Eriosomatine aphids (Hemiptera: Aphididae: Eriosomatinae) associated with moss and roots of conifer and willow in forests of the Pacific Northwest of North America

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Abstract—Apterous adult morphs of eriosomatine aphids associated with moss (Bryophyta) and/or roots of conifer (Pinaceae) or willow (*Salix* Linnaeus (Salicaceae)) in forests of the North American Pacific Northwest including Alaska are described, illustrated, and keyed. In total, seven species (*Clydesmithia canadensis* Danielsson, *Melaphis rhois* (Fitch) (moss only feeder), *Pachypappa rosettei* (Maxson), *Pachypappa sacculi* (Gillette), *Prociphilus americanus* (Walker) (fir root only feeder), *Prociphilus xylostei* (De Geer), and *Thecabius populimonilis* (Riley)) are characterised from their secondary host habitats. Secondary host forms of *C. canadensis* and *T. populimonilis* are described for the first time. The morphotypes from the secondary hosts were confirmed through deoxyribonucleic acid sequence matching with those from the primary hosts.

Résumé—Nous décrivons et illustrons les morphes adultes aptères de pucerons ériosomatinés associés aux mousses (Bryophyta) et(ou) aux racines de conifères (Pinaceae) et de saules (*Salix* Linnaeus (Salicaceae)) dans les forêts du Nord-Ouest Pacifique américain y compris l'Alaska et nous fournissons des clés pour leur identification. En tout, sept espèces (*Clydesmithia canadensis* Danielsson, *Melaphis rhois* (Fitch) (se nourrissant seulement de mousses), *Pachypappa rosettei* (Maxson), *Pachypappa sacculi* (Gillette), *Prociphilus americanus* (Walker) (se nourrissant seulement de racines de sapin), *Prociphilus xylostei* (De Geer) et *Thecabius populimonilis* (Riley)) sont caractérisées d'après les habitats de leur hôte secondaire. Nous décrivons les formes des hôtes secondaires de *C. canadensis* et de *T. populimonilis* pour la première fois. Les morphotypes des hôtes secondaires ont pu être confirmés par comparaison de leurs séquences d'ADN avec celles des morphotypes des hôtes primaires.

Introduction

A rich assortment of mosses (Bryophyta) in the coastal and interior forests of the Pacific Northwest is frequented by a diversity of arthropods, including eriosomatine aphids (Hemiptera: Aphididae: Eriosomatinae). At times, these are common in Berlese funnel extractions. *Melaphis rhois* (Fitch)

Received 26 August 2011. Accepted 18 October 2011.

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doi:10.4039/tce.2012.49

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is a true moss feeding aphid (Baker 1919; Heie 1980; Moran 1989; Hebert *et al*. 1991), while others are suspected or known to be root feeders (Smith 1969, 1974; Stroyan 1975; Danielsson 1990b) feeding in whole or in part on the roots of selected conifers (Pinaceae) or willow (*Salix* Linnaeus (Salicaceae)) with roots intertwined at times in moss at the moss–soil interface zone. Smith and Knowlton (1975) reported finding unidentifiable pemphigines (now named as Eriosomatinae; Nieto Nafría *et al*. 1998) in moss using Berlese funnels.

The Eriosomatinae are characterised by host alternation from a primary host (trees and shrubs) on which they form galls or pseudogalls, to various secondary hosts, usually the subterranean parts. The morphological forms (morphs) on the secondary hosts differ significantly from the forms on the primary hosts. As a result, it has been difficult to link the different parts of the life cycles without rearing and host transfer experiments. All of the aphids treated here were originally described from their gall-producing or leaf-curling forms on the primary host. In this study, the identity of the morphs on moss, or moss and fine roots (fir and spruce [*Abies* Miller and *Picea* Dietrich (Pinaceae)] and willow), or roots was confirmed by matching deoxyribonucleic acid (DNA) sequences with specimens obtained from the primary hosts. The secondary host forms of each species are characterised morphologically and an identification key is provided.

Materials and methods

Species descriptions, character measurements, and DNA sequences were based on specimens from authors' field collections obtained through Berlese extraction of moss and roots of conifer and willow from a wide range of sites in coastal and interior forests of the Pacific Northwest, including Alaska, or from galls and pseudogalls on primary hosts from various locations in North America. Extracted aphids were preserved in ethanol, with part used for DNA analysis (namely, DNA barcodes; Foottit *et al*. 2008) to confirm species identification, and part used for permanent slide mount preservation. Voucher specimens for morphological characterisation were cleared and slide mounted in Canada balsam following methods by Foottit and Maw (2000) and deposited in Washington State University (WSU) Aphid Collection, Prosser, Washington, United States of America unless otherwise indicated. Descriptive nomenclature is after Foottit and Richards (1993) and Pike *et al*. (2003). Full synonymies for aphids studied are available from Remaudière and Remaudière (1997). Plant names are after the United States Department of Natural Resources Conservation Service plant profiles (USDA 2009); full moss names with authors are shown in Table 1.

The following abbreviations are used in collection records: ap, aptera vivipara; Boro., Borough; CG, campground; Co., county; coll., collector; Cr, creek; E, east; ex, eriosomatines extracted or taken from; FR, forest road; Hwy, highway; im, immature; jct, junction; Lk, lake; mi, mile or miles; Mtns, mountains; Pk, park; N, north; NP, national park; nr, near; S, south; SP, state park; W, west. Identifying letters in authors' collection codes (*e.g*., A1A108): A# = year (*i.e.*, A1 = 2001, A2 = 2002, etc.); centre letter indicates collector, A, A. Pantoja, A. Hagerty, and S. Emmert; G, G. Graf; K, K. Pike; 108, sample number. Anatomical and other descriptive abbreviations are as follows: ABD, abdomen or abdominal; ANT, antenna; ASI, II, etc., antennal segment I, II, etc.; B, basal length of ultimate antennal segment (part up to and including primary rhinarium); Htbs, metatibia apical seta; Htars, metatarsus I apical seta; L/W, length/width; PT, processus terminalis of ultimate antennal segment (*i.e.*, part beyond primary rhinarium); 2° RHIN, antennal secondary rhinaria; URS, ultimate rostral segment (penultimate and ultimate segments).

Illustrations were drawn from images taken with a DEC13M digital eyepiece camera through a Zeiss Axiolab compound microscope (model 450907) (Carl Zeiss, Göttingen and Jena, Germany); morphological measurements (all recorded in millimetres, with segment length measured unless otherwise indicated) and character ratios are derived using image-measuring software (Pike *et al*. 2005).

Sequence data for mitochondrial cytochrome *c* oxidase subunit I (COI), 5′ end ("DNA barcoding" region) of exemplar specimens (Table 2) selected from authors' collections were compared to provide an indication of molecular coherence and distinctness of species. A few sequences of related aphids were included for comparison purposes. Details on primers and specimen processing follow

Table 1. Aphid eriosomatine associations with moss in the Pacific Northwest including Alaska (based on Berlese funnel extractions) for *Clydesmithia canadensis* (Cc), *Melaphis rhois* (Mr), *Pachypappa rosettei* (Pr), *Pachypappa sacculi* (Ps), *Prociphilus xylostei* (Px), and *Thecabius populimonilis* (Tp).

Mosses		Cc	Mr*	Pr	Ps	Px	Tp
Amblystegiaceae	*Hygrohypnum ochraceum* (Turner ex Wilson) Loeske			●			
	Sanionia uncinata (Hedw.) Loeske	●		●	●	●	
Aulacomniaceae	*Aulacomnium palustre* (Hedw.) Schwägr.			●	●		
Bartramiaceae	*Philonotis fontana* (Hedw.) Brid.	●					●
Brachytheciaceae	*Brachythecium starkei* (Brid.) Schimp.				●		
	Brachythecium sp.	●				●	
	Isothecium stoloniferum Brid.					●	
	Kindbergia oregana (Sull.) Ochyra					●	
	Kindbergia praelonga (Hedw.) Ochyra		●				
	Tomentypnum nitens (Hedw.) Loeske				●		
Bryaceae	*Pohlia* sp.					●	
Climaciaceae	*Climacium dendroides* (Hedw.) F. Weber & D. Mohr	●					
Dicranaceae	*Dicranum fuscescens* Turner				●		
	Dicranum scoparium Hedw.		●†		●	●	
Grimmiaceae	*Racomitrium* sp.					●	
Hylocomiaceae	*Hylocomium splendens* (Hedw.) Schimp.				●	●	
	Pleurozium schreberi (Brid.) Mitt.			●	●		
	Rhytidiadelphus loreus (Hedw.) Warnst.		●			●	
Mniaceae	*Leucolepis acanthoneuron* (Schwägr.) Lindb.		●				
	Plagiomnium insigne (Mitt.) T. Kop.	●					
	Plagiomnium sp.					●	
	Rhizomnium magnifolium (Horik.) T. Kop.	●			●		
	Rhizomnium sp.					●	
Polytrichaeae	*Polytrichum commune* Hedw.			●	●	●	
	Polytrichum juniperinum Hedw.				●		
	Polytrichum lyallii (Mitt.) Kindb.					●	
	Polytrichum sp.			●	●	●	
Sphagnaceae	*Sphagnum capillifolium* (Ehrh.) Hedw.				●		
	Sphagnum rubellum Wilson				●		
	Sphagnum russowii Warnst.			●			
	Sphagnum sp.			●	●	●	
Thuidiaceae	*Claopodium crispifolium* (Hook.) Renauld & Cardot		●	●			

*Associations reported in Europe (Holman 2009): *M. rhois* – *Eurhynchium striatum* (Schreb. ex Hedw.) Schimp. (Brachytheciaceae), *Hylocomium armoricum* Wijk & Marg., *Hypnum* sp. (Hypnaceae), *P. commune*, and *Sphagnum* sp.; in Arizona (Moran 1989) – *Haplocladium microphyllum* (Hedw.) Broth. (Thuidiaceae).

† Large numbers of *M. rhois* extracted; possible preferred moss or moss habitat (moss on coastal sands intermixed with dune grasses, adjacent to or under lodgepole pine or spruce).

Foottit *et al*. (2008). Information on sequences, collections, and taxonomy for each specimen was entered in the Barcode of Life Data System (Ratnasingham and Hebert 2007). All sequences obtained in this study were deposited in GenBank (Table 2). Where available, voucher specimens from the same collection sequenced are deposited in WSU or the Canadian National Collection (CNC) of Insects, Arachnids and Nematodes (Agriculture and Agri-Food Canada, Ottawa, Ontario).

Pairwise nucleotide sequence divergences were calculated using the Kimura two-parameter model of base substitution (Kimura 1980) and neighbour-joining analysis (Saitou and Nei 1987) was used to examine relationships among taxa and population samples. Although distance calculations are based on a particular evolutionary model, the neighbour-joining tree presented is intended as a graphical representation of phenetic sequence divergences among samples

Table 2. Material used for deoxyribonucleic acid (mitochondrial cytochrome *c* oxidase subunit 1) sequence comparisons.

