*: 29, hypopharynx and labial palps, ventral view. Scale bars = 0.03 mm (Figs. 23, 24), 0.05 mm (Figs. 25–27), and 0.03 mm (Figs. 28, 29).



one (*a.gen.*) short, reaching just beyond alveolus of *p.gen*. Subgenal seta (*s-gen.*) long, slender, almost reaching posterior margin of head capsule. Postclypeal seta (*p-cl.*) less than half the length of *p-ant*. Postmandibular seta (*p-man.*) long, slender, reaching to alveolus of *pa-gul*. Postmaxillary seta (*p-max.*) reaching alveolus of *pa-gul.* Paragular seta (*pa-gul.*) long, slender, reaching alveolus of *p-man*; *p-man*., *p-ant*., and *pa-gul*. all the same length. In addition, there are three microsetae (cervicals, *cer.*) immediately posterior to the ventrolateral margin of the head capsule. Sensillation: there are normally 20 campaniform sensilla on each half of the head capsule; positions are slightly variable but typically as in Figures 21 and 22. **Labrum (Figs. 23, 24):** a broadly semicircular, anteriorly projecting disc. Dorsal surface

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smooth, some reticulation anterior to long setae; each half with one long seta, two short setae, four basiconic sensilla, and two campaniform sensilla. There is one campaniform sensillum(?) medially on the dorsal surface. Ventral surface with long, thin spines on either side of midline along distal margin and a broad central patch of spines, which are very small basally, gradually becoming fine and hairlike medially and distally; each half with two campaniform sensilla among the spines. **Mandible (Fig. 25):** broadly triangular, with one large, pointed apical tooth, inner margin with 8–10 low, flat, irregular cusps; three setae basally, one long, two short; two campaniform sensilla basally. **Maxilla (Figs. 26, 27)** with a long medial apodeme directed posteriorly. Cardo: ventral face with one long and one short seta, their alveoli almost touching, each accompanied by a campaniform sensillum; one campaniform sensillum on sclerite between cardo and stipes. Stipes: dorsal face with a dense patch of short spines medially, extending well over margin to ventral face; one campaniform sensillum among the spines. Ventral face with one short seta accompanied by a campaniform sensillum, and four basiconic sensilla among the spines. A short, blunt anterolateral lobe beyond the palp insertion. Maxillary palp of two cylindrical segments: basal segment with a minute seta and a campaniform sensillum ventrally; distal segment truncate, with four minute, terminal basiconic sensilla. **Hypopharynx (Fig. 28):** a very short, blunt lobe extending anteriorly between the maxillae, with two very long apical setae at least twice the length of the longer of the labial palp processes. **Labial palp (Fig. 28):** short, cylindrical, with four processes, two short, cylindrical, blunt, and two slender, tapering, two to three times as long. **Antenna (Fig. 10):** shaft cylindrical and elongated, slightly swollen at base; sense organ near apex, appearing to have two internal chambers; axial seta slightly less than one-half length of antennal shaft; a corona of four basiconic sensilla. Antennal mound papillae α_1, β_1, α_2, β_2, and α_3, together with sensilla γ and δ, subtend about 150° along lateral margin of antennal mound; sensillum ϵ on medial side of mound; papillae conical, α_1–α_3 tall, slender, occasionally with a short terminal filament, β_1–β_1 less than half height of α_1–α_3.

Thorax (Figs. 30, 31). Th I: dorsal plate, *D*, covering much of dorsal surface, reaching over sides of segment. Spiracle at an indentation at posterolateral edge of *D*. Setation and sensillation: anterior row of five setae: a_1–a_3 short, slender, on *D*; a_4 and a_5 longer and stouter, on separate tiny platelets between *D* and *VL* and *VL* and *V*, respectively. Posterior row of five setae: *D* with three long, slender setae, d_1, d_2, and d_3; ventrolateral plate, *VL*, with one long seta, *vl*, reaching to mid-length of Th II; ventral plate, *V*, with one slender seta, *v*, almost half the length of *vl*. One microseta anterolateral to *VL*; two minute supplementary setae, s_1 and s_2, midway between *vl* and a_4. *D* with two sensilla in each of dorsal and ventral rows, medial of a_1 and a_2 and d_1 and d_2. **Th II–III:** *D* limited to dorsal surface; dorsolateral plate, *DL*, present. No spiracles. Setation: anterior row of five setae: a_1–a_3 short and slender, a_1 on *D*, a_2 at edge of *D*, a_3 anterolateral of *DL*, a_4 and a_5 as in Th I. Posterior row of five setae: d_1, d_2, *dl*, and *vl* long and slender; *v* short and slender, considerably less than one-half length of *vl*. Microsetae: an irregular row of six towards the anterior margin of each segment; two minute supplementary setae midway between *vl* and a_4. Sensillation: *D* with one sensillum in anterior row, anterior of a_1; two sensilla in posterior row as for Th I.

