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# CONTENTS

<table>
<thead>
<tr>
<th>Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Guest Editorial — Northwestern Caddisflies</td>
<td>1</td>
</tr>
<tr>
<td>Nimmo — The adult Rhyacophilidae and Limnephilidae (Trichoptera) of Alberta and Eastern British Columbia and their post-glacial origin</td>
<td>3</td>
</tr>
<tr>
<td>Editorial — Publish or Perish?</td>
<td>235</td>
</tr>
<tr>
<td>Frank — Carabidae (Coleoptera) of an arable field in central Alberta</td>
<td>237</td>
</tr>
<tr>
<td>Chance — Correction for drag of a flight mill, with an example for <em>Agrotis orthogonia</em> Morr. (Lep. Noctuidae)</td>
<td>253</td>
</tr>
<tr>
<td>Sehgal — Biology and host-plant relationships of an oligophagous leaf miner <em>Phytomyza matricariae</em> Hendel (Diptera:Agromyzidae)</td>
<td>255</td>
</tr>
<tr>
<td>Erwin — Notes and corrections to a reclassification of bombardier beetles (Carabidae, Brachinida)</td>
<td>281</td>
</tr>
<tr>
<td>Book Review</td>
<td>282</td>
</tr>
<tr>
<td>Book Review</td>
<td>283</td>
</tr>
<tr>
<td>Book Review</td>
<td>284</td>
</tr>
<tr>
<td>Guest Editorial — Excellence has no Nationality</td>
<td>287</td>
</tr>
<tr>
<td>Sehgal — A Taxonomic Survey of the Agromyzidae (Diptera) of Alberta, Canada, with Observations on Host-Plant Relationships</td>
<td>291</td>
</tr>
<tr>
<td>Nimmo — Corrigenda on the Adult Rhyacophilidae and Limnephilidae (Trichoptera) of Alberta and Eastern British Columbia and their Post-Glacial Origin</td>
<td>406</td>
</tr>
<tr>
<td>Thomas — An Apparatus and Method for the Field Separation of Tabanid Larvae (Diptera:Tabanidae) from Moss</td>
<td>407</td>
</tr>
<tr>
<td>Announcement</td>
<td>409</td>
</tr>
<tr>
<td>Editorial — Four Men and a Moth</td>
<td>411</td>
</tr>
<tr>
<td>Jacobson — The pale western cutworm, <em>Agrotis orthogonia</em> Morrison (Lepidoptera: Noctuidae): a review of research</td>
<td>414</td>
</tr>
<tr>
<td>Cheung — Purification and properties of arginine phosphokinase from honeybees <em>Apis mellifera</em> L. (Hymenoptera, Apidae)</td>
<td>437</td>
</tr>
</tbody>
</table>
INDEX

Achillea 270, 276
A. millefolium 256, 335, 369, 386
A. sibirica 256-258, 262, 266-274, 305, 335, 369, 386
Actaea rubra 306, 384
Agonum cupreum 239, 242, 246
A. cupripenne 239
A. placidum 239, 242, 246
A. quadripunctatum 239
A. retractum 239
Agromyza 292, 294, 296-303, 384
A. albertensis 296-297
A. albipennis 296-298, 302, 309, 392
A. ambigua 297, 300
A. ambigua group 296, 384
A. aprillina 296-298
A. brevispinata 296-299, 302, 309, 392
A. canadensis 296, 299, 386
A. fragariae 296-297
A. hockingi 296-300, 309, 392
A. kincalidi 296-300, 309, 392
A. lucida 298
A. masculina 296-297, 300-302
A. nearctica 296-297, 301, 309, 392
A. nigripes 296-298, 302
A. nigripes group 296, 384
A. populoides 296-297, 302, 309, 385
A. pseudoreptans 296-297, 302
A. pseudorufipes 299
A. reptans 302
A. reptans group 296
A. rubi group 296
A. rufipes group 261, 296
A. spiraeae 296-297, 300-302, 383
A. spiraeae 296
A. sulfuriceps 296, 303
A. ulmi 298
A. urticea 302
A. vockerothi 296-297, 301-303
Agromyzidae
Alberta 291-405
adult characteristics 293-294
host-plant relationships 255-280, 291-405
taxonomy 291-405
Agropyron 322-323
Agropyron repens 387
A. smithi 387
Agrotis delorata 416
A. orthogonia 253-254, 411-436
A. orthogonia duae 416
Ahmad, T. 256
Ainslie, C.N. 422
Algonquian 107, 116, 143-144
Allegophylax 145
Allen, P. 256, 265
Allium cepa 268, 272, 274, 278
Allomyia 57-60
Amara 238, 247
A. apricaria 240, 242, 247
A. apricaria group 248
A. aulica group 248
A. avida 240, 242, 247
A. convexa 240
A. cupreolata 240
A. ellipsis 240, 242, 248
A. farcta 240
A. lacustris 239
A. laevipennis 240
A. latior 240, 242, 247
A. littoralis 240, 242, 248
A. lunicollis group 248
A. obesa 240
A. pallipes 240
A. patruelis 240, 242, 248
A. quenseli 240
A. sinuosa 240
A. torritha 239, 242, 246-248
Amaranthus 344
Amauromyza 292, 295, 326-327, 384
Amelanchier canadensis 317, 384
Amphicosmoecus 5, 50-51, 55-56, 207, 216
A. canax 55-56, 159, 162, 184, 203, 207, 213
Amphioxus lanceolatus 437
A. abnormalis 327
A. riparia 326-327, 396
A. shepherdiae 326-327, 386, 396
A. subinfumata 326-327
Anabolia 5, 83, 101, 124-128, 138, 210, 217
A. bimaculata 125-128, 177, 192, 203, 210, 213
A. bimaculata group 210
A. consocia 125-126, 176, 191, 204, 210, 213
A. maculata 128
A. medialis 126
A. osburni 125-127, 161, 177, 191, 204, 210, 213
A. sordida 210
Anabolina 108, 112, 120-121
Anacyclus 256
Andrewartha, H. G. 418, 429.
Andrews, P. 440
Anemone 353
A. canadensis 359, 374, 385
A. multifida 372, 385
A. riparia 359-360, 385
Angelica 353
A. arguta 382, 386
Anisogamus 96
Anolopsyche 108
Anthemis 256
Anthrax molitor 428
Antineura 344
Antirrhinum 266
Apaneteles griffini 428
Apatania 5, 64-71, 156, 207, 217
A. aenicta 69
A. alberta 65, 70-71, 165, 185, 203, 207, 214
A. arctica 65-66
A. auricula 66
A. complexa group 70-71
A. crymophila 65, 69-70, 165, 185, 204, 207, 213, 221
A. dalecarlica 66
A. fimbrata group 65-66
A. frigida 67
A. groenlandica 66
A. inornata 66
A. pallida 67
A. palmeni 66
A. shoshone 65, 68, 165, 185, 204, 207, 213, 221
A. shoshove 406
A. stigmatella 65-68, 165, 185, 204, 207, 213, 221
A. stigmatella group 67-68
A. wallengreni group 69-70
A. zonella 65-66, 159, 164, 185, 204, 207, 214, 221
Apataniinae 5, 50, 64-71
Apatanini 5
Apatelia 65-69
Apatidea 65-67
Apidae 437-446
Apis mellifera 437-446
Apium 271
Apolopsycha 108, 116
Aptinodorus 281
A. cyaneus 281
Aptinomorphus 281
Aptinus 281
Aquilegia 266, 271, 352, 357, 362-363, 384-385
A. brevistyla 355
A. formosa 355-356
Aralia 353
A. nudicaulis 357, 385
Arctocia 126
Arctoecia 125-126, 138
Arctopora 5, 83, 133-135, 211, 217
A. pulchella 134-135, 178, 192, 204, 211, 213
A. salmon 211
A. trimaculata 211
arginine phosphokinase 437-446
Arnett, R. H., Jr. 283-284
Arnica 352
A. cordifolia 358, 386
Artemisia 258, 266-269, 272-277, 325
Asclepias syriaca 278
Aster 295, 312, 328, 333
A. ciliolatus 267, 351, 360, 386
A. conspicus 358, 386
Asterias rubens 437
Asynarchus 5, 83, 128-132, 143, 210, 217
A. aldinus 129, 131-132, 178, 192, 203, 210, 213
A. batchewana 131
A. conerus 131
A. contunmax group 130
A. curtus 129-131, 177, 192, 203, 210, 213
A. lapponicus 132
A. lapponicus group 130
A. mutatus 129-130, 177, 192, 204, 210, 213
A. planifrons 131
Atecyclus septemdentatus 437
Atylotus 407-408
Avena 323
Badister obtusus 240
Bajkov, A. 76
Balduf, W. V. 76, 95, 119, 124-125, 128, 146
Baldwin, E. 437-439, 444-445
Ball, G. E. 54, 62, 97, 102, 113, 116, 124,
Bannister, L. H. 437

Baptisa tinctoria 331

Barnes, W. 416

Bayrock, L. A. 197-198

Beirne, B. F. 429

Bembidion 244, 248, 250, 251

B. bimaculatum 239-242

B. canadianum 239, 242-244

B. grapei 239

B. mutatum 239, 242, 244, 251

B. nitidum 239-243

B. nudipenne 239

B. obscurellum 239, 242-243, 251

B. quadrimagulatum oppositum 239, 242-244, 251

B. rapidum 239

B. rupicola 239, 242-243, 251

B. sordidum 241

B. timidum 243

B. versicolor 239, 242-243

beetles

bombardier 281

Colorado potato 276-278

Benjamin, F. H. 416

Berecyntus bakeri 428

Berry, E. W. 124-125


Betten, C., et al. 196

Bidens cernua 307, 386

Birch, L. C. 418, 429

Blakely, P. E. 418-424, 427, 431

Blethan, S. L. 437, 444

Blickle, R. L. (see Morse).

Bombyliidae 428

Bonnetia compta 428

Bowman, K. 416

Brachinida 281

Brachinus adustipennis 281

B. fulminatus 281

B. kavanaughi 281

B. microamericanus 281

B. senegalensis 281

B. vulcanoides 281

Braconidae 428

Bradycellus congener 240

B. lecontei 240

Bradytus 248

Branch, H. E. 95

Braschnikov, W. C. 310

Brassica 274

B. khaber 267, 272

B. oleracea 273-275

Braithwaite, F. 67, 98, 102

Brimley, C. S. 126

Brooks, A. R. 427-428

Brosem, R. W. 438

Brown, A. W. 431

Brues, C. T. 119, 140

Bryson, R. A. 199

Buhr, H. 277

Burks, B. D. 196

Buttomomyza 317

Butt, B. A. 424

caddisflies, Alberta species 1-234, 406

origins and relationships 196-223

taxonomy 3-195

Calamagrostis 321

Calathus ingratus 239, 246

Callinectus sapidus 437

Calliphora erythrocephala 437

Calosoma calidum 239-241

Calycomyza 292, 295, 325-326, 384

C. althaeae 325

C. artemisiae 325

C. cynoglossi 325

C. menthae 325, 386

C. solidaginis 325, 387

C. sonchi 325-326, 387

Campanula 267

Cancer pagurus 437

Cannabis 277

Cantu, S. 424

Carabidae 237-252, 281

Alberta 237-252

of arable fields 237-252

Carabus complanatus 281

C. maeander 239

C. serratus 239

C. taedatus 239

Caragana arborescens 267

Carcinus maenas 437
Carex 319-321
Carlson, C. W. 438
Carpenter, G. D. H. 97
Centrostephanus rodgersii 437
Cerodontha 292, 295, 317-325, 384
C. angulata 317-319
C. calamagrostidis 319, 321-322
C. capitata 319, 323
C. chaixiana 318-320
C. dorsalis 318, 324
C. eucaricis 317-320
C. flavocingulata 320
C. frankensis 295, 317-320
C. gibbardi 317-320
C. incisa 319-322, 387
C. inconspicua 319, 322
C. lateralis 323
C. longipennis 319, 324
C. muscina 319, 322-323
C. occidentalis 318, 324-325, 395
C. scirpi 317-321, 387
C. semipistica 319
C. superciliosa 319, 323, 387
C. ultima 318, 321
Chaetotaulus 118-119
Chalcididae 428
Chance, M. A. 253-254, 425
Chelonus 428
Chenopodium 267
C. album 271
Cheung A. C. 437-446
Chilostigma 149-150, 154
Chilostigmodes 5, 82, 148-156
Chilostigmodes 5, 148, 150-151, 212, 217
C. areolaris 150
C. areolata 150-151, 181, 194, 204, 212-214
C. forcipata 212
Chlaenius alternatus 240
Chlamys opercularis 437
Chryanda 5, 50, 143-144, 211, 216
C. centralis 143-144, 180, 193, 204, 211, 214
C. cordon 144
C. pallida 144
C. parvula 144
C. signata 144
Chrysanthemum 256, 258, 266-269, 272, 276-277, 369, 386
Chrysothamnus 425
Chrysops 407-408
Cicindela aequinoctialis 281
C. limbalis 239
Cirsium arvense 425
Clematis 384
C. verticillaris 267, 361, 385
Clisteroronia 5, 83, 120-122, 210-211, 216
C. caroli 121
C. flavicollis 210
C. formosa 211
C. maculata 211
C. magnifica 121-122, 176, 191, 203, 210, 214
Clisteroniella 83
Clostoeca 143
Cohen, M. 256, 263
Coleoptera 237-252
collecting methods
chadisflies 11-12
ground beetles 238
rove beetles 238
spiders 238
tabanid larvae 407-408
Colpotaulius 110-112, 125-126, 133
tcontrol, cutworms 430-431
Cook, W. C. 411, 415, 418, 421-431
Cooley, R. A. 424
Copidosoma bakeri 428
Coquillet, D. W. 344
Corbet, P. S. 65
Cornus 353
C. canadensis 354, 385
C. stolonifera 354, 385
Cotula 256
Craig, D. A. 282
Crastemyza 317
Crepis 383-384
C. gracilis 381, 386
C. tectorum 366, 386
Criddle, N. 108, 118, 154, 156
Crumb, S. E. 417, 429
Cucumis 267
Curtonotus 248
cutworms
pale western 411-436
predators 237
Cynindis cribricollis 240
C. planipennis 240
Dahlia 272
Darlington, P. J., Jr. 281
Davis, T. B. 256
Davis, M. B. (see Betten et al.)
Davis, P. H. 265, 383
Dejean, P. F. M. A. 281
Delphinium 267, 363, 384-385
Dendromyza 316
Depner, K. R. 419
DePew, L. J. 431
Deschampsia caespitosa 332, 387
Desmotaillus 127-128
Dethier, V. G. 276, 356, 427
Dicosmoecinae 5, 50-64
Dicosmoecus 5, 50-53, 206, 216
D. atripes 51-53, 162, 184, 203, 206
D. jucundus 51-53, 159, 162, 184, 203, 206, 213
Di Jeso, F. 437
Diptera 255-280, 291-405, 407-408, 428
Disease, cutworms 427-429
Dizygomyza 292, 316-321
Dodds, G. S. 19-20, 23, 26-27, 61-62, 76, 90, 100, 124, 128, 138-140, 143
Döhrer, W. 146
drag-flight 253-254
Dugesiella hentzi 437
Eames, A. J. 265, 383
Ecclisomyia 5, 50-51, 61-64, 207, 217
E. bilera 207
E. conspersa 61-63, 164, 185, 203, 207, 213
E. digitata 207
E. kamtschatica 207
E. maculosa 61-62, 159, 164, 185, 203, 207, 214
E. scylla 207
E. species one 61-64, 164, 185, 203, 207
Ecclisopteryx 149
Echinus esculentus 437
Edwards, D. K. 425
Ehrharta 323
Elkins, W. A. 119, 145
Elodi, P. 437, 444
Elson, J. A. 198-199
Elymus 323
Enderlein, G. 309, 312, 342
Ennor, A. H. 437-438, 444-445
Enoecyla 150
Enoicyla 145, 149-150
Erigeron 425
Ernestia radicum 428
Erwin, T. L. 281
Escherichia coli 437
Eshbaugh, F. P. 415
Eupagurus bernhardus 445
Eupatorium 277-278, 333
Euxoa ochrogaster 237
Eyer, J. R. 415, 421, 426-427, 431
Fabricius, J. C. 149
Fallén, C. F. 296, 302, 350, 375
Farstad, C. W. 419-421
Faulkner, L. R. 431
Feeney, P. P. 256, 278
Fernald, M. L. 198
Fink, S. C. 438
Fischer, F. C. J. 11, 15, 19, 22-23, 52-156
flight mill 253-254
flight ranges 253-254
flight speeds 253-254
forecasting, cutworms 430
Forsslund, K. H. 97, 102, 104
Fowler, K. S. 437
Fraenkel, G. S. 256, 276
Frank, J. H. 237-252
Frey, R. 327-328, 344
Friend, W. G. 256
Friganea 119
Frison, T. H. 196
Fristrup, B. 97
Frost, S. W. 298, 328, 331, 354, 366, 380
Galeopsis 277-278, 333
G. tetrahit 267, 272, 274, 278
Galium boreale 343-344, 386
Gammack, D. B. 444
Geum allepicum 296
Gibson, A. 415, 421
Giddings, J. L. 197
Giraud, P. 309
Glossosomatidae 16
Glyphopsyche 5, 148-156, 211-212, 216
G. bryanti 149
G. intercissa 149
G. irrorata 149-150, 160, 181, 194, 204, 211-212
G. missouri 211-212
Glyphotaelius 124, 149
Gnaphosa sp. nr. muscorum 250
G. parvula 250
Gonia aldrichi 428
G. breviforceps 428
G. brevipulli 428
G. capitata 428
G. longiforceps 428
G. longipulli 428
Goniotaulius 65, 91, 102, 119, 125, 127, 149
Goodrich, A. L. 53
Grammotaulius S, 83, 122-123, 140-141, 210, 217
G. betteni 210
G. interregationis 122-123, 176, 191, 204, 210, 214, 221
G. lorettae 210
G. praecox 122-123
G. sibiricus 123
Grant, D. R. 197-199
Gravenor, C. P. 197-198
Gray, H. E. 425, 427
Greene, C. G. 316
Greenslade, P. J. M. 250
Griffiths, D. E. 437-438, 444-445
Griffiths, G. C. D. 261, 277, 297-298, 361, 364, 370, 375, 380-381, 383
Grindelia squarrose 425
Groschke, F. 319
Guppy, R. 33-34, 62, 95, 99-103, 107, 110, 121, 137, 140, 143, 149, 155
Gupta, P. D. 278
Gupta, R. L. 256
Gurney, B. 277
Gutierrrezia 425
Haematopota 407-408
Halescus 121, 146
Hendlirsch, A. 95
Hansen, F. E. 276
Haplopyza 292, 295, 344
H. togata 344
Hardwick, D. F. 419, 426-427
Hardy, J. 380
Harmston, F. C. (see Knowlton).
Harpalellus basilaris 240
Harpalus 238
H. amputatus 240, 242, 249
H. desertus 240
H. funerarius 240
H. pleuriticus 240, 242, 249
H. uteanus 240
Harris, P. 256
Harris, T. W. 101, 145
Harvey, T. L. 431
Hawn, E. J. 429
Helianthus 266, 274-277, 333, 425
H. annuus 258, 266-269, 272
Heliocidaris erythrogramma 437
Heliothis zea 276
Heming, B. S. 284-286
Hendel, F. 294, 300, 303, 309-328, 333, 343-345, 360, 364, 369, 375, 379
Hennig, W. 383
Henrickson, K. L. 97
Heracleum 351, 367
H. lanatum 379, 386
Hering, E. M. 256, 261, 276, 311, 335, 340, 346, 382-383
Hesperophylax 5, 139-142, 211, 216
H. alaskensis 140
H. consimilis 140-141, 180, 193, 203, 211
H. designatus 140, 211
H. incisus 140-142, 180, 193, 203, 211, 214
H. magnus 211
H. minutus 211
H. occidentalis 140-141, 179, 193, 203, 211, 214
Hexomyza 292-295, 309, 384
H. albicula 309
H. schineri 309, 385
Heywood, H. B. 196
Heywood, V. H. 265, 383
Heydemann, B. 250
Hisaw, F. L. (see Dodds).
Hocking, B. 235-236, 253, 411-412, 419-420, 427
Hoerner, J. L. 431
Holothuria forskali 437, 445
Homarus americanus 437
H. vulgaris 437, 444
Homophylax 5, 50, 78-81, 207-208, 216, 406
H. acutus 78-80, 160, 167, 186, 203, 208, 214
H. adriana 208
H. andax 208
H. baldur 78-81, 160, 167, 186, 203, 208, 214
H. crotchi 78-79, 160, 167, 186, 203, 208, 214
H. flavipennis 208
H. insulas 208
H. nevadensis 208
H. renzi 208
honeybees 437-446
Hope, F. W. 281
Hopewell, W. 431
Hopkins, A. D. 276
Hopkins, D. M. 197
Hordeum 323
H. vulgare 268, 272, 274
host-plant relationships 255-280, 382-387
Hsiao, T. H. 256, 276
Hubenthal, W. 281
Hussey, N. W. 277
Hutchinson, J. 265, 383
Hybomitra 407-408
Hyland, K., Jr. 146
Hymenoptera 428, 437-446
Hypnotranus 57, 107
Ichneumonidae 428
Icteromyza 292, 317-318, 323-324
Ilex 378
Imania 5, 50-51, 56-61, 207, 217
I. acanthis 207
I. bifosa 207
I. bifosa group 60-61
I. cascadis 57-59, 159, 163, 184, 203, 207, 214
I. cidoibes 207
I. gnathos 207
I. hector 57-60, 159, 163, 184, 203, 207, 214
I. renzi 207
I. stylata 57
I. tripunctata 57-58, 159, 163, 184, 201-203, 207, 214, 220
I. tripunctata group 56-60
information storage and retrieval 283-284
Jacobson, G. C. 102, 122
Jacobson, L. A. 253, 411, 414-436
Jasus verreauxi 437, 444
Jeannel, R. 281
Jermy, T. 256, 276, 278
Johnson, C. W. 102, 104, 119, 125, 146
Juncus 323, 324
Kaltenbach, J. H. 302, 333, 370
Kaplan, N. O. 437, 444
Karl, O. 320
Kassab, R. 437, 444
Kasting, R. 422, 427, 429
Keller, J. C. 256
Kennedy, J. S. 256
Khan, M. R. 422
Kimmins, D. E. 16, 67
Kirby, W. 102
Kjellgren, B. L. (see Betten et al.).
Klotz, C. 444
Knowlton, G. F. 34, 53-54, 99, 140-143, 154
Kolbe, H. J. 66, 102, 112, 119, 122
Kolenati, F. 102
Kowarz, F. 380
Krafka, J. 126
Krafka, J., Jr. 95, 126, 128
Krivada, W. V. 150
Kruger, J. P. 252
Lactuca 278
L. scariola 366
Lampsana 333
Landon, M. F. 444
Lathyrus 334
L. odoratus 267, 271
L. ochroleucus 334, 380, 385
Layne, E. 438
leaf miners, biology 255-280
host-plant relationships 255-280, 382-387
taxonomy 291-405
Leech, R. L. 198
Leimnephila 119
Lemurimyza 292, 295, 341-342
L. dorsata 341
L. pacifica 341
L. pallida 341-342
Lenarchus 134
Lenarchus 5, 83, 134-139, 211, 217
L. brevipennis 135, 138-139, 179, 193, 203, 211, 214
L. crassus 135-136, 178, 193, 204, 211, 214
L. expansus 211
L. fautini 135-137, 179, 193, 203, 211, 213
L. gravidus 211
L. intermedius 137
L. rho 211
L. rillus 211
L. vastus 135-138, 179, 193, 203, 211, 213
Lepidoptera 237, 253-254, 411-436
Lepnev, S. G. 154
Leptacinus batyphrus 250
Leptinotarsa decimlineata 276
Leptocella 14
Leptoceridae 14
Lewis, S. K. 437
life history, cutworms 416-427
Likens, G. E. (see McConnachie).
Limnephila 119
Limnephilidae 3-234, 406
species one 157, 183, 195, 203
species two 157, 183, 195, 203
species three 157-158, 161, 183, 195, 203
species four 158, 161, 183, 195, 203
species five 158, 183, 195, 203
Limnephilinae 5, 50, 81-158
Limnephilini 5, 82-142
Limnephilus 5, 13, 67, 83-122, 125-141, 149-150, 208-210, 217
L. acenus 209
L. acrocurvus 210
L. acula 210
L. ademus 209
L. affinis 118
L. alberta 86-88, 114, 174, 190, 203, 210, 214
L. americanus 89
L. argenteus 85, 88, 113-114, 174, 190, 204, 210, 213
L. argenteus group 113-114, 210, 217
L. arreto 210
L. asiaticus group 115, 209, 217
L. assimilis 210
L. assimilis group 107-109, 210, 217
L. canadensis 85-87, 120, 175, 191, 204, 209, 213
L. castor 209
L. cockerelli 86, 105-106, 171, 189, 203, 209, 214
L. coloradensis 209
L. congner 99
L. decepta 101
L. dispar 209
L. diversus 209
L. diversus group 120, 209-210, 217
L. elegans 97
L. elongatus 208
L. externus 84, 87, 99-100, 170, 188, 203, 208, 213, 221
L. externus group 99-100, 208-209, 217
L. extractus 85, 88, 91, 168, 186, 204, 208, 213
L. exulans 98
L. fagus 209
L. femoralis 85, 87, 102-103, 171, 188, 203, 209, 213, 221
L. fenestraus 209
L. fenestraus group 115-117, 209, 217
L. forcipatus 118
L. frijole 209
L. hageni 84, 88, 91-92, 168, 187, 204, 208, 214
L. hingstonei 104, 406
L. hyalinus 85, 88, 109-110, 173, 189, 203, 209, 213
L. incisis group 109-113, 209, 217
L. indivius 84, 88, 95-96, 169, 187, 204, 208, 213
L. infernalis 85, 87, 96-97, 169, 187, 203, 208, 213
L. janus 85-86, 111-112, 173, 189, 204, 209, 213
L. kennicotti 85, 88, 116-117, 175, 190, 204, 209, 213, 221
L. labus 84-86, 115, 174, 190, 204, 209, 213
L. lopho 86-88, 107, 172, 189, 203, 209, 214
L. lunomus 209
L. luridus 209
L. luridus group 101-103, 209, 217
L. luteolus 99-100
L. macgillivrayi 89
L. merinhus 112
L. minusculus 85-86, 111, 116, 174, 190, 203, 213, 209
L. miyadi 98
L. moestus 85, 88, 104-105, 171, 188, 204, 209, 213, 406
L. morrisoni 209
L. morrisoni group 209, 217
L. nebulosus 102
L. nigriceps 85, 88, 117-118, 161, 175, 190, 204, 210, 214
L. nigriceps group 117-118, 210, 217
L. nogus 86-87, 103-104, 171, 188, 203, 209, 213
L. nogus group 103-104, 209, 217
L. notatus 98
L. occidentalis 210
L. ornatus 85-87, 97-98, 170, 187, 203, 208, 213
L. ornatus group 97-98, 208, 217
L. oslari 100
L. pallens 209
L. pallida 108
L. partitus 85-87, 92-93, 161, 168, 187, 204, 208, 214
L. parvulus 86-88, 107-108, 172, 189, 204, 210, 213
L. perforatus 102
L. perpusillus 84, 87, 112-113, 173, 190, 203, 209, 213
L. picturatus 85-87, 98-99, 170, 188, 204, 208, 214, 221
L. picturatus group 98-99, 208, 217
L. pilosula 118
L. productus 210
L. pulchellus 406
L. rhaeus 112
L. rhombicus 85-87, 118-120, 175, 191, 203, 208, 214, 221
L. rhombicus group 118-120, 208, 217
L. roberti 108
L. sansoni 84, 87, 90-91, 168, 186, 203, 208, 214
L. secludens 85, 88, 110-111, 173, 189, 204, 209, 213
L. sericeus 84, 86, 100-101, 170, 188, 204, 209, 213
L. sericeus group 100-101, 209, 217
L. sitchensis group 104-107, 209, 217
L. spinatus 85-87, 108-109, 172, 189, 203, 210, 214
L. stigma group 95-97, 208, 217
L. stipatus 102
L. striola 118
L. subcentralis group 88-95, 208, 217
L. subguttatus 95
L. sublunatus 84, 87, 89-90, 95, 161, 167, 186, 203, 208, 214
L. subpunctatus 102
L. susana 84, 87, 93-94, 169, 187, 203, 209, 214
L. sylviae 209
L. taloga 210
L. tarsalis 209
L. tersus 100
L. thorus 208
L. valhalla 85, 88, 106, 172, 189, 203, 209, 214
L. sp. one 88, 94-95, 169, 187, 203
Limnophila 119
Limnophilus 89-92, 95-122, 134, 137, 141
Limulus polyphemus 437
Lindoeth, C. H. 54, 62, 97, 102, 113, 116, 124, 137, 143, 198-200, 238, 241-251
Lindsay, I. S. 418, 427, 431
Ling, S. 30-31, 34
Linnaeus, C. 118
Lioy, Da Paolo 316
Lipke, H. 256
Liriomyza 292-295, 328-341, 384
L. arcticola 339
L. balcanica 330
L. balcanicoides 328-333, 396
L. baptisiae 329-333
L. bifurcata 328-337, 397
L. cannabis 277
L. conspicua 329, 332
L. cordillerana 329, 332, 387
L. eboni 329-333
Meteorus leviventris 428
M. vulgaris 428
Metopomyza 292, 295, 342-343
M. flavonotata 342
M. griffithsi 342-343, 399
M. interfrontalis 342-343
Mez, C. 383
Micaria sp. nr. alberta 250
Michel, C. E. 95
Michelbacher, A. E. 256
Mik, J. 328
milk drag 253-254
Miller, L. A. 407
Milliron, H. E. 95
Milne, D. J. 96, 116-120, 127, 130, 146
Milne, M. J. 31
Mitchell, B. 241
Monarda 325
Morales, M. F. 439
Moreland, B. 437, 444
Morrison, H. K. 416, 424
Morrison, J. F. 437-438, 444-445
Moseley, M. E. 16, 89-92, 95-97, 102, 112, 119, 122-125, 128, 145-146, 149-150
Moyhuddin, A. I. 279
Munroe, E. G. 197-198
Musca 238
Muttkowski, R. A. 26, 95, 119, 126, 145-146
Myxicola infundibulum 445
Nakahara, W. 97
Napomyza 292, 295, 349-350
N. immanis 349
N. lateralis 349
N. nugax 349-350
N. plumea 349-350
natural enemies, cutworms 427-429
Nayar, J. K. 256
Neave, F. 62, 76, 97-99, 108-109, 128, 140, 156
Needham, J. G. 95, 146, 196
Nemorimyza 292, 295, 327-328, 384
N. posticata 295, 328, 387
Nemotaulius 5, 83, 123-124, 210, 217
N. hostilis 124, 161, 176, 191, 203, 210, 213
Neophylacinae 5, 50, 71-77
Neothremma 5, 71-72, 75-77, 207, 216
N. alicia 76-77, 160, 166, 186, 203, 207, 214
N. didactyla 207
N. galena 207
N. latouresi 77, 183, 186, 203, 207, 214, 406
Neprolepis 267, 270, 271
Neprops norvegicus 437
Neuronia 145
Nicotiana tabacum 267, 271, 273
Nihei, T. 439
Nimmo, A. P. 3-234, 406
Noctuidae 237, 253-254, 411-436
Noda, L. 439
Nothofagus 200
Notiophilus aquaticus 239
N. semistriatus 239
Oatman, E. R. 256
Odum, E. P. 251
Oligophlebodes 5, 71-75, 207, 216
O. ardis 207
O. minuta 207
O. mostbento 207
O. ruthae 72-73, 160, 166, 185, 203, 207, 214
O. sierra 72-74, 160, 166, 186, 203, 207, 213
O. sigma 207
O. zelti 72-75, 166, 186, 203, 207, 214
Omphroph americanum 251
Onocosmoecus 5, 51-55, 206-207, 217
O. quadrinotatus 206
O. unicolor 54-55, 162, 184, 204, 206, 213, 221
Ophiomyia 292, 295, 310-316, 384, 385
O. asterivora 312
O. banffensis 310-312
O. decima 310-311, 314
O. labiatarum 311-312, 395
O. madizina 312
O. maura 311-312, 316, 387, 395
O. monticola 310-312
O. nasuta 310-312
O. nona 311-313
O. pinguis 312
O. praecisa 310, 313-315
O. prima 311-313, 316
O. pulicaria 310, 314, 395
O. pulicaria group 295
O. pulicarioides 310, 314
O. secunda 310, 314
O. septima 311, 314
O. sexta 311, 314-315
O. stricklandi 310, 315, 395
O. undecima 311, 315-316
O. wabamunensis 311, 316
O. yougi 312
Orcutt, A. W. (see Betten et al.).
Oriol, C. 444
Oxytropis campestris gracilis 372-373
O. splendens 372, 385
Packard, A. S. 102
Pagurus bernhardus 437
Palaemon serratus 437
Paniscus 428
Papaver 267
Parachiona 107, 143-144
Parahidippus marginatus 250
Paralenarchus 83, 135-139, 211, 217
Parapatania 67
Parapheropsophus 281
Paraphytophyza 292, 295, 345-349, 384, 385
P. flavocingulata 346
P. lonicerae 346, 386
P. luteoscutellata 348
P. nitida 346-347
P. orbitalis 346-348, 386, 399
P. plagiata 346-348, 386, 399
P. spenceri 346-349, 386, 399
P. tremulae 346
parasites, cutworm 428
Pardosa groenlandica 250
P. sp. nr. metlakatla 250
P. moesta 250
P. sp. nr. saxatilis 250
Parker, J. R. 415, 418-431
Parks, T. H. 256
Patrobus lecontei 239
Pecten maximus 437, 445
Peleteria anaxia 428
P. haemorrhhoa 428
P. robusta 428
Pennak, R. W. 119, 124-127
Penstemon 352
P. confer 373, 386
P. procerus 373, 386
Periplaneta 238
Petasites sagittatus 373, 387
Peterson, L. K. 421
Péwé, T. L. 197
Pfadt, R. E. 431
Phalaris 322
P. arundinacea 387
Phanocelia 5, 148, 155-156, 212, 216
P. canadensis 156, 160, 181, 194, 204, 212, 214
Pheropsophidius 281
Pheropsophus 281
P. complanatus 281
Philarcus 5, 83, 132-133, 211, 217
P. quaeris 133, 178, 192, 204, 211, 213
Philoscasca 5, 143, 147-148, 211, 216
P. thor 147-148, 161, 181, 194, 203, 211, 214
Philonthus concinnus 250
P. furvus 250
P. occidentalis 250
Phleum 322
Pholcus phalangioides 437
photomicrography 282
Phryganea 65-67, 98, 101, 117-119, 122, 145, 149
Phytagromyza 346-347
Phytobia 292, 295, 316-317
P. amelanchieris 316-317, 384
P. confessa 295, 316-317
P. flavohumeralis 316-317
Phytoliriomyza 292, 344-345
P. arctica 344-345
P. formosensis 344
P. immaculata 344
Phytomyza 292, 295, 350-382, 384
P. affinalis 256, 359, 365
P. agromyzina 353, 354, 385
P. albipes 375
P. aquilegaeae 355
P. aquilegiana 352-355, 358, 378, 385
P. aquilegioides 351-352, 355-356, 358, 378, 385, 400
P. aquilegiophaga 352, 356, 359, 367, 385
P. aquilegivora 353, 356-357, 381, 385
P. aralivora 353, 357, 385
P. arnicivora 352, 357-358, 386, 400
P. asterophaga 351, 355, 358, 360, 379, 386
P. atricornis 380, 383, 263, 277
P. atripalpis 379
P. banfensis 352, 355, 358
P. blairmorensis 352, 356-359, 365, 367, 400
P. canadensis 353, 359-360, 371, 385
P. caprifoilae 354, 360, 364, 373, 375, 386
P. chrysanthemi 263, 380
P. ciliolati 351, 358, 360, 386
P. cineracea 353, 360-361
P. clematipha 350, 361, 368, 375, 385
P. colemanensis 352, 361-362, 373-374, 401
P. columbinae 351, 362-363, 385, 401
P. crassiseta 386
P. delphinivora 352, 363, 385
P. edmonstonensis 353, 363-364, 401
P. erigerontophaga 360
P. evanescens 354, 364
P. flavicornis 350, 368
P. flavoscutellata 375
P. fuscula 352, 357, 364, 379
P. gelida 379
P. gregaria 354, 364-365, 370, 386, 401
P. horticola 277, 381
P. ilicis 378
P. illustris 351, 356, 359, 365
P. intermedia 370
P. involucratae 353, 365, 370
P. jasperensis 353, 365-366, 371, 380, 402
P. lactuca 351, 366, 386-387, 402
P. lanati 261, 351, 367
P. lupini 352, 359, 367, 385
P. lupinivora 353, 367, 372, 385
P. luteiceps 350, 351, 368, 371, 385, 402
P. major 350, 361, 368-369, 403
P. matricariae 255-280, 351, 369, 373, 378-379, 384-387
biology 259-262
immediate states 263-265
host-plant relationships, adult females 265-269, 276-277
host-plant relationships, larvae 270-275, 277-278
P. mertensiae 353, 364, 369-370, 374, 386, 403
P. merula 354, 370
P. milli 353, 370, 403
P. minuscula 356, 381
P. miranda 351, 370-371
P. misella 352, 371, 404
P. modica 363
P. multifidae 353, 371-372, 385, 404
P. nepetae 369
P. notopleuralis 354
P. oxytropodis 354, 367, 372-373, 385, 404
P. pallipes 363
P. pedicularicaulis 365-366, 371
P. penstemonis 352, 361, 373-374, 386
P. perklymeni 354, 364-365, 373-375, 386
P. petasiti 351, 373-374, 387
P. plantaginis 352, 361, 373-374, 386
P. prava 351, 353, 364, 369, 374, 385
P. puccinelliae 364
P. queribunda 354, 364, 375
P. ranunculi 350, 361, 368, 375, 385
P. riparia 351, 376, 404
P. rufipes 368
P. sehgalii 353, 369, 376-377
P. senecionella 352, 377, 387, 405
P. solidaginivora 351, 378
P. solidaginophaga 352, 378-379, 387, 405
P. spondylii 351, 367, 369, 373, 376, 379, 386
P. subalpina 352, 379-380, 405
P. subtenina 352, 365, 371, 380
P. subtilis 352, 380-381, 385
P. syngenesiae 277, 352, 374, 377, 380-383, 386-387
P. syngenesiae group 263
P. thalictricola 356
P. thalictrivora 353, 356, 381, 385
P. timida 352, 363, 381, 405
P. urbana 352, 380-382
P. vibena 375
Pieris brassicae 256
P. rapae 256
Pisum sativum 267, 271-278
Plantago major 374, 386
Platiphilax 145
Platyphyllax 140, 145, 149-150, 153
Plutella maculipennis 278
Poa 320
Poecilantrax sackenii 428
P. willistoni 428
Poemyza 292, 317-318, 321-323
Polycelis cornuta 445
Polyporus 302, 309
P. tremuloideos 346, 385
P. tremulus 346
Porosagrotis delorata 416
P. orthogonia 411, 416
P. orthogonia duae 416
Porthetria dispar 437
Portunus depurator 437
Potamobius astacus 437, 444
P. leptodactylus 437
Potentilla 267, 271, 296, 385
Pradel, L. A. 437, 444
Praspedomyza 292, 295, 343-344
P. gallivora 343-344, 386
Prest, V. K. 197-199
Proctor, W. 95-97, 104, 119, 125-126, 146
Proterorhopalus 281
Provancher, L. 89, 95, 102, 145, 149
Pruess, K. P. 415
Pseudomeriania nigrocornea 428
Pseudomonas aeruginosa 429
Pseudonapomyza 292, 295, 345
P. atr a 345
P. lacteipennis 345
Pseudostenophylacinae 5, 50, 77-81
Psychoglypha 5, 148, 151-155, 212, 216
P. alaskensis 152-155, 182, 195, 204, 212-213
P. avigo 212
P. bella 212
P. ormae 212
P. prita 152-153, 182, 194, 203, 212, 214, 406
P. rossi 212
P. schmidi 152-153, 182, 195, 203, 212, 214
P. subboreale 154
P. ulla 152, 155, 182, 195, 203, 212, 214
Pteridomyza 294
Pterostichus adstrictus 239, 242, 245-247
P. corvus 239, 245
P. femoralis 239
P. lucublandus 239, 242, 245
Pruess, K. P. 415
Putman, J. D. 53
Psychoglypha 5, 143-147, 211, 216
P. guttifer 145-147, 181, 194, 203, 211-213
P. guttifer group 211
P. lepida group 211
P. similis 146
P. subfasciata 145-146, 180, 193, 204, 211, 214
Quedius spelaeus 250
Racomitrium 66-69
Rampton, U. N. 197-199
Ranunculus 360, 364, 384
R. abortivus 375, 385
R. acris 361
Rawson, D. S. 119, 146
rearing methods, cutworms 427
Regnouf, F. 437, 444
Rhacophila 13, 16-48, 205-206, 215-216
R. acropedes 17, 19, 23-24, 38, 42, 47, 203, 205, 214
R. acropedes group 23-24, 205, 216
R. alberta 17-20, 38, 41, 203, 205, 214
R. alberta group 19-22, 205, 216
R. amabilis 205
R. angelita 18-19, 33-34, 40, 44, 48, 204, 206, 221
R. angelita group 33-34, 206, 216
R. anomala 26
R. belona 18, 25, 38, 42, 46, 203, 205, 213
R. betteni group 31-32, 206, 216
R. bifila 18, 26, 38, 42, 46, 203, 205, 213
R. bipartita 33
R. bruesi 31
R. chilsia 17, 32, 44, 47, 203, 206, 214
R. coloradensis 18, 26, 38, 42, 47, 203, 205, 213
R. complicata 31
R. doddsi 30
R. glaciera 16, 19-22, 38, 41, 46, 203, 205, 214
R. harmstoni 205
R. hyalinata 17-18, 27, 39, 42, 47, 203, 205, 214
R. hyalinata group 27, 205, 216
R. insularis 205
R. invaria group 24-26, 205, 216
R. iranda 206
R. kermada 205
R. kincaidi 205
R. milnei 17, 36-37, 40, 45, 48, 203, 206, 213
R. oregonensis 34
R. pellisa 17-19, 30-31, 39, 43, 47, 203, 206, 214
R. peripla 206
R. rickeri 17-19, 28, 39, 43, 47, 203, 206, 214
R. sibirica group 28-31, 205-206, 216
R. sonoma 205
R. stigmatica 26
R. tucula 17-21, 38, 41-46, 203, 205, 213
R. vaccua 17-18, 31-32, 39, 44, 48, 203, 206, 213
R. vagrita 17-19, 35-36, 40, 45, 48, 203, 206, 213
R. vagrita group 35-37, 206, 216
R. vao 205
R. venena 17-19, 24, 40, 45, 48, 203, 205, 406
R. vepulsa 17-19, 28-29, 39, 43, 47, 203, 206, 214
R. verrula 17-19, 34-35, 40, 45, 48, 203, 206, 213
R. verrula group 34-35, 206, 216
R. vobara 17-19, 32-33, 40, 44, 47, 203, 206, 214
R. vobara group 32-33, 206, 216
R. vocala 205
R. vofixa 17-18, 22, 38, 41, 46, 203, 205, 213
R. vofixa group 22, 205, 216
R. vuzana 206
R. sp. one 18, 37, 40, 45, 48, 203
R. sp. two 19, 37, 40, 45, 48, 203
Rhysacophilidae 3-234, 406
Rhysacophilinae 16
Ricker, W. E. 95, 128, 146, 196
Rivard, I. 244-247, 250-251
Robin, Y. 437, 444
Robineau-Desvoidy, J. -B. 346, 374, 379
Rock, P. J. G. 421
Rondani, C. 317, 324
Rosa acicularis 296
Roselle, R. 415
Rotramel, G. L. 196
Rowe, J. S. 220-221
Rubiozyma 345
Sabellav pavonina 444-445
Salix 309
Salsola pestifer 425
Salt, R. W. 421
Sasakawa, M. 296-298, 303, 312, 316, 375
Saville, D. B. O. 198
Say, T. 100-101, 145
Schaaf, A. C. 427
Schaupp, F. G. 245
Schiodt, J. C. 247
Schoonhoven, L. M. 256
Schrank, F. von P. 375
Scirpus 321, 387
Seamans, H. L. 411, 415-431
Sehgal, V. K. 255-280, 291-405
Senecio 381, 383, 387
S. congestus pallustris 377, 387
S. pauciflorus 377, 387
S. vulgaris 268, 272
Shepherdia 327
S. canadensis 327, 386
Shewell, G. E. 299, 302, 324, 344
Shizukuoa 316
Sibley, C. K. 95-97, 119, 124-126, 134, 146
Silene noctiflora 271
Siltala, A. J. 95
Simpson, C. B. 95
Simpson, G. G. 14
Sipunculus nudus 437, 444
Siridomyza 312
Smilacinastellata 268, 339, 387
Smith, G. M. 95, 119, 126, 146
Smith, J. B. 145-146, 416
Smith, S. D. 20-36, 55, 67-68, 73, 137, 152, 201, 211
Smulyan, M. T. 256, 263, 380
Snodgrass, R. E. 145
Solanum tuberosum 267, 273
Solidago 295, 312, 325, 328, 333, 378, 386, 268, 273, 278, 425
S. lepida 378-379, 387
Sonchus 326, 384, 425
S. arvensis 273
S. asper 345
S. uliginosus 268, 272, 275, 366, 387
Sønderup, H. P. S. 252
Sorenson, C. J. 415, 421-422, 425-429
Spencer, K. A. 256, 278, 291-294, 297-350, 354
spiders, Alberta 237, 250
spiders, arable fields 237, 250
Spirographis spallanzanii 444
Sprules, W. M. 125, 146
staphylinid beetles, Alberta 237, 250
staphylinid beetles, arable fields 237, 250
Stegmaier, C. E. 333-334
Steinhaus, E. A. 429
Stenaphylacini 253
Stenaphylax 96, 107, 116, 121, 125, 138, 145-146
Stenaphylax comma 240
Stenaphylacini 4, 82, 142-148
Stenophylax 96, 107, 116, 121, 125, 138, 145-146
Stentor coerules 437
Strand, A. L. 415, 418-431
Strickland, E. H. 291, 411, 419, 427-430
Stride, G. O. 256
Strobl, G. 303
Styella mamiculata 437
Sugiyama, S. 256
Symptetrum rubicundulum 437
Symphoricarpos 360, 384, 386
S. albus 346, 347, 386
S. occidentalis 349, 386
Symnuchus impunctatus 239
Szorényi, E. 437, 444
Tabanidae 407-408
Tachinidae 428
Tachyporus 250
Takhtajan, A. 265, 383
Tanacetum 256, 266, 270, 274-477
T. vulgare 256-261, 266-275, 335, 369, 387
Taraxacum 326, 384, 387
T. officinale 268, 272, 313, 340, 366
Tatchell, E. C. 437
Tauber, C. A. 256, 258, 261
Tauber, J. M. 256, 258, 261
Teskey, H. J. 407
Tetrahymena pyriformis 437
Thalictrum 352, 384-385
T. venulosum 356, 362-363, 381, 384, 385
Thienemann, A. 67
Thlaspi arvense 267, 271
Thoai, N. V. 437, 444
Thomas, A. W. 407-408
Thomson, C. G. 133
thorax, evolution 284-286
thorax, morphology 284-286
Thornley, H. F. 415, 421-422, 425-429
Thorsteinson, A. J. 256, 278
Thut, R. N. 28, 31, 34, 36
Tilden, J. S. 261
Tilman, H. W. 200
Trechus quadrirstris 241
Trehan, K. N. 280
Trichocellus cognatus 240, 242, 249
Trichoptera 1-234, 406
Trifolium repens 334, 385
Triticum 323
T. aestivum 387
Trophosa terricola 250
Tropaeolum 267
Tylomyza 312
Typha latifolia 268, 272, 274
Uhr, M. L. 437
Ulmus americana 296-298, 385
Unzicker, J. D. 26, 67, 76, 145
Urtica 296, 302, 305, 308, 368
U. gracilis 385
Veronica 386
Verschaffelt, E. 256
Viala, B. 437
Vicia americana 267, 334, 341, 385
Vigna 334
Villa alternata 428
V. willistoni 428
Virden, R. 437-439, 444-445
Vorhes, C. T. 119, 145
Wagneria rohweri 428
Walkden, H. H. 416, 419-421, 427-429
Walker, E. M. 196
Walker, F. 67, 91-92, 95, 102, 112, 119, 122, 125-127, 145-146, 149-150
Wall, R. E. 430
Watts, D. C. 437-439, 444-445
Watts, R. C. 444
Webster, F. M. 256
Wendland, W. M. 199
Wenner, B. J. 431
Westfall, M. J. 196
Westgate, J. A. 198-200
Westwood, J. O. 349
Whitehead, D. R. 283-284
Whittaker, R. H. 256, 278
Wiggins, G. B. 89, 97-99, 102-104, 109, 116, 119, 124, 133, 143, 146, 201, 211
Wray, D. L. 125, 145
Wyman, M. 287-289
Xyraeomyza 344
Xysticus californicus 250
Zea 323
Zele 428
Zetterstedt, J. W. 65-67, 98, 117, 122, 132, 323, 364
Zinnia 266, 268, 273, 275
Zizania 322
Quaestiones

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Volume 7 Number 1 19 February 1971

CONTENTS

Guest Editorial — Northwestern Caddisflies ......................... 1
Nimmo — The adult Rhyacophilidae and Limnephilidae (Trichoptera) of Alberta and Eastern British Columbia and their post-glacial origin .......... 3

Guest Editorial — Northwestern Caddisflies

It is a good half century since the world famous Russian trichopterist, Dr. A. B. Martynov, declared that the Trichoptera were an ideal group from the standpoint of obtaining meaningful bio-geographic inferences. Dr. Martynov himself never followed up his historic statement on the Trichoptera, but instead gradually became engrossed in the study of fossil insects. His prophetic remark has, nevertheless, been borne out as group after group of the caddisflies have been studied on a phylogenetic and bio-geographic basis.

As controversies have emerged in recent years concerning the past history of the continental masses, Dr. Martynov’s special field of caddisfly study, the biota of the far north, has gradually become of increased importance in contributing information of unusual interest concerning inter-continental dispersals. The northern caddisflies of Europe have been well known for over a century, thanks to the pioneer work of Zetterstedt in Scandinavia and McLachlan in England. These investigators assembled and studied material and information on the northern fauna of their native lands and regions. Early in his career, Martynov himself published many papers making known the characteristics and distribution of the Trichoptera of Russia and especially the fauna of Siberia.

During this time, little was discovered concerning the Trichoptera of northern North America. Barnston and Kennicott made the first extensive northern collections, the former in the area immediately south of Hudson Bay, the latter in north central areas of Canada, including Great Slave Lake. In more recent years, limnological investigators added many valuable collections and lately entomologists have collected many caddisflies in the Government of Canada’s massive northern insect survey.

Although taxonomic problems concerning many northern species of Trichoptera have been elucidated by a variety of authors, one facet necessary to achieving a synthesis of the Holarctic caddisfly fauna has been sorely lacking. This is a thorough study of the group for northwestern North America. For several years such a study appeared to be in the offing and was actually prepared by J. Jared Davis. But because of publication difficulties and other obstacles this useful manuscript never graced the printed page.

The study of the Alberta caddisflies presented in this publication is, therefore, a timely and invaluable contribution to our knowledge of the Trichoptera of the far north. It gives us, first, a basis of discriminating identification for all the species of the region for the families treated, and second, geographic and ecological parameters that will be helpful in integrating these species with their relatives in other parts of the northern Holarctic range. The excellent illustrations of Alberta specimens will be of inestimable value in subsequent studies of intra-specific variation and its implications concerning post-Pleistocene coloniza-
tion of deglaciated areas.

In this wise, Dr. Nimmo's study will become a keystone in a synthesis of the evolutionary history of the northern biota.

Herbert H. Ross
Department of Entomology
University of Georgia
Athens, Georgia

November 27, 1970
Of the Rhyacophilidae 22 species and of the Limnephilidae 91 species are recorded here from the area, making a total of 113 species. Each species is described, and keys are provided for identification of adult specimens to species.

Seven species of Limnephilidae are described as new: Imania hector; Apatania alberta; Homophylax baldur; Oligophlebodes zelti; Limnephilus susana; Limnephilus valhalla; and Philocasca thor.

The post-glacial origin of this fauna is examined, taking into consideration the possible effects of past and present climatic patterns, extent of glacial ice masses and locations of possible refugia, and locations and drainage patterns of major glacial and post-glacial lakes. Also examined are the 12 range patterns exhibited by the species, and the distributions of each species relative to the other species in its genus or species group. The 12 range patterns form two main groups: one group of six is restricted wholly to the western Cordillera of North America; and the remaining six are more widely distributed, being largely transcontinental in extent. Altitudinal distributions are also briefly examined.

The conclusions reached are that only 5% of the present fauna is derived postglacially from the Beringian refugium, while 95% is derived from North America south of the southern limit of glacial ice. Dividing the 95% portion further, 61% is derived from the western Cordillera of the United States, 8% from eastern North America, 7% from the central Great Plains, 18% from all of North America south of the ice, i.e. from transcontinental species, and 1% is of uncertain derivation. (Traduction française à la page 234).

CONTENTS

Materials ........................................ p. 5
Methods .......................................... p. 11
The Family Rhyacophilidae Stephens ................. p. 16
The Family Limnephilidae Kolenati .................. p. 49
Origins and relationships of the fauna .............. p. 196
References ....................................... p. 224

Purpose of the study

The primary objective of this study is to determine the composition of the fauna of two families of Trichoptera, the Rhyacophilidae and Limnephilidae, in Alberta and eastern British Columbia. Secondly, by an examination of species distributions and relationships it is hoped to elucidate the post-glacial origins of the fauna.

While these are the major objectives of the study, there are some subsidiary benefits to be derived from the results. The first is the additional knowledge of North American Trichoptera which accrues, as to distributions, correlation of the sexes in species in which the female was previously unknown, and the discovery of new species. A second advantage of such a compilation as this, on a regional fauna, is the facilitation of ecological and other
studies of the adult Trichoptera of the area. Identifications should be possible without recourse to a scattered and difficult literature.

The third benefit is facilitation of studies of the immature stages of the species of the two families in the study area. The immature stages of most species are unknown at present, and it is hoped that the identification facilities supplied in this study will permit the immatures to be correctly correlated and identified. Once this is done ecological studies on the immature stages can be carried out.

The taxa studied

Originally I had hoped to examine all families of Trichoptera in the study area, but the large number of species, estimated at close to 200, and limitations of time precluded this. Consequently two families were decided upon: the Rhyacophilidae and Limnephilidae. A minimum of 113 species of these two families is recorded here from the study area.

Apart from my intrinsic interest, these two families were selected for the following reasons. The Rhyacophilidae are a distinctly mountain group of Trichoptera and should thus prove useful in tracing faunal changes in the study area. The Limnephilidae occur in both mountains and plains, with distinctive large faunas in each area, and should prove useful in elucidating faunal changes in both areas.

The Rhyacophilidae are represented in the study area by 22 species of one genus, Rhyacophila. These species represent 11 species groups which, in the text, are presented in the sequence of Ross (1956). The Limnephilidae are represented in the study area by 91 species. These variously represent a total of five subfamilies, four tribes, and 26 genera. In this study Schmid's (1955) order of presentation is used. Table 1 presents the names and organisation of the higher taxa of the Limnephilidae of the area.

The study area

Geographically the investigation embraces the Province of Alberta and the Rocky Mountains of eastern British Columbia. The western limits in British Columbia comprise the line from Kimberly to Golden, thence to Revelstoke, to Avola, and finally to the Mount Robson area. By these limits the northern portion of the Selkirk Mountains is also included.

Some information is also included which was derived from a collection from the Simpson Islands of Great Slave Lake, Northwest Territories. The lake is just over 50 miles north of the northern boundary of Alberta and the area was, until recently, difficult of access. It is felt that any faunal information on Trichoptera from the lake would be applicable to northern Alberta and I took the opportunity in 1964 of arranging with Mr. D. J. Larson, Lethbridge, Alberta, to collect adult Trichoptera for me while in the area.

Figure 1 illustrates the positions of the localities from which insects recorded here were taken. Figures 1a and 1b are enlargements of certain portions of Fig. 1 in which too many localities are recorded for inclusion in that figure. In Fig. 1, 1a, and 1b, many localities are listed as such-and-such a lake or river. This refers to the point at which the nearest road touches on, or crosses these bodies of water.

The study is limited to the area outlined above for two main reasons. It is a convenient delimited area located immediately across the mountain and plains routes between Alaska and the remainder of North America, and can be expected to yield evidence of faunal changes or dispersals due to glaciations or climatic changes. Also, embracing as it does both mountain and plains regions (Fig. 2), and ranging from boreal forest in the north, through aspen parkland, to near desert grassland in the south (Fig. 3), the area could be expected to yield a large and most interesting fauna of Trichoptera.
Table 1. The family Limnephilidae in Alberta and eastern British Columbia.

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<th>Subfamily</th>
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<td>Dicosmoecus</td>
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<td>Onocosmoecus</td>
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<td>Apataniinae</td>
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<td>Neophylacinae</td>
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<td>Oligophlebodes</td>
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<td>Neothremma</td>
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<td>Pseudostenophylacinae</td>
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<td>Limnophilinae</td>
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<td>Glyphopsyche</td>
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<td>Psychoglypha</td>
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<td>Phanocelia</td>
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MATERIALS

Total number of specimens

I examined 7,604 specimens of both sexes: 2,915 specimens of Rhyacophilidae; and 4,689 specimens of Limnephilidae. The total number of specimens of each species examined, by numbers per sex, is given at the end of its description in the text.

Sources of material

Most of the above material was collected by me during the summers of 1965, 1966,
Fig. 1. Alberta showing major highways, secondary roads, and collecting points. See also Fig. 1a and 1b.
Fig. 1a. Outline map of the Forestry Trunk Road between Hinton and Nordegg (left), and Nordegg and Cochrane (right). • collecting points
Fig. 1b. Forestry Trunk Road and connecting roads between Waterton and Banff (left); Banff-Jasper Highway between Banff and Jasper (right); • collecting points.
Fig. 2. Major physical features of Alberta and eastern British Columbia, showing rivers, lakes, and three levels of altitude.
Fig. 3. Forest Regions of Alberta and eastern British Columbia (adapted from Rowe, 1959).
1967, and 1968. Some specimens were obtained from the collections of the Department of Entomology, University of Alberta. A very small proportion was obtained on loan from the following institutions: Canadian National Collection, Ottawa; Royal Ontario Museum, Toronto; Illinois Natural History Survey, Urbana, Illinois, United States; and the United States National Museum, Washington, D. C., United States. The source of the borrowed material is given with species descriptions wherever applicable. Some material was obtained from graduate students in the Department of Zoology, University of Alberta, who obtained it in the course of their own studies, and passed it on to me for identification. The material recorded from Great Slave Lake was the result of a collection made in the summer of 1964 by Mr. D. J. Larson, and passed on to me. A small collection was obtained on loan from the Banff National Park Museum, Banff, Alberta.

In the text, locality records have been condensed to map form. Lists of localities and dates are given for new species only. A complete list of all such data is deposited in the Department of Entomology, University of Alberta, Edmonton, and is available to interested workers.

Disposition of material
All borrowed material was returned to the lending institutions.

Type material. — All type material is deposited in the Canadian National Collection, Ottawa, unless stated otherwise in the descriptions of new species. Borrowed material here designated as type material was returned to the lending institution. Where sufficient para-type material exists in unborrowed material, at least one of each sex is deposited in the Strickland Museum, Department of Entomology, University of Alberta.

Other material. — Most of the remainder of the material, all of which was obtained in the field in the course of this study, is deposited in the Strickland Museum of the Department of Entomology, University of Alberta. All remaining material, with the agreement of the Department of Entomology, University of Alberta, forms part of my own reference collection, or was distributed to other institutions or workers who expressed an interest in obtaining such material.

Determination of species present in the study area
It was too much to hope that all species known from the study area would be represented in my field collections. Therefore recourse was had to the literature pertaining to North American Trichoptera, and to Fischer’s ‘Trichopterorum Catalogus’ (1960, 1967, 1968) in a search for species recorded from Alberta, but not represented in my collections. The collections of the Canadian National Collection, Royal Ontario Museum, and the Illinois Natural History Survey were searched for specimens from the area, both to add to my records and to supplement the list of species. These methods proved most successful, and the names of several species were added to the list in consequence.

METHODS

Collecting methods
Several methods were employed in collecting the adult specimens used in this study. First was hand-netting, either of individuals in flight, or by sweeping vegetation adjacent to bodies of fresh water. Specimens were collected from a variety of vegetation, including trees overhanging the water, and sedges in the water. The next method involved searching the undersides of bridges, or the interior surfaces of culverts under roads. This method was very effective, but was of maximum use only after much practice.
The above methods were employed in daytime collecting. Collection of adult Trichoptera is also possible at nighttime, by the use of light sources of various types. As the insects generally land close to the light source, a white sheet is used below the light to render them more conspicuous and thus easier to pick up. The best times and conditions for light trapping are from twilight to about 1 or 1½ hours later, at air temperatures greater than 55°F, on cloudy evenings with no wind other than the most gentle air movements (see Nimmo, 1966b).

The first light source was a kerosene pressure lamp. This method is of use on warm, humid evenings only. Car headlights were also used. They were aimed toward the body of water from which the insects were expected to arrive in flight. An electric lamp rich in the ultra-violet wavelengths was especially productive, even on cooler evenings. It was most reliable when connected to a mains supply of current. This, however, was rarely possible and other sources were used, including a portable gasoline generator, and a portable 12-volt battery and DC-AC rectifier. The generator and battery sources, however, were unreliable.

**Preservation of material**

I collected all specimens directly into 80% ethanol, which both killed and preserved the specimens. While this preservative may fade some specimens it permitted me to manipulate whole specimens under the microscope. Storage is also facilitated. Dried, pinned specimens are difficult to handle, shrivel up on drying, and are much more liable to damage.

**Sorting of collections**

All material acquired at one time and locality was collected into a single vial and labelled with pertinent information. In the laboratory the contents of each vial were sorted to species and all specimens of each species, from each collecting episode, were placed collectively and permanently in a new vial of 80% ethanol and labelled. After this initial sorting the vials were sorted to groups, each of which contained specimens of one species.

**Association of males and females.** — On occasion it was difficult to correlate correctly the specimens of the two sexes of a species. On the initial sorting of field collections this was accomplished in one of three ways. Firstly, if both sexes were already described in the literature no problem was encountered. Secondly, if pairs *in copula* were taken in the field, each pair was segregated immediately to a separate vial. Later examination in the laboratory provided the information required to correctly associate specimens of the two sexes of any one species in mixed field collections, and specimens of each sex collected individually and in separate vials. And finally, if the above two sources of information were not available, wing colour patterns, venation, and various other body characters were used for associative purposes. Frequently the general facies of the specimens was all that was required. Also, a knowledge of the general facies of the genera involved assisted in narrowing the field. Rarely were very closely related species taken together. This last method was, in retrospect, found to have worked remarkably well; improper associations were rare and were later corrected.

**Identification of material.** — In identifying the material collected, the available literature was consulted. The specimens of Rhyacophilidae were identifiable with the assistance of Ross’ (1956) publication. For the Limnephilidae Schmid’s (1955) publication was used to the generic level. Identification to species was then made with the aid of scattered minor literature referred to by Schmid for each species. In case of doubt, material was forwarded to F. Schmid, of the Entomology Research Institute, Ottawa, G. B. Wiggins, of the Royal Ontario Museum, Toronto, H. H. Ross, of the Illinois Natural History Survey, Urbana, Illinois, or to D. G. Denning, Moraga, California for identification. I also spent one week at the Illinois Natural History Survey examining the collections, both for records, and for purposes of identifying material.
Type material was not normally examined. Little such material was available at the institutions which I visited. Many of my identifications were made from specimens identified by workers who had previously had access to such type material. For a very few species type material was all that was available and this was either borrowed, or drawings made from the type were obtained on loan from the original authors.

Preparation of material. — To identify the Trichoptera recorded as occurring in the study area genitalic characters were used at the species level, and venational, genitalic, and other non-genitalic characters were used at the supraspecific level. Material for identification and drawing was prepared as set out below.

The wings. The wings of the right side of the thorax were illustrated. These were torn off cleanly at their bases with stiff, needle-pointed forceps. They were then passed through 95% ethanol for washing and stiffening, and spread on a clean glass slide. A second slide, with 2.0 mm wide strips of cellulose tape along each lower edge, was then placed on top of the first and the whole assemblage placed in a small hand-sized press. After clamping the slides into the press the long edges were united by an application of Lepage’s white ‘Bondfast’ glue, which was found effective in binding the two slides together on drying. The cellulose tape prevented seepage of glue between the slides. The slides were then unclamped, labelled, and filed for future use. The wings were taken from the males, unless sexual dimorphism was evident on in situ examination, in which case the female wings were also treated as above, and illustrated. When only the female was known, the wings of this sex were illustrated.

The genitalia. The male and female genitalia were prepared for examination and illustration by removing the entire abdomen of a specimen and boiling it in a very strong solution of KOH, to dissolve the abdominal organs and tissues. The abdomen was then removed immediately to glacial acetic acid for clearing. After using this procedure for some time, I discovered that, while in the acid, a vigorous evolution of gas occurred within the abdominal contents; this gas was violently expelled on return to the boiling KOH, removing the abdominal contents in large part. Several such transfers between the two solutions resulted in swift removal of the abdominal contents. The genital capsule and abdomen together were then returned to the vial of 80% ethanol which contained the donor specimen.

Preparation of drawings

Wing drawings were made with a camera lucida mounted on a stereo binocular microscope. Slides were made of the wings of all species recorded here, but not all are illustrated as, in Limnephilus for example, the venation varied little between species.

Genitalic drawings were made using a square-grid eyepiece in a stereo binocular microscope. The image was imparted to a segment of bristol board lined in pencil with a similar squared grid. The size of the grid squares varied according to the size of the specimen, as it was desired to produce drawings of similar sizes for all species. The genital capsule being drawn was held steady, in a dish of 80% ethanol under the microscope, by a piece of wire of sufficient weight inserted anteriorly into the abdominal cavity.

In the drawings of the male the genital segments (IX and X) are frequently extracted from their normal position, retracted into segment VIII; this was done for greater clarity, but was not possible with the specimens of certain species. In the drawings of the male genital capsule of Rhyacophila spp. the lateral aspect shows the mesal face of the far (right hand) side clasper as this is the face which bears important characters.

Measurements and scales

Wing length is used to indicate relative sizes of species to each other. It is the distance,
in millimeters, from the fore wing tip to the base at the costal edge where the wing folds over at rest. Males were measured, unless only females were available. Scale bars are provided for the genitalic and wing drawings. The genitalic scale bars represent 0.5 mm or 0.25 mm, depending on the size of the specimen. The wing scale bars represent 4.0 mm. All measurements and scale bars were obtained by use of a micrometer eyepiece in a stereo binocular microscope. The scale bars for the genitalic drawings are immediately adjacent to the lateral aspect of the male genital capsule. All drawings, male and female, with the exception of wing drawings, which are located elsewhere, for any one species are to the same scale. When only the female is known no scale is given. Drawings derived from sources other than specimens available to me, have no scale, since the original sources had none.

Criteria employed

Inasmuch as this study is not a revision but a faunal survey, I restrict my remarks to taxa at the species level. For higher taxa I have adhered to the work of Ross (1956) and Schmid (1955). It is desirable to outline criteria at the species level as several new species are described.

Characters used in distinguishing species. — In the study of Trichoptera at the species level, with the exception of the species of a very few genera, the genitalic characters are of prime importance. Species are segregated and recognised on the basis of differences in genitalic characters. Other characters may be referred to in combination as distinguishing one species from another. Such are, the colour pattern of the fore wing, if sufficiently distinctive and constant, spur formula, coloration of the thorax, head or legs, and form and setation of designated areas or parts of the body. But the use of such characters individually is strictly subsidiary, as they are rarely sufficiently distinctive by themselves to provide a basis for erection of species. On the other hand, such characters may be utilised in the erection of higher taxa, when common to two or more species of still higher taxa. Wing pattern is, however, of paramount importance in distinguishing species of certain genera (e.g. Leptocella, of the Leptoceridae) where genitalic characters are highly variable and of dubious utility.

In the study of genitalic structures at the species level, form, structure, setation or spination are the important characters to be observed. Coloration, for example, is usually held to be of no importance, varying with age of the specimens. While it is accepted, indeed expected, that the characters in which interspecific differences may be detected vary intraspecifically, in most species recorded here this variation is limited and can, with practice, be recognised for what it is. In opposition to certain other groups of insects, Trichoptera species may be distinguished by critical examination of the general facies of the characters selected. No application of statistical techniques has yet been found necessary.

While supraspecific taxa are generally excluded from this discussion, it may be noted that, in initially segregating species of higher taxa to membership in these taxa, the characters employed are frequently venational, or are a variety of general body characters, and are frequently genitalic, involving considerations of characters less varied than at the specific level, and more revealing of the broader evolutionary history of the group.

Criteria at the species level. — Simpson (1961) defines the genetical species as follows: ‘Species are groups of actually or potentially inter-breeding natural populations, which are reproductively isolated from other such groups’. This biological species definition is the ideal, which I accept, but it is normally impractical to use it as a working definition due to lack of information. Simpson discusses this at some length. He also states that, in practice, this definition employs morphological criteria, but without the adverse implications of the ‘morphospecies’.
In dealing with Trichoptera species only morphological and distributional data are available at present, as outlined above. The data are, however, applied with the intentions of the above definition in mind; morphological differences are taken as evidence of reproductive isolation.

In this study I employ the following definition: A species is that group of individuals which is recognized as a unit by a multiplicity of characters, the nature of forms of which are peculiar to, and constant within, the available specimens, and which are distinguished from specimens of the presumed most closely related species by pronounced discontinuities in any or all of the characters. Interspecific variation, as mentioned above, is taken into account with regard to the constancy of characters within a species, and the discontinuities between species.

While, in most species of the Alberta Rhyacophilidae and Limnephilidae, the interspecific discontinuities are sufficiently evident as to require no comment, in some genera or species groups the recognised species are very similar. This may lead to some confusion in sorting if specimens of two similar species are collected simultaneously. With regard to such species, particularly if described as new, I reserved judgement as to their separate identity until I had sufficient information on which to base a decision. This information was acquired in the form of collecting data. Specimens of the species concerned had to be collected separately at different localities sufficiently often to instil confidence in regarding them as separate entities.

Miscellaneous notes

Notes on the descriptions. — General body descriptions are derived from the male. Sexual dimorphisms of the female are noted wherever applicable. Wing colours are of the male unless stated otherwise; the hind wings are hyaline in most species. The costal area referred to is that part of the wing between the costa and subcosta, extending from the humeral cross-vein to the point at which the costa and subcosta meet distally.

Notes on the text. — Most species recorded herein are strictly nearctic in distribution. The literature for each of these species is, to the best of my knowledge, complete to early 1970. However, for the holarctic species in the study area, only references to nearctic literature are recorded here, and the reader is referred in appropriate cases to Fischer’s ‘Trichopterorum Catalogus’ (1967; 1968) for a complete listing of palaearctic literature. This system is adopted as the literature on these holarctic species is too extensive for complete inclusion here. Synonymies for each species are complete, however. Type localities are named for each specific epithet, and are given in the citation for each species.

The keys used here for supraspecific taxa are adapted in translation from Schmid (1955). They are adapted by restricting them to the taxa recorded from the study area. At the species level, keys have been constructed for the males, and females, of each genus, if known. The character synopses for the supraspecific taxa of the Limnephilidae are adapted in translation from Schmid (1955), and are greatly condensed.

Immediately following each species description is a short statement of the known, or suspected, habitats, and biology, including notes on emergence if available and flying season, of the species. This information was largely derived from personal notes.

Notes on distribution maps. — The range maps presented here give only an approximate outline of collecting localities in the study area due to limitations of scale (see above, p. 11, for information on exact listing of collecting localities for each species). The inset maps of North America give only the nearctic distributions of each species. In the cases of holarctic species the palaearctic ranges are described briefly in the text.
THE FAMILY RHYACOPHILIDAE STEPHENS

This family is represented in Alberta and eastern British Columbia by the genus Rhyacophila Pictet only, belonging to the subfamily Rhyacophilinae Ulmer. Immediately following are synopses of the familial characteristics of the Rhyacophilidae, as adapted from Mosely (1939) and Mosely and Kimmins (1953), excluding the Glossosomatidae, and the subfamilial characteristics of the Rhyacophilinae, as adapted from Mosely (1939) and Ross (1956). The synopsis of characteristics for the genus Rhyacophila is adapted from Mosely (1939) and Ross (1956). The grouping of species within the genus is adopted from Ross (1956).

Character synopsis of the Rhyacophilidae. — Ocelli three. Maxillary palpi each of five articles in both sexes; basal articles short, remainder long, cylindrical. Metascutellum with or without warts. In some genera the middle tibia is dilated considerably. Spurs 3, 4, 4 in both sexes. Wings elongate, roughly parabolic, obliquely truncated apically. Hind wings shorter, narrower than fore wings. Venation generally complete (Fig. 4). Fore wings with apical cells f1-f5 present. Hind wings with only f2 and f5 present in some genera. Discoidal cell open or closed on fore and hind wings, or lacking on hind wings. R1 of fore wings forked apically or not. Thyridial cell present, sub-radial present or absent.

Character synopsis of the Rhyacophilinae. — Middle tibia not dilated. Fore wings with apical cells f1-f5 present; hind wings with f1-f3, and f5, present. Discoidal cell of both fore and hind wings open. Male genitalia with anal sclerite generally present, rarely absent.

The genus Rhyacophila Pictet

Synopsis of characters. — Antennae slender, shorter than wings; pedicel very short. Second article of maxillary palpus short, globular. Tergum VIII of male rarely modified postero-dorsally. Segment IX wide throughout, but varying in width. Claspers of two articles; of varied size; large, conspicuous. Segment X with anal sclerite in most species. Female genitalia long, tapered, slender, with pair of terminal cerci. Segments IX-XI membranous. Segment VIII with basal portion sclerotized, in some species complexly, with attendant lobes.

The genus Rhyacophila in Alberta and eastern British Columbia. — As presented in this study the genus is represented by 22 species, of which two are represented by unassociated females. The species are primarily confined to the mountain and foothill areas, but several range eastward to the plains, and two are transcontinental.

Following are separate keys to the males and females of the genus known to be present in the area.

Key to the Males of the Alberta and eastern British Columbia species of Rhyacophila Pictet

1a. Aedeagus simple, limnephiloid in general appearance, with paired lateral arms and simple median shaft (Fig. 25, 29, 33). Segment X rather like bird’s head in lateral aspect; the crown with multiple rounded depressions (Fig. 24, 28, 32) ................................................................. 2

1b. Aedeagus not limnephiloid, ranging from very small and simple (Fig. 91) to large and complex, with as many as five lobes (Fig. 52) ................... 4

2a.(1a) Distal article of clasper very deeply cleft, with ventral lobe lanceolate, dorsal lobe finger-like (Fig. 32). Lateral arms of aedeagus fringed distally with tuft of fine hairs (Fig. 33) ........................................ R. glaciera Denning, p. 21.

2b. Distal article of clasper not constructed ........................................... 3

3a.(2b) Distal article of clasper with dorsal lobe directed strongly meso-anterald along mesal face of basal segment (Fig. 24). Anal sclerite flanked by simple, laterally
uncleft, ventral lobes of segment X ............... *R. alberta* Banks, p. 19.
3b. Distal article of clasper with dorsal edge thick, fleshy; horizontally almost cylindrical. Anal sclerite flanked by two lobes of segment X on each side (Fig. 28) .......................................................... *R. tucula* Ross, p. 20.

4a.(1b) Postero-dorsal edge of tergum VIII with one or more lobes (Fig. 54, 86) .... 5
4b. Postero-dorsal edge of tergum VIII unmodified ................................. 6

5a.(4a) Tergum VIII with one small, rounded lobe (Fig. 54) ............ *R. rickeri* Ross, p. 28.
5b. Tergum VIII with three distinct lobes; lateral lobes large, rounded distally and flanking curved, square tipped median lobe (Fig. 86, 87) ........................................................................ *R. verrula* Milne, p. 34.

6a.(4b) Postero-dorsal edge of segment IX with distinct tuft of long, thick setae, directed posterad (Fig. 96) .......................................................... *R. vomina* Milne, p. 24.
6b. Postero-dorsal edge of segment IX quite clear of setae or hairs ............. 7

7a.(6b) Postero-dorsal edge of segment IX developed posterad as distinct lobe projected well beyond segment (Fig. 39, 51, 89, 93) ................................. 8
7b. Postero-dorsal edge of segment IX not so developed .................. 11

8a.(7a) Segment X with long, thin, curved and folded strap-like median lobe (Fig. 89, 93) ................................................................. 9
8b. Segment X without strap-like median lobe ........................................ 10

9a.(8a) Lobe of segment IX bilobed distally, in dorsal aspect (Fig. 90) ............ *R. vagrita* Milne, p. 35.
9b. Lobe of segment IX trilobed distally, in dorsal aspect; lateral lobes shorter than median lobe (Fig. 94) .......................................................... *R. milnei* Ross, p. 36.

10a.(8b) Segment X without anal sclerite. Aedeagus small, with median shaft short and with two rounded lateral wings (Fig. 39); lateral arms ventral, membranous, terminated by brush of stout, dark spines (Fig. 40) .......................................................... *R. acropedes* Banks, p. 23.
10b. Segment X with anal sclerite and large, dish-like tergal strap; segment X of two thin, vertical plates (Fig. 51). Aedeagus huge, with membranous base, long clavate lateral arms, hooded tip on median shaft and two lanceolate ventral lobes (Fig. 52) .......................................................... *R. hyalinata* Banks, p. 27.

11a.(7b) Distal article of clasper bilobed (Fig. 35, 57, 65, 69, 75, 79) ................. 12
11b. Distal article of clasper not bilobed ............................................... 16

12a.(11a) Distal article of clasper cleft apically, appearing scissors-like (Fig. 69, 75) ................................. 13
12b. Distal article of clasper not scissors-like ......................................... 14

13a.(12a) Anal sclerite small, with two button-like disto-lateral lobes (Fig. 70) curved dorsad (Fig. 69) .......................................................... *R. vaccua* Milne, p. 31.
13b. Anal sclerite larger, with two simple, rectangular distal lobes (Fig. 76) directed ventrad from segment X (Fig. 75) .......................................................... *R. chilisla* Denning, p. 32.

14a.(12b) Segment X massive, convoluted plate (Fig. 57, 58) longer than claspers. No evident anal sclerite .................................................. *R. vepulsa* Milne, p. 28.
14b. Segment X shorter than claspers. Anal sclerite evident ............................................ 15

15a.(14b) Distal article of clasper with acuminate, triangular dorsal lobe (Fig. 35) ............... *R. vofixa* Milne, p. 22.
15b. Dorsal lobe of distal article minute, hooked ventrad (Fig. 65) .................. *R. pellisa* Ross, p. 30.
15c. Dorsal lobe of distal article large, rectangular (Fig. 79) ....................... *R. vobara* Milne, p. 32.

16a.(11b) Segment X long, plate-like, cleft deeply, in dorsal aspect (Fig. 63, 83) ........ 17
16b. Segment X short, of two lateral plates flanking anal sclerite (Fig. 42, 47) ... 18
17a.(16a) Aedeagus large plate with lateral edges curled dorsad, ejaculatory duct prolonged by slender, tapered, dorsally curved median tube (Fig. 62) ........................................ R. belona Ross, p. 29.
17b. Aedeagus complex, with two very long, membranous lateral arms terminated by spatulate, setose distal plate (Fig. 84) ............ R. angelita Banks, p. 33.
18a.(16b) Lateral plates of segment X simple (Fig. 42, 43) .......... R. bifila Banks, p. 25.
18b. Lateral plates of segment X bilobed (Fig. 47, 48) .................. R. coloradensis Banks, p. 26.

Key to the Females of the Alberta and eastern British Columbia species of Rhyacophila Pictet
1a. Basal portion of segment VIII strongly sclerotized, clearly demarcated from membranous distal portion (Fig. 26) ........................................ 2
1b. Basal portion of segment VIII weakly sclerotized, merged almost imperceptibly with distal membranous portion (Fig. 85) ................ 15
2a.(1a) Sclerotized portion of segment VIII with distinct lobes or processes quite free from main body of segment, except at bases (Fig. 26, 38, 45, 53, 65, 73) ... 3
2b. Sclerotized portion of segment VIII without such processes (Fig. 30, 34, 41, 61, 68, 92, 100) ........................................ 9
3a.(2a) Distal portion of segment VIII, and segments IX-XI shortened, partly retracted within sclerotized base of segment VIII (Fig. 45) ................ 4
3b. Distal portion of segment VIII, and segments IX-XI long, tapered gradually distad ........................................ 5
4a.(3a) Ventral lobes of segment VIII long, thin, arcuate, in ventral aspect (Fig. 46) ........................................ R. bifila Banks, p. 25.
4b. Ventral lobes of segment VIII short, rounded apically, on common pedicel (Fig. 50) .... R. coloradensis Banks, p. 26.
5a.(3b) Segment VIII with one medial ventral process, (Fig. 26, 27) ................ 6
5b. Segment VIII with two ventro-lateral processes (Fig. 38, 53, 65) ................ 7
6a.(5a) Ventral process acute-triangular, but with deep v-shaped distal cleft; process extended well posterad under membranous portion of segment (Fig. 73, 74) ........................................ R. vaccua Milne, p. 31.
6b. Ventral process short, triangular, with rounded apex (Fig. 27) ........................................ R. alberta Banks, p. 19.
7a.(5b) Membranous distal portion of segment VIII flanked on either side, just distad of sclerotized base by lightly sclerotized, oblong plate (Fig. 53) ........................................ R. hyalinata Banks, p. 27.
7b. Membranous distal portion of segment VIII without sclerotized plates ... 8
8a.(7b) Spermathecal sclerites long, slender, each with deep narrow hook at posterior end (Fig. 38) ........................................ R. vofixa Milne, p. 22.
8b. Spermathecal sclerite long, triangular in lateral aspect (Fig. 64) ........................................ R. belona Ross, p. 29.
9a.(2b) Posterior edge of sclerotized portion of segment VIII with dorsal portion offset anterad, with dorsal and ventral edges joined by long sloping edge (lateral aspect) (Fig. 61, 100) ........................................ 10
9b. Posterior edge not offset as above ........................................ 11
10a.(9a) Anterior sclerotized edge of segment VIII with retractor rod attached (Fig. 100) ........................................ R. species 1, p. 37.
10b. Anterior sclerotized edge of segment VIII without retractor rod attached (Fig. 61) ........................................... R. vepulsa Milne, p. 28.

11a.(9b) Membranous portion of segment VIII emergent from upper half of sclerotized portion; lower half pinched off in form of thin, plate-like keel posteriorly (Fig. 41) ........................................... R. acropedes Banks, p. 23.

11b. Membranous portion of segment VIII emergent from entire diameter of sclerotized portion ......................................................... 12

12a.(11b) Dorsal surface of segment VIII immediately distad of sclerotized portion, minutely spinate (Fig. 30) ........................................... R. tucula Ross, p. 20.

12b. Membranous portion of segment VIII not spine ........................................... 13

13a.(12b) Sclerotized portion of segment VIII with posterior edge indented ventrally, laterally, and dorsally, as two pairs of lateral extensions (Fig. 81) ........................................... R. vobara Milne, p. 32.

13b. Sclerotized portion of segment VIII with posterior edge circular, or only slightly sinuate ......................................................... 14

14a.(13b) No evident spermathecal sclerites (Fig. 34) .................. R. glaciera Denning, p. 21.

14b. Spermathecal sclerite long, narrow strap in ventral aspect, with slightly wider, darker, posterior end and distinctly widened, pierced, anterior end (Fig. 68) ......................................................... R. pellisa Ross, p. 30.

14c. Spermathecal sclerite long, thin, irregular rod in lateral aspect; tip small, pick-like (Fig. 92) ........................................... R. vagrita Milne, p. 35.

15a.(1b) Abdomen in area of segments VIII-X with one or more distinct annular swellings (Fig. 88, 102) ......................................................... 16

15b. No such annular swellings present ......................................................... 17

16a.(15a) Tergum X clearly sclerotized ........................................... R. verrula Milne, p. 34.

16b. Tergum X not sclerotized. Spermathecal sclerite spindle shaped in lateral aspect, with anterior end attenuated (Fig. 102) .................. R. species 2, p. 37.

17a.(15b) Spermathecal sclerite spindle shaped in lateral aspect (Fig. 56, 85) ........ 18

17b. Spermathecal sclerite relatively long, tapered posterad in ventral aspect; anterior end cleft, with distinct median fissure (Fig. 99) .................. R. venna Milne, p. 24.

18a.(17a) Spermathecal sclerite with both ends (in lateral aspect) attenuated (Fig. 85) ........................................... R. angelita Banks, p. 33.

18b. Spermathecal sclerite (in lateral aspect) sigmoid in outline (Fig. 56) ........................................... R. rickeri Ross, p. 28.

The alberta group

Males of this group are characterised by large anal sclerites, simple tenth terga and, especially, by simple, limnephiloid aedeagi, with simple lateral arms and median shaft. The group contains four species of which three are found in Alberta.

Rhyacophila alberta Banks, 1918
(Fig. 4a, 4b, 24-27, 104)


Males of this species are distinguished from males of other species of the alberta group by
dorsal lobe of distal article of clasper directed meso-anterad (Fig. 24). The rounded triangular lobe on lower posterior edge of segment VIII is characteristic of females of this species (Fig. 27).

Description. — Antennae very pale yellow. Vertex of head mottled red-brown. Fore wing length of male 11 mm; pale yellowish brown, heavily irrorate, with dark areas concentrated on veins. Stigma pale, opaque. Venation of fore and hind wings as in Fig. 4a, 4b.

Male genitalia. (Specimen from Gap, near Exshaw, Alberta). Segment IX rectangular dorsally, tapered sharply antero-ventrad to lateral sutures then widened ventrally (Fig. 24). Claspers each with massive rectangular basal article concave mesally, especially at base. Distal article with long triangular ventral lobe, and dorsal lobe directed meso-anterad along mesal face of basal article. Segment X with dorsal portion rather like skull and beak of bird, with small rounded depressions at peak. Ventral part of segment cleft dorso-ventrally, flanking divided anal sclerite. Aedeagus with median shaft long, thin, bulbous at mid point (Fig. 25); lateral arms long, with large, rounded, ventral lobe distally with five long, curved spines.

Female genitalia. (Specimen from Gap, near Exshaw, Alberta). Basal quarter of segment VIII sclerotized, proximal edge slightly bulged and divided from distal area by thin annular line; distal edge produced ventrally as short, stout, triangular tooth (Fig. 26, 27). Cerci short, hyaline.

Notes on biology. — Adults of this species appears to emerge from streams ranging from small mountain brooks to large, turbulent mountain torrents. The flying season extends from August 12 to October 9.

Geographical distribution. — The known range of this species extends from Alaska to Colorado and Utah (Fig. 104) apparently being confined largely to the Rocky Mountain chain. In Alberta this species is found in the mountains and foothills at altitudes between 4,000' and 6,500'. Dodds and Hisaw (1925b) recorded it from Colorado, between 9,000' and 11,000'.

I have examined 174 specimens, 131 males and 43 females, from the study area.

Rhyacophila tucula Ross, 1950

(Fig. 5a, 5b, 28-31, 105)


Males of this species are distinguished from males of other members of the alberta group by bifid lateral flaps of segment X enclosing anal sclerite, and by long, rectangular dorsal ridge or fold of distal article of clasper (Fig. 28). The spinate dorsal surface of membranous portion of segment VIII (Fig. 30) is distinctive of females.

Description. — Antennae pale yellow. Vertex of head red-brown, with distinct cruciform pattern posteriorly, formed from two intersecting sutures. Thorax straw yellow, to red-brown dorsally. Spurs dark brown. Fore wing length of male 9.5 mm; pale red-brown, irregularly irrorate with no distinct stigma. Venation of fore and hind wings as in Fig. 5a, 5b.

Male genitalia. (Specimen from Sundance Creek, west of Edson, Alberta). Segment IX laterally rectangular but with large triangular bight in lower half of posterior edge (Fig. 28). Claspers each with long, rectangular basal article channeled along entire length of mesal face. Segment X laterally similar to birds head, with two bifid ventral lobes flanking anal sclerite. Aedeagus with long, slender median shaft; distal portion of shaft very slender tube, basal portion long slender bulb; lateral arms long, slender, smoothly expanded distally, each with distal spine, and mesal edge with heavy, dark spines (Fig. 29).
Female genitalia. (Specimen from Alaska; in Illinois Natural History Survey). Segment VIII with basal half sclerotized, tapered (Fig. 30); proximal half of sclerotized portion light brown, remainder darker, clearly demarcated. Dorsal surface of membranous portion of segment VIII minutely spinate. Spermathecal sclerite long, almost hyaline (Fig. 31); distal end constricted as circular head (ventral aspect); lateral edges darker than remainder.

*Notes on biology.* — Smith (1968) records the larvae from “...small to medium streams with mixed rubble bottoms”, in Idaho. My records indicate fairly fast, rock filled streams to be the habitat of larvae of this species. Smith also records the adult flying season as September-October. My records indicate a flying season of August 24 to October 12.

*Geographical distribution.* — The known range of this species extends from Alaska to Wyoming and Oregon (Fig. 105). It extends east to the Rockies but appears to be centered primarily in the Coast Ranges. In Alberta the species is known only from one locality in the low eastern foothills near Edson. The two localities shown in eastern British Columbia are also at low altitude (under 4,000').

I have examined six males from the area.