	Plant host	Location	Collection code*	BOLD specimen ID	GenBank accession no.
Clydesmithia canadensis (Danielsson)	Moss	Alaska	A7K237	CNC#HEM059486	JN201206
	Moss	Alaska	A7K258	CNC#HEM061734	JN201205
	Poplar gall	Saskatchewan	2010EM-0264A	CNC#HEM070133	HQ970647
	Poplar gall	Manitoba	2010EM-0271	CNC#HEM070145	HQ970650
	Moss	Washington	A8G191	CNC#HEM061742	JN201204
	Moss	Washington	A9G157	CNC#HEM064039	GU668242
	Moss	Washington	A7G057	CNC#HEM058033	JN201207
	Moss	Washington	A8G282	CNC#HEM061747	JN201203
	Poplar gall	Washington	A9G027	CNC#HEM064129	GU668241
	Fir roots	Washington	A9G200	CNC#HEM063911	GU668315
	Moss	Washington	A9G302	CNC#HEM063934	GU668317
	Moss	Montana	A9G373	CNC#HEM063955	GU668318
	Poplar gall	Alberta	FM36	CNC#HEM064337	GU668741
	Poplar gall	Alberta	2009EM-0301	CNC#HEM063441	GU668665
	Poplar gall	Alberta	2009EM-0418	CNC#HEM063558	GU668574
	Moss	Montana	A9G380	CNC#HEM063959	GU668320
	Spruce roots	Montana	A9G381	CNC#HEM063960	GU668322
Melaphis rhois (Fitch)	Moss	Washington	A5K256	CNC#HEM113727	EU701750
	Moss	Washington	A5K318	CNC#HEM113755	EU701749
	Sumac gall	Ontario	2000-55-1	CNC#HEM059738-4	GU667135
	Sumac gall	Ontario	93-11-15	CNC#HEM059540-15.1	GU668897
	Sumac gall	Ontario	94-19-2	CNC#HEM059508-2	GU667187
	Sumac gall	Ontario	2008EM-0359	CNC#HEM061578	JN201208
	Sumac gall	Ontario	92-57-5	CNC#HEM059611-5	GU668895
	Sumac gall	Ontario	2000-21-4	CNC#HEM059733-4	GU667134
	Sumac gall	Ontario	93-4-13	CNC#HEM059536-13	GU667142
	Sumac gall	Ontario	93-10-5	CNC#HEM059539-5.2	GU668915
	Sumac gall	Ontario	2000-7-3	CNC#HEM063878-3	GU668929
	Sumac gall	Ontario	92-58-22	CNC#HEM059612-22	GU667127
	Moss	Washington	A9K077	CNC#HEM063053	GU668200
	Sumac gall	Ontario	91-48-19	CNC#HEM059628-19	GU668872
	Sumac gall	Ontario	2000-5-1	CNC#HEM059737-11	GU667151
Pachypappa rosettei (Maxson)	Spruce roots	Washington	A9G188	CNC#HEM064054	GU668245
	Spruce roots	Washington	A7G138	CNC#HEM058046	JN201217
	Moss	Washington	A7G197	CNC#HEM058050	JN201216
	Poplar gall	Colorado	2010EM-0049	CNC#HEM069896	HQ970778
	Moss	Washington	A8G181	CNC#HEM061741	JN201209
	Spruce roots	Washington	A9G076	CNC#HEM064027	GU668244
	Moss	Washington	A9K029	CNC#HEM063038	GU668197
	Spruce roots	Washington	A9G138	CNC#HEM064035	GU668246
	Fir roots	Washington	10K152	CNC#HEM070709	JF883837
	Moss	Alaska	A7A107	CNC#HEM061691	JN201214
	Moss	Alaska	A7A171	CNC#HEM061726	JN201210
	Moss	Alaska	A7A155	CNC#HEM061717	JN201213
	Moss	Alaska	A7A170	CNC#HEM061725	JN201211
	Moss	Alaska	A9A084	CNC#HEM068359	HQ971275
	Moss	Alaska	10A014	CNC#HEM070229	JF883532
	Moss	Alaska	A7A168	CNC#HEM061724	JN201212
	Moss	Alaska	A7K213	CNC#HEM059482	JN201215

Table 2. *Continued*

	Plant host	Location	Collection code*	BOLD specimen ID	GenBank accession no.
Pachypappa sacculi (Gillette)	Poplar gall	British Columbia	2001EM-0375	CNC#HEM039530	EU701826
	Poplar gall	British Columbia	2000EM-0531	CNC#HEM033116	EU701828
	Moss	Alaska	A7A172	CNC#HEM061727	JN201220
	Moss	Washington	A8G307	CNC#HEM061754	JN201218
	Moss	Alaska	A7K139	CNC#HEM058106	JN201223
	Moss	Alaska	A7A118	CNC#HEM061699	JN201222
	Moss	Alaska	A7A177	CNC#HEM061731	JN201219
	Moss	Alaska	A9A011	CNC#HEM063887	GU668311
	Spruce roots	Washington	A9G045	CNC#HEM064015	GU668243
	Moss	Washington	10K064	CNC#HEM070674	JF883711
	Moss	Alaska	A7A126	CNC#HEM061703	JN201221
	Moss	Washington	A5G164	CNC#HEM113243	EU701827
	Moss	Washington	10K106	CNC#HEM070705	JF883833
Prociphilus americanus (Walker)	Fir roots	Washington	A9G068	CNC#HEM064022	GU668223
	Fir roots	Washington	A9G168	CNC#HEM064042	GU668222
	Fir roots	Washington	A9G318	CNC#HEM063944	GU668292
	Fir roots	Washington	A9G309	CNC#HEM063941	GU668294
	Fir roots	Idaho	A9G390	CNC#HEM063966	GU668295
	Fir roots	Washington	A9G217	CNC#HEM063916	GU668293
	Fir roots	Washington	A9G090	CNC#HEM064030	GU668220
	Ash	Washington	A6K074	CNC#HEM055890	JN201227
	Ash	British Columbia	2007EM-1032	CNC#HEM057942	JN201225
	Ash	British Columbia	CK2008-025	CNC#HEM061900	JN201224
	Fir roots	Montana	A9G385	CNC#HEM063962	GU668291
	Ash	Quebec	NIS 2006-161	CNC#HEM055915	JN201226
Prociphilus xylostei (De Geer)	Fir roots	Washington	A9K108	CNC#HEM064067	GU668229
	Moss	Alaska	A9A105	CNC#HEM068370	HQ971284
	Moss	Washington	A5K261	CNC#HEM113728	EU701865
	Moss	Washington	A6K251	CNC#HEM114039	JN201231
	Honeysuckle	British Columbia	2001EM-0469	CNC#HEM039632	EU701872
	Moss	Washington	A9K114	CNC#HEM064071	GU668227
	Moss	Washington	A8G295	CNC#HEM061750	JN201230
	Fir roots	Washington	A9G011	CNC#HEM063996	GU668230
	Moss	Washington	A7G236	CNC#HEM058055	JN201232
	Moss	Washington	A9G018	CNC#HEM063998	GU668232
	Moss	Washington	A9K011	CNC#HEM063030	GU668113
	Moss	Washington	A5K311	CNC#HEM113749	EU701866
	Moss	Washington	A8K064	CNC#HEM061756	JN201229
	Moss	Washington	A9K041	CNC#HEM063044	GU668199
Thecabius populimonilis (Riley)	Poplar gall	Manitoba	2010EM-0276	CNC#HEM070151	HQ970652
	Poplar gall	Alaska	10A198	CNC#HEM070651	JF883696
	Willow root	Alaska	10A001	CNC#HEM068338	HQ971336
	Moss-willow root	Washington	A9G036	CNC#HEM064009	GU668248
	Poplar gall	Washington	A9G199	CNC#HEM063910	GU668331
	Poplar gall	Washington	A9G316	CNC#HEM063943	GU668332
	Poplar gall	Idaho	A9G387	CNC#HEM063964	GU668334
	Poplar gall	Alberta	2009EM-0469	CNC#HEM063602	GU668552
	Poplar gall	British Columbia	2007EM-0826	CNC#HEM057530	JN201235
	Poplar gall	Manitoba	2007EM-0413	CNC#HEM057079	JN201236

Table 2. *Continued*

	Plant host	Location	Collection code*	BOLD specimen ID	GenBank accession no.
	Poplar gall	Ontario	2007EM-0332	CNC#HEM056999	JN201237
	Poplar gall	Wisconsin	2009EM-0199	CNC#HEM063338	GU668459
	Moss–willow root	Washington	A8K224	CNC#HEM061788	JN201233
	Moss–willow root	Washington	A8G305	CNC#HEM061753	JN201234
	Poplar gall	Utah	2010EM-0128	CNC#HEM069977-1a	HQ970830
	Poplar gall	Colorado	2010EM-0107	CNC#HEM069954	HQ970817
	Poplar gall	Montana	A9G365	CNC#HEM063949	GU668336
	Poplar gall	Alberta	2009EM-0259	CNC#HEM063397	GU668405
Other eriosomatines					
Pachypappa pseudobyrsa (Walsh)	Poplar gall	Utah	2010EM-0112	CNC#HEM069959	HQ970821
Prociphilus fraxinifolii (Patch)	Ash	Ontario	98EM-0135	CNC#HEM025928	EU701859
Prociphilus tessellatus (Fitch)	Alder	Ontario	92EM-228	CNC#HEM061535	EU701863
Smynthurodes betae (Walsh)	Tomato			CNC#HEM063294	GU668202
Thecabius gravicornis (Patch)	Poplar gall	Alberta	2009EM-0452	CNC#HEM063585	GU668564

Note: Full collection data for all samples available on the BOLD System (http://www.boldsystems.org; 'published projects' link, in projects RDBA and RFKPE); sequence data available on BOLD as well as on GenBank.

*Collection codes for the moss–root inhabiting eriosomatines correspond to collection numbers in specimens examined sections listed in the text. Other collections from ash, honeysuckle, poplar, and sumac are standards (confirmed species) for comparative species sequence match evaluation.

BOLD, Barcode of Life Data.

and should not be interpreted as a phylogenetic hypothesis.

Results

Specimens obtained during the course of this study were identified as belonging to the following species: *Clydesmithia canadensis* Danielsson, *M. rhois* (Fitch), *Pachypappa rosettei* (Maxson), *Pachypappa sacculi* (Gillette), *Prociphilus americanus* (Walker), *Prociphilus xylostei* (De Geer), and *Thecabius populimonilis* (Riley) (Figs. 1–32). Associations of aphid species with moss species are summarised in Table 1.

COI sequences for each species formed distinct clusters well separated from other species, with the moss/root forms falling within the clusters defined by the corresponding primary host forms (Fig. 33). Values for sequence divergences within and between clusters are given in Table 3. Maximum within-species sequence divergence was 4.18% while the minimum sequence divergence among clusters was 6.40%.

The secondary host forms of *C. canadensis* and *T. populimonilis* are described here for the first time.