Abdomen (Figs. 30–33). Ab 1–7: *D* narrower than on Th II–III. Setation and sensillation: anterior row with six slender setae; a_1 on *D*, length approximately half the distance to alveolus of d_1; a_2 closely in front of *DL*, anteroventral to spiracle; a_3 well anterior of a_2 and a_4; a_5 between *VL* and *V*; a_6 slightly medial to *V*. Posterior row of six setae: d_1, *dl*, and *vl* long and slender; d_2 shorter than d_1 on Ab 1–6, on Ab 7 nearly equal in length; two *v* setae, v_2 usually half to two-thirds the length of v_1. Microsetae: an irregular row of five towards the anterior margin of each segment. Sensilla as in Th II–III. **Ab 8:** *D* as on Ab 1–7. Spiracle as on Ab 1–7. Setation and sensillation: anterior row: a_1–a_6 slender, relative positions of a_1 and a_3–a_6 as on Ab 1–7, but a_2 between *D* and *DL*, anterodorsal to spiracle. Posterior row: *D* with three very long *d* setae, reaching rear of Ab 9; *dl* and *vl* almost as long; one long *v* seta, reaching alveoli of anterior-row setae on Ab 9. Microsetae as on Ab 1–7. Sensilla as on Ab 1–7. **Ab 9:** *D* as on Ab 1–8. No spiracle. Setation and sensillation: anterior row of five slender setae, slightly longer than on Ab 8; relative positions of a_1 and a_2 as on Ab 1–8, a_3 between *DL* and *VL*, a_4 between *VL* and *V*, a_5 anterior to *V*. Posterior row: *D* with three *d* setae; *d* setae and *dl* stout and very long, often reaching tip of anal

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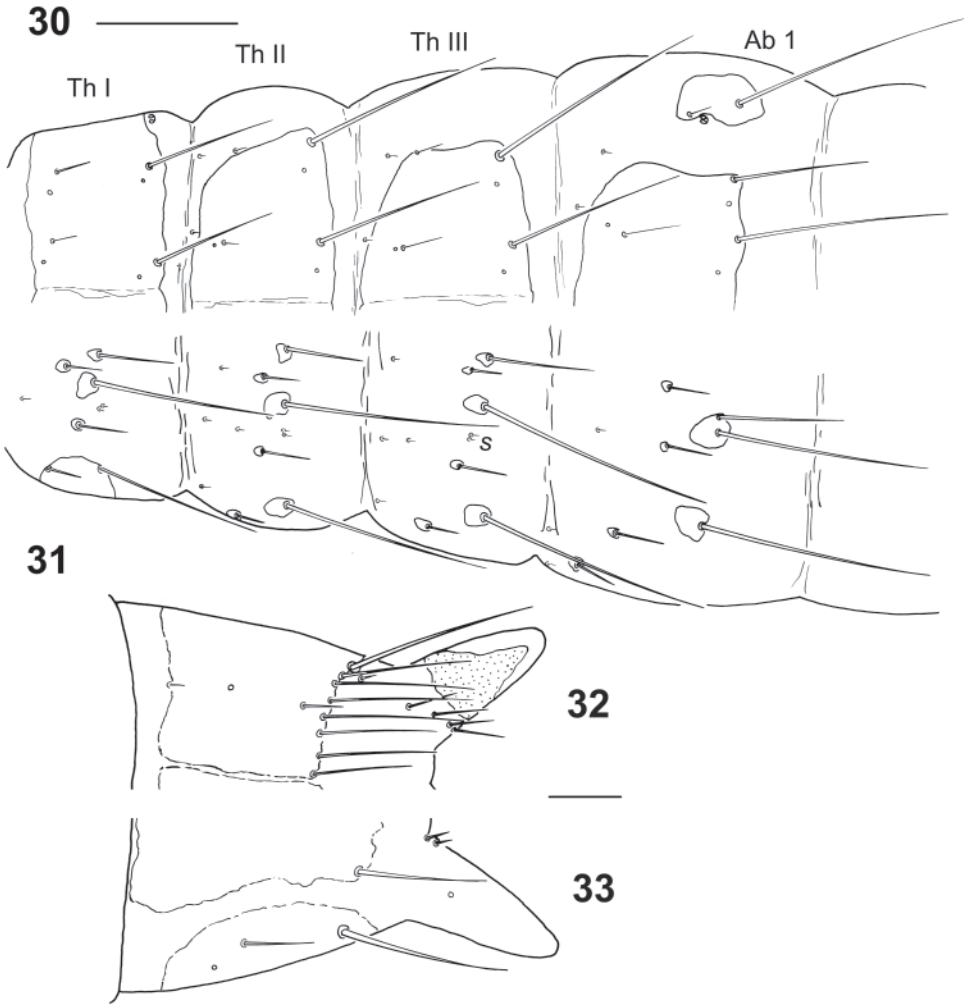
Figs. 30–33. *Paratyphloceras oregonensis*, thoracic segments one to three (Th I–III) and abdominal segment one (Ab 1): 30, dorsal view, right half; 31, ventral view, right half. Tenth abdominal segment: 32, dorsal view; 33, ventral view. *s*, supplementary setae. Scale bars = 0.3 mm (Figs. 30, 31) and 0.2 mm (Figs. 32, 33).



strut; *vl* and *v* approximately equal in length, reaching beyond rear margin of segment. Three microsetae towards anterior margin of segment; one dorsal, approximately in front of a_1, two ventral, approximately in front of a_4 and a_5. Sensilla as on Ab 1–8. **Ab 10 (Figs. 32, 33):** with two weakly sclerotized dorsolateral plates, which almost meet middorsally, and a single median ventral plate. No spiracle. Setation and sensillation: one microseta near anterior margin of dorsolateral plate; three stout ventrolateral setae (*v-l*), two on each dorsolateral plate reaching at least to mid-length of anal strut, the third on the ventral plate shorter; anterodorsal seta, *a-d*, shortly in front of comb row; anteroventral seta, *a-v*, slender, not usually reaching alveolus of nearest *v-l*; post-ctenidial seta (*p-ct*) minute, slender, just behind lateral portion of anal comb. Anal comb a single row of 6–8 setae on each half. Two campaniform sensilla on dorsolateral plate, one anterior to *a-d* seta, one anterior to *a-v* seta. **Anal strut and anal mound:** strut about half length of segment, fingerlike, bluntly rounded at tip, slightly curved ventrally; dorsal surface with a strip of scaly, sclerotized cuticle; one sensillum on ventral surface. Anal mound with 5–7 short setae in a single row.