*Rhyacophila glaciera* Denning, 1965

(*Fig. 6a, 6b, 32-34, 106)*


Males of this species are distinguished from males of other species of the *alberta* group by long, deeply cleft distal article of clasper. Females are distinguished by relatively unmodified segment VIII: posterior rim of sclerotized portion only very shallowly indented laterally.

*Description.* — Antennae light yellowish brown. Vertex of head deep reddish brown, except warts paler. Thorax brownish yellow, to red-brown dorsally. Spurs brown. Male fore wing length 8.8 mm; clear mottled greyish brown; stigma evident but light. Venation of fore and hind wings as in Fig. 6a, 6b.

Male genitalia. (Specimen from Mt. Edith Cavell, Jasper, Alberta). Segment IX with or without small dorsal, hyaline fin (Fig. 32). Segment IX strongly pinched in at lateral sutures, as in *R. tucula*. Claspers each with short basal article channeled on mesal face; distal article large, with very deep u-shaped cleft dividing it to rounded, finger-like, dorsal lobe and knife-like ventral lobe. Segment X with dorsal body only sparsely indented, forming rough semicircle. Aedeagus (Fig. 33) with median shaft in two distinct parts; distal part long, very thin; proximal part much thicker, continued thus to base. Lateral arms clavate in dorsal aspect; terminated by thick brush of setae.

Female genitalia. (Specimen from Mt. Edith Cavell, Jasper, Alberta). Basal part of segment VIII sclerotized, truncated, cone with slightly sinuate postero-lateral edges (Fig. 34). No cerci evident.

A *note on taxonomy.* — In his original description Denning (1965a) states that this species is not related to any other species of the genus. This may appear to be so, but an examination of the male genitalia, and a close comparison with the genitalia of *R. alberta* and *tucula* places this species in the *alberta* group beyond doubt. The virtual identity of the aedeagi of specimens of these species is of special importance in this connection.

*Notes on biology.* — This species frequents mountain streams ranging from small, turbulent, rocky creeks, to very small alpine trickles. The adult flying season extends from August 19 to October 7. I have taken specimens of this species crawling about on one to two feet of snow in October at the Mt. Edith Cavell alpine meadows in Jasper National Park. The nearby stream was largely frozen, but with occasional open holes in the thin ice.
Geographical distribution. — The known range of this species is very small. The species was only recently described from Montana. It is known only from the Rocky Mountains and Alberta. Altitude range is from 5,000’ to 7,000’.

Eight specimens, six males and two females, were examined from the study area.

The vofixa group

This group, represented here by only one species, is characterised by simple male genitalia in which the anal sclerite is divided into two large, ovate, lateral lobes. Aedeagus with large, finger-like, dorsal process; median shaft flanked by two finely divided lateral lobes like sheaves of spines. There are only two known species in this group, of which one occurs in Alberta.

Rhyacophila vofixa Milne, 1936
(Fig. 7a. 7b, 35-38, 107)


Males of this species are recognized by form of distal article of clasper, with acuminate triangular dorsal lobe and thick, fleshy, triangular ventral lobe (Fig. 35). Females are recognized by hooked spermathecal sclerites (Fig. 38).


Male genitalia. (Specimen from Rapids Creek, Gap, Alberta). Segment IX wide dorsally, narrower in ventral third of total height. Extreme ventral area segregated by dark suture lines (Fig. 35). Claspers each with large, trapezoidal, mesally concave, basal article. Distal article bilobed; dorsal lobe acuminate triangular; ventral lobe triangular, larger than dorsal, rounded distally, heavy. Segment X with concave dorsal plate; lateral walls sharp edged. Anal sclerite of two rounded, mesally concave, lateral flaps located ventrad of distal tip of segment X (Fig. 36). Aedeagus relatively small, with ejaculatory duct terminated on peculiar pick-like, hyaline, median shaft; median shaft flanked basally by membranous lobes tipped by numerous long, thin spines. Base of aedeagus surmounted by large, fleshy, dorsal lobe terminated by dark, folded, sclerotized pocket (Fig. 37).

Female genitalia. (Specimen from Rapids Creek, Gap, Alberta). Basal portion of segment VIII sclerotized in form of truncated cone terminated in two pairs of lateral lobes (Fig. 38). Segment XI with pair of small, hyaline cerci. Spermathecal sclerites two, parallel to each other, lightly sclerotized, tapered finely anterad, with heavier, deeply hooked posterior ends.

Notes on biology. — Adults emerge from non-turbulent, smoothly flowing, but swift, mountain brooks. to smaller, but very turbulent mountain torrents. The flight season extends from July 15 to August 31.

Geographical distribution. — The known range of this species extends from Alaska to Idaho and Washington (Fig. 107), apparently ranging throughout the northern Cordillera. My collecting in Alberta indicates that the species is confined to the mountain and foothill areas, between 3,000’ and 6,500’. The type locality is given as Edmonton by Milne (1936) which is at 2,000’.

I have examined 255 specimens, 184 males and 71 females, from the study area.
The acopedes group

Males of this group, represented here by two species, are characterised by simple aedeagus (Fig. 40) with lateral arms in form of membranous, extensible lobes with multi-spinate tips. One branch of this group has segment X with anteriorly directed basal processes (Fig. 96). In the second branch segment X is cleft dorsally down the middle. There are eight known species in this group, of which one is known from Alberta.

*Rhyacophila acopedes* Banks, 1914
(Fig. 8a, 8b, 39-41, 108)


Males of this species are distinguished from males of other species of the acopedes group by lateral ‘wings’ on median shaft of aedeagus, and by acuminate lobe dorsad of segment X, attached to segment IX. Females are distinguished by postero-ventral keel of segment VIII.

*Description.* — Antennae yellow-brown. Vertex of head uniformly deep red-brown. Thorax deep yellow-brown, to deep red-brown dorsally. Spurs brown. Fore wing length of male 10.8 mm; colour grey-brown; costal area hyaline, stigma weak, indistinctly irrorate. Veneration of fore and hind wings as in Fig. 8a, 8b.

Male genitalia. (Specimen from Cold Creek, Nojack, Alberta). Segment IX essentially rectangular, with irregular posterior edge (Fig. 39); postero-dorsal edge produced posterad as broad, triangular plate dorsad of segment X. Claspers each with basal article arcuate; basal area laterally flattened, distally tubular. Heavy distal article bilobed, with small pyramidal dorsal lobe, and massive ventral lobe roughly triangular in cross section. Segment X of two approximately rectangular, vertical plates side by side; base of each plate with broad lateral flange. Median shaft of aedeagus simple tapered tube (Fig. 40), flanked just distad of base by two rounded lateral ‘wings’. Lateral arms large, membranous, tubes each terminated by sheaves of long, dark spines.

Female genitalia. (Specimen from Cold Creek, Nojack, Alberta). Basal portion of segment VIII heavily sclerotized; antero-lateral edges slightly depressed; ventro-posterior surface keeled, tapered gradually to sharp posterior edge; membranous remainder of segment emergent only above keel (Fig. 41). Spermathecal sclerites two, indistinct, simple. tapered.

*Notes on biology.* — This species emerges from a variety of stream types ranging from torrential, rocky, mountain streams, to swift, smoothly flowing, shallow streams on pebble beds, to very quiet, sluggish streams on earthen beds. Smith (1968) gives the adult flight period in Idaho as late July to early August; peak emergence is in late July. My records give the flight period in Alberta as July 1 to August 22. I have a record from Jaffray, in south eastern British Columbia, dated May 10; seven of each sex were taken. Smith states that the species overwinters in Idaho as third or fourth instar larvae; pupation occurs in late May and June. He also adds that the adults are active in the afternoon, ceasing flight at dusk, and do not come to light. My own observations confirm this, specimens usually being taken under bridges or culverts. Both Smith (1968) and Denning (1948a) report that both sexes emit an unpleasant odour when handled. I have not noticed this phenomenon.

*Geographical distribution.* — The known range of this species extends from British Colum-
nia in the west to Labrador in the east, and south as far as Colorado (Fig. 108). This is one of the two transcontinental species of *Rhyacophila* known to occur in the study area. From the map there is seen to be a gap in mid-continent; this may be genuine or an artifact of collecting. In Alberta the species seems to be largely confined to the mountain and foothill regions. However, two localities well away from the main Cordillera are recorded. One, near Whitecourt (Chickadee Creek), is on the south west edge of the Swan Hills, an isolated rise of land; the other is at Cold Creek, Nojack, which is quite outside any unusual elevation of land, and about 50 miles from the eastern extremity of the foothills. This stream is peculiar in affording a rather large selection of otherwise mountain caddis-flies while, at the same time, affording a selection of plains species. This species ranges between 2,500' and 7,000' altitude.

I have examined 698 specimens, 449 males and 249 females, from the study area.

*Rhyacophila vemna* Milne, 1936

(Fig. 21a, 21b, 96-99, 120)


Males of this species are distinguished from males of other species in the *acropedes* group by long tuft of setae on posterior edge of tergum IX (Fig. 96), and by long, twisted, distal article of clasper. Females are distinguished by open-ended, mesally fissured spermathecal sclerite (Fig. 99).

**Description.** — Antennae red-brown. Vertex of head red-brown. Thorax light red to yellow-brown, darker dorsally. Spurs brown. Fore wing length of male 18.1 mm; chocolate-brown to reddish brown, heavily irrorate, with thick stigma. Hind wings with distal half stained clear brown. Venation of fore and hind wings as in Fig. 21a, 21b.

Male genitalia. (Specimen from Gap, near Exshaw, Alberta). Segment IX with anterior edges essentially straight, vertical; posterior edges with large, smooth, ventral indentation; dorsal portion curved antero-dorsad to narrow dorsal ridge (Fig. 96). Clasper with distinct mesal ledge basally on basal article; distal article twisted as if part of coil, with thick, rounded, distal lip. Dorsal part of segment X of two thin, short, vertical plates; distally with darkened, folded, deeply incised plate, denticulate on dorsal surface (Fig. 97). Median shaft of aedeagus slender, tapered; lateral arms membranous, very thick, terminated by heavy brushes of long, amber setae; these lobes surmount median shaft (Fig. 98).

Female genitalia. (Specimen from Gap, near Exshaw, Alberta). Basal half of segment VIII simple, tapered, lightly sclerotized tube. Spermathecal sclerite in ventral aspect (Fig. 99) spanner-like in appearance, with anterior end open; spindle shaped fissure located mesally. Cerci minute.

**Notes on biology.** — This species inhabits small, swift, gravel bedded, mountain streams. The flight period of the adults in Alberta extends from May 17 to July 7.

**Geographical distribution.** — The known range of this species extends from the Cascade Mountains of Washington to the Rockies of Alberta.

I have examined 21 specimens, 12 males and nine females, from the study area.

The *invaria* group

Members of this group are characterised by essentially simple male genitalia. Anal sclerite large, with deep root. Aedeagus with two lateral arms, complex median shaft, and specialised ventral lobes. Tergal strap attached to aedeagal base; expanded into sclerotized apical band.
There are two main branches of this group (Ross, 1956): one is located in eastern North America, the other in western North America. The western branch includes five species, of which two are dealt with here.

Rhyacophila bifila Banks, 1914
(Fig. 9a, 9b, 42-46, 109)


Males of this species are distinguished from males of other species in the *invaria* group by long, thin, conical, very dark lateral arms of aedeagus; by heavy, blade-like ventral lobes. Segment X is divided to two simple, lateral, tergal flaps (Fig. 42, 43). Females are distinguished by ventral lobes of segment VIII long, thin, arcuate, in ventral aspect (Fig. 46) arising from separate bases.

Description. — Antennae brown; each article annulated dark brown distally. Vertex of head very dark chocolate-brown. Thorax brown, to dark chocolate-brown dorsally. Legs yellow, distal ends of articles dark brown. Spurs brown. Fore wing length of males 10 mm; dark chocolate-brown, irrorate; stigmatic area almost black. Venation of fore and hind wings as in Fig. 9a, 9b.

Male genitalia. (Specimen from Canmore, Alberta). Tergum IX projected well posterad; remainder of segment IX narrow, tapered slightly ventrad (Fig. 42). Clasper short, massive; basal article roughly trapezoidal, mesal face occupied by two, almost contiguous, short ridges. Distal article of clasper polygonal, distal edge slightly concave; mesal face ridged, partly with fine setae. Segment X divided, as pair of flared, dorso-lateral plates; ventro-lateral of each plate is single, large, rounded lobe which appears as dorsal extension of tergal strap. Anal sclerite divided mesally (Fig. 43), arched dorsoap. Median shaft of aedeagus thick, with rounded dorsal lobe overhanging tip (Fig. 44); attached ventrad of median shaft are two massive, folded, sclerotized lobes terminated by short, stout, acuminate plates with tips directed dorsoap. Lateral arms of aedeagus long, conical, attached at aedeagal base, with distal quarter very finely attenuated as a hair.

Female genitalia. (Specimen from Canmore, Alberta). Segment VIII short, sclerotized, with short, membranous distal portion enclosed by short, widely separated, blunt, dorsal lobes, and blunt, vertically thin, ventral lobes attached to polygonal sternum (Fig. 45, 46). Dorsal and ventral lobes connected by thin lateral band anterad of which segment VIII is weakly sclerotized. Segments IX-XI short, stout. Cerci represented by two minute papillae. Spermathecal sclerites absent.

Notes on biology. — This species emerges from a great variety of streams and rivers, ranging from fast and turbulent to slow, from boulder strewn to pebble bottomed. Denning (1965) records it from clear, cold mountain streams. Smith (1968) records the Idaho flight period of the adults as late June to early September, peaking in late June. My records give the Alberta flight period as May 22 to August 23. Smith (1968) states that the species is crepuscular and its members are attracted to light.

Geographical distribution. — The known range of this species extends from British Columbia and Alberta to California and Wyoming (Fig. 109). In Alberta this species is found in the lower river courses, between 3,000' and 5,000', of the mountains and foothills.

I have examined 161 specimens, of which 102 were males, and 59 females.
Rhyacophila coloradensis Banks, 1904
(Fig. 10a, 10b, 47-50, 110)


Males of this species are distinguished from males of R. bifila Banks by bilobed, dorso-lateral sclerites of segment X (Fig. 47, 48). Females are distinguished by paired ventral lobes of segment VIII attached to common pedicel (Fig. 50) in R. coloradensis.

Description. — Antennae brown. Vertex of head virtually black. Thorax deep chocolate-brown, to virtually black dorsally. Spurs dark brown. Fore wing length of male 10 mm; dark chocolate-brown, irrorate, stigmatic area solid brown. Hind wings clear, dark brown distally, stigma slightly darker. Venation of fore and hind wings as in Fig. 10a, 10b.

Male genitalia. (Specimen from Chancellor Peak, Yoho, British Columbia). Segment IX virtually rectangular laterally, slightly wider dorsally than ventrally (Fig. 47), traversed by lateral sutures. Basal article of clasper short, stout, almost square; mesal face with short ventral ridge. Distal article of clasper massive, polygonal, with slightly concave mesal face with distal half with short setae. Dorso-lateral sclerites of segment X mesally concave, with dorsal hooks (Fig. 47, 48). Anal sclerite cleft mesally, arched dorsad, paralleling sclerites of segment X. Tergal strap terminated as two small lobes laterad of anal sclerite. Median shaft of aedeagus very similar to that of R. bifila Banks (Fig. 44, 49), but ventral lobes massive, rounded, folded, sclerotized, not acuminate distally; lateral arms rod-like, tipped with minute spines (Fig. 49).

Female genitalia. (Specimen from Chancellor Peak, Yoho, British Columbia). Sclerotized basal portion of segment VIII similar to that of R. bifila Banks laterally, except ventral lobes horizontal, not vertical; in ventral aspect both lobes arise from common pedicel (Fig. 50).

Notes on biology. — This species frequents both the fast, turbulent mountain creeks with boulder beds, and the slower, smoother flowing, pebble-bottomed creeks. Smith (1969) gives the Idaho flight period as March, April, May, and September, indicating two peaks of emergence, one in Spring, the other in Fall. My records indicate only one period of emergence in Alberta, albeit rather an extended one, from May to August, peaking in May (May 7 to August 30). I have one record, from Banff, Alberta, on April 17, 1915, by N. B. Sanson. Smith (1968) indicates that the adults are most active at dusk in Idaho, but start flying in the afternoon.

Geographical distribution. — The known range of this species extends from Alberta and British Columbia to California, New Mexico, and all intervening states except Nevada (Fig. 110). It appears to be truly widespread throughout the Cordillera. In Alberta the species is found in the foothills, but primarily in the mountains. In altitude it ranges from at least 3,000’ to about 6,000’. Dodds and Hisaw (1925b) recorded it from Colorado at between 6,000’ and 11,000’.

I have examined 268 specimens, 127 males and 141 females, from the study area.
The *hyalinata* group

Males of species in this group are characterised by wide apical band of tergal strap projecting beyond ventral corner of tergum X (Fig. 51); by truncate anal sclerite with definite root, and by simple tergum X (Ross, 1956). There are four species in this group of which one is known to occur in Alberta.

*Rhyacophila hyalinata* Banks, 1905
(Fig. 11a, 11b, 51-53, 111)


Males of this species are distinguished from those of other species by dorsally arched postero-dorsal extension of segment IX; by shape of distal article of claspers, which are parallel sided but bowed ventrad (Fig. 51), and by complex aedeagus (Fig. 52).

Description. — Antennae red-brown. Vertex of head deep chocolate. Thorax chocolate-brown, to darker chocolate dorsally. Spurs brown. Fore wing length of male 13.7 mm; dark purplish-brown, especially on veins; cells lighter, irrorate; stigma very thick. Venation of fore and hind wings as in Fig. 11a, 11b.

Male genitalia. (Specimen from Vicary Creek, north of Coleman, Alberta). Segment IX wide; anterior edges bowed anterad, posterior edges angular. Postero-dorsal edge developed as triangular, cup-like process overtopping segment X (Fig. 51). Basal article of clasper short, rectangular. Distal article bowed ventrad; swollen tip with fine hairs. Segment X of two large, warped, dorsal plates fused diagonally along mesal faces. Anal sclerite long, thin, angular laterally, apical band of tergal strap engaged distally. Tergal strap horizontal, lateral edges curled dorsad, apical band in form of recurved distal horn. Median shaft of aedeagus heavily sclerotized (Fig. 52) with distal tip overhung by dorsally concave lobe; acute triangular plate flanked basally by two lateral pads ventrad to ejaculatory duct. Lateral arms attached to membranous bases; each clavate, long, terminated by small, acuminate spine. Median shaft and lateral arms of aedeagus distad of massive membranous base overhung basally by acuminate, ventrally concave plate.

Female genitalia. (Specimen from Vicary Creek, north of Coleman). Basal portions of segment VIII sclerotized, flanked laterally by pair of lateral flaps, two acute triangular lobes ventrad (Fig. 53). Two lightly sclerotized, dorso-lateral plates posterad. No evident spermathecal sclerites, or cerci.

Notes on biology. — This species frequents the faster, more turbulent types of mountain stream with rocky beds; it is also, however, found in the faster, smoother flowing, pebble-bottomed streams. Smith (1968) records the adult flying season as late June to early August in Idaho. My records give a total span from July 5 to September 12 in Alberta, with the peak in later July.

Geographical distribution. — The known range of this species extends from Alberta and British Columbia to California and Colorado. The species is widespread in the Cordillera (Fig. 111). In Alberta it appears to be confined to the mountain areas. In altitude it ranges between 3,500' and 6,000'. Dodds and Hisaw (1925b) record it from Colorado at 9,000' to 11,000'.

I have examined 428 specimens, 270 males and 158 females, from the study area.
The sibirica group

Males of this group are characterised by ventral fusion of lateral arms, forming ventral membranous base terminated by ovate or elongate scoop with dorsal brush of hair (Fig. 54, 60) (Ross, 1956). Some species have lost this structure (Fig. 62). There are 26 species in this group, of which four are known to occur in Alberta.

*Rhyacophila rickeri* Ross, 1956
(Fig. 12a, 12b, 54-56, 112)


Males of this species are distinguished from males of other species of the *sibirica* group by postero-dorsal lobe of tergum VIII, and similar lobe of tergum IX (Fig. 54). Tergal strap wide, telescoped, with ventral aperture for aedeagus distinctive.

*Description.* — Antennae brown. Vertex of head dark brown anteriorly, lighter posteriorly. Thorax dark yellow-brown laterally, speckled dark brown on lighter ground. Spurs yellow-brown. Fore wing length of male 11.2 mm; light greyish brown, transparent. Venation of fore and hind wings as in Fig. 12a, 12b.

Male genitalia. (Specimen from Mt. Edith Cavell, Jasper, Alberta). Tergum IX with bulbous postero-dorsal process dorsal of segment X (Fig. 54). Segment IX rectangular laterally, with sinuate posterior edge. Basal article of clasper large, thick, directed postero-dorsad; distal article long, tapered, setose. Segment X with two distinct cerci whose bases pass mesad to two mesal protrusions (Fig. 55); thin flaps flank three-arched anal sclerite ventrolateral of cerci. Tergal strap prominent, dark, sinuate, with ventral aperture for passage of aedeagus. Median shaft of aedeagus long, thin, with distinct basal piece (Fig. 54); attached to large flared base, which flanks it; ventral process membranous, highly extensible, with dorsally concave tip spinate internally.

Female genitalia. (Specimen from Mt. Edith Cavell, Jasper, Alberta). Proximal third of segment VIII sclerotized; wide, shallow, longitudinal groove dorsally. Spermathecal sclerite warped, dorsal surface concave, ventral convex, at posterior end, reversed at anterior end. Laterally sclerite sigmoid in appearance (Fig. 56).

*Notes on biology.* — This species inhabits small, very shallow, cold alpine streams, in high moraine country. These streams are little more than trickles but persist throughout the year. I have taken specimens at Mt. Edith Cavell, on 1 to 2 feet of fresh snow in early October.

*Geographical distribution.* — The known range of this species extends from Alaska to Alberta and British Columbia (Fig. 112). I have taken specimens at only two localities, both at about 7,000’ altitude.

I have examined 23 specimens, 20 males and three females, from the study area.

*Rhyacophila vepulsa* Milne, 1936
(Fig. 14a, 14b, 57-61, 113)


Males of this species are distinguished from males of other species of the *sibirica* group by
massive segment X (Fig. 57, 58) and by asymmetrical distal cup of ventral process of aedeagus (Fig. 60). Females are distinguished by angularly offset dorsal and ventral surfaces of segment VIII (Fig. 61).

**Description.** — Antennae uniform chocolate-brown. Vertex of head dark chocolate. Thorax dark reddish-brown dorsally, grey-brown laterally. Spurs dark brown. Fore wing length of male 8.5 mm; uniform dull grey-brown; stigmatic area faint. Venuation of fore and hind wings as in Fig. 14a, 14b.

Male genitalia. (Specimen from Rowe Creek, Waterton National Park, Alberta). Segment IX slightly narrower ventrally than dorsally (Fig. 57). Basal article of clasper with straight dorsal edge, sinuate ventral edge. Distal article polygonal, slightly indented distally, ventral lobe swollen. Segment X massive plaque (Fig. 57, 58) weakly bilobed distally; dorsal surface irregular in lateral aspect, with distinct anterior hump; ventral surface concave anteriorly and posteriorly, convex between. Median lobe of aedeagus long, thin, with thinner distal quarter directed postero-dorsad (Fig. 59); attached ventrad of dorsally arched basal plate with disto-ventral surface produced as dorsally directed, slender, rounded, distally spinate, process. Proximad of basal complex of aedeagus is short, rounded, minutely spinate process directed anterad above aedeagal base. Ventral process of aedeagus attached to membranous base on slender pedicel; massive, ladle-like, setose around lateral walls; lateral walls asymmetrical (Fig. 59, 60).

Female genitalia. (Specimen from Rowe Creek, Waterton National Park, Alberta). Basal half of segment VIII simple, sclerotized, tapered cone; distal edge angular laterally (Fig. 61).

**Notes on biology.** — I have records of adults of this species taken in the vicinity of large, turbulent rivers, and from small, pebbly slow streams. Smith (1968) records the larvae from "... ripples of headwaters streams with compact, pebbly bottoms", in Idaho. He also gives the Idaho adult flight season as late July. My records for the study area are few, but they indicate a flight season in early August (August 1-5). This is not a common species.

**Geographical distribution.** — The known range of this species extends from Alaska to California and Montana (Fig. 113). In Alberta my records are too few to state with certainty the range of the species, but it appears to be confined to the mountains. Altitudinally it occurs from 4,000' to 6,000'.

I have examined eight specimens, five males and three females, from three localities in the study area.

*Rhyacophila belona* Ross, 1948

(Fig. 15a, 15b, 62-64, 112)


Males of this species are distinguished from males of other species of the *sibirica* group by long, thin, dorsally curved median shaft of aedeagus, with basal two-thirds flanked laterally by thin up-curved wings (Fig. 62). Females are distinguished by lateral aspect of spermathecal sclerite, which is triangular (Fig. 64).

**Description.** — Antennae almost black. Vertex of head black. Thorax black-brown, to black dorsally. Spurs dark brown. Fore wing length of male 8.4 mm; very deep purplish brown, with patches of slightly lighter purple-brown. Hind wings transparent chocolate-brown. Venuation of fore and hind wings as in Fig. 15a, 15b.

Male genitalia. (Specimen from Mt. Edith Cavell, Jasper, Alberta). Segment IX wide dorsally, sharply narrowed ventrad (Fig. 62). Basal article of clasper straight, tapered distad; distal article acute-triangular except for basal constriction, ventral edge thickened. Segment
X large, complexly folded, distally bilobed process (Fig. 62, 63) with roots well inside segment IX. Ventrad of base of segment X is rugose, domed plate. Aedeagus simple, slender, smoothly up-curved, tapered tube flanked along basal two-thirds by thin, dorsally curved, lateral wings (Fig. 62).

Female genitalia. (Specimen from Mt. Edith Cavell, Jasper, Alberta). Basal portion of segment VIII sclerotized, truncated-conical tube (Fig. 64); ventro-posterior edge with two small processes; dorsad of these are two larger, triangular flaps. Cerci simple, papillate.

Notes on biology. — This species inhabits high alpine brooks in moraine topography. The flight season of the adults extends from June 1 to July 21.

Geographical distribution. — This species is known only from Alberta and Montana (Fig. 112). It ranges from 6,000' to 7,000'.

I have examined 14 specimens, 10 males and four females, from the study area.

*Rhyacophila pellisa* Ross, 1938a
(Fig. 16a, 16b, 65-68, 114)


Males of this species are distinguished from males of other species of the *sibirica* group by very long claspers, very short segment X and simple aedeagus with long, thin, tapered median shaft and simple, setose ventral process (Fig. 66). In dorsal aspect segment X is simple, rounded, bilobed and deeply cleft (Fig. 64); another similar species which may eventually be found in Alberta has similar segment X but with only very shallow cleft. Females are distinguished by long, proximally pierced spermathecal sclerite (Fig. 68).

Description. — Antennae dark brown. Vertex of head almost black. Thorax dark chocolate-brown, to almost black dorsally. Spurs dark brown. Fore wing length of male 8.4 mm; uniform deep reddish brown; cells translucent, stigma prominent.

Male genitalia. (Specimen from Gap, near Exshaw, Alberta). Segment IX with robust, rectangular dorsal area separated from partially keeled, narrower ventral area by fine suture (Fig. 66). Basal article of clasper massive, tapered distad, variably channelled on mesal face; distal article somewhat trapezoidal, with thick ventral lobe, minute ventrally hooked, dorsal lobe. Segment X small, set dorsally on segment IX, deeply cleft mesally, with short, rounded lobes (Fig. 64); merged ventrally with flat, square-cut plate dorsad of anus. Tergal strap and apical band as smoothly curved distal hook. Median shaft of aedeagus long, thin, tapered, recurved tube (Fig. 67); ventral process long, with membranous base, short sclerotized pedicel, and slightly wider, setose, distal body.

Female genitalia. (Specimen from Gap, near Exshaw, Alberta). Basal half of segment VIII strongly sclerotized (Fig. 68), dorsal surface slightly shorter than ventral. Spermathecal sclerite in ventral aspect long, thin, clavate anteriorly; anterior end pierced; posterior end slightly expanded, darker, with two-arched hyaline line near tip.

Notes on biology. — This species frequents streams ranging from small, pebble-bottomed brooks, to larger, fast, rocky rivers. The Idaho flight season is given by Smith (1968) as late July to early August. The Alberta flight season is from July 19 to August 31. Smith states that daily flight is confined to late morning.

Geographical distribution. — The known range of this species extends from Alberta to
California and Colorado (Fig. 114). In Alberta it is largely confined to the mountain areas, but appears to extend eastward in the foothills. Its altitudinal range is 3,500' to 6,000'.

I have examined 142 specimens, 98 males and 44 females, from the study area.

The betteni group

This group is characterised, in males, by unusually long lateral arms of aedeagus; these are ventral in position, and fused in some species. Of the eight known species of this group, two are known to occur in the study area.

*Rhyacophila vaccua* Milne, 1936
(Fig. 13a, 13b, 69-74, 116)


Males of this species are distinguished from males of other species of the *betteni* group by abrupt ventral narrowing of segment IX (Fig. 69), by dorsally curved process of anal sclerite, and by narrow tenth segment (Fig. 70). As the female of *R. chilsea* Denning is unknown I cannot give comparative details within the group. However, females of this species are distinguished from all others by distinctive sternum of segment VIII (Fig. 73, 74), and by complex spermathecal sclerites (Fig. 73).

Description. — Antennae dark brown. Vertex of head uniformly very dark brown. Thorax dark grey-brown, mottled by almost white areas. Spurs dark brown. Fore wing length of male 10.4 mm; dark grey-brown interspersed with hyaline areas. Veneration of fore and hind wings as in Fig. 13a, 13b.

Male genitalia. (Specimen from Red Earth Creek, Banff National Park, Alberta). Segment IX with distinct, narrow, sternum (Fig. 69); tergum large, widened dorsally, dorsal surface sloped antero-ventrad. Basal article of clasper rectangular laterally, with mesal shelf at base joined medially with identical member of opposing clasper. Distal article bifid; dorsal lobe acuminate, with basal median flange overlapped with basal lateral flange of thumb-like ventral lobe. Segment X small, recessed dorsally into segment IX, channeled longitudinally along dorsal surface (Fig. 70). Anal sclerite small, bilobed distally, curved dorsad. Tergal strap large, curved, with apical band horizontal, attached to segment X disto-ventrally. Median shaft of aedeagus long, thick, distal end cleft horizontally, with rounded dorsal lobe overhanging ejaculatory duct (Fig. 71); median shaft completely shielded dorsally by thin, arched, distally acuminate plate (Fig. 71, 72); lateral arms fused except for heavily spinate distal lobes.

Female genitalia. (Specimen from Gap, near Exshaw, Alberta). Basal portion of segment VIII heavily sclerotized, partly free distally from membranous portion, very deeply cleft dorsally and ventro-laterally (Fig. 73, 74); sternum distinct from tergum, posterior edge produced posterad as acuminate-triangular lobe, with v-cleft distally. Spermathecal sclerites two long, slender, ventral rods, slightly bulbous posteriorly, set close together; dorsad of these rods is located a large, dorsally arched structure tapered anterad; single unit with light and dark areas as in Fig. 73.

Notes on biology. — This appears to be rather a ubiquitous species, being taken in the vicinity of a great variety of streams. I have collected specimens in the vicinity of large and
small, fast and slow, rocky and pebbly streams. Smith (1968) records the larva from small to medium, clear streams with mixed rubble bottoms, in Idaho. He also gives the adult flight season in Idaho as September and October. The Alberta flight season is August 19 to October 4.

**Geographical distribution.** — The known range of this species extends from Alberta and British Columbia to California and Wyoming (Fig. 116). In Alberta it is confined largely to the mountains, with a few records from the foothills. Most records are from south of Banff. In altitude it ranges between at least 3,500' and 6,000'.

I have examined 72 specimens, 47 males and 25 females, from the study area.

*Rhyacophila chilsia* Denning, 1950

(Fig. 75-78, 115)


Males of this species are distinguished from those of *R. vaccua* Milne by minute dorsal lobe of distal article claspers, by segment X well separated dorsally from segment IX, and by ventrally directed, angular, anal sclerite (Fig. 75).

The only known specimen of this species is a male, from Maligne Canyon, Jasper, Alberta. Being thus unable to prepare my own drawings, Dr. D. G. Denning very kindly lent me his original drawings of the species, which I have partly redrawn and present here (Fig. 75-78). I also present Denning's original description of the male, altering only his figure numbers to mine.

**Description.** — 'Length [?] 9.5 mm. Fore and hindwing fuscous, veins and pterostigma somewhat darker. Body, head, palpi and antennae yellowish; legs and spurs luteous. Sixth and seventh abdominal sternites with a short acute mesal spine.

Genitalia as in Fig. 75-78. Ninth segment gradually widened dorsally, meso-apical margin of tergum in the form of a sub-acute projection. Tenth tergum narrow plate-like structure; meso-dorsal margin projected caudad as acute process, pair of small acute mesal projections close to ventral margin and best discernible from dorso-caudal aspect; mesal surface of tergum concave; ventral process cleft nearly entire length (Fig. 75), and capable of only slight dorso-ventral movement; dorsal aspect of tergum as in Fig. 77. Apical segment of clasper gradually narrowed distally, distal margin cleft to form acuminate digitate process, setation sparse. Structures in association with aedeagus as in Fig. 78; apex of lateral arms somewhat asymmetrical, but each divided into four acute projections' (Denning, 1950).

**Notes on biology.** — I do not know which part of Maligne Canyon is meant, but the Maligne River in the area is fast, fairly smooth water on rocky, but not boulder, bottom; in the canyon itself the river is considerably narrowed, deeper, with frequent pools and cascades. Date of capture of the male was July 23.

**Geographical distribution.** — The position of the one known locality is indicated in Fig. 115. It is at an altitude of 3,800'.

The *vobara* group

Males of this group are distinguished by apical band of the tergal strap attached directly to inner ends of anal sclerite (Fig. 79). One of the two known species occurs in Alberta.

*Rhyacophila vobara* Milne, 1936

(Fig. 17a, 17b, 79-81, 115)

Males of this species are distinguished by thin, high segment IX with sinuate edges (Fig. 79), by massive proximo-mesal swelling of basal article of claspers, and by dorsal toothed plate at aedeagal base (Fig. 80).

Description. — Antennae dark brown. Vertex of head deep chocolate-brown, warts almost white. Thorax dark brown. Spurs brown. Fore wing length of male 8.5 mm; pale to dark chocolate-brown, with large irrorations, primarily at distal ends of peripheral cells. Stigma weak. Veneration of fore and hind wings as in Fig. 17a, 17b.

Male genitalia. (Specimen from Ranger Creek, Jasper Park, Alberta). Segment IX high, narrow, pinched ventrad of mid-line (Fig. 79). Basal article of clasper sinuate, with massive bulge on mesal face. Distal article almost square; distal edge irregular, with thick ventral lobe. Segment X irregular longitudinally folded sclerite. Anal sclerite large, tapered basad, with dark distal edge; articulated with ventral corner of segment X, which flanks it laterally. Apical band of tergal strap curved, attached to segment X at ventral edge. Median shaft of aedeagus short, thin, between two sclerotized, acuminate lateral arms; longer, thin, tubular process dorsad of shaft (Fig. 80). Aedeagal base roofed over by heavy, dark, flat, plate with large dorsal thorn; base ventrad of this plate enclosed in lightly sclerotized tube.

Female genitalia. (Specimen from Ranger Creek, Jasper Park, Alberta). Basal portion of segment VIII sclerotized (Fig. 81) with two pairs of disto-lateral lobes; dorsal lobes rounded, ventral lobes somewhat triangular.

Notes on biology. — Specimens of this species have been taken in the vicinity of small, fast, turbulent mountain creeks, small, gravelly alpine trickles, and slow, deep streams emerging from alpine peat bogs. The flight period of Alberta adults is from July 3 to September 10.

Geographical distribution. — The known range of this species extends from the Yukon Territory to Idaho. In Alberta my records are all from the mountains, except for one locality in the northern foothills. In altitude this species ranges from at least 3,500' to over 6,000'.

I have examined 36 specimens, 20 males and 16 females, from the study area.

The angelita group

Males of this group are characterised by large dorsal lobe of segment X (Fig. 82), by deep root of anal sclerite, and by an extra pair of lateral lobes on aedeagus (Fig. 84). One of the three known species in this group occurs in Alberta.

Rhyacophila angelita Banks, 1911
(Fig. 18a, 18b, 82-85, 117)


Males of this species are distinguished by large, elliptical bilobed dorsal lobe of segment X (Fig. 83), and by structure of aedeagus (Fig. 84).

Description. — Antennae yellow. Vertex of head brownish yellow. Thorax brownish yellow to straw. Spurs yellow-brown. Fore wing length of male 10.1 mm; hyaline, with very faint yellow-brown pattern; veins dark red-brown. Stigma weak. Venation of fore and hind wings as in Fig. 18a, 18b.

Male genitalia. (Specimen from Gap, near Exshaw, Alberta). Segment IX very wide dorsally; bowed, saddle-like; segment narrowed gradually ventrad; sternum curved anterad at lateral sutures (Fig. 82). Basal article of clasper long, parallel-sided, sinuate. Distal article mesally concave, with wide ventro-mesal ledge. Segment X small, enclosed plate, produced postero-dorsad as massive dorsal plate cleft deeply mesally (Fig. 83). Anal sclerite large, with deep root, flanking base of segment X. Tergal strap heavy, with laterally triangular apical band. Median shaft of aedeagus small, tapered, thin (Fig. 84); flanked laterally by pair of wide, dorsally hooked lobes. Two short, rectangular plates ventrad of median shaft. Lateral arms long, with membranous, extensible bases and spatulate tips with mesal concavities setose. Vertically bilobed prominence directed posterad on dorsum of aedeagal base.

Female genitalia. (Specimen from Gap, near Exshaw, Alberta). Basal portion of segment VIII tapered, sclerotized, truncated cone merged distally with membranous portion (Fig. 85). Dorsal surface of segment VIII base with deep channel; distally extended into dorsal swelling. Spermathecal sclerite simple, folded longitudinally, attenuated at each end.

Notes on biology. — This species appears to be cosmopolitan in its choice of habitat, specimens being taken near almost every type of water course available in the mountain area. The adult flight season extends in Alberta from July 7 to October 18. I have records for May 23 and June 20 also, but most of my records are within the range stated above.

Geographical distribution. — The known range of this species extends from the Yukon Territory to California and Colorado (Fig. 117). The species has also been recorded from the northern Appalachians of New Hampshire (Smith, 1968) which, in the present state of knowledge of this species, is a very isolated record probably representing a post-glacial remnant of a previously truly transcontinental species.

I have examined 530 specimens, 324 males and 206 females, from the study area.

The verrula group

This group contains only one known species of singular peculiarity. The detailed description following will serve to characterise the group.

*Rhyacophila verrula* Milne, 1936

(Fig. 19a, 19b, 86-88, 118)


Males of this species are distinguished by trilobed posterodorsal edge of tergum VIII (Fig. 86), by fused posterodorsal lobes of segment IX, hooked ventrad (Fig. 86, 87), and by curious dorsal process of aedeagal base. Females are distinguished by sclerotized tergum X
and by two annular swellings of segment IX (Fig. 88).

Description. — Antennae dark brown, scapes yellow. Vertex of head dark brown anteromesally; remainder, and warts, yellow. Thorax mottled yellow and dark brown. Spur formula of males 2, 4, 5; pro-thoracic spurs short, meso-apical spur of hind legs stout, long, distally bifid, in form of pincers; remainder normal. Spur formula of females 3, 4, 4; fore leg spurs short, remainder normal. Fore wing length of male 12 mm; light yellow-brown; pattern somewhat banded, colour alternated with hyaline areas; stigma opaque white. Venation of fore and hind wings as in Fig. 19a, 19b.

Male genitalia. (Specimen from Gap, near Exshaw, Alberta). Postero-dorsal edge of tergum VIII with projected median lobe dorsal of dorsal strap (Fig. 86, 87); flanked by two flap-like lateral lobes. Segment IX with narrow, short, dorsal strap ventrad of which postero-dorsal edges produced as two large, arched lobes fused distally but parted just at tips; each lobe with blunt, ventral, process basally fused to equivalent member opposite. Postero-lateral edges of segment IX rolled meso-anterad (Fig. 87). Basal article of clasper massive, rectangular; distal article small, rounded, concave on mesal face. Segment X small, arched, dorsal roof with two small distal lobes attached distally to ventral processes of lobes of segment IX. Anal sclerite as second, internal arch. Median shaft of aedeagus bulbous basally, thin, tapered distally, in deep, thin walled, sclerotized trough (Fig. 86), connected with stout, membranous, base; dorsal surface of base with long, slender, finger-like dorsal process, sinuate, fitted distally with anal sclerite.

Female genitalia. (Specimen from Gap, near Exshaw, Alberta). Segment VIII long, tapered, dilated annularly at distal extremity, lightly sclerotized for most of length (Fig. 88). Segments IX and X with annular swelling at point of junction. Segment X with posterior two-thirds of tergum sclerotized. Cerci small, membranous. No evident spermathecal sclerite.

Notes on biology. — Smith (1968) reports that the larvae of this species are totally phytophagous, which sets the species apart from other species of the genus. He reports larvae from small, cold, pebbly riffles of clear streams. I have usually taken specimens near larger, swift, deep, boulder strewn mountain creeks, and occasionally from smaller, shallower, pebbly creeks. Smith (1968) reports the Idaho adult flight period to be September to October, peaking in September. My records indicate the Alberta flight season to range from August 20 to October 12.

Geographical distribution. — The known range of this species extends from Alaska to California and Colorado (Fig. 118). In Alberta the species is found in the mountains and high foothills, between 3,500' and 4,000'.

I have examined 64 specimens, 47 males and 17 females, from the study area.

The vagrita group

Males of this group are characterised by prominent postero-dorsal, strap-like, lobes of both segments IX and X (Fig. 89, 93), by small, very simple aedeagi (Fig. 91), and by interlocking of segment X, anal sclerite, and apical band of tergal strap; anal sclerite encloses small, spherical, tip of segment X, and is itself flanked laterally by apical band (Fig. 86, 93). Both species of this group are known from Alberta.

Rhyacophila vagrita Milne, 1936
(Fig. 20a, 20b, 89-92, 119)

Rhyacophila ventrally.
wide, length postero-mesally species and it membranous cal VIII dorsal cerci similar basally.

Males of this species are distinguished from males of other species of the vagrīta group by distal article of claspers with acuminate dorsal lobe and thick, rounded, fleshy ventral lobe, and by bilobed postero-dorsal process of segment IX (Fig. 89, 90). Only the female of this species is known so no comparison can be made.

Description. — Antennae dark brown. Vertex of head dark brown anteriorly, laterally; postero-mesally light. Thorax dark grey-brown, to richer reddish brown dorsally. Fore wing length of male 9 mm; light grey-brown with scattered, rectangular, hyaline windows; stigma distinct, brown. Venation of fore and hind wings as in Fig. 20a, 20b.

Male genitalia. (Specimen from Snaring River, Jasper National Park, Alberta). Segment IX wide, with narrower dorsal strap peaked along anterior edge (Fig. 89); posterior edge of dorsal strap developed as long, sinuate, distally bilobed, thin, strap-like process (Fig. 89, 90). Basal article of clasper with very narrow base, approximately triangular, with mesal ledge basally. Distal article of clasper lanceolate, curved, acuminate dorsally, rounded and fleshy ventrally. Segment X with long, sinuate, dark brown dorsal process immediately ventrad of similar process of segment IX (Fig. 89, 90); ventrad of base of lobe are two small, peg-like cerci between which is located sclerotized, strap-like body of segment X, terminated between lateral horns of anal sclerite. Tergal strap sinuate, with apical band terminated at antero-ventral corner of anal sclerite. Aedeagus minute; ejaculatory duct directed dorsad from dorsal plate; dorsal process short, pick-like laterally; joined to sclerotized base (Fig. 91).

Female genitalia. (Specimen from Snaring River, Jasper National Park, Alberta). Segment VIII with short sclerotized tube at base (Fig. 92), with sigmoid posterior edges. Spermathecal sclerite long, thin, irregular, with minute, pick-like posterior tip; located centrally in membranous internal tube. No evident cerci.

Notes on biology. — Little is known of this species. The one locality at which I have taken it was adjacent to a wide, swift, smooth-flowing river with pebble and small boulder bottom.

Geographical distribution. — The known range of this species extends from Alberta and British Columbia to Utah (Fig. 119). In Alberta the two known localities are at the bottoms of major valleys at about 3,500'.

I have examined one specimen of each sex from the study area.

Rhyacophila milnei Ross, 1950
(Fig. 93-95, 119)


Males of this species are distinguished from those of R. vagrīta Milne by trilobed postero-dorsal process of segment IX (Fig. 93, 94), by saddled dorsal area of segment IX, and by parallelogram shaped distal articles of claspers.

Description. — Antennae brown. Vertex of head very deep brown, almost black. Thorax deep reddish brown, to very dark brown dorsally. Spurs yellow-brown; spurs of middle and hind legs long and heavy. Fore wing length of male 8 mm; translucent red-brown. Venation of fore and hind wings identical to that of R. vagrīta Milne.

Male genitalia. (Specimen from Banff, Alberta; paratype, in Illinois Natural History Survey). Segment roughly rectangular laterally (Fig. 93); dorsal surface longitudinally channeled, with posterior edge of two lateral arches over minute, stubby, cerci; postero-dorsal edge produced posterad as long, curved, trilobed strap; lateral lobes shorter than medial. Basal article of clasper slightly narrowed basad, with thick, rounded dorsal edge, and thin,
ledged, ventro-mesal edge. Distal article of clasper fused to basal article; parallelogram-like, with distinct acuminate dorsal lobe, and thick, rounded ventral lobe. Segment X with long, thin, sinuate, dorsal process immediately ventrad of that of segment IX (Fig. 93, 94); ventral surface concave. Ventral body of segment rounded, tubular, semi-circular laterally. Anal sclerite large, enclosing tip of segment X, open dorsally. Aedeagus minute; ejaculatory duct minute, directed postero-dorsad from membranous base below evenly rounded dorsal process; dorsal groove extended from base of aedeagus to top of dorsal process (Fig. 95).

Female unknown.

Geographical distribution. — The known range of this species is presently restricted to the type locality, which is simply ‘Banff, Alberta’ (Fig. 119).

Only one male of this species, a paratype, has been examined. The date of capture was September 5.

Unassociated females

*Rhyacophila* species 1
(Fig. 23a, 23b, 100-101, 121)

Description. — Antennae dark brown. Vertex of head deep reddish brown. Thorax light red-brown, to dark chocolate dorsally. Spurs brown. Fore wing length of female 8.0 mm; pale, clear brown, veins dark, stigma brown; hind wings much the same colour as fore, except anal area hyaline. Veneration of fore and hind wings as in Fig. 23a, 23b.

Female genitalia. (Specimen from Lusk Creek, Kananaskis, Alberta). Basal half of segment VIII sclerotized; posterior edges angular, dorsal edge offset anterad (Fig. 100). Spermathecal sclerite laterally spindle-like with long membranous sack attached anteriorly; distal end and adjacent edges dark; ventrally tip square-cut; double hook pattern just anterad of tip of dark coloration (Fig. 101), with shaft of hood faded anterad.

Notes on biology. — The two creeks from which I have taken specimens of this species are shallow, slow riffled streams on small pebble beds. The dates of capture were May 18 in southeastern British Columbia, and July 15 at Lusk Creek, in the Kananaskis valley of Alberta.

Geographical distribution. — Only two records are available for this species at present (Fig. 121). Both are from low altitudes, about 3,000'
Rhyacophilidae and Limnephilidae

Fig. 104-109. Maps of geographical distribution of *Rhyacophila* species in Alberta, and North America.
Fig. 110-115. Maps of geographical distribution of *Rhyacophila* species in Alberta, and North America.
Fig. 116-121. Maps of geographical distribution of *Rhycophila* species in Alberta, and North America.
THE FAMILY LIMNEPHILIDAE KOLENATI

This family is represented in Alberta and eastern British Columbia by 91 species belonging to 26 genera. The names of the genera are presented in Table 1 according to the scheme used by Schmid (1955).

The species in the study area are discussed individually in the text. Within genera, divisions to subgenera, or groups, follow Schmid (1955). Immediately following is a synopsis of familial characteristics translated and greatly condensed from Schmid (1955). The synopses of the subfamilial groups, including genera, are also derived and condensed from Schmid (1955), as are the keys to all taxa to the generic level. Schmid (1955) should be consulted for a complete exposition of the family and its constituent taxa. The keys include only those groups found in the study area. Keys are provided to the males of the species of each genus and are original unless stated otherwise. In the family as a whole the keys are applicable primarily to the males, as male genitalic characters are used sufficiently often to exclude the females. This situation is due to an insufficient knowledge of the females of the various taxa within the family, only the males being known for many species. The situation is aggravated by the relatively great homogeneity of body characters within the family, other than in the genitalia. Keys are provided to the females of some genera, but at present the best way to identify females is by association with males.

Some species are holarctic in distribution, ranging as far west as Europe. For such species there is a very large European literature. In this work only the literature pertaining to such species in North America is given in detail; the reader is referred, at the end of the literature and synonymy list for each species, to the appropriate volume of Fischer’s ‘Trichopterorum Catalogus’ for a complete listing.

Character synopsis of the Limnephilidae. — Ocelli three. Antennae as long as, or little shorter than fore wings; thickened, not fine; scapes generally as long as head, cylindrical, thickened. Maxillary palpi of straight, sub-cylindrical articles; with three articles in males, five in females. Pronotum short. Dorsal line (i.e. pale coloured median stripe from inter-ocellar space of head to metanotum) present or absent. Legs commonly long, heavy, not hairy or silky but spinate; spines most abundant on the tibiae and tarsi, generally black. Spurs yellowish, modified or not. Spur formula 1,3,4 to 1,1,1, variable intergenerically and interspecifically. Femora and tarsi of fore legs of males of certain genera provided with opposing brushes of short, stout, black spines. Fore wings of some genera basally narrow, distally expanded at stigma, with widely rounded apex; hind wings much larger, with well developed anal area (some dicosmoecine genera and all Limnephilinae). In all other genera the hind wing is reduced to varying degrees of similarity to the fore wing by reduction of anal area. Venation generally as in Fig. 122. Cross-vein R1-R2 of fore wing absent; f4 absent, median cell open. R1 of fore wing with distal kink of varied intensity, followed by smooth curve to encompass stigma, if present. Radial sector four branched, to encompass cells f1 and f2; discoidal cell longer than wide. Median and cubital veins each three branched to delimit f3 and f5 respectively. Thyridial cell between M and Cu1. All veins except Sc and R1 connected by cross-veins to form irregular, dispersed line known as anastomosis or chord. Venation of hind wing almost identical to that of fore wing, except chord more dispersed. Anal veins five in number. R1 without distal kink and bow, generally parallel to Sc.

Tergum VIII of male unmodified of variously developed and clothed with spines or hairs. Segment IX single, rigid, heavily sclerotized tube of fairly uniform width all round, or of varied widths; ventral area produced posterad to form shelf below aedeagus, or not produced; dorsal area reduced to strap of varied widths, or obsolete. Postero-ventral edges recessed, or not. In posterior aspect segment IX divided to dorsal and ventral cavities by
mesally directed extensions of lateral walls, or not divided. Claspers movable or fused to segment IX; composed of one or two articles, horizontal; if of two articles then curved, pincer-like; if of one article then short, plaque-like. Segment X small or large, with or without many lobes or branches.

Female genitalia less varied than those of males. Segment VIII unmodified or, in some genera, with slight concavity in sternum. Segment IX short, cylindrical, cleft ventrally, or lateral walls shortened to isolate ventral angles. In most genera segment IX of distinct terga and sterna. Segment X more or less incised, sclerotized tube distinct from segment IX, or fused to it. Supra-genital plate present except in a few genera, dorsad of genital cavity. Vaginal aperture on sternum IX or between sterna VIII and IX. Vulval scale ventrad of vaginal aperture, either as simple chitinous pad or strongly sclerotized, trilobed structure.

**Key to the Subfamilies and certain Genera of Limnephilidae in Alberta and eastern British Columbia**

1a. Discoidal cell of hind wing open distally, or R1 of fore wing united to Sc by cross-vein terminated at wing edge (Fig. 129a) ... Apataniinae, p. 64.

1b. Discoidal cell of hind wing open basally; i.e. RS divided from wing base; or F3 of hind wing absent, or both (Fig. 130, 131) ... Neophylacinae, p. 71.

1c. Discoidal cell of hind wing closed; f3 present. ... 2

2a.(1c) Chord of fore wing a single, irregular line (Fig. 133-135) ... Homophylax (Pseudostenophylacinae), p. 78.

2b. Chord of fore wing in two distinct lines (Fig. 138) ... 3

3a.(2b) Fore wing reddish, narrow. Male maxillary palpus very large ... Chyranda (Limnephilinae), p. 143.

3b. Fore wing not narrowed. Maxillary palpus of normal size ... 4

4a.(3b) Fore wing reddish, large, rounded; fl with long common boundary with discoidal cell (Fig. 128). Mesal face of male clasper with one or more sclerotized spines (Fig. 195) ... Ecclesiomyia (Dicosmoecinae), p. 61.

4b. Characters otherwise ... 5

5a.(4b) Clasper of male two-articled and movable. Vaginal aperture of female on segment IX ... Dicosmoecinae, p. 50.

5b. Clasper of male of one article only, and fused to segment IX. Vaginal aperture of female between segments VIII and IX ... Limnephilinae, p. 81.

**The Subfamily Dicosmoecinae Schmid**

**Synopsis of characters.** — Head very large; eyes large. Pronotum short; macrochaetae well developed. Spur formula 1,3,3; 1,2,2; or 1,3,4. Fore wings medium to large, parabolic. Hind wings much larger than fore wings or only slightly larger; anal edge smoothly convex. Venation of species in study area as in Fig. 122-128, basically simple and unmodified.

Male genitalia complex, varied. There is feeble specialization of appendages, or strong reduction in their numbers in some genera. Segment IX recessed into segment VIII in very few genera; of fairly uniform width except for dorsal lobes in certain genera, such as Dicosmoecus. Segment X not projected in most genera; large, roof-like over the aedeagal recess. There are four pairs of appendages which are reduced or absent in some genera. Claspers very large, pincer-like, two-articled, as in Dicosmoecus (Fig. 146), or smaller, with articles tending to fuse, as in Amphicosmoecus (Fig. 164). In certain genera (e.g. Imania) the claspers are complex, with distal article missing; not fused to segment IX. Aedeagus
highly varied in form and size; long and slender in some genera.

Segment IX of female genitalia of one piece, or of two distinct parts. Dorsal part well developed, but reduced in certain genera; in form of long tube; appendages absent. Segment X well developed, in form of simple cone (e.g. *Onocosmoecus* Fig. 162), bilobed dorsally with ventral plate. Supra-genital plate present. Vulval orifice on segment IX. Vulval scale similar to that of other subfamilies but formed from posterior edge of segment IX, not VIII; trilobed.

**Key to the Genera of Dicosmoecinae in Alberta and eastern British Columbia**

1a. Fore wing reddish, large, rounded; f1 with long common border with discoidal cell (Fig. 128a).......................... *Ecclisomyia*, p. 61.

1b. Fore wing with f1 short, common border with discoidal cell (Fig. 122-127) .... 2

2a.(1b) Small insects, fore wing length less than 12 mm; fore wing very dark, brownish black ........................................... *Imania*, p. 56.

2b. Much larger insects, fore wing length over 17 mm; fore wing reddish brown or grey to grey-black ........................................... 3

3a.(2b) Clasper of male with both articles fused, not articulated. Lateral lobes of female vulval scale stout, fleshy, with distal ends concave. Supra-genital plate arched dorsad, projected prominently posterd, free of remainder of genitalia (Fig. 164, 168, 169).......................... *Amphicosmoecus*, p. 55.

3b. Clasper of male with both articles articulated (Fig. 146). Median lobe of female vulval scale projected free, between thin, placoid lateral lobes. Supra-genital plate not as above; not projected freely and prominently (Fig. 151, 152, 156, 162, 163).......................... 4

4a.(3b) Thorax abundantly clothed with silky hairs; large, black insects ............... ............................................... *Dicosmoecus*, p. 51.

4b. Thorax without many silky hairs; smaller, red-brown insects .......................... *Onocosmoecus*, p. 53.

The Genus *Dicosmoecus* McLachlan

This genus is represented in the study area by two species.

**Synopsis of characters.** — Head very large; ocelli large, close-set. Spur formula 1,3,4. Pleural sclerites, metanotum, and wing bases clothed with long, fine, silky hairs.

Male genitalia with segment IX narrow throughout, except for meso-ventral tongue which encloses the clasper bases. Claspers very long, two-articled, in form of semi-circular pincer; bases of claspers produced mesad as wide ledges divided by vertical ridge (Fig. 147); distal article tapered sharply. Aedeagus long, thin; lateral arms slender, finely spinate; variably fused to ensheath median shaft (Fig. 149).

Female genitalia with segment IX of two almost separate parts; tubular piece narrow, projected. Segment X flared, narrowed basally. Supra-genital plate large, short, thick. Vulval scale simple, pad-like, trapezoidal and convex (Fig. 151, 152).

**Key to the Males of species of *Dicosmoecus* found in Alberta and eastern British Columbia**

1a. Mesal ridge of clasper bases in posterior aspect vertical, roughly rectangular in outline, with smaller rectangular lateral lobe (Fig. 147) ............... *D. jucundus* Banks, p. 52.

1b. Mesal ridge of clasper bases in posterior aspect not vertical, only outer edge visible; long axis oriented obliquely dorso-ventrad; lateral lobe small, acuminate (Fig. 154) .......................... *D. atripes* (Hagen), p. 53.
Key to the Females of species of *Dicosmoecus* found in Alberta and eastern British Columbia

1a. Median lobe of vulval scale sub-equal in length to lateral lobes. Segment X projected posterad, deeply cleft, the two halves thin, plate-like (Fig. 151) 

* D. jucundus* Banks, p. 52.

1b. Median lobe of vulval scale only half as long as lateral lobes. Segment X short, cleft to two short, rounded, fleshy lobes (Fig. 156) 

* D. atripes* (Hagen), p. 53.

*Dicosmoecus jucundus* Banks, 1943

(Fig. 122a, 122b, 146-152, 593)


Males of this species (which Flint, 1966, considers to be a synonym of *D. atripes*) are most easily distinguished from males of *D. atripes* by posterior aspect of basal ridge of clasper (Fig. 147, 153), as defined in preceding key. Females are distinguished by length of median lobe of vulval scale relative to lateral lobes (Fig. 151, 156).

Description. — Antennae dark brown; antero-mesal faces of scapes with longitudinal glabrous, yellowish stripe. Vertex of head dark brown; warts yellowish. Thorax yellowish laterally, yellow to red-brown dorsally in form of cruciform pattern on nota, with base of cross directed posterad. Femora yellow, tibiae and tarsi chocolate-brown. Fore wing length of male 25 mm; dark brownish grey, with prominent, almost black veins; costal area almost hyaline and a clear area located at divergence of veins M1+2 and M3. Venation of fore and hind wings as in Fig. 122a, 122b. Male genitalia. (Specimen taken 2 miles west of Hinton, Alberta). Segment IX high, very narrow, of irregular width (Fig. 146). Sternum produced posterad as broad shelf ventrad of clasper bases. Clasper massive, two-articled; distal article bowed slightly ventrad, with distal tooth directed postero-ventrad. Basal article with meso-ventral edge developed mesad as broad shelf (Fig. 147); shelf with two lobed vertical ridge extended meso-laterad; each lobe rectangular in posterior aspect, lateral lobe smaller, almost at right-angles to mesal lobe (Fig. 148). Median lobes of segment X short, rounded, spinate and semi-membranous. Intermediate lobes of segment X long, finger-like, each flanked laterally by thin ridge (Fig. 146); lobes connected by high, thin-legged bridge with flat, plate-like crown (Fig. 147). Cercus long, rounded-rectangular, setose distally. Aedeagus long, slender, head little wider than stem. Lateral arms short, with thick basal half, needle-like distal half; four heavy, dark spines near middle and tip with two or three spines in tight cluster (Fig. 149, 150). Mesal faces of clasper bases and base of aedeagus joined by continuous, thin, sclerotized strap, looped around aedeagal base (Fig. 147).

Female genitalia. (Specimen from 2 miles west of Hinton, Alberta). Posterior edge of sternum VII with long, narrow fringe of short, hyaline hairs. Segment VIII with sternum markedly narrowed by antero-mesal constriction (Fig. 151). Vulval scale massive; lateral lobes around vaginal aperture; median lobe tapered slightly distad, tip rectangular, attached completely distad by membrane. Segment IX small, notum massive, connected to vulval scale by lateral lobes with broad ventral extremities (Fig. 152); lateral lobes darker than notal area. Supra-genital plate small, membranous, located between vulval scale and segment IX, in membranous sheet. Segment X of two large, convoluted lobes joined smoothly to segment IX.

Notes on biology. — Specimens of this species appear to emerge from small to large, smoothly flowing, pebbled streams and rivers. I have records of captures made along lake
edges, but it is possible that these are instances of individuals flying in from nearby streams. Adults are found from the last week in July to the last week in August.

Geographical distribution. — The known range of this species extends from Alberta and British Columbia to California (Fig. 593). In Alberta the species is confined to the low mountain valleys and foothills at altitudes between 3,400' and 5,450'.

I have examined 27 specimens, 20 males and seven females, from the study area.

_Dicosmoecus atripes_ (Hagen), 1873

(Fig. 153-156, 592)


Description. — Meso-basal ledge of male clasper with ridge; in posterior aspect (Fig. 154) this ridge viewed along its crest; bi-partite, with larger lobe set at angle of about 40° along its long axis; smaller lobe tooth-like, with distinct acuminate tip, located latero-anterad of larger lobe. Distal article of clasper with distal tooth directed posterad from unbowed finger-like extension of article (Fig. 153). Lateral arms of aedeagus each tipped by dense cluster of spines; mid-point with four close-spaced lateral spines; basad with short single spine (Fig. 155).

Female genitalia essentially similar to that of _D. jucundus_ in lateral aspect, but differing markedly in ventral aspect (Fig. 156). Vulval scale massive, with short, tapered median lobe square tipped; lateral lobes huge, bulbous, with distinct antero-lateral concavities. Supr genital plate minute, triangular, located in sheet of membrane. Vaginal aperture roofed over by large sclerotized, straight-edged plate. Lateral lobes of segment X thick, fleshy, rounded, completely separated ventrally.

Geographical distribution. — The known range of this species extends from Alberta (Beaver Creek (Banks, 1943)) and British Columbia to California and New Mexico (Fig. 592). I have no records from Alberta in my own collections. The drawings were taken from Utah specimens in Illinois Natural History Survey.

The Genus _Onocosmoecus_ Banks

This genus is represented by one species in the study area.

Synopsis of characters. — Spur formula 1,3,4. Pleural sclerites without silky hairs; macrochaetae less developed than in _Dicosmoecus_. Fore wings large, bluntly parabolic apically; hind wings larger than fore wings, with posterior edge regularly convex. Chord of fore wing markedly broken; posterior part slightly oblique to body axis. Chord of hind wing only slightly disrupted; posterior part oblique to body axis.

Male genitalia much as in _Dicosmoecus_. Aedeagus relatively shorter; median shaft expanded apically; lateral arms quite large, partly free, armed with few heavy spines (Fig. 159).
Female genitalia differing appreciably from *Dicosmoecus*. Segment IX massive, very strong, of one piece; ventrally vulval scale flanked by two large lobes (Fig. 162, 163). Segment X conical. Supra-genital plate small. Vulval scale thick, trilobed; lateral lobes semiglobose apically; small, tongue-like median lobe enclosed by lateral lobes (Fig. 163).

*Onocosmoecus unicolor* (Banks), 1897
(Fig. 157-163, 594)


Specimens of this species are distinguished from other limnephilids in the study area by large size of body and wings, and by smoothly rounded parabolic form of wing tips. Specimens of this species may be confused with the still larger specimens of *Dicosmoecus* in the study area, and may be separated from them by general body coloration, which is red-brown rather than grey to black as in *Dicosmoecus*.

**Description.** — Antennae straw-yellow; antero-mesal face of scapes setaless; each article with distal half and anterior face depressed. Vertex of head dark straw-yellow. Thorax generally yellow, to brownish dorsally except for yellowish warts. Spurs dark yellow. Forewing length of male 18.4 mm; warm orange-brown except for grey-brown areas at proximal ends of the four distal radial cells, and at first bifurcation of M. Anal area slightly darker brown. Venation of fore and hind wings identical to that of *Dicosmoecus* (Fig. 122a, 122b).

Male genitalia. (Specimen from Gorge Creek, 20 miles west of Turner Valley, Alberta). Segment IX high, narrow, sinuate (Fig. 157); with sparse fringe of setae round clasper base, and denser patch ventrad of base. Clasper large, two-articled, with rather spindly distal article black tipped. Basal article with ventro-lateral band of setae set in lighter coloured area. Meso-basal ledge of clasper with transverse, rounded, ridge at postero-mesal corner (Fig. 158). Median lobes of segment X long, narrow, partially fused; separated from ventral portion of segment by wide membranous area. Ventral portion of segment X truncate-triangular in dorsal aspect, with high sclerotized ridge on each side. Cercus large, blunt, lanceolate in lateral aspect, with concave mesal face. Aedeagus large, simple, sinuate (Fig. 159); lateral arms heavy, short, armed with three to five straight, black spines of varied lengths, with one dominantly large spine basally. Two large, black spines arise from dorsal membranous area between median shaft and lateral arms of aedeagus (Fig. 160). Aedeagal base flanked by two twisted, strap-like sclerites attached to antero-mesal edge of claspers (Fig. 161).

Female genitalia. (Specimen from Gorge Creek, 20 miles west of Turner Valley, Alberta). Posterior edge of sternum VII with wide fringe of fine, hyaline hairs, Vulval scale relatively small, complex. Median lobe squat, triangular, rounded (Fig. 163); lateral lobes rounded, spatulate on mesal faces, tending to enclose median lobe. Lateral lobes laterally enveloped by two folds of membrane. Segment XI massive, tapered ventrad, with large lateral bulges (Fig. 162, 163). No apparent supra-genital plate. Segment X large, tubular, merged imperceptibly with segment IX; with large, projected, roof-like dorsal area, and shorter, hemicylindrical ventral area with dentate posterior edge.
Notes on biology. — Larvae of this species apparently inhabit streams ranging from very small to rivers, with no apparent preference as to nature of the bottom. There is some indication that larvae might also inhabit lakes. The adult flight season extends from early May to late September, peaking in August.

Geographical distribution. — The known range of this species extends from Alaska to the New England states and New Mexico (Fig. 594). In Alberta the species is commonest in the low mountain valleys, but has been recorded well out in the plains, and is known from Saskatchewan. In Alberta the known altitudinal range is from around 2,000' to 5,450'. I have examined 225 specimens, 154 males and 71 females, from the study area.

The Genus Amphicosmoecus Schmid

The single species of this genus is found in Alberta and eastern British Columbia.

Synopsis of characters. — Spur formula 1,2,4. Wings very large; fore wings bluntly rounded apically; hind wings with large anal area and M2 present (Fig. 123b).

Male genitalia with narrow dorsal strap on segment IX; remainder of segment greatly expanded ventrally (Fig. 164). Median lobes of segment X long, dorsally arched blades. Clasper large, long, blunt, pincer-like (Fig. 165); two-articled, both articles fused. Aedeagus small, housed in membranous pocket; lateral arms spiniform, armed with short, fine spines (Fig. 166).

Female with segment VIII unmodified. Vulval scale huge, massive; median lobe small, located in deep cleft between lateral lobes which are fleshy, and enclose vaginal aperture laterally (Fig. 168, 169). Segment IX large, of one piece, with no central lobes. Supra-genital plate large, projected well posterad, sclerotized (Fig. 169). Segment X small, recessed into segment IX; fused to segment IX; with long, thin median lobes.

Amphicosmoecus canax (Ross), 1947
(Fig. 123a, 123b, 164-169, 595)


Males of this species are distinguished from all others by large, sickle-shaped, median lobes of segment X, and by claspers with fused articles. Females are distinguished by massive vulval scale, with small, minutely trilobed median lobe, and by long, slender median lobes of segment X.

Description. — Antennae orange-brown; scapes dark brown, with yellow, glabrous anteromesal faces. Vertex of head dark straw-yellow with light brown areas. Thorax yellow to light brown especially laterad of terga. Spurs straw-yellow. Fore wing length of male 17.8 mm; pale greyish brown except for hyaline areas at extremity of Cu2, and initial bifurcation of M. Anal area posterad of Cu2 darker, slightly irrorate. Venation of fore and hind wings as in Fig. 123a, 123b.

Male genitalia. (Specimen from 2 miles east of Nordegg, Alberta). Segment IX with large ventral body; dorsal strap narrow, heavy, bilobed (Fig. 165); slight concavities occur at ventro-lateral faces of segment. Clasper large, two-articled, with articles fused; sharp, narrow, ledge along ventro-mesal face, and distinct groove on dorso-lateral face of basal portion thumb-like (Fig. 164, 165). Median lobes of segment X long, dorsally arched, thin blades; sickle-like, with acuminate tips. Cercus spatulate, setose, attached to large, bowl-shaped, lateral plates of segment. Aedeagus very simple (Fig. 166); tip slightly dilated, base slightly
wrinkled dorsally. Lateral arms very simple, plain rods with five to six simple, long spines distally. Aedeagus connected basally to clasper bases by lateral straps bent at angle of about 60° at point of departure from aedeagal base; terminated by large, hollow, spherical structures (Fig. 167).

Female genitalia. (Specimen from 2 miles east of Nordegg, Alberta). Posterior edge of tergum VII with short, narrow brush of short, yellow hairs. Vulval scale huge, with massive, fleshy lateral lobes, and small, trilobed median lobe (Fig. 169). Segment IX composed of single, trapezoidal tergum (Fig. 168). Supra-genital plate large, convoluted, with lateral edges turned dorsad. Segment X small, complex, with two short, stout, lateral lobes and two long, thin, hyaline, mesal lobes; bases of lobes produced ventrad as two broad, triangular flaps fitted loosely into two dorsal channels of supra-genital plate. Segment X recessed into segment IX.

Notes on biology. — Larvae of this species inhabit a wide variety of streams, from small, quiet brooks, to large rivers and turbulent mountain streams. The adult flying season extends from mid-September to late October.

Geographical distribution. — The known range of this species extends from Alberta and eastern British Columbia to Utah and California. Records are very scattered however (Fig. 595). In Alberta the species occurs mainly in the mountain and foothill areas. There is one record from Cold Creek, Nojack, however, which is well outside of this area. My records indicate an altitude range from at least 2,500' to 4,200'.

I have examined 67 specimens, 51 males and 16 females, from the study area.

The Genus *Imania* Martynov

This genus is represented in the study area by four species, one of which is here described as new. Ross (1950) divided the genus into four species groups, of which the *tripunctata* and *bifosa* groups are known to occur in the area.

Synopsis of characters. — Form of head varied. Spur formula 1,3,4. Macrochaetae poorly developed. Wings of different lengths; fore wings apically parabolic; hind wings slightly larger than fore wings, hardly indented posterad of apex (Fig. 124-127). Venation complete; fore wings unmodified, venation of hind wing slightly reduced. R1 of fore wing arched or not at stigma, or joined to Sc by cross-vein. Chord of fore wing strongly disrupted, concave to body. Hind wing with chord only slightly disrupted, posterior part oblique to body; Cu1a absent. Frenulum of seven or eight strong, curved spines at costa base.

Male genitalia with segment IX narrow laterally, with wide dorsal process (Fig. 170). Segment X elongate, slender; of two long, sclerotized, free or fused, portions (Fig. 171). Clasper large, two-articled; not pincer-like, complex, directed dorso-posterad; basal article long, subcylindrical, not baso-mesally enlarged, with baso-mesal area in some species developed as one or more sclerotized spines; distal article short, bilobed, with dorsal lobe with heavy, short, black teeth. Aedeagus small; lateral arms slender, spiniform, free or basally fused as sheath to median shaft (Fig. 175).

Female genitalia with segment IX of two parts not entirely separated; dorsal part simple, narrow, quite long, Segment X of two very large dorsal plates, strongly sclerotized. Vaginal aperture flanked by ventral lobes of segment X. Supra-genital plate large, not prominent. Vulval scale reduced to one lobe, membranous, wrinkled (Fig. 176, 177).

Key to the Males of species of *Imania* found in Alberta and eastern British Columbia

1a. Basal article of clasper with long, slender, acuminate spine attached to baso-mesal face (Fig. 171, 174, 184) ................................. (tripunctata group) 2a
1b. Basal article of clasper without such spine (Fig. 179) ..... *I. bifosa* Ross, p. 60.
2a.(1a) Aedeagus with lateral arm bases fused to form sheath around aedeagal base (Fig. 175) .................. *I. cascadis* Ross, p. 58.
2b. Aedeagus without basal sheath (Fig. 171, 185) .................. 3a
3a.(2b) Median shaft of aedeagus tapered to tip (Fig. 172); segment X deeply cleft, of two heavy, black, large spiniform lobes (Fig. 171) *I. tripunctata* (Banks), p. 57.
3b. Median shaft of aedeagus not tapered distally (Fig. 185); segment X not deeply cleft, with two short, acuminate distal lobes (Fig. 184) .................. *I. hector* Nimmo n. sp., p. 59.

**Key to the Females of three species of Imania found in Alberta and eastern British Columbia**

1a. Single, median, lobe of vulval scale massive, rectangular, dorsally directed flap (Fig. 176, 177) .................. *I. cascadis* Ross, p. 58.
1b. Median lobe of vulval scale small, dorsally directed (Fig. 181, 186). .................. 2a
2a.(1b) Ventral aspect of lateral lobes of segment X triangular; short, wide, rounded in lateral aspect (Fig. 187) .................. *I. hector* Nimmo n. sp., p. 59.
2b. Ventral aspect of lateral lobes of segment X trapezoidal (Fig. 181); in lateral aspect long, ventrally curved, slender (Fig. 182) .................. *I. bifosa* Ross, p. 60.

**The tripunctata group**

There are three species of this group known from the study area, one of which is new. Males of species in this group are characterised by long, sinuate, blade-like spines developed from baso-mesal face of clasper (Fig. 174). Females are recognizable by roughly triangular ventral aspect of lobes of segment X (Fig. 176, 187).

**Imania tripunctata** (Banks), 1900

(Fig. 126a, 126b, 170-172, 596)


*Hypnotranus ? tripunctatus*; Ulmer, 1907a:72.


Males of this species are distinguished from males of other species of the *tripunctata* group by massive, spiniform, heavily sclerotized distal lobes of segment X in ventral aspect (Fig. 171), and by smoothly tapered median shaft of aedeagus (Fig. 172).

**Description.** — Antennae chocolate-brown. Vertex of head dark chocolate with reddish tinges laterally. Thorax deep, warm red-brown laterally, darker dorsally. Spurs brown. Fore wing length of male 11.4 mm; dull red-brown, with hyaline areas along veins. Venacon of fore and hind wings as in Fig. 126a, 126b.

Male genitalia. (Specimen from Cascade River, Banff National Park, Alberta). Posterior edge of sternum VIII with long, single parallel row of heavy, hyaline setae (Fig. 170). Segment IX with very narrow ventral and lateral walls, broadened dorsad of clasper bases.
Nimmo

Clasper massive, with high base, narrowed distad to uniform width along distal half of basal article. Baso-mesal face of clasper with long, thin, sinuate black spine. Distally basal article with flared fringe of long, stout setae. Distal article of clasper bilobed, claw-like, with dorsal lobe flat ventrally, armed with many stout, short, black pegs. Ventral lobe rounded, short, with some black spines distally. Segment X with median lobes overhung by large, rounded, dorsal bulge. Median lobes long, thin, acuminate structures curved dorso-lateral distally. Cercus long, almost rectangular plate (in Fig. 170 they are seen end-on, however, as they project laterad). Lateral arms of aedeagus sclerotized, finely tapered, with curved base (Fig. 172). Median shaft tapered, with attenuated tip; ejaculatory duct opens on dorsal surface of tip, between two lateral flanges.

Female genitalia. Unknown.

Geographical distribution. — The known range of this species extends from Alaska to Washington and Colorado (Fig. 596). I have only one record of the species in Alberta, from an altitude of 6,500’, several miles northeast of Banff, on the Cascade Fire Road.

I have examined a single male of this species, on loan from Illinois Natural History Survey. The date of collection is May 30.

Imania cascadis Ross, 1950
(Fig. 124a, 124b, 173-177, 597)


Allomyia cascadis; Fischer, 1967:70.

Males of this species are distinguished from males of other species of Imania by basal aedeagal sheath of lateral arm bases (Fig. 175); by foreshortened basal article of clasper (Fig. 174); and by almost unleft segment X, each half of which is more or less square cut distally in ventral aspect. Females are distinguished by very wide, long median lobe of vulval scale (Fig. 176).

Description. — Antennae reddish chocolate-brown; scapes with antero-mesal faces dark brown, remainder pale yellow. Vertex of head deep chocolate-brown; warts pale. Thorax deep red-brown laterally, almost black dorsally; warts pale. Fore wing length of male 10.4 mm; pale red-brown, lightly irrorate. Venation of fore and hind wings as in Fig. 124a, 124b.

Male genitalia. (Specimen from Spray River, at Banff, Alberta). Tergum VIII with single row of long, thick setae parallel to posterior edge. Segment IX high, uniformly narrow, bowed anterad (Fig. 173). Basal article of clasper with massive base and clearly delineated distal clumps of setae originated from pale surficial areas. Baso-mesal face of clasper with long, thin, sinuate black spine. Distal article of two short, stout lobes with teeth or pegs only at distal edges. Segment X of two parallel, concave plates with distal edges thin, sharp, directed dorsal (Fig. 173, 174). Cercus short, rounded lobe. Lateral arms of aedeagus arched high over distal portion; attached to massive, plate-like bases (Fig. 175). Ejaculatory duct of median shaft opening dorsally, well basad of cleft tip.

Female genitalia. (Specimen from Spray River, at Banff, Alberta). Tergum VIII with straight, single row of long, stout setae parallel to posterior edge. Sternum VIII unpigmented medially. Vulval scale of single, wide, dorsally curved median lobe (Fig. 176). Segments IX and X imperceptibly fused (Fig. 177) as massive, sigmoid structure in lateral aspect, cleft medially as two lateral plates abutted dorsally, each at angle of about 45°. Supra-genital plate semi-circular, hyaline.

Geographical distribution. — The known range of this species extends from Washington to
Alberta (Fig. 597). In Alberta it is known only from the Spray River, Banff, at an altitude of about 5,500'.

I have examined two specimens from the study area, one of each sex, in Illinois Natural History Survey. The date given is May 30.

*Imania hector* Nimmo n. sp.

(Fig. 127a, 127b, 183-187, 597)

Males of this species are distinguished from males of other species of *Imania* by form of segment X in ventral aspect (Fig. 184); segment cleft distally, two halves spread wide apart, blade-like and acuminate. Median shaft of aedeagus short, blunt, with distinct distal head (Fig. 185). Females are distinguishable by triangular form of lateral lobes of segment X in ventral aspect (Fig. 186), and by long, narrow, dorsally directed median lobe of vulval scale.

**Description.** — Antennae dark brown. Vertex of head dark brown to black. Thorax dark red-brown. Femora of legs dark brown, remainder lighter brown. Fore wing length of male 7.6 mm; uniform dark brown except for slight irrorations along R1, and three hyaline areas at bases of F2 and F3, at bifurcation of M1+2 and M3, and at end of Cu2. Venation of fore and hind wings as in Fig. 127a, 127b.

Male genitalia. (Specimen from Sunshine Lodge, Banff National Park, Alberta). Tergum VIII with single row of long setae parallel to posterior edge. Segment IX high, narrow, essentially parallel sided (Fig. 183). Basal article of clasper massive, cylindrical throughout, armed with long, light brown, sinuate spine on baso-mesal face (Fig. 183, 184). Distal article bilobed; dorsal lobe parallel sided, moderately toothed ventrally. Segment X fused to segment IX dorsally. Median lobes fused at bases; distally separate, triangular, spinulate. Main body of segment X folded roof-like over anal aperture. Cercus long, narrow, in dorso-lateral depression of segment X. Aedeagus with two pairs of lateral arms; dorsal pair short, heavy, scythe-like; ventral pair long, straight, spatulate, in form of cylindrical sheath to membranous median shaft (Fig. 185). Ejaculatory duct open dorsally between distal flanges.

Female genitalia. (Specimen from Sunshine Lodge, Banff National Park, Alberta). Posterior edge of tergum VIII with single line of widely spaced hyaline hairs parallel to edge. Vulval scale single, long, rectangular median lobe; distal half wrinkled, curved dorsal (Fig. 186, 187). Vulval scale and vaginal aperture flanked by two large, sclerotized bodies. Segments IX and X fused; comprising two large, rounded lobes with flat mesal faces sloped meso-dorsal in form of roof-like structure; each lobe in ventral aspect triangular.

**Notes on biology.** — Individuals of this species appear to emerge from fast, turbulent mountain creeks with boulder beds. The flight season extends from June 1 to July 9.

**Geographical distribution.** — The known range of this species includes three localities close to the continental divide in Banff National Park, Alberta (Fig. 597). The altitudinal range extends from around 6,000' to 7,000'.

I have examined 13 specimens, nine males and four females, from the study area.


**Allotype.** — Female. Same data as holotype.

**Paratypes.** — Same data as holotype; four males, one female. Sunshine Lodge, Banff National Park, Alberta; July 9, 1962; K. C. Herrmann; four males. Hector Creek, at Banff-Jasper Hwy. north of Lake Louise, Banff National Park, Alberta; June 15, 1967; A. Nimmo; one female. Moraine Creek at Moraine Lake, Banff National Park, Alberta; June 1, 1958; W. E. Ricker; one female.
All type material is in the Canadian National Collection, Ottawa (type number 10,583) with the exception of the female from Hector Creek, which is in the Strickland Museum, Dept. of Entomology, University of Alberta, Edmonton.

This species is not named for Hector Creek but for the character of the same name in ancient Greek literature.

The *bifosa* group

One species of this group is known from the study area.

Males of the group are distinguished by absence of long, blade-like spine at baso-mesal face of basal article of clasper (Fig. 179); by presence of a short, acuminate extension of basal article of clasper, at meso-distal edge; and by presence of two pairs of long, curved, blade-like lateral arms on aedeagus (Fig. 180). Females are distinguished by lack of median cleavage of segment X (Fig. 181); by trapezoidal outline in ventral aspect, of lateral bulges of segment X; and by long, narrow, dorsally curved median lobe of vulval scale.

*Imania bifosa* Ross, 1950

(*Fig. 125a, 125b, 178-182, 597*)


*Allomyia bifosa*; Fischer, 1967:70.

Males of this species are distinguished from males of other species of the genus by absence of baso-mesal spine on clasper base. Females are distinguished by trapezoidal lateral bulges of segment X.

*Description.* — Antennae dark brown to black. Vertex of head black. Thorax black to very dark brown. Fore wing length of male 8.5 mm; uniform dark chocolate-brown, appearing black in living insects. Venation of fore and hind wings as in *Fig. 125a, 125b*.

Male genitalia. (Specimen from Mt. Edith Cavell, Jasper National Park, Alberta). Tergum VIII with single line of long setae parallel to posterior edge. Segment IX very narrow, bowed anterad in lateral aspect. Clasper large, with massive basal article of uniform width (Fig. 178). Basal article with meso-distal edge produced posterad as short, acuminate spine (Fig. 179). Distal article bilobed; ventral lobe thin, parallel sided in lateral aspect; dorsal article irregular, arched dorsad, with heavily toothed ventral surface. Segment X with short, bulbous cercus; median lobes triangular in lateral aspect, curved postero-laterad; intermediate lobes small, located on ventral edges of median lobes. Segment X roof-like, with carinate dorsal ridge. Aedeagus with median shaft curved ventrad; ejaculatory duct terminated in dorsal groove. Two pairs of lateral arms; basal pair long, slender, arched dorsad; distal pair similar but shorter and wider (Fig. 180).

Female genitalia. (Specimen from Mt. Edith Cavell, Jasper National Park, Alberta). Posterior edge of tergum VIII with single line of well spaced setae. Vulval scale with single, median lobe originated from fold of membrane, curved dorsad. Segment IX with semi-cylindrical dorsum almost completely dissociated from two ventro-lateral lobes around genital cavity (Fig. 182). No evident supra-genital plate. Segment X fused completely with segment IX and cleft mesally very shallowly (Fig. 181).

*Notes on biology.* — Individuals of this species emerge from cold, alpine streams which originate primarily as glacial melt-water and flow over moraine debris. The adult flight season extends from June 29 to July 22.

*Geographical distribution.* — The known range of this species is restricted to southern
Alberta and British Columbia (Fig. 597). In Alberta the species is known only from high mountain regions close to the continental divide, at altitudes between 6,000' and 7,500'. I have examined 116 specimens, 71 males and 45 females, from the study area.

The Genus *Ecclisomyia* Banks

Three species of this genus are known from the study area. Of these one is unidentified as only a single female is known.

*Synopsis of characters.* — Spur formula 1,3,4. Wings of normal size, elongate; fore wing rather narrowly parabolic; hind wing little larger. Venation complete, almost unmodified. Fore wing with long, narrow, discoidal cell; chord strongly disrupted, posterior part oblique to body. Hind wing with very long discoidal cell, chord not so disrupted, and posteriorly oblique to body (Fig. 128a, 128b).

Male genitalia with lateral walls of segment IX very wide; segment greatly narrowed dorsally and ventrally (Fig. 188, 194). Cercus very large, long, mesally concave. Median lobes of segment X fused in form of long process, concave basally, flattened distally. Clasper small, not recessed into segment IX, of one article, conical, with one or more stout, or long and thin, spines on baso-mesal face (Fig. 189, 195).

Female genitalia with segment IX very large, massive, of one piece. Segment X conical. Supra-genital plate short. Vaginal aperture along entire length of segment IX, partially obstructed by single, median, membranous vulval scale (Fig. 192, 193).

**Key to the Males of two species of *Ecclisomyia* found in Alberta and eastern British Columbia**

1a. Colour pale yellow-red. Clasper of genitalia with two pairs of long, fine, baso-mesal spines (Fig. 188, 189). Size smaller ............... *E. maculosa* Banks, p. 61.

1b. Colour dark purple-brown. Clasper of genitalia with single, massive, black, heavily sclerotized baso-mesal spine (Fig. 195). Size larger .... *E. conspersa* Banks, p. 62.

**Key to the Females of species of *Ecclisomyia* found in Alberta and eastern British Columbia**

1a. Colour pale yellow-red. Single median lobe of vulval scale massive, with distinct v-notch on distal edge (Fig. 192); supra-genital plate very large, very deeply cleft mesally. Size smaller .............................. *E. maculosa* Banks, p. 61.

1b. Colour dark red-, or purple-brown. Vulval scale and supra-genital plate not as above. Size larger .................................................. 2a

2a.(1b) Vulval scale very wide, long, rectangular, point of origin in membrane between segments VIII and IX (Fig. 200) ............................ *E. sp. 1*, p. 63.

2b. Vulval scale with rectangular tip, membranous, originated imperceptibly from membrane between segments VIII and X (Fig. 199) . . *E. conspersa* Banks, p. 62.

*Ecclisomyia maculosa* Banks, 1907

(Fig. 128a, 128b, 188-193, 598)


Males of this species are distinguished from males of other species of *Ecclisomyia* by two
pairs of long, fine spines on each clasper (Fig. 188, 189). Females are distinguished by large, distally notched, median lobe of vulval scale. Specimens may be distinguished with the naked eye simply by their small size, and pale yellowish red coloration with scattered irruptions.

**Description.** — Antennae light yellow-brown; antero-mesal face of scapes paler, glabrous. Vertex of head with antero-mesal area brown bounded by yellow. Thorax pale reddish or yellowish brown. Lateral faces of maxillary palpi black or otherwise; mesal faces light brown to yellow. Lateral faces of front and middle tibiae black. Fore wing length of male 7.9 mm; very light reddish or yellowish brown, uniformly irrorate, except for hyaline costal area. Venation of fore and hind wings as in Fig. 128a, 128b.

Male genitalia. (Specimen from Lake Agnes, Lake Louise, Alberta). Segment IX with wide lateral walls, and narrower but strong dorsal strap (Fig. 188, 189). Clasper of one article, large, longer than thick, with two pairs of long, dark spines on baso-mesal face; basal pair about three times longer than distal pair (Fig. 188). Median lobe of segment X skittle-like in dorsal aspect (Fig. 189), with small dilated tip; laterally fringed with sparse, short, sharp setae. Intermediate lobes short, blunt. Cercus long, rounded, mesally concave. Aedeagus very simple, with dorsally directed, scoop-like tip extended over ejaculatory duct as hood; ejaculatory duct opening in padding of hyaline membrane on ventral surface of dorsal hood (Fig. 190, 191). Distal edge of hood dark brown, with u-shaped mesal notch.

Female genitalia. (Specimen from Lake Agnes, Lake Louise, Alberta). Vulval scale large, with median ridge between two rounded, ventral concavities; sides roughly parallel, posterior edge with shallow, wide v-notch (Fig. 192). Segment IX high, narrow, of one piece (Fig. 193). Tufts of long, yellow setae laterally, about mid-point. Supra-genital plate large, long, rectangular, divided in two rounded, rectangular lobes by very deep v-cleft. Segment X of two rounded, conical lobes joined dorsally toward base; each lobe with mesally directed flanges on basal half of ventral edges (Fig. 192).

**Notes on biology.** — Individuals of this species emerge from small, riffled mountain creeks, running gently over fine gravel bottoms. The adult flying season extends, in the study area, from July 14 to August 14.

**Geographical distribution.** — The known range of this species extends from Alberta and British Columbia to Oregon and Colorado (Fig. 598). In Alberta it is confined to the mountains and foothills, ranging in altitude from 4,500’ to 7,000’.