Clydesmithia canadensis (Danielsson, 1990)

(Figs. 1–5; Table 4)

Specimens examined

ex moss (new habitat association) (moss sometimes with fine conifer roots intertwined)

Aptera viviparae and immatures: **UNITED STATES OF AMERICA (new distribution records). Alaska:** Matanuska Susitna Boro., nr Wasilla-Palmer, Old Glen Hwy, 6-viii-2007, ex *Climacium dendroides* (Hedw.) F. Weber & D. Mohr (Climaciaceae) (1ap – A7K237);

Table 3. Summary of pairwise distances (percent difference in mitochondrial cytochrome *c* oxidase subunit 1 sequences) between moss–root eriosomatine species (above the diagonal), maximum observed within-species divergence (on the diagonal), and minimum observed distances between sampled eriosomatines and nearest other eriosomatine species (right-hand column).

	Moss and/or fir, spruce, or willow root eriosomatine*							
	Clydesmithia canadensis	*Melaphis rhois*	*Pachypappa rosettei*	*Pachypappa sacculi*	*Prociphilus americanus*	*Prociphilus xylostei*	*Thecabius populimonilis*	Nearest other eriosomatine
C. canadensis ($n = 17$)	2.82	14.84–17.99 (16.89 ± 0.51)	9.50–12.25 (10.76 ± 0.80)	9.31–10.79 (10.11 ± 0.45)	14.42–16.73 (15.46 ± 0.36)	11.94–13.36 (12.49 ± 0.31)	11.63–13.48 (12.8 6± 0.36)	10.40 (*Pachypappa pseudobyrsa*)
M. rhois ($n = 15$)		4.18	12.27–15.63 (14.17 ± 0.73)	13.37–15.68 (14.73 ± 0.48)	14.49–17.45 (16.23 ± 0.72)	12.45–13.48 (12.93 ± 0.21)	10.31–11.56 (10.91 ± 0.40)	13.61 (*Smynthurodes betae*)
P. rosettei ($n = 17$)			3.31	7.97–9.55 (8.67 ± 0.43)	15.83–17.61 (16.68 ± 0.47)	12.27–15.76 (13.35 ± 0.76)	8.11–12.03 (9.33 ± 0.86)	10.42 (*P. pseudobyrsa*)
P. sacculi ($n = 13$)				0.62	14.58–15.64 (15.02 ± 0.27)	13.40–14.86 (13.88 ± 0.31)	10.54–11.11 (10.77 ± 0.13)	10.21 (*P. pseudobyrsa*)
P. americanus ($n = 12$)					2.84	10.15–13.64 (12.56 ± 0.81)	15.24–16.40 (16.03 ± 0.23)	10.86 (*Prociphilus fraxinifolii*)
P. xylostei ($n = 15$)						0.77	10.49–11.39 (10.77 ± 0.22)	11.56 (*Prociphilus tessellatus*)
T. populimonilis ($n = 18$)							0.93	6.40 (*Thecabius gravicornis*)

Note: Between-species values are given as the range, followed by the mean ± standard deviation in parentheses for all pairwise comparisons of the main studied eriosomatines.
*Includes representative primary host morphs in sequence divergence distance determinations.

Figs. 1–10. Eriosomatinae (aptera vivipara) of moss and/or roots of fir or spruce. 1–5, *Clydesmithia canadensis*: **1**, adult; **2**, ultimate rostral segment; **3**, antennal segments I–V; **4**, metatarsus and apex of tibia (lines point to size differences in setae on tarsus I and apex of tibia); **5**, wax gland plate. 6–10, *Melaphis rhois*: **6**, adult; **7**, ultimate rostral segment; **8**, antennal segments I–IV; **9**, metatarsus and apex of tibia (tarsus I and II fused); **10**, wax gland plate. Scale bars: 0.20 mm for Figures 1, 6; 0.05 mm for Figures 3, 4; 0.03 mm for Figures 2, 7, 8, 9.

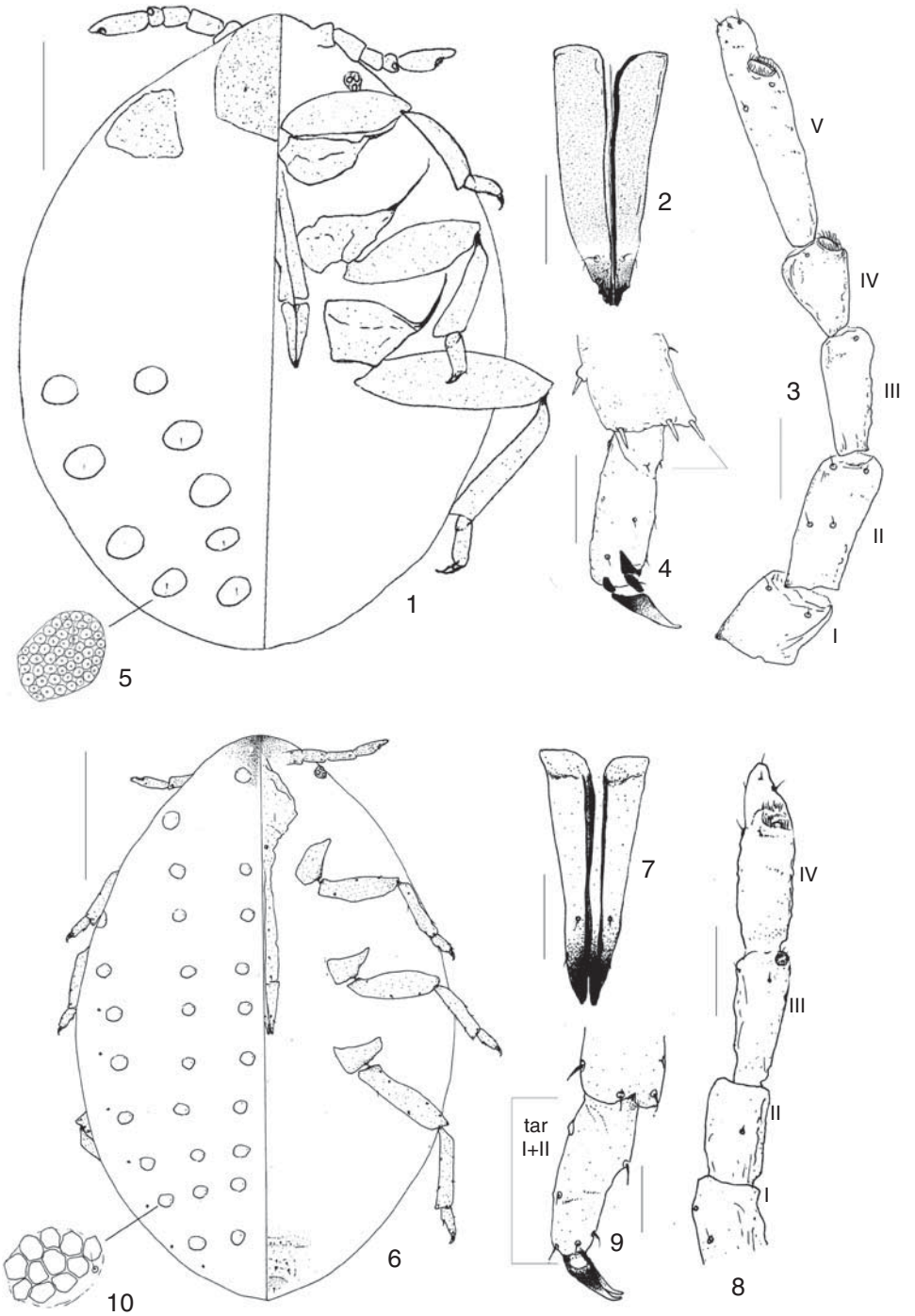


Table 4. Host/habitat and morphological measurements (mm) and comparisons of adult aptera viviparae of *Clydesmithia*, *Melaphis*, *Pachypappa*, *Prociphilus*, and *Thecabius* associated with mosses and/or roots of conifer or willow in the interior and coastal forests of the Pacific Northwest.

Features	*Clydesmithia canadensis* $n = 5$ Mean (range)	*Melaphis rhois* $n = 9$ Mean (range)	*Pachypappa rosettei* $n = 10$ Mean (range)	*Pachypappa sacculi* $n = 11$ Mean (range)	*Prociphilus americanus* $n = 9$ Mean (range)	*Prociphilus xylostei* $n = 32$ Mean (range)	*Thecabius populimonilis** $n = 5$ Mean (range)
Primary host	*Populus*	*Rhus*[†]	*Populus*	*Populus*	*Fraxinus*, *Syringa*	*Lonicera*	*Populus*
Alternate (secondary) host-habitat	Conifer roots–moss[‡]	Moss	Conifer roots–moss[‡]	Conifer roots–moss[§]	Conifer roots‖	Conifer roots–moss[‡]	Willow root–moss
Measurements[¶]	Aptera adult form on moss and/or roots						
Body	1.34 (1.03–1.63)	0.99 (0.79–1.20)	1.10 (0.84–1.41)	1.28 (0.94–1.76)	1.90 (1.39–2.34)	0.98 (0.78–1.22)	1.85 (1.49–2.43)
Head (width)	0.31 (0.27–0.37)	0.25 (0.21–0.29)	0.28 (0.23–0.33)	0.29 (0.22–0.38)	0.46 (0.40–0.59)	0.23 (0.19–0.27)	0.40 (0.36–0.45)
ANT (ASI–V)**	0.32 (0.24–0.42)	0.16 (0.12–0.19)	0.33 (0.27–0.39)	0.36 (0.26–0.48)	0.81 (0.65–1.02)	0.33 (0.26–0.45)	0.42 (0.28–0.54)
ASI	0.04 (0.03–0.05)	0.02 (0.02–0.03)	0.04 (0.03–0.04)	0.04 (0.03–0.05)	0.06 (0.05–0.07)	0.04 (0.03–0.05)	0.06 (0.04–0.07)
ASII	0.07 (0.05–0.09)	0.03 (0.03–0.04)	0.07 (0.05–0.07)	0.07 (0.05–0.09)	0.11 (0.09–0.14)	0.06 (0.05–0.08)	0.07 (0.05–0.09)
ASIII	0.06 (0.04–0.08)	0.04 (0.03–0.06)	0.08 (0.06–0.09)	0.08 (0.05–0.12)	0.22 (0.17–0.24)	0.07 (0.04–0.11)	0.10 (0.05–0.15)
ASIII + IV fused[††]					0.43 (0.33–0.55)		
ASIV	0.04 (0.02–0.06)	0.05 (0.04–0.08)	0.04 (0.03–0.05)	0.05 (0.03–0.07)	0.20 (0.15–0.28)	0.05 (0.03–0.08)	0.06 (0.03–0.09)
ASV	0.12 (0.09–0.14)		0.13 (0.10–0.15)	0.13 (0.10–0.15)	0.21 (0.17–0.26)	0.11 (0.09–0.14)	0.14 (0.10–0.17)
B	0.09 (0.07–0.12)	0.05 (0.04–0.06)	0.10 (0.08–0.11)	0.10 (0.08–0.12)	0.17 (0.12–0.28)	0.09 (0.07–0.12)	0.11 (0.08–0.13)
PT	0.02 (0.02–0.03)	0.01 (0.01–0.02)	0.03 (0.02–0.03)	0.03 (0.02–0.03)	0.04 (0.03–0.05)	0.03 (0.02–0.04)	0.03 (0.02–0.04)
URS	0.11 (0.09–0.14)	0.08 (0.07–0.09)	0.10 (0.09–0.11)	0.10 (0.08–0.12)	0.19 (0.16–0.22)	0.10 (0.09–0.12)	0.10 (0.09– 0.11)
URS (basal width)	0.05 (0.04–0.06)	0.04 (0.03–0.04)	0.04 (0.03–0.05)	0.04 (0.04–0.05)	0.06 (0.05–0.08)	0.03 (0.02–0.04)	0.05 (0.04–0.06)
URS accessory setae (no.)	0.00 –	0.00 –	0.00 –	0.00 –	16.6 (12.0–20.0)	1.72 (0.00–2.00)	0.00 –
Thorax							
Metafemur–trochanter	0.37 (0.28–0.46)	0.15 (0.12–0.19)	0.29 (0.23–0.36)	0.32 (0.22–0.42)	0.46 (0.38–0.55)	0.30 (0.22–0.40)	0.45 (0.30–0.59)
Metafemur (width)[‡‡]	0.10 (0.09–0.12)	0.04 (0.04–0.05)	0.07 (0.06–0.09)	0.08 (0.06–0.10)	0.10 (0.08–0.12)	0.06 (0.04–0.07)	0.09 (0.06–0.11)
Metatibia	0.33 (0.25–0.44)	0.14 (0.11–0.20)	0.32 (0.25–0.40)	0.36 (0.24–0.50)	0.66 (0.55–0.82)	0.27 (0.21–0.39)	0.47 (0.29–0.63)
Htbs[§§]	0.14 (0.13–0.15)	0.07 (0.04–0.09)	0.13 (0.10–0.15)	0.12 (0.09–0.13)	0.27 (0.22–0.32)	0.13 (0.11–0.17)	0.11 (0.11–0.11)
Metatarsus	0.11 (0.09–0.13)	0.05 (0.04–0.07)	0.10 (0.09–0.12)	0.12 (0.08–0.15)	0.20 (0.18–0.22)	0.09 (0.07–0.12)	0.13 (0.09–0.17)
Metatarsus (width at midpoint)	0.03 (0.03–0.03)	0.02 (0.02–0.03)	0.03 (0.02–0.03)	0.03 (0.02–0.03)	0.04 (0.04–0.04)	0.03 (0.02–0.03)	0.03 (0.02–0.03)
Htars[§§]	0.07 (0.06–0.07)	0.07 (0.04–0.10)	0.07 (0.06–0.08)	0.09 (0.07–0.11)	0.12 (0.18–0.31)	0.13 (0.11–0.16)	0.08 (0.08–0.08)