First-instar larva (L_I)

As $L_{II–III}$ except as follows. **Egg burster (Figs. 17, 18):** almost one-half length of head capsule, sunken into a depression between the frontal sutures especially anteriorly; not quite

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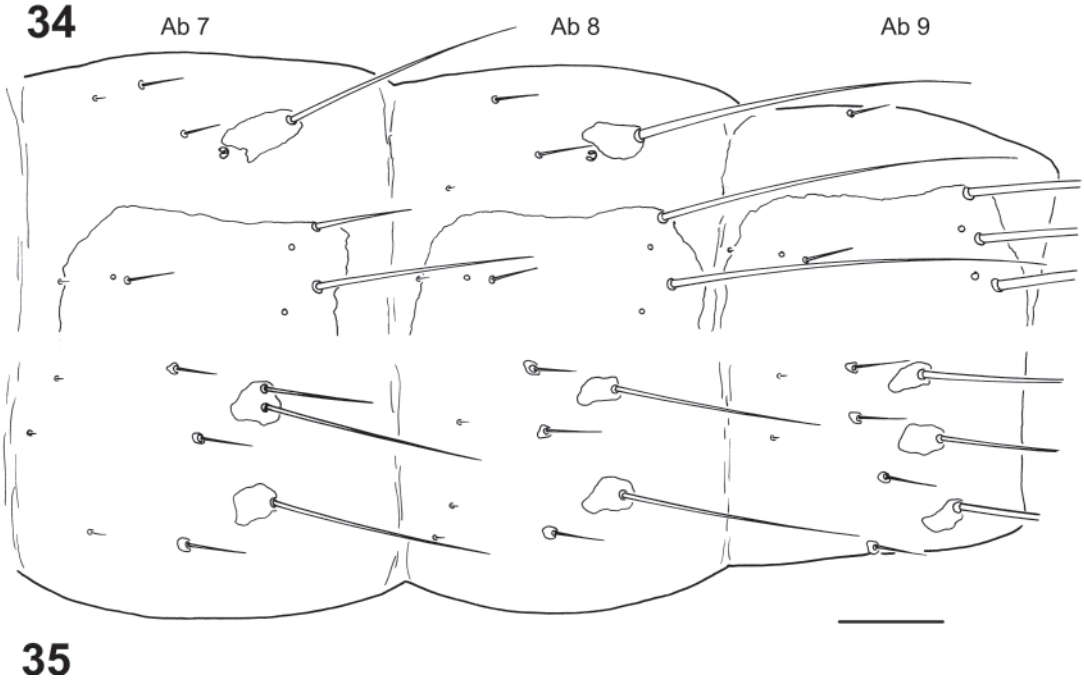
Figs. 34–35. *Trichopsylloides oregonensis* abdominal segments 7–9: 34, dorsal view, right half; 35, ventral view, right half. Scale bar = 0.1 mm.



reaching rear margin of capsule posteriorly; egg tooth small, at rear end of anterior portion, with a sharp, forwardly curved tip. **Antenna:** shaft cylindrical, uniform in diameter, shorter than in later instars, but axial seta greater than one-half length of shaft.

Remarks

This species also is a specific parasite of *A. rufa*, known from California to Washington (Lewis *et al.* 1988), though it is expected to be found in Canada as well (Holland 1985). See additional remarks under *T. oregonensis*.

Trichopsylloides oregonensis Ewing, 1938

(Figs. 29, 34, 35)

Material examined

UNITED STATES. Oregon: Lincoln Co., 4.8 km south of Burnt Woods, 12.iv.1981, *ex A. rufa* nest, D. Gettinger, one $L_{II–III}$ (+1♀); 18.iv.1981, *ex A. rufa* nest, D. Gettinger, five L_I; 16.xii.1981, *ex A. rufa* nest, coll. D. Gettinger, six $L_{II–III}$ (+7♂♂, 10♀♀). Benton Co., 6.4 km south, 4.8 km west Blodgett, 20.v.1981, *ex A. rufa* nest, coll. D. Gettinger, three L_I, nine $L_{II–III}$ (+2♀♀). **Washington:** Grays Harbor Co., 32 km north of Montesano, 25.v.1966, *ex A. rufa* nest, coll. unknown, CNC (BRC-L-89-06, tube No. 2), three $L_{II–III}$.

Description

Structurally almost identical with *P. oregonensis*, except as follows: all instars smaller than even L_I of *P. oregonensis*; Ab 8, *D* plate (Fig. 34) with only two *d* setae; Ab 1–6, d_2 setae more slender and less than half length of d_1; hypopharynx extended, apex truncate, with two long apical setae (Fig. 29); labial palp short, cylindrical, with four processes, three short, cylindrical, blunt, and one slender, tapering, about two to three times as long (Fig. 29).