I have examined 59 specimens, 54 males and five females, from the study area.

**Ecclisomyia conspersa** Banks, 1907

(Fig. 194-199, 599)


Males of this species are distinguished by massive, black, heavily sclerotized spine on baso-mesal face of clasper (Fig. 195). Females are distinguished by membranous, tapered, rectangular tipped median lobe of vulval scale (Fig. 199).

**Description.** — Antennae brown; scapes dark brown, antero-mesal faces white in female, pale brown in male. Vertex of head dark brown, posterior edge and angles paler. Thorax light to dark chocolate-brown; warts of terga yellowish. Spurs dark brown. Fore wing length of male 13.8 mm; dark reddish brown, uniformly coloured costal area. Venation as in *E.
maculosa.

Male genitalia. (Specimen from Kicking Horse Campground, Yoho National Park, British Columbia). Segment IX almost equilateral-triangular in lateral aspect (Fig. 194). Dorsal strap wide, short. Basal half of anterior edges banded with light and dark brown; remainder pale to hyaline. Clasper large, stubby; two articles fused but traces of suture evident. Setae on ventral, disto-ventral, and distal surfaces. Baso-mesal face occupied by massive, black, strongly sclerotized spine (Fig. 195), hooked laterad at tip; base of spine hemispherical. Median lobe of segment X acute-triangular in ventral aspect (Fig. 195), with disto-ventral hook. Intermediate lobes small, setose, placoid. Cercus large, rectangular, distally rounded, slightly concave on mesal face. Aedeagus large, with ejaculatory orifice on large, fleshy lobe between two stout, dark brown, distal spines (Fig. 196). Duct ventral on aedeagus, flanked by two lateral folds. Aedeagal strap roughly triangular (Fig. 197) at attachment point, with two thin straps connected to clasper bases.

Female genitalia. (Specimen from Kicking Horse Campground, Yoho National Park, British Columbia). Sternum VIII divided mesally by band of membrane of two lateral sternites (Fig. 199). Vulval scale rectangular distally, with rippled surface; attached to tapered fleshy extension of sternum VIII. Segment IX massive, trapezoidal in lateral aspect, fused almost imperceptibly to segment X, except ventrally (Fig. 198). Supra-genital plate cleft distally in form of two lobes; plate arched laterally, flanged to form partly enclosed passage to vagina. Segment X large, triangular in lateral aspect, with small notch distally. Ventral edges arched over and beyond anal aperture.

Notes on biology. — Individuals of this species emerge from small to large mountain creeks flowing turbulently over small stone or boulder bottoms. I have observed pupae of this species emerge from Whitehorse Creek, Cadomin, Alberta, at an altitude of about 6,500', on May 21. The pupae crawled out of the water onto streamside boulders or ice indistinguishably, remained still for about 10 minutes, then started to emerge as adults from the pupal skin, which required about 5 minutes. Upon completion of emergence the adults were active, but did not attempt to fly for about another 10-15 minutes. A total of 33 males and 17 females were collected on this occasion. The adult flight season extends from May 17 to September 12 in the study area.

Geographical distribution. — The known range of this species extends from Alaska to California and New Mexico (Fig. 599). In the study area the species is confined to the mountain and foothill areas, ranging in altitude from 2,600' to 7,300'.

I have examined 180 specimens, 131 males and 49 females, from the study area.

Ecclisomyia species I
(Fig. 200-201, 600)

Only a single female is known to me, which is distinguished from the females of the other species of Ecclisomyia treated here by very large, rectangular, median lobe of vulval scale. This lobe has definite point of origin from membrane between segments VIII and IX, and is concave dorsally, convex ventrally (Fig. 200, 201).

Description. — Antennae yellow-brown; scapes darker, with antero-mesal faces almost white, glabrous. Vertex of head dark brown centrally, lighter round edges. Thorax deep yellow-brown laterally, to dark brown dorsally. Spurs brown. Fore wing length of female 15.8 mm; red-brown, heavily irrorate, except for clear costal area. Venation identical to that of E. maculosa.

Female genitalia. Vulval scale single, large, rectangular, median lobe (Fig. 200), concave dorsally, convex ventrally, i.e. spatulate. Segment IX massive, trapezoidal in lateral aspect
(Fig. 201). Supra-genital plate short, wide, bilobed. Segment X relatively large, closed dorsally, deeply cleft ventrally; very slightly bilobed distally, with lateral walls constricted antero-ventrad.

**Geographical distribution.** — The single known female specimen was taken under a road bridge over the Miette River, about 1 mile south of Jasper, Alberta, on highway 93a (Fig. 600), on July 6. It was already dead and trapped in cobwebs.

The Subfamily Apataniinae Ulmer

Head rather long, both sides convex; eyes, ocelli and cephalic warts small. Pronotum short; macrochaetal development slight. Spur formula varied, identical in both sexes of the same species. Wings constant, identical in both sexes; fore wing elongate, obliquely parabolic; hind wing hardly larger than fore, with convex trailing edge; clearly indented at termination of Cu2. Frenulum of three strong spines at base of costa of hind wing; spines curved basally, sharp, flattened distally. Venation complete, somewhat modified. R1 of fore wing of most species arched distally, united to Sc by cross-vein. Chord single line, irregularly disposed. Hind wing with distally open discoidal cell, very short f1 and four anal veins. See Fig. 129a, 129b.

Male genitalia with segment IX lengthened longitudinally slightly; clasper bases enclosed or not. Dorsally segment IX only weakly narrowed, with or without two basal lobes. These lobes various in size, separate or fused together, or fused to median lobes of segment X. Segment X sclerotized, annular, around anus; slightly developed and inconspicuous; with or without three pairs of appendages. Clasper always large, two-articled, movable, pincer-like in certain groups. Distal article various, little reduced. Aedeagus with median shaft and two lateral arms, freely movable.

Female genitalia with segment IX of one piece; wide dorsally, latero-ventrally attenuated with large, conical, ventral lobes. Segment X slender, poorly sclerotized; in some taxa long, tubular, with lateral concavities. Supra-genital plate present in most taxa; membranous or concave, rigid. Vulval scale membranous lobe of sternum VIII or with small lateral lobes. Vaginal aperture along length of sternum IX.

In the study area the subfamily Apataniinae is represented by one genus, *Apatania* Kolenati, of the tribe Apataniini (Martynov). In consequence, no outline of characters of the subfamily or genus is given. The species of *Apatania* are distinguished by the key to subfamilies on page 50. Schmid (1953, 1954a, 1955) presents a detailed account of the subfamily and its constituent taxa.

The Genus *Apatania* Kolenati

This genus is represented in the study area by five species belonging to four groups. One of these species is new.

**Key to the Males of species of *Apatania* found in Alberta and eastern British Columbia**

1a. Intermediate lobes of segment X with tips hooked antero-lateral, darker than remainder of genitalia (Fig. 206, 207) .................................................. 2a

1b. Intermediate lobes of segment X not so hooked, not necessarily darker than remainder of genitalia (Fig. 202, 221) .................................................. 4a

2a.(1a) Lateral arms of aedeagus attached to fleshy dorsal lobes at base; long, laminate blades (Fig. 208, 213) .................................................. 3a

2b. Attachment of lateral arms not as above; median shaft of aedeagus thick, short,
Key to the Females of species of Apatania found in Alberta and eastern British Columbia

1a. Segment X separate and distinct from segment IX (Fig. 219, 224) .......................... 2a

1b. Segment X and IX fused solidly together (Fig. 204, 210, 214) .......................... 3a

2a. (1a) Median lobe of vulval scale abruptly widened distally to rectangular tip (Fig. 225) .......................... A. alberta Nimmo n. sp., p. 70.

2b. Median lobe short, simple (Fig. 220) .......................... A. crymophila McLachlan, p. 69.

3a. (1b) Segment X large, visible, fused solidly to segment IX; with acuminate distal lobes (Fig. 204, 214) .......................... A. shoshone Banks, p. 68.

3b. Segment X minute, concealed by posterior lobes of segment IX; segment IX massive, formless, rounded .......................... A. shoshone Banks, p. 68.

4a. (3a) Segments IX and X fused (Fig. 214) .......................... A. stigmatella (Zetterstedt), p. 67.

4b. Ventro-lateral lobes of segment IX present, distinct, separated by broad band of membrane (Fig. 204) .......................... A. zonella (Zetterstedt), p. 65.

The fimбриата group

One species of this group is presently known from the study area.

Synopsis of characters. — Fore wing sexual dimorphism strong in certain species; male fore wing stigma well marked or not; C thickened. R1 of hind wing arched at stigma or not, in contact with Sc.

Male genitalia with cerci and median lobes only of segment X present, free (except in A. kyotensis), large in most species. Cerci long, simple, like slender pegs in most species. Claspers medium sized; distal article distinct; small, bilobed in certain species. Aedeagus spinate; lateral arms laminate blades.

Female genitalia with dorsum of segment IX not prominent; simple and convex; shortened in some species. Supra-genital plate sclerotized, fused solidly to segment X. Segment X short, small, as large as segment IX.

Apatania zonella (Zetterstedt), 1840
(Fig. 129a, 129b, 202-205, 600)

Phryganea stigmatella var. zonella Zetterstedt, 1840:1066. (Type locality; Lapland).
Apatelia zonella; (Literature Palaearctic; see Fischer, 1967:125-126).
Apatidea zonella; (Literature Palaearctic; see Fischer, 1967:126).
Goniotaulius arctica Boheman, 1865. (Literature Palaearctic; see Fischer, 1967:127-129).
Goniotaulius arcticus; (Literature Palaearctic; see Fischer, 1967:127).
Apatelia arctica; (Literature Palaearctic; see Fischer, 1967:127-128).
Apatidea arctica; (Literature Palaearctic; see Fischer, 1967:129).
Radema arctica; Ross, 1944:297.

Apatidea auricula not Forsslund; (Literature Palaeartic; see Fischer, 1967:129).


Apatelia; See Fischer, 1967:129.

Radema groenlandica; Ross, 1944:297.


Apatelia inornata; See Fischer, 1967:129.


Apatidea palmeni; See Fischer, 1967:130.

Apatelia palmeni; See Fischer, 1967:130.

Apatania stigmatella not Zetterstedt; See Fischer, 1967:130.

Apatania zonella (Zetterstedt) var. dalecarlica Forsslund; See Fischer, 1967:130.

Males of this species are distinguishable from males of other species of Apatania by very short claspers, with bilobed distal article (Fig. 204). Females are distinguishable by acuminat postero-ventral lobes of segment X and presence of ventro-lateral lobes of segment IX (Fig. 204).

Description. — Antennae dark brown; scapes with antero-mesal faces glabrous. Vertex of head black. Thorax very dark brown. Femora of legs irregularly patterned with dark and lighter brown. Spurs yellow-brown. Fore wing length of male 8.5 mm; translucent dark brown, with thick, irregular stigma. Venation of fore and hind wings as in Fig. 129a, 129b. Stigma of female fore wing weaker than male.

Male genitalia. (Specimen from Lake Hazen, Ellesmere Island, Northwest Territories). Tergum VIII with irregular single row of long setae parallel to posterior edge. Segment IX with narrow dorsal strap pinched in at each side as distinct crown; segment gradually expanded ventrad (Fig. 202). Clasper stout, short, with basal article laterally flattened, narrowed basally, disto-ventrally with long setae. Distal article bilobed; ventral lobe flattened dorso-ventrally, directed mesad. Segment X with irregularly dentate, pedicilate cerci. Median lobes large, hooked ventrad distally, with smooth dorsal edges and irregularly dentate ventral edges. Intermediate lobes fused in form of small, ventrallyhooked lobe ventrad of median lobes. Aedeagus simple, with large, warped, sword-like lateral arms attached to membranous base dorsad of median shaft (Fig. 203). Median shaft arched dorsad, distally acuminated, bilobed, with cluster of basally directed spines disto-ventrally.

Female genitalia. (Specimen from Vermilion Lakes, Banff, Alberta). Posterior edge of sternum VII with narrow band of short, hyaline hairs. Vulval scale with single, median lobe (Fig. 205), slightly rugose distally. Segment IX small, parallel-sided in lateral aspect (Fig. 204); with large, irregular latero-ventral lobes separated by band of membrane. Supra-genital plate not evident. Segment X larger than IX with wide, smooth, warped ventral surface. Dorsal surface concave laterally, with median ridge.

Notes on biology. — This species is known to me in the study area from only two localities of the most opposite characteristics. The first is Lake Agnes, at Lake Louise, in Banff National Park, Alberta, at an altitude of 6,885', in the alpine meadows. The second is Vermillion Lakes just west of Banff, Alberta, at an altitude of 4,538'. This locality is a dense, valley bottom swamp in the Bow River valley. The collecting dates were July 21, and July 5 respectively.

Geographical distribution. — The known range of this species is Holarctic, extending in North America, from northernmost Canada (Ellesmere Island) to British Columbia, Montana, and Minnesota (Fig. 600).

I have examined three females of this species from the study area, and one male and seven females from Lake Hazen, Ellesmere Island, Northwest Territories.
The *stigmatella* group

Two species belonging to this group are known from the study area.

**Synopsis of characters.** — Cerci and intermediate lobes of male segment X large, massive, concave mesally. Median lobes of segment X on mesal faces of intermediate lobes (Fig. 207); very short and slender. Female genitalia with segment IX very long, without latero-ventral lobes (Fig. 210). Supra-genital plate poorly developed. Segment X very small.

*Apatania stigmatella* (Zetterstedt), 1840
(Fig. 211-215, 602)

*Phryganea stigmatella* Zetterstedt, 1840:1066. (Type locality: Lapland).

*Limmephilus stigmatellus*; Walker, 1852:50.


*Parapatania stigmatella*; See Fischer, 1967:119.


Males of this species are distinguished by irregularly sinuate median shaft of aedeagus (Fig. 213), and by distal tooth set dorsally on intermediate lobes of segment X (Fig. 211). Females are distinguished by absence of latero-ventral lobes of segment IX, by segment X visible in lateral aspect (Fig. 214), and by simple, narrow, median lobe of vulval scale (Fig. 215).

**Description.** — Antennae brown; scapes white, with antero-mesal faces brown, glabrous. Vertex of head black, warts white. Thorax dark brown to almost black dorsally. Femora blotchy brown, light brown, hyaline. Spurs brown. Fore wing length of male 9.6 mm; light, clear yellow-brown, no pattern. Venation identical with that of *A. zonella*.

Male genitalia. (Specimen from Simpson Islands, Great Slave Lake, Northwest Territories). Tergum VIII with single row of long, well spaced setae parallel to posterior edge. Segment IX roughly rectangular, wider laterally (Fig. 211); dorsal strap segregated by two lateral grooves, bulged slightly dorsad. Clasper massive, with cylindrical, fluted basal article; distal article semi-circular, claw-like, fringed internally with long setae (Fig. 211, 212). Segment X with large, flared, triangular cerci. Median lobes long, thin, merged basally with cerci. Intermediate lobes complex, dark, with dorsal processes closely associated with cerci and lateral of them; with distal lateral and dorsal teeth. Aedeagus with median shaft irregularly sinuate (Fig. 213); aperture of ejaculatory duct disto-dorsad, between lateral flaps; lateral arms mounted dorsad of median shaft, long, slender, laminate blades.

Female genitalia. (Specimen from Simpson Islands, Great Slave Lake, Northwest Territories). Posterior edge of sternum VII with wide band of short, hyaline hairs. Vulval scale single, strongly dorsally curved median lobe (Fig. 214, 215). Segment IX large, irregular, with large postero-ventral cavity. Segment X small, with anterior edges slanted from vertical
Nimmo

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208).

209).

Males

Male

Female

geographical

distribution.

The

known range of this

species

is Holarctic; in North

America it extends from

Alaska to Colorado, in the

south, and Newfoundland,

in the east (Fig. 602). The

Colorado record is curious

and, I suspect, open to

some doubt. The species

has not yet been

recorded from Alberta

but is included here as

there is a high

probability of it occurring

in the far north of the

province, which is similar to

the area surrounding

Great Slave Lake, and

less than 100 miles distant.

I have examined a single

specimen of each sex, from

Great Slave Lake. These

were taken on August 29.

Apatania shoshone

Banks, 1924

(Fig. 206-210, 601)

Apatania shoshone

Banks, 1924:442. (Type local-ity:

Yellowstone National Park, Wyoming).


Apatania shoshone; Betten, 1934:380.


Radema shoshone; Ross, 1944:297.

Males of this species are distinguished by long, slender distal hooks of intermediate lobes

of segment X (Fig. 206), and by strongly ventrally curved median shaft of aedeagus (Fig.

208). Females are distinguished by massive, formless segment IX, and minute segment X

(Fig. 209, 210).

Description. — Antennae dark brown; antero-mesal face of scapes yellow, glabrous. Vertex

of head very dark brown. Thorax dark brown, with interspersed lighter areas. Spurs yellow.

Fore wing length of male 8.3 mm; pale, clear brown. Cross-vein Cu-R1 white line across stigma.

Venation identical to that of A. zonella.

Male genitalia. (Specimen from Waterton National Park gate, Hwy. 5, Alberta). Tergum

with single line of long, well spaced setae parallel to posterior edge. Segment IX of roughly

uniform width throughout, sinuate (Fig. 206). Clasper massive, with cylindrical basal article,

and smaller distal article strongly hooked mesad, with ventral tooth (Fig. 206, 207). Seg-

ment X with short, cylindrical median lobes, projecting, triangular cerci, and large, dark,

trifid intermediate lobes hooked antero-lateral distally (Fig. 206, 207). Median shaft of

aedeagus stout, curved strongly ventral; ejaculatory pore in membranous area between dis-

tal flaps (Fig. 208). Lateral arms long, each laminate blade on single membranous dorsal

process of aedeagal base.

Female genitalia. (Specimen from Cameron Lake, Waterton National Park, Alberta). Vul-

val scale of single median lobe; rectangular except for slightly expanded tip; distal end of

lobe rugose ventrally (Fig. 209). Segment IX massive, of indefinite shape (Fig. 210); open

ventrally and posteriorly with two short lateral lobes lateral of segment X and posterior

opening. Supra-genital plate small, membranous, ventral of postero-dorsal opening of seg-

ment IX. Segment X minute, bilobed, between lateral lobes of segment IX.

Notes on biology. — I am uncertain as to the possible emergence sites of this species. The

single female from the Waterton Park gates may have emerged from the adjacent Waterton

River, or flown in from the nearby Maskinonge Lake. The remainder of my records are from

locations adjacent to large lakes. The adult flight season extends from July 23 to August 19.

Geographical distribution. — The known range of this species extends from Alberta to

Colorado (Fig. 601). In Alberta I have records from the extreme south west corner of the

province, at altitudes between 4,189' and 5,445'.

I have examined 19 specimens, 14 males and five females, from the study area.
The *wallengreni* group

One species belonging to this group is known to occur in the study area.

*Synopsis of characters.* — Fore wing stigma usually weak; costal vein not thickened. Sc and R1 of hind wing parallel throughout.

Male genitalia with segment IX narrow. Cerci setose, slightly concave mesally; triangular and projected well posterad (Fig. 216). Median lobes of segment X very slender; separate, or fused. Claspers unmodified, elongated, not thick, with basal article cylindrical; distal article as long as basal or shorter, sickle shaped in most species.

Female genitalia with dorsal part of segment IX characteristic, with pits and ridges, large; ventral lobes prominent (Fig. 219). Segment X long, slender; 1/3-1/4 times diameter of segment IX; quite divided to dorsal and ventral parts in certain species. Supra-genital plate triangular, shorter than segment X, weakly sclerotized.

*Apatania crymophila* McLachlan, 1880

(Fig. 216-220, 601)


*Radema aenicta*; Ross, 1944:297.

Males of this species are distinguished from males of other species of *Apatania* by dilated, heavily setose, distal article of clasper (Fig. 216), and by short, crooked, distally bulbous, median shaft of aedeagus (Fig. 218). Females are distinguished by simple median lobe of vulval scale (Fig. 220), and segment X distinctly separated from segment IX (Fig. 219).

*Description.* — Antennae dark brown to almost black. Vertex of head black. Thorax black. Legs black to deep brown. Spurs red-brown. Fore wing length of male 9.8 mm; uniform greyish brown, with large, opaque, stigmatic area. Venation identical to that of *A. zonella*.

Male genitalia. (Specimen from Simpson Islands, Great Slave Lake, Northwest Territories). Postero-dorsal edge with single line of long setae. Segment IX high, narrow (Fig. 216); with row of about six short, heavy setae near clasper base. Clasper massive, with laterally compressed distal article heavily setose. Median lobes of segment X sinuate, bilobed; cerci attached laterad of median lobes, distally splayed. Intermediate lobes massive, hooked plates (Fig. 216, 217). Median shaft and lateral arms of aedeagus attached to common base (Fig. 218); lateral arms dorsad of median shaft. Median shaft distally bulbous, tip directed ventrad. Lateral arms as long as median shaft, thin, recurved.

Female genitalia. (Specimen from Simpson Islands, Great Slave Lake, Northwest Territories). Sternum VII with posterior edge clothed by broad band of scattered, fine, hyaline hairs. Vulval scale small, short, rectangular, disto-ventrally rugose, median lobe (Fig. 220). Segment IX high, narrow, parallel-sided, with broad, short, lateral lobes laterad of segment X (Fig. 219). No apparent supra-genital plate. Segment X with bilobed portion, and fused, plate-like, median lobes with common central spur (Fig. 219).

*Geographical distribution.* — The known range of this species is Holarctic; in North America it extends from Alaska to Manitoba (Fig. 601). It is not yet recorded from Alberta, but occurs in Great Slave Lake, Northwest Territories, which is so close to the northern boundary of Alberta that it is reasonable to expect that it occurs in the Province.
I have examined 71 specimens, 43 males and 28 females, from Simpson Islands, Great Slave Lake.

The complexa group

One species belonging to this group is known from the study area, and is here described as new.

Synopsis of characters. — Male genitalia slightly enlarged. Segment IX with very long, slender, paired, dorsal lobes (Fig. 221); fused with marked median channel or not. Cerci small, oval. Intermediate lobes of segment X very long, slender. Median lobes varied in size, small in some species, slender; interlocked with lobes of segment IX, shorter. Claspers varied. Basal article long, cylindrical. Distal article much shorter, spinate; in some species long, spiniform. Aedeagus short, stout.

Female genitalia with segment IX long throughout (Fig. 224). Segment X long, divided to dorsal and ventral parts. Supra-genital plate very short, thick, unsclerotized, fused to segment IX.

Apatania alberta Nimmo n. sp.  
(Fig. 221-225, 602)

Males of this species are distinguished from males of other species of Apatania by aedeagus (Fig. 221) with lanceolate lateral arms attached laterad of aedeagal base at point where aedeagus bends sharply ventrad. Females are distinguished by single, median lobe of vulval scale abruptly broadened distally into rectangular head (Fig. 225).

Description. — Antennae very dark brown to black. Vertex of head black, setae hyaline. Thorax quite black. Spur formula 1,2,4; brown. Fore wing length of male 8.5 mm; uniform black. Cross-vein C-R1 white. Venation identical to that of A. zonella.

Male genitalia. (Specimen from Rapids Creek, Gap, Alberta). Tergum VIII with distinct postero-distal ridge with single row of long setae. Segment IX with high-peaked dorsal strap (Fig. 221); gradually widened ventrad, with small postero-ventral process. Clasper long, slender, with tip of distal article with short, stout setae. Base of proximal article with slight lateral depression; distal portion of article with long, slender setae. Segment IX with paired postero-dorsal processes, long, tapered, acuminate blades, fused basally. Median lobes of segment X directed postero-lateral, bilobed, with ventral lobe smaller; dark brown. Intermediate lobes ventrad of median lobes, with bifid base recessed into segment IX, and long, rounded, distally slightly dilated process in lateral aspect (Fig. 221). Intermediate lobes acute triangular plates in dorsal aspect (Fig. 223); abruptly pinched off at tip. Cercus small, dark, triangular, dorso-lateral of median lobe bases. Aedeagus with semi-cylindrical median shaft; open on dorsal surface (Fig. 221, 222). Lateral arms angular, directed dorso-lateral, attached lateral of aedeagal base.

Female genitalia. (Specimen from Rapids Creek, Gap, Alberta). Sternum VII with posterior edge clothed with short, hyaline hairs. Vulval scale with single, massive, median lobe (Fig. 224, 225); distal portion abruptly expanded laterally, rectangular, ventrally rugose. Segment IX large, semi-rectangular in lateral aspect (Fig. 224), with slightly expanded ventral portion. No evident latero-ventral lobes, or supra-genital plate. Segment X distinct from segment IX, rounded rectangular in lateral aspect, with disto-lateral clefts; with membranous ventral lobe dorsal of vaginal orifice; segment X completely open ventrally.

Notes on biology. — Adults of this species are usually associated with small, turbulent creeks, but, on occasion, some are near large, smooth-flowing rivers. A flight season from
May 5 to June 22 is indicated.

Geographical distribution. — To date this species is known only from the Banff area of Alberta (Fig. 602). All records are from areas at about 4,250' to 4,550' altitude.

I have examined 17 specimens, four males and 13 females, from the study area.


Allotype. — Female. Same data as holotype.

Paratypes. — Same data as holotype; four females. Forty Mile Creek at Trans-Canada Hwy., Banff National Park, Alberta; June 15, 1967; A. Nimmo; five females. Bow River at Trans-Canada Hwy., Canmore, Alberta; A. Nimmo; one male, three females. As previous record; May 23, 1967; A. Nimmo; one male. Road to Sundance Canyon, Banff, Alberta; June 22, 1962; G. B. Wiggins; one male.

The type series has been assigned the type number 10,584 in the Canadian National Collection, Ottawa.

The holotype, allotype, and seven female paratypes are in the Canadian National Collection. One male and two female paratypes are in the Royal Ontario Museum, Toronto, Ontario. One male and two female paratypes are in the United States National Museum, Washington. The remaining male and female paratypes are in the collection of the Strickland Museum, Dept. of Entomology, University of Alberta, Edmonton, Alberta.

This species is named for the Province of Alberta.

The Subfamily Neophylacinae Schmid

Head short, large, eyes prominent. Ocelli small, placed well anterad. Pronotum short, chaetose. Spur formula 1,2,2; 1,2,3; 1,2,4; 1,3,3; or 1,3,4. Meso-apical spur of male hind leg modified in certain taxa. Wings rather variable, not reduced. Fore wings narrow, but greatly widened at chord in some taxa. Hind wings shorter than fore. Fore wings irrorate in certain taxa, hind wings darkened. Frenulum large; subcosta of hind wing with three to four very long, basal spines. Fore wing venation complete; hind wings rather incomplete, with strong sexual dimorphism. Fore wing R1 strongly arched at stigma, in some taxa united to Sc by cross-vein. Discoidal cell long, narrow; chord strongly disrupted. Hind wings of Oligophlebodes and Neothremma with much reduced but constant venation coupled with sexual dimorphism.

Male genitalia of short pieces in form of peculiar massive ensemble. Segment VIII setiferous. Segment IX very large, enclosing remainder of genitalia, especially claspers; strongly convex ventrally in form of plate fused to claspers; segment with pronounced lateral relief (Oligophlebodes) or large appendage (Neothremma); dorsally very narrow, indistinguishable from segment X. Dorsal lobes absent. Segment X visible only by three pairs of appendages. Claspers small, not prominent, well recessed into segment IX; two articulated, with basal article reduced. Aedeagus, except in Neothremma, emergent from centre, or higher, of segment IX; slender, barely movable; lateral arms present or absent.

Female genitalia with segments IX and X very small, closely fused. Segment IX of two distinct parts; dorsal part short, or vestigial. Segment X fairly large, prominent, of two large, lateral, quite distinct pieces; narrowly cleft dorsally, quite open ventrally. Vaginal aperture wide and open on segment IX. Vulval scale simple or bilobed, attached to segment IX. Ventral lobes of segment IX more or less fused to vulval scale.

Key to the Genera of Neophylacinae in Alberta and eastern British Columbia

1a. Segment X of male two blunt lobes and two protuberant appendages (Fig. 226).

Clasper small, recessed into segment IX. Ventral lobes of female segment IX large,
fused anterad of vulval scale (Fig. 230) ..................... Oligophlebodes, p. 72.

1b. Segment X of male two very long blades strongly hooked ventrad (Fig. 244). Mesal face of segment IX with long, bilobed spine. Claspers almost entirely fused. Ventral lobes of female segment IX quite free (Fig. 248) .............. Neothremonia, p. 75.

The Genus Oligophlebodes Ulmer

This genus is represented in the study by three species, one of which is described as new.

Synopsis of characters. – Spur formula 1,3,3. Apico-mesal spur of hind tibia thickened basally, bristled on mesal face. Fore wing obliquely parabolic apically; hind wing slightly larger, notched apically (Fig. 131). Venation constant, sexually dimorphic on hind wings. R1 of fore wing joined to Sc by short cross-vein; chord disrupted little; posteriorly oblique to body. R5 absent in male hind wing; only f2 present. Female hind wing with f1, f2, and f5 present.

Male genitalia with segment IX strongly developed, with pronounced lateral process attached to median lobes of segment X. Median lobes of segment X rounded, concave, separated by wide space. Aedeagus very small, embedded in membranous mass, very high in segment IX. Claspers small, recessed in fissure of segment IX.

Female genitalia with ventral lobes of segment IX transverse plates, massive, not prominent, weakly sclerotized, fused to ventral surfaces of vulval scale; also fused to sternum VIII.

Key to the Males of species of Oligophlebodes found in Alberta and eastern British Columbia

1a. Distal spine of clasper, short, curved dorsad (Fig. 238) ..................... O. zelti Nimmo n. sp., p. 74.

1b. Distal spine of clasper straight (Fig. 226), or with disto-ventral tooth (Fig. 232) .................................. O. ruthae Ross, p. 72.

2b. Distal spine of clasper short, stout, with disto-ventral tooth (Fig. 232) ................................. O. sierra Ross, p. 73.

Key to the Females of species of Oligophlebodes found in Alberta and eastern British Columbia

1a. Segment X in ventral aspect deeply cleft, lateral lobes roughly triangular (Fig. 231) ..................... O. ruthae Ross, p. 72.

1b. Segment X in ventral aspect not deeply cleft, or, if so, not widely separated or triangular (Fig. 237, 243) ..................... O. sierra Ross, p. 73.

2b. Lateral lobes of segment X in ventral aspect bilobed (Fig. 243), with semi-circular dorsal lobes ............................. O. zelti Nimmo n. sp., p. 74.

Oligophlebodes ruthae Ross, 1944
(Fig. 130a, 130b, 131a, 131b, 226-231, 603)

Males of this species are distinguished from males of other species of *Oligophlebodes* by long, straight distal spine of clasper (Fig. 226). Females are distinguished by deeply divided, well separated, triangular lateral lobes of segment X in ventral aspect (Fig. 231).

**Description.** — Antennae dark brown; scapes somewhat darker. Vertex of head uniformly dark brown. Thorax more or less uniform dark brown. Spur formula 1,2,2, in both sexes in specimens examined here. Male only with mesal spur of hind leg swollen basally; curved, with short, thin process on inner face of curve. Fore wing length of male 7.4 mm; uniform light yellow to yellow-brown. Venation of male and female wings as in Fig. 130-131.

Male genitalia. (Specimen from Cameron Creek, Waterton National Park, Alberta). Ter-gum and sternum VIII each with single, distinct row of long setae parallel to posterior edge. Segment IX with high, thin dorsal strap and small, thin, irregular ventral body (Fig. 226). Ventral area produced posterad as long, narrow, triangular plate, ventrad of claspers (Fig. 227). Clasper fused to segment IX, large, complex, partly recessed into segment IX; with distinct, basally directed, long, dark, distal tooth; in ventral aspect tooth hooked mesad (Fig. 226, 227). Segment X with cerci trapezoidal, small. Median lobes well separated, with setose posterior edges. Lateral arms of aedeagus close to base of ejaculatory duct projected below them (Fig. 228, 229); distal end of lateral arms curved mesad.

Female genitalia. (Specimen from Cameron Lake, Waterton National Park, Alberta). Posterior edge of sternum VII with narrow fringe of short, fine setae. Vulval scale small, semi-circular, dark, median lobe partly enclosed ventrally by ventro-lateral lobes of segment IX (Fig. 231). Segment IX rectangular in ventral aspect, internally hollow, with ventral cleft; in effect large hood. Supra-genital plate not evident. Segment VIII with simple invagination on postero-lateral edge. Segment X bilobed (Fig. 231); lobes connected only basally; fused almost imperceptibly to segment IX (Fig. 230).

**Notes on biology.** — The adult flight season extends from July 3 to August 29. The adults appear to emerge from the mountain creek type of stream, ranging from relatively slow, gentle, gravel-bottomed foothills creeks to the more torrential, boulder strewn creeks.

**Geographical distribution.** — The known range of this species extends from Alberta and British Columbia to Oregon and Utah (Fig. 603). In Alberta it is found only in the mountain and foothill areas, ranging in altitude from about 5,000’ to 6,000’.

I have examined 52 specimens, 35 males and 17 females, from the study area.

**Oligophlebodes sierra** Ross, 1944

(Fig. 232-237, 604)


Males of this species are distinguished from males of other species of *Oligophlebodes* by short, stout distal spine of claspers, with disto-ventral tooth (Fig. 232). Females are distinguished by closely appressed lateral lobes of segment X, and by ventro-lateral concavities of vulval scale.

**Description.** — Antennae light brown. Vertex of head uniform reddish brown. Thorax uniformly yellow or pale purplish brown. Spur formula 1,3,3; meso-apical spur of male hind tibia swollen basally, with short, thin process on inner edge of curve. Fore wing length of male 7.6 mm; uniform pale brown, almost hyaline; no pattern except for pale grey stigma. Venation identical to that of *O. ruthae*.
Male genitalia. (Specimen from Athabasca River, Entrance, Alberta). Tergum and sternum of segment VIII with single rows each of setae parallel to posterior edges. Segment IX with small ventral body; high, very thin dorsal strap (Fig. 232). Clasper relatively large, fused to segment IX, distally black, with small disto-ventral tooth; with distinct, mesally directed, horizontal hooks (Fig. 233). Segment X with median lobes well separated, with irregularly dentate edges, and with distinct medially directed process (Fig. 233). Cercus large, rounded triangular, attached to horizontal dorsal edge of segment IX. Aedeagus minute; ejaculatory duct syringe-like, with bulbous inner end at attachment of membranous sperm duct (Fig. 234, 235); otherwise straight tube. Lateral arms dorsal and posterad of duct, overhung by large fold of hyaline membrane.

Female genitalia. (Specimen from Idaho; in Illinois National History Survey). Tergum VIII very large, separated from small, ventral sternum by wide band of folded membrane (Fig. 236); with row of strong setae parallel to posterior edge. Vulval scale single, median, dark, ventro-laterally concave lobe (Fig. 237). Segment IX fused almost indistinguishably to segment X; antero-laterally invaginated anterad into segment VIII. Segment X of two closely appressed lateral lobes.

Notes on biology. — My only record of this species in the study area is a single male taken at black-light about 100' above the Athabasca River, at the point where the Forestry Trunk Road crosses, at Entrance, Alberta. At that point the river is quite turbulent, with an obviously rocky bed. The date was July 25.

Geographical distribution. — The known range of this species extends from Alberta and British Columbia to California and Colorado (Fig. 604). The only Alberta record as given above was at an altitude of about 3,270'.

**Oligophlebodes zelti** Nimmo n. sp.  
(Fig. 238-243, 604)

Males of this species are distinguished from males of other species of *Oligophlebodes* by short, black, dorsally curved distal lobes of claspers (Fig. 238), which are more widely separated than in the similar *O. sigma* (Fig. 239). Also ventral plate of segment IX prominent, horizontal and projected further posterad than in *O. sigma*. Females are distinguished by bilobed lateral lobes of segment X in ventral aspect (Fig. 243).

Description. — Antennae light to dark brown. Vertex of head dark brown. Thorax uniform dark reddish brown. Spur formula 1,2,2; meso-apical spurs of male hind legs basally enlarged, claw-like, with small spine basally, on inside of claw. Fore wing length of male 8.4 mm; pale yellowish brown, no pattern. Venation identical to that of *O. rathae*.

Male genitalia. (Specimen from South Creek, Forestry Trunk Road, 20 miles south of Nordegg, Alberta). Segment VIII with single band of long, fine setae each side of tergum, parallel to posterior edge. Segment IX with high, narrow dorsal strap, with large, rounded triangular ventral body, and with short, dark, triangular plate projected posterad, ventrad of claspers (Fig. 238, 239). Clasper distally black, with distal process curved dorsad; in ventral aspect tip hooked mesad, otherwise squat triangular. Segment X with membranous median lobe and large, rectangular, setose, lateral lobes. Cercus small, dark, trapezoidal. Aedeagus with short, stout ejaculatory tube surmounted by two dark, bowed, lateral arms slightly bulbous distally (Fig. 240, 241). Median shaft of aedeagus surmounted by rectangular, membranous mass lightly spinate dorsally. Sperm duct passed anterad by way of large, oval aperture situated ventrally on membranous aedeagal sheath.

Female genitalia. (Specimen from South Creek, at Forestry Trunk Road, 20 miles south of Nordegg, Alberta). Posterior edge of sternum VII with narrow band of short, fine well
75

mal
basally

Notes on biology. — Individuals of this species emerge from small, turbulent, boulder or coarse gravel mountain streams. The adult flying season extends from July 14 to August 19.

Geographical distribution. — This species is presently known only from the mountains and foothills of Alberta (Fig. 604) between 4,700' and 5,500' in altitude. I have examined 55 specimens, 16 males and 39 females, from the study area.

Holotype. — Male. South Creek, Forestry Trunk Road, 20 miles south of Nordegg, Alberta; August 8, 1965; A. Nimmo.

Allotype. — Female. Same data as for holotype.

Paratypes. — Same data as for holotype; 36 females. Same data as for holotype, except July 14, 1967; one male. Red Earth Creek, Trans-Canada Highway, Banff National Park, Alberta; July 30, 1967; A. Nimmo; one male. Helen Creek, Banff-Jasper Hwy., north of Lake Louise, Alberta; August 10, 1967; A. Nimmo; one female. Rowe Brook, Waterton National Park, Alberta; August 19, 1965; A. Nimmo; one male. Lynx Creek, Forestry Trunk Road, north of Clearwater River, Alberta; July 14, 1967; A. Nimmo; five males, one female. South Creek, Forestry Trunk Road, 20 miles south of Nordegg, Alberta; August 12, 1968; A. Nimmo; five males, one female. Wampus Creek, Cadomin, Alberta; August 18, 1967; K. Zelt; one male.

The type series has been assigned the type number 10,589 in the Canadian National Collection.

The holotype, allotype, and three male and 36 paratypes are in the Canadian National Collection. The Lynx Creek paratypes are in the Strickland Museum, Dept. of Entomology, University of Alberta, Edmonton, Alberta. One male and one female paratype are in the United States National Museum.

This species is named for Ken Zelt, a graduate student in the Dept. of Zoology, University of Alberta, who collected a single male near Cadomin.

The Genus Neothremma Banks

Two species of this genus are known from the study area.

Synopsis of characters. — Lateral ocelli almost immediately posterad of exceptionally large anterior cephalic warts. Spur formula 1,3,4. Maxillary palpus of male with long brush of distally hooked setae (Fig. 249). Fore wing venation unmodified; hind wing venation much reduced, with some sexual dimorphism. Fore wing f3 tapered proximally to point; chord strongly irregular (Fig. 132a). Hind wing with minute discal cell, f1 with long proximal stem; male M1+2, M3+4, Cu1, Cu2 all separate; with three anal veins. In the female hind wing M similar but Cu of three veins.

Male genitalia with segment IX well developed, not enclosing any appendages; laterally with very long, bifid, sclerotized lobe directed postero-mesad. Segment X much smaller than IX, well separated; median lobes long, simple, postero-ventrally arched blades, well separated basally by membrane of anus (Fig. 244). Clasper along ventral edges of segment IX; two-articled, with basal article of each clasper fused mesally as ventral plate; distal article baso-dorsal on basal article; large, fused to segment IX, covered with distinct tubercles.
Female genitalia with segment IX of two pieces (Fig. 247). Segment X of two large dorsal pieces, and ventral scale. Vulval scale large, bifid (Fig. 248). Ventral lobes of segment IX large, slightly concave mesally, laterad of vulval scale.

**Key to the Males of species of Neothremma found in Alberta and eastern British Columbia**

1a. Distal tooth of second article of clasper dorso-anterad of distal extremity (Fig. 244); intermediate lobes of segment X roughly rectangular in lateral aspect

........................................................................................................... *N. alicia* Banks, p. 76.

1b. Distal tooth of second article of clasper a postero-dorsal continuation of article (Fig. 591a); intermediate lobes of segment X trifid in lateral aspect

........................................................................................................... *N. laloukesi* Schmid, p. 77.

*Neothremma alicia* Banks, 1930

(Fig. 132a, 132b, 244-249, 605)


*Neothremma alicia*; Ross, 1938b:45.

Males of this species are distinguishable by high-arched, blade-like median lobes of segment X; by lateral processes of posterior edges of segment IX; and by fused basal articles of claspers. Females are recognizable by massiveness of genitalia (Fig. 247), with huge, rounded, latero-ventral lobes of segment IX.

**Description.** — Antennae dark brown, scapes paler, six times longer than pedicel, with long bunch of hyaline hairs on mesal faces. Vertex of head red-brown. Frons with scattered, spatulate-tipped hairs. Maxillary palpus of male with article III cylindrical, fringed on posterior face with distinct, even brush of long, black, distally hooked hairs (Fig. 249). Thorax light yellow to red-brown. Spurs yellow-brown. Fore wing length of male 7.7 mm; light red-brown; no pattern. Venation as in Fig. 132a, 132b.

Male genitalia. (Specimen from Banff, Alberta). Tergum VIII with single line of long, slender setae parallel to posterior edge. Segment IX with narrow, distinct, dorsal strap; wide ventrally, with small, rounded, ventro-posterod process (Fig. 244, 245). Clasper massive, articulated to segment IX, with disto-dorsal teeth; two-articled, with distal article dorsal of basal article, rounded, setose. Claspers fused ventrally together at basal articles. Segment IX with long, distally bifid latero-posterod processes. Median lobes of segment X long, dorsally arched, acuminate blades. Intermediate lobes roughly rectangular, flared ventro-lateral. Aedeagus with massive membranous base (Fig. 246) connected to base of proximal clasper articles; each clasper base with short, stout, black spine at point of fusion. Median shaft of aedeagus tapered, sclerotized, scoop-shaped structure with ejaculatory duct projected dorsal as thin, isolated tube.

Female genitalia. (Specimen from Bow River, at Trans-Canada Hwy., west of Lake Louise, Alberta). Tergum VIII with single, dorsal line of long setae. Vulval scale with squat, tapered, distally bifid median lobe (Fig. 248). Segment IX small, rectangular, with massive, rounded latero-ventral lobes (Fig. 247). Segment X with large, triangular lateral lobes laterad of mesal structure like inverted bowl. Vaginal orifice flanked by two lateral plates of segment X.

**Notes on biology.** — Specimens of this species emerge from small to large mountain streams, usually of the less turbulent variety. Adult flight season extends from June 22 to
August 13.

Geographical distribution. — The known range of this species extends from Alberta and British Columbia to Oregon, Utah and Colorado (Fig. 605). In Alberta it is restricted to the mountain areas close to the continental divide, ranging in altitude from 4,500' to 7,000'.

I have examined six specimens, two males and four females, from the study area.

Neothremma laloukesi Schmid, 1968
(Fig. 591a, 591b, 605)


Males of this species are distinguished from males of N. alica by the characters presented in the key to males of Neothremma known from the study area.

The only known specimen of this species is a male, from Lake Louise, Alberta. Being thus unable to prepare my own drawings, Dr. F. Schmid very kindly lent me his original drawings of the species, which are presented here (Fig. 591a, 591b). I also present Schmid’s original description of the male, in translation from the French, altering only his figure numbers to mine.

Description. — 'Fore wings uniformly golden brown. Head abundantly clothed by very long, golden hairs which are slightly denser between the scapes of the antennae. Male maxillary palpi short, thick, with dense clusters of black hairs on mesal faces, as in N. alica Banks. Vena test similar to alica. Wing expanse of male 13 mm.

Male genitalia. Very similar to alica, but basal article of clasper distinctly longer and narrower (Fig. 591a). Distal article of clasper also longer in lateral aspect, with clear outline gradually tapered from base to apex; distally curved dorsal at obtuse angle; regularly trapezoidal in ventral aspect (Fig. 591b), tapered distad.'

Female genitalia. Unknown.

Notes on biology. — Date of capture of the single known male was June 7.

Geographical distribution. — The single locality is indicated in Fig. 605.

The Subfamily Pseudostenophylacinae Schmid

Head short, very large; eyes large. Ocelli large, protuberant. Thoracic macrochaetae long, dense. Spur formula 1,2,2; 1,3,3; or 1,3,4. Wings large; fore wing of varied sizes, apically elliptical. Hind wing not larger than fore wing except when anal area well developed; anal edge convex or not; anal area sexually dimorphic in some taxa. Certain taxa with fore wings strongly granular, densely clothed with fine, bristly hairs; hind wings similar. Fore wings brown, irrate. Vena test complete. R1 of fore wing not arched at stigma; discoidal cell very long; chord irregularly disrupted, markedly curved in most taxa; f5 and thyridial cell sessile. Hind wing chord similar, but more oblique to body.

Male genitalia segment VIII with strongly marked, spinate zone, or not. Segment IX very short in lateral aspect, or longer. Cerci small, lateral, fused to intermediate lobe bases; intermediate lobes large, massive, generally paired, or as single horizontal plate, or paired plates elongated meso-dorsad. Claspers one-articled, reduced in certain taxa to simple buttons along edge of segment IX. Aedeagus very large in certain taxa; voluminous but short; membranous or sclerotized. Lateral arms enormous in most taxa, varied, membranous.

Female genitalia well sclerotized, loosely connected. Segment IX of two separate parts; dorsal part simple, without appendages. Segment X not prominent, of two lateral lobes. Ventro-lateral lobes of segment IX small, well sclerotized, well separated; meso-ventral part small, membranous, attached to lateral lobes. No supra-genital plate. Vaginal aperture be-
between segments VIII and IX. Vulval scale small, strongly sclerotized; lobes lightly connected, movable; median lobe very small, narrow, very thick in some taxa; lateral lobes strongly sclerotized, voluminous, very thick.

This subfamily is represented in the study area by one genus, *Homophylax*.

The Genus *Homophylax* Banks

This genus is represented in the study area by three species, of which one is described as new. Females of only two species are known.

**Synopsis of characters.** — Spur formula 1, 3, 4. Wings large; fore wing markedly widened at chord, bluntly parabolic apically; hind wing blunted apically, scarcely larger than fore wing. Venaition complete, modified, with strong sexual dimorphism in hind wings. Fore wing chord single line, slightly oblique to body anteriorly, not disrupted. Male hind wing with small, narrow discoidal cell; R and M crowded toward C; f1 petiolate, f2 tapered proximad to point, f3 with long petiole. Hind wing of female with very large, triangular, discoidal cell.

Male genitalia with sclerotized, smooth, posterior bulge to tergum VIII. Segment IX very wide laterally, ventrally. Median lobes of segment X in form of two symmetrical, sclerotized cavities dependent from very thin dorsal strap; fused mesally as strongly sclerotized mesal ridges with dark, dorsal and ventral paired lobes. Intermediate lobes stout, twisted, lobed plates fused to segment IX; interlocked with meso-dorsal blades of claspers. Claspers with small, ventral plates; antero-mesal angles produced postero-dorsally as long, thin, acuminate, strongly sclerotized, dark blades. Cerci large, somewhat oval lobes in lateral aspect (Fig. 250); fused at bases with sclerotized cavities of intermediate lobes. Aedeagus very small, stout.

Female genitalia with dorsum of segment IX small. Segment X rather narrow, long tube (Fig. 253). Ventral lobes of segment IX large, prominent, vertical, separate plates. Vulval scale blunt, recurved; two or three lobed. Supra-genital plate very small.

**Key to the Males of species of *Homophylax* found in Alberta and eastern British Columbia**

1a. Meso-dorsal lobes of clasper long, narrow (Fig. 250); median processes of segment X with flat-topped dorsal spines with lateral teeth distally (Fig. 251) ........... 

1b. Meso-dorsal lobes of clasper short, wide, heavy (Fig. 225, 261). Dorsal spines of median lobe of segment X without disto-lateral tooth .......... 2a

2a.(1b) Median lobe dorsal spines fused basally, parallel sided (Fig. 256), with ventrally directed distal hook (Fig. 255) ................. *H. acutus* Denning, p. 79.

2b. Median lobe dorsal spines well separated basally, tapered, directed postero-laterad (Fig. 262) ....................... *H. baldur* Nimmo n. sp., p. 80.

**Key to the Females of two species of *Homophylax* found in Alberta and eastern British Columbia**

1a. Segment X in ventral aspect (Fig. 254) narrow, with deep ventral cleft, shallow dorsal cleft ................. *H. crotchi* Banks, p. 78.

1b. Segment X in ventral aspect (Fig. 258) wide, with dorsal cleft at least as deep as ventral

*Homophylax crotchi* Banks, 1920

(Fig. 133a, 133b, 250-254, 606)

Males of this species are distinguished from males of other species of *Homophylax* by small, laterally toothed dorsal spine of median lobes (Fig. 251), and by long, thin mesodorsal lobe of clasper. Females are distinguished by narrow segment X in ventral aspect (Fig. 254), with unequal dorsal and ventral clefts.

**Description.** — Antennae light red-brown. Vertex of head red-brown. Thorax warm light red-brown. Spurs brown. Fore wing length of male 16.4 mm; light brownish yellow, interspersed with slightly darker, irregular areas. Venation as in Fig. 133a, 133b. Without basal fore wing pouch and longitudinal hind wing fold between Rs and M (see Fig. 134, 135).

Male genitalia. (Specimen from Washington State, United States; in United States National Museum, Washington, D. C.). Tergum VIII with postero-dorsal area with distinct tooth close to posterior edge; with distinct lateral concavities (Fig. 250). Segment IX with dorsal strap narrowed laterally to junction with main body, expanded evenly ventrad. Claspers with ventral lobes slightly separated (Fig. 251), short, rounded; lateral lobes finger-like, thick, fleshy; median lobes long, narrow blades with slightly thickened black tips. Median lobes or plates of segment X large, cupped laterad, with small, spiniform, recurved ventral lobes, larger, flat-topped, dorsal lobes each with distinct disto-lateral tooth. Intermediate lobes extended laterad from anal membrane, curved posteroad above base of claspers. Cercus large, arched slightly dorsad; short, rounded distally. Aedeagus with large, membranous, dorsal lobe dorsad of median shaft (Fig. 252); like inverted trough, with concave ventral surface.

Female genitalia. (Specimen from Banff, Alberta). Sterna IV, V, and VI each traversed by thin dark line parallel to posterior edge interrupted mesally by roughly triangular tooth. Vulval scale with median lobe of two inconspicuous, small protuberances of posterior edge (Fig. 254). Lateral lobes curved dorsad to enclose two sclerites projected from vagina. Segment IX with laterally triangular, shell-like lateral lobes suspended from short, narrow dorsum. No supra-genital plate evident. Segment X long, tubular, of two lateral lobes distally projected well posteroad of all other structures (Fig. 253).

**Geographical distribution.** — The known range of this species extends from Vancouver Island and Washington State to Alberta. In Alberta I have only two records of the species: Banff, at about 5,000' on Sulphur Mountain; and Lost Lake, Waterton National Park, at 5,500'.

Dates of capture were September 10 and August 17 respectively. I have not taken any specimens of this species myself.

I have examined one male and two females of this species; only the females are from the study area, however.

*Homophylax acutus* Denning, 1964
(Fig. 134a, 134b, 255-259, 606)


Males of this species are distinguished from males of other species of *Homophylax* by short, wide, heavy mesal lobes of claspers, and by large, basally fused, ventrally hooked dorsal spines of median lobe of segment X (Fig. 255). Females are distinguished by large, short segment X, with equal dorsal and ventral clefts (Fig. 258).
**Description.** — Antennae brownish yellow. Vertex of head pale yellow. Fore wing length of male 16.4 mm; dull brownish yellow, with darker areas especially in posterior parts of wing. Venation as in Fig. 134a, 134b. Hind wing with large, longitudinal fold posterad of Rs; fold with numerous scales, especially basally. Male fore wing with soft, membranous fold basally; female without fold.

Male genitalia. (Specimen from Mt. Edith Cavell, Jasper National Park, Alberta). Segment IX with thread-like dorsal strap; main body of segment wide ventrally, tapered abruptly dorsad, with slight concavities ventrad of peak (Fig. 255). Clasper with mesal lobe short, wide, bowed mesad in dorsal aspect (Fig. 256); lateral lobe bifid distally, separated by deep mesal cleft. Segment X with median processes of two toothed plates flared laterad in form of deep, sclerotized concavities; dorsal hooks only slightly parted, square tipped; ventral hooks directed dorsad, recurved. Intermediate lobes triangular, acuminate in lateral aspect. Cercus with straight ventral edge, dorsal edge curved gradually ventrad. Aedeagus with smooth, sclerotized, basal sheath followed by high, peaked dorsal lobe; median lobe sclerotized distally.

Female genitalia. (Specimen from Moraine Lake, Banff National Park, Alberta; in Canadian National Collection). Similar to *H. crochi*, but lateral lobes of vulval scale larger; median lobe more pronounced (Fig. 259); vaginal sclerites more globose, with concave mesal faces. Ventro-lateral lobes of segment IX triangular but more rounded than in *H. crochi*. Segment X heavier, larger, shorter; dorsal cleft deeper than ventral (Fig. 258).

**Notes on biology.** — This species is recorded from only two localities in Alberta to date. One locality is a deep, morainic mountain lake; the second is located in high, alpine meadows, with shallow pools and small water trickles. Altitudes are 6,200' and 7,000' respectively. Dates of capture were August 6 and 22.

**Geographical distribution.** — The known range of this species extends from Idaho to Alberta (Fig. 606). In Alberta it appears to be confined to high altitude creeks or pools.

I have examined two males and one female from the study area.

*Homophylax baldur* Nimmo n. sp.
(Fig. 135a, 135b, 260-263, 607)

Males of this species are distinguished by spiniform, widely separated dorsal processes of median lobes of segment X (Fig. 262) and by small membranous dorsal lobe of aedeagus (Fig. 263).

**Description.** — Antennae light yellow-brown; scape with antero-mesal faces devoid of long setae. Vertex of head yellowish to reddish brown, with red-brown band between lateral ocelli. Thorax uniformly reddish yellow. Spurs red-brown. Fore wing length of male 17.3 mm; light yellowish brown, with slightly darker bands mesally and posteriorly. Anal flap of fore wings with white scales. Venation as in Fig. 135a, 135b. Fore wing with basal flap or pouch (Fig. 135a, 260). Hind wing with pronounced fold anterad of Cula; fold internally with hyaline scales; scales commonest in basal area of wing.

Male genitalia. (Specimen from Cameron Lake, Waterton National Park, Alberta). Postero-dorsal edge of tergum VIII triangular, raised plaque; in lateral aspect an overhanging tooth (Fig. 261). Segment IX with anterior edges produced anterad; posterior edge continuous to peak of dorsal strap. Dorsal strap virtually non-existent. Clasper with heavy, black, meso-dorsal process directed postero-dorsad; with straight dorsal edges, sinuate ventral edges; base warped at 90° to meet lateral lobe of clasper (Fig. 262). Median lobe of clasper fused ventrally, weakly divided. Segment X with two vertical median plates; plates toothed dorsally and ventrally; produced laterad as sclerotized concavities; dorsal teeth separated, acuminate;
ventral teeth small, button-like. Cercus almost triangular, with rounded tips. Aedeagus with small, membranous, dorsal process originated from membranous middle portion; bilobed in dorsal aspect.

Female genitalia. Not known.

Notes on biology. — The one Alberta record of this species is a high (5,445'), large mountain lake. The Utah record listed below is situated at 9,700'. Dates of capture were August 19, and September 17 respectively.

Geographical distribution. — The known range of this species is restricted to two localities (Fig. 607): one in extreme south west Alberta, the other in Utah.

I have examined 23 specimens from the study area, all males, and one other male, from Utah.


Paratypes. — Same data as for holotype; 22 males. La Baron Lake, Circleville Mountain, 15.9 miles west Junction, Pinto County, Utah, United States; September 17, 1967; G. E. Ball; one male.

The type series has been assigned the type number 10,585 in the Canadian National Collection, Ottawa. The holotype and 19 paratypes are in the Canadian National Collection; the Utah specimen is in the Strickland Museum, Dept. of Entomology, University of Alberta, Edmonton, Alberta; and one paratype each are in the Royal Ontario Museum, Toronto and the United States National Museum, Washington.

This species is named for Baldur, a character of Norse mythology encountered in my reading.

The Subfamily Limnephilinae Ulmer

Synopsis of characters. — Spur formula 1,3,4, but the following combinations are also found: 1,1,1; 0,2,2; 1,2,2; 2,2,2; 0,3,3; or 1,3,3. Wings very varied in size, from very large to little more than scales, dicosmoecine in shape in certain genera; hind wings with well developed anal area; fore wing colour highly varied; hind wings hyaline in most genera. Frenulum barely evident, of some long setae at extreme base of subcosta. Venation complete, only feebly varied except in Enoicyla and Phanocelia; identical in both sexes. Fore wing discoidal cell one to three times longer than its own stem; thyroidial cell pedicillate in very few taxa. Hind wing chord more or less broken, generally very oblique posterad; with five anal veins.

Male genitalia simple, with three pairs of appendages. Tergum VIII with spine or setose postero-dorsal process or not. Segment IX constant; more or less elongate laterally, somewhat shortened ventrally; in most genera very reduced dorsally. Segment as whole deeply recessed into segment VIII. Cerci rounded lobes; concave mesally, unarmed or not, with or without teeth, ridges, or crenulations; small to very large, strongly sclerotized. Intermediate lobes of segment X sclerotized, not very varied in form but varied in size; between cerci, not fused. Lateral angles of segment IX tapered or not, curved mesad to effect a certain amount of separation between anal and aedeagal cavities. Clasper one-articled, fused to segment IX; generally comparable in form to very oblique cone, with apex directed dorso-posterad. Aedeagus highly variable in form and size, long or not, slender, with distal spines; membranous basally or distally; lateral arms generally large, with all degrees of reduction among taxa.

Female genitalia with segment IX of two parts. Dorsal part large or not, conical, tapered to segment X. Segment X variable; tubular, cylindrical or conical; cleft dorsally, ventrally, or even laterally, various parts reduced to independent scales in certain genera. Ventral parts
of segment IX of two lobes and median part. Supra-genital plate present or absent. Vaginal aperture between segments VIII and IX. Vulval scale trilobed or not; thickened, fleshy; three lobes fused basally or not, but in the Limnephilini lateral lobes not entirely fused to median; relative proportions of lobes highly variable among taxa.

Following is a key to tribes of Limnephilinae, using males only. The females proved intractable in the attempt to discover cohesive key characters and are best identified in association with the male, or by comparison with drawings. This key is good only for the study area.

Key to the Males of the Tribes of Limnephilinae found in Alberta and eastern British Columbia

1a. Lateral arms of aedeagus simple, spiniform, or apparently so (Fig. 542), with no accessory spines or lobes; originated dorsad or ventrad of aedeagal base (Fig. 531, 547, 568, 580), not laterad .......................................................... 2a

1b. Lateral arms clavate, multi-lobate, multi-spinate, parti-membranous, or combination of these (Fig. 473, 486, 527); or if spiniform (Fig. 367), attached laterad of aedeagal base .......................................................... Limnephilini, p. 82.

2a.(1a) Ejaculatory duct terminated at extreme tip of median shaft of aedeagus, including lateral lobes or processes, excepting lateral arms (Fig. 531, 536, 547) .......................................................... Stenophylacini, p. 142.

2b. Ejaculatory duct terminated basad of extreme tip of median shaft, on dorsal surface of shaft (Fig. 550, 553), or between longer distal lobes (Fig. 565) .......................................................... Chilostigmini, p. 148.

The Tribe Limnephilini Schmid

Character synopsis of the Limnephilini. — Pronotum more developed than in other tribes of subfamily. Base of pro-femur and apex of opposing tibia with or without black brushes. Spur formula varied. Wings medium or small, not reduced, similar in both sexes. Fore wing evenly strap-like, little wider at stigma, with oblique, truncated apex. Hind wings much larger than fore. Fore wing coloration strongly contrasted; with large clear streak in mid-wing, second at proximal end of apical cells, third at distal end of M4+5, and fourth in thyroidal cell. Chord of fore wing very oblique to body, narrowly broken. Hind wing chord parallel to body, zigzagged regularly, strongly accentuated.

Male genitalia with posterior edge of tergum VIII finely, not densely, spinate. Segment IX with postero-lateral edges convex or not, as supported to cerci. Cerci very varied in size and form. Intermediate lobes of segment X varied, pincer-like in opposition to neighbouring cerci or not; with lateral teeth or not. Claspers varied, base button-like, to almost vestigial; free part slender, directed almost horizontally. Aedeagus strong, large; median shaft very simple, unarmed, folded and extensible at base or not. Lateral arms with slender base and expanded, spinate tip.

Female genitalia with segment IX of two parts in most taxa, well developed, close set. Dorsal part prominent or not, without prominent lobes. Appendages present or not; large, free; fused solidly, either to segment IX, or segment X. Segment X much smaller than segment IX; cylindrical, slender, deeply cleft or not. Segment X large, with thick, fleshy walls, hardly cleft at all; extended as one piece, not separate scales as in Stenophylacini. Ventral lobes of segment IX large, convex, in contact ventrally. Supra-genital plate large, free, prominent, ogival. Vulval scale trilobed, incompletely fused to sternum VIII, intervening sutures clearly visible.
Key to Genera and Subgenera of Limnephilini found in Alberta and eastern British Columbia

1a. Apex of fore wing notched (Fig. 141a) .......... *Nemotaulius* (*Macrotaulius*), p. 123.

1b. Apex of fore wing smooth, without indentations ................. 2a

2a.(1b) Apical spur of fore tibia large, triangular .................. *Philarctus*, p. 132.

2b. Spurs normal .................................................. 3a

3a.(2b) Fore wing with one or more longitudinal, median, silver lines bordered with black ............... *Hesperophylax*, p. 139.

3b. Fore wings without such lines .................................. 4a

4a.(3b) R4+5 of hind wings strongly tinted brown ........... *Grammotaulius*, p. 122.

4b. R4+5 of hind wing not so coloured. Spur formula 1,3,4; 1,2,3; or 1,2,2 .......... 5a

5a.(4b) Dorsal strap of segment IX well developed .............. 6a

5b. Dorsal strap of segment IX very narrow, recessed into segment VIII .......... 8a

6a.(5a) Wing span less than 20 mm; fore wing weakly irrate ....... *Arctopora*, p. 133.

6b. Wing span greater than 25 mm; fore wing strongly irrate .......... 7a

7a.(6b) Dorsal strap of segment IX of male large plate overhanging remainder of genitalia (Fig. 495) ............... *Lenarchus* (*Lenarchus*), p. 135.

7b. Dorsal strap of segment IX of male quite short, but prolonged by large plate formed by fused cerci (Fig. 501) .......... *Lenarchus* (*Paralenarchus*), p. 136.

8a.(5b) Cercus of male strongly toothed, segment IX narrow throughout (Fig. 440) ............... *Clistoronia* (*Clistoroniella*), p. 120.

8b. Characters otherwise ............................................ 9a

9a.(8b) Sc. of hind wing turned sharply anterad distally (Fig. 138b) ............... *Limnephilus*, p. 83.

9b. Sc. of hind wing only slightly turned anterad (Fig. 142b) .......... 10a

10a.(9b) Intermediate lobes of male segment X much smaller than cerci, button-like .......... *Asynarchus*, p. 128.

10b. Intermediate lobes of male segment X plate-like, spiniform, or reduced .......... 11a

11a.(10b) Fore wing reddish, uniformly irrate, or with regularly spaced minute patches of brown .......... *Anabolia*, p. 124.

11b. Fore wings otherwise colored; patterned with bars or large patches of colour, ranging from black to almost hyaline .......... *Limnephilus*, p. 83.

The Genus *Limnephilus* Leach

This genus is represented in the study area by 33 species, of which two are new, and one is known only from the female. In 1955 Schmid arranged the species of the genus in species groups. Sixteen groups are known from the study area. Besides these are three species which he did not classify, even though he placed other single species in groups of their own. In this study these three single species are placed in monotypic groups. According to Schmid (1955) the characters of this genus are the same as for the tribe.

Key to the Males of species of *Limnephilus* from Alberta and eastern British Columbia

1a. Postero-dorsal edge of tergum VIII spinate or setose (Fig. 370, 402) .......... 2a

1b. Postero-dorsal edge of tergum VIII not spinate or setose (Fig. 309) .......... 23a

2a.(1a) Spinate area of tergum VIII produced posterad, or ventrad, to varying degrees (Fig. 326, 342, 385, 427) ............... 3a

2b. Spinate area of tergum VIII not produced (Fig. 273, 370, 421) .......... 21a

3a.(2a) Spinate area of tergum VIII light or heavy bulbous lobe projected well posterad of membranous connection to segment IX (Fig. 291, 390, 402, 408) .......... 4a
3b. Spinate area of tergum VIII not projected well posterad of membranous connection to segment IX; not bulbous or spinate ............................................. 18a
4a.(3a) Mesal face of cercus with one or more black, strongly sclerotized teeth (Fig. 270b, 292, 321) ............................................. 5a
4b. Mesal face of cercus without such teeth ............................................. 13a
5a.(4a) Teeth basad of distal edge of cercus in single, dorso-ventral row (Fig. 265, 278, 301, 320) ............................................. 6a
5b. Teeth of cercus not arranged thus ............................................. 11a
6a.(5a) Lateral arms of aedeagus distally as acuminate, meso-dorsal, sclerotized teeth flanked by at least partly membranous, extensible ventro-lateral lobe (Fig. 266, 280, 293) ............................................. 7a
6b. Lateral arms of aedeagus, if distally divided, with ventro-lateral lobes sclerotized, rigid, not membranous or extensible (Fig. 299, 322) ............................................. 10a
7a.(6a) Median lobes of segment X long, laminate, narrow, dorsally curved blades (Fig. 264, 291) ............................................. 8a
7b. Median lobes of segment X not as above; short, wide basally, tapered distally (Fig. 270b, 278) ............................................. 9a
8a.(7a) Median lobes of segment X parallel almost to tips (Fig. 264); spinate dorsal process of tergum VIII large, globose .......... L. sublunatus Provancher, p. 89
8b. Median lobes of segment X tapered evenly and gradually distad (Fig. 291); spinate postero-dorsal process of tergum VIII long, tapered, directed ventrad ............................................. L. susana Nimmo n. sp., p. 93
9a.(7b) Distal process of clasper long, thin, tapered (Fig. 270a); spinate process of tergum VIII large, globose ............................................. L. sansoni Banks, p. 90
9b. Distal process of clasper short, stout, blunt (Fig. 278); spinate process of tergum VIII small, thumb-like .......... L. hageni Banks, p. 91
10a.(6b) Tip of clasper black, strongly sclerotized, with dorsally directed tooth (Fig. 320); median lobes of segment X hooked postero-ventrad ............................................. L. externus Hagen, p. 99
10b. Tip of clasper not so armed, blunt (Fig. 298); median lobes of segment X tapered, directed directly postero-dorsad, with no hook ............................................. L. indivisus Walker, p. 95
11a.(5b) Median lobes of segment X directed directly postero-dorsad (Fig. 326); spinate lobe of tergum VIII directed ventrad, located between cerci ............................................. L. sericeus (Say), p. 100
11b. Median lobes of segment X wide basally, tapered abruptly to thin tooth curved dorso-anterad (Fig. 385, 402); spinate process of tergum VIII directed backwards over genitalia ............................................. 12a
12a.(11b) Clasper with wide base, tapered gradually postero-dorsad (Fig. 385) ............................................. L. perpusillus Walker, p. 112
12b. Clasper originated abruptly from base, almost rectangular in lateral aspect, divided shallowly distally (Fig. 402) ............................................. L. labus Ross, p. 115
13a.(4b) Median lobes of segment X with distal portion curved dorsad (Fig. 305, 365, 408) ............................................. 14a
13b. Median lobes of segment X otherwise ............................................. 17a
14a.(13a) Median lobes of segment X long, narrow, evenly tapered throughout length (Fig. 304, 390) ............................................. 15a
14b. Median lobes of segment X otherwise ............................................. 16a
15a.(14a) Clasper with wide base, abruptly narrowed to finger-like distal portion (Fig.
Rhyacophilidae and Limnephilidae

304) ...........................................  L. infernalis (Banks), p. 96.

15b. Clasper short, blunt, with short base (Fig. 390) .... L. argenteus Banks, p. 113.

16a.(14b) Clasper base very short; cercus narrow, long, dark, strongly sclerotized on distal edge (Fig. 408, 409) ............... L. minusculus (Banks), p. 116.

16b. Clasper with long base; cercus with wide base, short, rounded (Fig. 365) ............... L. spinatus Banks, p. 108.

17a.(13b) Both cerci and median lobes of segment X short, strongly sclerotized, massive (Fig. 433, 434) ........................................... L. canadensis Banks, p. 120.

17b. Both cerci and median lobes of segment X long, slender, tapered, strongly sclerotized (Fig. 332, 333) ............... L. femoralis (Kirby), p. 102.

18a.(3b) Lateral arms of aedeagus distally bilobed (Fig. 286, 429); cercus relatively short, broad ........................................... 19a

18b. Lateral arms of aedeagus simple (Fig. 344, 350); cercus very long, slender .... 20a

19a.(18a) Cercus long, parallel-sided; clasper short (Fig. 427) .................. L. rhombicus (L.), p. 118.

19b. Cercus short, triangular; clasper with long, narrow distal process (Fig. 284) ............... L. partitus Walker, p. 92.

20a.(18b) Postero-dorsal edges of segment IX distinctly concave; clasper long, acuminate (Fig. 350) ........................................... L. valhalla Nimmo n. sp., p. 106.

20b. Postero-dorsal edges of segment IX not concave; clasper short, blunt (Fig. 342) ............... L. moestus Banks, p. 104.

21a.(2b) Clasper massive, with distinct dorsal tooth (Fig. 421) ........................................... L. nigriceps (Zetterstedt), p. 117.

21b. Clasper otherwise (Fig. 370) ........................................... 22a

22a.(21b) Median lobes of segment X long, with irregular edges; disto-lateral tooth present (Fig. 273, 274); no teeth on mesal face of cercus . . L. extractus Walker, p. 91.

22b. Median lobes of segment X short, with smooth edges; directed postero-mesad to teeth of mesal faces of cerci (Fig. 370, 371) .... L. hyalinus Hagen, p. 109.

23a.(1b) Clasper with long, narrow base (Fig. 375, 414) ........................................... 24a

23b. Clasper with short base (Fig. 337, 355, 360) ........................................... 27a

24a.(23a) Lateral arm of aedeagus expanded distally; blade-like, fringed peripherally with spines or setae (Fig. 311, 317) ........................................... 25a

24b. Lateral arm not expanded distally (Fig. 377, 416) ........................................... 26a

25a.(24a) Cercus deeply cleft distally, with distal ends of each lobe black, strongly sclerotized (Fig. 309, 310) ........................................... L. ornatus Banks, p. 97.

25b. Cercus not cleft, trapezoidal in lateral aspect (Fig. 315); meso-distal edge with distinct, regular, black tooth or spine (Fig. 316) ........................................... L. picturatus McLachlan, p. 98.

26a.(24b) Lateral arm of aedeagus reduced; simple, distally spinate, membranous lobe (Fig. 377); cercus triangular, vertically high (Fig. 375) ........................................... L. secludens Banks, p. 110.

26b. Lateral arm of aedeagus long, thin, with three or four distal spines across median shaft (Fig. 416, 417); clasper large, thin plate directed mesad, with black, dentate, dorsal edge (Fig. 414, 418) ........................................... L. kennicotti Banks, p. 116.

27a.(23b) Tips of median lobes of segment X directed dorso-lateral (Fig. 355, 380) .... 28a

27b. Tips of median lobes of segment X not directed dorso lateral (Fig. 337, 347, 360, 395) ........................................... 29a

28a.(27a) Clasper with disto-lateral tooth (Fig. 380) ........................................... L. janus Ross, p. 111.

28b. Clasper without such tooth; much smaller than median lobes of segment X
Key to the Females of species of Limnephilus from Alberta and eastern British Columbia

1a. Segment X distinct from segment IX, either by distinct suture line or abrupt decrease in size, or both. Segment X partly recessed into segment IX or not (Fig. 268, 295, 331, 406, 431) ........................................ 2a

1b. Segment X fused to segment IX; no suture lines or abrupt decrease in size; demarcated by slight declivity or not (Fig. 296, 318, 359, 363, 400, 419, 426) ........................................ 17a

2a.(1a) Segment IX with ventro-lateral lobes separate, distinct; demarcated by sutures (Fig. 271, 290, 324, 431, 438) ........................................ 13a

2b. Segment IX with ventro-lateral lobes, or not; if present, an integral part of segment, not separated by sutures (Fig. 268, 331, 340, 369, 388, 406) ........................................ 3a

3a.(2b) Segment IX with distinct dorsal and ventral portions joined by laterally constricted strap; segment X flanked dorsally and ventrally, not laterally (Fig. 268, 295, 388) ........................................ 11a

3b. Segment IX not constricted laterally, or segment X not flanked dorsally, or ventrally (Fig. 336, 369, 406, 412) ........................................ 4a

4a.(3b) Segment X with dorso-lateral lobes (Fig. 313, 331, 336, 383, 406, 412) ........................................ 5a

4b. Segment X without dorso-lateral lobes (Fig. 340, 369) ........................................ 10a

5a.(4a) Opposing edges of median and lateral lobes of vulval scale very close, at least at base; if close only at base, in form of v-pattern (Fig. 330, 384, 407, 413) ........................................ 6a

5b. Opposing edges of vulval scale lobes markedly separated (Fig. 314, 336) ........................................ 9a

6a.(5a) Dorso-lateral lobes of segment X tapered in lateral aspect (Fig. 383, 412) ........................................ 7a

6b. Dorso-lateral lobes of segment X not tapered; blunt or rounded distally (Fig. 331, 406) ........................................ 8a

7a.(6a) Lateral lobes of vulval scale with concave ventral faces in lateral aspect (Fig. 383) ........................................ L. janus Ross, p. 111

7b. Lateral lobes of vulval scale in lateral aspect with ventral faces not concave, median lobe markedly longer than lateral lobes (Fig. 412) ........................................ L. minusculus (Banks), p. 116

8a.(6b) Meso-dorsal lobes of segment X, immediately dorsad of anus, black, long, very thin, acuminate in lateral aspect (Fig. 331) ........................................ L. sericeus (Say), p. 100

8b. Meso-dorsal lobes of segment X immediately dorsad of anus short, triangular, blunt in lateral aspect (Fig. 406) ........................................ L. labus Ross, p. 115

9a.(5b) Dorso-lateral lobes of segment X long, thin, finger-like (Fig. 313)
9b. Dorso-lateral lobes of segment X short, squat, triangular (Fig. 335, 336) .................. L. ornatus Banks, p. 97.

10a.(4b) Segment IX with distinct, trapezoidal, lateral lobes projected postero-lateral of segment X (Fig. 340) .................. L. femoralis (Kirby), p. 102.

10b. Segment X without such lobes, with minute dorsal portion (Fig. 369) .................. L. spinatus Banks, p. 108.

11a.(3a) Cercus short, squat, rounded, appressed to top surface of segment X (Fig. 295, 388). .................. L. sublunatus Provancher, p. 89.

11b. Cercus long, lamellar, attached to segment IX basally, otherwise free (Fig. 268) ........ 12a

12a.(11a) Median lobe of vulval scale approximately equal to lateral lobes (Fig. 389); segment X oriented vertically in lateral aspect (Fig. 388) .................. L. perpusillus Walker, p. 112.

12b. Median lobe of vulval scale projected well beyond lateral lobes, up to twice their length (Fig. 294); segment X oriented antero-posterad (Fig. 295) .................. L. susana Nimmo n. sp., p. 93.

13a.(2a) Genitalia with cercus or cercus-like lobes dorsad of segment X (Fig. 271, 290, 324, 431) .................. L. canadensis Banks, p. 120.

13b. Genitalia without cerci; segment X conical in ventral aspect (Fig. 437) .................. L. partitus Walker, p. 92.

14a.(13a) Vulval scale small, shallowly recessed into sternum VIII (Fig. 290, 325); cercus in lateral aspect not divergent from segment X (Fig. 290, 325) ........ 15a

14b. Vulval scale large, deeply recessed into sternum VIII (Fig. 272, 432); cercus in lateral aspect divergent widely from segment X (Fig. 271, 431) ........ 16a

15a.(14a) Ventro-lateral lobe of segment IX divided as two sclerites (Fig. 290) .................. L. rhombicus (L.), p. 118.

15b. Ventro-lateral lobe of segment IX undivided, of one piece (Fig. 324) .................. L. externus Hagen, p. 99.

16a.(14b) Base of cercus dorsad of segment X (Fig. 271), squarely cleft disto-laterally .......... 18a

16b. Base of cercus antero-dorsad of segment X (Fig. 431); segment X not disto-laterally cleft L. rhombicus (L.), p. 118.

17a.(1b) Ventro-lateral lobe of segment IX separate and distinct from dorsal part of segment by suture or membrane (Fig. 307, 318, 363, 419) ........ 18a

17b. Ventro-lateral lobe of segment IX not distinguished from dorsal part of segment by suture (Fig. 282, 346, 378, 400) ........ 25a

18a.(17a) Segment X with pair of dorso-lateral lobes or cerci (Fig. 302, 307, 318, 374) ........ 19a

18b. Segment X without dorso-lateral lobes (Fig. 363, 394, 419, 426) ........ 22a

19a.(18a) Distal end of segment X pair of meso-dorsal lobes or scales and single ventral lobe (Fig. 308, 319) ........ 20a

19b. Distal end of segment X without such lobes (Fig. 303, 373) ........ 21a

20a.(19a) Ventro-lateral lobes of segment IX roughly rectangular in lateral aspect, oriented vertically (Fig. 318), the two lobes meeting but not fused ventrally (Fig. 319) ........ L. picturatus McLachlan, p. 98.

20b. Ventro-lateral lobes of segment IX triangular in lateral aspect (Fig. 307); not meeting ventrally (Fig. 308) ........ L. infernalis (Banks), p. 96.

21a.(19b) Dorso-lateral lobes of segment X flanked laterally by rectangular walls (Fig.
Nimmo

373, 374) .................. *L. hyalinus* Hagen, p. 109.

21b. Dorso-lateral lobes of segment X free, not flanked laterally (Fig. 302) ........... *L. indivisus* Walker, p. 95.

22a.(18b) Segment X composed of massive, mesally completely cleft, postero-dorsal plate (Fig. 419, 420) .................. *L. kennicotti* Banks, p. 116.

22b. Segment X otherwise .................. 23a

23a.(22b) Segment X indistinguishable from segment IX; massive, blunt, with small, simple anal aperture at extreme posterior end (Fig. 425, 426) .................. *L. nigriceps* (Zetterstedt), p. 117.

23b. Segment X not massive; deeply cleft mesally, tapered posterad in lateral aspect (Fig. 364, 394). .................. 24a

24a.(23b) Ventro-lateral lobes of segment IX high, narrow, oriented vertically (Fig. 394) .................. *L. argenteus* Banks, p. 113.

24b. Ventro-lateral lobes of segment IX almost as high as wide, with no special orientation (Fig. 363) .................. *L. parvulus* (Banks), p. 107.

25a.(17b) Ventro-lateral part of segment IX produced posterad as narrow, tapered lobe (Fig. 282, 296, 346, 353). .................. 26a

25b. Ventro-lateral part of segment IX produced posterad at most as very broad-based, abruptly tapered lobe (Fig. 276, 359, 378, 400). .................. 29a

26a.(25a) Dorso-lateral lobes, or cerci, of segment X long, thin, well separated from remainder of vulval scale much longer than lateral lobes .................. 27a

26b. Dorso-lateral lobes, or cerci, of segment X short, rounded distally, lamellar (Fig. 346, 354); median lobe of vulval scale no longer than lateral lobes .................. 28a

27a.(26a) Segment X cleft laterally (Fig. 296). .................. *L. species l*, p. 94.

27b. Segment X not cleft laterally (Fig. 282) .................. *L. hageni* Banks, p. 91.

28a.(26b) Segment X with dorsal lobes located laterally (Fig. 354) .................. *L. valhalla* Nimmo n. sp., p. 106.

28b. Segment X with dorsal lobes more mesally located (Fig. 345) .................. *L. moestus* Banks, p. 104.

29a.(25b) Segment X cleft laterally (Fig. 276, 378). .................. 30a

29b. Segment X not cleft laterally (Fig. 359, 400). .................. 31a

30a.(29a) Dorso-lateral lobes, or cerci, of segment X small, short, reaching no more than halfway to extremities of segment (Fig. 378) .................. *L. secludens* (Banks), p. 110.

30b. Dorso-lateral lobes, or cerci, of segment X large, triangular, equally as long as segment (Fig. 276) .................. *L. extractus* Walker, p. 91.

31a.(29b) Segment X deeply cleft dorsally (Fig. 401) .................. *L. alberta* Denning, p. 114.

31b. Segment X not deeply cleft dorsally (Fig. 358) .................. *L. lopho* Ross, p. 107.

The *subcentralis* group

Members of this group are recognizable in the field by wing pattern. This consists of a series of dark brown bars on lighter background; initially with median longitudinal band in vicinity of subradial cell, terminated at chord; distad of chord are two shorter bands, one between f1 and f2, the other on f4; remainder of wing irrorate to very irregularly patterned. Males are distinguished by thin, slightly concave mesal cerci, usually with short or long row of black teeth basad of distal ends; and by lamellate, tapered, median lobes of segment X (Fig. 273, 278, 291). Females are distinguished by presence of cerci or cercus-like postero-dorsal lobes of segment X, and by segment X being separated from remainder of genitalia by suture line (Fig. 268, 271, 290).
**Limnephilus sublunatus** Provancher, 1877

*(Fig. 138a, 138b, 264-269, 607)*


Males of this species are distinguished from males of other species of the group by long, smoothly curved, lamellate cerci (Fig. 264), and by similar median lobes of segment X which are curved dorsad and rather blunt distally. Females are distinguished by thin, delicate cerci of segment X, which are apparently attached to segment IX; segment X recessed into segment IX, long, tapered, thin walled, in lateral aspect (Fig. 268).

**Description.** — Antennae pale yellow. Vertex of head brown-yellow, except for paler warts. Thorax pale yellow, with light brown patches on dorsal areas of pleura. Brush of anterior femur of male half length of femur; sparse, with short, black spines. Fore wing length of male 13.9 mm; orange-brown, clear areas hyaline; costal margin clear for two-thirds of length. Stigma light brown. Venation as in Fig. 138a, 138b.

Male genitalia. (Specimen from Canmore, Alberta). Postero-dorsal edge of tegumen VIII produced posterad as large spinate bulb; spines black, sparse. Dorsal strap of segment IX of uniform width, overhanging main body of segment at angle of about 45° (Fig. 264). Main body of segment IX almost square; posterior edge directed mesad under postero-dorsal corner, which has finger-like aspect laterally. Clasper long, with wide base tapered quickly to finger-like dorsal portion. Segment X with median lobes long, thin, lamellate; distal third of dorsal edges black; lobes slightly up-turned in lateral aspect, warped in dorsal aspect (Fig. 265). Cercus long, narrow, of uniform width, with distal end black-toothed; with slightly darker dentate ridge two-thirds of distance from base (Fig. 265). Lateral arms of aedeagus bipartite distally; dorsal lobe scleritized, dorsally directed spine (Fig. 266); ventral lobe membranous except for clear, scleritized tip with fringe of brown setae.

Female genitalia. (Specimen from Canmore, Alberta). Vulval scale with slight concavities at posterior edges of lateral lobes; median lobe distally blunt, longer than lateral lobes (Fig. 269). Segment IX with lateral faces deeply depressed, recessed anterad as flanges. Ventral area directed posterad under segment X as acuminate plates (Fig. 268). Supra-genital plate large, semicircular, with hyaline basal area; with rectangular, membranous, basal area. Segment X very deeply cleft mesally (Fig. 269), with acuminate distal tips to lateral lobes; in lateral aspect segment tapered gradually posterad to tips. Cercus long, narrow, distal half clothed with short, fine, hyaline setae; cercus slightly longer than segment X, apparently attached to segment IX.

**Notes on biology.** — Specimens of this species appear to emerge from pools, sloughs or lakes fringed with horse-tails, or sedges. The flight period extends from July 1 to October 3. My records are insufficient to define a peak.

**Geographical distribution.** — The known range of this species extends from British Co-
lumbia, Idaho and Colorado to New Hampshire and Quebec (Fig. 607), with a large, mid-continental blank. In Alberta it is confined to the passes, and low valleys, of the mountains and foothills. In altitude it ranges from about 4,100' to 6,878'. I have taken specimens at the upper limit, but on the whole it is usually taken at the lower altitudes.

I have examined 45 specimens, 17 males and 28 females, from the study area.

_Limnophilus sansoni_ Banks, 1918

(Fig. 270a-272, 608)


Males of this species are distinguished from males of other species in the group by long, thin, tapered, dorsal process of clasper; by laterally toothed tip of median lobes of segment X; and by row of heavy, black teeth on mesal face of cercus (Fig. 270b). Females are distinguished by large, isolated ceri of segment X, and by segment X cleft squarely on latero-mesal faces (Fig. 271). Venation identical to that of _L. sublunatus._

_Description._ — Antennae dark brown; scapes darker, with antero-mesal faces pale, glabrous. Vertex of head almost black in ocellar triangle; remainder brown, with warts yellow. Thorax generally dark brown. Body of female generally rich red-brown, with dark brown only dorso-laterally. Brushes of male anterior femora of strong, black spines on basal half only. Spurs yellow. Fore wing length of male 14.0 mm; light brown; costal area clear to distal end of sub-costa. Stigma present. Clear areas other than costal margin slightly cloudy brown to clear yellow.

Male genitalia. (Specimen from Totem Creek area, Banff-Jasper Hwy., north of Lake Louise, Alberta). Postero-dorsal edge of tergum VIII prolonged posterad as large, black, spinate bulb. Segment IX with very narrow dorsal strap directed postero-dorsad at about 45°. Main body of segment square; posterior edge indented at clasper bases as wide, thumb-like process dorsally (Fig. 270a). Clasper with long, narrow base and long, thin, finger-like dorsal process. Median lobes of segment X with small disto-lateral tooth; dorso-lateral edges black, denticulate; attached to mesal edges of small, basal plates. Cercus triangular, with posterior edges black, dentate; with strongly sclerotized, dorso-ventral, black, dentate ridge (Fig. 270b). Aedeagus essentially identical to that of _L. sublunatus_, except for slightly broader dorsal lobe.

Female genitalia. (Specimen from Totem Creek area, on Banff-Jasper Hwy., north of Lake Louise, Alberta). Vulval scale median lobe blunt, little tapered, longer than lateral lobes (Fig. 272). Ventro-lateral lobes of segment IX square, with acuminate, concave process directed posterad (Fig. 271). Supra-genital plate attached ventrad of segment IX, wide, with slightly flanged lateral edges, flanges folded mesad. Segment X rectangular in lateral aspect, with square lateral clefts; in ventral aspect wide, triangular basally; cleft ventrally only slightly; dorsal cleft complete to cercal bases. Cercus located on posterior half of segment X, projected posterad beyond segment for half its length.

_Notes on biology._ — Adults of this species are collected almost exclusively in the vicinity of sedge ponds or sloughs. The adult flight season extends from July 25 to October 3 with an apparent peak of emergence from mid-August to mid-September.

_Geographical distribution._ — The known range of this species extends from Alaska to Colorado, though records are few (Fig. 608). In Alberta it is confined to the mountain and foothill areas, ranging in altitude from 3,700' to 5,350'.
I have examined 276 specimens, 103 males and 173 females, from the study area.

**Limnophilus extractus** Walker, 1852  
(Fig. 273-277, 609)

*Goniotaulis* extractus; Hagen, 1864: 815. 
*Limnophilus* (Goniotaulis) *extractus*; Hagen, 1861: 260.  
Males of this species are distinguished from males of other species of the group by long, slender, black, median lobes of segment X; by inconspicuous posterior lobe of tergum VIII; and by short, trapezoidal claspers (Fig. 273). Females are distinguished by almost completely cleft segment X (Fig. 277); by lack of separate and distinct ventro-lateral lobe of segment IX (Fig. 276); and by laterally cleft segment X.  
Description. — Antennae yellow to pale brown. Vertex of head yellow, to very pale brown in patches. Thorax pale yellow with slight local darkenings to pale brown. Male with brush of fore leg spinate, black, occupying only basal half of mesal face, in narrow band. Spurs yellow. Fore wing length of male 12.4 mm; pale brown to yellow; costal margin clear to wing tip and beyond. Venation identical to that of *L. sublunatus*.  
Male genitalia. (Specimen from Cold Lake, Alberta). Postero-dorsal margin of tergum VIII lightly setose; bounded laterally by depressions; setae pale. Segment IX with short dorsal strap; strap with mesal process directed ventrad (Fig. 273). Main body of segment abruptly expanded ventrad of dorsal strap, rectangular and featureless. Clasper small, blunt, attached to lower half of posterior edge of segment IX; trapezoidal in lateral aspect. Median lobes of segment X finger-like in lateral aspect; projected well posteral of cerci, black, each with small, distinct disto-lateral tooth (Fig. 274). Cercus triangular, concave on mesal face, not projected posteral of segment IX. Aedeagus simple; lateral arms originated dorsal of median shaft (Fig. 275); tips fringed with heavy setae along dorsal edges only; setae increase in length distally. Median shaft attached to distinct basal, sclerotized collar.  
Female genitalia. (Specimen from Flatbush, Alberta). Vulval scale large, lobes well spaced; median lobe longer than lateral lobes, square-tipped, slightly tapered from base (Fig. 277); lateral lobes curved mesad distally. Segment IX large, higher than wide (Fig. 276); with slight latero-posterior lobes. Supra-genital plate semi-circular. Segment X fused to segment IX; of two pairs of lobes; cerci broad, triangular in lateral aspect; main body of segment cleft completely in vertical plane (Fig. 277); cleft slightly in horizontal plane.  
Notes on biology. — This is a lake species. Adults are collected near sedge and other water weed-choked ponds and lakes. The adult flight period extends from May 22 to July 11.  
Geographical distribution. — The known range of this species is primarily boreal, extending from Great Slave Lake and central Alberta to the northern New England States (Fig. 609). In Alberta it is confined to the central and northeast lowlands.  
I have examined 27 specimens, 25 males and two females, from the study area.