Table 4. *Continued*

Features	*Clydesmithia canadensis* $n = 5$ Mean (range)	*Melaphis rhois* $n = 9$ Mean (range)	*Pachypappa rosettei* $n = 10$ Mean (range)	*Pachypappa sacculi* $n = 11$ Mean (range)	*Prociphilus americanus* $n = 9$ Mean (range)	*Prociphilus xylostei* $n = 32$ Mean (range)	*Thecabius populimonilis** $n = 5$ Mean (range)
Abdomen							
Cauda setae (no.)	2.00 (2.00–2.00)	2.00 (2.00–2.00)	2.00 (2.00–2.00)	2.44 (2.00–4.00)	21.4 (15.0–32.0)	2.03 (2.00–3.00)	2.00 (2.00–2.00)
Comparisons							
ANT/body	0.24 (0.21–0.26)	0.16 (0.12–0.20)	0.30 (0.28–0.34)	0.29 (0.27–0.31)	0.44 (0.36–0.56)	0.34 (0.29–0.43)	0.22 (0.18–0.23)
PT/B	0.26 (0.22–0.29)	0.28 (0.21–0.39)	0.27 (0.22–0.31)	0.25 (0.22–0.29)	0.23 (0.15–0.38)	0.29 (0.20–0.40)	0.28 (0.24–0.29)
PT/ASIII	0.43 (0.35–0.56)	0.29 (0.21–0.42)	0.37 (0.27–0.43)	0.32 (0.27–0.38)	0.13 (0.06–0.16)	0.38 (0.26–0.57)	0.34 (0.24–0.48)
URS (L/W)	2.34 (2.00–2.64)	2.15 (2.02–2.36)	2.48 (2.21–2.86)	2.50 (2.24–2.92)	3.05 (2.57–3.48)	3.25 (2.80–4.38)	1.87 (1.71–2.05)
URS/metatarsus	1.07 (0.95–1.16)	1.55 (1.28–1.75)	0.94 (0.88–1.01)	0.88 (0.77–1.01)	0.98 (0.85–1.09)	1.11 (0.93–1.31)	0.72 (0.63–0.82)
Metafemur–trochanter (L/W)	3.57 (3.00–4.02)	3.40 (2.89–3.91)	4.07 (3.68–4.97)	4.07 (3.78–4.56)	4.79 (4.13–5.48)	5.32 (4.15–6.30)	5.20 (4.56–5.84)
Metatarsus (L/W)‖‖	3.32 (2.75–3.86)	2.57 (2.15–3.07)	3.96 (3.42–4.38)	4.31 (3.38–5.22)	5.00 (4.04–5.52)	3.67 (2.99–4.47)	4.68 (4.00–5.38)
Htbs//Htars	3.11 (2.84–3.23)	0.93 (0.78–1.33)	1.99 (1.60–2.31)	1.34 (1.21–1.57)	3.35 (2.93–3.94)	0.94 (0.84–1.10)	3.88 (2.81–6.89)
Tarsus I chaetotaxy	2-2-2	2-2-2	3-2-2	3-2-2	3-2-2	2-2-2	3-2-2
URS with preapical light zone	Yes	No	Yes	Yes	No	No	Yes

*Measurments and comparisons based on morphs with five-segmented antennae.
†Known on *Rhus* in eastern North America and Arizona, but strictly anholocyclic on moss in Europe and the Pacific Northwest.
‡*Abies grandis* (Douglas ex D. Don) Lindl. – grand fir and *Picea engelmannii* Parry ex Engelm. – Engelmann spruce.
§*Picea engelmannii* Parry ex Engelm. – Engelmann spruce.
‖*A. grandis* (Douglas ex D. Don) Lindl. – grand fir.
¶Segment lengths measured, unless otherwise indicated.
**M. rhois* ASI–IV.
††*P. americanus* ASIII–IV often fused.
‡‡Measured at widest point.
§§Measurements are length in mm × 10.
‖‖*Melaphis* measurements based on single tarsomere present; other genera based on tarsomere II.
ANT, antenna; AS, antennal segment; B, base ultimate antennal segment; PT, processus terminalis; URS, ultimate rostral segment; Htbs, metatibial apical seta; Htars, metatarsus I seta; L/W, length/width.

Municipality of Anchorage, nr Portage Glacier, 8-viii-2007, ex *Rhizomnium magnifolium* (Horik.) T. Kop. (Mniaceae) and *Sanionia uncinata* (Hedw.) Loeske (Amblystegiaceae) (4im, barcode verified – A7K258); **Montana:** Mineral Co., I-90 Saltese exit, 12-viii-2009, ex moss (no mounts, barcode verified – A9G380); **Washington:** Kittitas Co., Manastash Cr Rd, 9-viii-2005, ex moss (1ap – A5G139) and 19-vii-2007, ex *Philonotis fontana* (Hedw.) Brid. (Bartramiaceae) (2im, barcode verified – A7G057) and 11-ix-2008, ex moss mix *P. fontana* and *Brachythecium* sp. (Brachytheciaceae) (2im, barcode verified – A8G283); Klickitat Co., Trout Lake-Glenwood Rd, 11-viii-2008, ex mixed moss *Plagiomnium insigne* (Mitt.) T. Kop. (Mniaceae) and *Brachythecium* sp. (2im, barcode verified – A8G191); Skamania Co., nr Trout Lake, FR30 past berry field E of FR24 jct, 25-vi-2009, ex moss (no mounts, barcode verified – A9G157); Yakima Co., South Fork Athanum, FR A1000, 28-vii-2009, ex moss (2ap – A9G302).

ex roots of fir, *Abies* and spruce, *Picea* (new host records)

Aptera viviparae and immatures: **UNITED STATES OF AMERICA. Montana:** Mineral Co., I-90 Saltese exit, 12-viii-2009, ex *Picea engelmannii* Parry ex Engelm (1ap, 1im – A9G381); **Washington:** Kittitas Co., Teanaway River Rd, 14-vii-2009, ex roots of *Abies grandis* (Douglas ex D. Don) Lindl. (1im, barcode verified – A9G200).

Diagnosis

Clydesmithia canadensis apterae from moss and/or conifer roots are distinguished from other moss or root feeding eriosomatines by a combination of features, namely anal plate not protruding (*P. americanus* with conspicuously protruding anal plate); URS with preapical light zone (*M. rhois* and *Prociphilus* spp. without a preapical light zone); tarsus I chaetotaxy 2-2-2 (*Pachypappa* spp., *P. americanus*, and *T. populimonilis* 3-2-2); ANT with five antennal segments (*M. rhois* with four antennal segments; *P. americanus* with four to five antennal segments; *T. populimonilis* with five to six antennal segments).

Description

Aptera vivipara (Figs. 1–5): Body oval, pale. Anterior upper portion of the head, antennae, coxae, femora, tibia, tarsi, rostrum, cauda, genital, and anal plates light brown to brown. Setae sparse, very short, and inconspicuous on body and antennae. Dorsum smooth, with indistinctly visible dorsal wax glands (see Figs. 1 and 5, for relative size, form, number, and distribution). Body length 1.03–1.63 mm; head width across eye 0.27–0.37 mm; ANT with five antennal segments, short 0.21–0.26× body, and without 2° RHIN; ASV longer than other individual segments; PT short, 0.22–0.29× B; rostrum extending to metacoxae; URS length 2.00–2.64× width, with a subapical pale zone (Fig. 2), and without accessory setae; tibial setae at apices stout, length >2× tarsus I setae (Fig. 4); tarsus I chaetotaxy 2-2-2; caudal setae 2. For a full range of morphological measurements and comparisons, see Table 4.

Natural history and distribution

The aphid is recognised from Alaska, Idaho, Montana, Washington, and Canada (Alberta, British Columbia, Manitoba, and Saskatchewan) on black cottonwood (*Populus balsamifera trichocarpa* (Torr. & A. Gray) Brayshaw (Salicaceae), primary host with sexual phase; Danielsson 1990a) where it produces linear galls on leaves. Its secondary host habitats include moss and/or roots of fir (*A. grandis* (Douglas ex D. Don) Lindl.; Pinaceae) or spruce (*P. engelmannii* Parry ex Engelm.; Pinaceae), and black cottonwood (Aoki *et al*. 1997). Sexuparae (winged migrants) are thought to return to *Populus* in late summer-early fall, with some anholocyclic populations possibly remaining on roots or in the moss–root substrata through the winter.