Remarks

The nature of the mandible in this species and in *P. oregonensis* is similar to that of known larvae in Rhadinopsyllini (Cotton 1970; Bartkowska 1972). Although the adults of *T. oregonensis* and *P. oregonensis* are of very distinct appearance (Holland 1985), the larvae are very similar, apart from being quite different in size.

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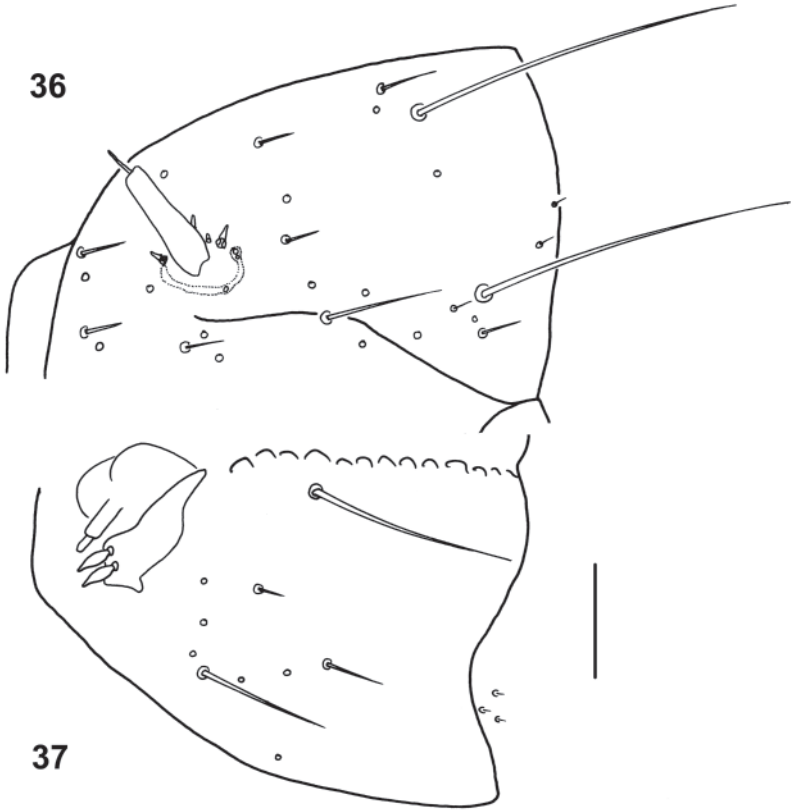
Figs. 36–37. *Dolichopsyllus stylosus*: 36, dorsal view of head capsule, right half; 37, ventral view of head capsule, right half. Scale bar = 0.1 mm.



Family Leptopsyllidae Baker, 1905

Subfamily Amphipsyllinae Ioff, 1936

Tribe Dolichopsyllini Baker, 1905

Dolichopsyllus stylosus (Baker, 1904)

(Figs. 11, 19, 20, 36–47, 51–53)

Material examined

UNITED STATES. Oregon: nest, 12.iv.1981, *ex A. rufa* nest, D. Gettinger, one L_I; 18.iv.1981, *ex A. rufa* nest, D. Gettinger, eight L_I, 15 $L_{II–III}$.

Description

Second- and third-instar larvae (L_{II} and L_{III})

Head (Figs. 36, 37, 51, 52). Setation: there are normally 17 acicular setae on each half of the head capsule, as follows. Three parietals (*par.*): outermost very long, slender, reaching mid-length of Th I; innermost very short, fine; middle parietal seta minute, usually slightly anterior to other parietals. Two minute occipitals, anterior (*a.occ.*) and posterior (*p.occ.*); *p.occ.* near posterior margin of head capsule. Frontal seta (*fr.*) long, slender, reaching at least midway to alveolus of outermost *par.* Interantennal seta (*i-ant.*) short. Two clypeal setae, median (*m.cl.*) and lateral (*l.cl.*); lengths approximately equal to basal diameter of antennal shaft. Postantennal seta (*p-ant.*) short. Two genal setae: posterior one (*p.gen.*) long, slender, approximately length of outermost *par.*; anterior one (*a.gen.*) short, barely reaching alveolus of *p.gen.* Subgenal seta (*s-gen.*) short, slender. Postclypeal seta (*p-cl.*) short. Postmandibular seta (*p-man.*) long, slender, not reaching alveolus of *s-gen.* Postmaxillary seta (*p-max.*) very short. Paragular seta (*pa-gul.*) long, reaching posterior margin of head capsule. In addition,