**Limnophilus hageni** Banks, 1930  
(Fig. 278-283, 610)
**Limnophilus hageni** Banks, 1930a:226. (Type locality: Fort Resolution, Great Slave Lake).


Males of this species are distinguished from males of other species in the group by high, narrow clasper bases, with thick, blunt dorsal process (Fig. 278); by row of black teeth extended only half way across cerci; and by dorso-laterally directed tips of median lobes of segment X. Females are distinguished by long, thin, cerci extended more than half their length beyond segment X; by absence of discrete ventro-lateral lobes of segment IX; and by very long median lobe of vulval scale (Fig. 282, 283).

**Description.** — Antennae light yellowish brown. Vertex of head with diamond-shaped black area with two corners occupied by lateral ocelli. Thorax light yellowish brown, with darker areas on thorax. Brush of male fore leg of single row of black spines extended along basal half of femur. Spurs yellow-brown. Fore wing length of male 11.8 mm; light brown, clear areas hyaline. Costal area quite clear; stigma slight. Venation identical to that of *L. sublunatus*.

Male genitalia. (Specimen from Forestry Trunk Road in area of Kananaskis Lakes, Alberta). Postero-dorsal edge of tergum VIII produced as short, black-spinate bulb. Segment IX with long, tapered dorsal strap; main body of segment stout, rectangular, with postero-dorsal angle directed mesad, furrowed (Fig. 278). Clasper short, blunt distally; base high, narrow. Median lobes of segment X short, stout in lateral aspect, black distally, with tips curved dorso-laterad (Fig. 278, 279). Cercus large, with dorsal edge curved gently distad; posterior edge black, irregularly dentate; mesal face with short, curved dentate line from dorsal edge. Median shaft of aedeagus with distinct distal head; opening of ejaculatory duct at extreme tip. Lateral arms large, each bifid, ventral lobe membranous, extensible, distally fringed with long setae; dorsal lobe sclerotized, toothed distally, with tooth directed dorso-mesad (Fig. 281).

Female genitalia. (Specimen from Forestry Trunk Road in area of Kananaskis Lakes, Alberta). Vulval scale with long, narrow, median lobe (Fig. 283); lateral lobes small, widely spaced, lateral edges slightly flanged. Segment IX large, rectangular, with small ventro-lateral lobes (Fig. 282). Supra-genital plate large, semi-circular. Segment X indistinct from segment IX; deeply cleft dorsally. Cerci long, thin, well separated from segment X.

**Notes on biology.** — Adults of this species are found in smaller ponds or sloughs with dense sedge and horse-tails present. The adult flight period extends from July 15 to September 22; my records are insufficient to indicate a peak period.

**Geographical distribution.** — The known range of this species extends from British Columbia to Ontario and Great Slave Lake (Fig. 610). In Alberta it is confined to the mountains and foothills, ranging in altitude from 4,600' to 5,350'.

I have examined 26 specimens, 16 males and 10 females, from the study area, and one (male) from Great Slave Lake.

**Limnophilus partitus** Walker, 1852
(Fig. 139a, 139b, 284-290, 611)


**Limnophilus partitus**; Betten and Mosely, 1940:127-129.
Males of this species are distinguishable by irregular posterior edges of segment IX (Fig. 284); by high, narrow-based claspers, with dorsal process long, thin, directed dorso-posterad; by very wide dorso-posterior process of tergum VIII (Fig. 285); and by small, sclerotized ventral lobe of lateral arm (Fig. 286). Females are distinguished by divided ventro-lateral lobes of segment IX (Fig. 290).

Description. — Antennae black. Vertex of head black, warts dark brown. Thorax black in male, brown in female. Spars light brown. Fore wing length of male 12.3 mm; brown, with large clear areas. Costal margin clear for about four-fifths of length. Stigma present, with distinct, white area immediately basad. Venation as in Fig. 139a, 139b; both fore and hind wings with cell between f2 and f3 pedicellate.

Male genitalia. (Specimen from pond 2 miles east of Nordegg, Alberta). Tergum VIII black with pale ventro-lateral edges; postero-dorsal edge produced posterad as black-spinate bulge dorsad of genitalia. Dorsal strap of segment IX hyaline, discrete from remainder of segment (Fig. 284); narrow in posterior aspect (Fig. 285). Main body of segment squat, with distinct bulge on dorsal edge. Clasper with base coincident with entire posterior edge of segment IX; dorsal process finger-like. Median lobes of segment X attached to mesal edges of lateral, concave lobes; massive, directed dorso-posterad; quite black. Cercus with distal edge black, dentate; with thin, weak line of teeth on mesal face. Lateral arms of aedeagus bilobed (Fig. 286); dorsal lobe heavily sclerotized, distally spiniform, directed dorsally; ventral lobe hyaline, spatulate, fringed distally with setae.

Female genitalia. (Specimen from pond 2 miles east of Nordegg, Alberta). Vulval scale wide (Fig. 289); lateral arms with concave distal faces; median lobe wide basally, gradually tapered distad, rounded. Segment IX with small dorsal body, divided to ventro-lateral lobes (Fig. 290). Supra-genital plate large, projected well posterad of vulval scale. Segment X completely cleft dorsally; anal opening wide, flared. Cerci short, acute-triangular in ventral aspect, held close to segment X.

Notes on biology. — Adults of this species are collected near ponds or sloughs thickly vegetated with sedges, or sedges and horse-tails. The adult flight period extends from August 7 to October 3. Peak emergence appears to be from mid-August to mid-September.

Geographical distribution. — The known range of this species extends from British Columbia and Great Slave Lake, to Newfoundland (Fig. 611). In Alberta it is confined to the mountains and foothills, ranging in altitude from 3,800' to 5,200'.

I have examined 77 specimens, 49 males and 28 females, from the study area and Great Slave Lake.

Limnophilus susana Nimmo, n. sp.
(Fig. 291-295, 612)

Males of this species are distinguished from males of other species in the group by evenly tapered, dorsally directed median lobes of segment X (Fig. 291); and by tapered, ventrally curved lobe of tergum VIII. Females are distinguished by short, stout cerci closely appressed to segment X and of equal length (Fig. 295); and by vulval scale median lobe twice as long as lateral lobes (Fig. 294).

Description. — Antennae red-brown. Vertex of head reddish to yellowish brown except for dark, chocolate-brown between ocelli, in cruciform pattern in male. Thorax very dark brown laterally and dorsally. Brush of male fore leg of scattered short, black spines on basal half of femur. Spurs light red-brown. Fore wing length of male 14.6 mm; chocolate-brown, with lighter, reddish brown, areas. Costal area almost hyaline. Venation identical to that of L. sublunatus.
Male genitalia. (Specimen from Forestry Trunk Road, at Pembina River, Alberta). Postero-dorsal lobe of tergum VIII broad, somewhat flattened, tapered, curved ventrad. Segment IX high, narrow, with main body nearly rectangular in lateral aspect (Fig. 291); with deep furrow at postero-dorsal angle. Dorsal strap deep, vertical band. Clasper large, with long, sinuate base; dorsal process of uneven width, directed dorsal distally, twisted slightly to form ridge at right angles to body axes. Median lobes of segment X long, narrow, evenly tapered, dorsally upturned blades; with disto-lateral tooth (Fig. 292) and large concave plates basally. Circus massive, curved, of approximately uniform width; distally with row of dark teeth; second series of three to four dark teeth two-thirds of distance from base (Fig. 292). Median shaft of aedeagus stout, dorsally curved; lateral arms massive, bilobed (Fig. 293). Dorsal lobe heavy, distally toothed, sclerotized; ventral lobe membranous but with lightly sclerotized distal edges with long, stout setae dorsally.

Female genitalia. (Specimen from Forestry Trunk Road, at Pembina River, Alberta). Vulval scale large, with long, rectangular, median lobe, rectangular, almost square, lateral lobes (Fig. 294); all lobes well separated; median lobe twice as long as lateral lobes. Supragnital plate large, pentagonal in ventral aspect. Segment IX with two thin, ventral lobes, and triangular dorsal portion, all connected by narrow lateral straps (Fig. 295). Segment X robust, terminated distally by two pairs of lobes; dorsal lobes thin, triangular; ventral lobes vertically thin, wide in lateral aspect. Cerci short, closely attached to dorsal surface of segment X; rounded, spindle-shaped.

Notes on biology. — Known only from a single slough with thick growth of horse-tails, and a fine-bladed sedge; water shallow. Date of capture was September 22.

Holotype. — Male. Forestry Trunk Road about 1 mile north of crossing of Pembina River, Alberta (Fig. 612); September 22, 1968. A. Nimmo.

Allotype. — Female. Same data as holotype.

Paratypes. — Same data as for holotype; one male, two females.

The holotype, allotype, and one female paratype are in the Canadian National Collection, Ottawa, where they have been assigned the type series number 10,586. The remaining male and female paratypes are in the Strickland Museum. Dept. of Entomology, University of Alberta, Edmonton, Alberta.

This new species is named for my wife, Susan.

Limnephilus species 1
(Fig. 296-297, 612)

Females of this species are distinguished from females of other species in the group by large dorsal body to segment IX, by long, distally up-turned segment X, and by long, slender, tapered cerci not appressed dorsally to segment X (Fig. 296).

Description. — Antennae yellow-brown. Vertex of head deep red-brown. Thorax yellow-brown. Spurs dark brown; formula 1,3,3. Fore wing length of female 11.8 mm; red-brown, with hyaline areas typical of the pattern for the subcentrals group, except no evident longitudinal bars at wing tip. Venation identical to that of L. sublunatus.

Male genitalia. Unknown.

Female genitalia. (Specimen from 2 miles north of Athabasca Falls, on Hwy. 93a, Jasper National Park, Alberta). Median lobe of vulval scale much longer than lateral lobes, with square tip, gradually tapered. Lateral lobes sub-triangular (Fig. 297). Segment IX large, with two ventro-lateral, rounded, not separate, lobes (Fig. 296). Dorsal portion convex, bounded by lateral declivities which result in concave sides of segment. Segments IX and X partly separated by faint suture. Supra-genital plate relatively small, convex ventrally; polygonal in
ventral aspect. Segment X cylindrical, deeply cleft mesally; not so deeply cleft laterally; dorsal lobes thus formed small, triangular in lateral aspect; ventral lobes larger, wider. Cerci long, tapered, thin, free from dorsal surface of segment X.

The specimen of this species known to me was taken from a small musk lake 2 miles north of Athabasca Falls, on Hwy. 93a, Jasper National Park, Alberta, September 10, 1966 (Fig. 612).

**The stigma group**

Males of this group are characterised by relatively small claspers, with high, ventrally tapered bases, and short, blunt dorsal processes; by small postero-dorsal lobes of tergum VIII projected well posterad from membranous connection to segment IX (Fig. 304). Females are characterised by presence of separate and discrete ventro-lateral lobes of segment IX (Fig. 302).

**Limnophilus indivisus** Walker, 1852

*(Fig. 298-303, 614)*


Males of this species are distinguished from males of other species of the group and genus by distally flared or expanded cerci (Fig. 298); and by short, narrow, tapered, median lobes of segment X. Females are distinguished by right-angled, ventro-lateral lobes of segment IX (Fig. 302); and by long, thin, acute-triangular cerci of segment X closely appressed to the dorso-lateral surface of segment X.

**Description.**—Antennae pale yellow; scapes darker, with longitudinal band of fine, short setae on antero-mesal faces. Vertex of head reddish brown, warts paler. Thorax yellow, tending to light reddish brown dorsally. Spurs dark reddish yellow. Fore wing length of male 14.9 mm; yellow to pale brown. Costal area clear to distal end of costa. Venation identical to that of *L. sublunatus*; with short area of short, black hairs on vein R2 of male hind wing (as in Fig. 140b); absent in female. Abdominal sterna VI and VII of male with short, triangular lobes in middle of posterior edges; similarly in female, but on sterna V and VI.
Male genitalia. (Specimen from Gorge Creek, 20 miles west of Turner Valley, Alberta). Postero-dorsal process of tergum VIII with short, black spines. Dorsal strap of segment IX not arched highly, directed postero-dorsad, with distinct, spatulate ventro-mesal process (Fig. 298, 301) connected to segment X. Body of segment IX wide dorsally, narrowed ventrad; with distinct black band of varied width along anterior edges. Clasper short, blunt, with high, narrow base. Median lobes of segment X conical, short, thin, tapered distad, black; attached to mesal edges of basal plates; directed slightly dorso-laterad. Cercus broadened distad; short, with distal rim black, dentate; with row of heavy, black teeth vertically on mesal face (Fig. 301); with tufts of black setae at distal corners. Lateral arms of aedeagus bilobed, with bifid bases (Fig. 299); ventral lobe rounded, spatulate, with fringe of heavy, dark setae on dorsal edge; dorsal lobe directed dorso-mesad (Fig. 300), with black, spiniform tip and hyaline lateral flange; posterior edge with four very heavy, black spines.

Female genitalia. (Specimen from Gorge Creek, 20 miles west of Turner Valley, Alberta). Vulval scale with two triangular lateral lobes, uniformly tapered median lobe. Vento-lateral lobes of segment IX distinct, discrete (Fig. 302), bent at right angles around base of segment X. Dorsal portion of segment IX small, almost indistinguishable from segment X. Supra-genital plate small, smoothly curved (Fig. 303). Segment X deeply cleft dorsally; conical in ventral aspect, situated between cerci. Cerci closely appressed to dorso-lateral surfaces of segment X, tapered to finger-like tips.

Notes on biology. — I have frequently taken adults of this species in the vicinity of small lakes or sloughs which are thickly bordered by cattail rushes, or coarse sedges. The adult flight period extends from July 14 to September 30; records are insufficient to determine a peak.

Geographical distribution. — The known range of this species extends from British Columbia to Illinois, Nova Scotia and Quebec (Fig. 614). In Alberta it is found in the plains, foothills, and low mountain passes.

I have examined 25 specimens, 15 males and 10 females, from the study area.

**Limnephilus infernalis** (Banks), 1914
(Fig. 304-308, 613)

*Anisogamus infernalis* Banks, 1914:154-156. (Type locality: Pinnacle Mountain, Fulton County, New York).


Males of this species are distinguished by antero-dorsally directed median lobes of segment X (Fig. 304); by large, mesally concave cerci heavily clothed on mesal faces with long setae; and by meso-ventral process of dorsal strap of segment IX connected to segment X (Fig. 305). Females are distinguished by large ventro-lateral lobes of segment IX (Fig. 307); and by large, triangular cerci fused to posterior edges of segment IX.

Description. — Antennae uniformly pale yellow. Vertex of head yellow except for darker area mesad of lateral ocelli. Thorax pale yellow, to brownish yellow. Brush of male fore leg extended barely half length of femur; composed of very stout, black spines.

Male genitalia. (Specimen from Sturgeon River, St. Albert, Alberta). Postero-dorsal lobe of tergum VIII small, bulbous distally; with short, stout, sparsely scattered, black spines. Segment IX with very high, thin dorsal strap; strap with large, ventro-mesally directed horn
connected to segment X; main body of segment small, irregular (Fig. 304, 305). Clasper thumb-like, widened slightly at high, very narrow base. Median lobes of segment X attached to mesal edges of slightly concave, basal plates; curved antero-dorsad, with slight distal swelling. Cercus very large, concave mesally; mesal face thickly clothed with long setae. Aedeagus simple; ejaculatory duct terminated at extreme tip, lateral arms attached to dorsal membranous base of aedeagus, with slightly dilated, setose tips (Fig. 306).

Female genitalia. (Specimen from Sturgeon River, St. Albert, Alberta). Vulval scale with short, tapered, blunt median lobe (Fig. 308); lateral lobes deeply channelled on mesal faces. Ventro-lateral lobes of segment IX triangular in lateral aspect (Fig. 307); main body of segment relatively large, not distinct from segment X. Segment X inconspicuous, ventrad of massive, triangular cerci; of simple, triangular dorso-lateral lobes fused to ventral surfaces of cerci (Fig. 308), and ventral, concave, triangular plate ventrad of anal orifice. Supra-genital plate visor-like, arched dorsal.

Notes on biology. — Adults of this species emerge from lakes, sloughs and quiet streams bordered with thick growths of sedges and cattail reeds. The adult flight period extends from August 14 to September 22.

Geographical distribution. — The known range of this species extends from Alaska to Alberta, Michigan and Maine (Fig. 613). In Alberta it is confined to the plains, low foothills, and low mountain passes.

I have examined 256 specimens, 206 males and 50 females, from the study area and Great Slave Lake.

The ornatus group

Males of the single species of this group are characterised by massive, distally bifid cerci (Fig. 309); by claspers with high, narrow bases and short, stubby dorsal processes; and by simple aedeagus (Fig. 311). Females are characterised by massive segment IX without ventro-lateral lobes (Fig. 313); by segment X which is discrete from segment IX; and by long, tapered cerci well separated from segment X.

Limnephilus ornatus Banks, 1897
(Fig. 309-314, 615)


Description. — Antennae yellow. Vertex of head uniformly yellow. Thorax pale yellow to light reddish brown. Brush of male fore leg narrow row of black setae along mesal face of basal half of femur. Spurs yellow. Fore wing length of male 14.3 mm; pale yellow to light reddish brown, with large hyaline areas. Costal area clear except for opaque area in distal
third of stigma. Venation identical to that of *L. sublunatus*.

Male genitalia. (Specimen from Indian Head, Saskatchewan). Tergum VIII without postero-dorsal process. Segment IX with short, thin dorsal strap. Main body with large, blunt lobe at postero-dorsal angle; with distinct row of heavy setae along ventral half of posterior edge (Fig. 309). Clasper with high, narrow base and short, blunt, thumb-like dorsal process. Median lobes of segment X attached to complexly folded baso-lateral plates; ventral edges and lateral faces minutely dentate; lobes black distally. Cercus large, bifurcated distally; distal lobes black, heavily sclerotized at tips (Fig. 310). Lateral arms of aedeagus slightly expanded distally (Fig. 311); distal half warped, concave mesally (Fig. 312) with fringe of setae along posterior edge.

Female genitalia. (Specimen from Indian Head, Saskatchewan). Vulval scale with short, rectangular median lobe; lateral lobes narrow, distinctly separated distally from median lobe (Fig. 314). Segment IX without discrete latero-ventral lobes (Fig. 313); curved slightly to embrace segment X. Supra-genital plate small, rounded, almost elliptical, set into ventral depression of segment IX. Segment X of inter-leaved dorsal and ventral parts distally; dorsal lobes darker, fused basally to ventral trough. Cerci long, thin, tapered, well separated from dorsal surface of segment X.

**Notes on biology.** — I have not taken individuals of this species in the study area, but the records available indicate that they inhabit sloughs and small lakes. The adult flight period extends from July 13 to September 10.

**Geographical distribution.** — The known range of this species extends from Alaska to Illinois and Greenland (Fig. 615) in North America. It is actually a Holarctic species with records extending west to Europe and Iceland. In Alberta it is confined to the plains or long, low mountain valleys leading to the plains.

I have examined 11 specimens, three males and eight females, from the study area.

The *picturatus* group

Males of the single species are characterised by large, mesally concave claspers with distomesal spine (Fig. 315, 316); by absence of postero-dorsal process of tergum VIII; and by short, relatively wide dorsal strap dorsad of large, trapezoidal segment IX. Females are distinguished by massive ventro-lateral lobes of segment IX (Fig. 318); by complete lack of separation of segments IX and X dorsally; and by minute, triangular cerci closely appressed to dorso-lateral surfaces of segment X.

**Limnophilus picturatus** McLachlan, 1875

(Fig. 315-319, 616)


(See Fischer, 1968:256, 258, for Palaearctic literature).


*Limnophilus miyadii* Tsuda, 1924. (See Fischer, 1968:258).

*Phryganea notatus* Zetterstedt, 1840. (See Fischer, 1968:258-259).

**Description.** — Antennae dark brown; scapes and pedicels black; yellowish brown throughout in females. Head entirely black. Thorax black; brush of male fore leg on basal two-thirds of femur; opposing face of tibia minutely spinate. Spurs yellow. Fore wing length of male
9.1 mm; pale brownish yellow; costal area clear; not patterned. Venation identical to that of *L. sublunatus*.

Male genitalia. (Specimen from Bow Pass, Banff National Park, Alberta). Segment IX with short dorsal strap; main body robust (Fig. 315). Clasper with long, narrow base; dorsal process short, with irregular edges, directed dorso-posterad. Median lobes of segment X narrow basally, widened at mid-point, narrowed distally to dorso-lateral hooks (Fig. 315, 316); black throughout. Median lobes attached to simple latero-basal plates. Lateral arms of aedeagus simple, gradually widened distad to narrow, acuminate tips with several tufts of setae or spines (Fig. 317).

Female genitalia. (Specimen from Sunwapta Pass, Jasper National Park, Alberta). Vulval scale triangular in general outline (Fig. 319); median lobe blunt, almost rectangular; lateral lobes semi-triangular, with straight posterior and mesal edges. Segment IX with massive, rectangular, ventro-lateral lobes (Fig. 318); dorsal body of segment small, indistinguishable from segment X. Supra-genital plate small, crescentic. Segment X small, with two minute dorsal lobes and single ventral lobe. Cerci small, triangular, immovable, closely appressed to dorso-lateral surfaces of segment X.

Notes on biology. — Adults of this species are found near shallow, sedge-fringed sloughs or small pools. The adult flight period extends from August 5 to September 22. There appears to be a peak at about the end of August and beginning of September.

Geographical distribution. — The nearctic range of this holarctic species extends from Alaska to Hudson’s Bay, and to Colorado (Fig. 616). In Alberta it is confined to the mountains and foothills, ranging in altitude from about 5,000’ to 6,880’.

I have examined 71 specimens, 42 males and 29 females, from the study area.

The *externus* group

Males of the single species of this group present in the study area are distinguishable by small, triangular cerci (Fig. 320); by black-spinate postero-dorsal bulb of tergum VIII; and by small, vertical, posteriorly hooked median lobes of segment X. Females are distinguished by massive ventro-lateral lobes of segment IX (Fig. 324); and by large, roughly triangular cerci of segment X very close to segment X.

**Limnephilus externus** Hagen, 1861

(Fig. 320-325, 617)


*Limnophilus congener* McLachlan, 1875:56-57. (See Fischer, 1968:100, for Palaearctic literature).

*Limnophilus congener*; (Palaearctic; see Fischer, 1968:100).

Limnophilus oslari; Essig, 1926:176.

Description. — Antennae uniform yellowish brown. Vertex of head black immediately mesial of lateral ocelli, otherwise brown. Thorax light reddish brown. Brush of male fore leg single row of black spines on basal half of mesal face of femur. Spurs hyaline to yellow. Fore wing length of male 21.6 mm; greyish brown, with hyaline areas. Costal area clear to distal end of sub-costa. Venation identical to that of L. sublunatus.

Male genitalia. (Specimen from Wapta Lake, Kicking Horse Pass, Yoho National Park, British Columbia). Postero-dorsal process of tergum VIII distinctly bulbous, with mesal band of dark spines. Dorsal strap of segment IX arched posterad, with ventro-mesal process (Fig. 320). Main body of segment rectangular, slightly curved, with distinct groove at postero-dorsal angle. Clasper short, slender, with virtually non-existent base; dorsal process with single, dorsally directed distal tooth. Median lobes of segment X black distally, each with two small distal teeth, dorsally and ventrally; lobes vertical, hooked posterad; bases bifid. Cercus triangular, with dorsal angles produced posterad; distal edges with row of prominent, black teeth (Fig. 321). Lateral arms of aedeagus distally fringed with dorsal row of setae directed anterad (Fig. 322, 323).

Female genitalia. (Specimen from Wapta Lake, Kicking Horse Pass, Yoho National Park, British Columbia). Vulval scale with evenly tapered median lobe; lateral lobes widely spaced (Fig. 325). Segment IX with massive, triangular ventro-lateral lobes in contact ventrad of segment X (Fig. 324, 325); dorsal portion of segment small, triangular in dorsal aspect. Supra-genital plate straight-edged in ventral aspect, with triangular distal edge. Segment X small, discrete from segment IX, with deep dorsal cleft, sinuate ventral edge. Cerci large, triangular, close to segment X.

Notes on biology. — Adults of this species are associated with smaller, sedge-fringed ponds and sloughs. The adult flight period extends from July 24 to October 4; I have one record from June 15, also. The peak appears to occur from mid-August to mid-September.

Geographical distribution. — The nearctic range of this holarctic species extends from Great Slave Lake to California and Newfoundland in North America (Fig. 617). In Alberta it occurs in the mountains and plains. It ranges in altitude from 2,000' to 5,340'.

I have examined 276 specimens, 108 males and 168 females, from the study area.

The sericeus group

Males of species of this group are characterised by high, narrow claspers with little or no dorsal process; by long, acute-triangular median lobes of segment X; and by meso-ventrally directed, relatively long, tubular, postero-dorsal process of tergum VIII (Fig. 326). Females of this group are characterised by segment IX without discrete ventro-lateral lobes; by very acuminate dorsal blade of segment X; and by rectangular, free cerci (Fig. 330, 331).

Limnophilus sericeus (Say), 1824
(Fig. 326-331, 618)


Anabolia decepta Banks, 1899:208-209. (Type locality: Washington State).

**Description.** — Antennae yellow-brown. Vertex of head dark chocolate-brown, except for lighter warts. Thorax yellow-brown, with darker areas. Male with very small brushes on anterior femora. Spurs yellow. Fore wing length of male 10.6 mm; light brown, clear areas hyaline. Costal area clear for most of distance to end of costa. Venation with humeral cross-vein either missing in both wings or reduced, otherwise as in *L. sublunatus*.

Male genitalia. (Specimen from Crimson Lake, Alberta). Postero-dorsal process of tergum VIII lengthened to cylindrical column directed meso-ventrad between cerci. Dorsal strap of segment IX narrow, high; main body of segment very slim in lateral aspect, with postero-dorsal angles blunt, curved mesad (Fig. 326). Clasper very acute-triangular with no dorsal process. Median lobes of segment X long, narrow, acuminate blades with dorsal edges dentate, black; attached to mesal edges of basal, convex plates which extend laterad to cerebral bases. Cercus trapezoidal in lateral aspect; mesal edge massively dentate, black. Median shaft of aedeagus short, stout, tapered; distal aspect of tip of median shaft as in Fig. 329. Lateral arm with sclerotized, dorsally rugose base, membranous distal part (Fig. 327); tips lanceolate, fringed with short setae.

Female genitalia. (Specimen from Crimson Lake, Alberta). Vulval scale long, tapered, distally rounded median lobe (Fig. 330); lateral lobes small, with concave ventral faces (Fig. 331). Segment IX without discrete ventro-lateral lobes; larger ventrally, extending postero-ventrad under segment X (Fig. 331). Segment X with tubular body; dorsal edge of anal orifice extended posterd as very thin, black blade (Fig. 331); slightly cleft distally (Fig. 330). Cerci long, quite free from body of segment X; parallel sided in lateral aspect.

**Notes on biology.** — Adults of this species emerge from a variety of habitats, ranging from ponds, lakes or sloughs fringed with sedges, cattail rushes, or horse-tails, to small or large streams and rivers of a quiet or smooth flowing nature. The flight season extends from June 15 to October 3, with no evident peak.

**Geographical distribution.** — The known range of this species extends from Alaska to Oregon, and east to Quebec and the New England States (Fig. 618). In Alberta it is found indiscriminately in the mountains, foothills and plains. In the mountain areas it is found to altitudes of 6,675'.

I have examined 81 specimens, 44 males and 37 females, from the study area.

The luridus group

Males of this group are characterised by minute claspers; by long, narrow cerci; by massive postero-dorsal bulbs of tergum VIII; and by ventrally narrow segment IX (Fig. 332). Females are characterised by massive segment IX without discrete ventro-lateral lobes; by small segment X; and by small, triangular cerci (Fig. 336).
**Limnephilus femoralis** Kolenati, 1848

(Fig. 332-336, 620)


**Description.** – Antennae light brown; scapes and pedicels darker. Vertex of head brown, warts paler. Thorax light to dark brown. Spurs yellow. Fore wing length of male 13.5 mm; light brown, irrorate, Costal area entirely clear. Venation identical to that of *L. sublunatus*.

Male genitalia. (Specimen from Simpson Islands, Great Slave Lake, Northwest Territories). Postero-dorsal edge of tergum VIII developed as massive, globular bulb clothed distally with small, stout, black spines. Dorsal strap of segment IX short, arched posterad; main body of segment roughly triangular in lateral aspect, with very narrow sternum (Fig. 332). Clasper minute, triangular. Median lobes of segment X black, long, acute-triangular, with rugose lateral faces; intermediate lobes of segment X small, cylindrical, black, rugose pegs laterad of median lobes (Fig. 333). Cercus long, narrow, distally rounded, with distal half of mesal faces black, rugose. Lateral arms of aedeagus expanded distally (Fig. 334), with toothed dorsal edges with four heavy setae; distal part fringed with short, dark setae, with thicker setae on mesal faces.

Female genitalia. (Specimen from Simpson Islands, Great Slave Lake, Northwest Territories). Vulval scale broad, triangular, with triangular lateral lobes well separated from blunt, tapered, median lobe (Fig. 335). Segment IX large, curved in lateral aspect; without discrete
ventro-lateral lobes (Fig. 336). Supra-genital plate short, narrow, lunate in ventral aspect. Segment X small, with two triangular dorsal lobes well separated from ventral channel of anal orifice. Cerci short, triangular, closely parallel to dorso-lateral surfaces of segment X; segment X as a whole discrete from segment IX.

**Notes on biology.** — The only collection made by myself was at the Vermilion Lakes, Banff National Park. These lakes are broad, shallow, sedge-fringed, swampy bodies of water. Adult flight season in July (July 1-19).

**Geographical distribution.** — The nearctic range of this holarctic species extends from Alaska to Greenland, Newfoundland, and Washington (Fig. 620), in North America. In Alberta the species appears to be a plains species found in the mountains only in the larger, low valleys. However, records are presently too few to allow proper conclusions.

I have examined 11 specimens, five males and six females, from the study area.

**The nogus group**

Males of the single known species of this group are characterised by wide dorsal strap in lateral aspect (Fig. 337); by narrow ventral region; by median lobes of segment X set dorsad of cerci; and by short claspers with short bases. Females are characterised by lack of discrete ventro-lateral lobes of segment IX (Fig. 340); and by curious triangular ventral lobe formed by fusion of segment IX ventrad of segment X (Fig. 341).

**Limnophilus nogus** Ross, 1944

(Fig. 337-341, 619)


*Limnophilus nogus*; Schmid, 1955:139.

**Description.** — Antennae uniform deep red-brown; antero-mesal faces of scapes without stout, heavy setae. Vertex of head uniform dark red-brown. Thorax dark chocolate-brown. Brush of male fore leg on basal third of femur; of short, black spines. Fore wing length of male 13.3 mm; dark red-brown, irregularly irrorate, with scattered larger hyaline areas. Venation identical to that of *L. sublunatus*.

Male genitalia. (Specimen from Oregon: Illinois Natural History Survey). Main body of segment IX robust, narrowed gradually dorsally and ventrally (Fig. 337); dorsal strap very thin only at meso-dorsal portion (Fig. 338). Clasper small, fused to segment IX; with short base and body; with disto-mesal tooth. Median lobes of segment X long, parallel-sided in lateral aspect; lyre-shaped in dorsal aspect, with distal dilations; attached to rectangular, sclerotized bases dorsad of cerci. Cercus long, narrow, slightly tapered. with disto-mesal tooth. Lateral arms of aedeagus bilobed distally (Fig. 339); dorsal edges of each lobe setose.

Female genitalia. (Specimen from Hosmer, British Columbia). Vulval scale roughly quadrangular (Fig. 341); with acute-triangular lateral lobes, long, rectangular median lobe. Segment IX of single unit; main body vertically narrow; with large, trapezoidal lateral lobes laterad of segment X (Fig. 340); with large, dorsally curved ventro-mesal processes fused ventrad in form of large triangular lobe (Fig. 341). Supra-genital plate wide, very small, short. Segment X massive, with lateral edges folded dorso-mesally to partly enclose dorsal surface of segment; in ventral aspect broad, rectangular plate with sinuate lateral edges and short, mesal cleft (Fig. 341) continued as ventro-mesal channel.

**Notes on biology.** — I have not collected specimens of this species. The only record within
the study area is a single female from Hosmer, British Columbia. The other records available to me from elsewhere indicate a flight season divided into two parts; the earliest flight occurs in May, the second in September and October.

Geographical distribution. — The known range of this species extends from British Columbia to California (Fig. 619). In the study area the single record is from an altitude of about 3,000'.

I have examined 18 specimens, two males and 16 females, from British Columbia. Seventeen of these specimens are from southwestern British Columbia and Oregon.

The sitchensis group

Males of this group are characterised by long, narrow cerci (Fig. 342); by short, wide-based, placoid claspers; by long, wide-based, triangular median lobes of segment X; and by aedeagi with tips of median shaft and lateral arms curved markedly dorsal; tip of median shaft flattened ventrally, occupied by ejaculatory duct pore (Fig. 344). Females are characterised by segment IX with ventro-lateral lobes distinct but not discrete from dorsal body; by large, thumb-like cerci fused solidly to segment IX, directed ventro-posterad along sides of segment X; and by thin walled, tubular segment X (Fig. 346, 353).

**Limnephilus moestus** Banks, 1908
(Fig. 342-346, 621)

*Limnephilus moestus* Banks, 1908b:61, 62. (Type locality: Grand Lake, Newfoundland).


Males of this species are distinguished by exceptionally long cerci (Fig. 342); by massive claspers deeply indented into segment IX; and by presence of lightly setose, incipient postero-dorsal process of tergum VIII. Females are distinguished by cerci projected well posterad of ventral extremity of segment X (Fig. 346); and by short tip to ventro-lateral extension of dorsal body of segment IX.

Description. — Antennae light brown; scapes dark brown, with antero-mesal faces paler, glabrous. Vertex of head dark brown. Thorax light brown, darker dorsally. Spurs yellow. Fore wing length of male 11.6 mm; medium brown. Costal area clear to mid-point of wing. Venation identical to that of *L. sublunatus*.

Male genitalia. (Specimen from Lethbridge, Alberta). Postero-dorsal edge of tergum VIII slightly protuberant, lightly setose. Segment IX overall rather narrow (Fig. 342); dorsal strap relatively thick, with distinct ventro-mesal process; ventral edge of segment with several stout setae. Clasper large, fused to posterior edge of segment IX; directed postero-mesad, with slight basal declivity; with three very distinct, long, black setae on ventral edge. Median lobe of segment X large, triangular (Fig. 342), with swollen bases (Fig. 343); black distally, light brown basally; minutely dentate disto-laterally; attached to mesal edges of basal plates which fit closely with bases of claspers and cerci. Cercus very long, narrow, tapered very gradually distad; mesally concave, with narrow meso-basal shelf (Fig. 343); distal half of mesal surface tuberculate. Median shaft of aedeagus without discrete head (Fig. 344); curved
dorsad, with three minute spines in orifice of ejaculatory duct. Lateral arms bifid basally; mesal branches fused together dorsally across base of median shaft; arms dilated slightly distally, curved dorsad, fringed ventrally and distally with setae.

Female genitalia. (Specimen from Bow Pass, Banff National Park, Alberta). Vulval scale with short, squat, slightly tapered median lobe; lateral lobes each rectangular (Fig. 345). Dorsal body of segment IX small, indistinguishable from segment X (Fig. 346); divided by lateral grooves from much larger, roughly triangular, ventro-lateral processes, with posterior process short. Supra-genital plate very wide, short, with straight posterior edge. Segment X small, tubular, darker than remainder of genitalia; deeply cleft ventrally, with short, v-cleft dorsally (Fig. 345); thin walled. Cerci relatively long, finger-like, dark brown, directed ventro-posterad, beyond ventral extremity of segment X.

Notes on biology. — Specimens of this species emerge from ponds or sloughs dominated by sedges. The adult flight period extends from July 19 to September 12.

Geographical distribution. — The known range of this species extends from British Columbia and Utah to Greenland and Newfoundland (Fig. 621). In Alberta most specimens were collected in the mountains, but I have one record from Lethbridge, well out in the plains. In the mountains it may attain altitudes of up to 6,878'.

I have examined 44 specimens, 35 males and nine females, from the study area and the Northwest Territories.

*Limnephilus cockerelli* Banks, 1900

(Fig. 347-349, 622)


Males of this species are distinguished by wide dorsal strap of segment IX (Fig. 347); by short, parallel-sided, bilobed claspers, with dorsal lobe thick, sharp, and ventral lobe thick, rounded; by short, triangular median lobes of segment X; and by relatively short aedeagus (Fig. 348).

Description. — Antennae brown; scapes darker except for paler, glabrous antero-mesal faces. Vertex of head mottled dark and light brown. Thorax light red-brown; brushes of male fore leg of thin, black spines along basal third of anterior edge of femur. Spurs brown. Fore wing length of male 14.9 mm; light yellow brown, irrorate; anterior half of wing virtually hyaline. Venation identical to that of *L. sublunatus*.

Male genitalia. (Specimen from Eisenhower Junction, Banff National Park, Alberta). Segment IX high, narrow, with wide dorsal strap (Fig. 347); narrow ventrally; postero-lateral angles of segment folded, directed mesal as finger-like process. Clasper articulated to segment IX; distally bilobed, with acuminate dorsal lobe, full, rounded, ventral lobe; setose. Median lobes of segment X black, with dentate disto-lateral faces (Fig. 349); short, triangular in lateral aspect (Fig. 347); attached to lateral edges of two deeply concave basal plates. Cercus long, narrow, parallel-sided, with concave, dentate mesal face. Median shaft of aedeagus curved sharply dorsad to large, slanted tip; lateral arms similarly curved, with slightly expanded tips fringed with setae (Fig. 348) extended part way across lateral faces.

Female genitalia. Unknown.

Geographical distribution. — The known range of this species extends from Alberta, south
along the Rocky Mountains to New Mexico. In Alberta it is known from a single locality, at Eisenhower Junction, Banff National Park, at an altitude of 4,600' (Fig. 622).

I have examined a single male specimen from the study area, in the Canadian National Collection, Ottawa.

*Limnephilus valhalla* Nimmo n. sp.
(Fig. 350-354, 622)

Males of this species are distinguished by exceptionally long cerci, bowed ventrad half way from base (Fig. 350); by distinct spinate process of tergum VIII; and by massive, triangular median lobes of segment X. Females are distinguished by distinct posterior process of ventro-lateral body of segment IX (Fig. 353); and by high, narrow, rectangular dorsal body of segment IX.

*Description.* — Antennae brown; scapes darker, with antero-mesal faces lighter, glabrous. Vertex of head black except for postero-lateral angles. Thorax light red-brown. Brush of male fore leg of thin, dark spines on basal third of anterior face of femur. Spurs yellow. Fore wing length of male 11.6 mm; dark brown, clear areas hyaline. Costal area clear. Venation identical to that of *L. sublunatus*; costa hyaline basad of humeral cross-vein.

Male genitalia. (Specimen from Mt. Edith Cavell, Jasper National Park). Postero-dorsal process of tergum VIII small, hemispherical, with short black spines. Dorsal strap of segment IX high, narrow. Main body of segment small, with postero-dorsal angle directed posterior; with fringe of setae on postero-ventral edge (Fig. 350). Clasper small, fused to segment IX, with several long, irregular setae on posterior edge. Median lobes of segment X with distal halves black; massive, triangular, thin plates. Cercus long, narrow, bowed ventrad at mid-point; slightly concave mesally, with black mesal faces on distal halves (Fig. 351). Median shaft of aedeagus curved strongly dorsad; lateral lobes similar, with distal portion at right angles to basal arm, fringed with setae (Fig. 352).

Female genitalia. (Specimen from Mt. Edith Cavell, Jasper National Park, Alberta). Vulval scale with very broad, short, slightly tapered median lobe (Fig. 354); lateral lobes rectangular, with concave distal faces. Segment IX high, narrow, with acute-triangular processes at postero-ventral angle (Fig. 353). Supra-genital plate short, wide, rectangular. Segment X relatively large, with scalloped posterior edges; lateral edge with large tooth dorsally; deeply cleft dorsally and ventrally (Fig. 354). Cerci short, thumb-like, directed postero-ventrad beside segment X.

*Notes on biology.* — Adults of this species were collected from small, sedge-lined, mountain lakes or pools.

*Geographical distribution.* — This species is known from only two localities; one in Alberta, at an altitude of 6,800'; the second is in British Columbia, at 5,220', 1 mile west of the continental divide (Fig. 622).


*Allotype.* — Female. Same data as holotype.

*Paratypes.* — Same data as holotype; one male, one female. Wapta Lake beaver pond, Kicking Horse Pass, Yoho National Park, British Columbia; August 10, 1967; A. Nimmo; one female.

The type series is in the Canadian National Collection, Ottawa, and has been assigned the number 10,587.

This species is named for 'Valhalla', home for those fallen in battle, as noted in my readings in Norse mythology.
**Limnophilus lopho** Ross, 1949
(Fig. 355-359, 623)


*Description.* — Antennae with basal two-thirds brown; distal third yellow; scapes, pedicels dark brown except for yellow, glabrous, antero-mesal faces of scapes. Vertex of head dark brown between lateral ocelli. Thorax black or dark brown; brush of male fore leg of long, fine, black spines on basal third of femur. Spurs yellow. Fore wing length of male 12.7 mm; brown to dark reddish brown. Costal area clear. Venation identical to that of *L. sublunatus*.

Male genitalia. (Specimen from Mt. Edith Cavell, Jasper National Park, Alberta). Dorsal strap of segment IX high, thick (Fig. 355). Main body of segment roughly triangular, with narrow sternum; anterior edges with distinct flanges. Clasper short, broad, thin plate with rounded tips. Median lobes of segment X large, triangular, black on distal halves, with tips directed dorso-laterally. Intermediate lobes small, rugose, bulbous pegs; black, heavily sclerotized. Cercus thumb-like in lateral aspect, with tip minutely dentate mesally, black (Fig. 356). Median shaft and lateral arms of aedeagus curved sharply dorsad (Fig. 357); lateral arms fringed distally, with short fringe on meso-ventral edges.

Female genitalia. (Specimen from Mt. Edith Cavell, Jasper National Park, Alberta). Vulval scale almost square (Fig. 358); lateral lobes rectangular; median lobe short, narrow, well separated from lateral lobes. Dorsal body of segment IX small, rectangular, separated dorsally from segment X by slight declivity (Fig. 359); ventro-lateral extremities triangular in lateral aspect, fused ventrally. Supra-genital plate wide, very short, sinuate. Segment X in lateral aspect plough-like; deeply cleft ventrally; shallowly but widely cleft dorsally (Fig. 358). Cerci short, broad, rounded lobes located base-laterad to segment X.

*Notes on biology.* — Adults of this species are found adjacent to small alpine pools or seepage slopes heavily clothed with sedges. The flight period extends from July 25 to August 5.

*Geographical distribution.* — The known range of this species extends from Oregon to British Columbia and Alberta (Fig. 623). I have taken it at altitudes of 6,600' and 6,800', on the east slope of Tonquin Valley, and at Mt. Edith Cavell, both in Jasper National Park.

The *assimilis* group

There are two species of this group present in the study area (see Fig. 360, 365). In genitalia characters these two species are so divergent that I cannot provide a list of common characters. Each species is characterised below.

**Limnophilus parvulus** (Banks), 1905
(Fig. 360-364, 623)

**Stenophylax ? parvulus** Banks, 1905:9-10. (Type locality: New Hampshire).

**Parachionia parvulus**; Banks, 1907a:39.

**Hyptontranus ? parvulus**; Ulmer, 1907a:72.


Limnophilus parvulus; Schmid, 1955:141.


Limnophilus pallidus; Fischer, 1968:254.


Males of this species are distinguished from males of other species of Limnophilus by massive, distally toothed claspers; by thin-bladed, black median lobes of segment X which are curved slightly ventrad (Fig. 360); and by lack of postero-dorsal process on tergum VIII. Females are distinguished by discrete ventro-lateral lobes of segment IX; and by small, tapered, thin segment X (Fig. 363).

Description. — Antennae light brown; scapes brown, with paler antero-mesal faces. Vertex of head with two dark areas between lateral ocelli. Thorax medium to light brown. Male fore leg with very slight brush of short, brown spines at base of femur. Spurs pale yellow. Fore wing length of male 10.5 mm; light yellowish brown; clear areas smoky white; coloured areas closely following venation; irrorate. Venation identical to that of L. sublunatus.

Male genitalia. (Specimen from Great Slave Lake, Northwest Territories). Dorsal strap of segment IX wide, with acuminate meso-ventral spine (Fig. 360). Main body of segment large, tapered slightly ventrad, with straight posterior edge, sinuate dorsal edge. Clasper with distodorsal tooth; mesal face of tooth concave, fringed with small, black dentations; base of clasper short. Median lobes of segment X long, tapered, bowed slightly ventrad; lateral faces black, ventral edges minutely dentate; lobes thin, with disto-lateral teeth (Fig. 361). Cercus short, sub-triangular in lateral aspect, fringed distally with long setae. Lateral arms of aedeagus hardly expanded distally, fringed along dorsal edges with setae (Fig. 362).

Female genitalia. (Specimen from Great Slave Lake, Northwest Territories). Vulval scale with distinct, straight base (Fig. 364); lateral lobes simple, curved mesad; median lobe rectangular. Dorsal body of segment IX small, tapered abruptly at junction with segment X (Fig. 363); ventro-lateral lobes large. Supra-genital plate with simple, curved posterior edge; small. Segment X small, long, tapered; deeply cleft mesally (Fig. 364). Cerci acute-triangular in lateral aspect; closely appressed to lateral surfaces of segment X.

Notes on biology. — Adults of this species are associated with lakes and sloughs with a heavy growth of sedges or Typha. The flight season extends from May 25 to July 5.

Geographical distribution. — The known range of this species extends from Alberta and Great Slave Lake to Quebec and New Hampshire (Fig. 623). In Alberta it is found largely in the plains, and in the low, major mountain valleys.

I have examined 38 specimens, 27 males and 11 females, from the study area and Great Slave Lake.

Limnophilus spinatus Banks, 1914 (Fig. 365-369, 624)


Anabolina spinata; Milne, 1935:41, 49.

Males of this species are distinguished from males of other species of Limnophilus by very
long base of the clasper (Fig. 365); by high, thin, dorso-anteriorly hooked, acuminated median lobes of segment X; and by presence of small, black-spinate, postero-dorsal lobe of tegum VIII. Females are distinguished by very massive ventro-lateral lobe of segment IX (Fig. 369); by minute dorsal body of segment IX; and by postero-ventrally slanted segment X.

**Description.** — Antennae dark brown; scapes dark chocolate-brown, with antero-mesal faces lighter, setaless. Vertex of head uniform dark brown. Thorax light brown, with darker areas. Brush of male fore leg well developed, of short, stout, black spines along entire length of femur. Spurs yellow. Fore wing length of male 10.8 mm; warm chocolate-brown. Costal area entirely clear. Venation identical to that of *L. sublunatus*.

Male genitalia. (Specimen from Hound Creek, 25 miles southeast of Cascade, Montana). Tergum VIII with small, black-spinate, postero-dorsal process. Dorsal strap of segment IX directed postero-dorsal (Fig. 365). Main body of segment of irregular outline, narrowed ventrad. Clasper with very high, narrow base, with long, thin, dorso-posteriorly directed dorsal process. Median lobes of segment X square in lateral aspect, with postero-dorsal angles produced as long, anteriorly curved, acuminated spines; lobes attached to mesal edges of rectangular, basal plates (Fig. 366). Cercus squat, distally rounded, with concave mesal face. Lateral arms of aedeagus very long, slender, spiniform (Fig. 367).

Female genitalia. (Specimen from Crowsnest Pass, 8 miles west of Coleman, Alberta). Vulval scale with broad, abruptly tapered median lobe (Fig. 368); lateral lobes with blunt lateral horns. Segment IX with minute dorsal body (Fig. 369), massive ventro-lateral lobes of indeterminate form. Segment X large, of two sets of sclerites; basal set longer, rectangular; distal set short, each roughly triangular in lateral aspect. Supra-genital plate wide, short, with almost straight posterior edge.

**Notes on biology.** — Adults of this species were found near small ponds or sloughs, and slow streams. The flight period extends from July 25 to August 30.

**Geographical distribution.** — The known range of this species extends from Alberta to California and Colorado (Fig. 624). In Alberta specimens have been collected in the plains and low mountain valleys of the southwestern corner of the province.

I have examined 22 specimens, 21 males and one female, from the study area and Montana (one male).

The *incisus* group

Four species of this group are known from the study area. As with the *assimilis* group there appears to be no significant community of characters to define the group (Fig. 370-398).

*Limnephilus hyalinus* Hagen, 1861

(Fig. 370-374, 627)


Males of this species are distinguished by close conjunction between distal edge of each median lobe of segment X and black line of teeth on mesal face of each cercus (Fig. 370, 371). Females are distinguished by scoop-shaped ventro-median lobes of segment IX (Fig. 373), which are discrete from dorsal body of segment; by large, triangular dorsal body of segment IX; and by long, thin cerci flanked laterally by latero-dorsal lobes of segment X.

Description. — Entire body and wings very pale, straw-yellow; warts, and costal area of fore wings almost white. Fore wing length of male 9.8 mm. Venation identical to that of L. sublunatus.

Male genitalia. (Specimen from Vermilion, Alberta). Postero-dorsal edge of tergum lightly setose. Dorsal strap of segment IX relatively short, thick. Main body of segment relatively narrow, slightly narrowed ventrad (Fig. 370). Clasper short, with wide base; triangular in lateral aspect. Median lobes of segment X short, distal halves black, tapered slightly distad (Fig. 371); distal edges vertical, straight, coincident with vertical line of black teeth on mesal faces of cerci. Cercus widened distad, slightly concave mesally, with vertical row of black teeth at mid-point of mesal face. Lateral arms of aedeagus long, expanded distad (Fig. 372), each with dorsal spine basad of membranous, irregular distal half.

Female genitalia. (Specimen from Manyberries, Alberta). Vulval scale almost circular, with curved, parallel-sided lateral lobes (Fig. 373), longer, tapered, median lobe. Segment IX with large, triangular dorsal body, larger, scoop-shaped, discrete, ventro-lateral lobes (Fig. 374). Supra-genital plate small, evenly rounded distally. Segment X composed of two dorso-lateral, rectangular lobes laterad of long, thin cerci, with small ventral lobe.

Notes on biology. — Adults of this species are found near sloughs and lakes which are thickly vegetated with sedges and cattail rushes. The flight season extends from July 5 to September 24, with a possible peak in August.

Geographical distribution. — This species is transcontinental, extending from Alaska to Oregon, Colorado, Illinois, and Newfoundland (Fig. 627). In the study area it occurs throughout the plains regions, and through the mountains along the low, major valleys reaching altitudes of 5,200'.

I have examined 91 specimens, 48 males and 43 females, from the study area and Great Slave Lake.

*Limnophilus secludens* Banks, 1914
(Fig. 375-379, 625)

*Limnophilus secludens* Banks, 1914:152. (Type locality: Penticton, British Columbia).


Males of this species are distinguishable by very short, membranous, distally spinate lateral arms of aedeagus (Fig. 377). Females are distinguished by short, tubular segment X with short, peg-like cerci solidly fused to dorso-lateral surfaces of segment (Fig. 378, 379).

Description. — Antennae brown; scapes lighter, setaless on antero-mesal faces. Vertex of head dark brown; lighter laterally. Thorax dark reddish brown; brush of male fore leg of short, black spines along full length of femur; opposing face of tibia with corresponding brush. Spurs very long, yellow-brown. Fore wing length of male 14.2 mm; light yellow-brown with darker areas; costal area clear except for slight distal darkening. Venation identical to that of L. sublunatus.
Male genitalia. (Specimen from Lethbridge, Alberta). Dorsal strap of segment IX short, with ventro-mesal process connected to segment X (Fig. 375, 376). Main body of segment tall, narrow, rectangular in lateral aspect. Clasper high, narrow, tapered, ventrad, acutetriangular. Median lobes of segment X short, narrow, black; tips directed dorso-laterad. Cercus short, irregular, deeply concave mesally. Median shaft of aedeagus with straight, thick basal portion (Fig. 377); distal third turned sharply dorsad, thin, narrow, acuminate. Lateral arms short, stubby, membranous; each with cluster of short, black spines distally.

Female genitalia. (Specimen from Lethbridge, Alberta). Vulval scale with median lobe longer than lateral lobes, tapered from wide base (Fig. 379); lateral lobes concave ventrally; Mesal edges sinuate, black. Dorsal body of segment X distinguished from segment X by posterior declivity (Fig. 378); ventro-lateral lobes almost separated from dorsal body; large; with straight, angular edges. Supra-genital plate squat, triangular. Segment X large, tubular, with minor dorsal and ventral projections. Cerci short, finger-like, fused solidly to dorso-lateral faces of segment X.

Notes on biology. — Adults of this species are found near lakes and sloughs with heavy growths of sedges and cattail reeds. The flight period extends from June 3 to September 23, with a possible peak in late July and August.

Geographical distribution. — The known range of this species extends from Great Slave Lake to Wisconsin, New Mexico, and California (Fig. 625). In Alberta it seems to be restricted to the plains, with occasional records from the foothills.

I have examined 372 specimens, 178 males and 194 females, from the study area and Great Slave Lake.

_Limnephilus janus_ Ross, 1938
(Fig. 380-384, 626)


_Limnephilus janus_ Ross, 1938:37. (Type locality: Tolland, Colorado). Ross, 1944:299.

_Limnophilus janus_; Schmid, 1955:140.

Males of this species are distinguished by high, very thin dorsal strap of segment IX (Fig. 380); by large, relatively long cerci with concave mesal faces and irregular dorso-mesal edges (Fig. 381); and by long, distally thin and acuminate median lobes of segment X. Females are distinguished by trilobed dorsal shield of segment X; and by absence of discrete ventro-lateral lobes of segment IX (Fig. 383).

Description. — Antennae pale yellow. Vertex of head pale yellow-brown, with dark areas adjacent to ocelli. Thorax pale yellow with some slightly darker areas. Brush of male fore leg composed of black spines along basal two-thirds of femur. Spurs pale yellow. Fore wing length of male 7.2 mm; greyish white, with scattered brown areas tending to follow veins. Vention identical to that of _L. sublunatus_.

Male genitalia. (Specimen from 6 miles south of Elk Point, Alberta). Dorsal strap high, narrow, with sharp dorsal edge (Fig. 380). Main body of segment IX wide, with distinct antero-ventral bulge. Clasper short, with short base; almost rectangular with dorso-distal tooth. Median lobes of segment X long, thin, each with wide base abruptly narrowed to thin distal process with tip directed dorso-laterad (Fig. 381). Cercus long, with disto-dorsal edge curled mesal, irregular, black. Aedeagus simple, with short, tapered median lobe, and long, dorsally curved, distally expanded, acuminate lateral arms, clothed on ventral edges with
setae (Fig. 382).

Female genitalia. (Specimen from 6 miles south of Elk Point, Alberta). Vulval scale with wide based, strongly tapered median lobe (Fig. 384); lateral lobes large, with concave lateral faces. Segment IX large, with no separate ventro-lateral lobes (Fig. 383). Supra-genital plate rectangular, set well ventrad of segment IX to which it is connected by band of folded membrane. Segment X large, separate from segment IX, with cylindrical ventral portion surmounted by trilobed dorsal roof, with lateral lobes.

Notes on biology. — I have collected specimens of this species only in the vicinity of large or small, shallow, sedge-edged lakes, ponds or sloughs. The flight season extends from July 12 to September 13, with peak about mid-August.

Geographical distribution. — This species is known from Alberta, Saskatchewan, Minnesota, and Colorado (Fig. 626). In Alberta it is a species of the plains and low foothills.

I have examined 40 specimens, 20 males and 20 females, from Alberta and Saskatchewan.

**Limnephilus perpusillus** Walker, 1852

(Fig. 385-389, 628)


**Anabolina perpusilla**; Betten, 1934:338.

**Anabolina perpusilla**; Betten and Mosely, 1940:140-142.

**Colpotaulius rhaeus** Milne, 1935:42, 50. (Type locality: Guelph, Ontario). Milne, 1936:60.


Males of this species are distinguished by small postero-dorsal, spinate lobe of tergum VIII (Fig. 385); by square median lobes of segment X with postero-dorsal angles developed as anteriorly hooked spines; and by large, black spine on dorso-mesal edge of cerci (Fig. 285, 386). Females are distinguished by massive, fleshy ventral body of segment IX (Fig. 388); and by vertically oriented segment X.

Description. — Antennae light reddish brown; scapes and pedicels darker, antero-mesal faces setaceous. Vertex of head with circular dark brown area between lateral ocelli. Thorax light brown, with darker areas. Brush of male fore leg composed of short, fine black spines along entire length of femur. Spurs yellow. Fore wing length of male 7.9 mm; light yellowish brown; very lightly irrorate in posterior regions. Costal area entirely clear. Venation identical to that of *L. sublunatus*.

Male genitalia. (Specimen from camp 3 miles east of Nordegg, Alberta). Postero-dorsal edge of tergum VIII with small, free, black-spinate lobe. Dorsal strap of segment IX narrow (Fig. 385). Main body of segment narrow, tapered ventrad; tapered dorsal to merge gradually with dorsal strap. Clasper with very long, narrow base produced dorso-posterad as finger-like dorsal process. Median lobes of segment X with square bases; postero-dorsal angles produced dorso-anterad as short, slender, hooked spines. Cercus short, triangular in lateral aspect, with dorso-mesal edge curled ventrad with single large spine (Fig. 385, 386).
Median shaft of aedeagus simple, short, tapered; lateral arms curved dorsad, each with distally expanded, acuminate tip fringed along ventral edge with setae (Fig. 387).

Female genitalia. (Specimen from pond 10 miles south of McLeod River, Forestry Trunk Road, Alberta). Vulval scale with squat, short median lobe tapered distad (Fig. 389). Lateral lobes almost rectangular, with deep channel on mesal edge of each lobe. Dorsal body of segment IX small; ventro-lateral extensions massive, fused ventrally (Fig. 388, 389). Supragenital plate membranous, lunate, of two wide lateral plates fused ventrally to form channel, with short, narrow, distal extension. Cerci short, thin, almost rectangular lobes attached between lateral plates of segment X.

Notes on biology. — Specimens of this species are collected near ponds with large quantities of sedge or bullrushes, or smaller creeks. The flight season extends from July 2 to September 6.

Geographical distribution. — The known range of this species extends from Alberta to Colorado and Newfoundland. In Alberta it occurs primarily in the plains and low foothills (Fig. 628).

I have examined 12 specimens, three males and nine females, from the study area.

The argenteus group

Males of the single species in this group are characterised by presence of spinate postero-dorsal lobe of tergum VIII; by large segment IX with short dorsal strap; by short, broad claspers; and by long, narrow, evenly tapered median lobes of segment X (Fig. 390). Females are characterised by discrete ventro-lateral lobes of segment IX; by segments IX and X being fused; and by minute, thin cerci (Fig. 394).

**Limnophilus argenteus** Banks, 1914


Description. — Antennae brown; scapes with anteromesal faces lighter, almost glabrous. Vertex of head with two dark brown areas mesad of lateral ocelli. Thorax brown with darker areas. Spurs light brown. Fore wing length of male 16.8 mm; light to dark brown, irrorate, clear areas very pale brown, not hyaline. Costal area sparingly irrorate. Venation identical to that of *L. sublunatus*.

Male genitalia. (Specimen from Vermilion Lakes, Banff). Postero-dorsal edge of tergum VIII produced posterd as small, black-spinate bulb. Dorsal strap of segment IX short, with sharp dorsal edge (Fig. 390). Main body of segment massive, irregular. Clasper short, broad, very stout, with short base. Median lobes of segment X long, narrow at bases, tapered evenly to acuminate tips; curved dorso-lateral (Fig. 391). Cercus short, almost square in lateral aspect, with wide baso-mesal extension dorsally; concave mesally. Median shaft of aedeagus attached to folded, membranous base, curved dorsad (Fig. 392); lateral arms straight basally, curved dorsad distally to expanded, flared, mesally concave tips.

Female genitalia. (Specimen from Worsley, Alberta). Vulval scale large, trapezoidal in general outline (Fig. 393); median lobe long, gradually tapered; lateral lobes thin, arched laterad. Dorsal body of segment IX small, fused imperceptibly to segment X (Fig. 394); ventro-lateral lobes discrete from dorsal body, high, narrow. Supra-genital plate large, evenly
rounded distally. Segment X small, distally dark; deeply narrowly cleft mesally (Fig. 393). Cerci two minute, thin, papillate structures attached to dorsal surface of segment X.

**Notes on biology.** — The single record which I have of this species from the study area is from large, sedge marshes just west of Banff, Alberta. The dates of capture in Alberta range from July 1 to July 12.

**Geographical distribution.** — The known range of this species extends from Alaska to Illinois and Ontario (Fig. 629).

I have examined 10 specimens, two males and eight females, from the study area and Great Slave Lake.

The **alberta** group

The single species known in this group is characterised by high, narrow segment IX (Fig. 395), with virtually no dorsal strap; by short, slender, tapered claspers; and by massive, thick, heavily sclerotized cerci (Fig. 396). Females are characterised by high, narrow segment IX (Fig. 400); and by vulval scale almost completely demarcated from sternum VIII (Fig. 401).

**Limnephilus alberta** Denning, 1958

*(Fig. 395-401, 629)*


**Description.** — Antennae dark brown; scapes with pale, glabrous antero-mesal faces. Vertex of head very dark brown, warts paler. Thorax dark brown; warts very pale. Spurs yellow. Fore wing length of male 14.9 mm; light brown, with darker areas; clear areas mostly hyaline. Costal area clear on basal two-thirds. Venation identical to that of **L. sublunatus**.

Male genitalia. (Specimen from 11 miles west of Banff, on Trans-Canada Hwy.). Dorsal strap of segment IX virtually non-existent (Fig. 395). Main body of segment sinuate, widened gradually dorsad from narrow ventral area. Clasper small, narrow, tapered, finger-like, with very short base. Median lobes of segment X small, trapezoidal, slanted dorso-mesad (Fig. 396). Cercus rectangular in lateral aspect, tapered basad from flat, black distal face, in dorsal aspect (Fig. 397). Median shaft of aedeagus short, stout, with large, discrete, distal head (Fig. 398). Lateral arms curved smoothly dorsad, not widened, each fringed along mesal face with long setae (Fig. 398, 399).

Female genitalia. (Specimen from 11 miles west of Banff, on Trans-Canada Hwy.). Vulval scale with angular anterior edge, almost separate from sternum VIII (Fig. 401); median lobe long, acute-triangular; lateral lobes stout, close to median lobe. Segment IX high, narrow, with slightly wider ventro-fataler area (Fig. 400). Supra-genital plate short, broad, suspended from segment IX by wide, wrinkled membrane. Segment X with hemi-cylindrical ventral portion short, and dorsal, mesally flattened, dorsally deeply cleft portion (Fig. 401) much longer, tapered. No evident cerci.

**Notes on biology.** — Specimens of this species are found near sedge lakes, ponds, and sloughs. The flight period extends from July 5 to September 10.

**Geographical distribution.** — The known range of this species is restricted largely to the continental divide area of Alberta and British Columbia (Fig. 629). In altitude it ranges from about 3,700' to 5,350'.

I have examined 28 specimens, eight males and 20 females, from the study area.
The *asiaticus* group

Males of this group are characterised by presence of postero-dorsal lobe on tergum VIII; by large, smooth tooth on dorso-mesal edge of cercus; and by wide-based claspers, with short, stout dorsal processes (Fig. 402). Females are distinguished by massive segment IX of single piece, without ventro-lateral lobes; and by massive, short lobed vulval scale (Fig. 406, 407).

*Limnephilus labus* Ross, 1941

(Fig. 402-407, 630)


**Description.** — Antennae reddish brown, scapes darker. Vertex of head dark brown between ocelli and posteral to posterior edge of cranium. Thorax reddish brown; brush of male fore leg composed of dense, stout, black setae along entire length of femur. Spurs reddish. Male fore wing length 9.5 mm; grey-brown, with darker areas close to posterior edge. Costal area clear to distal end of subcosta. Venation identical to that of *L. sublunatus*.

Male genitalia. (Specimen from Waterton, Alberta). Postero-dorsal edge of tergum VIII with small, thin, spinate lobe. Dorsal strap of segment IX short, wide (Fig. 402); main body of segment high, narrow, with anterior lobes; with short, blunt peg at postero-dorsal angles. Clasper with rectangular dorsal process and high, narrow base. Median lobes of segment X with broad bases tapered abruptly to small, acuminate postero-dorsal hooks. Cercus with very concave mesal face, with dorsal edge arched meso-ventrad (Fig. 403); with large, smooth, black spine. Median shaft of aedeagus long, irregular, curved dorsad (Fig. 404); lateral arms long, each curved sharply dorsad at mid-point, with expanded, acuminate distal lobe fringed ventrally with long setae (Fig. 404, 405).

Female genitalia. (Specimen from Waterton, Alberta). Vulval scale with massive, short lobes (Fig. 407); lateral lobes rectangular; median lobe very broad, blunt, with very little space between it and lateral lobes. Segment IX massive, of one rectangular piece (Fig. 406); segment X completely enclosed. Supra-genital plate very wide, short. Segment X distinct from segment IX; dorsal surface steep, terminated in two small, black-tipped dorsal lobes. Cerci large, stout, attached to dorsal surface of segment X; short, blunt.

**Notes on biology.** — Adults of this species are found near sedge or cattail ponds, lakes or sloughs. A very few (three) records indicate that this species may also inhabit rivers and smaller creeks. The flight season extends from July 25 to September 13, with a possible peak in late August.

**Geographical distribution.** — The known range of this species extends from Alberta and Saskatchewan to Idaho and Colorado (Fig. 630). In Alberta it is confined to the southern and central plains and lower foothills.

I have examined 40 specimens, 23 males and 17 females, from the study area.

The *fenestratus* group

Diagnostic genitalic characters are not available because of a too great diversity. Two species of the group are known from the study area.
Limnephilus minusculus (Banks), 1907
(Fig. 408-413, 631)

Stenophylax minusculus Banks, 1907b:120. (Type locality: Olympia, Washington). Banks, 1907a:39.


Algonquina minuscula; Milne, 1935:31, 49.


Limnophilus minusculus; Schmid, 1955:139.

Males of this species are distinguished from males of other species of Limnephilus by presence of postero-dorsal lobe of tergum VIII; by warped cerci with mesal projection and cross-axial ventral ridge (Fig. 408, 409); and by form of aedeagus. especially lateral arms (Fig. 410). Females are distinguished by single unit segment IX; by discrete segment X; and by double-lunate groove ventrad of segment X as seen in ventral aspect (Fig. 412, 413).

Description. — Antennae very dark brown; scapes darker. Vertex of head black. Thorax very dark brown; brush of male fore leg sparse, only on basal third of femur. Spurs dark yellow. Fore wing length of male 8.4 mm; pale chocolate-brown; costal area clear. Venation identical to that of L. sublunatus.

Male genitalia. (Specimen from Flatbush, Alberta). Postero-dorsal edge of tergum VIII with prominent, lightly spinate lobe. Dorsal strap of segment small, relatively narrowed, especially ventrally. Clasper short, with very short base; tapered evenly to rounded tip; directed postero-dorsad. Median lobes of segment X small, thin plates, with black tips; with wide bases, narrowed abruptly to small dorsal hooks; basal plates square, concave (Fig. 409). Cercus small, slender in lateral aspect, with tip at right angles, directed mesad, with black, dentate ventral edge (Fig. 409). Median shaft of aedeagus short, stout, tapered, with slightly dilated tip (Fig. 410, 411); lateral arms long, with very slender, sclerotized basal halves; distal halves membranous, extensible, with zigzag at bases; fringed distally, mostly on dorsal edges, with long setae (Fig. 410).

Female genitalia. (Specimen from Flatbush, Alberta). Vulval scale large, with short, stout median lobe, rectangular lateral lobes with groove along each median face (Fig. 413). Segment IX of one piece, roughly rectangular (Fig. 412); with slight postero-ventral lobes. Supra-genital plate membranous, wide, short, rectangular except for posteriorly indented edge. Segment X very small, discrete from segment IX in lateral aspect; tubular, short. Cerci short, dorso-ventrally flattened, rounded in ventral aspect; fused solidly to segment X.

Notes on biology. — Adults of this species are found associated with sedge or cattail reed sloughs or small lakes, and small streams or rivers on gravel beds. The flight season extends from May 25 to July 16, with peak in late June and early July.

Geographical distribution. — The known range of this species extends from Alaska to Washington, Colorado, New York, and Labrador (Fig. 631). In Alberta it is confined to the plains, low foothills, and major, low mountain valleys, up to about 4,500' altitude.

I have examined 106 specimens, 93 males and 13 females, from the study area.

Limnephilus kennicotti Banks, 1920
(Fig. 414-420, 632)

Fischer, 1968:199.

**Limnophilus kennicotti**; Schmid, 1955:139.

Males of this species are distinguished by massive claspers with very long bases (Fig. 414), mesally directed, thin, body (Fig. 418), and black-toothed dorsal edges. Females are distinguished by massive, mesally cleft dorsal body of segments IX and X combined (Fig. 419, 420).

**Description.** — Antennae dark brown; scapes darker, with pale, setaless, antero-mesal faces. Vertex of head very dark brown, warts paler. Thorax very dark brown, warts paler. Spurs brownish yellow. Fore wing length of male 8.9 mm; light brown; costal margin clear to end of subcosta; clear areas white. Venation identical to that of *L. sublunatus*.

Male genitalia. (Specimen from Canmore, Alberta). Dorsal strap of segment IX equal in height to main body; wide. Main body of segment very wide dorsally, narrowed ventrad (Fig. 414); with slight concavities at postero-ventral margins. Clasper massive, thin, directed mesad; with dorsal edges black-toothed (Fig. 418). Median lobes of segment X large, long, with wide bases tapered distad to rounded tips; very wide in dorsal aspect, with low, black-toothed ridge just basad of tips (Fig. 415). Cercus large, long, arched dorsal in lateral aspect; with slight declivity on mesal face, produced mesad as triangular ledge (Fig. 415). Median shaft of aedeagus long, slender; lateral arms shorter, slender, sclerotized, attached to dorsal surface of aedeagus; each with cluster of three spines distally, spines crossed over dorsal surface of aedeagus (Fig. 416, 417).

Female genitalia. (Specimen from Lethbridge, Alberta). Vulval scale small, with short, distally rounded median lobe (Fig. 420); lateral lobes very small, irregular, narrow, directed postero-laterad. Segment IX with discrete ventro-lateral lobes (Fig. 429); dorsal body indistinguishable from segment X. Supra-genital plate large, rectangular, visor-like in lateral aspect. Segment X massive, solidly fused to segment IX; rectangular in lateral aspect, with meso-dorsal hooks distally; in ventral aspect of two large, quite separate plates (Fig. 420).

**Notes on biology.** — Adults of this species are found near lakes and rivers. The flight period extends from June 24 to October 3, with a possible peak in August and September.

**Geographical distribution.** — The known range of this species extends from British Columbia to Newfoundland, and north to Greenland (Fig. 632). In Alberta it is found both on the plains, and in the foothills and mountains, to altitudes of about 6,675'.

I have examined 45 specimens, 10 males and 35 females, from the study area.

The **nigriceps** group

Males of the single species of this group are characterised by massive segment IX with short, narrow, dorsal strap (Fig. 421); by massive claspers with large, heavily sclerotized, black, dorsal tooth; and by small, light-coloured median lobes of segment X (Fig. 422). Females are characterised by discrete ventro-lateral lobes of segment IX (Fig. 426); and by solid, large segment X and dorsal body of segment IX fused.

**Limnophilus nigriceps** (Zetterstedt), 1840

(Fig. 140a, 140b, 421-426, 633)

**Phryganea nigriceps** Zetterstedt, 1840:1066. (Type locality: Lapland).


Limnophilus affinis Hagen (not Curtis), 1858. (See Fischer, 1968:245, for Palaearctic literature).

Limnophilus affinis; Fischer, 1968:245.

Pryganea pilosula (See Fischer, 1968:245).

Limnophilus pilosulus; (See Fischer, 1968:245).

Chaeotalius striola Kolenati. (See Fischer, 1968:245, 246, for Palaearctic literature).

Limnophilus striola; (See Fischer, 1968:246, for Palaearctic literature).

Limnophilus striola; (See Fischer, 1968:245-246, for Palaearctic literature).


Description. — Antennae dark brown; scapes black in males, pale yellow in females; antero-mesal faces paler, setaeless. Vertex of head black except for paler warts. Thorax deep black; brush of male fore leg composed of short, stout, black spines on basal half of femur. Spurs yellow. Fore wing length of male 11.6 mm; pale brown; anterior half of wing clear, posterior half irrorate. Venation of fore and hind wings as in Fig. 140a, 140b; R2 of hind wing with row of short, black hairs on ventral surface.

Male genitalia. (Specimen from Exshaw, Alberta). Postero-dorsal edge of tergum VIII lightly setose. Dorsal strap of segment IX short, curved posterad (Fig. 421). Main body of segment massive, widened ventrad, with postero-dorsal angle rounded, large. Clasper massive, short, wide, with large, black, heavily sclerotized disto-dorsal tooth. Median lobes of segment X small, directed dorso-posterad, with slight lateral hooks at tips (Fig. 422). Cercus large, parabolic, with large, black, heavily sclerotized disto-mesal tooth (Fig. 422, 423). Lateral arms of aedeagus long, slender, sclerotized, spinate distally, curved sharply dorsad (Fig. 424); large, wing-like, spinate, lobe on disto-ventral margin.

Female genitalia. (Specimen from Exshaw, Alberta). Vulval scale relatively small, with short, slender, tapered median lobe (Fig. 425); lateral lobes large, roughly triangular. Ventrolateral lobes of segment IX discrete, large, irregular in outline (Fig. 426). Dorsal body of segment indistinguishable from massive segment X. Supra-genital plate triangular, large. No evident cerci.

Notes on biology. — Adults of this species are found near small sedge ponds or sloughs. The flight season is from August 23 to September 22.

Geographical distribution. — The nearctic range of this holarctic species extends from Alaska to Alberta and Manitoba (Fig. 633). In Alberta I have collected specimens in the foothills and mountains, in the low valleys.

I have examined 20 specimens, 15 males and five females, from the study area.

The rhombicus group

Males of this group are characterised by postero-dorsal lobe on tergum VIII; by large, curved claspers with black, heavily sclerotized distal teeth; and by relatively small median lobes of segment X. Females are characterised by long distinct cerci; discrete ventro-lateral lobes of segment IX; and by separate segment X.

Limnophilus rhombicus (L.), 1758
(Fig. 427-432, 634)

Phryganea rhombica Linnaeus, 1758:548. (Type locality: Sweden). (See Fischer, 1968: 270-294, for Palaearctic literature).
Phryganea rhomboides; (See Fischer, 1968:271).

Friganea rhomboea; (See Fischer, 1968:271).

Chaetotaulis rhombicus; (See Fischer, 1968:272-273, for Palaeartic literature).

Limnephila rhombica; (See Fischer, 1968:272).

Limnophila rhombica; (See Fischer, 1968:282, 283).

Leimnephila rhombica; (See Fischer, 1968:274).


Limnophlus rhomnicus; (See Fischer, 1968:278).


Description. — Antennae yellow-brown. Vertex of head uniformly deep red-brown. Thorax uniform reddish brown; brush of male fore leg composed of fine, reddish hairs along basal half of anterior face of femur. Fore wing length of male 17 mm; reddish brown, partly irrorate, with large, irregular, hyaline areas. Vein A3 of fore wing dark brown, with heavy vestiture of stout, brown setae. Venation identical to that of L. sublunatus.

Male genitalia. (Specimen from 2 miles west of Lake Louise, Alberta). Postero-dorsal edge of tergum VIII extended sharply ventrad as rectangular, slightly bulbous, black-spinate screen (Fig. 427, 428). Dorsal strap of segment low, wide vertically; main body of segment stout, narrowed ventrad. Clasper small, with high, narrow base; dorsal process triangular. Median lobes of segment X small, short, black, with square-cut tips directed postero-lateral. Cercus massive, long, arched dorsad, with parallel sides; distal edge straight in lateral aspect, with ventral edge black, heavily sclerotized, dentate (Fig. 428). Lateral arms attached dorsally on adeagal base; distally bifid; ventral lobe large, flap-like, fringed dorsally (Fig. 429) with long spines; dorso-median lobes folded mesad, armed with several stout, black, distal teeth (Fig. 429, 430).

Female genitalia. (Specimen from Whitehorse. Yukon; in Canadian National Collection, Ottawa). Vulval scale large, deeply imbedded in sternum VIII (Fig. 432); median lobe short, truncate-triangular; lateral lobes clavate in ventral aspect. Ventro-lateral lobes of segment IX large, roughly triangular in lateral aspect (Fig. 431), discrete from dorsal body of segment; dorsal body small, triangular in dorsal aspect. Supra-genital plate large, semi-circular, hyaline. Segment X separable from segment IX; long, tubular, shallowly cleft mesad; with shallow groove on dorso-lateral surfaces, ventrad of cercal bases. Cerci long, with wide bases each abruptly tapered at mid-point.

Notes on biology. — The single male specimen examined was probably taken in the sedge sloughs just west of Lake Louise townsite, in Banff National Park. Date of capture was July 20.
Geographical distribution. — The nearctic range of this holarctic species extends from Yukon Territory to Colorado, Illinois, Newfoundland and Greenland (Fig. 634).

The diversus group

Males of this group are characterised by black-spinate, postero-dorsal lobes of tergum VIII; by short, stout, triangular, thick cerci and median lobes of segment X; and by wide-based claspers with long, distally heavily sclerotized, black-toothed tips (Fig. 433). Females are characterised by discrete, ventro-lateral lobes of segment X; and by segment X separate from segment IX (Fig. 438).

Limnophilus canadensis Banks, 1908
(Fig. 433-438, 635)


Limnophilus canadensis; Schmid, 1955: 142.

Description. — Antennae dark brown; scapes darker, with antero-mesal faces yellow, glabrous. Vertex of head dark brown, faded to brownish yellow lateral of lateral ocelli. Thorax dark brown; brush of male fore leg along entire length of femur; anterior tibiae with similar brushes on opposing faces. Spurs yellow, to brown. Fore wing length of male 7.0 mm; light reddish brown; costal area clear to end of subcosta; clear areas white; dark areas irrorate. Venation identical to that of L. sublunatus.

Male genitalia. (Specimen from Nordegg, Alberta). Postero-dorsal edge of tergum VIII with slender, prominent, black-spinate lobe. Dorsal strap of segment IX short, sharp edged dorsally (Fig. 433); main body of segment wide, narrowed ventrad, with sinuate dorsal edges. Clasper with high, narrow base; dorsal process long, directed dorsal, with distal edge black, heavily sclerotized, with two distinct teeth. Median lobes of segment X small, short, triangular, wide (Fig. 433, 434). Cercus similar, with dorsal angle setose, with long setae. Median shaft of aedeagus long, tapered, with distinct head; lateral arms shorter, expanded distally, acuminate, with disto-ventral edges fringed with short setae (Fig. 435, 436).

Female genitalia. (Specimen from Athabasca River, Grosmont, Alberta). Vulval scale rectangular (Fig. 437); median lobe short, tapered from wide base; lateral lobes longer, rectangular, each with slight distal widening. Dorsal body of segment IX small, high, narrow, with postero-dorsal process (Fig. 438); ventro-lateral lobes discrete, large, irregular. Supra-genital plate roughly rectangular, with squat triangular distal edge. Segment X large, tubular, conical in ventral aspect (Fig. 437), black disto-dorsally. No evident cerci.

Notes on biology. — Adults of this species are found near lakes, and slower, smoothly flowing rivers. The flight period extends from June 9 to August 12.

Geographical distribution. — The known range of this species extends from Alberta to Maine (Fig. 635). In Alberta it is confined to the plains or low foothills.

I have examined 12 specimens, five males and seven females, from the study area.

The Genus Clistoronia Banks

One species of this genus is known from the study area; it belongs to the subgenus
Clistoronia Banks.

Synopsis of characters. — Cephalic macrochaetae short, fine, sparse; pronotal macrochaetae very strong, abundant. Spur formula 1,3,3. Wings large; fore wings clearly widened at chord, truncated apically; hind wings rather narrow. Fore wing coloration varied, quite patchy. Fore wing venation much as in Limnephilus spp. but chord weakly disrupted, almost straight, oblique anteriorly; f3 narrowed basally. Hind wing chord strongly disrupted, distinctly concave to body.

Male genitalia with tergum VIII non-spinate. Segment IX very short, high (Fig. 439); postero-lateral angles prominent, support to segment X mesally. Cerci large, strong, heavily sclerotized; in lateral aspect triangular, bilobed distally. Median lobes of segment X spur-like, horizontal. Clasper weakly developed; distal portion long, conical, simple, directed mesad. Aedeagus large; median shaft much folded basally (Fig. 442); lateral arms spinate, each simple or bilobed.

Female genitalia with dorsal body of segment IX vestigial. Ventro-lateral lobes of segment IX quite large, convex plates, in close contact ventrally (Fig. 443, 444). Supra-genital plate large, ogival, prominent. Segment X varied, short, long, slender. Cerci or cercus-like lobes large, strongly flattened dorso-ventrally, fused to segment IX, or segment X, which is immediately ventrad. Median lobe of vulval scale varied in size; lateral lobes sub-quadrangular or rounded (Fig. 444).

Clistoronia magnifica (Banks), 1899
(Fig. 439-444, 635)

Clistoronia magnus; Banks, 1916:119.
Stenophylax magnificus; Milne, 1935:32, 52.
Limnephilus magnificus; Ross and Merkley, 1952:441, 451.
Anabolia caroli Denning, 1941b:196-197. (Type locality: Robson, British Columbia).
Limnephilus caroli; Ross, 1944:298.

Males of this species are distinguished from males of other species of Limnophilidae by large, triangular cerci (Fig. 439); by fused median lobes of segment X (Fig. 440); and by mesally directed black teeth on mesal faces of cerci. Females are distinguished by long, thin, acuminate dorsal lobes of segment X, ventro-mesad of cerci (Fig. 443).

Description. — Antennae yellow-brown; antero-mesal faces of scapes with few setae. Vertex of head deep red-brown. Thorax deep reddish brown. Fore wing length of male 18.1 mm; light chocolate-brown, irrorate, with larger hyaline areas. Venation identical to that of Limnephilus spp.

Male genitalia. (Specimen from Waterton, Alberta). Dorsal strap of segment IX very slim, incomplete dorsally (Fig. 439). Main body of segment vertically narrow, moderately expanded laterally, with postero-dorsal angles produced mesad as long, narrow processes. Clasper with narrow base, dorsal process long, tapered, acute-triangular in lateral aspect. Median lobes of segment X fused throughout length (Fig. 440), conical, rounded. Cercus massive, thick, triangular in lateral aspect, with short ventral tooth; mesal face with black, heavily sclerotized tooth. Median shaft of aedeagus short, stout, curved gently dorsad (Fig. 442); lateral arms parallel to median shaft, greatly widened distally; each distally bilobed, with
dorsal lobe longer, narrower, more acuminate than ventral. Both lobes fringed with setae.

Female genitalia. (Specimen from Waterton, Alberta). Vulval scale with squat, conical median lobe; lateral lobes triangular distally, well clear of median lobe (Fig. 444). Dorsal body of segment IX small, fused to segment X (Fig. 443); ventro-lateral lobes large, triangular in lateral aspect, fused ventrad of segment X; not discrete from dorsal body. Suprateginal plate small, semi-circular. Segment X large, tubular, deeply cleft laterally, not so deeply in vertical plane; dorsal lobes long, narrow; ventral lobes shorter, wide, darker. Cerci short, acuminate in lateral aspect, wide in ventral aspect.

Notes on biology. — Adults of this species are collected near sedge lakes or ponds. The flight period extends from June 11 to August 16, with a peak in mid-July.

Geographical distribution. — The known range of this species extends from Alberta and British Columbia to Utah (Fig. 635). In Alberta it is confined strictly to the area of the continental divide, but in the lower major valleys.

I have examined 17 specimens, 13 males and four females, from the study area.

The Genus Grammotaulius Kolenati

This genus is represented in the study area by a single species.

Synopsis of characters. — Head somewhat elongated, eyes small. Posterior cephalic warts very large, oval. Posterior ocelli surrounded by many hairs. Spur formula 1,3,4. Pronotum at least half as long as head. Wings large; fore wings uniformly, or patchily coloured. R5 of fore wing darkened in some species; always so on hind wing. Chord of fore wings very oblique anteriorly to body, not strongly disrupted. Hind wing chord parallel to body, strongly disrupted.

Male genitalia rigid, very large. Tergum VIII not spinate. Segment IX long longitudinally and vertically. Cerci very thick, to very large, slender; in some species short, massive, thick; dentate. Claspers poorly developed, not projected. Aedeagus very thick, similar to that of Limnephilus; lateral arms not erectile or setose, but simple or bilobed.

Female genitalia without discrete ventro-lateral lobes; dorsal body of segment IX narrow, elongated, with two free appendages. Segment X tubular, very large, short, sclerotized, barely cleft or mesally. Supra-genital plate small. Vulval scale large, with three large, sub-equal, projected lobes in most species.

Grammotaulius interregationis (Zetterstedt), 1840
(Fig. 445-450, 636)


Limnophilus interregationis; Walker, 1852:19.

Limnophilus interregationis; Hagen, 1861:254-255. (See Fischer, 1967:213, for Palaeartic literature).


Limnophilus praecox; Ross, 1941a:110.

Description. — Antennae light brown; scapes cream-white with glabrous antero-mesal faces. Vertex of head with black mesal diamond limited by lateral ocelli and median warts; remainder cream-white. Thorax black, shaded in areas to dark brown. Spurs brown. Fore wing length of male 20.9 mm; chocolate-brown to light reddish brown. Hind wing stigma light brown; R5 set in light brown band. Venation essentially identical to that of Limnophilus sublunatus.

Male genitalia. (Specimen from Wapta Lake, Kicking Horse Pass, Yoho National Park, British Columbia). Segment IX massive, rectangular; dorsal strap short, narrow to point of extinction dorsally (Fig. 445). Clasper small, blunt, short. Median lobes of segment X very small, short, with meso-dorsal black edges (Fig. 446). Cercus huge, thick, armed with heavily sclerotized teeth along distal edge; with ventral, black tooth directed postero-mesal. Median shaft of aedeagus simple. Lateral arms long, expanded slightly distally, each with two distal lobes (Fig. 447, 448); basal or dorsal lobe minute, with distal tuft of spines; ventral lobe large, lanceolate, fringed dorsally with short spines.

Female genitalia. (Specimen from Banff, Alberta). Vulval scale massive, triangular (Fig. 450); median lobe short, parallel-sided, lateral lobes with narrow bases, widened distally. Segment IX large, inseparably fused to segment X dorsally; ventral lobes much larger, with straight edges (Fig. 449). Supra-genital plate short, broad, with evenly curved posterior edge. Segment X relatively small, short, with pair of meso-lateral lobes. No evident cerci.

Notes on biology. — Adults of this species are found near sedge ponds, lakes or sloughs, and mountain streams of a turbulent and rocky nature. Flight season of the adults extends from July 4 to September 27.

Geographical distribution. — The nearctic range of this holarctic species extends from Yukon Territory to British Columbia, Minnesota, Nova Scotia, and Greenland (Fig. 636). In Alberta it is confined to the foothills and mountains, ranging in altitude from 4,500' to 6,800'.

I have examined 25 specimens, 13 males and 12 females, from the study area.

The Genus Nemotaulus Banks

A single species, of the subgenus Macrotaulus, is known from the study area.

Synopsis of characters. — Eyes quite small. Head quite elongate, with toothed ridge along occipital border. No cephalic warts present. Pronotum twice length of head in certain species. Spur formula 1,3,4. Fore wings coriaceous, apically indented (Fig. 141a). Hind wings very large, slightly indented. Fore wings very reddened, not irrorate. Venation of fore wings with very large discoidal cell; chord feebly disrupted, hardly oblique to body; hind wings similar.

Male genitalia with postero-dorsal edge of tegum VIII developed as large, black-spinate bulb. Segment IX usually large, well developed laterally. Claspers of medium size, massive in appearance, thick, concave, unarmed, not close to border of segment IX. Aedeagus large, strong, similar to that of Limnophilus spp.; lateral arms non-erectile, simple, fringed distally with setae or spines.