Melaphis rhois (Fitch, 1866)

(Figs. 6–10; Table 4)

Specimens examined

ex moss (new host species associations)

Aptera viviparae and immatures: **UNITED STATES OF AMERICA. Washington (new distribution records):** Clallam Co., Olympic NP, Ozette Lk, Swan Bay, 19-ix-2002 (3im – A2K236); Jefferson Co., Olympic NP, Hoh Rain Forest, 11-viii-2002, (1ap, 1im – A2K113); nr Kalaloch, Beach 3, 13-xii-2005, (1im, barcode verified – A5K256); and nr Quinault River, N Shore Rd, 15-xii-2005 (1ap, 6im – A5K318), 5-vi-2008, ex *Rhytidiadelphus loreus* (Hedw.) Warnst. (Hylocomiaceae)

(1im – A8K103) and a mix of *Leucolepis acanthoneuron* (Schwägr.) Lindb. (Mniaceae), *Claopodium crispifolium* (Hook.) Renauld & Cardot (Thuidiaceae) and *Kindbergia praelonga* (Hedw.) Ochyra (Brachytheciaceae) (1ap – A8K106); Pacific Co., nr Loomis SP, ex *Dicranum scoparium* Hedw. (Dicranaceae), 9-iv-2009, coll. K. and L. Pike (2ap – A9K080); nr Pacific Pines SP, 9-iv-2009, ex *D. scoparium*, coll. K. and L. Pike (21ap – A9K077, part deposited in CNC, UAF, USU, and WSU); Skagit Co., 3.6 mi from Hwy 20 on Baker Lk Rd, 24-ii-2005 (1ap, 20im – A5K009-10).

Diagnosis

Apterae are most easily distinguished from other moss-frequenting eriosomatines by differences in the number of tarsomeres (*M. rhois* one tarsomere versus two tarsomeres [*C. canadensis* tarsomeres often semi-fused]), antennal segments (*M. rhois* four antennal segments versus five to six antennal segments [*P. americanus* sometimes with four antennal segments, but then tarsi always with two tarsomeres]), and differences in the number, style, and arrangement of dorsal wax gland plates.

Description

Aptera vivipara (Figs. 6–10): Body oval, pale. Anterior upper portion of head, antennae, coxae, femora, tibia, tarsi, and rostrum light brown. Cauda, genital, and anal plates pale to slightly brown. Setae sparse, short, and inconspicuous on body and antennae. Dorsum smooth, with indistinctly visible multifaceted wax gland plates (see Figs. 6 and 10, for relative size, form, number, and arrangement). Body length 0.79–1.20 mm; head width across eye 0.21–0.29 mm; ANT with four antennal segments (rarely with five antennal segments), short 0.12–0.20× body, and without 2° RHIN; ASIV longer than other individual segments; PT short, about 0.28× B (range 0.21–0.39× B); rostrum extending to near metacoxae; URS length 2.02–2.36× width; legs short, tarsi with one tarsomere; caudal setae 2. For a full range of morphological measurements and comparisons, see Table 4.

Natural history and distribution

This aphid species is known from the central and eastern United States (Smith and Parron 1978), eastern Canada (Smith and Parron 1978; Hebert *et al*. 1991), and Arizona (Moran 1989), alternating between sumac, *Rhus* Linnaeus spp. (Anacardiaceae) (primary host with sexual phase) and moss, and from northwestern United States (Washington) as anholocyclic monoecious populations on moss. Outside of North America, *M. rhois* is known from Europe, but without heteroecy, feeding only on moss (Heie 1980). Its discovery in Washington State is new, collected from mosses in rainforests near Mt. Baker, the Olympic National Park, and from sandy coastal sites on Washington's Long Beach Peninsula.

Pachypappa rosettei (Maxson, 1934)

(Fig. 16; Table 4)

Specimens examined

ex moss (new habitat association) (moss sometimes with fine conifer roots intertwined)

Aptera viviparae and immatures: **UNITED STATES OF AMERICA. Alaska (new distribution records)** (mosses sampled mainly from spruce forest habitat (*Picea glauca* (Moench) Voss and *Picea mariana* (Mill.) Britton, Sterns & Poggenb.): Denali Boro., nr Cantwell, 4-viii-2007, ex *Pleurozium schreiberi* (Brid.) Mitt. (Hylocomiaceae) (2ap – A7K213); Fairbanks North Star Boro., Fairbanks, Spinach Cr Rd, 10-viii-2007 (4ap – A7K101, 104, 105, 107, 108), and ex mixed *Polytrichum* (Polytrichaeae) and *Sphagnum* (Sphagnaceae) (5ap, 1im – A7K150, 151, 152, 153, 154, 155); Juneau Boro., Juneau, Dredge Lake Rd, Pond Area A, 22-viii-2007 (no mounts, barcode verified – A7A211); Yukon-Kuyokuk Boro., Greyling Lake, 16-viii-2007, ex mixed *Polytrichum commune* Hedw. and *Sphagnum russowii* Warnst. (12ap – A7A170, part in CNC, UAF, and USU) and ex *Pleurozium schreberi* (no mounts, barcode verified – A7A171). **Washington** (mosses sampled mainly in spruce forest habitat (*Picea* spp.): Clallam Co., Olympic NP, Sol Duc River, ~2 mi SE of Sol Duc Hot Springs, 3-viii-2005 (3ap – A5K123); Kittitas Co., Manastash Rd and Lost Lk Trailhead, 11-ix-2008, ex *S. uncinata* (2im – A8G295); Pacific Co., nr Ilwaco, 8-iv-2009, ex *C. crispifolium* (2im, barcode verified – A9K029); Yakima Co., Bethel Ridge, FR1500, 1 mi N of Cash Prairie Jct, 6-viii-2008, ex *Aulacomnium palustre* (Hedw.) Schwägr.

(Aulacomniaceae) (no mounts, barcode verified – A8G181); FR 82 bridge across Bird Cr, 16-viii-2007, ex *Hygrohypnum ochraceum* (Turner ex Wilson) Loeske (Amblystegiaceae) (no mounts, barcode verified – A7G197); 5 mi N of Clear Lk, 27-vi-2007 (2ap – A7K108).

ex conifer roots, *Picea engelmannii* and *Abies*.

Aptera vivipara: **UNITED STATES OF AMERICA. Washington:** Skamania Co., nr Trout Lake, FR6621, between Goose Lk and South Prairie, 25-vi-2009, ex *P. engelmannii* (3ap – A9G138) and *Pseudotsuga menziesii* (Mirb.) Franco (Pinaceae) (probably errant on host, no mounts, barcode verified – A9G139); Yakima Co., Bethel Ridge, FR1500, 0.5 mi from Cash Prairie Jct, 8-vii-2009, ex *P. engelmannii* (3ap – A9G188); nr Clear Lk, N Fork Tieton Rd, 22-vi-2009, ex *P. engelmannii* (3ap – A9G076); Morse Cr, 10-ix-2010, ex *Abies* sp. (no mounts, barcode verified, 2im – 10K152).

Diagnosis

Pachypappa rosettei is nearly identical morphologically to *P. sacculi* but can be distinguished by a difference in length comparison of specific setae, that is, metatibia apical seta/metatarsus I seta (*P. rosettei* = 1.99 [range 1.60–2.31]; *P. sacculi* = 1.34 [range 1.21–1.57]). See key below to separate *P. rosettei* from other eriosomatines in moss or on conifer or willow roots.

Description

Aptera vivipara: Body oval, pale. Anterior upper portion of the head, antennae, coxae, femora, tibia, tarsi, and rostrum brown. Cauda, genital, and anal plates light brown. Setae sparse, very short, and inconspicuous on body and antennae. Dorsum smooth, with indistinctly visible dorsal wax glands (see Fig. 11, for relative size, form, number, and distribution). Body length 0.84–1.41 mm; head width across eye 0.23–0.33 mm; ANT with five antennal segments, short 0.28–0.34× body, and without 2° RHIN; ASV longer than other individual segments; PT short, 0.22–0.31× B; rostrum extending to metacoxae; URS length 2.21–2.86× width, with a subapical pale zone and without accessory setae; tibial setae at apices stout, length 1.60–2.31× tarsus I setae (Fig. 16); tarsus I chaetotaxy 3-2-2; caudal setae 2–4. For a full range of morphological measurements and comparisons, see Table 4.

Natural history and distribution

The aphid is recognised from Canada and the western United States on aspen (*Populus tremuloides* Michx. (Salicaceae) primary host with sexual phase) (Danielsson 1990b; Blackman and Eastop 1994), host alternating to roots of *Picea* spp., with the roots commonly entwined in moss on the forest floor. The habitat is typically moist or semi-moist and shaded. Based on Berlese extractions, *P. rosettei* uses roots of *P. engelmannii*, *P. mariana* (Mill.) Britton, Sterns & Poggenb., *Picea sitchensis* (Bong.) Carrière in the Alaska–Washington region, and probably other *Picea* spp. when present, *Abies*, and possibly *P. menziesii* (Danielsson 1990b). Sexuparae (winged migrants) return to aspen in mid-August to October, but also anholocyclic populations remain on roots of *Picea* (or *Picea* and moss) through the winter as manifested by *P. rosettei* presence on roots in the spring (aphid found in moss in April, see A9K029).

Pachypappa sacculi (Gillette, 1914)

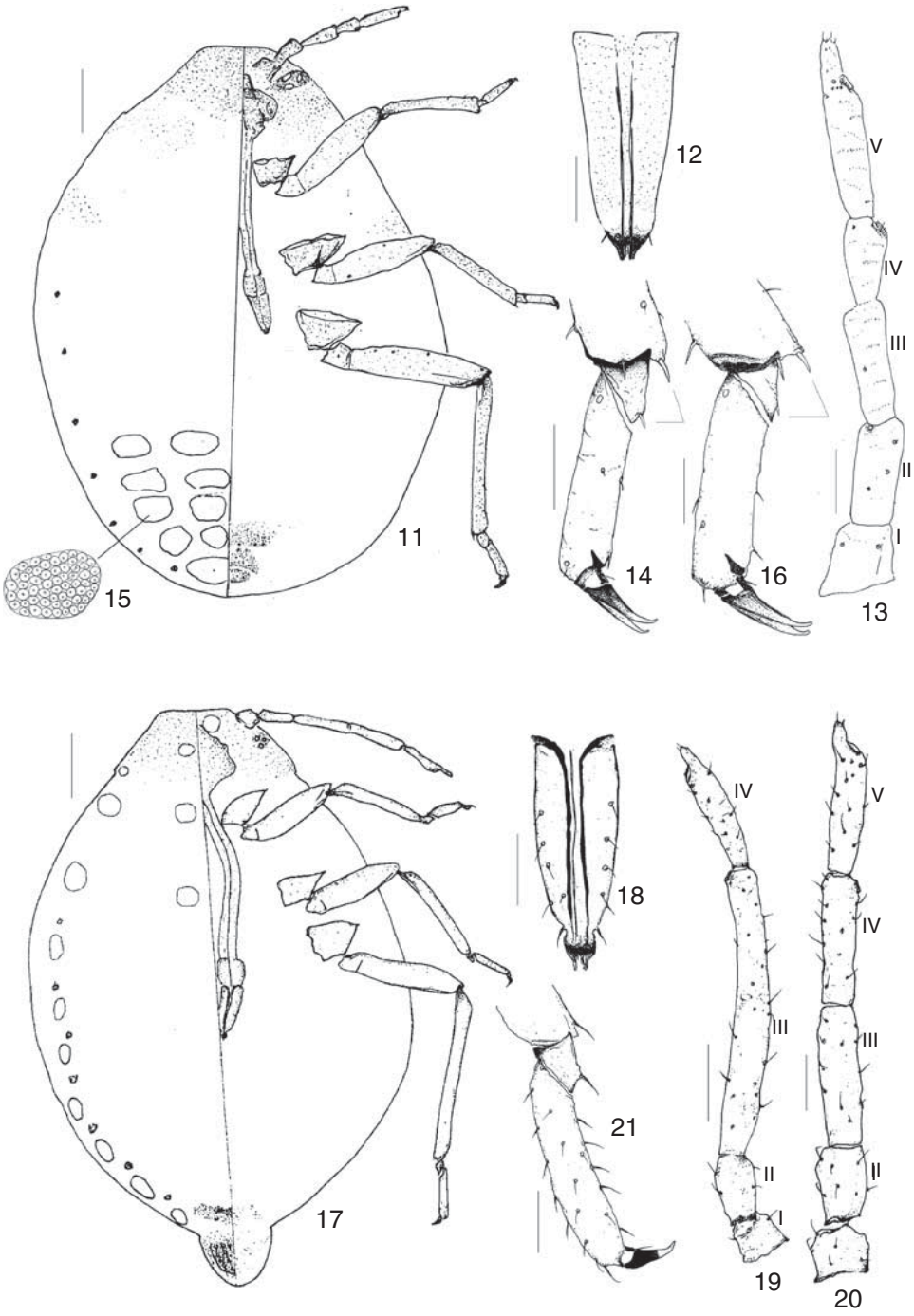
(Figs. 11–15; Table 4)