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there are three microsetae (cervicals, *cer.*) immediately posterior to the ventrolateral margin of the head capsule. Sensillation: there are normally 20 sensilla on each half of the head capsule; positions are variable but typically as in Figures 36 and 37. **Labrum (Figs. 38, 39):** a broad, semioval, anteriorly projecting disc with a narrow basal sclerite. The labrum is flexible at the anterior margin, so when mouthparts are dissected for study and prepared on slides, it may be difficult to obtain strictly dorsal-ventral orientation. Ventral surface (Fig. 39) basally with scattered small spines that gradually increase in size laterally and anteriorly, extending well on to dorsal surface; each half with three basiconic sensilla and two campaniform sensilla. Dorsal surface (Fig. 38) basally smooth, entire anterior portion with stout, recurved spines; each half with one long seta mid-laterally, four shorter setae, two basiconic sensilla, and three campaniform sensilla. There is one somewhat larger campaniform sensillum(?) medially on the dorsal surface. **Mandible (Figs. 40, 51):** broadly triangular, tapering to a sharp, apical tip, without additional teeth; base greatly swollen and bearing two enormously enlarged, tusklike setae; two sensilla near alveolus of upper seta. **Maxilla (Figs. 41, 42, 51):** with a long basal apodeme directed posteriorly. Cardo: ventrally with one long and one short seta and two campaniform sensilla, and one campaniform sensillum in sclerotized ring between cardo and stipes; dorsal face with faint, cuticular reticulations distally. Stipes: anterolaterally with an apparently flexible, trilobed flap adjacent to base of palp, dorsally covered with flat, plaque-like scales extending to a dense patch of coarse spines anteromedially, which continues over to ventral face; a campaniform sensillum among the spines. Ventral face with one short, stout seta and at least two basiconic sensilla posterior to spines. Maxillary palp of two cylindrical segments; basal segment short, stout, with a very short seta and a campaniform sensillum ventrally; distal segment slender, truncate, with four basiconic sensilla apically. **Hypopharynx (Fig. 43, 52):** an elongated, stout, protruding lobe with trilobed apex; dorsal face densely covered with stout spines. Two clear, circular structures (alveoli?) on ventral surface near base of median lobe. **Labial palp (Figs. 43, 52):** short, cylindrical, with five processes, two long, slender, and three shorter, stouter, approximately half as long. **Antenna (Fig. 11):** shaft cylindrical and elongated, distinctly swollen at the base; sense organ near apex, apparently with two internal chambers; axial seta approximately one-third length of shaft; a corona of four basiconic sensilla. Antennal mound papillae α_1, β_1, α_2, β_2, and α_3, together with sensilla γ and δ, subtend approximately 150° along lateral margin of antennal mound; sensillum ϵ on medial side of mound. Papillae conical, α_1–α_3 occasionally with a terminal filament, β_1–β_2 much shorter, rarely with a filament.

Thorax (Figs. 44, 45). (Note: descriptions for the thorax and abdomen are based largely on L_I. Patterns of setation and sensillation on later instars are identical; setae in later instars are stouter and longer in absolute length.) **Th I:** dorsal plate, *D*, covering much of dorsal surface, reaching over sides of segment. Spiracle at an indentation at posterolateral edge of *D*. Setation and sensillation: anterior row of five short, slender setae: a_1, a_2, a_3, and a_5 very short and fine, a_4 about twice as long; a_1–a_3 on *D*. Posterior row: *D* with three long, slender setae, d_1–d_3; *VL* with one long, slender seta, *vl*, longer than d_3, and one extremely minute supplementary seta at the posterodorsal margin of *VL*, more conspicuous in $L_{II–III}$; *V* with one very short, fine seta, *v*. One ventral microseta anterior to *VL*, near margin of segment. *D* with two sensilla in each of anterior and posterior rows, medial of a_1, a_2 and d_1, d_2. **Th II–III:** *D* limited to dorsal surface; dorsolateral plate, *DL*, present. No spiracles. Setation and sensillation: anterior row: a_1–a_5 short, slender; a_3 on or near *DL*. Posterior row: d_1, d_2, *dl*, and *vl* long and slender, d_1 longest; *v* very short, not reaching posterior margin of segment. Microsetae: an irregular row of six towards the anterior margin of each segment. One extremely minute supplementary seta at dorsolateral margin of *VL* on some specimens. *D* with one sensillum in anterior row, medial of a_1; two sensilla in posterior row as for Th I.

Abdomen (Figs. 44–47, 53). Ab 1–7: *D* narrower than on Th II–III. Setation and sensillation: anterior row of six short, slender setae; a_1 on *D*, a_2 anteroventral to spiracle; a_3 slightly anterior to a_2 and a_4; a_5 between *VL* and *V*; a_6 anterior to medial margin of *V*. Posterior row: d_1, d_2, *dl*, and *vl* very long and slender; *V* with three *v* setae (Fig. 53), v_1 longest, as long as *vl*, v_2 less than half length of v_1, v_3 one-half or less length of v_2. Microsetae: an irregular row of five towards the anterior margin of each segment. Sensilla as in Th II–III. **Ab 8:** *D*