Female genitalia with dorsal part of segment IX narrowed, triangular, weakly developed; no free appendages. Segment X continuous with segment IX, tubular; short, massive, poorly cleft mesally. Ventro-lateral lobes of segment IX huge, largely contiguous ventrally. Supra-genital plate small. Vulval scale very large, plate-like, entirely flanked by sternum VIII; median lobe very small, sunk between two sub-quadrangular lateral lobes.
Nimmo

*Nemotaulius hostilis* (Hagen), 1873

(*Fig. 141a, 141b, 451-455, 637*)


**Description.** — Antennae brown; scapes darker, with antero-mesal faces pale, almost glabrous. Vertex of head deep red-brown; flat, evenly covered with large pustulate bumps. Thorax pale yellow, with slightly darker areas laterally; dorsal areas flat, pustulate. Spurs yellow. Fore wing length of male 22.8 mm; grey-brown to almost black in mixture of solid blocks of colour, and irrorate areas. Costal area hyaline except for slight basal irroration. Venation as in Fig. 141a, 141b; distal edge of fore wing crenulate.

Male genitalia. (Specimen from George Lake, near Busby, Alberta). Postero-dorsal edge of tergum VIII developed as large, black-spinate bulb. Dorsal strap of segment IX short; complex, of sclerotized flanges merged gradually with main body (Fig. 451). Main body of segment high, spindle-shaped, not wide. Clasper with long, narrow base; dorsal process massive, short, thick; claw-like distally. Median lobes of segment X small, short, dorso-laterally hooked spines (Fig. 451, 452). Cercus small, wide, lobe without mesally concave face. Aedeagus large, with simple median shaft (Fig. 453); lateral arms long, with wide bases and distal tips; tips acuminate, fringed on edges with long setae.

Female genitalia. (Specimen from George Lake, near Busby, Alberta). Vulval scale relatively small, with very short, rounded, median lobe, massive, triangular lateral lobes (Fig. 455). Dorsal body of segment IX and segment X solid tapered tube, deeply cleft dorsally (Fig. 454). Ventro-lateral lobes of segment IX huge, discrete from dorsal body, irregular, fused solidly ventrally. Supra-genital plate small, triangular, membranous with sclerotized edges.

**Notes on biology.** — Adults of this species are found near lakes and sloughs overgrown with sedges or, particularly, cattail reeds. The flight period extends from June 3 to August 10.

**Geographical distribution.** — The known range of this species extends from Alaska to Colorado and Newfoundland (Fig. 637). In Alberta it is confined to the plains region.

I have examined 39 specimens, 28 males and 11 females, from the study area.

The Genus Anabolia Stephens

This genus is represented in the study area by three species.

**Synopsis of characters.** — Cephalic warts small, pronotum somewhat elongate. No dorsal line. Spur formula 1,3,4. Fore wings large, slightly truncated, rounded, or parabolic apically; hind wings variable in size. Coloration of wings characteristic, fairly constant; fore wings reddish brown, with no hyaline or darker areas; uniformly coloured or minutely irrorate. Venation somewhat variable; chord rectilinear, anteriorly oblique, weakly disrupted, concave to body; hind wing chord posteriorly oblique, disrupted.
Male genitalia with tergum VIII non-spinate. Segment IX generally well developed laterally, rigid, sclerotized; dorsal strap slender, with blunt elongate, median process in some species, dentate in most species. Median lobes of segment X more or less triangular, sclerotized lamellae. Claspers with slender, pad-like basal part fused to segment IX, sometimes twisted helically; dorsal process horizontal, slender, cylindrical. Aedeagus large; median shaft short, thick, folded at base; lateral arms slender, normally bilobed, spinate.

Female genitalia very stubby, not projected. Segment IX of two pieces in lateral aspect; dorsal part small, with appendages which are free, or fused at base of segment X. Segment X small, conical, cleft vertically. Ventro-lateral lobes of segment IX very large, massive, contiguous or separated ventrally. Supra-genital plate small. Vulval scale variable.

**Key to the Males of species of Anabolia found in Alberta and eastern British Columbia**

1a. Median shaft of aedeagus very short, stubby, with distal head recessed into basal part (Fig. 458) ................................................................. A. consocia (Walker), p. 125.

1b. Median shaft of aedeagus long, slender (Fig. 463, 468) ........................................ 2a

2a.(1b) Clasper with minute dorsal process and high, very slender base (Fig. 461) ................................................................. A. ozburni (Milne), p. 126.

2b. Clasper with large, conical, black-tipped dorsal process (Fig. 466) ................................................................. A. bicaculata (Walker), p. 127.

**Key to the Females of species of Anabolia found in Alberta and eastern British Columbia**

1a. Segment X with cerci or cercus-like lobes; vulval scale with median lobe longer than lateral lobes (Fig. 459, 460, 469, 470) ................................................................. 2a

1b. Segment X without such lobes; median lobe of vulval scale not longer than lateral lobes (Fig. 464, 465) ................................................................. A. ozburni (Milne), p. 126.

2a.(1a) Ventro-lateral lobes of segment IX massive, fleshy, with triangular posterior edge (Fig. 459) A. consocia (Walker), p. 125.

2b. Ventro-lateral lobes of segment IX small, roughly rectangular in lateral aspect, except for triangular postero-ventral lobe projected well posterad under segment X (Fig. 469) ................................................................. A. bicaculata (Walker), p. 127.

*Anabolia consocia* (Walker), 1852
(Fig. 456-460, 638)

*Limnephilus* (Goniotaullus) consocius Walker, 1852:33. (Type locality: North America).


*Goniotaullus consocius*; Hagen, 1864:815.


**Arctoecia conscia**; Sibley, 1926:107.

**Arctoecia conscia**; Muttkowski and Smith, 1929:259.


**Limnephilus medialis**; Ross, 1938b:36. Ross, 1944:190, 298.

Males of this species are distinguished from males of other species of the genus by short, blunt median shaft of aedeagus (Fig. 458) with distal head recessed into basal portion; by distally flared, black-edged claspers with deeply concave mesal faces (Fig. 456, 457); and by rectangular median lobes of segment X. Females are distinguished by massive, fleshy, ventrolateral lobes of segment IX (Fig. 459), with triangular posterior edge; by minute dorsal body of segment IX; and by median lobe of vulval scale slender, tapered, much longer than lateral lobes (Fig. 460).

**Description.** — Antennae yellowish brown. Vertex of head red-brown, with mesal longitudinal stripe of dark brown. Thorax pale yellow; with mesal longitudinal stripe of dark brown along terga. Thoracic warts fragmented to individual setal bases in some specimens. Male anterior femur without brush. Spurs pale yellow. Fore wing length of male 14.1 mm; light brownish yellow; faintly irrorate basally; veins irregularly darkened. Venation identical to that of *Limnephilus* spp.

Male genitalia. (Specimen from Cold Creek, Nojack, Alberta). Dorsal strap of segment IX with dorso-mesal process lightly setose (Fig. 456). Main body of segment wide dorsally, tapered gradually ventrad. Clasper small, with high, narrow base; dorsal process short, originated gradually from base, with distally black, clawed tip. Median lobes of segment X large, rectangular in lateral aspect, thick in dorsal aspect (Fig. 457), with distal third black; basal plates large, complexly folded. Cercus massive, distal edge black, with disto-ventral angle attenuated as black tooth (Fig. 457). Median shaft of aedeagus short, stout, with wrinkled base (Fig. 458); distal head recessed into basal body. Lateral arms stout, curved dorsal, tapered slightly distad; distally fringed on dorsal and ventral edges with short setae.

Female genitalia. (Specimen from Chicago, Illinois; in Illinois Natural History Survey). Vulval scale large; median lobe longer than lateral lobes (Fig. 460), narrow, evenly tapered distad; lateral lobes curved, widened distad, with concave mesal faces. Dorsal body of segment IX minute, narrow, strap-like (Fig. 459); ventro-lateral lobes massive, fleshy, with triangular posterior edges, discrete from dorsal body. Supra-genital plate small, wide, tapered posterad, truncated distally; convex ventrally. Segment X completely cleft ventro-mesally, dorsally two edges joined by sheet of membrane (Fig. 460); triangular in lateral aspect. Cerci roughly triangular, held closely to dorso-lateral faces of segment X; fused solidly to segment X.

**Geographical distribution.** — The known range of this species extends from Alberta to Virginia and Quebec (Fig. 638). The two records from Alberta available to me are from the plains region, at about 2,100'.

I have examined two specimens of this species from the study area, one adult and one pupal male. I have also examined a female from Illinois.

*Anabolia ozburni* (Milne), 1935

(Fig. 142a, 142b, 461-465, 639)

*Arctoecia ozburni* Milne, 1935:39, 49. (Type locality: Guelph, Ontario).

Males of this species are distinguished from males of other species of Anabolia by massive, thick cerci (Fig. 461); by minute dorsal process of claspers; and by dorso-mesal process of dorsal strap large, projected well posterad (Fig. 462). Females are distinguished by large segment IX fused solidly to segment X dorsally (Fig. 464); and by lack of cerci or cercus-like lobes.

Description. — Antennae dark brown; scapes very dark, with antero-mesal faces lighter, glabrous. Vertex of head very dark brown. Thorax dark to very dark brown. Spurs yellow. Fore wing length of male 10.8 mm; light reddish brown, irrorate; costal area clear. Venation as in Fig. 142a, 142b; leading edge of fore wing truncate and R1 straight to edge, not bowed. Hind wing with deep indentation at Cu.

Male genitalia. (Specimen from Cold Lake, Cold Lake, Alberta). Dorsal strap of segment IX laterally narrow, dorsally expanded to large triangular, horizontal plate with single seta in distal clear area. Main body of segment robust, narrowed abruptly ventrad (Fig. 461). Clasper with high, very narrow base surmounted by minute dorsal process. Median lobes of segment X massive, triangular, with distal halves black; tips hooked laterad as small teeth (Fig. 462). Cercus massive, rectangular in lateral aspect, with distal face wide, black, fringed with setae; attached to wide internal bases. Median shaft of aedeagus long, narrowed slightly at mid-point (Fig. 463), expanded to folded distal head. Lateral arms each of uniform width for two-thirds length, then widened slightly to thin, spatulate tip cleft distally as two acuminate spines; dorsal and ventral edges of tips setose; mesal faces with pair of heavy spines.

Female genitalia. (Specimen from Michigan; in Illinois Natural History Survey). Vulval scale small, with rectangular median lobe (Fig. 465); lateral lobes with concave mesal edges curved, lateral edges distinctly angular. Dorsal body of segment IX large, wide, fused to segment X dorsally, but divided from it ventradly by suture (Fig. 464). Ventro-lateral lobes of segment IX massive, almost square in lateral aspect, discrete from dorsal body of segment. Supra-genital plate minute, short, not projected laterally beyond distal extremities of lateral lobes of vulval scale. Segment X cylindrical internally, triangular in lateral aspect, with dorsal edges of mesal cleft sinuate; median cleft deep, with dorsal cleft angular, ventral cleft rounded (Fig. 465).

Geographical distribution. — The known range of this species extends from Alberta to Quebec, New Hampshire and Michigan (Fig. 639). In Alberta it is known only from Edmonton and Cold Lake to the northeast; both are plains localities, and Cold Lake is in the boreal forest region.

I have examined two males from the study area, and one female from Michigan. Dates of capture of the Alberta specimens were July 11 and 17.

Anabolia bimaculata (Walker), 1852
(Fig. 466-470, 640)
Limnephilus (Desmotaullus) bimaculatus; Hagen, 1861:263.
Desmotaulius bimaculatus; Hagen, 1864:811. 
Anabolia maculata; Dodds and Hisaw, 1925a: Fig. 1. Balduf, 1939:121. 
Males of this species are distinguished from males of other species of Anabolia in the study area by conical dorsal processes of claspers with black tips; by dorsal strap of segment IX without dorso-mesal process; and by small, triangular median lobes of segment X (Fig. 466). Females are distinguished by relatively small ventro-lateral lobes of segment IX with small, triangular ventro-posterior lobes; by ventro-lateral lobes in contact mesally (Fig. 470); and by small, low, dorsal body of segment IX (Fig. 469). 
Description. — Antennae brown; antero-mesal faces of scapes paler, glabrous. Vertex of 
head dark brown. Thorax dark brown dorsally but with paler meso-longitudinal line; laterally 
pale yellow. Spurs pale brown. Fore wing length of male 15.8 mm; deep chocolate-brown 
to pale yellowish brown; lightly irrorate; costal area clear, pale yellow. Venation not signifi-
cantly different from that of Limnephilus spp. 
Male genitalia. (Specimen from George Lake, near Busby, Alberta). Dorsal strap of 
segment IX short, slender, directed anterad (Fig. 466). Main body of segment roughly inverted-
triangular. Clasper with long, narrow base; dorsal process short, conical, heavily sclerotized, 
black distally. Median lobes of segment X short, triangular, black distally, each with minute 
disto-lateral tooth (Fig. 467). Cercus of medium size, rounded-triangular distally; with con-
cave mesal face, thick base. Median shaft of aedeagus slender, tapered evenly distad, with 
distinct distal head small (Fig. 468); lateral arms shorter than median shaft, each basally 
curved sharply dorsad, divided distally to long, acuminate dorsal lobe and small, triangular 
ventral lobe; short setae located only along edge between lobes. 
Female genitalia. (Specimen from George Lake, near Busby, Alberta). Vulval scale with 
three lobes well separated (Fig. 470); median lobe longer than laterals, conical in ventral 
aspect, rugose at base; lateral lobes with channelled mesal faces. Dorsal body of segment IX 
small, with short, triangular, dorsal extension; main part of dorsal body fused to segment X 
(Fig. 469). Ventro-lateral lobes of segment IX relatively small, rectangular in lateral aspect 
except for triangular postero-ventral angles; discrete from dorsal body. Segment X of irregu-
lar outline in lateral aspect; distally acuminate, deeply cleft mesally. Cerri short, fused at 
bases to dorso-lateral surfaces of segment X. Supra-genital plate small, rectangular. 
Notes on biology. — Adults of this species are found near cattail sloughs, lakes, or ponds, 
or smaller, quietly flowing, rivers and creeks. The flight period extends from June 11 to 
August 29 with a possible peak at end of July and beginning of August. 
Geographical distribution. — The known range of this species extends from Great Slave 
Lake to British Columbia, New Mexico, Michigan, and Maine (Fig. 640). In Alberta it is 
fairly ubiquitous throughout the plains and lower major mountain valleys. 
I have examined 417 specimens, 274 males and 143 females, from the study area. 
The Genus Asynarchus McLachlan 
This genus is represented in the study area by three species belonging to two groups. 
Synopsis of characters. — Head slightly elongate; eyes not prominent. Dorsal line barely
visible. Spur formula 1, 3, 4. Pronotum short. Wings of normal size, shortened in female of some species and cold adapted forms. Fore wings much as in *Limnephilus* spp. but more expanded at chord; hind wings somewhat larger than fore. Fore wings basically brown, with small irruptions and larger clear areas at thyridial cells, chord, and distally along M4+5.

Male genitalia with tergum VIII non-spinate. Segment IX laterally strongly convex and sclerotized. Cerci medium to large, varied; in certain species slender, strongly concave; distal edge heavily sclerotized, mesal faces with massive tooth or ridge in some species. Median lobes of segment X small, ventrad of cerci. Claspers with prominent basal pieces fused to segment IX; distal processes bifid, pincer-like, black. Aedeagus large, quite similar to that of *Limnephilus* spp.; lateral arms slender, bilobed.

Female genitalia with dorsal body of segment IX short, inconspicuous; with two large, laterally flattened, appendages fused basally to each other in some species. Segment X ventrad of these appendages; with thin, hardly cleft walls. Ventro-lateral lobes of segment IX huge, high, massive; in most species contiguous meso-ventrally. Supra-genital plate large. Vulval scale partly recessed into sternum VIII; lateral lobes long, oblique straps.

**Key to the Males of species of Asynarchus found in Alberta and eastern British Columbia**

1a. Clasper very large, blade-like, triangular (Fig. 471); median lobes of segment X large, triangular; dorsal strap relatively wide ........ *A. mutatus* (Hagen), p. 129.

1b. Claspers small, distally bifid (Fig. 476, 482); median lobes of segment X small hooks; dorsal strap very narrow ........................................ 2a

2a.(1b) Cercus hooked meso-ventrad distally, with second, ventral, black tooth distinct (Fig. 482) ....................... *A. aldinus* (Ross), p. 131.

2b. Disto-dorsal angle of cercus triangular in lateral aspect (Fig. 476), not divided from disto-ventral angle .............. *A. curtus* (Banks), p. 130.

**Key to the Females of species of Asynarchus found in Alberta and eastern British Columbia**

1a. Segment IX a single, massive unit, grossly enlarge ventrad (Fig. 474) .................. *A. mutatus* (Hagen), p. 129.

1b. Segment IX with clear, almost discrete ventro-lateral lobes (Fig. 480) .................. *A. curtus* (Banks), p. 130. *A. aldinus* (Ross), p. 131.

The *contumax* group

A single species of this group is known in the study area.

Males of this group are distinguished by short, thin-walled, mesally concave cerci; and by massive median lobes of segment X. Females are distinguished by very large ventro-lateral lobes of segment IX; and by narrow, oblique lateral lobes of vulval scale.

*Asynarchus mutatus* (Hagen), 1861
(Fig. 471-475, 641)


*Stenophylax mutatus*; Betten, 1934:345.


Males of this species are distinguished from males of other species of Asynarchus by large, triangular, blade-like claspers (Fig. 471); by high, short, triangular median lobes of segment X; and by short, irregular cerci. Females are distinguished by massive, unit segment IX (Fig. 474) which completely encircles segment X (Fig. 475).

Description. — Antennae brown; antero-mesal faces of scapes darker, glabrous. Vertex of head dark brown, warts yellowish. Thorax warm yellowish brown. Brush of fore leg of male slight, on basal third of femur only. Spurs dark brown. Fore wing length of male 15.0 mm; dark brownish grey, irrorate, with larger patches of solid colour; two major areas of clear membrane just distad of chord and immediately anterad of Cu1+2; veins of chord darker than others. Venation identical to that of Limnephilus spp.

Male genitalia. (Specimen from George Lake, near Busby, Alberta). Dorsal strap of segment IX simple, broad; main body of segment almost elipsoidal. Clasper long, thin, triangular blade with black tip (Fig. 471). Median lobes of segment X short, with denticulate dorsal edges; distal areas black, each with distinct disto-lateral tooth (Fig. 472). Cercus short, with cup-like disto-mesal faces, black, toothed posterior edges. Median shaft of aedeagus tapered slightly distad; directed postero-dorsad from base (Fig. 473); lateral arms curved in semi-circle, each with lanceolate, spinate distal lobe; two small, spatulate lobes on ventral edge of each arm; each lobe distally fringed with stout spines.

Female genitalia. (Specimen from Indian Head, Saskatchewan). Vulval scale with short, conical median lobe (Fig. 475); lateral lobes long, narrow, tapered, directed postero-lateral, well separated from median lobe. Segment IX massive, of one piece; dorsal portion slightly narrowed; ventral portion swollen, fused ventrad of segment X (Fig. 474, 475). Supra-genital plate very wide, short, hyaline. Segment X very short, tubular, not cleft. Cercal lobes not evident.

Notes on biology. — Adults of this species are found near sedge and cattail sloughs and lakes. The flight season extends from June 3 to July 23.

Geographical distribution. — The known range of this species extends from British Columbia to Great Slave Lake, Minnesota and Ontario (Fig. 641). In Alberta it is confined to the plains and eastern edges of the foothills in the lower valleys.

I have examined 11 males of this species from the study area and Great Slave Lake, and a female from Saskatchewan.

The lapponicus group

Two species of this group are known from the study area.

Males of this group are distinguished by large, projected, lanceolate cerci; and by small median lobes of segment X. Females are distinguished by discrete ventro-lateral lobes of segment IX; and by large, triangular lateral lobes of vulval scale.

Asynarchus curtus (Banks), 1920
(Fig. 476-481, 642)


Males of this species are distinguished from males of other species of Asynarchus by short, distally bifid claspers; by massive, disto-ventrally toothed claspers (Fig. 476); and by unclef distal edge of claspers. Females are distinguished by partially separate ventro-lateral lobes of segment IX (Fig. 480); and by laterally cleft segment X, with wide, triangular dorsal cerci. Females of this species are, however, inseparable from those of A. aldinus, except by association with the male in the field.

The males are of the form batchewana Denning (syn., conerus Ross) and differ consistently from the eastern curtus as illustrated by Ross (1950b). The synonymy followed here is that of Schmid (1952c), although Ross and Denning still consider batchewana a distinct species (in litt.).

Description. — Antennae clothed with black hairs, of overall dark brown colour; scapes clear yellow, glabrous. Vertex of head dark brown except for narrow area mesad of compound eyes. Thorax reddish brown, with intermixed darker areas. Brush of male fore leg sparse, pale, confined to basal quarter of femur. Spurs reddish yellow. Fore wing length of male 14.8 mm; red-brown, irrorate, with very few larger areas clear. Costal area also irrorate. Venaion identical to that of Limnephilus spp.

Male genitalia. (Specimen from Gorge Creek beaver pond, 20 miles west of Turner Valley, Alberta). Dorsal strap of segment IX short, narrow (Fig. 476). Main body of segment massive, with narrow sternal area. Clasper short, stout, distally bifid, black. Median lobes of segment X small, distally hooked dorsad, black. Cercus massive, with heavy longitudinal ridge along mesal face (Fig. 477); distally black. Median shaft of aedeagus long, curved dorsad from base (Fig. 478); lateral arms shorter, with disto-dorsal lobe long, scythe-like, curved dorso-anterad; with small ventral lobe setose (Fig. 479).

Female genitalia. (Specimen from Gorge Creek beaver pond, 20 miles west of Turner Valley, Alberta). Vulval scale large, with narrow median lobe slightly longer than large, triangular, lateral lobes (Fig. 481). Dorsal body of segment IX small, wide, partially separated from segment X (Fig. 480); ventro-lateral lobes large, rectangular, partially discrete from dorsal body. Supra-genital plate wide, incised on posterior edge, partly sunken in ventral depressions of segment IX. Segment X small, shallowly incised laterally, deeply incised dorsad; tubular. Cerci massive, set well dorsad of segment X, blunt distally.

Notes on biology. — Adults of this species are found in a wide variety of habitats, from small plains sloughs and lakes, to high mountain pass bogs, and smaller, quieter creeks. The flight period extends from July 5 to Sept. 25, with peak about the beginning of September.

Geographical distribution. — The known range of this species extends from Alaska to Colorado and Labrador (Fig. 642). In Alberta it is found throughout the plains, foothills, and mountains, to altitudes of around 7,350'.

I have examined 246 specimens, 96 males and 150 females, from the study area and Great Slave Lake.

Asynarchus aldinus (Ross), 1941
(Fig. 482-483, 643)


Males of this species are distinguishable from males of *A. curtus* by lateral aspect of cerci, with meso-distal angle separated from ventral tooth by lunate cleft, in form of distinct, postero-ventrally hooked tooth (Fig. 482). Females can only be determined in association with males.

*Description.* — Antennae light brown, with yellow, glabrous stripe along antero-mesal faces of scapes. Vertex of head dark brown, with lighter mesal band joining area between compound eyes with postero-mesal warts. Thorax warm reddish brown; terga lighter dorsally. Brush of male fore leg of short, black spines in narrow band on basal third of femur. Spurs yellow. Fore wing length of male 11.2 mm; brownish grey, sparsely irrorate. Venation identical to that of *Limnephilus* spp.

Male genitalia. (Specimen from Bow Pass, Banff-Jasper Hwy., Alberta). Dorsal strap of segment IX very narrow, short. Main body of segment large, angular, almost trapezoidal (Fig. 482). Clasper large, short, stout; distal extremity black, bifid; base long, tapered ventrad. Median lobes of segment X small, hooked dorsad distally. Cercus massive, with large ventro-distal tooth produced basad along mesal face (Fig. 483); in lateral aspect dorso-mesal extremity separated from ventral tooth as postero-ventrally curved hook (Fig. 482). Aedeagus essentially identical to that of *A. curtus*.

Female genitalia. This sex is known (Nimmo, 1965), but is indistinguishable from female of *A. curtus*.

*Notes on biology.* — Adults of this species are found in high alpine meadow and mountain pass areas, emerging from shallow, quiet pools or streams in sedge meadows. The flight period extends from July 25 to August 27.

*Geographical distribution.* — The known range of this species extends from Great Slave Lake to Idaho (Fig. 643). In Alberta it attains altitudes of up to 7,000'.

I have examined 16 specimens, eight males and eight females, from the study area.

*Asynarchus lapponicus* Zetterstedt, 1840

This species has been reported recently from the study area (Clifford, 1969), but I have been unable to confirm the record as the specimens involved are missing. Therefore I do not include full details on this species, but draw the reader's attention to the above record, and refer to Schmid (1954b:78-81) for figures and full description.

The Genus *Philarctus* McLachlan

A single species of this genus is known from the study area.

*Synopsis of characters.* — Head rather elongate, eyes and cephalic warts small. Antennae thick, shorter than wings. Anterior femora of male very thick; anterior tibiae equally thick, slightly flattened, each terminated by ridge; both clothed with brushes of stout spines along opposing faces; apical spur short, flat, triangular. Spur formula 1,3,4. Wings various in size; some species with *Limnephilus*-like wings; others quite shortened, apically parabolic. Coloration dark brown. Venation of fore wing with chord weakly disrupted, slightly oblique; hind wing chord strongly disrupted, parallel to body.

Male genitalia with well developed segment IX; dorsal strap short, wide, setose. Cerci very large, bulky, strongly sclerotized, fused ventrad of anal aperture and located laterad of it. Intermediate lobes of segment IX triangular or horizontal discs, ventrad of cerci. Claspers well developed, with long, slender dorsal process. Aedeagus similar to *Limnephilus* spp.; lateral arms very slender, expanded distally, finely spinate.

Female genitalia with dorsal body of segment IX short, blunt, projected, expanded laterad
Philarctus Limnephilus Colpotaulius peripherally.

at base; ventro-lateral lobes quite small, not contiguous ventrally. Supra-genital plate large, short. Segment X large, blunt, thick, weakly sclerotized, pilose; deeply cleft tube, more or less open ventrally. Cerci large, prominent, free. Median lobe of vulval scale long, narrow; lateral lobes short, thick, sub-quadrangular.

*Philarctus quaeris* (Milne), 1935

(Fig. 484-489, 644)


*Description.* — Antennae dark brown; antero-mesal faces of scapes yellow-brown, glabrous. Vertex of head dark reddish brown in triangular area between three ocelli; lighter peripherally. Thorax light brown laterally, dorsally. Brush of male fore leg confined to distal three-quarters of femur; anterior tibia also with brushes on entire length of opposite face. Spurs reddish brown. Fore wing length of male 8.7 mm; dark chocolate-brown, heavily irrorate; costal area hyaline throughout. Venation identical to that of *Limnephilus* spp.

Male genitalia. (Specimen from 17 miles north of Langdon Corner, on Hwy. 9, Alberta). Dorsal strap high, wide (Fig. 484); heavily setose. Main body of segment irregular in lateral aspect, with low, triangular postero-dorsal angles. Clasper with parallelogram-like base surmounted by short, thin, acuminate dorsal process. Median lobes of segment X not evident. Ventrad of dorsally fused cerci are two placoid lobes which appear to be intermediate lobes (Fig. 484, 485). Cercus large, fused at base to segment IX; distally acuminate plate fused dorsally as roof to anal passage. Median shaft of aedeagus long, very slender, with distinct, long distal head (Fig. 486, 487); lateral arms shorter, slightly expanded from narrow bases to shovel-like distal blades concave on mesal faces.

Female genitalia. (Specimen from 17 miles north of Langdon Corner, on Hwy. 9, Alberta). Vulval scale with roughly rectangular median lobe; lateral lobes triangular, close to median (Fig. 489). Dorsal body of segment IX high, narrow, distinct from segment X (Fig. 488); ventro-lateral lobes small, irregular, flap-like. Supra-genital plate trapezoidal. Segment X tubular, with lateral bulges; slightly cleft mesally; recessed slightly into segment IX. Cerci short, narrow, fused at base, projected clear of remainder of segment X.

*Notes on biology.* — Adults of this species are found near sedge and horse-tail sloughs or lakes of the plains or low mountain valleys. The flight period extends from June 18 to September 13, with a peak toward the end of August.

*Geographical distribution.* — The known range of this species extends from Great Slave Lake to Oregon, Colorado, and Minnesota (Fig. 644). In Alberta it is known from the plains and low mountain valleys.

I have examined 142 specimens, 69 males and 73 females, from the study area.

The Genus *Arctopora* Thomson

Schmid (1952c) erected the genus *Lenarchulus* to contain two species, with *Phryganea trimaculata* Zetterstedt as type species. Fischer (1966) pointed out that in fact Thomson (1891) erected the genus *Arctopora* to contain the single species *Phryganea trimaculata* Zetterstedt. *Arctopora* is therefore used here as the correct name for this genus which contains three species, one of which is known from Alberta.
Synopsis of characters. — Head rather elongated. Pronotum short. Spur formula 1,3,3. Wings quite large, fore wings large, truncated apically; hind wings not large, indented postero-apically. Fore wings with large brown patches; chord weakly disrupted, concave, slightly oblique to body posteriorly.

Male genitalia with tergum VIII setose at postero-dorsal edge. Segment IX elongated laterally, about as wide as sides dorsally. Cerci small, heavily sclerotized, thick, rounded. Median lobes of segment X small, blunt, heavy. Aedeagus of average size; median shaft slender; lateral arms similarly very slender except for widened tips.

Female genitalia with dorsal body of segment IX well developed, prominent, almost entirely overhanging small, inconspicuous, collar-like segment X. Ventro-lateral lobes of segment IX large, ovoid, closely contiguous ventrally. Supra-genital plate large, inconspicuous. Vulval scale large, partly flanked by sternum VIII; median lobe long, narrow; lateral lobes sub-quadrangular, divergent.

\textit{Arctopora pulchella} (Banks), 1908
(Fig. 490-494, 645)

\textit{Limnephilus pulchellus} Banks, 1908b:63. (Type locality: Grand Lake, Newfoundland).

\textit{Arctopora pulchella}; Fischer, 1969:59-60.

Males of this species are distinguished by massive, dorsal lobes of dorsal strap of segment IX (Fig. 490, 491); and by short, rounded, blunt median lobes of segment X. Females are distinguished by fused, inseparable segments IX and X (Fig. 493); by discrete ventro-lateral lobes of segment IX fused ventrally; and by minute segment X recessed into segment IX (Fig. 494).

\textbf{Description.} — Antennae dark brown, to dark reddish brown. Vertex of head very dark brown to black. Thorax deep red brown to black. Spurs red-brown. Fore wing length of male 9.5 mm; grey-brown, with large hyaline areas. Venation identical to that of \textit{Limnephilus}.

Male genitalia. (Specimen from Wapta Lake, Kicking Horse Pass, Yoho National Park, British Columbia). Postero-dorsal edge of tergum VIII slightly bulbous, sparsely setose (Fig. 490). Dorsal strap of segment IX massive, thick, projected well posterad over remainder of genitalia; distally narrowed, bilobed (Fig. 491); each lobe supported by only very slight antero-lateral straps to main body of segment. Main body of segment roughly rectangular, narrowed ventrad, curved slightly posterad. Clasper small, triangular, mesally concave. Lobes of segment X short, blunt, rounded distally; median lobes closely appressed along mesal edges (Fig. 491); intermediate lobes attached to lateral extensions of median lobes; cerci small, peg-like. Median shaft of aedeagus long, straight, hardly tapered, with slight, distinct distal head (Fig. 492); lateral arms longer, thinner, each expanded distally to clawed tip, with short, lightly spinate baso-dorsal lobe, and long, curved tapered distal lobe.

Female genitalia. (Specimen from Wapta Lake, Kicking Horse Pass, Yoho National Park, British Columbia). Vulval scale large, with median lobe basally narrow, expanded distally to slightly bilobed tip (Fig. 494); lateral lobes triangular, well separated. Dorsal body of segment IX large, high, rectangular, fused to segment X which it partly overshadows (Fig. 493); ventro-lateral lobes discrete, polygonal, fused ventrad of segment X. No apparent supra-
genital plate. Segment X minute, difficult to distinguish from segment IX; cleft ventrally.

Notes on biology. — Adults of this species are found near sedge sloughs or ponds and quiet streams. The flight period extends from June 28 to September 25.

Geographical distribution. — The known range of this species extends from British Columbia to Newfoundland (Fig. 645). In Alberta it is confined largely to the mountains and foothills, to altitudes of 6,675', it is however also found well away from the mountains, at Edmonton (2,000'), and at the Hay River, in northern Alberta.

I have examined 90 specimens, 47 males and 43 females, from the study area.

The Genus Lenarchus Martynov

Four species belonging to this genus, in two subgenera, are known from the study area.

Synopsis of characters. — Head short, in most species large, with prominent eyes. Spur formula 1,3,4. Wings large or of average size; fore wings clearly widened at chord; hind wings much larger. Fore wings strongly irrorate, brown or red; venation with chord strongly disrupted, somewhat concave, anteriorly oblique to body. Hind wing chord strongly disrupted, concave, parallel to body.

Male genitalia with segment IX elongate laterally, robust; short ventrally, produced dorsad as equally wide dorsal strap, developed posterad as massive, wide lobe over rest of genitalia (Fig. 495); lobe in some species formed from dorsal strap, but in others formed from fused cerci. Cerci large, thick, heavily sclerotized, dentate, when free. Median lobes of segment X elongate plates in most species. Claspers not prominent, fused so solidly to segment IX that suture not easily seen; dorsal process very slender in some species, long, horizontal. Aedeagus long, strong; median shaft folded basally; lateral arms slender, distally bilobed.

Female genitalia various. Segment IX of some species of two distinct parts. Ventro-lateral lobes very large, blunt, ventrally contiguous, or long, slender, not contiguous. Supra-genital plate large, short. Segment X tubular, variously cleft. Cerci long, slender, or fused to segment X. Vulval scale quite large; lateral lobes somewhat quadrangular; oblique, divergent.

Key to the Males of species of Lenarchus known from Alberta and eastern British Columbia

1a. Dorsal plate formed of posterior process of dorsal strap of segment IX (Fig. 495)

1b. Dorsal plate formed from fused cerci (Fig. 501)

2a.(1b) Clasper with long, very thin dorsal process (Fig. 504)

2b. Clasper otherwise (Fig. 501, 510)

3a.(2b) Dorsal plate with rectangular median cleft (Fig. 502)

3b. Dorsal plate with narrow, v-shaped, median cleft (Fig. 511)

L. (Lenarchus) crassus (Banks), p. 136.

L. (Paralenarchus) vastus (Hagen), p. 137.


L. (Paralenarchus) brevipennis Banks, p. 138.

Females of only two species are known, so that a key to the females of the species present in the study area is impracticable at present.

The Subgenus Lenarchus Martynov

This subgenus, of which one species is known from the study area, is characterised by large, irrorate fore wings; by dorsal plate formed from dorsal strap of segment IX of male; and by median lobes of segment X of male well developed.
Lenarchus crassus (Banks), 1920
(Fig. 495-500, 646)


Males of this species are distinguished from other species of Lenarchus by dorsal plate formed from dorsal strap of segment IX (Fig. 495); and by long, irregularly dorsally directed, black spine attached to dorso-mesal faces of claspers. Female unknown.

Description. — Antennae yellow-brown. Vertex of head red-brown, to dark brown mesally. Thorax dark yellowish brown to red-brown. Spurs red-brown. Fore wing length of male 15.1 mm; warm chocolate-brown, irrorate, with larger hyaline areas. Venation identical to that of Limnephilus spp.

Male genitalia. (Specimen from Eisenhower Junction, Banff National Park, Alberta). Segment IX massive, of roughly equal width throughout, curved anterad in lateral aspect (Fig. 495). Postero-dorsal edge produced posterad as wide, thick plate dorsad of remainder of genitalia, and weakly bilobed on posterior edge (Fig. 496). Clasper high, narrow, partly fused to segment IX; dorsal extremity with long, thin, heavily sclerotized spine attached to mesal face, curved angularly dorsad. Median lobes of segment X high, thin, polygonal, dark plates set vertically laterad of anus, connected ventrally by small sub-anal plate (Fig. 496, 497). Cercus rounded-triangular, fused to postero-ventral edges of dorsal plate of segment IX. Median shaft of aedeagus slender, tapered (Fig. 498), with tip deeply cleft (Fig. 499); lateral arms with long, narrow bases each abruptly widened to distal, spatulate tip fringed on dorsal edge with long setae; with small, spiniform, meso-dorsal lobe visible in dorsal aspect (Fig. 500).

Female genitalia. Not known.

Geographical distribution. — This species is known from few, widely separated localities in Alberta, Quebec, and New Hampshire (Fig. 646). In Alberta the single record is from a point along the Bow River Valley in the mountains, in an area of valley-bottom sedge marshes.

I have examined a single male of this species from Alberta; in the Canadian National Collection, Ottawa.

The Subgenus Paralenarchus Schmid

This subgenus, three species of which are known from the study area, is characterised in males by clear discontinuity between segment IX and dorsal plate, formed from fused cerci (Fig. 501); median lobes of segment X very long, or reduced.

Lenarchus fautili (Denning), 1949
(Fig. 501-503, 647)

Limnephilus fautili Denning, 1949a:46-47. (Type locality: Libby Flats, Albany County, Wyoming).


Males of this species are distinguished from males of other species of Lenarchus by short,
blunt, rounded claspers (Fig. 501); and by dorsal plate, attached to fused cerci, with deep, rectangular median cleft (Fig. 502). The female is unknown.

*Description.*—Antennae dark brown, joints yellow; scapes very dark, with slightly lighter, glabrous antero-mesal faces. Vertex of head uniformly black. Thorax dark brown to almost black. Spurs reddish brown. Fore wing length of male 8.6 mm; dark chocolate-brown; irregularly irrorate, especially along anterior edge. Venation identical to *Limnephilus* spp.

Male genitalia. (Specimen from Bow Pass, Banff National Park, Alberta). Segment IX high, narrow, except for large, rounded, latero-anterior lobes (Fig. 501); dorsal strap hardly narrower than remainder. Clasper scoop-like, with concave mesal face; rounded-rectangular in lateral aspect. Median lobes of segment X minute, short, hooked ventrad (Fig. 501, 502). Intermediate lobes massive, each bilobed; mesal lobes heavily sclerotized, dorsally curved, acuminate, black teeth; lateral lobes placoid, curved latero-dorsal to flank cercal bases laterally. Cercus massive, thick, long, fused mesally for half length (Fig. 502); decreased in width, directed weakly postero-lateral distad of fused bases. Median shaft of aedeagus long, slightly narrowed distad, with distinct, discrete distal head (Fig. 503); lateral arms sinuate, of uniform width to widened, bilobed, distal tips; dorso-mesal lobe curved, acuminate; latero-ventral lobe spatulate, fringed distally with short setae.

Female genitalia. Not known.

*Notes on biology.*—I have collected a single specimen from a small, sedge-fringed, peat-based, alpine pool at 6,878'. Flight season extends from July 17 to August 10.

*Geographical distribution.*—The known range of this species extends from Great Slave Lake to Alberta and British Columbia (Fig. 647). In Alberta it appears to be confined to alpine situations, but records are too scanty to be certain.

I have examined two males of this species from the study area, and one from farther west in British Columbia.

*Lenarchus vastus* (Hagen), 1861

(Fig. 504-509, 646)


Males of this species are distinguished by very wide dorsal strap (Fig. 504); by long, very thin, tubular dorsal process of claspers; and by long, tapered blades of segment X median lobes. Females are distinguished by almost entirely separated dorsal body and ventro-lateral lobes of segment IX (Fig. 508); and by large, pedicellate, trapezoidal cerci (Fig. 508, 509).

*Description.*—Antennae brown; scapes darker, with lighter, glabrous, antero-mesal faces. Vertex of head dark brown to black. Thorax dark brown dorsally; laterally reddish brown. Tibiae with alternating dark and light bands. Spurs brown. Fore wing length of male 18.7 mm; dark brown, heavily irrorate; some darker bars posterad of Cu1, with colour intensified by localised patches of black hairs. Venation identical to *Limnophilus* spp.

Male genitalia. (Specimen from Eisenhower Junction, Banff National Park, Alberta; in
Canadian National Collection, Ottawa). Segment IX massive, sub-rectangular in lateral aspect, with large, rounded lobes on antero-lateral edges (Fig. 504); posterior edges sinuate. Clasper at ventral angle of segment IX (Fig. 505), triangular, with long, very narrow dorsal extension with long, thin, tubular dorsal process. Median lobes of segment X long, narrow, tapered blades curved gently dorsad, each with black, minutely dentate dorsal edges (Fig. 504); intermediate lobes massive, thick, twisted plates ventrad of fused cerci (Fig. 504, 505). Cerci massive, fairly short, fused along most of mesal edges (Fig. 506); directed slightly postero-ventrad, with black extremities; somewhat concave on ventral surfaces. Median shaft of aedeagus stout, with wrinkled basal portion (Fig. 507); with distinct, discrete distal head partly recessed into basal part. Lateral arms longer, each of even width, narrow, with cleft tips.

Female genitalia. (Specimen from Eisenhower Junction, Banff National Park, Alberta; in Canadian National Collection, Ottawa). Vulval scale large, triangular in general outline (Fig. 509); with large, rectangular median lobe; lateral lobes with long, rectangular bases, rounded-triangular lobes on distal three-quarters of mesal edges. Segment IX with small, triangular, ventro-lateral lobes connected to acute-triangular (in lateral aspect) dorsal body by very narrow lateral bands (Fig. 508). Supra-genital plate wide, short, rounded. Segment X of two major parts, ventral part wide basally, tapered slightly posterad; posteriorly bilobed (Fig. 509); with ventral carina; dorsal part narrow strap of varied width, bent at right angles, widened laterad; black, pointed distally.

Notes on biology. — Adults of this species are found near smaller mountain or alpine sloughs or ponds fringed with sedges. They have also been collected from low, major valley systems of the Cordillera. The flight season extends from June 6 to August 24.

Geographical distribution. — The known range of this species extends from Alaska to Alberta, Idaho, and California (Fig. 646). In Alberta it is confined to the mountain areas, ranging in altitude from about 3,000' to about 6,800'.

I have examined 28 specimens, nine males and 19 females, from the study area. I have never taken males myself, but many females; all males recorded are in the Canadian National Collection, Ottawa.

*Lenarchus brevipennis* (Banks), 1899

(Fig. 510-514, 647)


*Limnophilus brevipennis*; Ross, 1938b:34. Ross, 1944:298.


Males of this species are distinguishable from males of other species of *Lenarchus* by dorsal plate formed of fused cerci; by dorsal plate with v-shaped median cleft (Fig. 511); by small, pale, thin-bladed, median lobes of segment X (Fig. 510); and by orbicular, distal concavities of cercal mesal surfaces. Females are distinguished by massive vulval scale with short, thin, median lobe (Fig. 514); by discrete, trapezoidal ventro-lateral lobes of segment IX (Fig. 513); and by acute-triangular cerci.

Description. — Antennae brown; antero-mesal faces of scapes lighter, glabrous. Vertex of
head very dark brown, except lighter laterally. Thorax very dark brown throughout. Spurs brown. Fore wing length of male 11.2 mm; pale chocolate-brown; densely and minutely irrorate; costal area clear. Venation not differing significantly from *Limnephilus* spp.

Male genitalia. (Specimen from Lewis Lake, Wyoming; in Illinois Natural History Survey). Segment IX high, relatively narrow, except widened laterally (Fig. 510). Ventro-lateral angles with tapered suture. Clasper small, with large, triangular ventral lobe, small, acuminate, dorsal lobe. Median lobes of segment X small, digitate, thin blades (Fig. 510). Intermediate lobes of segment X massive, folded plates; each meso-distal lobe short, thick, distally black-toothed spike; each latero-basal lobe rectangular in lateral aspect, curved dorsad. Cerci massive, fused along mesal edges for two-thirds of length (Fig. 511); with mesal carina, and orbicular distal concavities. Two short, thin, clavate papillae (Fig. 510, 511) baso-dorsad of cerci. Median shaft of aedeagus massive, thick throughout, with discrete distal head recessed into basal portion (Fig. 512); lateral arms attached to median shaft, not tapered distad, with disto-dorsal lobe curved, spiniform; disto-ventral lobe blunt, fringed with long setae.

Female genitalia. (Specimen from Waterton, Waterton National Park, Alberta). Vulval scale huge; median lobe long, thin, shorter than lateral lobes (Fig. 514); lateral lobes massive, almost trapezoidal. Dorsal body of segment IX high, narrow, merged indistinguishably to acute-triangular cercal lobes (Fig. 513); ventro-lateral lobes discrete, trapezoidal in lateral aspect; small. Supra-genital plate large, slightly angular laterally. Segment X small, recessed into segment IX; essentially cylindrical, with lateral edges incised, ventral surface flat, plate-like.

**Geographical distribution.** — The known range of this species extends from southern Alberta to Oregon and Colorado (Fig. 647). In Alberta it is known from a single female taken in the far southwest corner of the province.

I have examined two specimens of this species; one male from Wyoming, and a female from the study area.

**The Genus *Hesperophylax* Banks**

Three species of this genus are known from the study area.

**Synopsis of characters.** — Head short, very large, eyes large. Spur formula 1,2,2. Wings large, similar to *Limnephilus* spp. except hind wings rather narrow, not indented posterio-apically. Fore wings densely pilose, patterned; sub-radial cell with silvered line; distad of cell line trebles in width, tapered gradually to wing tip, silver line bordered with grey or black. Venation of fore wings with weakly disrupted chord, concave, anteriorly oblique to body; hind wing similar.

Male genitalia with narrow segment IX. Cerci very large, blunt, thin, weakly sclerotized. Median lobes of segment X fused as single lobe over membranous anal orifice. Claspers fairly large, not prominent; with long bases narrow; dorsal processes long, slender. Aedeagus fairly large, short, curved dorsad; median shaft slender, simple; lateral arms much shorter, each with short, thick base with two bundles of slender, sclerotized blades.

Female genitalia with dorsal body of segment IX short, weakly developed; ventro-lateral lobes very small, inconspicuous, fused to lateral edges of very large, thick, supra-genital plate. Segment X short, tubular, finely pilose. Cerci long, thin, fused to dorsal surfaces of segment X. Median lobe of vulval scale long, narrow; lateral lobes large, triangular.

**Key to the Males of the species of *Hesperophylax* found in Alberta and eastern British Columbia**

1a. Clasper long, narrow, acute triangular (Fig. 515, 525); median lobe of segment X
with distinct dorso-anterad hook acuminate ........................................... 2a
1b. Clasper with truncate tip, dorsal portion of uniform width (Fig. 520); median
lobe of segment X not acuminately hooked, clavate... \textit{H. incisus} (Banks), p. 142.
2a.(1a) Disto-dorsal edge of cercus with slight indentation (Fig. 515); clasper base wide
throughout entire height .................................................. \textit{H. occidentalis} (Banks), p. 140.
2b. Cercus without distal indentation (Fig. 525); clasper base evenly tapered ventrad
................................................................. \textit{H. consimilis} (Banks), p. 141.

Key to the Females of species of \textit{Hesperophylax} found in Alberta and eastern British
Columbia

1a. Median lobe of vulval scale narrow; at least as long as lateral lobes (Fig. 523, 529)
.......................................................... ........................................... 2a
1b. Median lobe of vulval scale very short, wide, with truncate tip (Fig. 519) ...........
.......................................................... ........................................... \textit{H. occidentalis} (Banks), p. 140.
2a.(1a) Vento-lateral lobes of segment IX large, irregular, prominent (Fig. 524) .......
.......................................................... ........................................... \textit{H. incisus} (Banks), p. 142.
2b. Vento-lateral lobes of segment IX small, barely evident (Fig. 528)
.......................................................... ........................................... \textit{H. consimilis} (Banks), p. 141.

\textit{Hesperophylax occidentalis} (Banks), 1908
(Fig. 515-519, 648)

\textit{Hesperophylax alaskensis}; Ross, 1938b:32.

The major distinguishing characters of the two sexes of this species are given in the above
keys.

\textit{Description}. — Antennae brownish yellow; anterio-mesal faces of scapes glabrous. Vertex
of head yellow-brown. Thorax reddish orange. Spurs yellow-brown. Fore wing length of
male 14.8 mm; pale yellow, with longitudinal silver line. Venation as in \textit{Limnephilus} spp.

Male genitalia. (Specimen from Logan, Utah; in Illinois Natural History Survey). Postero-
dorsal edge of tergum VIII minutely spinate. Dorsal strap of segment IX thin, warped
antero-mesally round cercal bases (Fig. 515). Main body of segment spindle-like in lateral
aspect. Clasper with high, wide base; large, acute-triangular. Median lobe of segment X in
lateral aspect widened distally, tapered abruptly to dorso-anterad directed, acuminate tip;
posterior aspect as in Fig. 516. Cercus large, concave on mesal face, with distinct indentation
on distal edge. Median shaft of aedeagus bent dorso-posterad at mid-point, at about 45°;
lateral arms with dorsal cluster of close-packed spines curved dorso-anterad (Fig. 517), each
with two small, separate groups of ventral spines; the whole attached to wide, membranous
base.
Female genitalia. (Specimen from High River, Alberta). Vulval scale equilateral-triangular in ventral aspect (Fig. 519); median lobe shorter than large triangular lateral lobes. Dorsal body of segment IX high, thin, indistinguishable from segment X; ventro-lateral lobes small, irregular, setose ventrally (Fig. 518). Supra-genital plate large, with rectangular base, triangular posterior edge. Segment X cylindrical, deeply cleft ventrally, with disto-dorsal angles flanged laterally. No evident cercal lobes.

**Geographical distribution.** — The known range of this species extends from Alberta and British Columbia to California and New Mexico (Fig. 648). It is known from a single locality in the plains of southwestern Alberta.

I have examined two specimens of this species, one of each sex.

**Hesperophylax consimilis** (Banks), 1900
(Fig. 525-529, 648)


The major distinguishing characteristics of each sex of this species are outlined in the keys above.

**Description.** — Antennae yellow; scapes slightly darker with glabrous, antero-mesal faces. Vertex of head reddish yellow. Thorax light reddish yellow, with mesonotum flanked by dark brown bars. Spurs yellow. Fore wing length of male 8.1 mm; light reddish yellow, with longitudinal silver line. Venation identical to *Limnophilus* spp.

Male genitalia. (Specimen from Little Bow Creek, High River, Alberta). Postero-dorsal edge of tergum VIII sparsely clothed with short setae. Dorsal strap of segment IX very thin, incomplete dorsally; main body of segment spindle-shaped (Fig. 525). Clasper with wide base tapered evenly ventrad; dorsal process long, thin, tapered distad, acuminate. Median lobe of segment X with dorso-ant erad process acuminate; with membranous folds about anus; high, narrow, triangular in posterior aspect (Fig. 526). Cercus large, polygonal, with concave mesal face. Median shaft of aedeagus much longer than lateral arms (Fig. 527), curved gently dorsad; lateral arms of dorsal sheaf of spines, several separate ventral spines; spines long, lamellar; attached to membranous base.

Female genitalia. (Specimen from Little Bow Creek, High River, Alberta). Vulval scale equilateral-triangular (Fig. 529); median lobe long, narrow, tapered evenly distad, rounded; lateral lobes acute-triangular, with carinae bisecting anterior angles. Dorsal body of segment IX small, high, narrow, separated from segment X by posterior declivity (Fig. 528); ventro-lateral lobes barely visible in lateral aspect, small. Segment X large, plate-like over anal aperture, bilobed, rounded, with distinct lateral lobes. No evident cerci. Supra-genital plate semicircular.

**Notes on biology.** — Adults of this species are collected near creeks of varied velocities, from mountain streams to sedge-choked plains streams. Flight season ranges from June 10 to August 15.

**Geographical distribution.** — The known range of this species extends from Alberta to Nevada (Fig. 648). In Alberta it is found primarily in the plains region, but has been taken at 5,000’ altitude at Cameron Creek, Waterton National Park.

I have examined 24 specimens, 18 males and six females, from the study area.
*Hesperophylax incisus* (Banks), 1943  
(Fig. 520-524, 649)

The major distinguishing characters are outlined in the keys to the species of *Hesperophylax*.  

**Description.** — Antennae light yellow-brown; each article with distinct brown band distally; scapes darker, antero-mesal faces lighter, glabrous. Vertex of head light to dark brown; warts lighter. Thorax reddish brown, with darker brown laterally on mesonotum. Spurs yellowish brown. Fore wing length of male 12.7 mm; light brown, darker postero-basally; with longitudinal, silver line. Venation as in *Limnephilus* spp.  

Male genitalia. (Specimen from Simpson Islands, Great Slave Lake, Northwest Territories). Postero-dorsal edge of tergum VIII lightly setose. Dorsal strap not developed, replaced by web of membrane (Fig. 520); main body of segment narrow, spindle-shaped. Clasper long, slender, of uniform width distally, with rectangular tip. Median lobe of segment X blunt, rounded distally; tripod-like in posterior aspect, high, narrow (Fig. 521). Cercus large, with disto-dorsal indentation; tip curved mesad (Fig. 521). Median shaft of aedeagus straight, thin basally, turned abruptly dorsad at 45° for final third of length; lateral arms each of single, large cluster of lamellate spines curved dorsad (Fig. 522).  

Female genitalia. (Specimen from Simpson Islands, Great Slave Lake, Northwest Territories). Vulval scale with long, rectangular median lobe (Fig. 523); lateral lobes directed postero-laterad, each triangular, narrow. Dorsal body of segment IX high, narrow, tapered ventrad; ventro-lateral lobes large, prominent (Fig. 524). Supra-genital plate large, square, rounded distally. Segment X large, separated from segment IX by shallow declivity; with ventrad curtains lateral of anal aperture; laterally with warped, large, rounded lobes (Fig. 523, 524). No evident cerci.  

**Notes on biology.** — Adults of this species are collected near lakes, and occasionally slow, gravelly streams. The flight dates extend from June 30 to August 30.  

**Geographical distribution.** — The known range of this species extends from Great Slave Lake to California and Colorado (Fig. 649). In Alberta it is confined to the mountains and foothills, ranging in altitude to 6,450'. An outlying population is found in the Cypress Hills in southeastern Alberta.  

I have examined 165 specimens, 113 males and 52 females, from the study area and Great Slave Lake.  

The Tribe Stenophylacini Schmid  

**Synopsis of characters.** — Head short, very large, with large, prominent eyes. Pronotum short; macrochaetae fine. Spur formula 1,2,2; 1,3,3; or 1,3,4; and 0,3,4 in males of some species. Male anterior femur of most species with brushes. Wings very varied; sexually dimorphic. Fore wings apically truncated; hind wings somewhat indented postero-apically, with large anal areas. Venation constant in most taxa. Fore wing chord only slightly disrupted, concave and posteriorly oblique to body. Hind wing chord markedly disrupted, very oblique posteriorly.  

Male genitalia less massive than in Limnephilini; more varied. Tergum VIII finely spinate. Segment IX slightly enlarged laterally, tapered dorsad. Cerci with little ventral support. Intermediate appendages not large, spur-like in most species, directed dorsad; paired except
in Clostoeca Banks. Claspers varied in size; rarely armed or toothed; not as prominent as in Limnephilini. Aedeagus very varied, median shaft long, simple, non-membranous. Lateral arms simple filaments to spinate, dentate plates.

Female genitalia with segment IX composed of two quite distinct parts in most species; dorsal body large, without appendages; ventro-lateral lobes prominent, produced laterad or posterad. Segment X simple, continuous prolongation of segment IX; entirely cleft to two lateral, ventral, and dorsal parts, or not. Supra-genital plate present or absent. Vulval scale medium or small, variable; three lobes often of different sizes; lateral lobes fused to sternum VIII.

Key to the Males of genera of Stenophylacini found in Alberta and eastern British Columbia

1a. Maxillary palpus very long ........................................ Chyranda Ross, p. 143.
1b. Maxillary palpi normal .................................................. 2a
2a.(1b) Clasper ventrad on segment IX, projected (Fig. 545) .... Philocasca Ross, p. 147.
2b. Clasper long, projected little, vertical (Fig. 535, 540) ................ Pycnopsyche Banks, p. 144.

The Genus Chyranda Ross

One species of this genus is known from the study area.

Synopsis of characters. — Antennae fine, longer than fore wings in male; much shorter in female. Maxillary palpi of male remarkably long, with very small basal article; female palpi normal. Spur formula 1,3,3. Male wings narrow, long; female wings wide, short.

Male genitalia with short segment IX. Cerci, median lobes of segment X of average size; thin, vertically oriented to form deep cavities. Claspers very large, fused to segment IX, not projected. Aedeagus very small; lateral arms spiniform, asymmetrical.

Female genitalia with dorsal body of segment IX short. Segment X small, produced as two large, dorsal, and one very small, ventral, lobes. Supra-genital plate small. Vulval scale of two lateral lobes separated by median cleft.

Chyranda centralis (Banks), 1900

(Fig. 530-534, 650)


Algonquina centralis; Milne, 1935:30, 49.


Algonquina pallida; Betten, 1934:370.


Parachiona signata Banks, 1907b:120-121. (Type locality: Idaho).
Algonquina signata; Betten, 1934:370.

Males of this species are distinguished by short, high, mesally directed claspers (Fig. 530); by left lateral arm of aedeagus corkscrewed dorsally over aedeagal tip (Fig. 531); and by cercal bases very little in contact with segment IX. Females are distinguished by segment X well separated from segment IX (Fig. 533); and by massive, bilobed vulval scale (Fig. 534).

Description. — Antennae warm reddish brown; scapes banded vertically, alternately black and yellow; scapes with antero-mesal faces very dark brown, glabrous. Vertex of head dark brown, except for warts. Thorax bright yellowish brown. Spurs light brown. Fore wing length of male 12.9 mm; pale yellow to light brown. Venation identical to Limnephilus spp.

Male genitalia. (Specimen from Sunwapta Pass, Jasper National Park, Alberta). Dorsal strap of segment IX very thin, almost to point of extinction dorsally (Fig. 530); main body of segment high, narrow, trapezoidal in lateral aspect. Clasper short, parallelogram-like in lateral aspect, with thin, acuminate dorsal angle; directed mesad (Fig. 532). Median lobes of segment X short, slightly tapered, blunt, rounded, with concave lateral faces. Cercus large, rounded, mesally concave flap. Median shaft of aedeagus short, stout, attached to membranous base (Fig. 531); lateral arms asymmetrical; left arm in form of corkscrew, curved dorsad over aedeagal tip.

Female genitalia. (Specimen from Sunwapta Pass, Jasper National Park, Alberta). Vulval scale massive, angular, with only two lobes, both lateral (Fig. 534). Dorsal body of segment IX large, high, narrow, curved (Fig. 533), of uniform width; ventro-lateral lobes distinct, but fused to dorsal body, triangular. Supra-genital plate semi-circular, hyaline, membranous, small. Segment X of two lateral, ear-like flaps; open dorsally; connected ventrally by warped plate with semi-circular projection between lateral plates.

Notes on biology. — Adults of this species are found near mountain ponds with heavy sedge growth, and occasionally mountain streams of some rapidity. They are also taken on seepage slopes on valley sides. Flight dates range from July 19 to October 8.

Geographical distribution. — The known range of this species extends from Alaska to Oregon, Colorado, and Quebec (Fig. 650). The Quebec record is curiously isolated, and may be of interest. In Alberta the species occurs in the mountains, foothills, and the Cypress Hills. Specimens have been found at altitudes as high as 6,880'.

I have examined 220 specimens, 118 males and 102 females, from the study area.

The Genus Pycnopsyche Banks

Two species belonging to this genus are known from the study area.

Synopsis of characters. — Spur formula 1,2,2; 1,3,3; 1,3,4. Wings not very large, variable in shape. Chord in both fore and hind wings markedly concave.

Male genitalia tergum VIII with posterior edge produced as two dorsal lobes, as two lateral lobes parallel to cerci, or as two dorso-lateral lobes; these lobes are specifically characteristic. Segment IX short, rather attenuated dorsally. Cerci varied, enclosing anal aperture to form horizontal platform. Median lobes of segment X conical or spiniform, or small to vestigial. Claspers vertical, not projected, with high bases fused to segment IX, and well developed dorsal processes. Aedeagus small; median shaft large, membranous; lateral arms each with bulbous base and group of fine spines or hairs distally.

Female genitalia with ventro-lateral lobes of segment IX large, blunt, fused to ventral surfaces of segment X. Vulval scale rather conspicuous, single fleshy lobe.
Key to the Males of species of *Pycnopsyche* found in Alberta and eastern British Columbia

1a. Tergum VIII with large, black-spinate, ventro-lateral lobes on posterior edge (Fig. 540); clasper without lamellate dorso-mesal process ............ *P. guttifer* (Walker), p. 146.

1b. Tergum VIII without ventro-lateral lobes of any kind on posterior edge (Fig. 535); clasper with high, thin lamellate process at meso-dorsal edge .................................................. *P. subfasciata* (Say), p. 145.

Key to the Females of species of *Pycnopsyche* found in Alberta and eastern British Columbia

1a. Segments IX and X solidly fused as simple tube without lobes or processes (Fig. 543) ................................................................. *P. guttifer* (Walker), p. 146.

1b. Segments IX and X distinctly separate (Fig. 538) with dorso-lateral cerical lobes ........ *P. subfasciata* (Say), p. 145.

*Pycnopsyche subfasciata* (Say), 1824  
(Fig. 535-539, 651)

*Neuronia? subfasciata*; Walker, 1852:11.

*Enoicyla subfasciata*; Hagen, 1861:269. Hagen, 1864:813.


*Stenophylax subfasciatus*; Milne, 1935:52.


The major distinguishing characters are given in the keys above.

Description. — Antennae brown; antero-mesal faces of scapes slightly lighter, with fewer setae than remainder. Vertex of head red-brown, warts paler; dark brown spots meded of each lateral ocellus. Thorax red-brown. Spurs yellow. Fore wing length of male 18.7 mm; light yellow-brown, with distinct darker areas between f2 and f3, and in middle of discoidal, sub-radial and thryrdial cells. Venation almost as in *Limnephilus* spp.

Male genitalia. (Specimen from Lethbridge; in Illinois Natural History Survey). Posterior edge of tergum VIII warped, with minute, hyaline spines (Fig. 535); small, acute-triangular lobes ventrad of spinate area. Dorsal strap thread-like in dorsal aspect (Fig. 537); main body of segment IX spindle-shaped with narrow ventral area. Clasper with high, thick base; postero-mesal edge with dorsal process long, lamellar, thin, tapered dorsal, with anteriorly directed distal hook. Median lobes of segment X minute spikes; intermediate lobes smaller, on bases of medians (Fig. 537). Cercus long, thin, narrow, with irregular dorsal edge. Median shaft of aedeagus of varied widths, abruptly narrowed to very thin distal stem (Fig. 536); lateral arms each with swollen base, and single, very slender distal spine.

Female genitalia. (Specimen from Illinois: in Illinois Natural History Survey). Vulval scale large, semi-circular except doubly-indented distally (Fig. 539); single lobe. Dorsal body of
segment IX high, narrow, abruptly declivous posteriorly to segment X (Fig. 538); ventro-lateral lobes minute, rounded. Supra-genital plate large, triangular, with sinuate edges. Segment X tubular, with rounded disto-lateral edges, with small, plate-like dorsal lobe. Cerci small, on dorso-lateral surfaces of segment IX.

Geographical distribution. — The known range of this species extends from Alberta to Illinois and New Hampshire (Fig. 651). It is known from only one locality in Alberta.

I have examined a single male from Alberta, and a single female from Illinois.

**Pycnopsyche guttifer** (Walker), 1852

*(Fig. 540-544, 652)*


*Pycnopsyche guttifer*; Milne (D. J.), 1943:192.


*Halesus* species no. 2; Betten, 1901:568-569.

The major distinguishing characters are given in the keys to species above.

Description. — Antennae reddish brown. Vertex of head reddish brown. Thorax yellow to light reddish brown. Spurs darker. Fore wing length of male 17.2 mm; dull greyish brown; distal and anal edges, chord area, and area of bifurcation of M all darker than remainder. Venation identical to that of *Limnephilus* spp.

Male genitalia. (Specimen from La Biche River, Charson Bridge, Alberta). Postero-dorsal edge of tegrum VIII thinly spinate; postero-lateral angles developed as black-spinate pads laterad of segment IX (Fig. 540, 541). Dorsal strap of segment IX very fine; main body of segment very narrow, high; spindle-shaped. Clasper with high, relatively wide base; prolonged dorsad as thin, acuminate, dorsally directed blade. Median lobes of segment X minute, peg-like, attached well dorsad of anal aperture, to mesal processes of cerci (Fig. 541). Cercus large, almost square in lateral aspect; mesally concave. Median shaft of aedeagus ventrally straight, dorsally sinuate, with abruptly tapered distal quarter recurved dorsad (Fig. 542); lateral arms attached dorsad of median shaft, each with short basal section terminated in sheaf of four or five fine spines.

Female genitalia. (Specimen from Blindman River, Hwy. 2, Alberta). Vulval scale simple, trapezoidal plate (Fig. 544). Segments IX and X fused, demarcated by slight dorsal declivity (Fig. 543); no ventro-lateral lobes of segment IX. Supra-genital plate triangular, with warped lateral extremities, attached to invagination dorsad of vulval scale (Fig. 544). Segment X
simple, tubular, with slight disto-lateral clefts.

Notes on biology. — Adults of this species are found near larger, fast flowing rivers with pebble bottoms. Flight dates range from August 23 to October 3.

Geographical distribution. — The known range of this species extends from Washington to Newfoundland, North Carolina, and possibly Georgia (Fig. 652). In Alberta it is found in the plains regions.

I have examined a total of one male and six females from the study area.

The Genus Philocasca Ross

A single species of this genus is known from the study area; it is here described as new.

Synopsis of characters. — Wings large, rounded; hind wings with very large anal area, R1 fused to Sc. Spur formula 1,3,4; 1,2,4; or 1,2,2.

Male genitalia with very short segment IX not attenuated dorsally. Cerci very large, horizontal plates. Median lobes of segment X ventrad of cerci; large, thick. Claspers blunt, projected, without free parts. Aedeagus entirely membranous, with internal sclerites; lateral arms spiniform.

The following characterisation of the females is derived from an examination of the drawings of females of the various species of Philocasca given by Wiggins and Anderson (1968). Segment IX of two parts; dorsal body tapered ventrad; ventro-lateral lobes large, blunt, not projected or contiguous ventrally. Segment X small, bilobed, lobes tapered. Supra-genital plate parabolic, distinct. Vulval scale with short, stubby lateral lobes; no median lobe; two small lobes laterad of lateral lobes.

Philocasca thor Nimmo n. sp.  
(Fig. 143a, 143b, 545-547, 653)

Males of this species are similar to those of Philocasca antennata Banks (see Fig. 17, Wiggins, 1968), but differ in smaller, more tapered cerci (Fig. 545); in wider median lobes of segment X arched dorsad, evenly tapered; in wider ventral area of segment IX; in longer, slightly tapered claspers; and in larger lateral plates between median lobes and cerci (Fig. 546).

Description. — Antennae pale straw-yellow; scapes dark reddish-brown, with antero-mesal faces pale, setaless. Vertex of head uniform red-brown; all setae hyaline, except for intense black setae of warts at posterior edge of compound eyes. Thorax pale yellow laterally; red-brown dorsally, with slight mesal stripe. Spur formula 1,2,4; spurs red-brown. Fore wing length of male 16.7 mm; pale greyish brown, uniformly and densely irrorate except for much paler costal area. Venation as in Fig. 143a, 143b; quite similar to Limnephilus spp.

Male genitalia. (Specimen from alpine meadows east of Mt. Edith Cavell, Jasper National Park, Alberta). Segment IX high, almost acute-triangular as dorsal strap and main body merge almost imperceptibly (Fig. 545). Clasper small, distally triangular, blunt, fused to segment IX, with two distinct tufts of setae. Median lobes of segment X smoothly arched, tapered disto-dorsad; attached to posterior edge of large, hemi-spherical cup in segment VIII (Fig. 546), from which large, short, rounded, slightly tapered cerci arise laterally. Median shaft of aedeagus short, stubby; ejaculatory duct terminated between two smooth, rounded, distal valves (Fig. 547); lateral arms short, stout, black, acuminate, spiniform; aedeagal base surmounted by heavy, black, sclerotized hood. Aedeagal straps from claspers triangular, with meso-ventral interconnection small, hook-like in lateral aspect.

Geographical distribution. — This species is known from a single locality (Fig. 653).
Holotype. — Male. Alpine meadows, east of Mt. Edith Cavell, Jasper National Park, Alberta; July 4, 1965; A. Nimmo. Type number 10,588 in the Canadian National Collection. This species is named for Thor, a character encountered in my reading of Norse mythology.

The Tribe Chilostigmini Schmid

Synopsis of characters. — Head of most species rather short, large, with very prominent eyes. Pronotum short, with relatively thin macrochaetae. Anterior femora of males with or without brushes. Spur formula 1,1; 1,2,2; 1,3,3; or 1,3,4. Wings varied, not sexually dimorphic. Fore wings quite narrow basally, with expanded, rounded, truncated, indented tips. Hind wings much larger than fore wings, indented posteral of apex or not. Venation of fore wings with large, coriaceous stigma in both sexes. R1 strongly arched, connected to Sc by cross-vein or not. R2 arched, parallel to R1. Chord anteriorly oblique to body, disrupted, or almost rectilinear. Posterior wing chord strongly disrupted, very oblique to body posteriorly.

Male genitalia with tergum VIII finely spinate posteriorly or not. Segment IX lengthened laterally; concave in some species. Ventrally produced as plaque ventral of claspers and aedeagus; dorsally narrow, developed anteral as two lateral, internal cavities. Cerci varied in size; large, sclerotized, or small, flexible, bilobed, and largely fused to bases of intermediate lobes of segment X. Claspers simple, conical, more or less concave on mesal faces; or bipartite, with prominent external lobe, and internal lobe.

Female genitalia with segment IX devoid of appendages; composed of one piece, or with poorly developed ventro-lateral lobes evident. Segment X short, tubular, or composed of two dorsal scales and ventral lobe. Supra-genital plate present or absent. Vulval scale varied in size, but usually very large; trilobed; triangular or quadrangular, concave or thick; lateral lobes large, fused to median basally; median lobe very small.

Key to the Genera of Chilostigmini found in Alberta and eastern British Columbia

1a. f3 petiolate on fore and hind wings .................. Phanocelia Banks, p. 155.
1b. f3 sessile .............................................. 2a
2a.(1b) Chord of fore and hind wings with regular, pronounced zigzag. Apical area very short .................. Chilostigmodes Martynov, p. 150.
2b. Chord of both wings with irregular, weak zigzag. Pronotum sparsely setose .... 3a
3a.(2b) Fore wing dusky brown, irrorate, with hyaline patches .................. Glyphopsyche Banks, p. 148.
3b. Fore wing reddish, with longitudinal white or silver line ............................... Psychoglypha Ross, p. 151.

The Genus Glyphopsyche Banks

A single species of this genus is known from the study area.

Synopsis of characters. — Spur formula 1,2,2. Wings very large; much larger in male than female. Hind wings very large. Fore wing chord virtually rectilinear, parallel to body or slightly oblique anteriorly; incomplete cross-vein between R1 and R2, at apex of discoidal cell.

Male genitalia with postero-dorsal edge of tergum VIII trilobed, densely spinate. Cerci small, bilobed, fused to segment X. Median lobes of segment X fused, curved dorsad. Claspers quadrangular, very prominent. Aedeagus of average size, robust, sclerotized; lateral
arms small, thick.

Female genitalia with dorsal portion of segment IX very short. Ventro-lateral lobes scarcely discernible. Segment X short, tubular, as large as segment IX; segments IX and X indistinguishable. Vulval scale small, quite thick with lateral lobes massive, large; median lobe slender.

**Glyphopsyche irrorata** (Fabricius), 1781
(Fig. 551-556, 654)


*Enoicyla irrorata*; Hagen, 1864:812.


*Platyphylax irroratus*; Hagen, 1873a:296.

*Ecclisopteryx irrorata*; Banks, 1892:364.


*Limnephilus (Goniotaulus) intercissus* Walker, 1852:30-31. (Type locality: Canada).


*Chilostigma intercissa*; McLachlan, 1876a:188.

*Ecclisopteryx intercissa*; Provancher, 1877:259. Provancher, 1878a:146.

*Ecclisopteryx intercissa*; Provancher, 1878b:134-135.

*Chilostigma intercissum*; Ulmer, 1905a:22.


Males of this species are distinguished by peculiar aedeagus (Fig. 553, 554); by trilobed postero-dorsal edge of tergum VIII; and by very prominent claspers (Fig. 551). Females are distinguished by virtual absence of ventro-lateral lobes of segment IX; and by massive unit formed by fused segment IX and X (Fig. 555, 556).

**Description.** – Antennae light reddish brown; scapes dark brown, with yellow, glabrous, antero-mesal faces. Vertex of head dark brown, posterior edge yellow. Thorax brown to light brown laterally, very dark brown dorsally, with reddish yellow median band except on metathorax. Spurs brown. Fore wing length of male 16.6 mm; greyish chocolate-brown, irrorate, with larger, hyaline patches scattered throughout; costal area lighter. Venation not significantly different from that of *Limnephilus* spp.

Male genitalia. (Specimen from Cold Creek, Nojack, Alberta). Postero-dorsal edge of tergum VIII with fine, short, black spines arranged in rough triangle (Fig. 551, 552). Dorsal strap of segment IX high, narrow, folded anterad; main body of segment irregular, with pyramidal peak, ventral area segregated by lateral folds. Clasper columnar in posterior aspect, with concave distal face flanked by small, semi-circular, knife-like ridge on mesal edge. Median lobes of segment X almost completely fused, black, each set high, hooked anterad; produced ventro-laterad as two lateral straps terminated just dorsad of clasper bases (Fig. 552). Cercus bilobed, smoothly rounded. Large, rectangular, concave shelf with flanged
edges ventrad of anal aperture. Median shaft of aedeagus large, distally cleft, ventrally black plate with lateral edges folded dorsad (Fig. 553, 554); membranous hood dorsad of base with small, short, conical, setose lateral arms.

Female genitalia. (Specimen from Cold Creek, Nojack, Alberta). Vulval scale large, with short, wide median lobe; lateral lobes roughly rectangular, slightly sinuate distally (Fig. 556). Segment IX relatively small, with antero-dorsal prolongation (Fig. 555); channelled ventrally as two ventro-lateral bulges. Supra-genital plate semi-circular, traversed dorsally by fold of membrane. Segment X fused to segment IX, large, with concave depressions dorso-laterally.

Notes on biology. — Adults of this species are found in a variety of habitats, including small, slow streams, but primarily sedge or cattail sloughs, ponds and lakes. The flight dates extend from September 9 to October 4. I also have records from March, April, and May, which, I suspect, represents adults which have overwintered to emerge in periods of warm spring sunlight.

Geographical distribution. — The known range of this species extends from Alaska to California in the west, and New Hampshire in the east (Fig. 654). In Alberta it is found in the plains, foothills, and mountains, but at low altitudes, in the low valleys and passes.

I have examined 37 specimens, 19 males and 18 females, from the study area.

The Genus Chilostigmodes Martynov

One species of this genus is known from the study area.

Synopsis of characters. — Spur formula, 1,1,1. Wings quite large; fore wings with quite large, rounded apex; hind wings strongly indented. Fore wing chord close to apex, parallel to body, strongly disrupted; apical cells short. Chord of hind wing clearly disrupted, even closer to apex than in fore wing.

Male genitalia with segment IX elongate laterally. Cerci large, very prominent, convergent, pincer-like; fused basally to segment X. Claspers conical, lanceolate. Aedeagus long, thin; median shaft without basal tubercles; lateral arms very slender.

Female genitalia unknown.

Chilostigmodes areolata (Walker) 1852
(Fig. 548-550, 655)

Limnephilus areolatus Walker, 1852:35. (Type locality: St. Martin's Falls, Albany River, Hudson's Bay).


Enopyla areolata; McLachlan, 1871:110. Banks, 1892:364.


Platyphylax areolata; Banks, 1907a:39.

Chilostigma areolaris; Banks, 1943:353.

Glyphopsyche areolatus; Milne, 1935:24, 50.

Chilostigmodes areolatus; Fischer, 1969:316-317.


Description. — Antennae dark brown; antero-mesal faces of scapes almost white, glabrous. Vertex of head totally black. Thorax very dark brown to black. Spur formula 1,1,1; brown.
Fore wing length of male 12.7 mm; membrane hyaline with scattered patches of light grey-brown; veins brown, narrowly flanked by brown membrane. Venation not different from Limnephilus spp. except for chord advanced somewhat apically.

Male genitalia. (Specimen from George Lake, near Busby, Alberta). Segment IX large, produced well posterad (Fig. 548); with suture located just below cerci, as continuation of posterior edge. Dorsal strap very low, thread-like (Fig. 549). Clasper with wide base, narrowed rapidly to mid-point, with finger-like distal portion. Median lobes of segment X minute, vertically oriented hooks directed posterad. Horizontal, concave plates laterad of median lobes fused laterally to cercal bases. Cercus large, widened distally, with finger-like disto-ventral process, with concave baso-mesal face. Aedeagus delicate, hyaline; median shaft simple, of uniform width, curved slightly ventrad; orifice of ejaculatory duct in disto-dorsal channel (Fig. 550); lateral arms long, very slender, each tapered distad, with ventrally directed distal spine; attached to dorsal surface of aedeagal base.

Female genitalia. Unknown.

Notes on biology. — This species is known from one locality in the study area which is a large Typha lake. Flight dates range from April 27 to May 13, with one record from October 25. It seems that this species emerges in late fall, overwinters, and reappears in early spring.

Geographical distribution. — The known range of this species is represented by scattered records from Alaska to Alberta to Labrador (Fig. 655). In Alberta it appears to be confined to the northern plains and boreal forest.

I have examined 10 males from the study area.

The Genus Psychoglypha Ross

Four species of this genus are known from the study area.

Synopsis of characters. — Cephalic and pronotal warts densely hirsute. Spur formula 1,2,2; 1,3,3. Wings quite large; fore wings narrow, truncated, or indented apically; costal area cleft basally. Hind wings fairly large, variously indented. Fore wings characteristically yellowish red with longitudinal silver line along sub-radial and fourth apical cells. Chord of fore wings oblique anteriorly to body, strongly disrupted.

Male genitalia with tergum VIII with one or two black-spinate zones along posterior edge. Segment IX laterally elongate as large, distinct cavity in conjunction with claspers; ventrally segment produced posterad as large shelf. Cerci not large, with two well separated lobes. Median lobes of segment X fairly well sclerotized, of varied size, concave dorsally; fused or connected by membrane; flared dorso-laterad of anal aperture; produced laterad to walls of segment IX. Claspers prominent, concave plates, fused to edges of segment IX with line of fusion indistinct; bilobed, laterally large, mesally small. Aedeagus very long, thin; lateral arms very thin, spiniform; median shaft bilobed distally, bulbous, spinate basally.

Female genitalia with segment IX large; dorsal part large, bilobed, segment X almost completely enclosed; ventro-lateral lobes small, fused to dorsal part as simple lateral flaps. Supragenital plate large. Vulval scale large, thick, quadrangular, with two large, lateral lobes, and very small, median lobe.

Key to the Males of species of Psychoglypha found in Alberta and eastern British Columbia

1a. Disto-dorsal portions of median lobes of segment X longitudinally oriented plates (Fig. 572, 578) .................................................. 2a
1b. Disto-dorsal portions of median lobes of segment X cross-axially oriented, anteriorly concave plates (Fig. 563, 567) .................. 3a
2a.(1a) Disto-dorsal portions of median lobes of segment X smoothly rounded (Fig. 562);
claspers convergent toward median lobes; pattern of spines of tergum VIII as in Fig. 563. ............................ P. prita (Milne), p. 152.

2b. Disto-dorsal portions of median lobes acuminate in lateral aspect (Fig. 566); claspers parallel to median lobes; pattern of spines of tergum VIII as in Fig. 567 ............................ P. schmidtii Nimmo, p. 153.

3a.(b) Median lobes of segment X small; segment IX high, narrow (Fig. 572); lateral arms of aedeagus short, thick, asymmetrical (Fig. 575) . . P. alaskensis (Banks), p. 153.

3b. Median lobes huge (Fig. 578); segment IX short, wide; lateral arms of aedeagus very long, thin, symmetrical (Fig. 580, 581) ........................ P. ulula (Milne), p. 155.

Key to the Females of two species of *Psychoglypha* found in Alberta and eastern British Columbia

1a. Segment X small, bell-shaped in lateral aspect (Fig. 570), little projected; lateral lobes of vulval scale in ventral aspect very large, square (Fig. 571) ............................ P. schmidtii Nimmo, p. 153.

1b. Segment X larger, acute-triangular in lateral aspect (Fig. 576), well projected posterad; lateral lobes of vulval scale smaller, almost triangular, with sinuate posterior edges in ventral aspect (Fig. 577) ........................ P. alaskensis (Banks), p. 153.

*Psychoglypha prita* (Milne), 1935
(Fig. 562-565, 657)

*Glyphopsycha pritus* Milne, 1935:25, 50. (Type locality: Banff, Alberta).


Males of this species are distinguishable from males of other species of *Psychoglypha* in the study area by relatively orbicular segment IX in lateral aspect (Fig. 562); by pattern of spines on posterior edge of tergum VIII (Fig. 563); and by cross-axially oriented, anteriorly concave, distally rounded median lobes of segment X. The female is unknown, but probably similar to that of *P. schmidtii* Nimmo (Fig. 570, 571).

Description. — Antennae dark brown; antero-mesal faces of scapes yellow, glabrous. Vertex of head almost black, with paler posterior warts. Thorax dark brown. Spur formula 1,2,2; dark reddish brown. Fore wing length of male 18.3 mm; pale orange-brown, irrorate; longitudinal silver line faint, merged with background; costal area clear. Venation not significantly different from *Limnephilus* spp.

Male genitalia. (Specimen from alpine meadows, east of Mt. Edith Cavell, Jasper National Park). Postero-dorsal edge of tergum VIII with short, stout, black spines; less dense anteriorly (Fig. 562, 563), mesally. Dorsal strap of segment IX wide, high, irregular, projected posterad over segment X. Main body of segment curved ventro-posterad, with deep notch on postero-lateral edges. Clasper small, fused to segment IX; directed dorso toward median lobes of segment X; lateral lobe acuminate in lateral aspect; median lobe short, rounded. Median lobes of segment X directed dorso-posterad; oriented cross-axially, with concave anterior faces, rounded tips. Cercus small, with lanceolate ventral lobe; dorsal lobe simple, lightly setose. Median shaft of aedeagus long, curved dorsad, with distal lobes one-third of length (Fig. 564, 565); ventral surface of shaft minutely spinate; lateral arms each shorter, also curved slightly dorso, long, thin, tapered to acuminate tips.

Female genitalia. Unknown.
Notes on biology. — The single locality in which I collected adults of this species is a very small, shallow, alpine pool at about 6,800', surrounded by sparse, short sedges. The specimens were all taken on October 3, crawling about on about 2 to 3 feet of fresh snow.

Geographical distribution. — The known range of this species extends from Alberta to Idaho (Fig. 657).

I have examined 17 males from the study area.

*Psychoglypha schmidi* Nimmo, 1965
(Fig. 566-571, 658)


Males of this species are distinguishable from males of *P. prita* (Milne) by pattern of spines on posterior edge of tergum VIII (Fig. 567); by claspers parallel to median lobes of segment X (Fig. 566); and by median lobes of segment X with acuminate tips in lateral aspect. Females are distinguishable from those of other species of *Psychoglypha* by small, bell-shaped segment X (Fig. 570); and by large, square, lateral lobes of vulval scale (Fig. 571).

Description. — Antennae orange-brown; scapes dark brown, with creamy, glabrous anteromarginal faces. Vertex of head orange-brown. Thorax dark reddish brown laterally, with pale yellow mesal stripe dorsally. Spur formula 1,2,2; spurs dark orange-brown. Fore wing length of male 20.3 mm; pale to dark orange-brown, faintly irrorate; stigmatic area grey-brown, costal area clear. Venation identical to *Limnephilus* spp.

Male genitalia. (Specimen from Bow Pass, Banff National Park, Alberta). Postero-dorsal edge of tergum VIII very densely clothed with short, black spines; depressed slightly, with two lateral protrusions (Fig. 566, 567). Segment IX relatively small, trapezoidal in lateral aspect. Clasper acute-triangular in lateral aspect, parallel to median lobes of segment X. Median lobes of segment X oriented cross-axially, with concave anterior faces, acuminate disto-anterad hook. Cercus bilobed; ventral lobe thumb-like; dorsal lobe inconspicuous, setose. Aedeagus very similar to that of *P. prita*, above, but lateral arms darker; base of median shaft pinched in (Fig. 568, 569).

Female genitalia. (Specimen from Bow Pass, Banff National Park, Alberta). Vulval scale very large, with massive, almost square lateral lobes (Fig. 571); median lobe very small, conical. Segment IX relatively small, irregular in outline, with ventro-lateral spines internally, directed anterad (Fig. 570); without ventro-lateral lobes. Supra-genital plate inconspicuous, with two median extensions directed posterad; very small. Segment X small, dark brown, bell-shaped in lateral aspect, open ventrally, with short, dorsal strap.

Notes on biology. — Adults of this species are found near small mountain and alpine streams ranging from trickles in alpine meadows to boulder strewn torrents. Flight dates range from September 10 to October 30.

Geographical distribution. — The known range of this species is in the western mountains of Alberta, close to the continental divide, and in British Columbia (Fig. 658). It ranges in altitude from 3,500' to 6,870'.

I have examined 31 specimens, 18 males and 13 females, from the study area.

*Psychoglypha alaskensis* (Banks), 1908
(Fig. 572-577, 659)

Glyphopsyche subborealis; Knowlton and Harmston, 1938:285.
Males of this species are distinguishable by short, thick, asymmetrical lateral arms of aedeagus (Fig. 574, 575); and by segment IX high, narrow in lateral aspect (Fig. 572). Females are distinguishable by long, projected, acute-triangular segment X (Fig. 576); by vulval scale massive, high, in lateral aspect; and by larger triangular lobes of segment IX lateral of segment IX.

Description. – Antennae pale yellow-brown; antero-mesal faces of scapes glabrous. Vertex of head pale yellow-brown. Thorax straw, to dark brown; dorsum of mesothorax with median, reddish yellow band. Spur formula 1,2,2; spurs dark brown. Fore wing length of male 16.6 mm; pale reddish brown. Venation essentially as in Limnephilus spp.; with large, pink stigmatic area.

Male genitalia. (Specimen from Wrigley Harbour, Mackenzie River, Northwest Territories). Postero-dorsal edge of tergum VIII with short, fine, dark brown setae dispersed in pattern shown in Fig. 572. Dorsal strap of segment IX narrow; main body of segment roughly rectangular in lateral aspect; high, narrow. Clasper short, flat posteriorly, fused to segment IX, short, high. Median lobes of segment X small, oriented longitudinally, directed mesodorsad (Fig. 573). Cercus bilobed, ventral lobe large, rectangular, slightly widened distally, setose; dorsal lobe small, bulbous. Median shaft of aedeagus thickset, minutely spinate basoventrally, with short, membranous distal lobes (Fig. 574, 575); lateral arms short, thick, asymmetrical in dorsal aspect (Fig. 575).

Female genitalia. (Specimen from Wrigley Harbour, Mackenzie River, Northwest Territories). Vulval scale large, truncate-triangular in ventral aspect; lateral lobes with lateral angles turned slightly dorsad, rounded, clothed with short setae; median lobe very short, triangular (Fig. 577). Segment IX quite small, sheathed laterally by rounded, triangular cerci (Fig. 576). Supra-genital plate short, very wide, crescentic in ventral aspect; with short setae. Segment X acute-triangular in lateral aspect; deeply incised dorsally; open ventrally.

Notes on biology. – Adults of this species are found near every sort of aquatic habitat from small, slow creeks to very large mountain rivers, and from sedge fringed ponds or sloughs. Flight dates range from September 10 to May 23 of the following year. I have records from the months of September, October, November, January, March, April and May, from the Banff area, collected by N. B. Sanson. Adults probably overwinter. The winter records presumably represent specimens emerging from hiding places in warm weather.

Geographical distribution. – The known range of this species extends from Alaska to Nevada and Michigan (Fig. 659). In Alberta it is found primarily in the mountains, but is also known from a very few localities well east of the mountains, which seem to contain a partly mountain fauna intermixed with a plains fauna. It has been recorded at altitudes up to 5,600'.

I have examined 51 specimens, 18 males and 33 females, from the study area and Northwest Territories.
Rhyacophilidae and Limnephilidae

Psychoglypha ulla (Milne), 1935
(Fig. 578-581, 660)


Males of this species are distinguished by massive, dorsally directed, longitudinally oriented, median lobes of segment X (Fig. 578); by setose postero-dorsal edge of tergum VIII; and by lateral arms of aedeagus attached well dorsad of median shaft, on membranous base (Fig. 580). Female unknown.

Description. — Antennae yellow; scapes slightly darker, with glabrous antero-mesal faces. Vertex of head red-brown, with yellow posterior warts. Thorax reddish, pale yellow laterally, to red-brown dorsally. Spur formula 1,3,3; dark reddish brown. Fore wing length of male 17.7 mm; stigmatic area pale rose; area anterad of longitudinal silver line pale yellow, with slightly darker areas between veins; immediately posterad of silver line is an area of chocolate brown posterad of which is an area of reddish brown to pale yellow. Venation identical to that of Limnephilus spp.

Male genitalia. (Specimen from Kicking Horse Camp, Yoho National Park, British Columbia). Postero-dorsal edge of tergum VIII protuberant, with mesal notch; with short, silky, somewhat hyaline setae. Dorsal strap of segment IX complex, with blunt, posteriorly directed process mesally (Fig. 578, 579); markedly truncate on ventral area. Clasper short, blunt, with concave inner face; with slight lateral flange. Median lobes of segment X large, distally black, oriented in vertical, longitudinal plane. Cercus distinctly bilobed; ventral lobe long, thin, clavate; dorsal lobe thumb-like, setose. Median shaft of aedeagus long, slender, widened slightly from very thin base; distal lobes long, membranous, held close together (Fig. 580, 581); lateral arms very long, thin, each of almost uniform thickness except for acuminate tip; black, attached well dorsad of base of median shaft.