Specimens examined

ex moss (new habitat association) (moss sometimes with fine conifer roots intertwined)

Aptera viviparae and immatures: **UNITED STATES OF AMERICA. Alaska** (mosses sampled mainly from spruce forest habitat [*P. glauca* and *P. mariana*]): Fairbanks North Star Boro., Calypso Farm, 30-vii-2007, ex *Sphagnum capillifolium* (Ehrh.) Hedw. (Sphagnaceae) (1im – A7K139), Chena Hot Springs Rd, 1-viii-2007, ex *P. schreberi* (1im, barcode verified – A7K168, A7K174), *Hylocomium splendens* (Hedw.) Schimp. (Hylocomiaceae) (4ap – A7A170, part in UAF), 1-vi-2009, coll. R. Pampell (no mounts, barcode verified – A9A002), 30-vi-2009, coll. R. Ranft (no mounts, barcode verified – A9A011), 27-vii-2009, coll. R. Pampell (no mounts, barcode verified – A9A032) and ex *P. commune*, coll. D. Fleming (no mounts, barcode verified – A9A038); Fairbanks, 31-viii-2007, ex *Polytrichum juniperinum* Hedw. (1ap – A7K162) and *A. palustre* (3ap – A7K165); Spinach Cr Rd, 10-viii-2007 (2ap – A7A103, A7A152-2), and ex *Polytrichum* sp. and *Sphagnum* sp. (1ap – A7A153), Rosie Cr Farm; 18-vi-2007, ex mixed *Dicranum fuscuscens* Turner (Dicranaceae), *P. schreberi*, *Ptilidium pulcherrimum* (Weber)

Figs. 11–21. Eriosomatinae (aptera vivipara) of moss and/or roots of fir or spruce. 11–15, *Pachypappa sacculi*: **11**, adult; **12**, ultimate rostral segment; **13**, antennal segments I–V; **14**, metatarsus and apex of tibia (lines point to size differences in setae on tarsus I and apex of tibia); **15**, wax gland plate. **16**, *Pachypappa rosettei*, metatarsus. 17–21, *Prociphilus americanus*: **17**, adult; **18**, ultimate rostral segment; **19–20**, antennal segments showing variation in number; **21** metatarsus. Scale bars: 0.20 mm for Figures 11, 17; 0.10 mm for Figures 19, 20; 0.05 mm for Figures 12, 13, 18, 21; 0.03 mm for Figures 14, 16.



Vain. (liverwort) (Ptilidiaceae), and *S. uncinata* (1ap – A7A134); Juneau Boro, Dredge Lk Rd, 22-viii-2007 (1ap, 1im – A7A126-127); North Slope Boro., N of pass, 15-viii-2007, ex *Tomentypnum nitens* (Hedw.) Loeske (Brachytheciaceae) (no mounts, barcode verified – A7A118); Yukon-Kuyokuk Boro., Dalton Hwy, 16-viii-2007, ex *H. splendens* (no mounts, barcode verified – A7A176) and *P. commune* (1ap – A7A177); Elliott Hwy, nr mi marker 71, 22-vi-2009, coll. R. Ranft (2ap – A9A030); Greyling Lake nr Dalton Hwy, 16-viii-2007, ex *D. fuscuscens* (no mounts, barcode verified – A7A174), and *Sphagnum rubellum* Wilson and *P. schreberi* (2ap – A7A172); Rd to Nolan, 14-viii-2007, ex *T. nitens* (2im, barcode verified – A7A111); **Washington** (mosses sampled mainly from spruce forest habitat [*P. engelmannii* or *P. sitchensis* (Bong.) Carrière]): Jefferson Co., Olympic NP, Queets River Rd, ~8 mi NE of Hwy 101, 14-xii-2005 (1ap, 1im – A5K268), 22-vi-2006 (1ap – A6K158), and ~5 mi NE of Lk Quinault on North Shore Rd, 21-iii-2006, ex *Polytrichum* (1ap – A6K026); Kittitas Co., FR112 1 mi from Manastash Rd, 10-ix-2002 (8ap, 1im – A2G313, part in CNC, UAF, USU), Lost Lk Trailhead, 10-ix-2002 (1ap, 1im – A2G310), ex *Polytrichum* (3ap, 2im – A2G311), and ex moss sampled from under *A. grandis* (2ap – A9K114), Tamarack Springs Rd, 11-ix-2008 (no mounts, barcode verified – A8G307); Lewis Co., 1 mi W of White Pass, 13-ix-2010, ex moss (no mounts, barcode verified – 10K106); Pacific Co., nr Loomis SP ex *D. scoparium*, coll. K. and L. Pike (2ap – A9K080); Skamania Co., nr Big Mosquito Lk, FR 24, 2.5 mi S of FR 8851, ex *Polytrichum*, 30-viii-2005 (3ap – A5G164) and 12-ix-2005 (2ap – A5G215), South Prairie, 1-ix-2010, ex moss (no mounts, barcode verified – 10K064); Yakima Co., Morse Cr Rd, 4-ix-2007, ex *Brachythecium starkei* (Brid.) Schimp. (1ap – A7G251); N Fork Tieton River, FR 1207, 22-vii-2008, ex *R. magnifolium* (1ap – A8G083).

ex *Picea* roots only (no moss)

Aptera viviparae: **UNITED STATES OF AMERICA. Washington:** Kittitas Co., Manastash Rd and Lost Lk Trailhead, 3-vi-2009, ex *P. engelmannii* (3ap – A9K109) and 16-vi-2009, coll. G. & D. Graf (no mounts, barcode verified – A9G045).

Diagnosis

Secondary host forms of *P. sacculi* are nearly identical morphologically to *P. rosettei*; to distinguish the species, see diagnosis statements for *P. rosettei*. Also see key below to separate it from other eriosomatines in moss or on conifer or willow roots.

Description

Aptera vivipara (Figs. 11–15): Body oval, pale. Anterior upper portion of the head, antennae, coxae, femora, tibia, tarsi, and rostrum light brown. Cauda, genital, and anal plates pale to light brown. Setae sparse, very short, and inconspicuous on body and antennae. Dorsum smooth, with indistinctly visible dorsal wax glands (see Figs. 11 and 15, for relative size, form, number, and arrangement). Body length 0.94–1.76 mm; head width across eye 0.22–0.38 mm; ANT with five antennal segments, short 0.27–0.31× body, and without 2° RHIN; PT short, 0.22–0.29× B; rostrum extending almost to metacoxae; URS length 2.24–2.92× width, with a subapical pale zone (Fig. 12), and without accessory setae; tibial setae at apices stout, length 1.21–1.57× tarsus I setae (Fig. 14); tarsus I chaetotaxy 3-2-2; caudal setae 2. For a full range of morphological measurements and comparisons, see Table 4.

Natural history and distribution

The aphid is recognised from across Canada and areas of the western United States and Alaska on aspen (*P. tremuloides*, primary host with sexual phase) (Danielsson 1990b; Blackman and Eastop 1994), host alternating to roots of *Picea* spp. (occasionally found on *A. grandis*), with the roots often intermingled in mosses on the forest floor. Based on Berlese extractions, *P. sacculi* uses roots of *P. engelmannii*, *P. mariana*, and *P. sitchensis* in the Alaska–Washington region, and other *Picea* spp. (Danielsson 1990b). Sexuparae return to aspen in mid-August to October, but also anholocyclic populations continue on roots of *Picea* (or *Picea* and moss) through the winter (aphid found in moss in March, see A6K026).

Prociphilus americanus (Walker, 1852)

(Figs. 17–21; Table 4)

Specimens examined

ex roots of fir, *Abies grandis*

Aptera viviparae or immatures (all collections by G. and D. Graf): **UNITED STATES OF**

AMERICA. Idaho: Kootenai Co., Beauty Creek, 12-viii-2009 (11ap – A9G390); **Montana:** Mineral Co., I-90 Lookout Pass, 12-viii-2009; **Washington:** Kittitas Co., Teanaway, FR9738, 14-vii-2009 (3ap – A9G217); Klickitat Co., Trout Lake-Glenwood Rd, 24-vi-2009 (12ap – A9G082, A9G090) and 25-vi-2009 (2ap – A9G169); Skamania Co., nr Trout Lake, FR66 & 6610 Jct South Prairie, 25-vi-2009 (1ap – A9G082), FR88 nr Trout Lake, 25-vi-2009 (1ap, 1im – A9G168); Yakima Co., North Fork of Tieton Rd, 22-vi-2009, (3ap, 1im – A9G067, A9G068); S. Fork Athanum, FR A1000 mi marker 7 and FR A2400 north side of Red Saddle, 28-vii-2009 (5ap – A9G309, A9G318).

Diagnosis

Prociphilus americanus is found on roots of fir, not on roots of spruce or willow, and not in moss. It is morphologically distinct from other moss–root eriosomatines found in the study area by a conspicuously protruding anal plate (versus no protruding anal plate), long rostrum, often extending well beyond metacoxae (versus not or only marginally extending beyond metacoxae), URS with preapical constriction (versus without preapical constriction), URS with >10 accessory setae (versus four or fewer), and cauda with ≥ 15 setae (versus four or fewer).