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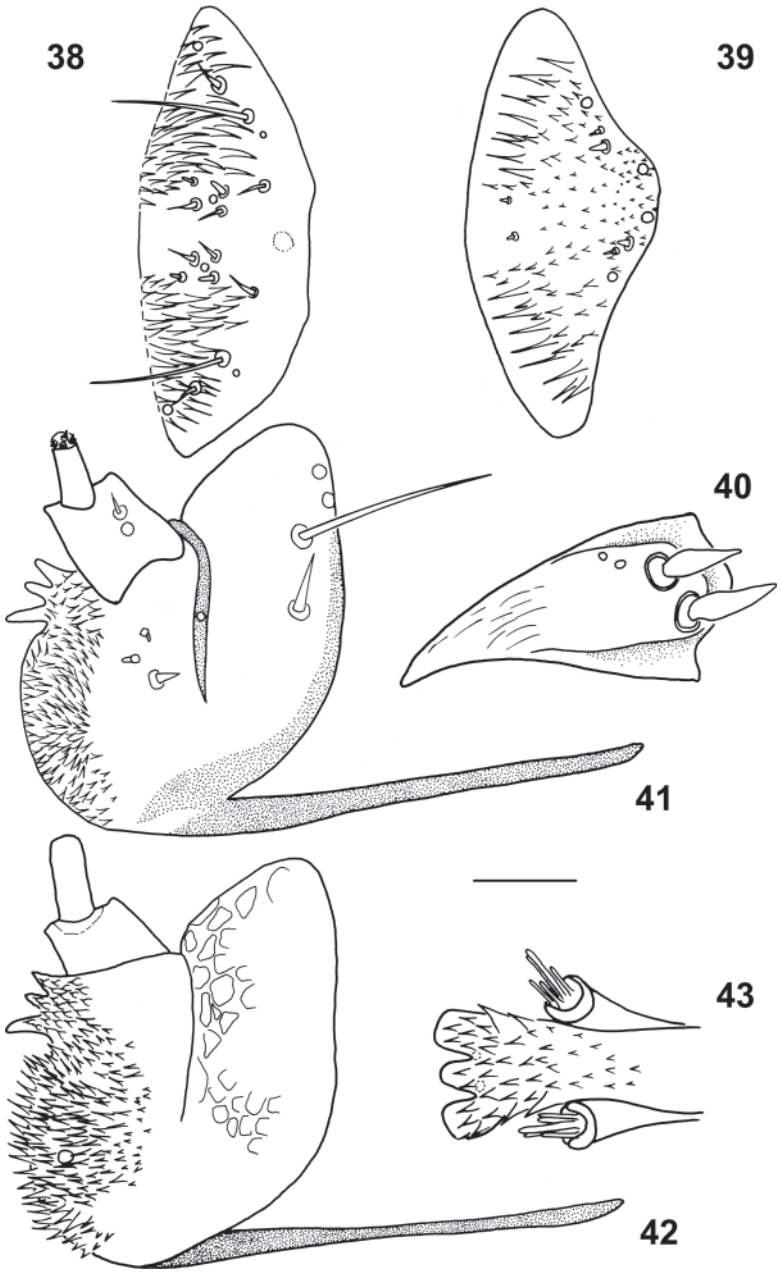
Figs. 38–43. *Dolichopsyllus stylosus*: 38, labrum, dorsal view; 39, labrum, ventral view; 40, mandible; 41, left maxilla, ventral view; 42, right maxilla, dorsal view; 43, hypopharynx and labial palps, dorsal view. Scale bar = 0.03 mm.



as on Ab 1–7. Spiracle as on Ab 1–7. Setation and sensillation: anterior row: a_1–a_6 short and slender, relative positions of a_1 and a_3–a_6 as on Ab 1–7, but a_2 anterodorsal to spiracle. Posterior row: d_1 long, slender, exceeding tip of anal strut; d_2 and *dl* long, slender, reaching base of anal strut; *vl* long, slender, reaching Ab 10; *V* with two *v* setae, v_1 similar in length to *vl*, v_2 less than one-third the length of v_1. Microsetae and sensilla as on Ab 1–7. **Ab 9:** *D* as on Ab 1–8. No spiracle. Setation and sensillation: anterior row of five short, slender setae, relative positions as on Ab 8. Posterior row: *D* with three *d* setae, d_1, d_2, and d_3; *d* setae and *dl*

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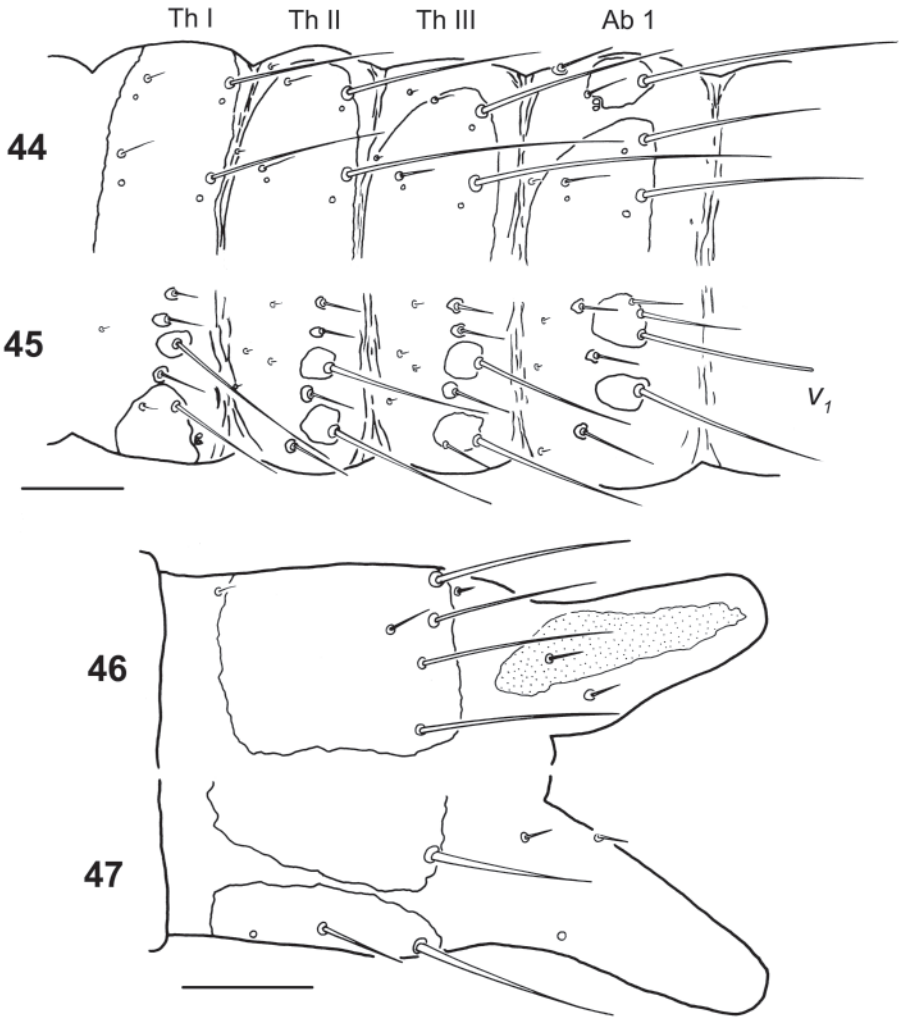
Figs. 44–47. *Dolichopsyllus stylosus*: 44, dorsal view of thoracic segments one to three (Th I–III), abdominal segment one (Ab 1), right half; 45, ventral view of Th I–III and Ab 1, right half (note truncated tip of v_1); 46, tenth abdominal segment, dorsal view, right half; 47, tenth abdominal segment, ventral view, right half. Scale bars = 0.1 mm (Figs. 44, 45) and 0.05 mm (Figs. 46, 47).