Female genitalia. Unknown.

Notes on biology. — Adults are found near mountain creeks and rivers, with gravel beds. Flight dates of adults range from August 19 to October 3, with one record from May 23, which may be indicative of adult overwintering.

Geographical distribution. — The known range of this species extends from Alaska to California, and east to Alberta, where it appears to be confined to the vicinity of the continental divide (Fig. 660).

I have examined five males from the study area.

The Genus Phanocelia Banks

There is a single species in this genus, which is here recorded from Alberta.

Synopsis of characters. — Spur formula 1,2,2. Wings large, narrow, elongate; fore wing rounded apically; hind wing not so large, clearly indented postero-apically. R1 of fore wing poorly arched, united to Sc by cross vein; chord zigzag as in Chilostigmodes. Hind wing chord less disrupted than in fore wing.

Male genitalia with tergum VIII slightly cleft mesally, clothed with fairly large spines. Segment IX well developed. Cercus cup-like, horizontal. Median lobes of segment X long, vertical, fused at bases to cerci. Clasper large, massive, concave mesally. Aedeagus large; median shaft thin, unarmed; lateral arms very slender.
Female genitalia with very large vulval scale; median lobe minute; lateral lobes large, triangular, suspended laterally by tapered lateral strap to segment IX. Segment IX large; ventro-lateral lobes evident, fused to dorsal body. Segment X small, recessed into segment IX.

Phanocelia canadensis (Banks), 1924
(Fig. 557-561, 656)


Description. — Antennae dark brown to almost black; scapes short, swollen, with anteromesal faces lighter, especially in females. Vertex of head black. Thorax very dark brown to black. Spurs almost black, shorter, stouter than usual in Limnephilidae. Fore wing length of male 11.2 mm; clear, tinted dark brown; veins dark brown. Venation not significantly different from that of Limnephilus spp.

Male genitalia. (Specimen from 2 miles east of Nordegg, Alberta). Postero-dorsal edge of tegrum VIII minutely spiculate on two rectangular, lateral areas. Segment IX narrow, bowed anterad (Fig. 557); dorsal strap narrow, tapered dorsad. Claspers large, each triangular in lateral aspect, with large lateral lobes and minute mesal lobes; fused together at midline of body (Fig. 558). Median lobes of segment X short, rectangular processes curved dorsad from posterior edges of concave basal plates which are partly fused mesally. Cercus small, triangular, fused to segment X (Fig. 557). Median shaft of aedeagus long, thick, of roughly uniform width except for slight distal widening, curved strongly ventrad (Fig. 559); lateral arms attached to membranous pouch dorsad of aedeagal base; long, very slender, curved ventrad, distally acuminate.

Female genitalia. (Specimen from 2 miles east of Nordegg, Alberta). Vulval scale with minute, triangular median lobe; lateral lobes massive, triangular (Fig. 561) suspended from segment IX by tapered lateral strap (Fig. 560). Dorsal body of segment IX large, trapezoidal; ventro-lateral lobes discernible, not entirely discrete; trapezoidal also, fitted at right angles to base of dorsal body; fused ventrally. No evident supra-genital plate. Segment X of two distal lobes of posterior edges of segment IX, and ventral median lobe connected by lateral flanges to lateral lobes.

Notes on biology. — I have taken adults of this species at one locality: a deep, man-made swamp with thick growths of horse-tails (Equisetum) throughout, except at deepest parts, and with thick growths of sedges around edges. Dates of capture are September 22 and October 9.

Geographical distribution. — The known range of this species extends from Alberta and Northwest Territories to New Hampshire (Fig. 656). In Alberta it is known only from near Nordegg, at 4,470' altitude.

I have examined seven specimens, four males and three females, from the study area.

Unidentifiable Species of Limnephilidae

Under this title are described the females of five species of Limnephilidae for which no certain identity can be given, even to genus. The males are, of course, unknown, or at least unassociated.
Limnephilidae species 1
(Fig. 582-583, 661)

Description. — Antennae yellow-brown; antero-mesal faces of scapes glabrous. Vertex of head deep red-brown. Thorax deep brownish yellow laterally, deep red-brown dorsally. Spur formula 1,2,4; spurs brown. Fore wing length of female 19.5 mm; light brown, evenly and minutely irrorate; costal area clear. Venation similar to Limnephilus spp.

Female genitalia. (Specimen from Rapids Creek, Gap, Alberta). Vulval scale massive, parallelogram-like (Fig. 583); lateral lobes rounded-triangular; median lobe shorter, blunt, rounded distally. Segment IX large dorsally, with ventro-lateral lobes evident but imperceptibly fused to dorsal portion (Fig. 582). Supra-genital plate of medium size, slightly bilobed distally. Segment X deeply cleft mesally, with lateral lobes curved slightly ventrad, rounded dorsally.

Notes on biology. — The single specimen was taken at a concrete culvert over a rocky, fast, smoothly flowing mountain stream on May 7.

Geographical distribution. — The only known locality of this species is at Gap, Alberta, at about 4,250' (Fig. 661).

Limnephilidae species 2
(Fig. 584-585, 661)

Description. — Antennae brown. Vertex of head deep brown. Thorax dark red-brown, to almost black dorsally. Spur formula 1,3,4; spurs brown. Fore wing length of female 13.1 mm; pale greyish brown, faintly irrorate; costal area clear. Venation essentially identical to Limnephilus spp.

Female genitalia. (Specimen from Blindman River, at Hwy. 2, Alberta). Vulval scale with median lobe projected well posterd of laterals; strongly tapered distally, with truncate tip; lateral lobes triangular, concave ventrally (Fig. 585). Segment IX high, narrow, spindle-shaped in lateral aspect (Fig. 584); no evident ventro-lateral lobes. Supra-genital plate wide, high, arched dorsad, hyaline. Segment X cylindrical, with black, deeply divided dorsal arch, and clear, bilobed ventral trough which is recessed into dorsal arch.

Notes on biology. — The single female was taken under a concrete bridge over a small, slow, mud-bottom river on August 29.

Geographical distribution. — The locality at which this species was collected is well east of the foothills, in the plains (Fig. 661).

Limnephilidae species 3
(Fig. 144a, 144b, 586-587, 662)

Description. — Antennae light brown, scapes chocolate. Vertex of head deep chocolate-brown. Thorax chocolate-brown, darker dorsally. Spurs pale yellow. Fore wing length of female 6.9 mm; pale grey-brown, with distinct hyaline areas. Venation as in Fig. 144a, 144b.

Female genitalia. (Specimen from 26 miles south of Teepee Creek, Forestry Trunk Road, north of Hinton, Alberta). Vulval scale with median lobe much longer than angular lateral lobes; parallel-sided, rounded distally (Fig. 587). Segment IX high, parallel-sided in lateral aspect (Fig. 586); bowed anterad; without discrete ventro-lateral lobes. Supra-genital plate minute, short, hyaline. Segment X small, cylindrical, fused to segment IX but distinct due to pronounced declivity; cerci long, acute-triangular, fused at bases to dorso-lateral faces of
Nimmo

Limnephilidae species 4
(Fig. 145a, 145b, 588-589, 662)

This species bears a strong resemblance to the females of some species of *Lenarchus* as illustrated by Schmid (1952c), as does the species following (Fig. 590, 591).

**Description.** — Antennae brown, scapes darker, with antero-mesal faces paler, glabrous. Vertex of head dark chocolate-brown. Thorax dark brown dorsally, slightly lighter laterally. Spur formula 1,3,4; spurs brown. Fore wing length of female 14.1 mm; chocolate-brown, heavily irrorate, with larger areas of hyaline membrane. Costal area hyaline. Venation as in Fig. 145a, 145b.

Female genitalia. (Specimen from Amethyst Lakes, Jasper National Park; collected by H. Goulet). Vulval scale with massive, irregularly rounded lateral lobes (Fig. 589); median lobe short, rounded-rectangular. Segment IX high, wide dorsally, separated from segment X dorsally by weak declivity (Fig. 588); ventro-lateral lobes large, polygonal, not delimited from dorsal body. Supra-genital plate wide, lunate, membranous. Segment X bilobed; roughly triangular in lateral aspect, held roof-like dorsad of anal aperture.

**Notes on biology.** — The single specimen was taken under a rock close by the sedge pools just east of Amethyst Lakes, in near-alpine meadow, on July 7.

**Geographical distribution.** — The locality at which this specimen was taken is at 6,450’ altitude (Fig. 662).

Limnephilidae species 5
(Fig. 590a-590b, 663)

As with species 4 above, the female described here bears a strong resemblance to females of certain species of *Lenarchus*.

**Description.** — Antennae red-brown; antero-mesal faces of scapes lighter, glabrous. Vertex of head dark red-brown. Thorax dark red-brown dorsally, lighter laterally. Spur formula 1,3,4; spurs brown. Fore wing length of female 15.0 mm; chocolate-brown, distinctly irrorate, with larger hyaline areas; costal area clear. Venation essentially identical to that of *Limnephilus* spp.

Female genitalia. (Specimen from 3 miles east of Nordegg, Alberta). Vulval scale large, triangular; median lobe slightly tapered, thin, recurved distally (Fig. 590a, 590b); lateral lobes roughly triangular. Segment IX large, wide dorsally; separated from segment X by shallow declivity; ventro-lateral lobes large, triangular, not discrete from dorsal body. Supra-genital plate short, wide, evenly semi-circular. Segment X small, cylindrical at base, surmounted by two large, triangular, roof-like distal lobes held roof-like over anal aperture.

**Notes on biology.** — The single female was taken from a large man-made pond thick with *Equisetum*, and fringed with thick growths of sedges. Date of capture was August 8.

**Geographical distribution.** — The species is known from a single locality at Nordegg, Alberta, at 4,470’ altitude on the eastern edge of the Rocky Mountains (Fig. 663).
Fig. 130-137. Fore (a) and hind (b) wings of males, and females where indicated, of species of Limnephilidae. 130. Oligophlebodes ruthae Ross. 131. O. ruthae Ross (female). 132. Neothrema alicia Banks. 133. Homophylax crotchi Banks. 134. H. acutus Denning. 135. H. baldur Nimmo n. sp. 136. Glyphopsyche irrata (Fabricius). 137. Phanocelia canadensis (Banks).
Rhyacophilidae and Limnephilidae

Rhyacophilidae and Limnephilidae

ORIGINS AND RELATIONSHIPS OF THE FAUNA

Aims of the study. — The putative origins and relationships of the fauna of Rhyacophilidae and Limnephilidae, represented by 22 and 91 species respectively, of Alberta and eastern British Columbia, are described. Dispersal into the study area from unglaciated areas, or refugia, after the last major glaciation of North America, the Wisconsin, is discussed, and an attempt is made to determine the contributions of the glacial faunas of possible source areas to the present day fauna.

At the glacial peak the study area was, to all intents and purposes, a slate wiped clean by total ice cover. There was at least one minor exception to this, mentioned below. Such faunal movements should be amenable to clarification to a greater extent than pre-Wisconsin faunas at the species level and provide a very convenient unit with which to work due to the essentially clean sweep of the study area by the ice.

Procedures employed. — I shall attempt to arrive at a reasonable answer to the problem thus stated by an examination of a variety of factors. Firstly, the Wisconsin and post-Wisconsin history of North America is reviewed, especially the full extent of the ice sheets and major outliers, the locations of possible refugia, the subsequent retreat of the ice fronts, and the major post-glacial lakes and river systems and their development to the present. Secondly, a brief review of the major weather systems at the Wisconsin peak and at the present time is presented. Thirdly, an examination is made of the ranges of the Alberta and eastern British Columbia Rhyacophilidae and Limnephilidae, and of Alberta’s position with respect to the range areas, and each species is relegated to the range pattern which it best fits. Also, the species are examined as to groupings by similar habitats, to determine how this may be instructive. Lastly, an examination is made of the range relationships of each species to the remainder of its genus, or species group within a genus.

Literature on aquatic orders of North American insects. — While there have been many major faunal works on the wholly aquatic orders of North American insects, such as Betten et al. (1934), Milne (1934, 1935, 1936), Ross (1944), Flint (1960), and Denning (1963) on Trichoptera, Needham and Heywood (1929), Needham and Westfall (1955), and Walker (1953, 1958) on Odonata, Needham and Claassen (1925), and Frison (1935) on Plecoptera, and Burks (1953) on Ephemeroptera, none has attempted to elucidate the zoogeography or origins of the fauna dealt with.

Ross (1967) presented a study of evolution and dispersal of the world Trichoptera as a whole. In 1956 he dealt more fully with three families of Trichoptera. He also dealt (1953, 1958, 1965) with the effects of the Pleistocene and subsequent events on various nearctic insect groups, utilising primarily members of the wholly aquatic orders.

Various smaller papers dealing with members of discrete groups within wholly aquatic orders in North America also exist, such as those by Ross (1951, 1959) on Trichoptera, Ricker (1963), and Ross, Rotramel, Martin, and McAlpine (1967) on Plecoptera. But there is none, so far as I am aware, which deals with the aquatic fauna, or part of it, of a distinct geographical area such as I deal with here.

While reference is made in the following to papers which deal with non-aquatic groups of insects, where appropriate, in the elucidation of the problem before us, I make no reference to any such papers at this point. In dealing with fresh water insects, more especially the wholly aquatic orders, one is dealing with insects of a distinctly circumscribed habitat, at least in the immature stages, which would seem to set distinct limits to their dispersal patterns and pose problems peculiar to such groups. Ross (1956) mentions this especially with reference to the cool-adapted Trichoptera.
Synopsis of the glacial history of North America from the peak of the Wisconsin glaciation to the present

Extent of Wisconsin glaciation. — Figure 664 (from Flint, 1957 and Prest, 1969) outlines the maximum extent of ice cover at the peak of the Wisconsin glaciation in North America. While the continental ice cover originated from several centers to form a series of coalescing ice fields, in effect the land mass of northern North America appears to have been under a single mass of ice which connected, by way of the Arctic archipelago, to the still extant Greenland ice cap. In the west the southern ice margin closely but irregularly paralleled the Canada-United States boundary. South of this margin were located many ice fields (as many as 70 according to Flint, 1957) of varied extents scattered throughout the Cordillera. In the east the ice margin extended further south. Both coasts and their outlying islands were apparently icebound, as was also the Arctic archipelago. Alaska was only partly glaciated, most of the Yukon valley being ice free; this condition extended over into north east Siberia. The line passing north west from southern Alberta to the Arctic Ocean is the location of the line of coalescence between the Laurentide ice sheet to the east and the Cordilleran ice sheet to the west, the eastern edge of which flowed east through the Rocky Mountains to the Great Plains, there to be forced south east by the Laurentide sheet.

The time of initiation of final degradation of the Wisconsin ice is uncertain, and could have varied from place to place, but evidence suggests an average value of about 10,000 B. P., despite at least some readvances in certain areas. Gravenor and Bayrock (1961) estimate the final recession, or melting back, of the Wisconsin ice from southern Alberta to have started about 11,000 years B. P. In that area they consider the ice to have receded in a northerly or north easterly direction. This refers to the Laurentide ice sheet retreating from the line of coalescence with the Cordilleran ice sheet of the Rocky Mountains. The Laurentide sheet is now extinct but the Cordilleran sheet still exists in the scattered glaciers and ice fields of the Rocky Mountains, and can be assumed to have melted much more slowly than the Laurentide, presumably due to higher altitudes and location in deeper valleys which might be supposed to provide some protection from ablation processes. Presumably, also, the ice would be deeper in the major valleys and simply take longer to melt. It is interesting to speculate on the possibility that, at the time of general recession, while the greater part of Canada may still have been under ice, a corridor of deglaciated territory may have opened between the northwestern United States, western Canada, and the Arctic Ocean, possibly even through to the unglaciated part of Alaska, as this was relatively close to the line of coalescence (Fig. 664). Such a corridor would, in all probability, permit biotic interchange between Alaska and southern North America prior to complete deglaciation, possibly with results different from those that might be expected if the ice were to disappear uniformly, leaving the northern half of North America open to unimpeded colonisation. I have been unable to discover any record of such a corridor in the literature.

Locations of possible unglaciated areas. — Areas which were unglaciated during the Wisconsin, or any other glaciation, are of prime interest to the biogeographer, as they may have acted as refugia or foci of redispersal for plants and animals at a later date. In Fig. 664 roman numerals indicate the locations of known, or postulated, unglaciated areas and, therefore, possible refugia.

The Beringian refugium (I) is known definitely to have existed and includes the unglaciated areas of Alaska and northeast Siberia (Ball, 1963; Munroe, 1956). Prest, Grant, and Rampton (1968) in their 'Glacial map of Canada', and Prest (1969), show the western areas of the Yukon to have been unglaciated also. As Pévé, Hopkins, and Giddings (1965),
in their Fig. 2, show the unglaciated area of central Alaska to have extended widely to the Alaska-Yukon boundary, to coincide at least approximately with the unglaciated portion of the western Yukon, this area must have formed part of the Beringian unglaciated area and, therefore, of the Beringian refugium. Flint’s map of Eurasia (1957: Fig. 24-1, and plate 3) shows a large unglaciated area between northeast Siberia and the remainder of Eurasia. From his map, however, it also appears that, at least in the Wisconsin glaciation, corridors may have existed to north or south of the glaciated area of Siberia, by which biotic movements may have occurred.

Flint (1957) shows all of northern Canada under ice, but three areas are thought to have been unglaciated and acting as refugia, at least for plants, at the time of the Wisconsin peak (Ball, 1963). There is some doubt as to the existence of the Mackenzie refugium (II) which, if it existed, was small. A refugium has been postulated for the western Arctic islands (III) but Savile (1961) and Munroe (1956) both express doubt on this point, for rather different reasons. Savile believed the islands to have been unglaciated but covered with snow for too long periods to permit survival. However, Leech (1966) does not believe that periods of snow cover, of one or more years, necessarily eliminate life. Munroe states that the islands were under such a load of ice that they were very largely submerged, as evidenced by pronounced emergence from the sea in recent times. Prest (1969) shows areas II and III to have been unglaciated. Leech (1966) is of the opinion that a refugium existed in northern Ellesmere Island, having investigated the spider fauna of the Lake Hazen area. The third possible refugium of the high Arctic is Peary Land in northern Greenland (IV), which seems definitely to have been unglaciated and to have acted as a refugium, for plants at least (Savile, 1961). Leech (1966), without limiting his statement to any one part of the biota, upholds the existence of the Peary Land refugium. As he decides that adjacent northern Ellesmere Island was a refugium for spiders, it is logical to assume that Peary Land would have been capable of supporting other animal life also.

One or more unglaciated areas have been postulated for eastern North America (V) (Fernald, 1925; Munroe, 1956; Lindroth, 1963) but, again it is uncertain whether they existed at all and, if so, where.

One other area within the ice sheet is known to have been unglaciated. This is the height of land of the Cypress Hills of southeastern Alberta and southwestern Saskatchewan (VI) (Westgate, 1964; Gravenor and Bayrock, 1961). The remaining unglaciated area, undoubtedly a refugium, is the entire southern half of North America (VII), except for the highland glaciers of the Cordillera.

Ross (1965) surmises that small, very local, refugia may have existed within the Cordilleran ice mass, on the higher mountain peaks rising above the ice.

Ball (1963) states that the distributions of most of the northern biota are explainable by dispersal from the two major unglaciated areas of central Alaska (I) and the area south of the main ice sheet (VII).

The distribution of the present day nearctic glaciers is given in Fig. 665.

Lakes of Wisconsin and post-Wisconsin time. — As an aid to understanding present distributions and dispersal routes of aquatic insects, the distribution and drainage patterns of the lakes of North America during the Wisconsin glaciation and after are examined. The information presented is derived from Flint (1957), Elson (1967), and Prest, Grant, and Rampton (1968). Figure 666 outlines the major lakes of North America during and after Wisconsin time. Lakes Lahontan and Bonneville lay south of the ice sheet. The remainder were covered by ice at the peak of the Wisconsin and formed along the southern edges of the ice as it retreated northward. In most cases each lake is reduced in size at the present time but only Lakes Ojibway-Barlow and Lahontan have essentially disappeared.
There were multitudes of small lakes, then and now, but they do not concern us here. The outlets of each lake are indicated, each having had several over a period of time as the ice edge retreated or readvanced.

Flint (1957) presents a history of the Great Lakes. Briefly, they drained south to the Mississippi River by various routes until eventually they were allowed to take their natural course east to the St. Lawrence River by the final recession of the ice. Lake Ojibway-Barlow was relatively small and drained south and east via the Ottawa valley. It was at one time joined to Lake Agassiz.

A history of Lake Agassiz is given by Elson (1967) in some detail. The lake varied greatly in size and position, draining first to the south and the Mississippi, then through several outlets, to the south as before, to the Great Lakes via Lake Nipigon, and to the north west and the Athabasca River. Finally, as the ice receded, it drained northeast to Hudson Bay and shrank to the present Lake Winnipeg. The Saskatchewan River drained eastward to Lake Agassiz and may at various times, though Elson does not provide information on this, have successively formed part of the Gulf of Mexico, Arctic, and finally the Hudson Bay watersheds. Prest, Grant, and Rampton (1968), in their 'Glacial map of Canada', show all western Canada, virtually to the western mountains, to have been under lake water at one time or the other since Wisconsin time. Presumably, apart from Lake Agassiz, small lakes or sloughs were involved.

Lake Lahontan apparently had no outlet. Lake Bonneville at one stage in its history drained north west to the Columbia River and the Pacific Ocean.

The study area of Alberta and eastern British Columbia embraces the headwaters of large rivers important to each of the major watersheds of North America except the Atlantic (Fig. 666; the darkened rivers). This curious juxtaposition of major watersheds seems to provide ideal conditions for dispersal of those aquatic organisms which, having their immature stages in aquatic habitats are, nevertheless, able to fly between neighbouring bodies of water as adults.

The large post-glacial lake system of North America, temporary though some of its constituents may have been, probably provided very suitable pathways for dispersal of aquatic organisms from east to west and vice versa, more particularly for still water forms. The entire system stretching from Alberta to Ontario, Quebec, and the northeastern United States has, at various times since the last glaciation, formed a gigantic, shifting network of waterways. It seems possible that the distribution patterns of Trichoptera may at least partially reflect this, and the point is examined below.

**Synopsis of climatic history of North America from Wisconsin time to the present**

Bryson and Wendland (1967) proposed a sequence of weather pattern shifts from the peak of the Wisconsin glaciation to the present. They describe the effects of the shrinking Laurentian ice mass on air masses and the subsequent effects on weather. They consider the effects of climatic changes on the biota, largely the forest and grassland biotas along the southern edges of the ice sheet as it contracted. They do not consider it reasonable to regard vegetation zones to be controlled and located where they are simply by single factors, no matter how closely the boundaries of the zone and any value of the factors may coincide. The control must be the result of a variety of factors acting as annual, or at least seasonal, means. They utilise the mean positions of the various frontal zones and determine the possible past positions by an examination of what is known about former and present vegetation zones. I summarize their plotting of the postulated winter and summer mean positions
of the Arctic frontal zones for the period about 10,000-13,000 years B. P., and for the present time (Fig. 667). The general trend towards the present was for the frontal zones to migrate north as the ice sheet dwindled. In the period 3,500-5,000 years B. P. they estimate that the fronts were actually further north of their present positions, but have readvanced slightly southward.

The Arctic frontal means are used as indicators of cooler areas of the continent, and hence of increasing warmer conditions south of the mean frontal zones as they tended northward. The result, as shown in Bryson and Wendland, has been a shift northward of the North American biotic zones, more particularly, for the central plains of North America, of the boreal forest, and the grasslands. At about the time of retreat of the glaciers from Alberta the area was under boreal forest, which has since moved northward to make way for the present day grasslands of the southern part of the province. A similar effect can be expected in the mountains, except that it would be an altitudinal shift. Bryson and Wendland indicate that there was essentially no tundra belt between the receding ice front and the encroaching boreal forest belt; that, in fact, the forest may have established itself immediately icebound moraine was uncovered. Exactly where tundra may have survived as such is not indicated, but it may reasonably be expected to have existed in the various far northern unglaciated areas, or refugia. The overall result was a general shift of the various floras and faunas northward, and upward in the Cordillera, with subsequent isolation of at least some species on scattered mountain ranges.

As to the speed with which the biota responded to climatic shifts, Bryson and Wendland indicate that deglaciation is due to climatic changes and lags behind these changes. The result is that the areas beyond, and close to the edges of the ice sheet, were climatically suitable for vegetation prior to removal of the ice. That is, there is no reason to doubt that, for example, there could be forest right up to the edges of the ice (see preceding paragraph). Lindroth (1965), investigating the vegetated area of Skaftafell adjacent to a receding glacier in Iceland, concludes that there is nothing unusual in vegetation occurring in immediate proximity to glacial ice, whether advancing or receding. Presence or absence of vegetation in such a situation is dependent on macro-climate rather than on the presence of the ice itself. A superb example of dense Nothofagus forest in Argentina within feet of an active glacier is given in plate 14 of Tilman (1957). Westgate (1964) presents evidence of ponds with vegetation and animals not only at the ice edge, but on the ice itself, wherever debris was sufficiently accumulated to provide a substrate for the biota.

In the west the mean frontal zones clearly trend north west toward Alaska or the Mackenzie delta area (Fig. 667). This is true of both the ancient and modern frontal zones, and for the zones of intermediate periods postulated by Bryson and Wendland. This appears probably to be due to the presence of the western Cordillera, which acts as a barrier, preventing the fronts from extending westward to the coast. Bryson and Wendland show the remaining ice mass (at about 8,000 years B. P.) to be located between Great Slave Lake and Labrador, and between northern Baffin Island and northern Ontario. It is reasonable then to suppose that the ice tended, at least at its southern and western boundaries, to retreat along the frontal zones. Here is some support for the corridor between Alaska and the unglaciated portion of North America, east of the mountains, and right through the study area, as postulated above.

Distribution of the Rhyacophilidae and Limnephilidae of Alberta and eastern British Columbia

The species of Rhyacophilidae and Limnephilidae known from the study area have been
found to fall into 12 basic distribution patterns. These are outlined in Fig. 668 and 669. I have grouped them into two primary types for convenience. The first type comprises those species which are confined strictly to western North America, tending generally to follow the various ranges of the western Cordillera (Fig. 668). The second type comprises those species which extend beyond, or exist only east of the Cordillera (Fig. 669). The patterns as illustrated outline the general area occupied by the species from which they are drawn. They are not exact delineations of species ranges.

The ranges of Trichoptera in North America are, as yet, relatively poorly known, and much intensive collecting is required before accurate statements can be made about range patterns. However, for the present study, current knowledge will have to suffice. The species ranges used in determining these range patterns do not necessarily extend throughout the full extent of the patterns to which they belong. The boundaries are really composites of species ranges which appear to follow a common pattern, however incompletely.

Table 2 lists the range patterns in numerical order, giving the species known from each, and the range map number of each species in the taxonomic portion of this study. Following is presented a brief outline of each range pattern, in numerical order.

Range pattern 1. This pattern extends from central Alaska south, embracing the entire western Cordillera, as far south as the southwestern United States. The Alberta species included are mostly mountain stream species, but a few are usually found at higher altitudes, in the bogs or pools of the high passes and alpine meadows. This pattern is equivalent to Munroe's (1956) type W5.

Range pattern 2. This pattern extends from central Alaska to Colorado, along the eastern ranges of the Cordillera. Only three Alberta species are included, two of which are species of the lower mountain streams; the third, *Imania tripunctata*, is found at higher altitudes and is rather uncommon.

Range pattern 3. This pattern is similar to type 1, but without the extension to the Yukon and Alaska. It contains a large number of species, most of which are inhabitants of mountain streams of varying degrees of rapidity and turbulence. This pattern is equivalent to Munroe's type W3.

Range pattern 4. This pattern extends from the Alberta Cordillera to California, via Idaho, Washington, and the Cascade ranges. It contains a small selection of species which inhabit the lower mountain streams and lakes.

Range pattern 5. Species included in this pattern follow the eastern ranges of the Cordillera from Alberta to Colorado, and inhabit mountain streams. This pattern is equivalent to Munroe's type W2.

Range pattern 6. This pattern embraces species which are either very restricted in range, largely to the Cordillera of Alberta, or are known only from the type localities; several are described above as new. It is not so much a pattern as a collection of species which cannot yet be assigned to any of the other patterns. Specimens of several of the species may simply be rarely taken, and thus are poorly known. The range pattern embraces the Cordillera of Alberta, British Columbia, Washington, and Idaho. The great majority of included species are found near mountain creeks or ponds ranging to the higher alpine meadows, and largely comprise members of genera which are reputedly rare (Ross, 1950b; Denning, 1964; Wiggins and Anderson, 1968).

Range pattern 7. This pattern embraces the greater part of North America, extending from Alaska east to Newfoundland and Greenland, and south east to New Mexico. In the United States it is restricted largely to the eastern ranges of the Cordillera. The species included in this pattern inhabit streams and rivers.
Fig. 664-669. 664. Maximum distribution of glacial ice in North America at the peak of the Wisconsin glaciation, showing locations of known and suspected unglaciated areas (roman numerals), and line of coalescence between the major ice masses (toothed line). Compiled from Flint (1957), Westgate (1964), and Prest, Grant, and Rampton (1968). 665. Present day distribution of nearctic glaciers. From Flint (1957). 666. Composite map of major periglacial and pluvial lakes of North America (black areas) and present major lakes (hatched areas), showing various drainage patterns which existed post-glacially and which are now extinct (arrows). A - Lake Aggasiz; B - Lake Bonneville; G - Great Lakes; L - Lake Lahontan; O-B - Lake Ojibway-Barlow. Compiled from Flint (1957), and Elson (1967). 667. Map of North America showing the mean positions of the Arctic frontal zone 10,000-13,000 years B. P. in summer (B. P. - S.) and winter (B. P. - W.). Derived from Bryson and Wendland (1967). 668. Range patterns 1-6 exhibited by Alberta species of Rhyacophilidae and Limnephilidae. 669. Range patterns 7-12 as exhibited by Alberta species of Rhyacophilidae and Limnephilidae.
Table 2. Species of Rhyacophilidae and Limnephilidae from the study area listed under the range pattern to which each belongs.

<table>
<thead>
<tr>
<th>Pattern no.</th>
<th>Species</th>
<th>Map Fig.</th>
<th>Pattern no.</th>
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*Limnephilus infernalii* (Banks) 613
*Limnephilus ornatus* Banks 615
*Limnephilus externus* Hagen 617
*Limnephilus femoralis* (Kirby) 620
*Limnephilus minusculus* (Banks) 631
*Limnephilus hyalina* Hagen 627
*Limnephilus rhombicus* (L.) 634
*Limnephilus sublunatus* Provancher 607
*Limnephilus perpusillus* Walker 628
*Pycnopysche guttifer* (Walker) 652
*Nemotacllae hostiliis* (Hagen) 637
*Asynarchus curtus* (Banks) 642
*Anabolia bimaculata* (Walker) 640
*Apatania stigmatella* (Zetterstedt) 602
Range pattern 8. This pattern comprises an eastern and a western region. The western region extends from Alaska to California and Colorado, and eastward almost to Manitoba. The eastern region extends from Manitoba eastward to Newfoundland. There are no records known, for any of the species which are included within this pattern, for the intermediate area, which variously includes all or parts of at least Saskatchewan and Manitoba. The species included here variously inhabit, in the study area, mountain creeks, the swamps of the lower mountain valleys, and the higher passes.

Range pattern 9. This pattern extends from Alaska southeastward, in a widening belt, to Colorado and Ontario. In the United States Cordillera it is confined to the eastern ranges south of Idaho. The included species inhabit primarily lakes, sloughs, or streams in low mountain valleys.

Range pattern 10. This pattern embraces the great central plains of North America and includes only two species. The pattern is equivalent to Munroe's (1956) type C4.

Range pattern 11. This pattern extends from the eastern edges of the Cordillera in Alberta, to the Great Lakes states of the United States, Labrador, and Newfoundland. Alberta represents the western limits for all the included species of this type. These species occur in lakes, sloughs, and slower streams. This pattern coincides with Munroe's (1956) type B.

Range pattern 12. This pattern embraces virtually all of Canada, with its southern boundary extending into the United States south of the Great Lakes. At least one species, *Apatania zonella*, is known to extend northward to the Arctic archipelago. The included species emerge from lakes, sloughs and, perhaps, the slower rivers.
Distributional relationships of Alberta species of Rhyacophilidae and Limnephilidae to the remainder of their respective genera or species group

In this section are examined the spatial relationships of the Alberta Trichoptera dealt with in this study to other species of their respective genera, or species groups within genera. The purpose in so doing is to determine whether it is possible to deduce the provenance of the Alberta species after the Wisconsin glaciation.

The Rhyacophilidae. — None of the North American species of Rhyacophilidae is known to be holarctic. With the exception of two transcontinental species, the Alberta species are restricted to the western Cordillera.

The alberta group. Of the four species known to belong to this group, kinaeidai, alberta, tucula, and glaciera, the last three are represented in the study area; kinaeidai is known only from the Cascade ranges of Washington (Ross, 1956); glaciera is known only from Montana and Alberta (Fig. 106). The two species alberta and tucula are known from Alaska to the Rocky Mountains of the United States (Fig. 104, 105). These two species are very similar and occupy somewhat mutually exclusive ranges, tucula to the west, alberta to the east; there are no records from the Yukon.

The voixia group. Of the two very similar species of this group only voixia is known from the study area; its range extends from Alaska and the Yukon to Idaho (Fig. 107). The other species, harmstoni, is known only from Colorado and Utah.

The acropedes group. Ross (1956) lists 11 species in this group, three of which are eastern Asiatic. According to Ross (1956) the seven North American species are confined to the western Cordillera, except for acropedes, which is also known from eastern North America. Ross considers that the group originated in eastern Asia, spread to western North America, whence a second, reverse, interchange occurred, back to Asia, to give the present set of species. As this undoubtedly occurred prior to the Wisconsin glaciation it is of little interest at present. According to Ross the North American species of the group are restricted to the western coastal ranges, except for acropedes (Fig. 108). Smith (1968) records vao from as far east as Idaho. I record vemna from Alberta; Smith records it from Idaho (Fig. 120). Thus these two species are not as restricted as Ross supposed. Ross derives acropedes from vao as the result of an eastward spread, after which acropedes spread west to coincide with vao. Thus the origin of the North American species of this group is apparently located in the coastal mountain ranges. It may be supposed that the ranges of the species prior to the Wisconsin glaciation were much as they are today, south of the southern limit of ice.

The invaria group. This group has an Appalachian branch of six species, and a Cordilleran branch of five species. Two of the western species, bifila and coloradensis, are known from the study area (Fig. 109, 110) and are general throughout the Cordillera. Two other species, amabilis and kernada, are known only from southern California, and the fifth, insularis, is known only from Vancouver Island.

The hyalinata group. This group, comprising four species, is of peculiar distribution; three species are located in western North America, while the fourth is known from the Caucasus. Ross (1956) cannot be certain that this European species belongs to this group, as he has seen only drawings. Only one North American species, hyalinata, is known from the study area; it is widely distributed in the Cordillera as a whole (Fig. 111). Of the remaining two species, sonoma is known only from California, and vocala from the Cascade ranges from Oregon to British Columbia.

The sibirica group. This is a large group of 26 species, four of which are known from the study area. These four species are rather dissimilar belonging to different lineages within the
group (Ross, 1956:95). One species is known from Europe, several more from eastern Asia, and the greater number from North America, being divided into eastern and western groups. Ross (1956) postulates a western North American origin for the group, with dispersal in time to Asia and eastern North America. There are no holarctic species. Of the Alberta species, two, *vepula* and *pellisa*, are widespread; *vepula* ranges from Alaska to California (Fig. 113); *pellisa* appears to be limited to Alberta in the north, is not recorded from British Columbia, though it almost certainly occurs there, and extends south by both the coastal and eastern ranges of the Cordillera (Fig. 114). Of the other two species, *belona* is restricted to the Idaho-Alberta area, and *rickeri* extends from the Alberta-British Columbia Cordillera to Alaska.

The *betteni* group. This group comprises eight species, all confined to the Cordillera of western North America. All but the two species known from the study area are confined to the Cascade ranges of California and Oregon. Of the two known from Alberta one, *chilsia*, is known only from the Alberta Cordillera (Fig. 115); the second, *vaccua*, is widespread, but barely extends south along the eastern ranges of the Cordillera (Fig. 116). Ross (1956) is of the opinion that the group originated in the coastal ranges and has spread eastward from there.

The *vobara* group. Two species comprise this group, *iranda* and *vobara*, of which the latter is known from the study area. The other species is known from the coastal ranges of Oregon.

The *angelita* group. This group contains three species, two of which, *perplana* and *vuzana*, are known only from the Cascade ranges of the coast; the third species, *angelita*, is widespread throughout the Cordillera, from the Yukon to California and Colorado (Fig. 117). It is also recorded from the northern Appalachians, in what must surely be an isolated population; it seems reasonable to suppose that isolation occurred post-glacially.

The *verrula* group. Only one species, *verrula*, is known in this group. It ranges widely from Alaska to California and Colorado (Fig. 118).

The *vagrita* group. The two very similar species of this group are both known from the study area. These are *vagrita* and *milnei* (Fig. 119). Only *vagrita* is widespread, extending to Utah; *milnei* is known only from the type locality at Banff, Alberta.

The Limnephilidae. — The 91 species known from the study area are not distributed so narrowly as the Alberta Rhyacophilidae. Some species are known only from the western Cordillera of North America; others are widespread transcontinentally, and from north to south; others are holarctic, if not circumpolar.

The genus *Dicosmoecus*. Of the 10 species of *Dicosmoecus* (Schmid, 1955), two are known from the study area. Of these two, *atripes* is widespread throughout the Cordillera, from Alberta and British Columbia to California and New Mexico (Fig. 592); *jucundus* (Fig. 593) has a similar distribution except that it is unknown from the eastern ranges. The remainder of the genus is distributed between eastern Asia (two species) and western North America (eight species). Of the North American species, the general distributional pattern is centered on the coastal ranges from California to British Columbia, with one species known only from Alaska.

The genus *Onocosmoecus*. Of the eight species of *Onocosmoecus* (Schmid, 1955) only one is known from the study area (*unicolor*). This species is distributed from Alaska to California, New Mexico (Fig. 594), and eastern North America, with a large gap between the eastern and western ranges. As this species is known from streams of the plains regions of Alberta the gap must be viewed with suspicion, as being due to insufficient collecting. One species of *Onocosmoecus* is known from eastern Asia, the remainder being North American and confined to the Cordillera with the exception of *quadrinotatus*,
which ranges from Newfoundland to Michigan and the White Mountains of New Hampshire.

The genus *Imania*. Of the 10 known species of *Imania*, Schmid (1955) lists eight; the ninth is described above as new; the tenth is described by Schmid (1968) as new. Four species are known from the study area: *bifosa, cascadis, tripunctata*, and *hector*. Of these, *hector* is known only from Alberta (Fig. 597); *bifosa* is known only from Alberta and British Columbia; *cascadis* from Washington, Oregon, and Alberta (Fig. 597); and *tripunctata* is widespread from Colorado and Washington to Alaska (Fig. 596). Ross (1950b) refers to *tripunctata* as occurring as isolated, higher altitude, populations, particularly in the southern extremities of its range. Of the genus as a whole one species is known from eastern Asia; the remaining four species are known from isolated localities in Colorado (*gnathos*), Nevada (*renoa*), and Washington (*acanthis* and *cidoibes*).

The genus *Amphicosmoecus*. This genus is represented by a single species, *canax*, which is widespread from Alberta and British Columbia to California and Utah (Fig. 595).

The genus *Ecclisomyia*. Of the six species of this genus (Schmid, 1955), two are known from the study area (*maculosa* and *conspersa*); a third, undescribed species is represented by a single female. Both Alberta species are widespread in the Cordillera. The species *conspersa*, which ranges from Alaska to California and New Mexico (Fig. 599), has a more extensive known range than *maculosa*. The latter ranges from Alberta and British Columbia to Colorado (Fig. 598). Of the remaining four species two, *digitata* and *kamtschatica*, are known only from eastern Asia, and the other two, *scylla* and *bilera*, are known only from British Columbia to Oregon, and California respectively.

The genus *Apatania*. This genus contains 50 species, five of which are known from the study area; one is described above as new. Twelve species are recorded from North America; of these, three are holarctic and known from Alberta or just north of Alberta. The remaining species of the genus are widespread through Eurasia. The species known from the study area, or closely adjacent areas, are *zonella, stigmatella, shoshone, crymophila*, and *alberta*. Of these species *zonella* (Fig. 600), *stigmatella* (Fig. 602), and *crymophila* (Fig. 601) are northern in distribution in North America, and holarctic in total. *A. stigmatella* has been recorded from Colorado; this is either an error, or represents a peculiarly isolated population. Of the remaining two species *shoshone* is known from Alberta south, along the eastern Cordillera, to Colorado; *alberta* is known only from around Banff, Alberta.

The genus *Oligophlebodes*. Of the seven species of *Oligophlebodes* three are known from the study area, one being described above as new. Of the Alberta species *zelti* is known only from several localities in Alberta (Fig. 604); *sierra* is widespread from Alberta and British Columbia to Colorado and California (Fig. 604); and *ruthae* is confined to the eastern ranges of the Cordillera, from Alberta and British Columbia to Oregon and Utah (Fig. 603). Of the four remaining species of the genus one is known only from Colorado (*ardis*), another is known only from New Mexico and Utah (*sigma*), the third is widespread from New Mexico to Wyoming and South Dakota, and is the most easterly species of *Oligophlebodes* (*minuta*), and the fourth (*mostbento*) is known only from Oregon.

The genus *Neothremma*. Of the four species of *Neothremma* (Schmid, 1955; 1968) two, *alicia* and *laloukesi*, are known from the study area; the total known range of *alicia* extends from Alberta and British Columbia to Oregon and Colorado (Fig. 605). At present *laloukesi* is known only from Alberta. The other two species (*didactyla* and *galena*) are known only from Washington.

The genus *Homophylax*. Denning (1964) revised this genus, and listed eight species. One further species was described above as new, raising the total to nine. Three species are
known from the study area (crotchii, acutus, and baldur). Of these crotchii is known only from a very small range, from southern Alberta to Vancouver Island and Washington (Fig. 606); acutus is known only from Idaho and Alberta (Fig. 606) but, being only recently described by Denning (1964) will almost certainly be found to extend further; and baldur is known only from Utah and far southwestern Alberta (Fig. 607). Of the remaining six species andax is known from southeast Alaska to Oregon; flavipennis is known from Colorado to Montana; insulas is known only from California; renzii only from California; nevadensis from California and Nevada; and adriana only from New Mexico. More so than other rare genera, Homophylax appears to be divided into distinct eastern and western species groups. Much more almost certainly remains to be known of the range of species of Homophylax. The genus is rarely represented in collections and appears to be rare in nature. This apparent rarity may, however, be due to secretive habits and high altitude distribution, thus making collection difficult.

The genus Limnephilus. This is one of the larger genera of Trichoptera, and the largest of the Limnephilidae. Schmid (1955) lists 140 species in the genus of which seven are incertae sedis. In this study two new species of Limnephilus are described, raising the total to 142. Of this number of species one is listed from South America, 63 from North America only, and seven are holarctic. Of the 33 species known to occur in the study area one is undescribed (the female only is known), and six are holarctic.

Of the rhombicus group only one species, rhombicus, is known from the study area. This species is holarctic in distribution with an extensive North American range (Fig. 634); the remaining four species are variously known from Asia and eastern Europe, but one is known from Spain (Schmid, 1955). This group would appear to be decidedly Eurasian in origin.

Of the 11 species of the subcentralis group six are known from the study area, including one new species. These species are sansoni, extractus, hageni, sublunatus, partitus, and susana. One other species is undescribed as only the female is known. None of the Alberta species are holarctic; sansoni extends from Alaska to Colorado, along the eastern ranges of the Cordillera (Fig. 608); extractus extends from Alberta and Great Slave Lake to New Hampshire (Fig. 609); sublunatus extends from British Columbia to Colorado and Quebec (Fig. 607); partitus extends from British Columbia to the Northwest Territories and Newfoundland (Fig. 611); and susana is known only from the type locality in Alberta (Fig. 612). The remaining five species are known variously from Europe to Siberia, with one species, elongatus, from the Northwest Territories.

Of the seven species of the stigma group two, infernalis and indivisus, are known from the study area. Both are distributed in a northern transcontinental pattern, infernalis from Alaska to New Hampshire (Fig. 613), and indivisus from British Columbia to Illinois and Nova Scotia (Fig. 614). The remaining five species are variously known from Europe to eastern Siberia.

Only one species, ornatus, is known in the ornatus group. Its range in North America is northern transcontinental, from Alaska to Illinois, Newfoundland and Greenland (Fig. 615). Schmid (1955) also reports it from Japan.

One of the two species of the picturatus group is known from the study area. This species, picturatus, is holarctic, ranging from Sweden to North America, where it extends from Alaska to Colorado and Hudson Bay (Fig. 616). The second species is known only from British Columbia.

Of the two species of the externus group, like the picturatus group, one, thorax, is isolated in North America, in Utah; the second species, externus, is holarctic, ranging from Europe to North America. In North America it ranges from Great Slave Lake to California.
and Newfoundland (Fig. 617).

The sericeus group, with two species, is limited to North America. The species known from the study area, sericeus, is northern transcontinental in range, from Alaska to Oregon and Maine (Fig. 618) with an apparent mid-continental gap. The second species, fagus, is known only from Oregon.

Of the three species of the morrisoni group one, lopho, is known from the study area. This species is restricted to Oregon, British Columbia, and Alberta (Fig. 623). The remaining two species, castor and morrisoni, are restricted to the western ranges of the Cordillera.

The stitchenis group contains seven species, of which three are known from the study area. These are moestus, cockerelli, and valhalla. The group is restricted to North America. With the exception of moestus, all are restricted to the western Cordillera. Of the Alberta species moestus is most widespread, ranging from British Columbia to Colorado, Newfoundland, and Greenland (Fig. 621); cockerelli is restricted to the eastern ranges of the Cordillera (Fig. 622); and valhalla is known only from the area of the Albertan continental divide (Fig. 622).

The single species of the luridus group known from the study area, femoralis, is holarctic in distribution, ranging from Europe to North America. It ranges from Alaska to Washington, Maine, and Greenland (Fig. 620) in North America. The other known species, luridus, is known only from northwest Europe.

Of the six species of the fenestratus group two, minusculus and kennicotti, are known from the study area. Of these two minusculus is widespread, ranging from Alaska to Colorado and Labrador (Fig. 631); kennicotti ranges from British Columbia to Newfoundland (Fig. 632), with records from Greenland, so it is probably also present in northern Canada, though there are no records known to me. The remaining four species are palaearctic (dispar), known only from Oregon (sylviae), restricted to the eastern ranges of the Cordillera (coloradensis), or holarctic (fenestratus).

The nógus group contains one species, nógus. It is not known from Alberta, but has been taken at Hosmer, British Columbia, only 30 miles from Alberta, and within the study area. Its known range extends from southern British Columbia south, along the western coastal ranges of the Cordillera (Fig. 619).

Of the nine species of the incisus group four, secludens, janus, hyalinus, and perpusillus, are known from the study area. Of these four secludens ranges from Great Slave Lake to Wisconsin, New Mexico and California (Fig. 625); janus ranges across the central plains of North America, from Alberta to Wisconsin and Colorado (Fig. 626); hyalinus is transcontinental, ranging from Alaska to Colorado and Newfoundland (Fig. 627); and perpusillus is distributed through the central plains (Fig. 628). Of the remaining five species in the group two are European, one is known only from Colorado (tarsalis), one from New Brunswick (ademus), and the last from California (acenestus).

The asiaticus group contains 12 species, of which eight are known variously from Europe and different parts of Asia, and four are North American. None are holarctic. Of the four North American species only one, labus, is known from the study area. It ranges from Alberta to Idaho and Colorado (Fig. 630). The remaining three species are restricted to the western ranges of the Cordillera (lunonus), to the southwestern United States and Mexico, and, according to Schmid (1955), has been reported from Oregon and Washington (frijole), and to Alaska and the Northwest Territories (pallens).

The four species of the diversus group are restricted to North America. The single species known from the study area, canadensis, is known only from scattered records from Alberta to Maine (Fig. 635). Of the remaining species in the group, diversus is known only from
Arizona and Colorado, *productus* from California and Utah, and *acula* simply from the western United States (Schmid, 1955).

Of the seven species of the *assimilis* group two are known from the study area. Of these two *parvulus* ranges from Alberta and Great Slave Lake to Quebec and New Hampshire (Fig. 623); *spinatus* is strictly western, ranging from Alberta to California and Colorado (Fig. 624). The remaining five species are restricted to North America; *assimilis* is known only from Arizona and California; *taloga* from Oklahoma and Utah; *acrocourvus* from Minnesota; *arreto* from the western ranges of the Cordillera in California, Oregon and Washington; and *occidentalis* from Oregon, Washington and British Columbia.

Of the *nigriceps* group one species, *nigriceps*, is known, ranging from Alaska to Manitoba (Fig. 633).

Only one species, *alberta*, is known for the *alberta* group. This species is known only from the Cordillera of Alberta and adjacent areas of British Columbia.

Again only one species, *argenteus*, is known in the *argenteus* group, ranging from Alberta and Great Slave Lake to Illinois (Fig. 629).

The genus *Grammatotaullius*. Of the nine species of *Grammatotaullius* only three are known in North America. The remainder are known variously from Europe and Asia. Of the North American species only one, *interregationis*, is known from the study area. This species ranges throughout northern North America (Fig. 636), from the Yukon to Nova Scotia and Greenland. Of the other two species *lorettae* is known only from Colorado, and *brettii* from Oregon and British Columbia. Schmid (1955) queries a record of *brettii* from Shanghai, as would I.

The genus *Nemotaullius*. Of the six species of *Nemotaullius* only one, *hostilis*, is known from North America, and the study area. It ranges across central North America from British Columbia to Newfoundland, and from Great Slave Lake to Colorado (Fig. 637). The remaining species are European or Asian in distribution.

The genus *Anabolia*. Of the three groups, and series of ungrouped species in this genus, members of only two groups are known from the study area, totalling three species. There are 15 species in *Anabolia* (Schmid, 1955) of which only four are nearctic. The remainder are Eurasian species. Two species, *consocia* and *ozburni*, are known from the study area; the remaining two species are palaearctic. *A. consocia* ranges from Alberta to South Dakota, Maine, and Quebec (Fig. 638); *ozburni* ranges throughout the same area but is less well recorded (Fig. 639). One species, *bimaculata*, of the *bimaculata* group, is known from the study area; it ranges extensively throughout North America (Fig. 640). The second species of the group, *sordida*, is very similar to *bimaculata* and ranges throughout central North America (Schmid, 1955).

The genus *Asynarchus*. Of the 17 species of *Asynarchus* (Schmid, 1955) two are *incertae sedis*, from North America, eight are strictly North American, and two are holarctic. The five strictly palaearctic species are variously distributed from northern Europe to Japan and Siberia. Of the species known from North America three, *aldinus*, *mutatus*, and *curtus*, are known from the study area. Of these three *aldinus* ranges from Great Slave Lake to Idaho (Fig. 643); *curtus* is northern transcontinental, from Alaska to Labrador and Colorado (Fig. 642); and *mutatus* ranges from British Columbia to Great Slave Lake and Ontario (Fig. 641). The remaining seven North American species are variously known from Utah, Michigan, British Columbia, the western Cordillera, Washington, or are northern holarctic.

The genus *Clistoronia*. All four species of *Clistoronia* are strictly North American; only one species, *magnifica*, is known from the study area, ranging from British Columbia and Alberta to Oregon and Utah (Fig. 635). Of the remaining three species *flavicollis* is known
only from Alaska and British Columbia; *formosa* from Utah and Idaho; and *maculata* from Arizona and New Mexico.

The genus *Philarctus*. This genus appears to be definitely Oriental in origin; of the seven species (Schmid, 1955) six are known from various parts of Siberia, central Asia, China, and the Himalaya. The seventh species, *quaeris*, is known only from North America, ranging from Great Slave Lake to Oregon, Colorado, and Minnesota (Fig. 644).

The genus *Arctopora*. The three species of *Arctopora* are known from North America. One, *triaculata*, is northern holarctic, and unknown from the study area. The second species, *pulchella*, limited to North America, is known from the study area, and ranges from British Columbia to Michigan, Maine, and Newfoundland (Fig. 645). The third species, *salmon* Smith (1969), is known only from Idaho.

The genus *Lenarchus*. Three subgenera, *Prolenarchus, Lenarchus*, and *Paralenarchus*, are recognized by Schmid (1955). The second and third are represented in the study area by four species. The subgenus *Prolenarchus* contains two species, one northern European, the other known only from Michigan and Ontario. The subgenus *Lenarchus* contains six species, one of which, *expansus*, is known from Siberia and Alaska; three others are known from various parts of Eurasia; and two, *crassus* and *rho*, are known only from North America. Of these two *rho* is known only from the coastal ranges from Oregon to British Columbia; *crassus* is known from the study area, ranging from Alberta to Quebec and Maine (Fig. 646). The Nearctic *Paralenarchus* contains five species, three of which, *fauitini, brevipennis*, and *vastus*, are known from the study area. *L. fauitini* ranges from Great Slave Lake to Wyoming (Fig. 647); *brevipennis* is widespread from Alberta to Oregon and Colorado (Fig. 647); and *vastus* ranges from Alaska to Alberta and California (Fig. 646). The remaining two species of the subgenus are known from California (*gravidus*) and Oregon and Montana (*rillus*).

The genus *Hesperophylax*. This genus contains six species, three of which, *occidentalis, consimilis*, and *incisus*, are known from the study area. *H. occidentalis* ranges from Alberta and British Columbia to California and New Mexico, but intermediate records are poor (Fig. 648); *consimilis* is known only from Alberta and Utah (Fig. 648); and *incisus* is widespread from Great Slave Lake to California and Colorado (Fig. 649). Of the remaining three species *designatus* is known from central and southern North America, *magnus* from Arizona and Mexico, and *minutus* from the coast ranges of California and Oregon.

The genus *Chyranda*. Only one species, *centralis*, is known in this genus; it is known from the study area and ranges from Alaska south to Oregon and Colorado (Fig. 650) and has also been recorded from Quebec.

The genus *Pycnopsyche*. The 14 species are arranged in five species groups (Schmid, 1955). Two groups and two species are represented in the study area: *guttifer*, of the *guttifer* group, and *subfasciata* of the lepida group. With the exception of these two species the genus is restricted to northeastern North America: *subfasciata* ranges from New Hampshire to Alberta (Fig. 651), and *guttifer* is transcontinental, ranging from Washington to Georgia and Newfoundland (Fig. 652). The origin of this group appears to center on northeastern North America.

The genus *Philocasca*. Six species of *Philocasca* are known of which one occurs in the study area. This species, *thor*, is known only from a single male taken at the alpine meadows of Mt. Edith Cavell, Jasper, Alberta (Fig. 653). Wiggins (1968) revised the genus, listing five species which are known only from scattered localities in the Alberta-Washington-northern California area.

The genus *Glyphopsyche*. Two species of *Glyphopsyche* are known, *irrorata* and *missouri*. 
Only *irrorata* is known from the study area, ranging from Alaska and California to New Hampshire, but with a gap in Saskatchewan (Fig. 654). The second species, *missouri*, is known from a single area in Missouri.

The genus *Chilostigmodes*. Only two species of *Chilostigmodes* are known, *areolata* and *forcipata*. Only *areolata* is known from the study area, ranging from Alaska to Labrador (Fig. 655); *forcipata* is known only from Siberia.

The genus *Psychoglypha*. This genus contains eight species of which four are recorded from the study area. Of these four (*prita, schmidi, alaskensis, and ulla*) *prita* is known only from Alberta and Idaho (Fig. 657); *schimdi* is known only from the area of the continental divide of Alberta and British Columbia (Fig. 658); *alaskensis* is widespread from Alaska to Utah and Michigan (Fig. 659); and *ulla* ranges throughout the Cordillera from Alaska to California (Fig. 660). Of the remaining four species of the genus, *avigo* and *ormiae* are known only from Utah and Oregon; *rossi* is known only from British Columbia; *bella* is known from British Columbia and California. With the exception of *alaskensis*, which is transcontinental, the genus is confined to the western Cordillera of North America.

The genus *Phanocelia*. The one species of this genus, *canadensis*, is known from the study area, at a single locality (Nordegg, Alberta). It ranges from Alberta and the Northwest Territories to Maine (Fig. 656) but is poorly known.

Altitudinal distribution of the Alberta species of Rhyacophilidae and Limnephilidae

The purpose of this section is to examine the altitudinal distributions of the Alberta species of the two families dealt with, and to relate this information in some manner to their geographical distributions. Table 3 presents a list of the Alberta species in order of increasing lower altitudinal limits. The altitudes given apply only to the study area, and are derived from adult records.

The species of range patterns 7-12 (more extensive ranges) occur primarily at the lower altitudes, and the species of range patterns 1-6, which are confined to the Cordillera, are found at the higher altitudes. Also, the species of range patterns 7-12 have a much greater altitudinal range, and many attain similar altitudes to the species of range patterns 1-6. However, as the lower altitudinal limit of a species is raised, the total range tends to decrease; similarly with the altitudinal range. It is of interest that those species of range patterns 7-12 which are found only at higher altitudes tend to have more northern total ranges.

The conclusion to be drawn from the above would appear to be that, under present ecological conditions, the high altitude species of range patterns 1-6 occupy relatively narrow zones. These zones are presently found only in the mountains. At the last glaciation (Wisconsin), their altitudinal distribution was probably greater, extending to lower altitudes. Probably some species extended to lower altitudes of the study area. Some, in fact, did and spread eastward across North America, south of the ice sheets. Post-glacial warming forced these species upward into the mountains, some so high that they are represented by what appear to be isolated relict populations. The species presently restricted to the Cordillera are so restricted simply because it is the only area which is capable of satisfying their ecological requirements. Many of the Cordilleran species inhabit turbulent, cold, glacial-melt streams; other, still-water forms, are restricted by undetermined factors. It should also be pointed out that the species which extend from the lower to the higher altitudes are still-water forms which inhabit lakes, ponds, or sloughs.
Table 3. Altitudinal distribution of the Alberta species of Rhyacophilidae and Limnephilidae based on adult records.

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<th>Altitude</th>
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Discussion

Introduction. – The problem now presented is to elucidate the source areas of the present Alberta fauna of Rhyacophilidae and Limnephilidae after the essentially clean sweep of the study area by the Wisconsin ice sheets. By ‘source areas’ I refer to those areas outside the study area in which populations of Alberta species survived the glaciation, and from which they were able to re-disperse at dissipation of the ice, to wider distributions, including the study area. I examine below the origins of the Alberta species in the sense of relationships in space with closest relatives, usually to the other species of their respective genera, or to the remaining species of their species groups in genera which are too large and diverse to be treated as single units.

Given above are data concerning the maximum extent of the Wisconsin ice; the possible unglaciated areas, or refugia, from which the fauna may have dispersed post-glacially, of which there are only two of any consequence; the retreat of the ice sheets; the locations and extent of glacial and post-glacial lakes and rivers; the possible effects of post-glacial climates on biotic movements and retreat of the ice sheets; the common range patterns exhibited by groups of species of the two families; and, finally, the relationships of each species known from the study area to the remaining species of their respective genera or species groups within genera.

It only remains to examine this information, in toto, and to determine, as far as possible, whence the present Alberta fauna of the two families dispersed into the study area post-glacially, and to examine briefly their broader relationships in space to their presumed closest relatives. The purpose in examining these spatial relationships is to attempt to educe the pre-glacial sources, or origins of the fauna. Are there, for example, Eurasian, Cordilleran, or eastern North American elements in the Alberta fauna, and what are they? The basis of decision in this matter is simply that a genus, or species group, is presumed to have originated in the geographical area which harbours the greater number of species of the group in question. In the context of this study this appears to be the only reasonable course. As has been stated elsewhere this study is not a revision and it is simply impossible to critically examine here the total of all species of all higher taxa represented in Alberta with a view to determining dispersals and phylogeny within each taxon. The foregoing presumption is based on the idea that the longer the period of time during which representatives of a group occupy a given geographical area the greater the amount of diversity, or speciation, which may occur. Thus, if a supraspecific taxon is represented in North America by fewer species than occur in Asia, it is presumed that the fewer North American species indicate that the taxon in question has been present in North America for a shorter time than in Asia, hence it originated in Asia. Undoubtedly this argument will prove to be incorrect in at least some cases, but it should be adequate for a broad general outline of pre-glacial faunal origins.

In certain cases, however, studies on the phylogeny and distribution of discrete taxa are available, with conclusions regarding geographical affinities or origins. These conclusions are used here.

Pre-Wisconsin affinities of the Alberta fauna. – The relationships of the Alberta species, or genera, of the two families are examined here by a consideration of the distribution of species related to the Alberta species. The ground has already been prepared above (pp. 205-212) and it only remains to condense the information presented to more manageable form.

The family Rhyacophilidae is represented in the study area by 11 species groups of the genus Rhyacophila. The family Limnephilidae is represented by 26 genera and 91 species. Eight of these species are represented by unidentifiable females and are not considered further. The distribution of the species in each genus or species group, and the putative
geographical area of origin of each genus or group is given in Table 4. From this table it would appear that the relationships of the Alberta fauna of Rhyacophila are primarily with North American groups, especially with western North American groups, and with one group of Asian ancestry.

Table 4. Geographical distribution of the higher taxa of the Alberta fauna of Rhyacophilidae and Limnephilidae and their probable source areas.

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<th>Number of species</th>
<th>Probable source area</th>
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Table 4 (continued)

| Name of taxon | Number of species | | | | | Probable source area |
|--------------|------------------|---|---|---|---|
|               | Holarctic | Palaeartic | Nearctic | Total |                         |
|               | West | Transcontinental | East |          |                        |
| Onocosmoecus  | 1   | 5   | 1   | 1     | 8   | Cordillera               |
| Imania        | 10  |     |     |       | 10  | Cordillera               |
| Ecclisomyia   | 2   | 4   |     | 6     | 7   | Asia                     |
| Philarctus    | 6   | 1   |     | 7     | 7   | Asia                     |
| Chilostigmodes| 1   | 1   |     | 2     | 2   |                         |
| Arctopora     | 1   | 1   |     | 3     | 3   |                         |
| Grammataulius | 6   | 2   | 1   | 9     | 9   | Eurasia                  |
| Nemotaulius   | 5   | 1   |     | 6     | 6   | Eurasia                  |
| Anabolia      | 11  | 4   |     | 15    | 15  | Eurasia                  |
| Asynarchus    | 2   | 5   | 5   | 1     | 15  |                         |
| Lenarchus     | 1   | 1   |     | 2     | 2   |                         |
| (Prolenarchus)|     |     |     |       |     |                         |
| (Lenarchus)   | 1   | 3   | 1   | 6     | 6   | Eurasia                  |
| (Paralenarchus)|    |     |     |       |     |                         |
| Limnephilus   |     |     |     |       |     |                         |
| Group         |     |     |     |       |     |                         |
| ornatus       | (1)**| 1   |     | 1     | 1   |                         |
| nigriceps     | 1   |     |     | 1     | 1   |                         |
| argentus      |     |     |     |       |     |                         |
| nogus         |     | 1   |     | 1     | 1   | Cordillera              |
| alberta       |     | 1   |     | 1     | 1   | Cordillera              |
| diversus      |     | 3   | 1   | 4     | 4   | Cordillera              |
| assimilis     |     | 5   | 2   | 7     | 7   | Cordillera              |
| morrisoni     |     | 3   |     | 3     | 3   | Cordillera              |
| stitchensis   |     | 6   | 1   | 7     | 7   | Cordillera              |
| rhombicus     | 1   | 4   |     | 5     | 5   | Eurasia                  |
| subcentralis  |     | 5   | 3   | 3     | 11  |                         |
| stigma        |     | 5   | 2   | 7     | 7   | Eurasia                  |
| asiaticus     |     | 8   | 4   | 12    | 12  | Eurasia                  |
| externus      | 1   |     | 1   | 2     | 2   | Cordillera              |
| picturatus    | 1   |     | 1   | 2     | 2   | Cordillera              |
| sericeus      |     |     |     |       |     |                         |
| luridus       | 1   | 1   |     | 2     | 2   | Eurasi                   |
| incisus       |     | 2   | 3   | 3     | 9   | North America            |
| fenestratus   | 1   | 1   | 2   | 2     | 6   | North America            |
| Genus         |     |     |     |       |     |                         |
| Apatania      |     |     |     |       |     |                         |
|                | 3   | 38  | 9   | 50    | 50  | Eurasia                  |

(?) = Ross (1956).
* Ross (1956).
** Schmid (1955)
The affinities of the Alberta species of Limnephilidae are varied and complex. Most of the taxa appear to be of western North American origin, with some elements from eastern North America, North America generally, Eurasia, and some indefinite.

Post-Wisconsin sources of the Alberta Rhayacophilidae and Limnephilidae. — There are several possible routes whereby the study area may have been reinvaded post-glacially by species of the two families considered here. These routes are suggested both by the distribution patterns as set forth in Fig. 667, 668, and by the spatial relationships or affinities of the Alberta species to their respective genera or species groups as described above. These routes are examined below and an attempt made to fit each of the 113 Alberta species of the two families to them. Some species fall easily and convincingly into their allotted route of post-glacial dispersal; others do not, and impart a measure of uncertainty to the conclusions.

As mentioned earlier, the range patterns of the Alberta species are grouped into two major classes. Those species belonging to the first major class are restricted entirely to the Cordillera, and those belonging to the second class range throughout North America in a variety of patterns, the only common feature of which is that each pattern embraces the study area.

The nine possible routes of post-glacial dispersal of species into the study area are as follows:

a). From the entire Cordillera, south of the ice.
b). From the coastal ranges of the Cordillera only.
c). From the eastern ranges of the Cordillera only.
d). From the area immediately south of, and adjacent to, the Cordilleran ice sheet.
e). From all of North America south of the ice sheets.
f). From the central plains of North America.
g). From eastern North America, to the northwest.
h). From Alaska, to the south and east.
i). From Alaska and the southern, unglaciated, portion of North America simultaneously, provided that the species involved maintained populations in both areas throughout the Wisconsin.

Dispersal route i is not seriously considered here, as the end result would be distributions similar to those which could result from any of the other eight routes, and intensive investigations, which are beyond the scope of this study, would be required to detect such a dispersal route. In any such investigations a first step would be intensive collecting in Alaska, the Yukon, and northern British Columbia, as records are very poor from these areas. In conjunction with, and following such collecting, morphological variation, possibly indicative of prolonged isolation of two populations from each other, would have to be searched for and examined in detail. If any species did in fact disperse post-glacially from the two foci, such an investigation might provide supporting evidence.

Prior to attempting to determine the dispersal routes of the Alberta species, several points of interest to the inquiry require examination. Habitat preferences of each species are important in elucidating past dispersal patterns. Suitable climatic conditions are inconsequential to individuals of a species if the habitat which they require is missing, for whatever reason. This is especially so in the Trichoptera, due to the very restricted habitat of the larvae: fresh water. Fresh water abounds in most of the area under consideration but in different forms: it may be fast and turbulent, fast and smooth flowing, slow flowing, standing, as in lakes, ponds, and sloughs, and it may be deep or shallow, permanent or intermittent, cold or warm. All types of fresh water bodies have their particular complement of trichopteran species.
The distribution of the various types of fresh water bodies has undoubtedly changed greatly since the beginning of the Wisconsin glaciation. While I can find no specific reference, it seems reasonable to assume that the area south of, but adjacent to, the southern edges of the ice sheets was occupied by lakes, creeks, and rivers sustained by glacial meltwater. This would result in cold water streams which, in all probability, were swift and turbulent. South of this band, in non-glacial drainage systems, were warmer bodies sustained by precipitation alone. Farther south still, conditions were different again, and so on. As the ice sheets melted and the southern edges retreated northward, the various types of fresh water habitats would alter and assume the character of the next southern type. In effect I propose that the water habitat types appeared to migrate northward behind the retreating ice sheets, just as the various biota are believed to have done. As the Laurentian ice sheet is now quite extinct, and retreated in a northerly direction, it follows that some of the water habitat types which followed behind it are now found only in the far north or are extinct, except in mountainous areas to east or west. This point is raised, as the transcontinental belt of cold water stream habitats created during glaciation would provide a means of dispersal of mountain species from west to east, or from east to west, with the possible result of isolated populations of species with large range gaps between the populations. There are in fact some such species known from the study area.

The post-glacial lakes and drainage patterns have altered greatly since the retreat of the ice and, in total, must have acted as a great network, in time, throughout central North America. This system is now essentially defunct, as glacial control has ceased and each watershed is now distinct and well separated from the next, with minimal, if any, variation. This post-glacial network of lakes and streams extended, in time, as well as space, from the Great Lakes to Great Bear Lake (Fig. 665), and probably provided an open road from eastern and central North America to the north west and northern North America, and possibly from Alaska to the south east. Such a 'road', consisting largely of lakes, ponds, and sloughs, but with streams of unknown character surrounding them, would probably be of greatest assistance to lake and pond species, of which there are many known from the study area. These species have range patterns which belong to the second major division of the range pattern series (Fig. 668).

The western Cordilleran species exhibit two dispersal routes. Species isolated south of the ice advanced northward, ultimately to Alaska, and the species isolated in the Alaska-Yukon refugium spread southward. Ordinarily the species spreading south from Alaska would be low altitude forms or, at least, forms which would not be forced to retreat upward to higher, colder, mountain areas to form isolated populations as the climate warmed following glacial retreat. High altitude forms would be isolated in the Alaskan highlands instead. Present day high altitude forms which, during the glacial maximum, would be enabled to survive at low altitudes south of the ice sheets, and form continuous populations, would advance northward behind the retreating glaciers, but would also advance, at the southern extremities of their ranges, higher into the mountains. Eventually they would attain such altitudes, at least in the south, so that isolated populations would result. Species exhibiting such isolated distributions can generally be assumed to have advanced from the south of the ice sheets. However, some present day high altitude forms may have dispersed from Alaska south, along the eastern slopes of the Cordillera. This is barely conceivable if one considers the slower disappearance of the Cordilleran ice sheet from southern British Columbia, and the presence of a corridor between northwestern United States and Alaska, along the eastern face of the Cordillera as the Laurentian ice sheet retreated to the north east. This dispersal would occur at low altitudes initially, and in a narrow band of suitable territory. As the Cordilleran ice sheet vanished, dispersal would then occur upward into the
high mountains, again resulting in isolated populations. At the present time, however, I cannot provide evidence of such a dispersal route.

To begin the detailed examination of the post-glacial origins of the Alberta Rhyacophilidae and Limnephilidae I shall first examine the groups of species included in range patterns 1-6 (Fig. 667). Table 2 (pp. 203-204) lists the species in each range pattern.

The species of range patterns 1-6 are confined to the Cordillera. They are largely fast, cool, mountain stream species, whose members would find it difficult, if not ecologically impossible, to disperse beyond the Cordillera post-glacially. Despite the limitations imposed by present knowledge of species ranges it seems reasonable to assume that the species belonging to range patterns 3-6 were confined to the Cordillera south of the Cordilleran ice sheet in British Columbia, and that they spread northward post-glacially, reaching their northern limits in the southern half of British Columbia and the Cordillera of Alberta. The species of range pattern 3 are widespread throughout the Cordillera, on both sides of the Great Basin of Utah and Nevada and northward. Despite the inclusion of that area within the pattern, in fact very few species are recorded therefrom. It may be they extended into the area during the Wisconsin pluvial and have since been driven out by increasingly drier conditions (see Ricker, 1963). This also applies to the species of range pattern 1. The species of range pattern 3 belong to dispersal route a.

The four species of range pattern 4 are confined to the coastal Cordillera, attaining the same northern limits as those of range pattern 3; they belong to dispersal route b.

The four species of range pattern 5 are confined to the eastern ranges of the Cordillera, with similar northern limits; they belong to dispersal route c.

The 28 species of range pattern 6 are known only from the very restricted area which includes Oregon, Washington, Idaho, Montana, southern British Columbia, and western Alberta. Many of these species are described as new, or are represented only by unidentifiable females. Others belong to genera which are rare, either because of intrinsic rarity, or difficulty in collecting specimens. Still others are restricted to isolated high altitude populations; these are species which were apparently unable to migrate northward post-glacially. It seems reasonable to suppose that many, at least, of these species have dispersed very little since retreat of the ice, simply moving northward into southern British Columbia and Alberta. They belong to dispersal route d.

The species included in range patterns 1 and 2 present greater difficulty as they could represent examples of dispersal patterns a, h, and i (range pattern 1) or c, h, and i (range pattern 2). For reasons given above the postulated dispersal pattern i is omitted from further consideration at this time. I. tripunctata, of range pattern 2 may represent an example of dispersal south of the Cordilleran ice sheet south of Alaska along the north-south corridor prior to melting of the Cordilleran ice sheet. In the study area it is now found isolated only at high altitudes, and does not extend south of Alberta. However, it might also represent dispersal from south to north, and upward, as the ice retreated. The remaining two species of range pattern 2 are low altitude forms and certainly belong to dispersal route c.

The 13 species of range pattern 1 exhibit a variety of altitudinal ranges but none could be referred to as high altitude isolates. All are known from the southern extremities of the Cordillera to, or almost to, Alaska. As most of the close relatives of each species are found largely in the area south of the former ice sheets it is reasonable to assume that the species of range pattern 1 belong to dispersal route a.

The species of range patterns 7-12 present greater problems for which less clear cut answers are available. They belong variously to dispersal routes e-i.

Many of the species included in these range patterns have far northern distributions in conjunction with southern extensions. Several are holarctic. Ross (1965) states that it
would be difficult to elucidate the loci of post-glacial dispersal of these species.

The species of range pattern 7 are the most widespread of the Alberta species. They are still water forms. Of these, four (L. externus, L. femoralis, L. rhombicus, and A. stigmatella) are holarctic, and can reasonably be assumed to have dispersed south and east from Alaska. While about half of the other species involved are recorded from Alaska, they are all very well represented from the southern limits of the pattern. Of particular interest is the heavy representation in the western Cordillera. This would be difficult territory to disperse into or through, and the process would indubitably take longer than in the plains. Also of interest is the fact that these species are found on both sides of the now arid Great Basin. It is most probable that at least the greater number of these species were well established, transcontinentally, south of the ice sheets, and spread northward behind the ice. With the exceptions of the four holarctic species, which appear to belong to dispersal route h, the species included in range pattern 7 appear to belong to dispersal route e.

The species included in range pattern 8 are a curious mixture of fast and still water forms. The fast water forms belong to R. acropedes, R. angelita, and O. unicolor. This pattern comprises two separate ranges for each included species, one eastern, the other western. The dispersal route involved here would appear to be e. Apparently the ice sheets created conditions along their southern edges which were suitable for these species and they were enabled to migrate eastward and become transcontinental in distribution (Ross, 1956). Ross (1958) mentions such a possibility in the Pleistocene as a whole. On recession of the ice these conditions became more and more restricted to the highlands of the east and west, and an intervening range gap resulted. Ricker (1963) proposes a similar situation for Plecoptera and also mentions, as is the case here, the few species which exhibit this distribution.

The seven species included in range pattern 9 are primarily low mountain valley forms of marshes or slow streams in Alberta. These conditions extend beyond the mountains to the plains in the east, however. These species, with the exception of the holarctic species L. picturatus and A. crymophila, appear to belong to dispersal route f. L. picturatus and A. crymophila may have followed dispersal route h.

The two species of range pattern 10 evidently belong to dispersal route f. Either their restricted ranges are due to incomplete knowledge of their distribution, or they are restricted ecologically.

The species included in range pattern 11 are primarily centered in northeastern North America; Alberta apparently represents the western extremities of their ranges. On the whole they appear to belong to dispersal route g, and to have spread both west and north from the eastern United States.

The six species included in range pattern 12 are still or slow water forms, transcontinental, and restricted almost entirely to Canada, with the exception of A. zonella which is circumpolar, though unknown from the western Arctic and Alaska at present. L. kennicotti and G. interregationis are also known from Greenland. A. zonella is known from the high Arctic Islands and Greenland, to British Columbia, but is primarily a far northern species. The post-glacial source of this species is uncertain, but it may well have spread from several foci, one of which is northern Ellesmere Island, and Peary Land. It may also have survived south of the ice sheets and spread north. The remaining species, on the whole, appear to have survived south of the ice sheets and spread northward; they belong to dispersal route e. None attain the high latitudes of A. zonella.

On a percentage basis the probable post-glacial sources of the Alberta fauna of Rhyacophilidae and Limnephilidae are as follows: from the western Cordillera south and west of the study area — 61%; from Alaska — 5%; from eastern North America — 8%; from trans-
continental species south of the ice — 18%; and from the central plains — 7%.

While certain of the preceding conclusions, with regard to some species, are doubtful, one species is more dubious than any other — A. zonella. This species is not included in any of the preceding figures but represents less than 1% of the total.

Four transcontinental species of range pattern 8 are nonetheless considered to be of western Cordilleran provenance. They are represented in the east in relatively isolated highland areas and are thought to have dispersed eastward during the Wisconsin glaciation itself, when suitable ecological conditions prevailed just south of the ice sheets, and to have been isolated there post-glacially.

The total of 33% of species thought to have dispersed into and through Alberta from the central plains, eastern North America, and southern transcontinental localities, are essentially all still water forms which almost certainly utilised the myriad lakes, ponds, and sloughs created during deglaciation, and as they exist at present.

In conclusion, only 5%, or possible 6%, of the Alberta fauna of the two families is derived from northern glacial refugia. The remaining 95 (94)% is derived from south of the major ice sheets, the greater portion being indubitably western Cordilleran.

While it is not part of the stated objectives of this study, it seems appropriate to examine briefly the broader implications of the data presented here, for the post-glacial recolonisation of northern North America as a whole. Ross (1965) examines this problem in detail. The holarctic species of Limnephilidae seem, on the whole, to have dispersed east and south from Alaska, or other possible far northern refugia. All other species appear to have dispersed northward post-glacially, from south of the ice sheets. There is a distinct western Cordilleran element which has remained restricted to the Cordillera. The eastern areas of North America also have a distinctive endemic fauna. There has been little interchange between the two areas, especially in the montane elements. What interchange there has been is restricted to west to east dispersals (Ross, 1956, 1965) when glacially imposed ecological factors were suitable. The remainder of the fauna has shuttled back and forth in a north-south pattern, with perhaps some northwestward dispersal by the eastern lowland fauna, to the northern Great Plains.

Conclusions

1. The affinities of the Alberta species of Rhyacophila are primarily with the western Cordillera of North America. One species group, while with a large North American complement, is apparently Asian in origin.

2. The affinities of the Alberta species of Limnephilidae are varied and complex. Regarding genera and species groups within larger genera indiscriminately, 21 taxa have their closest affinities with western North America, two with eastern North America, five with North America, but indefinite within the area, 12 with Eurasia, and three are indefinite between Eurasia and North America. The greater part, then, of the Alberta fauna appears to be North American in origin.

3. The post-glacial source of the Alberta fauna of the two families studied is almost entirely from the southern half of North America south of the former ice sheets, with a minor Beringian, or Alaskan, element. The greater part of the southern element is derived from the western Cordillera.

4. The western element is composed largely of cool stream species, which largely excludes their post-glacial dispersal eastward. The remainder are plains lake, pond, or slough forms, which were undoubtedly assisted in their northward dispersal by the great network of post-glacial lakes, ponds, and sloughs created by the retreating glaciers, and which are
now much diminished in size, and altered in drainage patterns. However, the remnants still provide a multitude of areas in which these species thrive.

Acknowledgements

I wish to extend my sincerest thanks to the following persons and institutions for their assistance in bringing this study to completion.

G. E. Ball, acting in the capacity of my thesis supervisor, has read and criticised the manuscript most constructively, and has provided many helpful suggestions prior to final writing. Not a few of the specimens examined in the course of this study were collected by him, and they have provided many useful records. B. Hocking, H. Clifford, and D. A. Craig, of the University of Alberta, and H. H. Ross, University of Georgia, Athens, Georgia, United States, acting as members of my committee, have also read, and commented most usefully on, the manuscript.

I also wish to acknowledge the varied contributions of my wife, Susan, who proofread certain parts of the manuscript, and provided moral support in the long months of writing, and was more than patient with a house full of thesis, truly a housewife’s nightmare!

Also most gratefully acknowledged are the contributions of the University of Alberta in various ways to my support and transportation costs during the course of the investigations, and similar support provided through National Research Council of Canada grant No. A.1399, held by G. E. Ball.

F. Schmid, of the Entomology Research Institute, Ottawa, very kindly checked certain identifications for me, lent me the original drawings of one species, and arranged for me to examine, and borrow material from, the collections of the Entomology Research Institute. I wish also to acknowledge the cooperation of G. B. Wiggins, and T. Yamamoto, of the Royal Ontario Museum, Toronto, for access to collections, loan of material, and checking of certain identifications. D. G. Denning very kindly lent me the original drawings of Rhyacophila chilisia Denning, and compared some of my material with his types. H. H. Ross gave me access to the collections of the Illinois Natural History Survey, and loaned much interesting material. O. S. Flint, Jr., United States National Museum, Washington, D. C., forwarded on loan certain specimens required in the study. S. D. Smith, of Central Washington State College, Ellensburg, Washington, very kindly agreed to my use of certain distributional records from Idaho, as yet unpublished. The assistance of F. C. J. Fischer, Amsterdam, Holland, in obtaining full citations for several obscure papers for my bibliography is greatly appreciated.

D. R. Whitehead cooperated in checking certain of my keys, and D. J. Larson, K. W. Richards, R. E. Leech and P. Graham, all of the University of Alberta, very kindly passed on to me any Trichoptera which they acquired in the course of their own work. Graduate students of the Department of Zoology, University of Alberta, too numerous to mention, also provided me with many interesting records when they requested assistance in identifying material for their own work.

N. F. Novakowski of the Canadian Wildlife Service, Edmonton, arranged accomodation and transport in Wood Buffalo National Park in northern Alberta; and the staffs of certain of the western National Parks allowed me access to fire roads to remote areas of the parks. I appreciate very much the cooperation of the Superintendent of Banff National Park, in arranging for me to borrow a small collection of Trichoptera, formed in the early 1900's by N. B. Sanson, from the Banff Museum.
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Nimmo


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Vingt-deux espèces de Rhyacophilidae et 91 espèces de Limnephilidae, faisant un total de 113 espèces, sont rapportées pour cette région. Chaque espèce est décrite et accompagnées de clefs permettant d'identifier les spécimens adultes par rapport aux espèces.

Dans les Lymnephilidae sept espèces sont décrites comme nouvelles: Imania hector; Apatania alberta; Homosphylax baldur; Oligophlebodes zelti; Limnophilus susana; Limnophilus valhalla; et Philocasca thor.

L'origine postglaciaire de cette faune est étudiée, considérant les effets probables des systèmes climatiques présents et passés, l'étendue des masses glaciaires et la position des refuges probables, et la position et le système de drainage des principaux lacs glaciaires et postglaciaires. De plus 12 modèles de distribution démontrés par les espèces, et la distribution de chaque espèce en relation à d'autres espèces dans leur genre et dans leur groupe, sont étudiés. Les 12 modèles de distribution se divisent en deux sections principales: la première, composée de six modèles, est entièrement limitée à la cordillère occidentale de l'Amérique du nord; et les six derniers sont transcontinentalement distribués. La distribution en fonction de l'altitude est brièvement examinée.

Les conclusions démontrent, d'un côté, que 5% de la faune contemporaine provient du refuge de Beringia après les glaciations, et d'un autre côté, que 95% provient de régions de l'Amérique du nord au sud de la limite sud des glaces. En divisant davantage cette dernière portion, 61% provient de la cordillère occidentale de l'Amérique du nord, 8% de l'est de l'Amérique du nord, 7% du centre des grandes plaines, 18% de toute l'Amérique du nord au sud des glaces, i.e. d'espèces transcontinentales, et 1% demeure incertain.
Publication of *Quaestiones Entomologicae* was started in 1965 as part of a memorial project for Professor E. H. Strickland, the founder of the Department of Entomology at the University of Alberta in Edmonton in 1922.

It is intended to provide prompt low-cost publication for accounts of entomological research of greater than average length, with priority given to work in Professor Strickland’s special fields of interest including entomology in Alberta, systematic work, and other papers based on work done at the University of Alberta.

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CONTENTS

Editorial – Publish or Perish? .......................................................... 235
Frank – Carabidae (Coleoptera) of an arable field in central Alberta ........ 237
Chance – Correction for drag of a flight mill, with an example for
Agrotis orthogonia Morr. (Lep. Noctuidae) ......................................... 253
Sehgal – Biology and host-plant relationships of an oligophagous leaf miner
Phytomyza matricariae Hendel (Diptera:Agromyzidae) .......................... 255
Erwin – Notes and corrections to a reclassification of
bombardier beetles (Carabidae, Brachinida) ....................................... 281
Book Review .................................................................................... 282
Book Review .................................................................................... 283
Book Review .................................................................................... 284

Editorial – Publish or Perish?

The admonition to publish or perish, with its oral equivalent: present a paper or stay at home, may be of value to the occasional administrator who has no better device for allocating travel monies, increments, or other rewards of virtue, but has certainly had some unhappy consequences. All of us, I am sure can recall more than one occasion when, sitting through some usually duller than normal submitted paper, the feeling has come over us that we have heard it all before. Anybody who has ever really tried to keep up with the literature will know of many frustrating examples of related one or two page papers, published in several usually obscure journals, by the same author (or authors in varied sequence) under different titles. When assembled through due process of inter-library loan or microfilm and subjected to critical comparative study, such papers often prove to say exactly the same thing. Often it wasn’t worth saying anyhow. Then there are the papers, often longer, which appear in the proceedings of a meeting, and again in a regular journal, with no great change. There are also coherent theses which are decimated for publication in a diversity of periodicals; for this the blame is also diverse: the facile acceptance of long lists of publications as an index of merit in both the papers and their author, editorial boards with a terror of long papers, and authors with an inordinate love for every word they have ever drafted.

But all of this is at the personal level; the current Canadian wave of nationalistic or perhaps we should call it tribalistic fervour, since our aboriginal peoples appear to be specifically excluded, has expanded the publish or perish dictum to the level of national publishing houses. These must be helped, maintained, kept Canadian, cherished, and above all kept uncontaminated by any other funds than Canadian dollars.

The first requirement for a Canadian publishing house to flourish, however, is that Canadians buy, even if they do not read them, Canadian books, because there are obstacles of various kinds, all unjustifiable, to the passage of books across many international boundaries. Canadians do neither of these things; at least not on the scale of most progressive peoples. Some 10 years ago I lived for a while in an African town of some 15,000 souls, more than half of them black or brown, which supported as many shelf-feet of bookshops as a Canadian city of 350,000.
Per million of population, Canada publishes one third of the average number of books published by western European countries and only about half the number published in the U.S.S.R. Some 10 years ago we could at least take comfort in the thought that we published nearly twice as many books per million people as our neighbours to the South, but their production is now well ahead of that of Canada. It is a strange fact that the more books per head a country publishes, the more copies of each it prints. This leaves Canada still further behind in numbers of copies of books printed, so that while bookish Britain prints a book per head in about 16 months, it takes Canada over six years to achieve this.

Business men tell me that Canadian publishers lack business ability; this may well be true. At the receiving end I know them to be slow, inaccurate, and expensive. It is almost always both quicker and cheaper to buy a British book from a British retailer than from a Canadian distributor, who is usually also a Canadian publisher. Prices may be as much as 65 per cent above British retail prices, and I am told that the average price increase is 30 per cent. But this money buys little service; from the consumer's viewpoint it would be hard to imagine a commercial group less interested in his needs than Canadian publishers. Telegraphic enquiries get surface mail replies if any, letters may languish for weeks. Foreign publishers have similar and more serious complaints about Canadian businesses which claim to act as distributors for them. Neither principal nor client is served. If and when books from a foreign publisher eventually arrive through a Canadian distributor they may be the wrong edition or the wrong book or both, they may be so damaged that they must be returned, they will probably be too few and too late for the purpose for which they were ordered, and the price will certainly be an anti-educational shock. Such businesses should be investigated, not subsidized. In respect of many one wonders, not that they go out of business, but that they have managed to stay in it for so long.

In most countries most of those who deal in books have an interest in education and take pleasure in the contributions they can make to it. In Canada this attitude is rare, though it pays no less than elsewhere; more often, distributors here prove to be inhibitors. The book trade should be cooperating with librarians to, in three words, make Canadians read: surely our climate is favourable. Clearly, until this is done it will remain possible, both at the personal and at the public level, for a nationalistic Canadian to both publish and perish.

Brian Hocking
CARABIDAE (COLEOPTERA) OF AN ARABLE FIELD IN CENTRAL ALBERTA

J. H. FRANK
Sugar Manufacturers’ Association
Research Department
Mandeville P. O., Jamaica

Quaestiones entomologicae 7: 237-252 1971

Sixty-three species of carabid beetles were collected in pitfall traps in an arable field in central Alberta. Data on life histories or biology are given for 26 of the more abundant species and discussed, and population densities are estimated for several of these. Six species of staphylinid beetles and 12 of spiders also taken in the study are listed. The spider species included Xysticus californicus Keys, a first record in Canada.


Larvae and adults of most species of Carabidae prey upon other insects. As part of a study of the economic importance of Carabidae as predators of cutworms, a study was made of the species inhabiting an arable field in Central Alberta. Mention is made of Staphylinidae and of spiders from the same habitat.

THE STUDY AREA

This was selected following a report of a cutworm attack on a field of barley near Calahoo, Alberta. The designation of the site is: section SW8, township 55, range 27, meridian W4, which is roughly 32 km (20 miles) northwest of Edmonton. The area is mapped as a mixture of three soils: two formed on fine-textured, stone-free lacustrine sediments (these are Mico silty clay loam, comprising 50% of the area and Maywood clay loam, comprising 20%); the other on a loam-textured, stony glacial till (this is Cooking Lake loam and comprises 30% of the area).