Description

Aptera vivipara (Figs. 17–21): Body oval, pale. Anterior upper portion of the head, antennae, coxae, femora, tibia, tarsi, and rostrum light brown to brown. Cauda and anal plate brown. Setae easily visible on body and appendages. Dorsum smooth. Abdomen with marginal wax glands; head and thorax with rounded wax glands (see Fig. 17, for relative size, form, number, and arrangement). Body length 1.39–2.34 mm; head width across eye 0.40–0.59 mm; ANT with four to five antennal segments, short 0.36–0.56× body, and without 2° RHIN; PT short, 0.15–0.38× B; rostrum long, distinctly extending beyond metacoxae; URS length 2.57–3.48× width, without a pale subapical zone (Fig. 18) and with 12–20 accessory setae; tibia setae at apices and tarsus I setae equal in size; tarsus I chaetotaxy 3-2-2; caudal setae 15–32. For a full range of morphological measurements and comparisons, see Table 4.

Natural history and distribution

This aphid species is widely distributed in North America (Smith 1969; Smith and Parron 1978), including Alaska, on roots of *Abies* (Blackman and Eastop 1994, 2006) host alternating to ash, *Fraxinus* Linnaeus (Oleaceae) (primary host with sexual phase; also reported on *Forsythia* Vahl (Oleaceae) and *Syringa* Linnaeus (Oleaceae)) (Blackman and Eastop 2006). Some anholocyclic populations continue on roots of *Abies* year around (Zak 1965; Smith 1969; DeFrancesco and Murray 2009).

Prociphilus (*Stagona*) *xylostei* (De Geer, 1773)

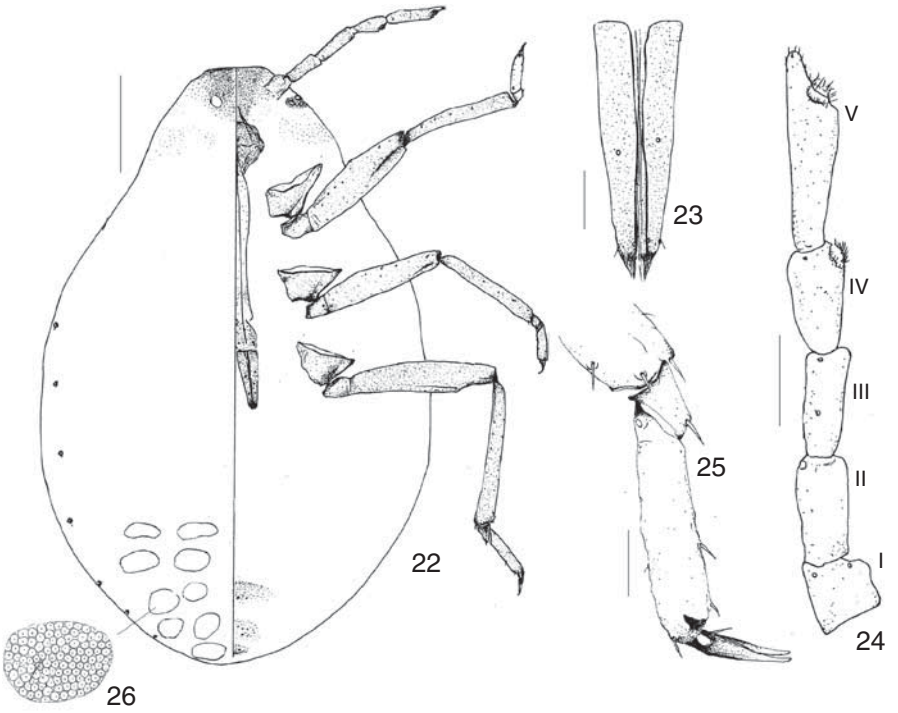
(Figs. 22–26; Table 4)

Specimens examined

ex moss (new habitat association) (moss sometimes with fine roots of conifer intertwined)

Aptera viviparae and immatures: **UNITED STATES OF AMERICA. Alaska (new distribution record):** Juneau Boro., nr Juneau, Montana Cr Trail, Area C, 28-viii-07, coll. E. Kunibe (no mounts, barcode verified – A7A129); Kodiak Island, 9-viii-09, coll. S. Lillard, (no mounts, barcode verified – A9A105); **Washington:** Grays Harbor Co. Olympic NP, Lk Quinault, North Shore Rd, 15-xii-2005 (4ap, 2im – A5K311-12), and ex *H. splendens* (5ap – A5K313, A5K320); Clallam Co., Olympic NP, Ozette, Sand Point Trail, 4-vi-2008, ex *Polytrichum lyallii* (Mitt.) Kindb. (1ap – A8K064); Jefferson Co., Olympic NP, nr Kalaloch, Beach 5, 12-viii-2004 (4ap, 1im – A4K084) and Big Cedar tree, 13-xii-2005 (2ap – A5K261); Lk Quinault, nr park entrance on South Shore Rd, 21-iii-2006 (1ap – A6K007); nr Ruby Beach, 15-ix-2006 (2ap – A6K251); Kittitas Co., Lost Lk Trailhead, 27-viii-2002 (1ap, 1im – A2G288), 10-ix-2002 (4ap – A2G310) and ex *Polytrichum* sp. (3ap – A2G311), 11-ix-2008, ex *S. uncinata* (2ap – A8G295), and 3-vi-2009, coll. G. & D. Graf, (1ap – A9K114); Manastash Rd & FR 112, 27-viii-2005, ex *Plagiomnium* sp. (1im – A2G296); FR 112, 1 mi from Manastash Rd, 10-ix-2002, (1ap – A2G313); Pacific Co., nr Black Lk, 8-iv-2009, coll. K. and L. Pike, ex *D. scoparium*, (4ap – A9K008, A9K019), ex *Isothecium stoloniferum* Brid. (Brachytheciaceae) (2ap – A9K009), ex *Kindbergia oregana* (6ap – A9K011, A9K017),

Figs. 22–32. Eriosomatinae (aptera vivipara) of moss and/or roots of fir, spruce or willow. 22–26, *Prociphilus xylostei*: **22**, adult; **23**, ultimate rostral segment; **24**, antennal segments I–V; **25**, metatarsus and apex of tibia; **26**, wax gland plate. 27–32, *Thecabius populimonilis*: **27**, adult; **28**, ultimate rostral segment; **29–30**, antennal segments showing variation in number; **31**, metatarsus and apex of tibia; **32**, wax gland plate. Scale bars: 0.20 mm for Figures 22, 27; 0.05 mm for Figures 24, 28, 29, 30, 31; 0.03 mm for Figures 23, 25.



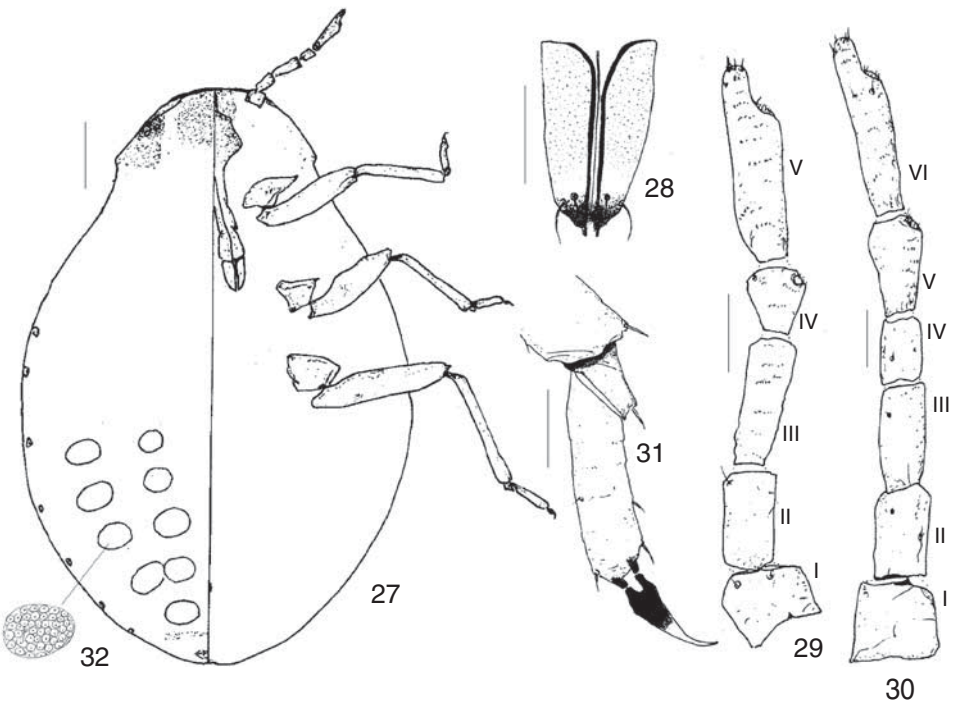
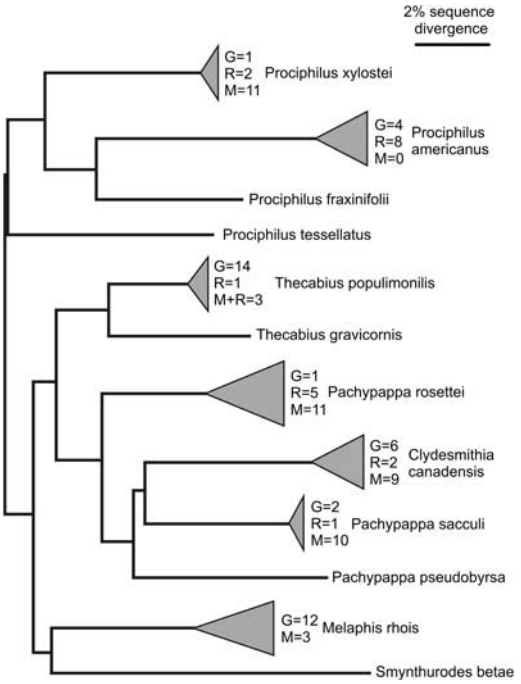


Fig. 33. Simplified neighbour-joining tree of cytochrome *c* oxidase subunit I sequence divergences among samples. Terminal clusters corresponding to species are represented by an enveloping triangle, with internal structure omitted. G = number of samples from galls or pseudogalls on primary host; R = number of samples from roots of secondary host; M = number of samples extracted from moss; M + R = number of samples from a mixture of moss and roots.



and ex *R. loreus* (1ap – A9K012); nr Loomis SP, 9-iv-2009, ex *K. oregana* (Sull.) Ochyra, coll. K. and L. Pike (1ap – A9K083); Skamania Co., FR 24, 2.5 mi S of FR 8851, nr Big Mosquito Lk, 12-ix-2005, ex *P. commune* (1ap – A5G215); FR 6030, 1 mi S of Forlorn Lk, 22-viii-2002 (3im – A2G280); Yakima Co., Bumping Lk Rd, 3 mi from Hwy 12, 10-x-2005, ex *Rhizomnium* sp. (2ap – A5K204) and *Brachythecium* sp., *K. oregana* and *Racomitrium* sp. (Grimmiaceae) (1ap, 1im – A5K211); Morse Cr, 1.5 mi from Hwy 410, 10-x-2005 (5ap – A5K218),ex *Rhizomnium* sp. (8ap, 2im – A5K220, part in CNC, UAF, USU), ex *Sphagnum* sp. (2ap, 1im – A5K216), and 10-vi-2009, coll. G. and D. Graf (2ap – A9G006); nr Morse Cr, Bear Gap Trailhead, 4-ix-2007, ex *Pohlia* sp. (Bryaceae) (2ap – A7G236).

ex roots of fir, *Abies grandis*

Aptera viviparae and immatures: **UNITED STATES OF AMERICA. Washington:** Kittitas Co., Manastash Rd and Lost Lk Trailhead, 3-vi-2009 (3ap – A9K108, part in CNC); Yakima Co., Morse Cr, 10-vi-2006, coll. D. & G. Graf (2ap, 2im – A9G011).