extremely long, slender, reaching well beyond tip of anal strut; *vl* shorter, reaching about to base of anal strut; *V* with two *v* setae, v_1 similar in length to *vl*, v_2 less than one-third the length of v_1. Three microsetae towards anterior margin of segment; one dorsal, approximately in line with a_2, two ventral, approximately in line with a_4 and a_5. Sensilla as on Ab 1–8. **Ab 10 (Figs. 46, 47):** with two weakly sclerotized dorsolateral plates, which almost meet mid-dorsally, and a single median ventral plate. No spiracle. Setation and sensillation: two stout ventrolateral setae (*v-l*) on dorsolateral plate reaching about mid-length of anal strut; the third *v-l* seta on ventral plate slightly shorter; a microseta near anterior margin of dorsolateral plate; anteroventral seta (*a-v*) stout, often reaching alveolus of nearest *v-l*; anteroventral sensillum well forward; post-ctenidial seta (*p-ct*) minute, just behind uppermost *v-l*. Anal comb of two distinct rows, anterior row with one short seta on each half, posterior row with three (occasionally four) longer, slender setae on each half. **Anal strut and anal mound:** strut fingerlike, bluntly rounded at tip, slightly curved ventrally, dorsal surface with an

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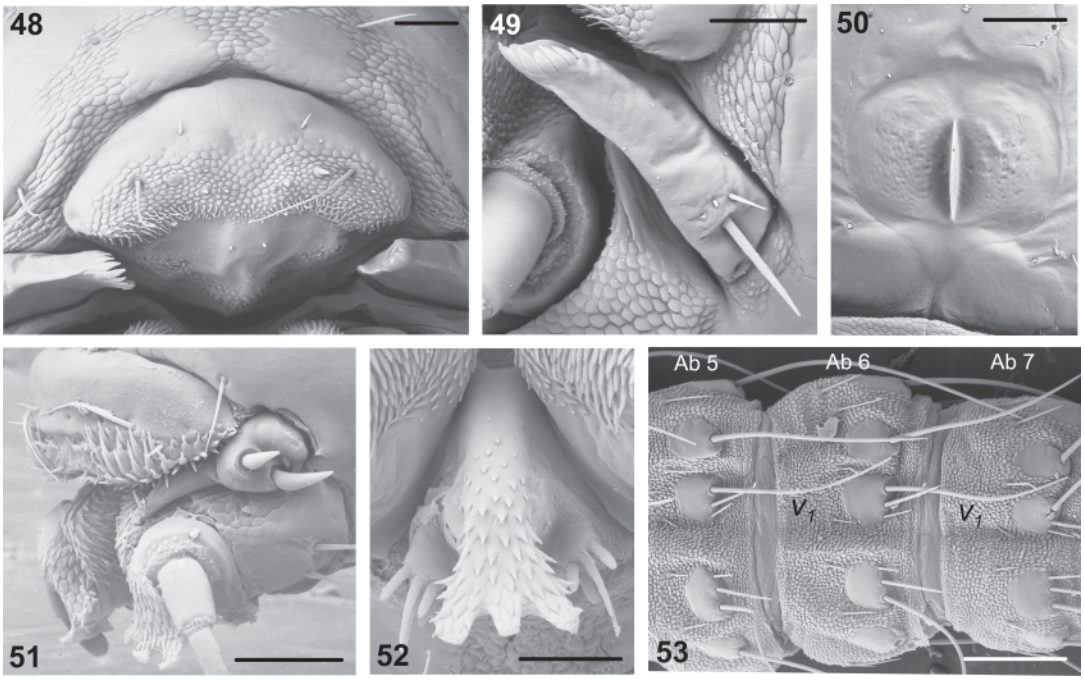
Figs. 48–53. *Hystrichopsylla schefferi*: 48, frontal view of labrum and mandibles; 49, left mandible, lateral view; 50, egg burster plate of L_I. *Dolichopsyllus stylosus*: 51, lateral view of mouthparts (note the pair of enlarged, tusklike setae near the base of the mandible); 52, dorsal view of hypopharynx and labial palps; 53, abdominal segments 5–7 (Ab 5, 6, 7), ventral view (note truncated tips on v_1 setae on Ab 5, 6). Scale bars = 40 μm (Figs. 48, 49, 51), 100 μm (Figs. 50, 53), and 20 μm (Fig. 52).



irregular, sclerotized strip; a campaniform sensillum on ventral surface. Anal mound with 4 (range 2–5) short setae.