The species of cutworm was determined as Euxoa ochrogaster Guenée (Lep; Noctuidae), the red-backed cutworm.

A study area of about 0.2 hectare (0.5 acre) was used, near the centre of the field. Partly because of its smallness and partly because of agricultural practices, which inhibit growth of other than the crop plant, the area was very uniform. The duration of the study was the frost-free periods of 1967 and of 1968, from June 1967. In 1968 a crop of oats was grown in the field.

THE CLIMATE

Frost occurred from early November 1967. In 1968 thawing was during the first week of May with more or less permanent frost from the first week in October. Frost limited the movement of Carabidae severely, so that the operation of pitfall traps during frost periods
was unproductive. Meteorological information was supplied by the Weather Office, International Airport, Edmonton. Maximum temperatures occurred in September 1967 (max. 33.6 C, 92.5 F), but in July 1968 (max. 31.0 C, 87.8 F). Minimum temperature of the study period was -32.3 C (-26.1 F), in January 1968. This air temperature range of 65 C (over 118 F), although modified by the field crop, must impose severe restrictions on the movement of surface active insects. Refuge from temperature extremes is provided by the ability of the adult and larval carabids to burrow into the soil. From the temperature aspect the season was more 'advanced' in 1968 than in 1967.

The rainfall patterns were similar over the two years, with July and August being the wettest months (total 120-145 mm, 5-6 inches, for the two months together) but September 1967 was an extremely dry month (0.76 mm, 0.03 inch) compared with September 1968 (37.34 mm, 1.47 inches).

METHODS

The principal means of capturing beetles was a grid of 10 x 10 unbaited pitfall traps spaced at 1 m intervals. This was in place throughout the study period except when agricultural operations (ploughing, seeding, and harvesting) were in progress, at which times it was taken up, to be replaced as soon as possible. The traps were of high impact polystyrene plastic and were 10.2 cm in height, 8.7 cm (O.D.) at top and 7.2 cm (O.D.) at base. The shape allowed stacking for transportation and the light weight also facilitated this. Individual traps which had become soiled while in use were replaced by clean traps as necessary, although the plastic resisted adherence of mud. A vinyl square 10.8 x 10.8 cm (quarter of a 9 inches x 9 inches floor tile) was supported on four small wooden stakes of length about 10 cm, at a height of about 2.5 cm above each trap to keep it dry. Insects caught in the pitfall traps were removed from the study area for identification and were not returned unless they were to be used for mark, release, and recapture studies. Those not returned were used to establish and maintain cultures, or were dissected.

Population estimates were made in a way similar to that described by Frank (1967). Released beetles had been marked by cutting a minute notch in the right elytron with spring scissors instead of marking with paint.

Larvae taken in pitfall traps were reared individually, at first in plaster of Paris blocks, later in 60 x 15 mm plastic petri dishes contained in a glass battery jar to maintain an adequate level of humidity. Entomophagous larvae were fed larvae of Musca or pieces of Periplaneta, and phytophagous larvae (species of Amara and of Harpalus would not survive for long on a diet of insects) were fed pieces of maize (corn) kernel. An identification label was attached to the inside cover of each petri dish with a smear of vaseline. Food had to be replaced daily to prevent growth of mould.

Cultures of adults were maintained on a damp peat substrate in 8 x 17.5 x 4.5 mm transparent plastic boxes and were fed in much the same way as were the larvae. Eggs and larvae, when found, were removed from these cultures and treated as were the pitfall-trapped larvae.

THE CARABIDAE

Names of the 63 species collected arranged according to Lindroth (1961), with data on those less frequently collected, are given in Table 1. Data on the more abundant species follow.
Table 1. A list of names of carabid species collected in the study area near Calahoo, Alberta, with notes, numbers, and dates for the less frequently encountered species (mature adults except where otherwise noted).

<table>
<thead>
<tr>
<th>Name of species</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Carabus taedatus</em> Fabricius</td>
<td>5 – VIII-IX.1967; 11 – V-VIII.1968</td>
</tr>
<tr>
<td><em>Calosoma calidum</em> Fabricius</td>
<td>text p. 241</td>
</tr>
<tr>
<td><em>Notiophilus semistriatus</em> Say</td>
<td>1 – 18.X.1967</td>
</tr>
<tr>
<td><em>Loricera pilicornis</em> Fabricius</td>
<td>2 – VII.1967</td>
</tr>
<tr>
<td><em>Bembidion nitidum</em> Kirby</td>
<td>text p. 241</td>
</tr>
<tr>
<td><em>Bembidion grapei</em> Gyllenhal</td>
<td>3 – between X &amp; XI. 1967</td>
</tr>
<tr>
<td><em>Bembidion bimaculatum</em> Kirby</td>
<td>text p. 241</td>
</tr>
<tr>
<td><em>Bembidion rupicola</em> Kirby</td>
<td>text p. 243</td>
</tr>
<tr>
<td><em>Bembidion obscurellum</em> Motschoulsky</td>
<td>text p. 243</td>
</tr>
<tr>
<td><em>Bembidion rapidum</em> LeConte</td>
<td>2 – VI.1968</td>
</tr>
<tr>
<td><em>Bembidion versicolor</em> LeConte</td>
<td>text p. 243</td>
</tr>
<tr>
<td><em>Bembidion quadrimaculatum oppositum</em> Say</td>
<td>text p. 243</td>
</tr>
<tr>
<td><em>Bembidion mutatum</em> Gemminger and Harold</td>
<td>text p. 244</td>
</tr>
<tr>
<td><em>Bembidion canadianum</em> Casey</td>
<td>text p. 244</td>
</tr>
<tr>
<td><em>Pterostichus lucublandus</em> Say</td>
<td>text p. 245</td>
</tr>
<tr>
<td><em>Pterostichus corvus</em> LeConte</td>
<td>text p. 245</td>
</tr>
<tr>
<td><em>Pterostichus adstrictus</em> Eschschoitz</td>
<td>text p. 245</td>
</tr>
<tr>
<td><em>Pterostichus femoralis</em> Kirby</td>
<td>1 – 30.IX.1968</td>
</tr>
<tr>
<td><em>Calathus ingratus</em> Dejean</td>
<td>text p. 246</td>
</tr>
<tr>
<td><em>Synuchus impunctatus</em> Say</td>
<td>few, all brachypterous; ♀ – 17.VII.1967 with 43 well-developed eggs; ♀ – 21.VIII.1967 with 40 eggs; ♀ – 21.VIII.1967 with tachinid larva parasite</td>
</tr>
<tr>
<td><em>Agonum quadripunctatum</em> DeGeer</td>
<td>1 – 26.X.1967</td>
</tr>
<tr>
<td><em>Agonum retractum</em> LeConte</td>
<td>1 – 18.X.1967; 2 – VI.1968</td>
</tr>
<tr>
<td><em>Agonum cupripenne</em> Say</td>
<td>2 – 17.VII.1967 &amp; 5.VII.1968</td>
</tr>
<tr>
<td><em>Agonum cupreum</em> Dejean</td>
<td>text p. 246</td>
</tr>
<tr>
<td><em>Agonum placidum</em> Say</td>
<td>text p. 246</td>
</tr>
<tr>
<td><em>Amara torrida</em> Panzer</td>
<td>text p. 246</td>
</tr>
<tr>
<td>Name of species</td>
<td>Notes</td>
</tr>
<tr>
<td>-------------------------------------</td>
<td>---------------------------------------------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td><strong>Amara latior</strong> Kirby</td>
<td>text p. 247</td>
</tr>
<tr>
<td><strong>Amara apricaria</strong> Paykull</td>
<td>text p. 247</td>
</tr>
<tr>
<td><strong>Amara avida</strong> Say</td>
<td>text p. 247</td>
</tr>
<tr>
<td><strong>Amara obesa</strong> Say</td>
<td>text p. 247</td>
</tr>
<tr>
<td><strong>Amara quenseli</strong> Schonherr</td>
<td>1 gravid ♀ - 28.VIII.1967</td>
</tr>
<tr>
<td></td>
<td>4 – 23.VIII &amp; 27.IX.1968 including 2 gravid ♂♂</td>
</tr>
<tr>
<td><strong>Amara farcta</strong> LeConte</td>
<td>text p. 248</td>
</tr>
<tr>
<td></td>
<td>1 – 1967; 2 – 1968, 1 immature (30.VIII)</td>
</tr>
<tr>
<td></td>
<td>text p. 248</td>
</tr>
<tr>
<td><strong>Amara patruelis</strong> Dejean</td>
<td>text p. 248</td>
</tr>
<tr>
<td><strong>Amara laevipennis</strong> Kirby</td>
<td>few – 30.VI &amp; 5.IX.1967 &amp; VIII.1968; gravid ♂ – 12.VII.1968</td>
</tr>
<tr>
<td><strong>Amara littoralis</strong> Mannerheim</td>
<td>3</td>
</tr>
<tr>
<td><strong>Amara convexa</strong> LeConte</td>
<td>text p. 249</td>
</tr>
<tr>
<td><strong>Amara pallipes</strong> Kirby</td>
<td>few – VI-VIII; immature adult – 9.VIII.1968</td>
</tr>
<tr>
<td><strong>Harpalus amputatus</strong> Say</td>
<td>text p. 249</td>
</tr>
<tr>
<td><strong>Harpalus funerarius</strong> Csiki</td>
<td>few – IX.1967 &amp; VII.1968; gravid ♂ – 18.VII.1968</td>
</tr>
<tr>
<td><strong>Harpalus uteanus</strong> Casey</td>
<td>6</td>
</tr>
<tr>
<td><strong>Harpalus pleuriticus</strong> Kirby</td>
<td>6 – VI-VIII.1968</td>
</tr>
<tr>
<td><strong>Harpalus desertus</strong> LeConte</td>
<td>text p. 249</td>
</tr>
<tr>
<td><strong>Harpalellus basilaris</strong> Kirby</td>
<td>1 – 2.XI.1967</td>
</tr>
<tr>
<td><strong>Trichocellus cognatus</strong> Gyllenhal</td>
<td>5 – VI-VII.1968; 2 gravid ♂♂ – 26.VII.1968</td>
</tr>
<tr>
<td><strong>Bradycellus lecontei</strong> Csiki</td>
<td>2 ♂♂, elytra iridescent – 27.X.1967 &amp; 23.IX.1968</td>
</tr>
<tr>
<td><strong>Bradycellus congener</strong> LeConte</td>
<td>text p. 249</td>
</tr>
<tr>
<td><strong>Bradycellus species ?</strong></td>
<td>6 – 18.VII.1968</td>
</tr>
<tr>
<td><strong>Stenolophus comma</strong> Fabricius</td>
<td>1 – 17.VI.1968</td>
</tr>
<tr>
<td><strong>Badister obtusus</strong> LeConte</td>
<td>1 – VI.1968</td>
</tr>
<tr>
<td><strong>Chlaenius alternatus</strong> Horn</td>
<td>1 – 18.IX.1968</td>
</tr>
<tr>
<td><strong>Metabletus americanus</strong> Dejean</td>
<td>text p. 249</td>
</tr>
<tr>
<td><strong>Cymindis planipennis</strong> LeConte</td>
<td>1 – 18.X.1967</td>
</tr>
<tr>
<td><strong>Cymindis cribricollis</strong> Dejean</td>
<td>♂ – 17.VII.1967; gravid ♂ – 31.VII.1968</td>
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63 species
**Calosoma calidum Fabricius**

No trace of this species was seen at Calahoo in 1967, but several examples were captured in 1968, with immature adults found on 16 and 26 August. Two eggs were laid by a captive ♀ on 20 June 1968 and one of these was reared to the third instar. A few living larvae were taken in pitfall traps (between 5 July and 3 August) and reared to the adult state. The average length of each stage was: egg 4 days, instar I 5 days, instar II 8 days, instar III 14 days, pupa 8 days. The life cycle is therefore complete in 5 to 6 weeks. No evidence suggests that there is more than one generation per year or that any larvae overwinter.

**Bembidion nitidum Kirby**

Specimens were trapped in June, September, and October 1967, and in May-July and again in late September-October 1968. The population density was estimated for 1968 as $\leq 1.0/m^2$.

A final instar larva, found in a culture of adults in the laboratory, on 2 January 1968, pupated on 6 January, but became infected with a fungal growth by the middle of the following month and died. Nineteen other larvae were taken from the same culture which was replenished by the addition of newly-trapped adults, in summer 1968. These appeared between 24 and 28 May and then not again until the end of July. None was reared to the adult; one, taken as an instar I larva on 24 May, underwent ecdisis on 28 May and again on 31 May, but the instar III larva was unable to pupate successfully and died on 10 June. Of the larvae which appeared at the end of July, some had reached instar III by 19 August. An instar II larva was trapped on 23 August.

Lindroth (1963) recorded immature beetles from early August and stated that hibernation is probably imaginal i.e. that larval growth takes place in the summer. However, there seem to be two breeding periods indicated first by peaks in number or activity (i.e. pitfall trap catches) in early May and late June (Fig. 1) and second by instar I larvae produced in culture only in late May and in late July. If this interpretation is correct, the immature adults recorded by Lindroth were probably from the second generation. The larva found in culture in January 1968 was perhaps properly from the first annual generation which had been produced early because of warm temperatures in the laboratory. Likewise the number or activity peak of September-October is possibly an early manifestation of that of the following May which is interrupted by freezing temperatures. A situation in some ways the reverse of this is discussed by Mitchell (1963) where a few adults of *Trechus quadristriatus* (Schrank) (which is stated to breed in September) overwinter and breed in the following spring. The development period of the supposed second annual larval generation is not necessarily of the same length as that of the first and if a third takes place during the winter, this last would obviously be much lengthened.

**Bembidion bimaculatum Kirby**

Many more specimens of this species were taken in August than in any other month and it appeared to have a single peak of numbers or activity (Fig. 1). Captured ♀♀ contained eggs between the end of July and early September, when as many as 17 mature eggs were contained in the abdomen of a single ♀. Larvae were taken from a laboratory culture on 4 November 1967. Lindroth (1963) considered the larva to hibernate.

The population size was estimated at $\leq 0.8/m^2$ in 1968. The related species *B. sordidum* Kby. was not recognised from Calahoo.
Fig. 1. Pitfall catches of Carabidae over fortnightly periods (log. scale) x time.
Carabidae of an arable field

Bembidion rupicola Kirby

A common species at Calahoo, with an estimated population size (1968) of 2.6/m². Adults showed a very similar pattern of numbers or activity to that shown by B. nitidum, with peaks in early May, late June, and October.

Several pairs of adults were observed mating in pitfall traps on 10 May 1968. Larvae were taken from a culture of adults in the laboratory at various dates between 24 May and 10 June 1968, but none was reared successfully, so that the duration of the larval instars cannot be given. However, an instar III larva, taken at Worsley, Alberta, on 11 July 1967, pupated on 14 July and the adult emerged on 20 July. Lindroth (1963) recorded immature beetles between 22 July and 3 August and stated that adults hibernate.

If an analogy is drawn with B. nitidum and B. quadrimaculatum, below, it would seem likely that the numbers or activity peaks of early May and late June (Fig. 1) correspond to two separate breeding periods. The first generation reaches the adult state in late June. Either these adults and their parents, or both, then breed giving rise to the second generation which reaches the adult state at the end of July and beginning of August. This second generation may normally overwinter and perhaps breed in May of the following year, but a certain number of larvae may be produced in October and may overwinter.

A single instar III larva trapped at Calahoo on 11 September 1968, pupated in the laboratory on 16 September and the adult emerged on 28 September. This raises the possibility of a third generation in the year, but because of the absence of a peak in numbers or activity in early August, it seems more probable that the occurrence of this larva was exceptional.

Bembidion obscurellum Motschoulsky

Far fewer adults of this species were trapped in late 1967 than of B. rupicola, but the former were more numerous at the beginning of 1968. Either B. obscurellum adults were not influenced so greatly to activity by the warm autumn of 1967, or they survived the winter better. Population size between June and August 1968 was estimated at 3.9/m².

The pattern of activity appears to be identical to that of B. rupicola, with three peaks in numbers or activity, one in early May, the second in late June and a smaller third in October (Fig. 1). Like B. rupicola, adults were found mating in pitfall traps on 10 May 1968. Larvae and eggs were taken from a culture of adults on 24, 25 and 26 May and not again until 26-31 July. Lindroth (1963) recorded immature adults in late July in Alberta.

Bembidion versicolor LeConte

This species had a rather similar pattern of numbers or activity (Fig. 1) to that of B. nitidum. It showed a peak in early May, a second in late June and a third in November. The third peak had its beginning earlier in 1967 than in 1968. Gravid ♀♀ were taken on 19 and 26 July 1968. No larvae were obtained.

The species is somewhat hygrophilous. Specimens of the related species B. timidum LeConte were not collected at Calahoo.

Bembidion quadrimaculatum oppositum Say

By far the most numerous carabid at Calahoo, its population size was estimated to be 20/m² in 1968 with a pattern of numbers or activity (Fig. 1) similar to that of B.
Several pairs of a laboratory culture were observed mating in late May 1968. Instar III larvae were recovered from this culture on 13 June and one of these pupated on 20 June and the adult emerged on 1 July. A ♀ taken in a pitfall trap on 26 July was found to be gravid. Larvae were again taken from culture between 26 and 31 July of which one pupated on 5 August but subsequently died.

Rivard (1964) has indicated for the subspecies a breeding period extending from May until July in eastern Ontario. This was based on dissection of 72 females captured between May and November 1963, of which 24 were gravid. During most of this May-July period, according to Rivard's Fig. 1, no more than 50% of the female beetles dissected were gravid, except in early July when approximately 100% were gravid. In Rivard's Fig. 1, a line is drawn through 10 points on a graph which relate to the 24 gravid beetles and a similar number of non-gravid ones. Thus a difference of one or two gravid beetles at any date could make a large difference to the shape of the graph line.

The numbers of individuals taken in pitfall traps at Calahoo (Fig. 1) are based upon the summation of pitfall trap catches over fortnightly periods. The number taken in early May was 924; in late May 769; in early June 294; in late June 1234; in early July 872 and in late July a mere 66. Unless the substantial drop in numbers in early June and substantial increase in late June are related to breeding activity they are difficult to account for; the explanation is hardly to be sought in direct temperature or rainfall variation effects.

If no significant drop in numbers occurs, but merely a period of quiescence, then the second peak must represent a resumption of breeding activity by the same generation of adults. Thus a single generation would have two temporally (at least partially) separated breeding periods.

If a real drop in numbers occurs, then the second peak must be associated with an increase in the adult population by the metamorphosis of pupae — but the continuance of breeding activity after this date is not disputed — and this suggests true bivoltinism. On this basis, because adults of this new generation must outnumber adults of the previous generation by at least four to one (Fig. 1) in late June and thereafter, then no more than 20% of trapped females should be gravid from late June onwards, if there is no bivoltinism. Rivard found 100% of females captured to be gravid only in early July.

The evidence points to the existence of two breeding periods at Calahoo. Several other species of Bembidion show a very similar pattern of numbers or activity.

_Bembidion mutatum_ Gemminger and Harold

Less numerous than the similar _B. quadririmaculatum_. The numbers trapped were small particularly in 1968, but indicate numbers or activity peaks (Fig. 1) similar to those of the above species, perhaps slightly delayed. A gravid ♀ was captured on 9 August 1968.

_Bembidion canadium_ Casey

As frequently trapped in late 1967 as _B. rupicola_, this species was only as numerous in 1968 as _B. mutatum_. The numbers taken in pitfall traps decreased from May 1968 until June, after which there was no activity until October (Fig. 1). The absence of a second summer peak in 1968 may indicate that the species is univoltine, if meaning can be inferred from the small numbers of individuals trapped.
Pterostichus lucublandus Say

The population size of this species was estimated at $\leq 0.7/m^2$ in the study area in 1968. The adults were active only during May-July of 1968, but in the milder autumn of 1967 there was another peak of numbers or activity in late September (Fig. 1). Approximately equal numbers were caught during each half-month period between early May and early July and there is no evidence to suggest that there are two activity peaks with the corollary of bivoltinism. Rivard (1964) also arrived at this conclusion of univoltinism for this species and his Fig. 1 indicated that the breeding period extends from May into September in eastern Ontario.

Females dissected on 20 May 1968 and 17 July 1967 contained large eggs. Mating of pairs caught in pitfall traps was observed on 21 May 1968 as well as in laboratory cultures during the last week of May. Eggs were produced by these cultures from 23 May until 5 June and from 8-16 July. The egg stage lasted 4-7 days, instar I 6-7 days, instar II 6-11 days, instar III 14-21 days and the pupa 8-10 days. Towards the end of July and in early August larvae were taken in pitfall traps frequently and one of these was reared to produce an adult on 23 August (pupal stage 7 days). Immature adults were taken in pitfall traps on 5 September 1968.

Larvae (apparently instar III) were described briefly by Schaupp (1881), one of which pupated on 26 August and the adult emerged on 5 September; another pupated on 18 August and the adult emerged on 29 August.

Pterostichus corvus LeConte

Not a single example of this species was taken in the study area in 1967, but 16 were taken in May-July 1968. By analogy with the related P. lucublandus, the population size may have been of the order of 0.07/m² in 1968.

Eggs were obtained from a laboratory culture on 30 June, 14, 15 and 26 July and 3 August 1968. The average duration of each stage was as follows: egg 6 days, instar I 6 days, instar II 6 days, instar III 16 days, pupa 7 days.

Because of the small numbers trapped it is not possible to specify the breeding period or periods with any certainty. The northernmost locality given by Lindroth (1966) for the occurrence of this species in Alberta is Morin, some 150 miles SSE of Calahoo.

Pterostichus adstrictus Eschscholtz

More than twice as numerous at Calahoo as P. lucublandus (estimated population size in 1968 1.8/m²), but apparently with a very similar life cycle. The second numbers or activity peak of late September 1967 shown by P. lucublandus was even more marked in this species and was repeated to some extent the following year (Fig. 1). There was a very slight diminution in numbers trapped from late May until June.

Gravid ?? were found as early as 10 May and as late as 17 July, while immature adults were trapped from 21 August until 5 September. Adults in a laboratory culture produced eggs between 23 May and 26 July and the resultant larvae were reared in the same manner as those of P. lucublandus. The egg stage lasted 4-8 days, instar I larva 4-6 days, instar II larva 4 days, instar III 17-18 days and pupa 6-7 days. Adults reared from instar III larvae taken in pitfall traps emerged at the end of July and beginning of August.

The related P. pennsylvanicus LeC., although abundant at George Lake, Alberta, a marshy, wooded locality little more than 16 km (10 miles) NNW of Calahoo, was never found in the study area.
Calathus ingratus Dejean

A few individuals only were taken, in June-August of both 1967 and 1968; the normal habitat is wooded localities.

Two ?? (with very reduced wings) were trapped on 17 July 1967, one of which contained eight large eggs, the other five. Another ?, taken on 24 July 1968, was also gravid. A (macropterous) ?, taken on 21 August 1967, contained no eggs, neither did brachypterous ?? taken at Scandia and at Tofield, Alberta in April 1968.

Agonum cupreum Dejean

Estimated to have a population size of 1.0/m² in 1968 at Calahoo, this species seemed to be less abundant than during the previous year. All examples from Calahoo, in which the wings were examined, proved to be macropterous.

None of the ?? caught at various states between 21 April (1968) and 17 July (1967) contained mature eggs (though one contained the pupa of a parasitic hymenopteron), but a ? taken on 21 August (1967) contained (only) two eggs, perhaps indicating the approaching end of the breeding season. An instar III larva, trapped on 30 August 1968, pupated on 15 September and the adult emerged on 21 September. An immature adult was taken in a pitfall trap on 16 September 1968. A pair was observed in copula, in the laboratory, on 20 November 1967. Lindroth (1966) recorded immature adults at the end of July and in August.

The graph of numbers or activity (Fig. 1) is difficult to interpret and it may be that there is a single breeding period extending from May into July, but numbers trapped are too small for certainty. The September-October peak possibly represents early incidence of the activity of the following year. If breeding occurs from May to July, immature adults would be expected from late July until late September. The apparent decline in numbers between 1967 and 1968 might be the result of unsuccessful overwintering possibly as a result of the high and perhaps untimely level of activity in late 1967.

Agonum placidum Say

Less frequently captured in 1967 than was A. cupreum, the situation was reversed in 1968, when A. placidum was more often captured and its population size was estimated at \( \leq 1.5/m² \).

Females with eggs were taken on 17 July 1967, the maximum number of eggs recorded per ? being 20. Of 20 ?? captured on 14 April 1968 at Scandia, Alberta, none contained eggs, but one contained two nematode parasites. Eight instar III larvae caught between 23 August and 9 September 1968 produced adults between 4 Sept. and 17 Sept., the average time for the pupal stage being 6 days.

A numbers or activity peak in July is well marked in this species (Fig. 1) and there is some evidence of a minor peak in the year (October 1967 and September-October 1968). The breeding period seemed to be restricted to July in 1968 at Calahoo. Rivard (1964) found gravid ?? between June and September in eastern Ontario. Lindroth (1966) quoted records of gravid ?? from June to August in southern Ontario.

Amara torrida Panzer

Lindroth (1968) wrote that the habitat of this species was similar to that of Pterostichus
adstrictus. Certainly both species were common at Calahoo. The population density of A. torrida was estimated by the mark, release and recapture technique as $\leq 0.6/m^2$ in 1968. In the same year, numbers taken in pitfall traps gradually rose to a single peak in early August and then declined more rapidly (Fig. 1).

Gravid $\varnothing$ were trapped in 1967 on 17 July, 21 August, 24 August and 1 September, while in 1968 gravid $\varnothing$ were taken on 19 July and 9 August, but $\varnothing$ trapped on 20 May and 30 September were not gravid. The maximum number of eggs contained by a single $\varnothing$ was 20 (24 August 1967). Pairs were observed in copula on 6 August 1967 and 16 August 1968. A pitfall trap emptied on 21 August 1968 contained a single adult $\sigma$ A. torrida together with two eggs (no other beetles present) which, unfortunately, did not prove to be viable. Five eggs were removed from a culture of adults in the laboratory, between 30 July and 2 August 1968, but these too were not viable. An immature adult was trapped on 17 July 1968.

This bears out the suggestion by Lindroth (1968) of larval hibernation and indicates a lengthy larval growth period. The single peak in numbers trapped, in early August, may well indicate the coincidence of the peak of the breeding period with the peak period of emergence of the new generation of adults.

Adults, each with a single parasitic dipterous larva, were captured on 10 May 1968 (1 example); 20 May 1968 (1 example); 9 August 1968 (3 examples). A male captured on 9 August 1968 was the host of a nematode.

-Amara latior- Kirby

Only a few individuals of this species were trapped in either year at Calahoo, the greatest number appearing in early July (Fig. 1). A gravid $\varnothing$ was taken on 5 September 1967. A larva, taken from soil on 11 July 1967 at Worsley, Alberta, pupated the same day and the adult emerged on 17 July. Lindroth (1968) recorded gravid $\varnothing$ in September and October in Ontario, while Rivard (1964) recorded others during August-October in eastern Ontario.

-Amara apricaria- Paykull

This species was commoner at Calahoo than species of Amara previously discussed, but numbers trapped were still too low to allow interpretation of the pattern of numbers or activity (Fig. 1). A single gravid $\varnothing$ was taken on 17 July 1968. The larva was described briefly by Schiødte (1867) but the date of capture was not given.

An individual parasitised by a dipterous larva was captured on 10 May 1968.

-Amara avida- Say

This species was apparently commoner at Calahoo in 1968 than was A. torrida ($\leq 0.9/m^2$) and like that species with a single peak in numbers or activity (Fig. 1). The peak, however, occurred in early July, a month earlier than the A. torrida peak. Some evidence of a second peak in September-October was seen in 1967 but not in 1968.

Gravid $\varnothing$ were taken on 17 July, 21 August and 24 August 1967 and 9 August 1968. As many as 11 eggs were dissected from a single $\varnothing$. Several eggs were laid singly by a $\sigma$ in a laboratory culture on 3 August 1968 and some of these hatched between 9 and 12 August, but none of the resultant larvae survived instar I. A single immature individual was taken among 17 mature adults on 10 July 1968. Lindroth (1968) noticed immature adults in June in British Columbia and Alberta.

Two individuals, each parasitised by a dipterous larva, were captured on 9 August 1968.
Specimens of this species were most frequently taken in late September and early October. Two gravid ♂♂ were taken at Calahoo on 17 July 1967 and two others on 21 April 1968 at Mill Creek, Edmonton. A pair was found in copula on 6 June 1968 and an immature adult was taken in a pitfall trap on 16 August 1968. Lindroth (1968) described A. patruelis as "a pronounced spring species" and stated that adults hibernate. It appears as if the larvae have a summer development period in contrast to the foregoing species of the subgenus Curtonotus (Amara aulica group Lth.) e.g. A. torrida, and Bradytus (Amara apricaria group Lth.) e.g. A. avida, but the pattern of numbers or activity (Fig. 1) is difficult to interpret because of the small numbers trapped.

Three ♂♂, the first captured on 20 May 1968, the others on 11 September 1968, each contained a single parasitic dipterous larva.

Amara ellipsis Casey

Not uncommon at Calahoo. The greatest number of individuals to be taken in a two-week period was in early October 1967 and a peak at this time of year was repeated in 1968 (Fig. 1). This late-year peak is a possible forerunner of the small peak of early May. There appears to be a second peak in July. There is similarity in this to the condition shown in the Bembidion species and on the basis of this and the following evidence two breeding periods per year are suggested.

An overwintering ♂, hand collected on 3 April 1968, contained eggs which were not fully developed. Pitfall trapped ♂♂ yielded eggs on 10 May and on 3 and 15 July 1968; none was trapped between the middle of May and the end of June; no ♂ trapped later in the year than July was gravid. An adult emerged successfully on 19 July 1967 from a pupa which had been collected as a larva on 22 June, the date of pupation being 7 July. An immature adult was taken at Calahoo on 24 July 1968. Lindroth (1969) found immature adults at the end of July.

Three ♂♂ captured on 26 July 1968, 21 August and 30 September each contained a single parasitic dipterous larva.

Amara littoralis Mannerheim

Present and active in largest numbers in July at Calahoo, the commonest species of subgenus Amara (Amara lunicollis group Lth.). It seems to have a life cycle similar to that of A. ellipsis, with a peak in numbers or activity (Fig. 1) in early May and a second one in July. A decline in numbers trapped in early August is not accounted for unless the peak of late August is the result of the emergence of adults of the second generation. Two breeding periods per year are suggested.

Dissected ♂♂ contained eggs on 10 May and on 20 May 1968; none was trapped thereafter until early July. In the latter month ♂♂ contained eggs on 3, 10, 12, 15, 18, 24, 26 and 31 July, but not thereafter. Lindroth (1968) found immature adults in July and at the beginning of August.

A ♂ taken on 17 July 1967 contained a larva of an unidentified tachinid, which occupied about half the volume of the host's abdomen. The empty chorion of the tachinid egg lay under the right elytron of the host. Four ♂♂, captured on 24 July 1968, 31 July (2 examples) and 3 August each contained a single parasitic dipterous larva.
Harpalus amputatus Say

According to Lindroth (1968) a xerophilous species, the most abundant of the large carabids at Calahoo in 1968, when its population size was estimated at 4.2/m². The pattern of numbers or activity probably indicates a single peak in early June (1968) and extending from May until July, with slight fluctuation. A slight autumnal peak was seen in 1967 (Fig. 1), but the species was not trapped in that year until early September.

Dissected ?? contained eggs on 8 May 1968, 17 July 1967, 9 August 1968 and 21 August 1967. Unfortunately no females captured in June 1968 were put aside for dissection, but all were used to establish cultures or in population estimations. The presence of gravid ?? in June would have established the existence of a single breeding period as indicated by the pitfall trap captures.

Harpalus pleuriticus Kirby

The population size of this species at Calahoo in 1968 was of the order of 1.0/m². The species is thus not only of smaller size but was of smaller population size than H. amputatus. It reached the zenith of what may be a single extensive peak in numbers or activity in July (Fig. 1). If this is, in fact, a single peak, then the breeding period may extend from May until August, as seems to be indicated with H. amputatus. An autumnal peak was seen in late September 1967.

Dissected ?? contained mature eggs on 17 July 1967, 12, 15, 17, 18, 19 and 24 July and 9 August 1968, but not thereafter and not in May 1968. As with H. amputatus, no ?? captured in June were set aside for dissection. A pair was observed mating in a laboratory culture on 8 July 1968. Immature adults were taken in pitfall traps on 18 and 24 July, 9 and 16 August 1968.

Adults captured on the following dates in 1968 contained parasitic dipterous larvae: 20 May (1 example); 9 July (1 example); 24 July (2 examples each with 2 parasites); 9 August (1 example with 2 parasites).

Trichocellus cognatus Gyllenhal

The adults of this species were taken at Calahoo only in late September-November, when large numbers (387 during October 1967, 465 during October 1968) were caught in pitfall traps. Freezing interfered with assessment of population size.

A pair was found mating in a pitfall trap on 2 October 1968. Lindroth (1968) stated that immature beetles are abundant from mid-July to the end of August, but this was not so at Calahoo. Larvae were taken from culture between 1 and 17 October 1968. Oviposition might well take place in October and November when temperatures allow, and larvae may overwinter.

Metabletus americanus Dejean

Adults of the species were present and active in May to mid-July and late September to November only (Fig. 1). None was captured between mid-July and late September, but a ? taken on 19 July 1968 was gravid. In the laboratory six instar I larvae were taken from a culture of adults between 10 and 18 July 1968, but none was reared successfully. Several instar I larvae were taken from culture on 20 November 1968, of which two underwent ecdysis to instar II on 5 December.
There was a decline in pitfall trap captures in early June, similar to that of some *Bembidion* species, so that two generations per year may be indicated. Some larvae may be produced in May and early June.

Other Arthropods

The following species of Staphylinidae were captured in the study area: *Leptacinus batychrus* Gyll., *Philonthus occidentalis* Horn, *P. concinnus* Grav., *P. furus* Nordm., *Quedius spelaeus* Horn, *Tachyporus* sp. The third, fourth, and fifth of these were trapped only occasionally.

Spiders taken in the study area were: *Trochosa terricola* Thor., *Pardosa groenlandica* (Thor.), *P. mackenziana* Keys, *P. moesta* Banks, *Pardosa* sp. nr. *saxatilis* (Htz.), *Pardosa* sp. of *metlakatla* complex, *Gnaphosa* sp. nr. *muscorum* (Koch), *G. parvula* Banks, *Micaria* sp. nr. *alberta* Gertsch, *Xysticus californicus* Keys (1 9, 21 June 1968, first Canadian record), *Paraphidippus marginatus* (Walck.). *Pardosa groenlandica* was the most frequently trapped of these.

**DISCUSSION**

Life cycles

Perhaps more ecological studies of Carabidae have been made than of any other family of Coleoptera, but the volume of knowledge of their life cycles is slender.

Rivard (1964) concluded that for 13 species studied in eastern Ontario, each had only a single generation per year, based on occurrence of mature eggs in the ovaries of adult ♀♀. He classified them into two major groups, spring breeders and autumn breeders, with a small third group overlapping the two periods. Greenslade (1965) arrived at similar conclusions in a study of 26 species of Carabidae in England, based on observations of activity periods of adults and larvae through numbers of individuals caught in pitfall traps and the association of these activity periods with breeding activity. However, Heydemann (1963) considered a number of species of carabids in maritime Germany to have more than one breeding period per annum. He cited some species of *Bembidion* and observed that (apparently in respect of insects in general) while carnivorous forms are mostly univoltine, saprophagous forms are frequently bivoltine or polyvoltine.

Rivard’s (1964) assumption that the breeding periods are coincident with the presence of mature eggs in [a high percentage of] ♀♀, with perhaps a 2-3 weeks delay between the maturity of the eggs and the onset of oviposition, is doubtless a good approximation for the population as a whole; but no allowance is made for periods of inactivity e.g. if gravid ♀♀ are inactive over the winter before oviposition. Nor is distinction made between different generations present in the population. Thus if the premise be expanded (beyond Rivard’s statements) one is led to infer that adult generation I breeds, producing eggs, larval instars, pupae and thus the resultant adult generation II. The fate of adult generation I is ignored, but possibly a considerable number of adults of generation I may survive and may breed again (at a time not necessarily coincident with the breeding period of generation II). This possibility is higher in species of lower reproductive potential or lower survival rate. The survival of these adults depends upon the combined effects of parasitism (including disease), predation, inter- and intraspecific competition, climatic factors and ‘natural senescence’. Lack of information on ‘natural senescence’ is a result of the difficulty of observing individuals in the field over long periods of time. Conditions in the laboratory must pro-
duce anomalous results. No individual beetle in the present study survived in the laboratory for much more than 1 year. However, an adult ♀ and ♂ of *Omophron americanum* Dejean (for which Rivard (1964) gives the breeding period as May to June) were captured at Chappice Lake, Alberta, on 29 May 1967, along with five other adults, and survived in captivity until May 1969. These individuals must have been produced, as eggs, not later than the summer before capture (on Rivard’s evidence) and so their total life span was at least 3 years. The ‘culture’ of seven adults produced eggs in June 1967 (the resultant larvae subsequently died) but none thereafter. This, however, is no proof that the normal life span approaches (or exceeds) 3 years, nor that each generation of adults breeds only once. It merely shows that adults of generation I could still form part of the population at the breeding period of adults of generation II and even of generation III.

Breeding periodicity in different parts of the geographical range of a species may differ and may or may not be directly influenced by climatic conditions. Heydemann (1963) (following Lindroth, 1945) remarked upon the different percentages of species with a summer larval growth period or with a winter larval growth period between habitats with a maritime climate and with a continental climate. The implication was that in a harsher (continental) climate, a greater percentage of species has a winter larval growth period.

Populations

The principal interest of the present study lies in the observed dominance of Carabidae among the larger soil-surface inhabiting insects of the study area and in the large number of species apparently coexisting in an apparently very uniform habitat.

On the assumption that there is at least some similarity of requirements between the *Bembidion* species, then there must be interspecific competition (Odum, 1959). If population size is taken as a measure of success in this competition, then *B. quadrimaculatum*, with a population size about double that of all other *Bembidion* species combined, must be seen as the most successful species. Similarity of requirements may not be unconnected with accepted taxonomic relationship. Nine of the 11 species belonging to different species groups of *Bembidion* (Lindroth, 1963) where there might be expected to be greater differences in requirements, but *B. rupicola* and *B. obscurellum* belong to the same species group, as do *B. quadrimaculatum* and *B. mutatum*. *Bembidion rupicola* and *B. obscurellum* were of comparable abundance in the study area in 1968, not so with *B. quadrimaculatum* and *B. mutatum*.

Few genera of Carabidae have been recorded in the literature as having restricted food preferences. It is to be expected that those species which were not merely stragglers into the area would have some food-chain relationship to the crop plant. Carabids might eat the crop plant or its seeds or stages of its decomposition, or they might be predators of other animals which do so.

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REFERENCES


A method of measuring the drag-speed relationship for an insect flight mill system is reviewed. Compensated free flight speeds and ranges for Agrotis orthogonia Morrison are given for Jacobson's (1965) data.

The use of insect flight mills as described by Hocking (1953) necessitates a consideration of mill drag. The additional drag of the device substantially lowers flight speed, and should be corrected for as follows.

The difference between power required to maintain a mill alone, and a mill loaded with a dead insect at a constant speed, is the power required to overcome drag on the insect alone at that speed. Free flight speed would be the speed at which power to overcome drag on the insect alone would equal power to overcome drag on the mill-insect combination at the observed mill speed. Correction for this requires the measurement of drag-speed relationships for the mill itself and for the insect.

I tested the mill used by Jacobson (1965). It is similar to those described by Hocking (1953), but gives a flight circumference of 0.893 meters. With the mill pivoted on a steel needle, the mill tip sweeps out a horizontal circle. Following Hocking's (1953) procedure, about the glass stem I wound two natural silk threads, passed these over light weight pulleys on either side of the glass stem, and attached a series of weights to their opposite ends. By measuring the terminal tip speed for each pair of weights the drag at this speed can be obtained from the following relationships:

\[
d = \frac{2Wrg}{R} \quad \text{and} \quad P = \frac{dc}{t} = \frac{2Wgrc}{Rt}
\]

where,

- \(d\) = equivalent drag on the system at the arm tip at terminal speed (kg m sec\(^{-2}\))
- \(W\) = weight on each thread (kg)
- \(r\) = radius of the glass stem (m)
- \(g\) = acceleration due to gravity (9.8 m sec\(^{-2}\))
- \(R\) = length of the mill arm (m)
- \(P\) = power to maintain a terminal tip speed (Joules sec\(^{-1}\))
- \(c\) = circumference swept out by the insect mount on the mill arm (m)
- \(t\) = time for one revolution (sec)

I used the means of two readings taken in each direction of rotation at each loading to plot drag-speed relationships (Fig. 1). For speeds too high for counting by eye I used Hocking's photocell system.

I plotted power against terminal speed for the insect and for the mill with a dead insect, without wings or legs, mounted on it in flight attitude. The appropriate drag value, i.e. that on the insect alone or that on the insect plus 'tip equivalent drag' for the mill, multiplied by the tip speed gives the power values. As suggested by Hocking (1953) by comparison of the mill mounted insect speed to the free insect speed at equal power, the free flight speed can be estimated. The dotted lines on Fig. 1 illustrate this procedure. Free flight speeds estimated, a proportional correction can also be made to equivalent flight ranges. An example using Jacobson's (1965) data follows.
The maximum mill speed of male *Agrotis orthogonia* Morrison is given at 4.5 mph or 2.01 m sec\(^{-1}\). From Fig. 1 the equivalent free speed is found by the projection at equal drag from the insect-mill curve to the free flight curve (dotted lines). The equivalent free flight speed is 2.47 m sec\(^{-1}\) or 5.5 mph. The mean free flight speed of the male is 20% faster than the mill speed, and the equivalent flight range is then 17.6 miles.

Equivalent Free Flight Speeds and Ranges of *A. orthogonia*

<table>
<thead>
<tr>
<th>Mill values</th>
<th>Free flight values</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>male</td>
</tr>
<tr>
<td>Mean speed (mph)</td>
<td>2.5</td>
</tr>
<tr>
<td>Max. speed (mph)</td>
<td>4.5</td>
</tr>
<tr>
<td>Max. range (miles)</td>
<td>14.7</td>
</tr>
</tbody>
</table>

REFERENCES


The members of this species feed in nature only on representatives of the plant genera Achillea, Chrysanthemum, Matricaria and Tanacetum belonging to the tribe Anthemideae, family Compositae. Natural incidence, mating, adult and larval feeding, oviposition, life cycle and immature stages on Tanacetum vulgare L. were observed. Thirty-eight plant species belonging to 17 families were tested for acceptability to gravid females for feeding and oviposition. Comparison of index of acceptability for feeding and oviposition with an index of plant relationship show that only plants closely related phylogenetically to the natural host-plant were acceptable for feeding and oviposition. This ovipositional preference by adult females is probably due to host-specific substances present only in selected plants. Studies on feeding and ovipositional preference by adult females when offered a choice of six acceptable plants show that maximum numbers of feeding punctures were on the plant from which flies were bred. Other preferred plants also served as hosts in nature. Two genera, Artemisia and Helianthus, though acceptable but not preferred in these studies do not serve as hosts in nature. The larva being a completely internal plant feeder is unable to select a more suitable food plant which might be available in its range. First instar larvae were manually transferred from the natural host-plants in various test plant species. Comparison of the success index for larval development with the index of plant relationship show that some plants widely removed phylogenetically but presumably lacking toxic or inhibitory substances were nutritionally adequate for completion of larval development.

Larven herbeizuführen. Es ist anzunehmen, dass in diesem Falle toxische oder hemmende Substanzen nicht vorhanden waren.

Most of our knowledge of the biology of agromyzid flies is due to the late Professor E. M. Hering who in 1951 reviewed all existing information and compiled an extensive bibliography on this subject. Numerous other workers have studied the biology of many leaf mining species in detail (Webster and Parks, 1913; Smulyan, 1914; Cohen, 1936; Ahmad and Gupta, 1941; Allen, 1956; Oatman and Michelbacher, 1958, 1959; Tauber and Tauber, 1968).

*Phytomyza matricariae* Hendel is an oligophagous species whose members feed in nature around Edmonton, Alberta, Canada, only on the representatives of the tribe Anthemideae, family Compositae. The plant species attacked are *Achillea millefolium* Michx. (Fig. 1), *Achillea sibirica* Ledeb. (Fig. 2), *Achillea* sp. (cultivated variety), *Chrysanthemum* sp. (cultivated soft leaf variety), *Matricaria matricarioides* (Less.) Porter (Fig. 3), and *Tanacetum vulgare* L. (Fig. 4). Hering (1957) lists *Achillea, Anacyclus, Anthemis, Cotula* and *Matricaria* as European hosts for the members of this species. However, the identity of flies bred from some of these hosts probably needs confirmation by examination of the male genitalia. Spencer (1969) lists *Tanacetum* also as a European host.

Literature on various aspects of host selection, feeding, and host preference in phytophagous insects has been reviewed by many authors (Lipke and Fraenkel, 1956; Friend, 1958; Thorsteinson, 1960; Kennedy, 1965; Dethier, 1966, 1970; Schoonhoven, 1968).

Verschaffelt (1910) for the first time demonstrated that host selection in *Pieris brassicae* and *P. rapae* is determined by mustard oil glucosides in cruciferous and related plant families. Since then the food ranges of many oligophagous insects have been explained by the botanical distribution of secondary plant chemicals (Fraenkel, 1959). Feeding or token stimuli which evoke special feeding responses in phytophagous insects have been investigated (Thorsteinson, 1953; Sugiyama and Matsumoto, 1959; Nayar and Fraenkel, 1962, 1963; Harris and Mohyuddin, 1965; Keller and Davich, 1965; Stride, 1965) and together with deterrents play an important role in determining the selection of host-plants (Thorsteinson, 1960; Jermy, 1961, 1964). Many recent studies on the host range of oligophagous species have shown that plants not closely related to natural host-plants may be acceptable for normal growth and development (Jermy, 1961, 1966; Hsiao and Fraenkel, 1968). The association between insects and their host-plants has been shown to be the consequence of the interaction of two independently mutating systems (Dethier, 1970), and of the evolutionary coadaptations to chemical interactions between them (Whittaker and Feeny, 1971).

Most research in the field of insect host-plant relationships has been on external plant feeders. Agromyzids having evolved as exclusively internal plant feeders are more closely bound to plants than any group of external feeders and are therefore ideal for the study of insect-food plant relationships. The female agromyzid deposits an egg individually inside the tissue of a selected plant. The emerging larva, unlike that of external plant feeders, is unable to select a more suitable food plant which might be available in its ecological range. The larva either feeds on the plant tissue selected for it by its mother or dies. Although an agromyzid larva is not concerned with the selection of a suitable food plant, it is directly involved with its acceptance. These larvae are therefore most suitable for the study of their potential to use various food plants for their development.

Host-plant relationships in Agromyzidae have been discussed by Hering (1951), Nowakowski (1962), Spencer (1964) and Sehgal (1971). Among Agromyzidae, monophagy and oligophagy are both of common occurrence. Strict monophagy is rare outside of monotypic genera. Extreme polyphagy is also rare; all known polyphagous species are restricted in their range of food plants. Most species therefore feed in nature on related plants.
Fig. 1–4. Leaf mines on natural host plants of *Phytomyza matricariae*. 1. *Achillea millefolium* Michx. 2. *Achillea sibirica* Ledeb. 3. *Matricaria matricarioides* (Less.) Porter. 4. *Tanacetum vulgare* L.
MATERIALS AND METHODS

Observations on biology, and host-plant relationships of adult females and larvae were made under laboratory conditions of 70 ± 1°F and 12 hours of daily illumination maintained inside a growth chamber. The flies used in these experiments were bred from *Tanacetum vulgare* L. Both greenhouse and field grown plants were used. Small cuttings from the test plants were kept in Sach’s culture solution for flowering plants. By changing the solution it was possible to keep the cuttings healthy during the test period.

**Biology of Phytomyza matricariae Hendel**

Observations on mating, oviposition, feeding habits, and life cycle, were made on *Tanacetum vulgare* L. In order to determine the incubation period, individual leaves were caged with a large population of flies. After six hours the leaves were removed, examined for eggs, and the positions of individual eggs marked. The leaves were then observed at 12 hour intervals. The progress of larval mines was marked with different water soluble colors every 12 hours and the mine examined for moulded mouth hooks, which can be seen inside the mine by transmitted light under a binocular microscope. Duration of larval stadia was estimated from the positions of moulded mouth hooks. The time of moulting during any 12 hour period was estimated by measuring the relative length of leaf mine before and after the position of moulded mouth hooks. This method of recording larval activity has been used by Allen (1956) and Tauber and Tauber (1968). It was thus possible to estimate the duration of larval stadia, length of leaf mine excavated by different instars, and observe the mining habits of the larva. Leaf mines were fixed in 'Formal Acetic Alcohol' (F.A.A.) for microscopy.

**Host-plant relationship in adult females**

**Range of food plants.** — Small twigs of various plant species, bearing young leaves, were exposed individually to five gravid females inside a muslin cage, for a period of 24 hours. At the end of the experiment, flies were removed from the cages and the leaves examined for feeding punctures and punctures with eggs.

**Feeding and oviposition preference by gravid females.** — A circular plastic petri dish 5½ inches in diameter was used as a choice chamber to test the feeding and oviposition preference of adult females. The young leaves of six different plants, grown under greenhouse conditions, were placed around the periphery of the dish equidistant from one another. The petioles of leaves were pulled out through small holes in the periphery of the dish and wrapped with cotton kept moist with distilled water. The plants used in this experiment were *Tanacetum vulgare* L., *Achillea sibirica* Ledeb., *Matricaria matricarioides* (Less.) Porter, *Artemisia sp.*, *Chrysanthemum sp.*, (cultivated variety) and *Helianthus annuus* L. Five gravid females from a laboratory culture maintained on *Tanacetum vulgare* L. were used in each test after being isolated from their food plant for one hour. They were anesthetized with CO₂ and then introduced at the centre of the petri dish.

**Host-plant relationships of the larva**

**Transfers of larvae from natural host-plants to test plants.** — First instar larvae normally less than 24 hours old were used in these experiments. The supply of healthy first instar larvae was from plants in which eggs were laid in the laboratory. Field collected larvae were not used in order to avoid any early parasitization by braconids or chalcidooids.

Only young and tender leaves which are easier to handle than the mature leaves were used in these experiments. A small slit was made in the leaf of a test plant, using fine insect
pins under a binocular microscope. It is normally easier to make the slit near the base of the leaf or near the mid rib, more so on one side of the leaf than the other, depending on the test plant. A first instar larva was then removed by opening its mine on the natural host-plant and transferred with a fine tip of a soft brush into the slit made on the leaf of the test plant. The larva was pushed inside the slit so that it was completely surrounded by the tissue of the test plant. The leaf of the test plant along with a small portion of petiole or twig was then enclosed inside a square plastic petri dish containing moist filter paper in order to prevent any sudden drying of the tissue around the slit. Two small holes were cut in upper corners of the petri dishes and covered with thin muslin cloth to permit transpiration and to prevent excessive condensation. The larva inside the test plant can be observed by transmitted light, moving its mouth hooks in an attempt to eat the new tissue. Leaves of the test plants were checked within a couple of hours of making the transfers. If the larva was still moving its mouth hooks, the transfer was considered successful; if the larva did not show any movement it was assumed to have been injured and the transfer was rejected. With patience and experience with particular test plant, it was possible to make good transfers of larvae, except to Artemisia because of the very woolly surface of the leaf. The transferred larva usually ended up inside the fibres on the leaf, rather than inside the leaf tissue.

Observations were made every 12 hours on larval feeding and pupation, if any, during the previous 12 hour period. The pupae obtained were kept individually in small vials containing moist sand, for emergence of adults. The emergence of adults was also checked every 12 hours.

**BIOLOGY OF PHYTOMYZA MATRICARIAE HENDEL**

**Natural incidence**

The adults of this species appear around Edmonton, Alberta during the first week of June. The leaf mines and larvae start appearing on various host-plants by the second week of June. There are numerous overlapping generations during July, August, and up to mid-September, when numbers start declining. At this time the host-plants also decline in vigor due to shorter days and lower temperatures. Towards the end of September, puparia go into winter diapause.

**Mating**

Mating was observed in the laboratory and it occurs many times in the life of both sexes, usually on the leaves of the food plant. The mating posture in a superimposed position is typical of other agromyzid flies. Its duration as in other agromyzid flies varies greatly, from ½ hour to approximately 2 hours.

**Adult feeding**

The flies feed upon plant exudates soon after emergence. The female selects a suitable spot on the leaf tissue, bends the tip of her abdomen vertically downwards, pierces the epidermis and then rotates the tip of her ovipositor within the leaf tissue. She then withdraws her ovipositor, turns around and imbibes the sap exuding from the wound. The puncture thus made is almost conical in shape. This method of feeding among agromyzid flies is of wide occurrence and has been described for many species.

The female spends most of her lifetime making punctures in leaf tissue. These punctures are made both on upper and lower surfaces of the leaf, but are usually more numerous on the upper surface. The males, which are incapable of making such punctures, feed on the sap from punctures made by females or on natural plant exudates and probably also on
nectar of flowers. Pollen grains could not be found in the guts of about 10 field collected males examined for this purpose.

Plants normally survive the injury made by feeding punctures on the leaf, but under severe laboratory infestations they become greatly etiolated and sometimes collapse.

**Oviposition**

The eggs are laid singly inside the leaf parenchyma in punctures made in a similar way to feeding punctures. The egg punctures, like feeding punctures, were found both on upper and lower surfaces of the leaf, but unlike feeding punctures were usually more common on the lower surface. Feeding punctures always greatly outnumber oviposition punctures. This method of oviposition is general among the leaf mining agromyzid flies and has been described in many species.

**Incubation period**

The incubation period (Table 1) ranged from 90-102 hours, with an average of approximately 91 hours or 3.8 days. The egg, originally translucent, becomes opaque white within the first 24 hours. The cephalopharyngeal skeleton appears as a darkly sclerotized structure at the end of 72 hours. At this time the embryo is almost fully developed and the mouth hooks can sometimes be seen to move horizontally.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Number of records</th>
<th>Duration in hours</th>
<th>Total average duration (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg</td>
<td>44</td>
<td>91.0 (90.0–102.0)*</td>
<td>3.8</td>
</tr>
<tr>
<td>First instar</td>
<td>20</td>
<td>64.2 (55.0–73.0)</td>
<td></td>
</tr>
<tr>
<td>Second instar</td>
<td>20</td>
<td>45.0 (40.0–51.5)</td>
<td></td>
</tr>
<tr>
<td>Third instar</td>
<td>20</td>
<td>56.4 (44.0–65.0)</td>
<td></td>
</tr>
<tr>
<td>TOTAL larval</td>
<td>20</td>
<td>165.6 (144.0–180.0)</td>
<td>6.9</td>
</tr>
<tr>
<td>Pupal stage</td>
<td>15</td>
<td>13.7 (13.0–14.5) (days)</td>
<td>13.7</td>
</tr>
<tr>
<td>TOTAL life cycle</td>
<td></td>
<td></td>
<td>24.4</td>
</tr>
</tbody>
</table>

*The values of 40 observations were 90.0 hours and four 102.0 hours.

**Larval activity**

The average duration of first, second, and third instars (Table 1) was 64.2, 45.0 and 56.4 hours respectively. The total larval period was 165.6 hours or 6.9 days on an average.

From hatching to shortly before pupation, the larva is completely endophagous. This results in the excavation of a linear leaf mine. The mine starts from the upper or lower surface of the leaf depending upon the site of oviposition and may terminate on either surface, when the larva leaves by cutting a small crescent shaped slit. The larva then falls to the ground and pupates. The larva like most other agromyzid larvae (Hering, 1951)
seems unable to re-enter the leaf once it is removed from it. The ability of the larvae of ‘Liriomyza pusilla’ Meigen’ (Tilden, 1950) and at least some members of the Agromyza rufipes group (Nowakowski, 1964; Griffiths, verbal communication) to re-enter the leaf seems very unusual.

The mouth hooks can be seen cutting through the leaf tissue in a lateral and semicircular motion. The larvae, like those of other agromyzids (Hering, 1951), mine the leaf while lying on their sides and they alternate from one side to the other. The frass is deposited in discrete granules along the sides of the mine alternately as the larva turns from side to side. Many larvae may start mining the same leaf simultaneously resulting in numerous mines crossing each other, however, every mine remains distinct and contains only one miner. The larvae normally feed only on the leaf tissue, but in heavy infestations also migrate to the petiole or mine under the epidermis of the stem.

Transverse sections of the mined leaves (Fig. 5, 6) show that larvae feed indiscriminately on the palisade and spongy mesenchymatous tissue between the two epidermal layers of the leaf. The larvae only consume the entire tissue between upper and lower epidermis when this is very heavily infested. Thus the leaf mine is normally more visible from one side of the leaf. The larvae are capable of crossing the leaf veins but the vascular bundles are not consumed, as also reported in some other agromyzid species (Trehan and Sehgal, 1963; Tauber and Tauber, 1968).

The lengths of mines excavated by first, second and third instar are given in Table 2. The total length of 142.0 mm is much shorter than 273.0 mm for “Phytomyza lanati Spencer” (Tauber and Tauber, 1968). Although the duration of the third larval instar is approximately the same as that of the first instar, the major portion of the mining activity was done by the third instar.

Table 2. Lengths of leaf mines excavated by different larval instars of Phytomyza matri- cariae Hendel in Tanacetum vulgare L.

<table>
<thead>
<tr>
<th>Stage of larva</th>
<th>Length of leaf mine in mm (each 19 observations)</th>
</tr>
</thead>
<tbody>
<tr>
<td>First instar</td>
<td>Range 8.0–18.4, Average 13.5</td>
</tr>
<tr>
<td>Second instar</td>
<td>Range 13.4–42.5, Average 29.1</td>
</tr>
<tr>
<td>Third instar</td>
<td>Range 71.2–127.0, Average 99.4</td>
</tr>
<tr>
<td>TOTAL larval life</td>
<td>Length 110.0–177.0, Average 142.0</td>
</tr>
</tbody>
</table>

Pupation

The mature larva when ready to pupate leaves the leaf mine and falls to the ground, where it seeks a suitable site for pupation. Often the larva remains sticking to the exit slit in the mine and there forms the puparium. Duration of the puparium averages 13.7 days but varies considerably. The pupae from the fall generation undergo winter diapause.
Fig. 5–6. Transverse sections of leaf mines of *Phytomyza matricariae*. 5. leaf mine on *Achillea sibirica* Ledeb. 6. leaf mine on *Matricaria matricarioides* (Less.) Porter.
DESCRIPTION OF THE IMMATURE STAGES

Egg

The egg (Fig. 7) when freshly laid is translucent white, smooth, elongate, ovo-cylindrical, slightly broader at the posterior end, and with a small, almost indistinguishable micropyle at the anterior end. The eggs of the members of the Phytomyza syngenesiae group have a similar micropyle (see Smulyan, 1914, ‘Phytomyza chrysanthemi Kowarz’ and Cohen, 1936, ‘Phytomyza atricornis Meigen’). The egg dimensions are given in Table 3.

Table 3. The dimensions in mm of egg, larva, cephalopharyngeal skeleton*, and puparium of Phytomyza matricariae Hendel. All measurements based on 10 observations.

<table>
<thead>
<tr>
<th>Stage</th>
<th>Length average (range)</th>
<th>Width average (range)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg</td>
<td>0.293 (0.283–0.316)</td>
<td>0.129 (0.100–0.141)</td>
</tr>
<tr>
<td>First instar larva</td>
<td>0.412 (0.300–0.550)</td>
<td>0.152 (0.116–0.208)</td>
</tr>
<tr>
<td>Cephalopharyngeal skeleton</td>
<td>0.121 (0.116–0.125)</td>
<td></td>
</tr>
<tr>
<td>Second instar larva</td>
<td>0.732 (0.592–0.825)</td>
<td>0.243 (0.208–0.300)</td>
</tr>
<tr>
<td>Cephalopharyngeal skeleton</td>
<td>0.220 (0.216–0.233)</td>
<td></td>
</tr>
<tr>
<td>Third instar larva</td>
<td>2.395 (2.125–2.625)</td>
<td>0.667 (0.625–0.750)</td>
</tr>
<tr>
<td>Cephalopharyngeal skeleton</td>
<td>0.316 (0.308–0.316)</td>
<td></td>
</tr>
<tr>
<td>Puparium</td>
<td>1.810 (1.675–1.950)</td>
<td>0.852 (0.800–0.925)</td>
</tr>
</tbody>
</table>

*includes mouth hooks, labial sclerite and paired paraclypeal phragma.

Larva

There are three larval instars which can be easily recognised by the sizes of their cephalopharyngeal skeletons (Table 3). The first instar larva when freshly hatched is translucent white, but soon becomes greenish due to the ingested leaf tissue. The second and third instar larvae are yellowish green in colour. The first instar larva is metapneustic, while the second and third instar larvae are amphipneustic. The anterior spiracles (Fig. 8) of the mature third instar larva have 7-9 small oval bulbs, while the posterior ones (Fig. 9) have 19-21 small oval bulbs. De Meijere (1926) illustrated the anterior and posterior spiracles in the European members of this species bred from Matricaria chamomilla L. He reported about 12 bulbs on the anterior and 18 bulbs on the posterior spiracles. The head (Fig. 10) bears two small longitudinal sclerites just above the mouth hooks, small but conspicuous maxillary palps, a pair of small antennae and numerous sense papillae. The muscle scars on the intersegmental membrane (Fig. 11) are small, oval and transversely elongated. The tubercle bands (Fig. 11) consist of small conical processes irregularly scattered along the intersegmental membrane. The tubercle bands as in other agromyzid larvae (Allen, 1957) are best developed along lateral portions of intersegmental membrane.

The cephalopharyngeal skeletons of the first, second, and third instar are illustrated in Fig. 12-14. They consist of paired mouth hooks or mandibles, labial sclerite, and paired paraclypeal phragma. The mouth hooks in the first instar larva are small, simple and sickle
shaped; while in second and third instars they are well developed with two teeth each, alternating with one another. The right mouth hook is higher than the left and both mouth hooks are joined at the base (Fig. 10). Labial sclerite and paracylpeal phragma are smaller in first and second instars, but are well differentiated in the third instar. The dorsal process of the paracylpeal phragma consists of a long, single, slender and darkly sclerotized arm; the ventral arm is short, lightly sclerotized, and has a conspicuous foramen towards its posterior end.

**Puparium**

The puparium dimensions are given in Table 3; it is conspicuously segmented and shining black in colour.

The hardening of the third larval skin is due to the deposition of the calcospherites (Frick, 1952; Allen, 1957) so that it can be softened by treatment with dilute hydrochloric acid and can be cut open for detailed examination. Although the puparium preserves the external morphology of the third instar, this is best studied in the larva itself.

**HOST-PLANT RELATIONSHIPS OF ADULT FEMALES**

The ovipositing female comes across numerous other plants besides those normally attacked in nature. In order to test the specificity of feeding and oviposition a selection of a wide range of plants was exposed to a batch of five gravid females, for a period of 24 hours. Plants used in this study included some common plants, which the female would encounter in the field, as well as some plants which are known for certain secondary substances like alkaloids, glycosides, etc. A total of 38 plant species belonging to 17 families were tested for feeding and oviposition. Feeding and oviposition preference of females when offered a choice of acceptable plants was also studied. Degree of phylogenetic relationship of the test plant to the natural host-plant was compared with the index of acceptability for feeding and oviposition.

**Index of plant relationship**

Botanical relationship of the test plant species, used in experiments on feeding and oviposition by adult females and transfers of larvae, to one of the natural food plants of *P. matricariae* was examined.

The phylogenetic relationships between plant families and orders is still a matter of controversy. Most plant classifications fall into two groups depending on the supposed nature of primitive angiosperm flowers (Davis and Heywood, 1965). One system is based on the assumption that the earliest angiosperms were wind-pollinated and that the monocotyledons and dicotyledons have arisen independently from hypothetical gymnosperms. According to the second system dicotyledons and monocotyledons were both derived from primitive angiosperms which were insect-pollinated. The second system has the support of most recent botanists (Eames, 1961; Hutchinson, 1964; Takhtajan, 1969). Hutchinson (1964) has maintained a basic division of dicotyledons into woody “Lignosae” and herbaceous “Herbaceae”, a system which allegedly leads to the wide separation of certain plant families which otherwise seem closely related in the structure of their flowers. The arrangement of plant families used in this study is after Takhtajan (1969), which is considered to reflect more closely the phylogenetic relationships between plant families. An index of plant relationship from 1 to 10 was used as follows:

<table>
<thead>
<tr>
<th>Relationship of the test plant species to natural host-plant</th>
<th>Index of plant relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Same species</td>
<td>10</td>
</tr>
</tbody>
</table>
2. Same genus 9
3. Same tribe (Asteraceae) 8
4. Same family (Compositae) 7
5. Same order (Asterales) 6
6. Same superorder (Asterid) 5
7. Same subclass (Asteridae) 4
8. Same class (Dicotyledoneae) 3
9. Same division (Angiospermae) 2
10. Same phylum (Tracheophyta) 1

Acceptability index for feeding and oviposition

Acceptability index (A.I.) of a test plant for feeding and oviposition relative to that of the natural food plant from which flies were obtained was calculated for comparison with the index of plant relationship. In experiments with feeding and oviposition studies, females used were obtained from the natural host-plant *Tanacetum vulgare* L. Data given in Tables 4 and 5 were used to calculate the acceptability index. In order to give a theoretical maximum value of 1 to the acceptability index, the sum of the components was divided by 2; thus:

\[
A.I. = \frac{1}{2} \left( \frac{\text{Feeding punctures}}{\text{Feeding punctures in } T. \text{ vulgare}} + \frac{\text{Oviposition punctures}}{\text{Oviposition punctures in } T. \text{ vulgare}} \right)
\]

Range of food plants

Data on the acceptability of plants for feeding and oviposition by gravid females is summarized in Table 4. Indices of plant relationship and of acceptability for feeding, and oviposition are given for each plant species. Of the 38 plant species tested only seven belonging to the family Compositae tribes Anthemidae and Heliantheae were acceptable both for feeding and oviposition. Among these *Artemisia*, *Helianthus* and *Zinnia* were not found attacked in nature. The acceptability index for feeding and oviposition based on the data in Tables 4 and 5 is plotted against the index of plant relationship in Fig. 15. Indices of acceptability were very low for most species of test plants, but high for indices of plant relationship of 8 or over.

Feeding and oviposition preference by gravid females

The preference of gravid females for feeding and oviposition when offered a choice of six acceptable plants was examined. The plants used in this study were *Achillea sibirica* Lede., *Artemisia* sp., *Chrysanthemum* sp., *Helianthus annuus* L., *Matricaria matricarioides* (Less.) Porter and *Tanacetum vulgare* L. belonging to the family Compositae. Results of this experiment are summarized in Table 5.

The number of feeding punctures on *Tanacetum* was significantly higher than on other plants tested. The numbers of feeding punctures on *Chrysanthemum*, *Achillea*, *Matricaria* and *Helianthus* were not significantly different from each other, but were significantly lower than on *Tanacetum*. The numbers of punctures with an egg on *Tanacetum*, *Chrysanthemum*, *Achillea* and *Matricaria* were not significantly different from each other, but were significantly higher than on *Helianthus* and *Artemisia*. No relationship was found between the numbers of oviposition punctures and the numbers of feeding punctures.

Feeding preferences by freshly emerged females

Feeding preference by freshly emerged females, which had not been exposed to any food plant, was examined in a similar experiment the results of which are summarized in Table 6. The only difference from Table 5 is that the numbers of feeding punctures on *Achillea*, *Matricaria* and *Chrysanthemum* were significantly higher than on *Helianthus* and *Artemisia*. 

---

*Note:* The text contains a table, figures, and further data analysis that are not fully transcribed here. The full context and details can be found in the original document.
Table 4. Feeding and oviposition by females of *Phytomyza matricariae* Hendel on various plant species.

<table>
<thead>
<tr>
<th>Test plant</th>
<th>Number of feeding punctures</th>
<th>Number of punctures with an egg</th>
<th>Index of acceptability</th>
<th>Index of plant relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>PTERIDOPHYTA</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Polypodiaceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Nephrolepis</em></td>
<td>2</td>
<td>0</td>
<td>0.002</td>
<td>1</td>
</tr>
<tr>
<td><strong>ANGIOSPERMAE-DICOTYLEDONEAE</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ranunculaceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Aquilegia</em> sp. (cultivated)</td>
<td>16</td>
<td>0</td>
<td>0.018</td>
<td>3</td>
</tr>
<tr>
<td><em>Clematis verticillaris</em> DC</td>
<td>12</td>
<td>0</td>
<td>0.013</td>
<td>3</td>
</tr>
<tr>
<td><em>Delphinium</em> sp. (cultivated)</td>
<td>0</td>
<td>0</td>
<td>0.000</td>
<td>3</td>
</tr>
<tr>
<td>Papaveraceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Papaver</em> sp. (cultivated)</td>
<td>11</td>
<td>0</td>
<td>0.012</td>
<td>3</td>
</tr>
<tr>
<td>Chenopodiaceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Chenopodium</em> sp.</td>
<td>5</td>
<td>0</td>
<td>0.005</td>
<td>3</td>
</tr>
<tr>
<td>Cucurbitaceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cucumis</em> sp.</td>
<td>11</td>
<td>0</td>
<td>0.012</td>
<td>3</td>
</tr>
<tr>
<td>Cruciferae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Brassica kaber</em> (DC.) Wheeler</td>
<td>3</td>
<td>0</td>
<td>0.003</td>
<td>3</td>
</tr>
<tr>
<td><em>Thlaspi arvense</em> L.</td>
<td>22</td>
<td>0</td>
<td>0.024</td>
<td>3</td>
</tr>
<tr>
<td>Rosaceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Potentilla</em> sp.</td>
<td>0</td>
<td>0</td>
<td>0.000</td>
<td>3</td>
</tr>
<tr>
<td>Leguminosae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Caragana arborescens</em> Lam.</td>
<td>3</td>
<td>0</td>
<td>0.003</td>
<td>3</td>
</tr>
<tr>
<td><em>Lathyrus odoratus</em> L.</td>
<td>0</td>
<td>0</td>
<td>0.000</td>
<td>3</td>
</tr>
<tr>
<td><em>Lupinus</em> sp. (cultivated)</td>
<td>0</td>
<td>0</td>
<td>0.000</td>
<td>3</td>
</tr>
<tr>
<td><em>Pisum sativum</em> L.</td>
<td>32</td>
<td>0</td>
<td>0.036</td>
<td>3</td>
</tr>
<tr>
<td><em>Vicia americana</em> Muhl.</td>
<td>0</td>
<td>0</td>
<td>0.000</td>
<td>3</td>
</tr>
<tr>
<td>Tropaeolaceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Tropaeolum</em> sp. (cultivated)</td>
<td>3</td>
<td>0</td>
<td>0.003</td>
<td>3</td>
</tr>
<tr>
<td>Solanaceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Lycopersicon esculentum</em> L.</td>
<td>3</td>
<td>0</td>
<td>0.003</td>
<td>4</td>
</tr>
<tr>
<td><em>Nicotiana tabacum</em> L.</td>
<td>4</td>
<td>0</td>
<td>0.004</td>
<td>4</td>
</tr>
<tr>
<td><em>Solanum tuberosum</em> L.</td>
<td>3</td>
<td>0</td>
<td>0.003</td>
<td>4</td>
</tr>
<tr>
<td>Scrophulariaceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Antirrinum</em> sp. (cultivated)</td>
<td>0</td>
<td>0</td>
<td>0.000</td>
<td>4</td>
</tr>
<tr>
<td>Labiatae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Galeopsis tetrahit</em> L.</td>
<td>5</td>
<td>0</td>
<td>0.005</td>
<td>4</td>
</tr>
<tr>
<td>Campanulaceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Campanula</em> sp. (cultivated)</td>
<td>0</td>
<td>0</td>
<td>0.000</td>
<td>5</td>
</tr>
<tr>
<td>Compositae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Achillea sibirica</em> Ledebl.</td>
<td>567</td>
<td>28</td>
<td>1.039</td>
<td>8</td>
</tr>
<tr>
<td><em>Artemisia</em> sp.</td>
<td>227</td>
<td>10</td>
<td>0.398</td>
<td>8</td>
</tr>
<tr>
<td><em>Aster ciliolatus</em> Lindl.</td>
<td>10</td>
<td>0</td>
<td>0.011</td>
<td>7</td>
</tr>
</tbody>
</table>
Table 4 (continued)

<table>
<thead>
<tr>
<th>Test plant</th>
<th>Number of feeding punctures</th>
<th>Number of punctures with an egg</th>
<th>Index of acceptability</th>
<th>Index of plant relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chrysanthemum sp. (cultivated)</td>
<td>467</td>
<td>34</td>
<td>1.012</td>
<td>8</td>
</tr>
<tr>
<td>Helianthus annuus L.</td>
<td>292</td>
<td>19</td>
<td>0.600</td>
<td>7</td>
</tr>
<tr>
<td>Matricaria matricarioides (Less.) Porter</td>
<td>441</td>
<td>30</td>
<td>0.926</td>
<td>8</td>
</tr>
<tr>
<td>Senecio vulgaris L.</td>
<td>54</td>
<td>0</td>
<td>0.060</td>
<td>7</td>
</tr>
<tr>
<td>Solidago sp.</td>
<td>12</td>
<td>0</td>
<td>0.013</td>
<td>7</td>
</tr>
<tr>
<td>Sonchus uliginosus Bieb.</td>
<td>4</td>
<td>0</td>
<td>0.004</td>
<td>7</td>
</tr>
<tr>
<td>Tanacetum vulgare L.</td>
<td>443</td>
<td>35</td>
<td>1.000</td>
<td>10</td>
</tr>
<tr>
<td>Taraxacum officinale Weber</td>
<td>124</td>
<td>4</td>
<td>0.139</td>
<td>7</td>
</tr>
<tr>
<td>Zinnia sp. (cultivated)</td>
<td>44</td>
<td>3</td>
<td>0.092</td>
<td>7</td>
</tr>
</tbody>
</table>

ANGIOSPERMAE-MONOCOTYLEDONAE
Liliaceae

| Allium cepa L.                                                            | 1                           | 0                               | 0.001                  | 2                           |
| Smilacina stellata (L.) Desf.                                             | 0                           | 0                               | 0.000                  | 2                           |

Gramineae

| Hordeum vulgare L.                                                        | 7                           | 0                               | 0.007                  | 2                           |

Typhaceae

| Typha latifolia L.                                                        | 0                           | 0                               | 0.000                  | 2                           |

Table 5. Feeding and oviposition preferences of female *Phytomyza matricariae* Hendel from a culture raised on *T. vulgare*.

<table>
<thead>
<tr>
<th>Test plant</th>
<th>Average* number of feeding punctures</th>
<th>Average number of punctures with an egg</th>
<th>Index of success</th>
<th>Index of plant relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tanacetum vulgare</td>
<td>519.5 a**</td>
<td>11.8 a'</td>
<td>1.000</td>
<td>10</td>
</tr>
<tr>
<td>Chrysanthemum sp.</td>
<td>200.5 b</td>
<td>13.3 a'</td>
<td>0.756</td>
<td>8</td>
</tr>
<tr>
<td>Achillea sibirica</td>
<td>181.6 b c</td>
<td>10.5 a'</td>
<td>0.614</td>
<td>8</td>
</tr>
<tr>
<td>Matricaria matricarioides</td>
<td>161.0 b c</td>
<td>15.0 a'</td>
<td>0.790</td>
<td>8</td>
</tr>
<tr>
<td>Helianthus annuus</td>
<td>58.5 b c</td>
<td>2.3 b'</td>
<td>0.153</td>
<td>7</td>
</tr>
<tr>
<td>Artemisia sp.</td>
<td>36.8 c</td>
<td>1.6 b'</td>
<td>0.102</td>
<td>8</td>
</tr>
</tbody>
</table>

* Averages are based on six replicates.

** Treatments which are not significantly different from each other have the same letter opposite; as calculated by Duncan’s multiple range significance level test.
Fig. 15. Graph showing the index of acceptability of test plant for feeding and oviposition, and the index of plant relationship.

Table 6. Feeding preferences of freshly emerged (<24 hours) females of Phytomyza matri-
cariae Hendel from T. vulgare.

<table>
<thead>
<tr>
<th>Test plant</th>
<th>Average number of feeding punctures*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tanacetum vulgare</td>
<td>250.8 a**</td>
</tr>
<tr>
<td>Achillea sibirica</td>
<td>174.6 b</td>
</tr>
<tr>
<td>Matricaria matricarioides</td>
<td>139.5 b</td>
</tr>
<tr>
<td>Chrysanthemum sp.</td>
<td>128.6 b</td>
</tr>
<tr>
<td>Helianthus annuus</td>
<td>28.3 c</td>
</tr>
<tr>
<td>Artemisia sp.</td>
<td>14.3 c</td>
</tr>
</tbody>
</table>

* Based on six tests.
** Treatments which are not significantly different from each other have the same letter opposite; as calculated by Duncan's multiple range significance level test.
HOST-PLANT RELATIONSHIPS OF LARVAE

In nature the larvae feed only on the plants accepted for oviposition by the female. Being completely internal plant feeders, they cannot select a more suitable food plant which might be available in its geographical range. In order to test the ability of larvae to use different plants as food which may be available in their geographical range, the first instar larvae obtained from the natural food plant were transferred into the tissue of the test plant. An index of success for larval development based on larval feeding, pupation, and emergence of imago was calculated for comparison with the index of plant relationship.

Index of success for larval development

An index of success (S. I.) for larval development was calculated from results obtained in the transfers of larvae from natural host-plant into recipient plant species, for comparison with the index of plant relationship. This calculation was based on three components as follows:

1. **Duration of larval survival in recipient plant.** — This was expressed in half days; the 12 hours immediately preceding the finding of a non-feeding larva was included since observations showed that the average survival time after the cessation of feeding was about 12 hours. Studies on the life history as summarized in Table 1 show that the average duration of a larval stage in *P. matricariae* on *T. vulgare* is 6.9 days. The first instar larvae used in transfer experiments were about 1 day old. Therefore under normal conditions the remainder of larval feeding time should average 5.9 days. Success in larval feeding was expressed as the ratio of the duration of feeding of larva on test plant to 5.9 days.

2. **Pupation.** — This is considered as successful termination of larval development. Success was expressed as the proportion of the transferred larvae pupating successfully on the test plant.

3. **Emergence.** — In most plants the larvae which pupated also emerged as adult flies. The emergence was given one-fourth as much weight as pupation in calculation of success index, that is, it was expressed as one quarter of the proportion of transferred larvae which yielded adult flies.

In order to give a theoretical maximum value of 1 to the Success Index (S. I.) the sum of these components was divided by 2.25; thus:

\[
S. I. = \frac{1}{2.25} \left( \frac{\text{Survival time (days)}}{5.9} + \frac{\text{Pupations}}{\text{Transfers}} + \frac{\text{Emergences}}{4 \times \text{Transfers}} \right)
\]

Transfers of larvae from natural host-plant to test plant

The number of larvae transferred individually from the natural host-plant to inside the tissue of recipient plant species was 20, except in two species where it was 10. Results of the transfers of larvae are summarized in Tables 7 and 8. Values for the success index and the index of plant relationship are also given graphically in Fig. 16.

Among Pteridophyta, only the greenhouse fern *Nepthrolepis* sp. tested for transfers of larvae from *Tanacetum*, could not be used by larvae as food for completing their development indicating the plant to be toxic or otherwise unacceptable.

Among dicotyledons, 28 plants belonging to 10 plant families were tested for transfers of larvae from *Tanacetum* (Table 7) and *Achillea* (Table 8). One larva at least completed its development on 16 plant species belonging to 5 families. Leaf mines formed after transfer of larvae from *Tanacetum* into four of the test plants are shown in Fig. 17-20.
Table 7. Results of transfers of larvae of *Phytomyza matricariae* Hendel from *Tanacetum vulgare* L. to other plant species. 20 transfers except where indicated. Note that transfers to *T. vulgare* represent a control.

<table>
<thead>
<tr>
<th>Recipient species</th>
<th>Duration of larval feeding in test plant (days)</th>
<th>Number of larvae pupated (<strong>emerged</strong>)</th>
<th>Index of success</th>
<th>Index of plant relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>PTERIDOPHYTA</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Polypodiaceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Nephrolepis</em> sp. (cultivated)</td>
<td><em>0.25 ± 0.0</em> (0.5—0.5)</td>
<td>0</td>
<td>0.018</td>
<td>1</td>
</tr>
<tr>
<td><strong>ANGIOSPERMAE-DICOTYLEDONEAE</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ranunculaceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Aquilegia</em> sp. (cultivated)</td>
<td><em>2.57 ± 3.0</em> (0.5—9.0)</td>
<td>3</td>
<td>0.276</td>
<td>3</td>
</tr>
<tr>
<td>Caryophyllaceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Silene noctiflora</em> L.</td>
<td><em>1.07 ± 0.3</em> (1.0—2.0)</td>
<td>0</td>
<td>0.080</td>
<td>3</td>
</tr>
<tr>
<td>Chenopodiacea</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Chenopodium album</em> L.</td>
<td><em>0.97 ± 0.5</em> (0.5—2.0)</td>
<td>0</td>
<td>0.072</td>
<td>3</td>
</tr>
<tr>
<td>Cruciferae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Brassica</em> khaber (DC.)</td>
<td><em>2.47 ± 2.0</em> (1.0—7.5)</td>
<td>2</td>
<td>0.241</td>
<td>3</td>
</tr>
<tr>
<td><em>Thlaspi arvense</em> L.</td>
<td><em>1.80 ± 0.8</em> (1.0—4.0)</td>
<td>0</td>
<td>0.135</td>
<td>3</td>
</tr>
<tr>
<td>Rosaceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Potentilla</em> sp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Melilotus officinalis</em> (L.) Lam.</td>
<td><em>3.07 ± 2.6</em> (1.0—9.0)</td>
<td>2 (1)</td>
<td>0.280</td>
<td>3</td>
</tr>
<tr>
<td><em>Pisum sativum</em> L.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Umbellifereae</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Apium</em> sp.</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td><em>Solanaceae</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Nicotiana tabacum</em> L.</td>
<td><em>0.25 ± 0.1</em> (0.2—1.0)</td>
<td>0</td>
<td>0.018</td>
<td>4</td>
</tr>
</tbody>
</table>
Table 7 (continued)

<table>
<thead>
<tr>
<th>Recipient species</th>
<th>Duration of larval feeding in test plant (days)</th>
<th>Number of larvae pupated (** emerged)</th>
<th>Index of success</th>
<th>Index of plant relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Labiatae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Galeopsis tetrahit L.</td>
<td>*3.65 ± 1.9 (1.0–7.0)</td>
<td>10</td>
<td>0.552</td>
<td>4</td>
</tr>
<tr>
<td><strong>Compositae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Achillea sibirica Ledeb. (10 transfers)</td>
<td>*4.65 ± 1.4 (1.0–6.0)</td>
<td>9 (8)</td>
<td>0.594</td>
<td>8</td>
</tr>
<tr>
<td>Artemisia sp. (10 transfers)</td>
<td>*0.25 ± 0.0 (0.5–0.5)</td>
<td>0</td>
<td>0.018</td>
<td>8</td>
</tr>
<tr>
<td>Chrysanthemum sp. (cultivated)</td>
<td>*4.07 ± 2.8 (1.5–8.5)</td>
<td>6</td>
<td>0.472</td>
<td>8</td>
</tr>
<tr>
<td>Dahlia sp. (cultivated)</td>
<td>*2.37 ± 1.8 (1.0–8.0)</td>
<td>2 (1)</td>
<td>0.228</td>
<td>7</td>
</tr>
<tr>
<td>Helianthus annuus L.</td>
<td>*2.97 ± 2.3 (0.5–6.0)</td>
<td>10</td>
<td>0.501</td>
<td>7</td>
</tr>
<tr>
<td>Matricaria matricarioides (Less.)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Porter (10 transfers)</td>
<td>*4.40 ± 1.4 (0.5–5.5)</td>
<td>9</td>
<td>0.580</td>
<td>8</td>
</tr>
<tr>
<td>Senecio vulgaris L.</td>
<td>*3.85 ± 2.2 (0.5–7.5)</td>
<td>6 (5)</td>
<td>0.450</td>
<td>7</td>
</tr>
<tr>
<td>Sonchus uliginosus Bieb.</td>
<td>*3.02 ± 2.6 (0.5–7.0)</td>
<td>9</td>
<td>0.476</td>
<td>7</td>
</tr>
<tr>
<td>Tanacetum vulgare L.</td>
<td>*5.57 ± 1.0 (2.0–7.0)</td>
<td>19</td>
<td>0.966</td>
<td>10</td>
</tr>
<tr>
<td>Taraxacum officinale Weber</td>
<td>*2.25 ± 2.3 (0.5–6.0)</td>
<td>4 (3)</td>
<td>0.274</td>
<td>7</td>
</tr>
<tr>
<td><strong>ANGIOSPERMAE-MONOCOTYLEDONEAE</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Liliaceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Allium cepa L.</td>
<td>*3.95 ± 2.4 (1.0–9.0)</td>
<td>6 (5)</td>
<td>0.458</td>
<td>2</td>
</tr>
<tr>
<td>Gramineae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hordeum vulgare L.</td>
<td>*2.67 ± 1.7 (1.0–7.0)</td>
<td>3</td>
<td>0.284</td>
<td>2</td>
</tr>
<tr>
<td>Typhaceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Typha latifolia L.</td>
<td>*0.55 ± 0.2 (0.5–1.0)</td>
<td>0</td>
<td>0.041</td>
<td>2</td>
</tr>
</tbody>
</table>

* mean ± S. D. (range) ** all emerged unless otherwise indicated.
Table 8. Results of transfers of larvae of *Phytomyza matricariae* Hendel from *Achillea sibirica* Ledeb. to test plants. 20 transfers except where indicated. Note that transfers to *A. sibirica* represent a control.

<table>
<thead>
<tr>
<th>Recipient species</th>
<th>Duration of larval feeding in test plant (days)</th>
<th>Number of larvae pupated (<strong>emerged)</strong></th>
<th>Index of success</th>
<th>Index of plant relationship</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>ANGIOSPERMAE-DICOTYLEDONEAE</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cruciferae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Brassica oleracea</em> L.</td>
<td><em>1.50 ± 0.9</em> (0.5–5.5)</td>
<td>1</td>
<td>0.140</td>
<td>3</td>
</tr>
<tr>
<td>Leguminosae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Lupinus</em> sp. (cultivated)</td>
<td><em>1.45 ± 1.3</em> (0.5–7.0)</td>
<td>0</td>
<td>0.108</td>
<td>3</td>
</tr>
<tr>
<td><em>Pisum sativum</em> L.</td>
<td><em>4.17 ± 1.2</em> (2.0–6.0)</td>
<td>10</td>
<td>0.591</td>
<td>3</td>
</tr>
<tr>
<td>Solanaceae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Nicotiana tabacum</em> L.</td>
<td><em>0.80 ± 0.4</em> (0.5–2.0)</td>
<td>0</td>
<td>0.060</td>
<td>4</td>
</tr>
<tr>
<td><em>Solanum tuberosum</em> L. (10 transfers)</td>
<td><em>0.50 ± 0.4</em> (0.5–1.5)</td>
<td>0</td>
<td>0.037</td>
<td>4</td>
</tr>
<tr>
<td>Compositae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Achillea sibirica</em> Ledeb.</td>
<td><em>4.72 ± 1.6</em> (1.0–7.5)</td>
<td>15</td>
<td>0.772</td>
<td>10</td>
</tr>
<tr>
<td><em>Solidago</em> sp.</td>
<td><em>0.67 ± 0.4</em> (0.5–2.0)</td>
<td>0</td>
<td>0.050</td>
<td>7</td>
</tr>
<tr>
<td><em>Sonchus arvensis</em> L.</td>
<td><em>1.50 ± 1.3</em> (1.0–6.0)</td>
<td>0</td>
<td>0.112</td>
<td>7</td>
</tr>
<tr>
<td><em>Tanacetum vulgare</em> L. (10 transfers)</td>
<td><em>5.05 ± 1.1</em> (2.5–6.5)</td>
<td>9</td>
<td>0.880</td>
<td>8</td>
</tr>
<tr>
<td><em>Zinnia</em> sp. (cultivated)</td>
<td><em>2.72 ± 1.5</em> (1.0–5.5)</td>
<td>6 (5)</td>
<td>0.365</td>
<td>7</td>
</tr>
</tbody>
</table>

* mean ± S. D. (range)  ** all emerged unless otherwise indicated.
Fig. 16. Graph showing the success index of test plant for larval development against index of plant relationship.

▲ Transfers from Tanacetum vulgare L. ■ Transfers from Achillea sibirica Ledeb.

On the basis of available data, although it is not possible to make statistical comparisons of the relative success of larval development on these plants, nevertheless some of these plants were clearly more suitable for larval development than others. Two species outside the Compositae, Pisum sativum L. and Galeopsis tetrahit L., were at least as good as Tanacetum, their natural food plant, if not better, in their suitability for larval development. Brassica spp. tested were quite resistant to larval development; besides others, one reason was the formation of callus in the injured area of the young leaf. Among other plants tested, the formation of callus in the punctures made for feeding and oviposition, and in other small injuries, was very frequent in the young leaf of Helianthus.

Twelve dicotyledons were not used by larvae as food for complete development, though they did survive for a certain length of time in most of these plants. Among these plants the failure of larvae to mature in Artemisia sp. was probably due to the fact that they would bite their way out into the woolly fibres of the leaf. In all other plants the experimental larva died inside the tissue of the recipient plant.