Diagnosis

Prociphilus xylostei has general features similar to *Pachypappa* spp. described above, but differs in URS pigmentation (*P. xylostei* without a preapical light zone versus *Pachypappa* spp. with a preapical light zone); URS accessory setae usually two versus none; dorsal wax glands on head present versus absent; and setae at apex of tibia and tarsus I equal in size versus unequal. See key below to distinguish it from other eriosomatines in moss or on conifer or willow roots.

Description

Aptera vivipara (Figs. 22–26): Body oval, pale. Anterior upper portion of the head, antennae, coxae, femora, tibia, tarsi, and rostrum light brown. Cauda, genital, and anal plates pale to light brown. Setae sparse, very short on body and antennae. Dorsum smooth, with indistinctly visible dorsal wax glands including a round pair on the head (see Figs. 22 and 26, for relative size, form, number, and arrangement). Body length 0.78–1.22 mm; head width across eye 0.19–0.27 mm; ANT with five antennal segments, short 0.29–0.43× body, and without 2° RHIN; PT short, 0.20–0.40× B; rostrum extending almost to metacoxae; URS length 2.80–4.38× width, without a pale subapical zone, and usually with two accessory setae; setae at apex of tibia and tarsus I equal in size; tarsus I chaetotaxy 2-2-2; caudal setae usually 2. For a full range of morphological measurements and comparisons, see Table 4.

Natural history and distribution

The aphid is widely distributed in Eurasia and in North America (New Brunswick, Maine, Alaska, Colorado, Utah, Oregon [Smith 1969], and Washington) on black twinberry (*Lonicera involucrata* (Richardson) Banks ex Spreng., Caprifoliaceae, primary host with sexual phase) (Smith 1969), host alternating to moss and/or roots of conifer (confirmed on *A. grandis* in Washington; reported on *Picea* in Europe [Blackman and Eastop 1994]). Sexuparae (winged migrants) return to

Lonicera Linnaeus in October–November (Blackman and Eastop 1994); in the Pacific Northwest and possibly throughout its geographical range, some anholocyclic populations continue on roots of conifer (or conifer and moss) through the winter (aphid found in moss in March, see A6K007).

Thecabius populimonilis (Riley, 1879)

(Figs. 27–32; Table 4)

Specimens examined

ex moss (new habitat association) (with *Salix* roots intertwined)

Aptera viviparae and immatures: **UNITED STATES OF AMERICA. Washington:** Kittitas Co., FR 3111 1 mi NE of Buck Meadows 11-ix-2008, ex *P. fontana* (9ap – A8G305, A8K224) and 16-vi-2009 (5ap, 2im – A9G036).

ex roots of willow, likely *Salix rotundifolia* Trautv. ssp. *dodgeana* (Rydb.) Argus

Aptera viviparae and immatures: **UNITED STATES OF AMERICA. Alaska (new distribution record):** Kenai Peninsula Boro., nr Nunatak, Harding Ice Field, 13-vii-2007, coll. M. Bowser (3ap, 1im – 10A001).

Diagnosis

Thecabius populimonilis is the only eriosomatine found in the moss–willow root habitat in the Pacific Northwest; it is not found on conifer roots. It differs in tarsus I chaetotaxy from *C. canadensis* and *M. rhois* (*T. populimonilis* 3-2-2 versus 2-2-2) and from other moss–root eriosomatines by its short URS (*T. populimonilis* URS length/width usually <2.0 [range 1.71–2.05] versus > 2.2 [range 2.21–4.38]).

Description

Aptera vivipara (Figs. 27–32): Body oval, pale. Anterior upper portion of the head, antennae, coxae, femora, tibia, tarsi, rostrum, cauda, genital, and anal plates light brown. Setae sparse, very short, and inconspicuous on body and antennae. Dorsum smooth, with indistinctly visible dorsal wax glands (see Figs. 27 and 32, for relative size, form, number, and distribution). Body length 1.49–2.43 mm; head width across eye 0.36–0.45 mm; ANT with five to six antennal segments, short 0.18–0.23× body, and without 2° RHIN; ultimate antennal segment longer than other individual antennal segments; PT short, 0.02–0.04; URS length 1.71–2.05× width, with a subapical pale zone, and without accessory setae; tibia setae at apices and tarsus I setae equivalent in length (Fig. 31); tarsus I chaetotaxy 3-2-2; caudal setae 2. For a full range of morphological measurements and comparisons, see Table 4.

Natural history and distribution

This aphid species is widely distributed in North America (Smith 1969; Blackman and Eastop 1994) on poplar (galls produced on *Populus* spp., primary host with sexual phase), with at least some members host alternating to roots of willow, *Salix* (observed in California (Lange 1943) and Washington), and others apparently recolonising poplar (Blackman and Eastop 1994).

Key to aphid eriosomatines (aptera vivipara morph) associated with moss and/or roots of fir, spruce, or willow in forests of the Pacific Northwest

1	Anal plate conspicuously protruding (Fig. 17); URS with >10 accessory setae; cauda with >10 setae; on roots of fir	***Prociphilus americanus* (Walker)**
—	Anal plate not protruding (Figs. 1, 6, 11, 22, 27); URS with zero to four accessory setae; cauda with two to four setae; on moss and/or roots of fir, spruce or willow	2
2(1)	Antennae with four segments (rarely five); tarsi with one tarsomere (tarsomere I and II completely or partially fused), with setae in tarsus I position similar or equal in length to metatibia apical setae) (Fig. 9); head with wax gland plates; URS without preapical light zone or accessory setae; on moss	***Melaphis rhois* (Fitch)**
—	Antennae with five segments (rarely six); tarsi with two tarsomeres, if partially fused, then tarsus I setae shorter than metatibia apical setae and head without wax gland plates; other features variable	3
3(2)	Tarsus I chaetotaxy 3-2-2	4
—	Tarsus I chaetotaxy 2-2-2	6

4(3) URS length/width <2.0; antenna with five to six segments; on roots of willow sometimes intertwined with moss at the moss-soil interface zone . . . . . ***Thecabius populimonilis* (Riley)**

— URS length/width >2.0 (usually >2.2); antenna with five segments; on moss and/or roots of fir or spruce 5

5(4) Metatibia apical seta/tarsus I seta, mean = 2.0 (range 1.6–2.3) (Fig. 16) ***Pachypappa rosettei* (Maxson)**

— Metatibia apical seta/tarsus I seta, mean = 1.3 (range 1.2–1.6) (Fig. 14) ***Pachypappa sacculi* (Gillette)**

6(3) URS with a preapical light zone and no accessory setae (Fig. 2); tarsomeres I and II semi-fused (Fig. 4) ***Clydesmithia canadensis* Danielsson**

— URS without a preapical light zone and with usually two accessory setae (Fig. 23); tarsomeres I and II distinct (Fig. 25). . . . . ***Prociphilus* (*Stagona) xylostei* (De Geer)**

Discussion

All of the eriosomatines discussed above were originally described from their gall-producing or leaf-curling forms on their primary hosts. These same species on their secondary hosts or alternate habitats are not equivalent morphologically to those on the primary host, and some had not been previously recognised or described. DNA sequence comparisons were used to match morphs of the primary host with those on the alternate host habitats. Of the numerous eriosomatine aphid–moss associations discovered through Berlese extraction (Table 1), most are reported here for the first time.

Of the seven eriosomatines in the moss–root substrata in forests of the Pacific Northwest, only one, *M. rhois*, is clearly recognised to use moss as a food source. *Thecabius populimonilis* is found in moss but only when roots of willow are present, implying that willow is its true secondary host. *Prociphilus americanus* is found strictly on roots of fir in soil below the forest floor mosses. *Clydesmithia canadensis*, *P. rosettei*, *P. sacculi*, and *P.* (*Stagona*) *xylostei* occur in mosses with conifer roots, but also in mosses free of roots. The latter situation suggests that these aphids exploit mosses in some fashion, but their specific relationships or interactions with the mosses are little studied. It may be that they feed on moss directly, but it is also possibly that they are simply dispersing through the moss, or because of a diverse suite of mycorrhizal fungi that interact with moss (Davey and Currah 2006; Ptaszyńska *et al*. 2006), they frequent mosses to feed on fungi. It has been reported previously that *Pemphigus piceae* (Hartig) (now a junior synonym of *P. rosettei* or *P. sacculi*, see Danielsson 1990b; Carter and Danielsson 1991; Remaudière and Remaudière 1997) and a similar aphid feed on mycorrhizal fungi associated with conifers (Zak 1965).

Most of the eriosomatines found in the moss–root forest habitats of the Pacific Northwest are relatively obscure and of little or no known economic importance. None have direct useful purposes for humans, but they are part of the ecological structure or food web used by a variety of organisms. Those that frequent moss, whether feeding on moss or not, have no observable effect on moss health. Those that feed on the roots of fir, spruce, or willow in old growth or managed forests likewise have little or no apparent effect on plant health. The only reported damage or stress to trees caused by conifer root feeding aphids (*P. americanus*) has been in Christmas tree fir plantings (O'Donnel 2008; DeFrancesco and Murray 2009). Also, as an above ground winged migrant, *P. americanus* can be a nuisance for participants in outdoor activities when it occurs in large numbers as it migrates from roots of fir to ash trees in the fall (Mack 2010). On ash, the aphid overwinters in the egg stage, then feeding by new generation aphids in the spring cause developing leaves to curl and twist. Homeowners sometimes treat for the aphid to minimise its impact on ash.

Acknowledgements

The authors express thanks to D. Graf, (Washington State University technical staff), D. Fleming, B. Kunibe, S. Lillard, R. Pampell, and R. Ranft (United States Department of Agriculture-Agricultural Research Services, Alaska); M. Bowser (Kenai National Wildlife Refuge, Soldotna, Alaska), and L. Pike (Prosser, Washington) for assistance in field collecting and Berlese extraction; and D. Graf for specimen clearing and mounting. For the loan of specimens or making

collections available for study they thank R. L. Blinn, North Carolina State University, Raleigh, North Carolina; J. Pitts, Utah State University, Logan, Utah; G. Miller, United States Department of Agriculture, Systematic Entomology Laboratory, Beltsville, Maryland; and the Canadian National Collection of Insects, Arachnids and Nematodes (Agriculture and Agri-Food Canada, Ottawa, Ontario). The authors also thank the United States National Forest Service for permission to sample, and J. Frelich and G. Hunter for facilitating collections in the Olympic National Park. DNA sequencing was supported through funding to the Canadian Barcode of Life Network from Genome Canada (through the Ontario Genomics Institute), Natural Sciences and Engineering Research Council of Canada and other sponsors listed at www.BOLNET.ca.

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