First-instar larva (L_I)

As in $L_{II–III}$ except as follows. **Egg burster (Figs. 19, 20):** approximately one-third length of head capsule, rear end lying at posterior margin of head capsule, coronal suture absent; paddle-shaped, greatest width about three-quarters of total length, with a sharp, distinct egg tooth at about one-third the length from the anterior margin. **Antenna:** shaft uniform in diameter, shorter than in later instars, but axial seta greater than half the shaft length. **Abdomen:** v_1 seta on Ab 1–9 with truncated tip (Fig. 53).

Remarks

This remarkable species is a common parasite of *A. rufa* from California to British Columbia (Hubbard 1947; Holland 1949, 1985). Medvedev and Kotti (1992) emphasized the unique characters of adults of *D. stylosus*, the species being the sole representative of the Dolichopsyllini, and considered *D. stylosus* basal to the entire Leptopsyllidae. Significantly, the species has occupied a solitary position in almost every taxonomic arrangement of the family. The larva also exhibits a number of unique characters: the labrum, maxillae, and hypopharynx (which is, further, uniquely trilobed) are partially covered by extremely large spines; the mandibles bear two enormous, tusklike setae on an enlarged base. It would be very interesting to observe these larvae alive, to determine by what means and upon what materials they feed. Pilgrim (1991) has drawn attention to the very great differences in the form of mouthparts, especially mandibles, in various flea larvae. The three distinct forms of mouthparts described in this paper are clear evidence of the possibility of a divergent range of food and/or feeding methods among species in the same nest.

The larva of *D. stylosus* is the only one that we have seen that has five processes instead of four on the labial palps. Another extraordinary character of the larva is the regular occurrence of three *v* setae on each *V* plate on Ab 1–7. The

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only other larvae known to have three *v* setae are those of *Notiopsylla* spp., where the numbers range, irregularly, from one to four (Pilgrim 1998). The two circular structures on the ventral surface of the hypopharynx may be the alveoli of the two setae present in this position in other flea larvae. However, we have not seen setae on the hypopharynx of any specimen of *D. stylosus* that we have examined. It is possible that the setae have all been broken off, but it is more likely that they are truly absent, with only the alveoli remaining. In the first instar only of *D. stylosus*, the truncated tip of v_1 is also of particular note; all the *v* setae stain less intensively than do the other posterior-row setae but, whereas the shorter v_2 and v_3 appear stiff, v_1 seems to be soft and flexible; its lumen also appears to be open at the tip.

The larvae of fewer than half the genera of the Leptopsyllidae (mostly in Leptopsyllinae) are known, and even fewer have been adequately described. It is important that larvae of all the genera be collected and descriptions undertaken; the phylogeny of Medvedev and Kotti (1992) for this family can then be tested with respect to larval characters.

Discussion

The fact that *A. rufa* is often held to be the oldest extant species of rodent, and that it is host to a unique assemblage of fleas, makes the collection and description of the larvae of these fleas exciting. Larvae of at least *H. schefferi*, *P. oregonensis*, and *T. oregonensis* conform to the known characters for their respective subfamilies and tribes. However, there are no previous descriptions of larvae for members of the former subgenus *Hystroceras* or the monotypic genera *Paratyphloceras* and *Trichopsylloides*, other than the contribution by Pilgrim (in Elbel 1991).

As Holland (1985) pointed out, there was earlier confusion about the taxonomic status of *T. oregonensis*. The larvae of *P. oregonensis* and *T. oregonensis* are very similar and clearly belong to the Rhadinopsyllini, supporting the current taxonomic placement. How the fleas in these two genera became specifically associated with the same host can only be a matter of speculation.

Certainly the adults of *D. stylosus* have been recognized for a long time as phylogenetically distinct (Holland 1949; Medvedev and Kotti 1992). The basal position of the genus *Dolichopsyllus* within the Leptopsyllidae adds to the importance of the larval characters in *D. stylosus*. However, larvae of so few of the genera in the family have been described that it is premature to attempt an interpretation of the relationships within the family based on larval characters.

As is the case with all families of fleas, there is a great need for collection and careful association of larvae with known adults. It is evident from the four species treated within this paper that there are abundant characters available in the order for the development of a reconstructed phylogeny including larval characters. Adult fleas are subjected to intense selection pressures from an alert and fastidious host intent on grooming out the source of the annoying bites. It may be that larval characters will display less evidence of convergent evolutionary processes, something that has plagued analysis based on adults. It is essential that flea workers undertake detailed and consistent descriptions of the larvae of as many taxa as possible so that the potential values of the immature stages can be appreciated.

Acknowledgements

We very much appreciate the contribution of Don Gettinger (Department of Biology, University of Central Arkansas, Conway, Arkansas). Without his diligence and hard work in collecting the nests of the mountain beaver, the larvae of these fascinating fleas would still be a mystery. We thank E.E. Lindquist (Eastern Cereal and Oilseed Research Centre, Canadian National Collection of Insects, Agriculture and Agri-Food Canada, Ottawa) for the loan of specimens and Jan McKenzie for carefully preparing specimens for examination using the scanning electron microscope. We also thank Carol Galloway for her skilled assistance with production of the plates. Financial support provided by the New Zealand Lottery Grants Board (R.L.C.P.), the University of Manitoba, and the Natural Sciences and Engineering Research Council of Canada (T.D.G.) is gratefully acknowledged. We also thank the School of Biological Sciences, University of Canterbury, for their continuing support.

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