Among three monocotyledons, two species, Allium cepa L. and Hordeum vulgare L. were used by larvae to complete development to adult flies. The failure to use the third species Typha latifolia L. was, besides other factors, probably also due to the presence of large air spaces in the leaf tissue.
Fig. 17–20. Leaf mines formed after transfers of larvae of *Phytomyza matricariae* from *Tanacetum vulgare* to various recipient species. 17. leaf mine on *Brassica oleracea* L. 18. leaf mine on *Pisum sativum* L. 19. leaf mine on *Sonchus uliginosus* Bieb. 20. leaf mine on *Zinnia* sp. (cultivated).
DISCUSSION

Host-plant relationships of adult female

Range of food plants. — Even though females made varying numbers of feeding punctures on many plants, eggs were only deposited in members of the family Compositae belonging to the tribes Anthemideae and Helianthae. Plants which are not accepted for both feeding and oviposition are considered as non-hosts. The physical characteristics of the plant do not seem to be important, although they may play some role in host preference. The acceptability of closely related plants for both feeding and oviposition indicate that chemical factors are involved in the very high degree of host-plant specialization. That many plants are not acceptable as hosts by *P. matricariae* is indicative of deterrent effects in the plants. Plants acceptable for feeding must therefore have stimulating substances and at the same time lack deterrent substances. Since the females oviposited only on closely related members of the family Compositae, the plants accepted for oviposition must also have substances which provide adequate stimuli for egg laying and these are not necessarily the same substances as those which stimulate feeding. Hsiao and Fraenkel (1968) working with Colorado potato beetle, *Leptinotarsa decemlineata* (Say), suggested that host specific stimuli from some solanaceous plants were required in the oviposition behavior of this species.

When the index of success in feeding and oviposition was compared with the index of plant relationship (Fig. 15), only plants most closely related to natural food plants were acceptable for feeding and oviposition, thus confirming the observed oligophagy of *P. matricariae* in nature.

Hering (1951) pointed out numerous species of mining insects in which the ovipositing females committed errors in their choice of host-plants and concluded that such instances of erroneous oviposition were quite common and yet escaped our attention. Later Nowakowski (1962) examined such known instances in the family Agromyzidae and found that these were mainly due to misidentifications of the insects. The results of the experiments on the host range of *P. matricariae* indicate that the females are unlikely to make the mistake of ovipositing on the wrong host under normal circumstances.

Feeding and oviposition preference of females. — When females were offered a choice of six acceptable plants for feeding and oviposition, *Tanacetum*, from which the flies used were obtained, was most preferred for feeding (Table 5); however, the numbers of eggs laid were not significantly higher than on some other plants in the test. In another experiment in which freshly emerged females obtained from pupae bred on *Tanacetum* were used, *Tanacetum* was still most preferred (Table 6) in number of feeding punctures. The preference for feeding on *Tanacetum* may either be explained by the preconditioning of the females in their own life, or by preconditioning in their larval life as defined by Hopkins’ (1917) host selection principle, or by the greater quantity of substances which stimulate feeding, or just by the taste preference of the females. This however, cannot be clarified at present and would need further detailed studies. However, behavior in which insects prefer the plant species previously eaten is in agreement with the observations of Jermy, Hanson and Dethier (1968) on *Manduca sexta* (Johanssen) and *Heliothis zea* (Boddie). It may be pointed out that *Tanacetum* appeared to be more heavily attacked in nature than other host-plants. This, however, may also be due to various other factors like greater abundance of this plant in the habitat.

Among other plants used in the study *Achillea*, *Chrysanthemum*, and *Matricaria* were almost equally preferred, while *Helianthus* and *Artemisia* were least preferred for both feeding and oviposition (Tables 5, 6). The first three plants belong to the same tribe Anthemideae as *Tanacetum* and also serve as host-plants in nature. In *Chrysanthemum* only the
soft leaf variety was found to be attacked in nature. This suggests some importance of physical characteristics of plants in their selection. *Artemisia*, although closely related to *Tanacetum*, was not preferred, probably because the leaves used had a thick covering of woolly fibres on their lower surfaces, which may act as a physical barrier for females of this species. *Helianthus* which was also not preferred, is not as closely related to *Tanacetum*. It was also not found to be attacked in nature.

Hussey and Gurney (1962) suggested the use of feeding punctures to egg ratio as a method of assessing host preference in agromyzid species. The most ‘preferred’ host plant would have the lowest feeding puncture to egg ratio. They worked with a polyphagous species ‘Phytomyza atricornis Meigen’ which was later shown by Griffiths (1967) to consist of two distinct species, *Phytomyza syngenesiae* (Hardy) feeding predominantly on composites and *Phytomyza horticola* Goureau feeding on composites and other families so that their results cannot be properly evaluated. In the populations used they found that feeding puncture to egg ratio was lower on preferred plants and concluded that preferred plants are nutritionally superior. It appears that the differential feeding and oviposition in their experiments with different varieties of *Chrysanthemum* was due to chemical factors which act as stimulants or deterrents rather than to nutritional differences.

**Host-plant relationships of larvae**

The ability of the larva to use 16 plants belonging to five different families for its development clearly shows that it is far less sensitive to deterrents than the adults which would only feed and oviposit on certain members of the family Compositae. The larvae having evolved a completely internal parasitic mode of life have reduced or poorly developed sense organs, which in turn reduces their ability to discriminate between various plant species. This is further supported by the observation that the larva starts feeding almost as soon as it is transferred to the test plant. The act of feeding was inferred from the movement of larval mouth hooks inside the test plant. However, the larva is capable of distinguishing between various kinds of tissue within the leaf, as only the mesenchymatous tissue is eaten. It is apparent that plants widely separated phylogenetically are nutritionally adequate for the completion of larval development, if they lack substances which are toxic or inhibitory.

Buhr (1937) was the first to carry out transplantation experiments with agromyzid larvae. He found that among the plants tested, the transferred larvae developed only on plants phylogenetically related to their natural food plant and died on plants not related to the normal host-plant. *Liriomyza eupatorii* (Kaltenbach) was exceptional, but it was already known to feed on *Eupatorium* (Compositae) and *Galeopsis* (Labiatae). He also succeeded in transferring larvae of *Liriomyza cannabis* Hendel from *Cannabis* (Urticaceae), to *Eupatorium* and *Galeopsis*. However it is not known whether these two “species”, *Liriomyza eupatorii* (Kaltenbach) and *L. cannabis* Hendel, represent host races or sibling species, as was considered by Nowakowski (1962), since there is no clear morphological distinction between them.

Admittedly, the possibility that the agromyzid female would oviposit in nature on plants not closely related to the natural host-plant is very small. But, if the female did oviposit on plants outside the normal range, there is a good possibility that the larva would complete development, if the plant is not toxic or inhibitory. This is contrary to Nowakowski’s (1962) suggestion that the probability of larval survival is very small.

This ability of the larvae to use successfully certain plants outside the range of normal host-plants of the ovipositing female in *P. matricariae*, can explain observed patterns in agromyzids and also in external feeders. *Liriomyza eupatorii* (Kaltenbach) normally feeds
in nature on *Eupatorium*, family Compositae and *Galeopsis*, family Labiatae. *Liriomyza brassicae* (Riley), an oligophagous species feeding on Cruciferae and related families, has also been reported to feed on *Pisum*, family Leguminosae (Spencer, 1964; Sehgal, 1965). Gupta and Thorsteinson (1960) showed that the leaves of non-cruiferous plants were normally accepted by the caterpillars of *Plutella maculipennis*, which normally feed on cruciferous plants. Jermy (1961) showed that Colorado potato beetle, normally a solanaceous feeder, accepted the leaves of *Asclepias syriaca* L., family Asclepiadaceae and *Allium cepa*, family Liliaceae. He later (1966) suggested that in these plants some other substances replace the specific phagostimulants. Hsiao and Fraenkel (1968) working on Colorado potato beetle found the leaves of *Asclepias* (Asclepiadaceae) and *Lactuca* (Compositae) to be the most suitable non-solanaceous plants and these plants could support reproduction and continuous culturing. They further reported that these plants were not fed upon in the presence of normal solanaceous hosts. They therefore concluded that host selection in this species was determined not only by the presence of adequate feeding stimuli and nutrients, but also by the presence of host specific substances which induce the initial feeding behavior. In *P. matricariae* such host specific substances could be important in the specificity of oviposition on certain members of the family Compositae, but not in the larval feeding on various test plants.

Jermy (1966) suggested that certain plants like *Pisum sativum* L. and *Malva sylvestris* L. seem to be in general free of strong feeding inhibitors, while others like *Solidago* are strongly deterrent. Results of transfers of larvae of *P. matricariae* support this view, as *Pisum sativum* was quite suitable for larval development while *Solidago* was not. *Galeopsis tetrahit* probably also belongs to a similar category of non-inhibitory plants.

The majority of species in the family Agromyzidae are restricted feeders, being monophagous or oligophagous (Sehgal, 1971). This study of insect host-plant relationships of adults and of larvae of *P. matricariae*, as well as recent studies involving other oligophagous species have shown that botanically unrelated plants can also serve as adequate food plants for normal development. However, in nature an oligophagous species normally selects botanically related plants for feeding and oviposition. Restricted feeding in nature on botanically related plant species or on unrelated plant species having similar secondary substances is probably the result of numerous evolutionary coadaptations of the phytophagous insect to the allelochemics (Whittaker and Feeny, 1971), allomones and kairomones, of the host-plant(s).

ACKNOWLEDGEMENTS

I am grateful to B. Hocking, Chairman, Department of Entomology, University of Alberta, for providing the opportunity and support for this project and for his supervision, criticism of manuscript, and keen interest throughout this study. I am grateful to G. E. Ball, Department of Entomology, University of Alberta, for advice and valuable criticism of the manuscript. I am also grateful to K. A. Spencer, London, England and G. C. D. Griffiths, Department of Entomology, University of Alberta, for numerous useful discussions and valuable suggestions. I would like to thank D. A. Craig and W. G. Evans, Department of Entomology, University of Alberta and G. Pritchard, Department of Biology, University of Calgary for numerous suggestions and helpful criticism of the results. I thank J. G. Packer, Department of Botany, University of Alberta for help in identification of host-plants, H. S. Welling for help in greenhouse culturing of plants, J. S. Scott for help in preparing photographs and J. Rickert for help in translating the abstract into German.
REFERENCES


NOTES AND CORRECTIONS TO A RECLASSIFICATION OF BOMBARDIER BEETLES (CARABIDAE, BRACHINIDA)

TERRY L. ERWIN
Division of Coleoptera
Department of Entomology
Smithsonian Institution
Washington, D. C. 20560

Quaestiones entomologicae 7: 281 1971

Since publishing my "A reclassification of bombardier beetles and a taxonomic revision of the North and Middle American species (Carabidae:Brachinida)" (Quaest. ent. 6:4-215, 1970) a number of points have come to my notice. These follow seriatim, page numbers and references are to that paper.

Page 17, line 29: Read uniperforate for uniporforate.

Pages 34-37: Jeannel (1949:1084) designated Brachinus senegalensis Dejean (1825:308) as type of Pheropsophus Solier (1833:463). Unfortunately, I followed his designation and failed to see Hope's previous designation of Carabus complanatus Fabricius (1775:242) in his Coleopterist's Manual (1838:99). Since P. complanatus Fab. is a New World species (type from Santo Domingo) Pheropsophus Solier is the generic name for all the New World species and Pheropsophidius Hubenthal (1911:547) is a synonym (Pheropsophidius Hubenthal, type Cicindela aequinoctialis Linné 1763:395...aequinoctialis L. = complanatus F. according to Castelnau 1835:51). Thus, Pheropsophus is not available for the Old World species as they represent a genus different from the New World group. The first available name is Stenaptinus Maindron (1906:15), type species S. krichna Maindron (1906:15) designated by Jeannel (1949:1084). The following list summarizes the correct names of the subtribe Pheropsophina:

Genus Stenaptinus Maindron
Subgenus Stenaptinus s. str.
Subgenus Parapheropsophus Hubenthal (= Pheropsophus auct.)
Subgenus Aptinomorphus Jeannel

Genus Pheropsophus Solier
Subgenus Pheropsophus s. str. (= Pheropsophidius auct.)
Subgenus Protopheropsophus Hubenthal

The name Parapheropsophus Hubenthal must be raised from synonymy (Darlington, 1968:234) to become available for the taxon called Pheropsophus by Jeannel (1949), myself (1970), and others. The above was drawn to my attention by Basilewsky (in litt.) and I thank him kindly.

Page 38: The type species of Aptinus was designated by Hope (1838:99) not Jeannel.


Pages 59, 81, 108, 153, 155: The following species were described by me in Opusc. ent. 34(3):287-288, cf. 1969b in the list of references: Brachinus microamericanus, B. adustipennis, B. kavanaughi, B. fulminatus, and B. vulcanoides.

Page 164, line 42: Read extant for extent.

Page 211, line 30: Read 21(2) for 1(2).
Book Review


Loveland, a former research associate of the Kodak Research Laboratories, has produced a book that is indeed a comprehensive account of photomicrography. He deals with all the major aspects of the subject without neglecting the more recent developments in this field.

In Volume I he gives a general consideration of the compound microscope, photomacrography, the optics of illuminating lamps, the quality of illumination, image contrasts and finally the eyepiece and roll-film cameras. This is followed by the appendices where depth of field, focal length of lenses and illumination for photomacrography are considered further; by a list of equations used in the text; and by the index which includes the subjects in Volume II. Loveland believes illumination to be very important and he pursues this subject further in Volume II where he considers special methods of illumination, flash photomicrography and the photographic spectrum. Consideration is then given to the selection of photographic materials, the determination of exposure, and processing and printing. He also deals with the advantages and problems of color photomicrography, with fluorescence photomicrography and cinemicrography. This is followed by appendices where he deals with exposure formulas, special immersion fluids and an illuminator for far-ultraviolet photomicrography, the equations used in the text, and an index as in Volume I.

In the foreword, Loveland indicates that the book has been written not only for the professional but also for the "neophyte" and he never loses sight of this. Ample warnings of the difficulties and disadvantages of various techniques are given and in some cases neophytes are warned off certain techniques. Each chapter is begun with a general consideration of the topic and then moves rapidly into the theoretical aspects. Loveland never neglects the practical problems and he always gives a good account of the various instruments available from the major manufacturers. He has obviously had much experience for when there is not a commercially manufactured piece of equipment to solve a problem, he gives photographs or line diagrams of the equipment he had built.

Loveland's style of writing is good; even in the more technical portions of the text it is a pleasure to read. The book's usefulness as a reference text is much enhanced by the printing of important sections of the text in italics or bold face type. These two volumes will be a very useful teaching aid for photomicrography and should be in every laboratory where photomicrography is practised.

D. A. Craig
Department of Entomology
University of Alberta
Edmonton 7, Alberta
Book Review


This interesting little book is a guide to sources of entomological information, and an introduction to current information storage and retrieval theories, problems, and accomplishments as they relate to entomology. The book is intended not only as peripheral reading material, but as a student text. Accordingly, each chapter except the first contains suggested assignments, optional assignments, and a series of review questions. The writing is clear, the printing quality is good, and the illustrations are pertinent and well reproduced.

Arnett's book has a rather complex organization, with 11 text chapters, a glossary, four appendices, and subject and author indices, in addition to preface, postface, and colophon. Chapter one contains introductory observations, chapters two through eight deal with original information, and the closing three chapters deal with secondary information. Chapter two is of particular importance, since it concerns information storage and retrieval theory, the main subject of the book. In chapters three, four, and five Arnett discusses stored information, and original documents and their preparation for storage. Chapter six concerns the preparation of these documents for information retrieval. The remaining five chapters, which are more general and to some extent superficial, concern search resources, abstracts and indices, synthetic literature, popular literature, and societies, institutions, and personnel. The four appendices are: a bibliography of basic types of entomological literature; a selected list of commercial publishers and dealers in this literature; a list of entomological equipment and supply companies; and a list of major North American entomological libraries.

The arrangement of the references, or bibliography, is unfortunate. This bibliography contains 237 entries, at least one being a repetition. As a key to various types of literature, its organization by chapter and subject headings is quite suitable. Perhaps, though, the many additional text references to serials, and to other works such as the Zoological Record, should be included in it. As a key to references cited, however, this bibliography leaves much to be desired. Some citations repeated in two or more text chapters are not listed accordingly in the bibliography, and thus are not readily located (retrieved?). For example, there is in chapter four a reference to the Conference of Biological Editors, but this is listed in the bibliography under the heading of chapter five. I suggest that, if a second edition of this book is published, there should be a separate section for references cited.

Several acronyms used repeatedly in the text add to the complexity of the book, and any reader unfamiliar with these acronyms should turn first to the glossary and learn their various meanings. The information boxes used in numerous places are useful to summarize main points and to supply ancillary information, but some seem to me to detract from the book. I wonder, for instance, if the list of purposes of publication on page 66 is really needed; if this list is to be included, then I think each of its elements needs further discussion.

These criticisms are minor, but relate to the information storage and retrieval features of the book itself!

I strongly recommend that student entomologists, in particular, acquire and use this book as a guide. Many will find that the last several chapters will help reduce the time required for, and increase the efficiency of, any literature searches they may need to do. Regrettably, the book is somewhat regional in scope, and as a guide will be of limited use outside of North America.
However, the book is especially timely and pertinent to the information explosion problems of the present decade. Chapters two through six are of especially great importance to all entomologists, since procedures for the preparation and dissemination of entomological information are already beginning to undergo some radical changes and will continue to do so in the near future. Indeed, in terms of its information storage and retrieval concerns, Arnett hopes that his book will introduce entomologists to those changes now in progress, and that by so doing it will help accelerate its own obsolescence. For the professional entomologist, therefore, the time to read this book is now.

Donald R. Whitehead  
Department of Entomology  
University of Alberta  
Edmonton 7, Alberta

Book Review


This is the second in a series of monographs by Matsuda analyzing structural evolution in insects. He began this project to organize the large quantity of published information which had accumulated since the appearance of Snodgrass' textbook on the subject in 1935. Perusal of the bibliography supports his rationale: of 744 references only 186 appeared before 1935. There are 424 references in English, 180 in German, 79 in French and 61 in other languages chiefly Russian and Italian. As the German and French contributions have importance out of proportion to their numbers the appearance of a review in English is of great value to English-speaking entomologists.

This book deals with the thorax but considers the wings and legs only briefly. Matsuda's conclusions are based largely on his reading, interpretation, and digestion of published works although he contributes original information where required to fill in gaps.

The book is divided into two parts: a discussion of general topics on 87 pages, and a discussion on 314 pages which treats in detail selected representatives of each insect order. For most biologists the first part is of greater use. In it Matsuda establishes the primitive organization of the pterygote thorax. This necessitates a summary of his conclusions from part II. He discusses the neck, tergum, sternum, intersegmental regions, pleuron and aspects of the wings, coxae and spiracles, comments on their embryological and evolutionary origins, analyzes the various theories proposed to explain their evolution, and emphasizes the strengths and weaknesses of each theory. Finally, he presents his own conclusions, synthesizing a theory of homology from descriptive and experimental embryology, postembryonic development, genetics, comparative morphology, paleontology and phylogeny.

In his discussion of wings Matsuda concentrates on their origin, a subject which has intrigued many workers as evidenced by the plethora of theories published to explain their presence. His most interesting discussion here concerns the validity of separating the pterygotes into the Paleoptera and Neoptera. Matsuda concludes that this separation is phylogenetically unsound since the wing mechanism of the Ephemeroptera is very much like that of most neopterous pterygotes, while that of Odonata is not.
In the second half of part I, Matsuda considers the thoracic musculature. First, he presents an illustrated and tabulated description of the musculature of the apterygote Lepisma saccharina L. based on the work of Barlet. This serves as a standard of reference for his general discussion of pterygote musculature which follows. Here, he introduces a system of abbreviations used in part II for naming muscles.

The final section of part I (Major evolutionary features of thoracic musculature) is the strongest section in the book. Matsuda concludes that the predominant evolutionary trend of the adult thoracic muscles in insects has been a reduction in number. At the same time however, some muscles have been added and in their turn these secondary muscles have decreased in number also in the higher pterygotes. Thus, the thoracic musculature includes two kinds of muscles of different evolutionary origin: (i) those inherited from a wingless antecedant and (ii) those which have arisen de novo in the Pterygota. The former Matsuda calls paleogenetic muscles; the latter neogenetic muscles. A third group, the caenogenetic muscles, are those which have developed exclusively in the immature stages and which have no recognizable homologues in the adults.

Matsuda discusses the gross developmental pattern of the thoracic muscles. There are few if any caenogenetic muscles in paurometabolous insects, but in holometabolous insects these tend to increase. Also, the time of appearance of imaginal muscles and degeneration of larval muscles during metamorphosis varies from one order to another (heterochrony). Immature pterygote insects tend to preserve muscles present in the Apterygota whereas the adults of these insects lack them. There is also a tendency for nymphal and larval insects to preserve muscles present in the adults of related but less derived groups. This last observation, as emphasized by Matsuda, accords with the biogenetic law of Müller-Haeckel i.e. that ontogeny recapitulates phylogeny.

Matsuda closes part I with a discussion of the underlying developmental mechanisms for production of new muscles. Differences in the growth rate of epidermal cells and differences in times of connection between muscles and the epidermal cells in various insects result in the production of homologous muscles with new points of attachment and hence new functions. The development of ectodermal parts is often dependent on muscles after the connection of the two is established but not before. Here, Matsuda should have cited the work of Sahota and Beckel (1967. Can. J. Zool. 45:407-434) who showed experimentally that in Galleria mellonella L., the topographic relationships between flight muscle myoblasts and the epidermis is the causative factor in determining the orientation of developing flight muscles. Homologous muscles may be inserted on the cuticle in Pterygota and on the epidermis in Apterygota and larval Pterygota. Some muscles are replaced by ligamentous structures which are ectodermal in origin.

The flight muscles have been derived differently in different orders. Fibrillar and close-packed types of flight muscles are specializations of the normal, non-flight muscles which are tubular. Much of this argument is based on Tieg's (1955) classic study of flight muscles, a paper which, in this book, finally receives the recognition it deserves.

In part II, each account of an order is illustrated with fully-labelled drawings. Most of these are modified from other works, but some are based on Matsuda's own observations. Many of the copied illustrations are not of the quality of the originals but all of them show clearly what they are intended to show. Most of the analyses are accompanied by a table providing a uniform system of designation for the muscles found by different investigators in different species. Each table is followed by a list of remarks muscle by muscle. Where information is available both adult and larval musculature and its metamorphosis are discussed. The structural basis for flight is summarized and alary polymorphism is referred to if it occurs in the group under discussion.
Matsuda’s phylogenetic conclusions, which are highly controversial, are derived with an appreciation for Hennig’s (1966) principles and terminology. He suggests that Embioptera and Phasmida are derived sister groups of Plecoptera. His belief that the Blattaria, Isoptera, Mantodea, Grylloblattodea, and Orthoptera belong together is evidenced by his tabular comparisons of the thoracic muscles of individuals in these different orders. He supports Crampton’s (1918) idea that the Dermaptera and Coleoptera are closely related to each other and thus implies that the beetles are only distantly related to the other holometabolous orders. Zoraptera are related both to the hemipteroid orders and to the Isoptera and Plecoptera and Matsuda proposes that the hemipteroids were derived from the same protorthopteroid ancestry as Isoptera. Suprisingly, Matsuda does not discuss the relationships of the panorpoid complex but in grouping most of these orders (Mecoptera, Diptera, Lepidoptera, Trichoptera) together he implies support for Hinton’s (1958, A Rev. Ent. 3:181-206) interpretation. Hymenoptera he considers to be a sister group of the Mecoptera and the placing of Strepsiptera, he says, requires further study.

In leaving consideration of Odonata to the end of the book, Matsuda underlines his belief that these insects are only distantly related to the other pterygotes. He proposes that this order could have arisen from a machilid- or japygid-like ancestor and intimates that odonate peculiarities have been derived in such a way as to obscure this order’s relationships with the Machilidae and Diplura. I am not convinced by Matsuda that the ectognathous Odonata are closely related to entognathous Diplura.

As the structures comprising the thorax of insects form a functional complex, they are liable to change with changes in the mode of life of the organisms. Thus, insects in different orders with similar methods of locomotion could have similar thoraces arising through convergence. Adaptive features often are of limited value in phylogenetic hypothesizing if they are not used in conjunction with many other characters of different functional significance. I suggest that phylogenies erected on the basis of thoracic structure alone will not persist for very long.

I respect this author for his ability at synthesis. Some workers have criticized Matsuda for relying too heavily on the work of others. Nevertheless Matsuda’s conclusions are his own and could only be arrived at by one who has a comprehensive appreciation of thoracic complexity in the whole of the Insecta. To have mastered this amount of information and still found time for original investigation is a remarkable accomplishment.

The book reveals that insect morphology is an active field of investigation, points out that a great amount of information remains to be obtained particularly in the developmental area, and hopefully, shows non-morphologists that this is not the dull subject that many of them believe it to be. I am looking forward to the appearance of future volumes by Matsuda.

Bruce S. Heming
Department of Entomology
University of Alberta
Edmonton 7, Alberta
Publication of *Quaestiones Entomologicae* was started in 1965 as part of a memorial project for Professor E. H. Strickland, the founder of the Department of Entomology at the University of Alberta in Edmonton in 1922.

It is intended to provide prompt low-cost publication for accounts of entomological research of greater than average length, with priority given to work in Professor Strickland's special fields of interest including entomology in Alberta, systematic work, and other papers based on work done at the University of Alberta.

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CONTENTS

Guest Editorial — Excellence has no Nationality ........................................... 287
Sehgal — A Taxonomic Survey of the Agromyzidae (Diptera) of Alberta, Canada, with Observations on Host-Plant Relationships ................................. 291
Nimmo — Corrigenda on the Adult Rhyacophilidae and Limnephilidae (Trichoptera) of Alberta and Eastern British Columbia and their Post-Glacial Origin ...... 406
Thomas — An Apparatus and Method for the Field Separation of Tabanid Larvae (Diptera: Tabanidae) from Moss ......................................................... 407
Announcement .................................................... 409

Guest Editorial

A committee has been established in the Province of Alberta to enquire into non-Canadian influence in post-secondary education in the province. There is a non-Canadian component in this university and especially in the distribution list of Quaestiones entomologicae. To these people among others both the existence of this committee and the following statement of the president of the university will be of interest:

Excellence has no Nationality

Let me begin by making it clear to members of the Committee that I appear before you as one person, not as a representative of The University of Alberta. Although I am aware that other people and other groups from The University of Alberta will present ideas to you, no consensus of opinion has been sought, and there will be no opinion given by anyone or any group which might be interpreted as the official opinion of The University of Alberta.

It is also important for me to say that I am aware of the unemployment situation in Canada, and that the possibility of high unemployment at all levels is of major concern to me. The University of Alberta employs several thousands of people, both with and without university degrees. It therefore goes without saying that our University must adopt employment procedures which will help to alleviate the high incidence of unemployment among Canadian citizens, and among those to whom our government has granted the right to live and work in Canada.

However, the purpose of your inquiry is not economic in nature, and I mention employment procedures for the sole purpose of saying that universities are aware that their situation in the 1970's will be far different from what it was in the 1960's.

The question of "who should teach at The University of Alberta" is not new. Let me quote from the minutes of a meeting of a governing body of this University:

"Dr. Jenkins expressed his disapproval of the idea of appointing all the professors and assistants outside of the province. He was strongly in favor of utilizing the material available in the province and he felt sure that many men now engaged in educational work were eminently qualified to undertake the higher branches of learning and he felt an injustice would be done the whole of the teaching profession of the province if only outsiders were appointed."
The sentiment was expressed at the first meeting of the Senate of The University of Alberta on March 30, 1908. This was before a single member of the staff, other than the President, had been appointed to The University of Alberta. Fortunately the matter was not taken further. I say "fortunately" because I feel strongly that this University would not enjoy the respect it has today if Dr. Jenkins had had his way sixty-three years ago.

Since you are a Committee of Inquiry into non-Canadian Influence in Alberta Post-Secondary Education, sooner or later you will have to define what will be meant by a "non-Canadian influence," and to propose the procedures by means of which such an influence can be measured. Presumably you will have to be able to identify a good "non-Canadian influence" from one that, by some means or other, will be deemed to be bad. Your task will not be easy because in a rather restricted sense one might say that there is no real Canadian content in the science and mathematics courses taught in Canada today. Let me explain what I mean.

Education generally, and higher education particularly, is a world of ideas. If one traces the sources of the big ideas of science and mathematics, they will not be found to be Canadian, nor, in fact, were they discovered in the United States. Up until the middle of the present century, these ideas came from Great Britain, France, Germany, Switzerland, Italy, and even smaller countries like Denmark made major contributions to the world of ideas. During the first fifty years of the present century, it was common practice for the men and women of Canada and the United States to go abroad for post-graduate education. Indeed, these people coupled with the thousands of people who were brought to this continent from abroad developed the educational systems of Canada and the United States.

Who were the people who dominated the world of scientific ideas during the first half of the twentieth century? As illustration only, there was Einstein of Germany, Fermi of Italy, Weyl of Switzerland, Dirac of England, Bohr of Denmark, Wigner and Von Neumann of Hungary, and De Broglie of France. Even if the list were complete, no Canadian and few Americans would be contained among those who contributed to the world of big ideas up till 1950. Since that time the United States and Russia have come to the fore. The ideas that led to the development of computer technology, to the exciting ideas being developed in genetics and the life sciences, to laser technology, and to transportation and communications technologies, to name but a few, should make us aware that the time has not yet come when Canadians can arrogantly say that we shall lock out the world of ideas that exists beyond our borders, and go the rest of the way by ourselves.

How does one classify the study of arithmetic, dependent as it is on the Arabic number system? Is this a non-Canadian influence? How does one classify the study of geometry, dependent as it is on the ideas of Euclid and Pythagoras? Is this a non-Canadian influence? I do not envy you the task that has been placed into your hands, and do not know how you will accomplish it.

It is my fear however that groups are raising the "non-Canadian influence" issue on a meaningless statistical basis, and that conclusions will be drawn, and, indeed, have already been drawn, which are not warranted by the statistics. If these issues develop into a witch-hunt in Canada, then I want no part of it. I lived through the McCarthy era, and friends of mine were made uncomfortable and unwelcome at their universities. Some were dismissed and some went to jail, not because they were Communists, but because they chose to fight for academic freedom, the right to seek truth as they saw fit and the right to teach and publish the truth as they saw it.

During the 1960's, Canada sought and brought men and women from the four corners of the world to help us solve what then seemed to be an insoluble problem: the problem of expanding enrolments with too few people qualified to teach. If, after making a major con-
tribution to our country, such men and women are made to feel uncomfortable and unwel-
come, then this will indeed be a sorry way to show our gratitude.

There is no reason to believe that the search for truth will ever end at the borders of
Canada. We are a young country and a small nation. There is every reason to believe that
the majority of the big ideas of science, by means of which scientific knowledge is acquired,
will come from outside our borders for many years to come. But Canada must pursue excel-
ience, and it must pursue excellence wherever excellence exists. Therefore, Canadians must
continue to go outside of our country for study, and leaders of excellence must be brought
to Canada to teach their ideas on Canadian soil.

Although I have nothing but respect and admiration for the accomplishments of Canadian
universities during recent years, we have no Harvards nor Oxfords in our midst. Banting and
Best shared the Nobel Prize for their discovery of insulin about half a century ago. No other
Nobel Prize in science has been awarded to a Canadian nor have we been able to attract such
people to work in and for Canada.

As I said at the beginning, concern over unemployment in Canada is genuine, and univer-
sities must help our people to find interesting and rewarding work. However, we must not
adopt a policy which will give a short-term gain but will turn into a long-time evil. It will be
a tragedy if ever Canada posts signs, or enacts legislation, which will tell the members of the
world of ideas they are not welcome here. Excellence attracts excellence, and such a policy
will discourage desirable people from coming to Canada, and may, in the long run, encourage
desirable Canadians to leave Canada.

Max Wyman
University of Alberta
A TAXONOMIC SURVEY OF THE AGROMYZIDAE (DIPTERA) OF ALBERTA, CANADA, WITH OBSERVATIONS ON HOST-PLANT RELATIONSHIPS

VINOD K. SEHGAL
Department of Entomology
University of Alberta
Edmonton 7, Alberta

Thirty-one new species are described and eleven further are recorded from Alberta for the first time. This brings the total of Albertan Agromyzidae to 170 and that for Canada and Alaska to 321 species. Genitalia of all males representing new species are illustrated. Keys to Albertan genera and species, diagnostic characters and data on larval host-plants are given. Host-plant relationships are discussed.


This survey of the family Agromyzidae in Alberta was started in the summer of 1966, when this was one of the most poorly known families of cyclorrhaphous Diptera in Canada. Strickland (1938, 1946) listed 20 species as occurring in Alberta. The only comprehensive treatment for North American Agromyzidae was by Frick (1959) who included those known from Canada. Since the publication of Frick’s synopsis, the concept of certain genera of Agromyzidae has been revised by Nowakowski (1962) on the basis of his studies of male genitalia. As new characters of male genitalia were discovered, it became necessary to confirm all determinations of species, which were previously based on external morphology and sometimes only on female specimens. One of my main objectives was to collect, determine, and describe as many species as possible in order to assess the family Agromyzidae in Alberta and in Canada, and to provide keys for the determination of genera and species. This investigation in Alberta was started parallel to Spencer’s 1969 synopsis of the Agromyzidae of Canada and Alaska. As a preliminary report on these investigations I described 13 new species from Alberta (Sehgal, 1968). Spencer examined all previously known records of Canadian and Alaskan Agromyzidae and confirmed a total of 290 species.

Among the Canadian species Spencer (1969) recorded 128 described species as occurring in Alberta. As a result of this study 31 new species are described from Alberta and 11 further species have been recorded for the first time as occurring in Alberta. This brings the total of Albertan Agromyzidae to 170 and that of Canadian and Alaskan Agromyzidae to 321 described species (Table 1). The male genitalia of almost all Albertan species have been examined. Any record of Albertan Agromyzidae outside the present work must be considered tentative, until confirmed on the basis of male genitalia.
Table 1. Distribution among genera of new species, new Alberta records, and all known species of Agromyzidae from Alberta, and Canada and Alaska.

<table>
<thead>
<tr>
<th>Genus</th>
<th>New species</th>
<th>New Alberta records</th>
<th>Total number of species now known from:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Alberta</td>
</tr>
<tr>
<td>Agromyza</td>
<td>2</td>
<td>2</td>
<td>17</td>
</tr>
<tr>
<td>Melanagromyza</td>
<td>3</td>
<td>—</td>
<td>9</td>
</tr>
<tr>
<td>Hexomyza</td>
<td>—</td>
<td>—</td>
<td>1</td>
</tr>
<tr>
<td>Ophiomyia</td>
<td>1</td>
<td>—</td>
<td>17</td>
</tr>
<tr>
<td>Phytobia</td>
<td>—</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Cerodontha</td>
<td>—</td>
<td>2</td>
<td>7</td>
</tr>
<tr>
<td>Dizygomyza</td>
<td>—</td>
<td>—</td>
<td>5</td>
</tr>
<tr>
<td>Poemyza</td>
<td>—</td>
<td>—</td>
<td>2</td>
</tr>
<tr>
<td>Icteromyza</td>
<td>—</td>
<td>—</td>
<td>2</td>
</tr>
<tr>
<td>Cerodontha</td>
<td>—</td>
<td>—</td>
<td>2</td>
</tr>
<tr>
<td>Calycomyza</td>
<td>—</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Amauromyza</td>
<td>2</td>
<td>—</td>
<td>2</td>
</tr>
<tr>
<td>Nemorimyza</td>
<td>—</td>
<td>—</td>
<td>1</td>
</tr>
<tr>
<td>Liriomyza</td>
<td>6</td>
<td>1</td>
<td>27</td>
</tr>
<tr>
<td>Lemurimyza</td>
<td>—</td>
<td>—</td>
<td>1</td>
</tr>
<tr>
<td>Metopomyza</td>
<td>1</td>
<td>—</td>
<td>2</td>
</tr>
<tr>
<td>Praspedomyza</td>
<td>—</td>
<td>—</td>
<td>1</td>
</tr>
<tr>
<td>Haplomyza</td>
<td>—</td>
<td>—</td>
<td>1</td>
</tr>
<tr>
<td>Phytoliriomyza</td>
<td>—</td>
<td>—</td>
<td>1</td>
</tr>
<tr>
<td>Paraphytomyza</td>
<td>1</td>
<td>—</td>
<td>5</td>
</tr>
<tr>
<td>Pseudonapomyza</td>
<td>—</td>
<td>—</td>
<td>2</td>
</tr>
<tr>
<td>Napomyza</td>
<td>—</td>
<td>—</td>
<td>3</td>
</tr>
<tr>
<td>Phytomyza</td>
<td>15</td>
<td>4</td>
<td>59</td>
</tr>
<tr>
<td>Other genera</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>TOTAL</td>
<td>31</td>
<td>11</td>
<td>170</td>
</tr>
</tbody>
</table>

MATERIALS AND METHODS

As a part of this study I made intensive collections of agromyzid specimens from the province of Alberta, Canada, including the Alberta Rockies. Some specimens collected by others, especially G. C. D. Griffiths, K. A. Spencer, the late Professor E. H. Strickland, and B. Hocking, from Alberta localities were also examined and are acknowledged in the list of material.

Attempts were made to rear adults from immature stages as far as possible. This permitted me to clarify the biology of many species. I studied approximately 1200 specimens and examined genitalia preparations of 620 specimens. Genitalia of all males representing new species and a few other species where necessary for their specific determination have been illustrated. Reference is made to good earlier illustrations of male genitalia. The holotypes and allotypes of all new species will be deposited in the Canadian National Collection, Ottawa.
The terminology used in describing new species is that employed by Spencer (1969) and other workers in Agromyzidae. The frons width and eye width are measured at the level of the median front ocellus from above. The term gena here means the area below the eyes including the lower orbits. The ratio of genal and eye heights are measured mid-way between vibrissal and posterior margins. The terminology of the aedeagus is that used by Frick (1952) and Spencer (1969).

**Abbreviations**

acr, arcostichal hair; Adap, aedeagal apodeme; Ar, arista; As3, third antennal article; Bsph, basiphallus; C, costa; dc, dorsocentral bristles; Dph, distiphallus; Ejap, ejaculatory apodeme; Ejb, ejaculatory bulb; Ejd, ejaculatory duct; Hypa, hypandrium; m-m, medial crossvein; M1·2 and M3·4, median veins; Mph, mesophallus; oc, ocellar bristles; Ori, lower orbital bristles; Ors, upper orbital bristles; os, orbital setulae; Pgo, postgonites; Phph, phallophore; Prgo, pregonites; Pvt, postvertical bristles; R1, R2·3 and R4·5, radial veins; r-m, radiomedial crossvein; Sc, subcosta; Vi, Vibrissa; Vte, outer vertical bristle; Vti, inner vertical bristle.

**CHARACTERISTICS OF THE FAMILY AGROMYZIDAE**

The main distinguishing characters of the members of this family are as follows:

**Head.** — Postvertical bristles divergent; distinct orbital bristles present, normally two strong upper orbital bristles, Ors, directed upwards and two lower orbital bristles, Ori, directed inwards and upwards; orbital setulae present; distinct vibrissal hair present, represented by a bunch of fused hairs or ‘vibrissal horn’ in some males of the genus *Ophiomyia* Braschnikov; centre of frons without bristles or setulae.

**Mesonotum.** — Distinct dorsocentral bristles present, normally 3+1, sometimes a few anterior bristles are reduced or lost; variable number of acrostichals present; scutellum normally with four scutellar bristles, two in subgenus *Cerodontha* Rondani.

**Wing.** — Costa broken at end of subcosta, extended to apex of vein R4·5 or M1·2; subcosta weakly developed distally, adjacent to, and either joined to or independent from R1 distally; crossvein r-m present; anal vein shortened, not extended to the wing margin.

**Male genitalia.** — Hypandrium large and well developed; pregonites and postgonites normally well differentiated, former sometimes fused with hypandrium; epandrium large and conspicuous; surstyli and cerci normally well developed and with characteristic setae or setulae; aedeagus complex; aedeagal apodeme large and darkly sclerotized; aedeagal hood conspicuous; aedeagus with distinct basal section consisting of basiphallus and phallophore and distal section consisting of various sclerites forming mesophallus, paraphallus, and distiphallus; terminal section of ejaculatory duct inside distiphallus normally bifid; ejaculatory apodeme normally well developed, sometimes reduced, bulb conspicuous.

**Female postabdomen.** — Seventh segment completely sclerotized, forming a conical ovi-poster sheath; eighth segment elongate, retractible into seventh, bearing numerous anteriorly directed denticles; pair of egg guides around gonopore; anus well beyond gonopore; two spermathecae.

**Larvae.** — Anterior spiracles on first abdominal segment approximate; posterior spiracles on last or eighth abdominal segment approximate or widely separated; mouth hooks well developed and almost vertical in relation to labial sclerite; paraclypeal phragma normally with dorsal and ventral arms; muscle scars and tubercle bands strongly developed along lateral portions of abdominal segments.
**Biology.** — Larvae feed inside the living tissue of angiosperms (except those of *Pteridomyza* Nowakowski, *Liriomyza felti* (Mall.) and *Phytomyza scolopenderii* R.-D. which feed on ferns and few representatives of the genus *Liriomyza* Mik feeding on horsetails and liverworts). Larvae show varying host-plant specificity, but normally feed on one plant organ. Most species feed as leaf miners, some feed inside the stems, seeds, and other parts of plants; a few cause galls (*Hexomyza* Enderlein).

**TAXONOMIC TREATMENT**

The generic concept used in this study is the one which has come to be generally accepted (Spencer, 1969), but is certainly not final in agromyzid classification. As recent studies progress on the male genitalia, the need for defining some of the larger genera on a monophyletic basis becomes more apparent. No attempt is made in this study to undertake any generic revision of the existing classification.

According to the biological species concept (Mayr, 1963), species are defined to be groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups. I accept this species definition. The application of this species concept presents many practical difficulties and some of these have been discussed by Mayr (1969). The reproductive isolation of a population is usually inferred indirectly from comparisons of external morphology. In Agromyzidae, besides the evidence of external morphology, various other evidences are helpful. The majority of agromyzid species are restricted feeders, either monophagous or oligophagous, confined to botanically related plant species. It seems highly unlikely that significant gene interchange occurs between populations restricted to unrelated host-plants, even if the morphological differences between them are minor. Such populations can be assumed to represent distinct species, so long as the observed differences are shown consistently. Often other evidence such as larval morphology or shape of mine is available to support this assumption.

Spencer (1969) discussed briefly the significance of various taxonomic characters currently in use in agromyzid taxonomy; the same criteria have been accepted here. The characters of male genitalia have been used as far as possible in order to provide a basis for more accurate determination of species. Information on Albertan host-plants and biology, wherever available, has been included. The following key represents a further development of that originally produced by Hendel (1931) and modified by Frick (1952, 1959) and Spencer (1969).

**Key to genera of Albertan Agromyzidae**

1(0). Subcosta developed throughout its length, coalesced with R₁ before contact with costa .................................................. 2

2(1). Prescutellars absent; dorsocentrals, two, three or four pairs, if three or four pairs halteres black ........................................... 3

- Prescutellars present; at least three pairs of dorsocentrals; halteres yellow .................................................. *Agromyza* Fallén, p.296

3(2). Mesonotum or abdomen normally with greenish, bluish or coppery metallic sheen; antennae not separated by conspicuous keel; aedeagus with basiphallus U-shaped; larvae normally with conspicuous horn in centre of posterior spiracles; larvae feed inside stems or seeds ................................. *Melanagromyza* Hendel, p.303

- Mesonotum and abdomen black; aedeagus with basiphallus with long side arms; posterior spiracles of larva without central horn ........................................ 4
<table>
<thead>
<tr>
<th>Number</th>
<th>Description</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>4(3)</td>
<td>Antennae separated by conspicuous raised facial keel (absent from <em>pulicaria</em></td>
<td><em>Ophiomyia</em> Braschinkov, p. 310</td>
</tr>
<tr>
<td></td>
<td>group); male with or without distinct vibrissal horn; larval posterior</td>
<td></td>
</tr>
<tr>
<td></td>
<td>spiracles with more than three bulbs; larva feeds below stem epidermis or</td>
<td></td>
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<td></td>
<td>as leaf miner.</td>
<td></td>
</tr>
<tr>
<td>5(1)</td>
<td>Orbital setulae erect or reclinate, rarely absent.</td>
<td><em>Hexomyza</em> Enderlein, p. 309</td>
</tr>
<tr>
<td>6(5)</td>
<td>Costa extended to apex of vein M₁,₂; if only to R₄,₅ then either crossvein m-</td>
<td></td>
</tr>
<tr>
<td></td>
<td>m-absent (<em>Phytobia confessa</em> Spencer) or lunule broad, distinctly higher</td>
<td></td>
</tr>
<tr>
<td></td>
<td>than semicircle (<em>Cerodontha (Dizygomyza) frankensis</em> Spencer).</td>
<td></td>
</tr>
<tr>
<td>7(6)</td>
<td>Scutellum normally dark, concolourous with mesonotum.</td>
<td></td>
</tr>
<tr>
<td>8(7)</td>
<td>Halteres with knob white or yellow.</td>
<td></td>
</tr>
<tr>
<td>9(8)</td>
<td>Crossvein m-m absent.</td>
<td><em>Haplomyza</em> Hendel, p. 344</td>
</tr>
<tr>
<td>10(9)</td>
<td>Vein R₄,₅ ending nearest wing tip; larvae cambium miners.</td>
<td><em>Phytobia</em> Lioy, p. 316</td>
</tr>
<tr>
<td>11(10)</td>
<td>Vein M₁,₂ ending nearest wing tip.</td>
<td></td>
</tr>
<tr>
<td>12(11)</td>
<td>Third antennal article with conspicuous spine anterodorsally, scutellum</td>
<td></td>
</tr>
<tr>
<td></td>
<td>with only two bristles; or lunule higher than semicircle, narrow or</td>
<td></td>
</tr>
<tr>
<td></td>
<td>triangular; or lunule broad, antennal bases widely separated, third</td>
<td></td>
</tr>
<tr>
<td></td>
<td>antennal article in male distinctly enlarged.</td>
<td><em>Cerodontha</em> Rondani, p. 317</td>
</tr>
<tr>
<td>13(12)</td>
<td>Frons dark; orbits raised above plane of frons.</td>
<td><em>Praspedomyza</em> Hendel, p. 343</td>
</tr>
<tr>
<td>14(7)</td>
<td>Frons yellow, orbits in same plane as frons.</td>
<td><em>Calycomyza</em> Hendel, p. 325</td>
</tr>
<tr>
<td>15(14)</td>
<td>Crossvein m-m absent; one Ors.</td>
<td><em>Haplomyza</em> Hendel, p. 344</td>
</tr>
<tr>
<td></td>
<td>Crossvein m-m present (absent in <em>Liriomyza singula</em> Spencer); two Ors.</td>
<td></td>
</tr>
<tr>
<td>16(15)</td>
<td>Prescutellar area yellow; orbital setulae normally erect; aedeagus with</td>
<td><em>Lemurimyza</em> Spencer, p. 341</td>
</tr>
<tr>
<td></td>
<td>sclerotized paired tubules in the distiphallus, epandrium with</td>
<td></td>
</tr>
<tr>
<td></td>
<td>conspicuous black spines.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Prescutellar area normally dark, sometimes yellow; orbital setulae</td>
<td><em>Liriomyza</em> Mik, p. 328</td>
</tr>
<tr>
<td></td>
<td>reclinate; aedeagus variable in form, but not as in the genus <em>Lemurimyza</em></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spencer.</td>
<td></td>
</tr>
<tr>
<td>17(6)</td>
<td>Crossvein m-m either absent, or if present well beyond r-m.</td>
<td><em>Paraphytomyza</em> Enderlein, p. 345</td>
</tr>
<tr>
<td>18(5)</td>
<td>Crossvein m-m basal to r-m.</td>
<td><em>Pseudonapomyza</em> Hendel, p. 345</td>
</tr>
<tr>
<td></td>
<td>Crossvein m-m basal to or at same level as r-m.</td>
<td><em>Napomyza</em> Westwood, p. 349</td>
</tr>
<tr>
<td></td>
<td>Crossvein m-m absent.</td>
<td><em>Phytomyza</em> Fallén, p. 350</td>
</tr>
</tbody>
</table>
Genus *Agromyza* Fallén


The main distinguishing characters of this genus are subcosta developed throughout its length and coalesced with R₁ before contact with costa; at least three pairs of dorsocentrals; prescutellars present and halteres yellow.

This genus is represented in Alberta by 17 species, of which two are described as new. The species in this genus form a very diverse assemblage of many groups. The species in the *ambigua* group, *albertensis* Sehgal, *aprilina* Malloch and *kincaidi* Malloch; as well as species in the *nigripes* group, *albipennis* Malloch, *brevispinata* new species, *hockingi* Spencer and *nigripes* Meigen; like other members of the *ambigua/nigripes* groups (Griffiths, 1963) form a single group of grass mining species with similarity in shape of the distiphallus. Members of the *ambigua* group differ from those of the *nigripes* group only by a shortened costa, not extended beyond the apex of vein R₄₋₅, and longer distiphallus. The *Urtica* miner, *pseudoreptans* Nowakowski, belongs to the *reptans* group, while the *Mertensia* miner, *canadensis* Malloch, belongs to the *rufipes* group.

The species in the *spiraeae* group, *populoides* Spencer, *vockerothi* Spencer, *fragariae* Malloch, *masculina* Sehgal and *spiraeae* Kaltenbach, are believed to be closely related due to similarities in the male genitalia. This concept was first proposed by Sasakawa (1961). The species in this group have asymmetric sclerotization of the basiphallus and mesophallus.

*A. aristata* Malloch, whose larvae mine the leaves of *Ulmus americana* L., family Ulmaceae, is probably close to the *rubi/spiraeae* group of Sasakawa (1961). Another group of species whose members are characterized by 3+1 strong dorsocentrals and yellow frons is represented in Alberta by *nearctica* new species. Three further females belonging to this group cannot be identified in the absence of males. The leaf mines on members of *Geum allepicum* Jacq., *Potentilla* sp., and *Rosa acicularis* Lindl., of the family Rosaceae probably represent those of the members of the *spiraeae* group, but no flies have been bred from these hosts.

**Key to Alberta species of the genus *Agromyza* Fallén**

1(0). Dorso-centrals 3-6, decreased significantly in size anteriorly; presuturals as well as anterior post-sutural dorso-centrals usually not distinguishable from acrostichals

- Dorso-centrals 3+1, strong and distinct ........................................... 2

2(1). Wing tip near apex of vein M₁₋₂ ................................. *sulfuriceps* Strobl, p.303
- Wing tip near apex of vein R₄₋₅ or midway between R₄₋₅ and M₁₋₂ ............................. 3

3(2). Legs largely yellowish ................................................................. 4
- Legs largely black or brown ............................................................. 5

4(3). Antennae yellow, smaller specimens, wing length 2.2 to 2.7 mm; larvae leaf miner on *Ulmus americana* L. ................................. *aristata* Malloch, p.298
- Antennae dark brown; larger specimens, wing length about 3.0 mm ..........................

................................. *canadensis* Malloch, p.299

5(3). Costa extended to apex of vein R₄₋₅ ........................................... 6
- Costa extended to apex of vein M₁₋₂ ................................................ 8

6(5). Squamal fringe brown or black; larger specimens, wing length about 2.7 to 3.5 mm ................................. *kincaidi* Malloch, p.300
- Squamal fringe pale or whitish, smaller specimens ............................................. 7

7(6). Third antennal article with distinct angle or point anterodorsally; eyes upright, normal ................................. *albertensis* Sehgal, p.297
Third antennal article rounded at end; eye distinctly slanted .......................... aprillina Malloch, p. 298

8(5).  Mesonotum at least weakly shining black; mesophallus and distiphallus single
S-shaped sclerotization ................................................................. 9

- Mesonotum distinctly mat black; mesophallus and distiphallus separate sclerotizations
  ........................................................................................................ 9(8).

9(8).  Third antennal article with distinct angle anterodorsally .......................... 10

- Third antennal article rounded at tip ............................................... 11

10(9).  Squamal fringe pale or whitish; ejaculatory bulb very broad
  ........................................................................................................ 10(9).

- Squamal fringe dark or brown; ejaculatory bulb narrower
  ........................................................................................................ 11(10).

11(9).  Surstyli with 3-6 distinctly large spines (Fig. 6) .................. hockingi Spencer, p. 300

- Surstyli with smaller spines (Fig. 5); aedeagus as in Fig. 3, 4 .................. brevispinata n. sp., p. 298

12(1).  Frons reddish yellow; orbits black; second and third antennal articles black;
aedeagus as in Fig. 10 .................................................................. nearctica n. sp., p. 301

- Frons dark, brown or black ................................................................ 12

13(12).  Squamal fringe pale ................................................................. populoides Spencer, p. 302

- Squamal fringe darker, brown or black ........................................... 14

14(13).  Mid-tibia with a strong bristle posteriorly ......................... vockerothi Spencer, p. 303

- Mid-tibia without a distinct bristle .................................................. 15

15(14).  Frons distinctly brown ............................................................ fragariae Malloch, p. 300

- Frons distinctly mat black ............................................................ 16

16(15).  Gena narrow one-eighth to one-tenth eye height; basiphallus and mesophallus
  with sclerotized strips .................................................................... masculina Sehgal, p. 301

- Gena broader, about one-fifth eye height; distiphallus separated from basiphallus
  by long membranous section ......................................................... spiraeae Kaltenbach, p. 302

**Agromyza albertensis** Sehgal


**Comparisons and diagnostic characters.** — The members of this species differ from those of a similar species,*kincaidi* Malloch, in smaller size, wing length 2.0-2.7 mm and in having pale squamal fringe, and from those of *ambigua* Fallén in having frons less projected above eyes in profile. The main distinguishing characters are the conspicuous angle on the third antennal article and distinct male genitalia. Sehgal (1968) illustrated the head, wing and male genitalia characteristic of this species. Spencer (1969) also figured the aedeagus.

**Biology.** — Not confirmed, but larvae probably mine leaves of grasses (Gramineae).

**Geographical distribution.** — Known only from Alberta, from the following localities: CANADA. Alberta: Banff, Blairmore, Elkwater.

**Agromyza albipennis** Meigen


**Diagnostic characters.** — The members of this species may be recognised by the combination of characters given in the key. The distinctive aedeagus and ejaculatory bulb are as illustrated (Fig. 1, 2). Sasakawa (1961) and Griffiths (1963) described in detail and illustrated significant diagnostic characteristics of this species.
Biology. — Larvae are known to mine the leaves of grasses (Gramineae) (Sasakawa, 1961; Griffiths, 1963).

Geographical distribution. — The members of this species are Holarctic in distribution, known from numerous localities in Europe (Griffiths, 1963), Japan (Sasakawa, 1961) and Canada (Spencer, 1969). I have examined three specimens from the following localities:


*Agromyza aprilina* Malloch


Comparison and diagnostic characters. — The members of this species resemble closely those of *A. kincaidi* Malloch and can be reliably separated only by examination of the characters of male genitalia. Other external differences are pale squamal fringe, smaller size and distinctly slanting eyes. Spencer (1969) illustrated the aedeagus characteristic of this species.

Biology. — Not confirmed, but the larvae probably mine the leaves of grasses (Gramineae).

Geographical distribution. — The members of this species are Nearctic in distribution and are known from United States and Canada. The known Alberta locality is:

CANADA. Alberta: Banff (Spencer, 1969).

*Agromyza aristata* Malloch


*Agromyza ulmi* Frost 1924:54; Frick, 1957:199.

Diagnostic characters. — The members of this species may be recognized by the combination of characters given in the key. Spencer (1969) illustrated the distinctive aedeagus.

Biology. — Larvae make elongated blotch mines on the upper surface of the leaves of *Ulmus americana* L., family Ulmaceae. The leaf mines appear in great numbers around Edmonton during the second week of June. The members of this species have only one generation a year in Alberta.

Geographical distribution. — The members of this species are widespread in United States (Frick, 1959) and are also known from Canada (Spencer, 1969). I have examined the following material from Alberta:


*Agromyza brevispinata* new species

Comparison and diagnostic characters. — The male of this species differs from those of the similar species *hockungi* Spencer and *lucida* Hendel in having a weakly shining or somewhat mat mesonotum and distinct male genitalia. This species is included in Spencer’s (1969) key to Canadian species of the genus *Agromyza* Fallén by amending and extending the couplet as follows:

26. Third antennal segment distinctly cut away below (Spencer, 1969, Fig. 5) . . . .

.......................................................... *nigripes* Meigen
- Third antennal segment rounded at tip ........................................ 26a
26a. Mesonotum somewhat mat or weakly shining black; surstyli with 8-10 small spines; aedeagus as in Fig. 3, 4 ............................... brevispinata n.sp.
- Mesonotum entirely shining black ............................................ 27

Description. — Head. Frons slightly wider than width of eye at level of front ocellus, not projected in front of eye margin in profile; two strong Ors directed upwards; two Ori directed inwards and upwards; orbital setulae retracted; eyes oval, approximately 1.3 times higher than their length; gena deepest at rear, approximately one-fifth eye height midway between vibrissal and posterior margins; third antennal article rounded at tip; arista long and pubescent.

Mesonotum. Two strong dorsocentrals; acr in about nine irregular rows.

Wing. Length in male about 2.8 mm; costa extended to apex of vein M₁₂; wing tip nearest to vein R₄₅; crossvein r-m approximately at centre of discal cell.

Male genitalia (Fig. 3-5). Hypandrium with short apodeme and broad pregonites; surstyli (Fig. 5) with 8-10 small spines; aedeagus as illustrated (Fig. 3, 4).

Colour. Frons and orbits mat black; ocellar triangle weakly shining black; mesonotum weakly shining mat black; squamae yellow, fringe dark brown.

Derivation of the specific name. — The name brevispinata is given in view of the small spines on surstyli.

Biology. — Not confirmed, but larvae probably mine leaves of grasses (Gramineae).

Geographical distribution. — This species is known from a single male collected at the following locality:


Agromyza canadensis Malloch


Comparison and diagnostic characters. — The members of this species are large flies, wing length approximately 3.0 mm and are distinctive in having yellowish brown legs and dark antennae.

They have male genitalia which appear indistinguishable from those of A. pseudornifipes Nowakowski. The two previously known Canadian specimens of this species are brownish flies (Shewell, 1953) while the members of European A. pseudornifipes are darker in colour. This was the basis of Spencer's (1969) accepting them as different species. The bred male from Yukon Territory, Canada, however, is darker in colour. The discovery of this dark specimen casts doubt on the separation of these two species on the basis of colour. The name A. pseudornifipes Nowakowski will probably prove to be a junior synonym of A. canadensis Malloch.

Biology. — Larvae make blotch mines on the leaves of Mertensia paniculata (Ait.) G. Don, family Boraginaceae. Pupation takes place outside the leaf mine.

Geographical distribution. — The members of this species are known from Western and Eastern Canada (Frick, 1959; Spencer, 1969). I have examined the following material referable to this species:

CANADA. Alberta: Numerous leaf mines on Mertensia paniculata (Ait.) G. Don, Edmonton, river bed near University of Alberta campus; White Mud Creek park, July to September 1968; Yukon Territory: 1 ♂ Dawson City, from leaf mines on Mertensia paniculata (Ait.) G. Don, 5.viii.1968, emerged 22.vi.1969, coll. G. C. D. Griffiths.
**Agromyza fragariae** Malloch

*Agromyza fragariae* Malloch 1913a:307; Spencer, 1969:42.  

**Comparisons and diagnostic characters.** — The members of this species resemble closely those of *A. spiraeae* Kaltenbach and *A. masculina* Sehgal but differ in having distinctly brownish frons and distinctive aedeagus. The aedeagus has a characteristic sclerotization in the mesophallus as illustrated by Spencer (1969).  

**Biology.** — Larvae are known to mine the leaves of *Fragaria virginiana* Duchesne, family Rosaceae in United States.  

**Geographical distribution.** — The members of this species are known from United States and Canada (Spencer, 1969). From Alberta, Canada they are known from the following localities:  

**CANADA.** Alberta: Blairmore; Onefour (Spencer, 1969).

---

**Agromyza hockingi** Spencer

*Agromyza hockingi* Spencer 1969:44.  

**Diagnostic characters.** — The members of this species are small shining black flies, having pale or slightly brownish squamal fringe and distinct male genitalia. Spencer (1969) illustrated the aedeagus. The number of bristles on surstyli (Fig. 6) is variable, from three to six.  

One male collected from Edmonton, White Mud Creek park, 13.vi.1966 is tentatively referred here as it has the aedeagus very similar to that of *hockingi* Spencer, but has distinctive surstyli (Fig. 7) with two very long spines and a small indistinguishable bristle. This probably represents a further species, but more material is necessary to confirm this opinion.  

**Biology.** — Larvae probably mine leaves of grasses (Gramineae).  

**Geographical distribution.** — Known from Alberta, New Brunswick, Ontario and Quebec (Spencer, 1969). I have examined the following material from Alberta:  


---

**Agromyza kincaidi** Malloch


**Comparisons and diagnostic characters.** — The members of this species are large shining black flies, wing length about 3.0 mm, with costa extended to vein R₄₊₅ and dark squamal fringe. The aedeagus (Fig. 8, 9) and surstyli are also very distinctive.  

Hendel (1931) synonymised the name *kincaidi* Malloch with *ambigua* Fallén. Frick (1952, 1959) also accepted it synonymous with *ambigua* Fallén. Spencer (1965d) concluded that specimens of *ambigua* Fallén sensu Hendel represented *nigrella* Rondani and not the true *ambigua* Fallén. He later (1969) rejected Hendel's synonymy and re-established this species.  

**Biology.** — Larvae probably mine leaves of grasses (Gramineae).  

**Geographical distribution.** — Known from Alaska and widespread in Canada (Spencer, 1969. I have examined the following material from Alberta:  

**CANADA.** Alberta: 1 ♀ Cypress Hills, Elkwater Lake, 24.vi.1966; 1 ♂ Edmonton, White Mud Creek park, 10.vi.1966, 1 ♀ same locality, 6.vii.1966; 1 ♀ same locality, viii.1968; 1 ♀ Edmonton, 110 St. 84 Ave., 15.vi.1968; 1 ♀, 2 ♀♀ Jasper, 17.vi.1966.
Agromyzidae of Alberta

Agromyza masculina Sehgal

Agromyza masculina Sehgal 1968:59.

Comparisons and diagnostic characters. — The members of this species resemble externally those of spiraeae Kaltenbach and vokerothi Spencer and can be reliably recognized by examination of the male genitalia. Sehgal (1968) illustrated the head, wing and aedeagus characteristic of this species.

Geographical distribution. — Known only from Alberta from the following localities: CANADA. Alberta: Blairmore, Okotoks.

Agromyza nearctica new species

Comparison and diagnostic characters. — The specimen of this species is distinctive in having reddish frons and 3+1 strong dorsocentraIs. It is distinguished in Spencer's (1969) key to Canadian species of the genus Agromyza Fallén by amending and extending couplet 29 as below:

29. Third antennal segment yellow. .......................... 30
- Third antennal segment black .......................... 29a

29a. Second and third antennal segments completely black; orbits black; frons distinctly projected in profile; aedeagus as in Fig. 10 ...... nearctica n. sp.
- Third antennal segment black .......................... sp. indet. (Spencer)

Description. — Head. Frons approximately twice width of eye at level of front ocellus distinctly projected in front of eye margin in profile. Two strong Ors directed upwards; three Ori directed inwards and upwards; orbital setulae numerous, reclinate. Orbits broad, each approximately one-fifth frons width. Eyes oval, 1.2 times higher than their length, bare; ocellar triangle small. Gena approximately one-fourth eye height. Third antennal article rounded at tip, with normal pubescence; arista normal, pubescent.

Mesonotum. DorsocentraIs 3+1 strong bristles; acr numerous, approximately in six rows; strong prescutellars present.

Wing. Length in male approximately 2.5 mm; costa extended to vein R₄₋₅; costal segments 2-4 in the ratio of 1 : 0.22 : 0.21; crossvein m-m present; basal portion of M₃₋₄ slightly longer than distal (1 : 0.9).

Male genitalia (Fig. 10-12). Hypandrium (Fig. 12) V-shaped, with narrow side arms and short but distinct apodeme; pregonites broad; postgonites elongate; surstyli with approximately 8 spinules placed anteriorly; cerci long; aedeagus (Fig. 10) characteristic with bag of spinules between two arms of basiphallus as illustrated; ejaculatory apodeme (Fig. 11) small and narrow, bulb small, membranous.

Colour. Frons reddish; orbits black; gena paler; lunule reddish; ocellar triangle weakly shining black; both Vt's on dark ground; first antennal article reddish; second and third antennal articles black; mesonotum, scutellum and pleura mat black; legs black, only distal tips of femora yellow; squamae yellow, fringe light brown; halteres yellow.

Derivation of the specific name. — The name nearctica indicates that the known member of this species is from the Nearctic.

Geographical distribution. — This species is known from a single male from the following locality:

*Agromyza nigripes* Meigen


**Comparison and diagnostic characters.** — The members of this species resemble closely those of *A. albipennis* Meigen and are separated reliably by examination of the characters of male genitalia. Spencer (1969) illustrated the aedeagus characteristic of this species.

**Biology.** — In Europe the larvae are known to mine the leaves of various genera belonging to the tribes Glycerieae, Aveneae and Agrostaeae of the family Gramineae (Griffiths, 1963).

**Geographical distribution.** — The members of this species are known from Europe and Canada (Spencer, 1969). From Alberta, Canada they are known from the following localities:


*Agromyza populoides* Spencer

*Agromyza populoides* Spencer 1969:52.

**Diagnostic characters.** — The members of this species are very distinctive in having pale squamal fringe, characteristic aedeagus (Spencer, 1969, Fig. 53) and biology.

**Biology.** — Larvae make large black blotch mines on *Populus* spp., family Salicaceae.

**Geographical distribution.** — Known from United States, and Alberta, Ontario, Quebec and Saskatchewan in Canada. I have examined the following material from Alberta:

CANADA. Alberta: Paratype 1 ♂ Edmonton, University of Alberta campus, near Aberhart Hospital, 1.vi.1966; 1 ♂ Edmonton, White Mud Creek park, from leaf mines on *Populus tremuloides* Michx., coll. 4.ix.1968, emerged 15.iii.1969; 1 ♀ same data, emerged 3.vi.1969.

*Agromyza pseudoreptans* Nowakowski


*Agromyza reptans*; Frick, 1952:373 (not Fallén 1823a).

**Diagnostic characters.** — The members of this species had previously been confused with *reptans* Fallén, but possess very distinct male genitalia. Nowakowski (1964) illustrated the distinctive male genitalia of a specimen of this species under the name *urticae* Nowakowski. Frick (1952) also illustrated the characteristics of this species under the name *reptans*.

**Biology.** — Larvae make irregular blotch mines on the leaves of *Urtica* spp., family Urticaceae.

**Geographical distribution.** — Known from Europe, Japan, United States and Canada (Spencer, 1969). I have examined the following material from Alberta:

CANADA. Alberta: 1 ♀ Blairmore, 4.ix.1966, det. K. A. Spencer

*Agromyza spiraeae* Kaltenbach


**Comparisons and diagnostic characters.** — The diagnostic characters of the members of this species are: frons mat black, not projected in front of eye margin in profile; mesonotum and scutellum weakly shining black; wing length approximately 2.4 mm; costa extended to vein M1+2; Spencer (1969) figured the distinctive aedeagus.

The adults resemble those of *A. vockerothi* Spencer and *A. masculina* Sehgal and are separated by characteristics of male genitalia. The description of *A. spiraeae* Kaltenbach
from Japan indicates a probable further species because of slight differences in the structure of distiphallus as figured by Sasakawa (1961).

**Biology.** — Larvae mine leaves of various members of the subfamily Rosoideae, family Rosaceae (Hering, 1954).

**Geographical distribution.** — The members of this species are widespread in North America and Central Europe (Hering, 1954; Spencer, 1969). I have examined the following material from Alberta:


*Agromyza sulfuriceps* Strobl

*Agromyza sulfuriceps* Strobl 1898:270; Spencer, 1969:58.

**Diagnostic characters.** — The members of this species are small flies, wing length approximately 2.4 mm (Spencer, 1969). The main distinguishing characters are: antennae yellow, frons yellowish below and darker above, orbits black; mesonotum mat grey, legs black, costa extended to vein M₁+₂, wing tip near apex of vein M₁+₂; aedeagus as illustrated by Spencer (1969).

**Biology.** — Larvae mine leaves of various members of the family Rosaceae in Europe and United States.

**Geographical distribution.** — The members of this species are Holarctic in distribution and are known from North America, Europe and Mongolia (Spencer, 1969). From Alberta, Canada they are known from the following locality:

CANADA. Alberta: Wabamun (Spencer, 1969).

*Agromyza vockerothi* Spencer

*Agromyza vockerothi* Spencer 1969:60.

**Comparison and diagnostic characters.** — The members of this species resemble those in the *spiraeae* group and differ only in having a mid-tibial bristle. The examination of male genitalia is necessary for correct identification. Spencer (1969) illustrated the aedeagus, characteristic of this species.

**Geographical distribution.** — Known from Alberta, British Columbia, Ontario and Nova Scotia (Spencer, 1969). I have examined the following material from Alberta:


**Genus Melanagromyza** Hendel

*Melanagromyza* Hendel 1920:126.

The distinguishing characters of the genus *Melanagromyza* Hendel are: subcosta developed throughout its length and coalesced with R₁ before contact with costa; normally two to three pairs of dorsocentals, four only in *setifrons* (Melander); halteres black; prescutellars lacking; antennal bases approximate; conspicuous facial keel lacking; aedeagus with basiphallus U-shaped; posterior puparial spiracles normally with black horn or scar in centre.

This genus is represented in Alberta by nine species. Three new species are described in this treatment. The members of this genus are mostly stem borers as shown by the known life histories of four Albertan species: *achilleana* n. sp. and *bidenticola* n. sp. feed on Compositae; *martini* Spencer on Urticaceae, and *actaeae* n. sp. on Ranunculaceae. Three further males tentatively discussed here as *Melanagromyza* sp. might represent a new species. But as the males of a closely related species *actaeae* n. sp. have not been bred these specimens
cannot be definitely determined for the time being.

**Key to Alberta species of the genus Melanagromyzia Hendel**

1(0). Squamal fringe pale or white ............................................. 2
   - Squamal fringe dark, black or brown ..................................... 5
2(1). Orbits distinctly projected above eyes in profile .................... 3
   - Orbits not significantly projected above eyes in profile .......... 4
3(2). Posterior puparial spiracles widely separated, each with approximately 30 bulbs; larva stem borer in Actaea .................................... *actaeae* n. sp., p. 305
   - Posterior puparial spiracles approximate, each with 15-18 bulbs; larva stem borer in *Urtica* .................................................. *martini* Spencer, p. 308
4(2). Orbits about one-fourth width of frons, not projected above eyes in profile; orbital setulae numerous, in three irregular rows; aedeagus as in Fig. 27 ... *bidenticola* n. sp., p. 306
   - Orbits about one-fifth width of frons, slightly projected above eyes in profile; orbital setulae fewer, in two rows; aedeagus as in Fig. 14 .... *achilleana* n. sp., p. 304
5(1). Dorsocentrals 3 or 4; larger specimens, wing length 3.2 mm ........ 6
   - Dorsocentrals 2, at most 3; smaller specimens ......................... 6
6(5). Frons strongly projected .................................................. 7
   - Frons not significantly projected .......................................... 8
7(6). Abdomen greenish, broad, low keel separating base of antennae ........ 8
   - Abdomen black, facial keel normal ..................................... 8
8(7). Orbits and ocellar triangle distinctly shining black ................. 9
   - Orbits and ocellar triangle not shining black ......................... 9

**Melanagromyzia achilleana** new species

**Comparisons.** — The members of this species differ from those of similar species, *M. matricarioides* Spencer, in having proclinate orbital setulae and distinct male genitalia (Fig. 14). *M. achilleana* and *M. bidenticola* n. sp. described below are distinguished in Spencer’s (1969) key to Canadian species of the genus *Melanagromyzia* Hendel by amending and extending the couplet 8 as below:

| 8. Orbits conspicuously broad, each almost one-third width of frons | 9 |
| - Orbits narrower, at most one-quarter width of frons | 8a |
| 8a. Orbital setulae proclinate, with few reclinate hairs below | 8b |
| - Orbital setulae erect or reclinate, not proclinate above | 10 |
| 8b. Orbits about one-quarter width of frons, not projected above eyes in profile; orbital setulae numerous, in three irregular rows; aedeagus as in Fig. 27 ... *bidenticola* n. sp. | |
| - Orbits about one-fifth width of frons, slightly projected above eyes in profile; orbital setulae fewer, in two rows; aedeagus as in Fig. 14 .... *achilleana* n. sp. | |

**Description.** — Head (Fig. 13). Frons slightly broader than width of eye (1.0 : 0.9) at level of front ocellus, slightly projected above eye margin in profile; orbits broad, approximately one-fifth of frons width; ocellar triangle small; lunule almost semicircular above; eyes oval approximately 1.3 times higher than their length, hairy; gena deepest at middle, approximately one-fifth of eye height; two strong *Ori* directed upwards; two *Ori* directed inwards; distance between *Ori* approximately three times distance between upper *Ori* and lower *Ori*; orbital setulae numerous, in two irregular rows, largely proclinate, with few reclinate hairs
Mesonotum. Two strong postsutural dc; acr numerous, in 10-11 irregular rows.

Leg. Mid-tibia with two strong bristles medially.

Wing. Length 2.2 mm in ♂♂, 2.6 mm in ♀♀; costa extended strongly to vein M₁+2; wing tip nearest to apex of vein R₄+₅; crossvein r-m beyond middle of discal cell; distal section of M₃+₄ approximately 0.7 times basal section.

Male genitalia (Fig. 14-17). Hyandrium (Fig. 16) with distinct apodeme, side arms and pregonites broad; surstyli (Fig. 17) with group of conspicuous spines anteriorly; aedeagus (Fig. 14) with basiphallus U-shaped and close to distiphallus complex; ejaculatory apodeme (Fig. 15) broad, bulb small and well sclerotized.

Colour. Frons mat black; orbits and ocellar triangle weakly shining black; antennae black; mesonotum, scutellum and abdomen shining black with greenish lustre; halteres and legs black; squamal fringe and margin pale or white.

Description of immature stages. — Puparium creamish yellow, elongate and cylindrical in shape, measures 3.0 x 1.3 mm.

Larval mouth parts obtained from puparium are illustrated (Fig. 18). Mandibles sickle-shaped, left larger than right, each with large apical and small second tooth; short U-shaped sclerite present above mandibles; lateral sclerites at base of mandibles well developed; labial sclerite short and darkly sclerotized; paraclypeal phragmata approximately 2.5 times length of labial sclerite, weakly sclerotized.

Muscle scars on abdominal segments elongate anteroposteriorly; tubercles small and scattered.

Anterior spiracles (Fig. 19) short, with eight small bulbs arranged in two rows; posterior spiracles (Fig. 20) widely separated, with almost complete circlet of 10-11 bulbs; small black horn present in centre of posterior spiracles.

Derivation of the specific name. — This species is named after the genus of its larval food plant, Achillea sibirica Ledeb.

Biology. — Larva feed inside the stem of Achillea sibirica Ledeb., family Compositae. Pupation occurs inside the stem during August-September.

Geographical distribution. — The members of this species are known only from type locality:

CANADA. Alberta: Holotype ♂ Elk Island park, from stems of Achillea sibirica Ledeb., emerged 12.viii.1967; Paratypes 2 ♀♀ same data.

Melanagromyza actaeae new species

Comparisons. — The members of this species resemble those of M. martini Spencer in external morphology, but have distinct biology and larval morphology. This species is distinguished in Spencer's (1969) key to Canadian species of the genus Melanagromyza Hendel by amending and extending couplet 6 as below:

6. Orbits shining black, very strongly projected; large species, wing length 3.4 mm in male ........................................... miranda Spencer
- Orbits weakly shining; smaller species, wing length 2.5-3.0 mm .......................... 6a
6a. Posterior puparial spiracles widely separated, each with approximately 30 bulbs; larva stem borer in Actaea ................................................... actaeae n. sp.
- Posterior puparial spiracles approximate, each with 15-18 bulbs; larva stem borer in Urtica ................................................... martini Spencer

Description. — Head (Fig. 21). Frons broad, approximately twice width of eye at level of
front ocellus, distinctly projected in front of eye margin in profile; orbits narrow, each about one-sixth of frons width; ocellar triangle small; lunule higher than semicircle along upper margin; eyes oval, approximately 1.2 times higher than their length, almost bare or with very fine pubescence; gena deepest at middle, approximately one-fourth eye height; two Ors directed upwards; 3 Ori directed inwards; distance between lower and middle Ori about three times distance between middle and upper Ori; orbital setulae numerous, in two to three rows, erect or reclinate below and proclinate above; antennal bases approximate; third antennal article rounded at tip.

Mesonotum. Two distinct postsutural dc; acr numerous, in 10-12 irregular rows.

Leg. Mid-tibia with one or two small bristles medially.

Wing. Length 3.0 mm in ⇑⇓, costa extended to vein M_{1+2}; apex of vein R_{4+5} nearest wing tip; crossvein r-m slightly beyond middle of discal cell; distal portion of M_{3+4} approximately 0.7 times basal portion.

Colour. Frons mat black, orbits and ocellar triangle weakly shining black; lunule and antennae black; mesonotum, scutellum and abdomen shining black with slight greenish lustre; legs and halteres black; squamal margin and fringe pale or white.

Description of immature stages. — Puparium yellow, elongate and cylindrical in shape, measures 4.0 mm x 1.5 mm.

Larval mouth parts obtained from puparium are illustrated (Fig. 22). Mandibles sickle-shaped, left larger than right, each with large apical and small lower tooth; short U-shaped sclerite present above the mandibles; labial sclerite small and darkly sclerotized; paracyclopelid phragmata approximately 3.0 times labial sclerite, weakly sclerotized.

Muscle scars (Fig. 23) on abdominal segments elongate anteroposteriorly; tubercles small and scattered.

Anterior spiracles (Fig. 24) short with 16 small bulbs arranged in two rows; posterior spiracles (Fig. 25) widely separated, each with approximately 30 small scattered bulbs, distinct horn present in the centre of each spiracle.

Derivation of the specific name. — This species is named after the genus of its larval food plant.

Biology. — The larvae feed inside the stems of *Actaea rubra* (Ait.) Willd, family Ranunculaceae. The host plant, commonly known as Red and White Baneberry, is fairly common in moist places in forests near Edmonton. This is the first *Melanagromyza* species to be recorded whose members feed on plants of the family Ranunculaceae.

Geographical distribution. — Known only from the locality of type specimens as below:

CANADA. Alberta: Holotype ⇑ Edmonton, White Mud Creek park, from stems of *Actaea rubra* (Ait.) Willd., coll. 4.ix.1968, emerged 27.x.1968; Paratypes 3 ⇑⇑ same data, coll. 4-6.ix.1968, emerged 18-23.x.1968. One paratype female presented to K. A. Spencer.

*Melanagromyza bidenticola* new species

Comparison. — The members of this species differ from those of a similar species *M. virens* (Loew) in having narrower orbits and distinct male genitalia. This species is distinguished in Spencer's (1969) key to Canadian species of the genus *Melanagromyza* Hendel as shown earlier at the beginning of the description of *M. achilleana* n. sp.

Description. — Head (Fig. 26). Frons slightly broader than width of eye (1 : 0.9) at level of front ocellus, not projected in front of eye margin in profile; orbits broad, approximately one-fourth of frons width; ocellar triangle small; lunule higher than semicircle along upper margin; eyes oval, approximately 1.2 times higher than their length, hairy; gena deepest at middle, approximately one-seventh of eye height; two strong Ors directed upwards; two Ori
directed inwards; orbital setulae numerous, in about three irregular rows, largely proclinate, with erect or reclinate hairs below; antennal bases approximate; third antennal article rounded at tip, arista pubescent.

Mesonotum. Two strong poststural dc; acr numerous, in 12-15 irregular rows. Leg. Mid-tibia with two strong bristles medially.

Wing. Length 2.5-2.8 mm; costa extended to vein M₁+₂; wing tip near the apex of vein R₄₊₅; crossvein r-m slightly beyond middle of discal cell; distal portion of M₃₊₄ approximately 0.7 times basal portion.

Male genitalia (Fig. 27, 28). Hypandrium (Fig. 28) with short, broad apodeme, side arms and pregonites broad; surstyli with small spines at base; aedeagus (Fig. 27) with basiphallus U-shaped and close to distiphallus complex; distiphallus as illustrated, ejaculatory apodeme broad, bulb small and well sclerotized.

Colour. Frons and orbits mat black; ocellar triangle weakly shining black; lunule and antennae black; mesonotum, scutellum and abdomen shining black with distinct greenish and coppery lustre; halteres and legs black; squamal margin and fringe pale or white.

Description of immature stages. — Puparium pale yellow, elongate and cylindrical in shape, measures 3.4 mm x 1.3 mm.

Larval mouth parts obtained from puparium are illustrated (Fig. 29). Mandibles sickleshaped, left larger than right, each with large apical and small lower tooth; short U-shaped sclerite present above mandibles; labial sclerite short and more darkly sclerotized along lower margins; paracylpeal phragmata approximately 3.0 times length of labial sclerite, weakly sclerotized.

Muscle scars on abdominal segments elongate anteroposteriorly; tubercles small and scattered.

Anterior spiracles (Fig. 30) short with about 10-11 bulbs arranged in two rows; posterior spiracles (Fig. 31) widely separated, each with almost complete circket of 15-17 small bulbs, small distinct horn present in centre of each spiracle.

Derivation of the specific name. — This species is named after the genus of its larval food plant.

Biology. — Larvae feed and pupate inside the stems of Bidens cernua L., family Compositae. Puparia are found inside the stems during August-September. Puparia remain inside the stems during winter and the flies emerge towards the end of June. Specimens of Bidens cernua L. are fairly abundant around Edmonton along stream banks.

Geographical distribution. — The members of this species are known only from the type locality:


Melanagromyza fastosa Spencer


Comparison and diagnostic characters. — The members of this species differ from those of a similar species, laetifica Spencer, in having shining black orbits and ocellar triangle and deep gena, about one-fourth to two-fifths eye height. Spencer (1969) has figured the distinctive aedeagus.

Geographical distribution. — Known only from Alberta and Quebec. Known Alberta locality is as follows:
Melanagromyza laetifica Spencer

Melanagromyza laetifica Spencer, 1969:68.

Diagnostic characters. — The main diagnostic characters of the members of this species are: strongly projected frons, dark squamal fringe and abdomen. Spencer (1969) has illustrated the aedeagus characteristic of this species.

Geographical distribution. — The members of this species are known only from Alberta and Manitoba in Canada (Spencer, 1969). Alberta localities are:

CANADA. Alberta: Manyberries, Mountain View.

Melanagromyza martini Spencer

Melanagromyza martini Spencer, 1969: 70.

Comparison and diagnostic characters. — The members of this species resemble those of M. actaeae n. sp. but have different biology and larval morphology as shown in the key. Spencer (1969) illustrated the aedeagus characteristic of this species.

Biology. — Larvae feed inside the stems of Urtica, family Urticaceae.

Geographical distribution. — The members of this species are known from Alberta, British Columbia, Ontario and Saskatchewan in Canada (Spencer, 1969). I have examined the following material from Alberta:

CANADA. Alberta: Paratype 1 ♂ Blairmore, 26.vi.1966; 1 ♀ same data; 1 ♂ and 1 ♀ Edmonton, Rainbow Valley, from stems of Urtica gracilis Ait. (Urticaceae), emerged 24.iii.1968; 1 ♀ Edmonton, White Mud Creek park, 23.vi.1966; Paratype 1 ♂ George Lake, near Busby, 1.vii.1966; 2 ♀♀ same locality, 1-5.vii.1966.

Melanagromyza occidentalis Spencer

Melanagromyza occidentalis Spencer, 1969:73.

Diagnostic characters. — The main distinguishing characters of the members of this species are dark squamal fringe, frons normally not projected, mat black mesonotum and greenish abdomen. Spencer (1969) illustrated the aedeagus characteristic of this species.

Geographical distribution. — The members of this species are known from Alberta, British Columbia and Saskatchewan in Canada (Spencer, 1969). The Alberta localities are:

CANADA. Alberta: Banff, Elkwater and Jasper

Melanagromyza setifrons (Melander)

Agromyza setifrons Melander, 1913:260.

Melanagromyza setifrons (Melander) Frick, 1959:366; Spencer, 1969:75.

Diagnostic characters. — The main distinguishing characters of the members of this species are dark squamal fringe and three or four dorsocentrales. Spencer (1969) illustrated the aedeagus characteristic of this species.

Geographical distribution. — The members of this species are known from United States, and Alberta and British Columbia in Canada. The Alberta locality is as below:

CANADA. Alberta: Blairmore (Spencer, 1969).
Melanagromyza shewelli Spencer

Melanagromyza shewelli Spencer, 1969:75.

Diagnostic characters. — The main distinguishing characters of the members of this species are: dark squamal fringe, distinctly projected orbits, facial keel and deep gena. Spencer (1969) illustrated the aedeagus characteristic of this species.

Geographical distribution. — The members of this species are known from Alberta and British Columbia in Canada (Spencer, 1969). The Alberta localities are:

CANADA. Alberta: Frank and Mountain View.

Melanagromyza sp.?

Comparisons and diagnostic characters. — The males resemble externally those of *M. actaeae* n. sp., but as the males of the latter species have not been bred, these males cannot be definitely associated. The aedeagus (Fig. 32) has a characteristic gap between basiphallus and distiphallus. Such a gap is also characteristic of *Melanagromyza* sp. (Steyskal) (Spencer, 1969) and *M. angelicae* (Frost), but the adults differ from them in having narrower orbits and smaller size. The wing length in male is about 2.5 mm.

Geographical distribution. — I examined three males from the following localities:

CANADA. Alberta: 1 ♂ Edmonton, Emily Murphy park, 11.vi.1968; 2 ♂♂ George Lake, near Busby, 22.v.1968.

Genus Hexomyza Enderlein

Hexomyza Enderlein, 1936:182.

The members of this small genus are similar to those of the genus *Melanagromyza* Hendel in external morphology. Hendel (1931) included all known species in the genus *Melanagromyza* Hendel. Frick (1952) combined the members of the genus *Hexomyza* Enderlein with those of the large genus *Melanagromyza* Hendel. Later Spencer (1966a) in view of distinct male genitalia and larval biology resurrected this genus to include gall causing species.

Of the two species known in Canada only one, *H. schineri* (Giraud), has been confirmed in Alberta. The other species, *H. albicula* Spencer, gall producer on *Salix* twigs, probably also occurs in Alberta.

Hexomyza schineri (Giraud)

Agromyza schineri Giraud, 1861:484.


Hexomyza schineri (Giraud), Spencer, 1966a:42, 1969:81.

Comparison and diagnostic characters. — The members of this species differ from those of *H. albicula* Spencer in having costa extended to apex of vein M₁, ₂, and distinct male genitalia. Spencer (1969) illustrated the aedeagus characteristic of this species.

Biology. — Larvae produce twig galls on *Populus tremuloides* Michx., family Salicaceae.

Geographical distribution. — The members of this species are known from Western Europe, U. S. A. and Canada (Spencer, 1969). I examined the following material from Alberta:

Genus *Ophiomyia* Braschnikov

*Agromyza* Fallén, subgenus *Ophiomyia* Braschnikov, 1897:40.


The main distinguishing characters of the genus *Ophiomyia* Braschnikov are: subcosta developed throughout its length and coalesced with *R*₁ before contact with costa; two to three pairs of dorsocentrales; halteres black; prescutellars lacking; antennal bases usually separated by distinct, bulbous facial keel; aedeagus with basiphallus elongate, with two distinct side arms.

The species in this genus are extremely difficult to separate on the basis of external morphology alone. Recent examination of characters of the male genitalia of most of North American species (Spencer, 1969) has greatly facilitated the identification of closely related species. The species in the *pulicaria* group, *decima* Spencer, *pulicaria* (Meigen) and *pulicarioides* Sehgal, resemble externally those in the genus *Melanagromyza* Hendel, but possess aedeagus typical of the genus *Ophiomyia* Braschnikov. Spencer (1964c) transferred species in the *pulicaria* group from the genus *Melanagromyza* Hendel to the genus *Ophiomyia* Braschnikov due to similarities in the characters of the male genitalia.

The genus is represented in Alberta by 17 species. The members of this genus usually mine below the stem epidermis of various herbaceous plants, but a few mine the tissue in the leaf. Biology of most species in Alberta remains to be determined as information is available about host-plants of only four species.

**Key to Alberta species of the genus *Ophiomyia* Braschnikov**

1(0). Antennal bases separated by distinct, swollen facial keel or male with vibrissal horn or both

- Antennal bases not separated by distinct keel; vibrissa normal; aedeagus with basiphallus elongate, with two distinct side arms

2(1). Peristomial hairs long, conspicuous .................. *decima* Spencer, p. 311
- Peristomial hairs normal

3(2). Aedeagus as in Fig. 35 .......................... *pulicaria* (Meigen), p. 314
- Aedeagus as illustrated (Fig. 12, Sehgal, 1968) .................. *pulicarioides* Sehgal, p. 314

4(1). Orbital setulae proclinate, upper orbital bristles lacking in male; three pairs of posttural dorsocentrales

- Orbital setulae reclinate

5(4). Costa extended to apex of vein *R₄,₅*, male without vibrissal fasciculus

- Costa extended to apex of vein *M₁,₂*, male with vibrissal fasciculus

6(5). Squamae pale, margin slightly darker, facial keel narrow

- Squamae darker grey, margin dark brown; facial keel broader

7(5). Vibrissal angle at most 60°

- Vibrissal angle between 70° and 90°

8(7). Gena deep, one-fourth to one-third eye height

- Gena narrower, one-tenth to one-sixth eye height

9(8). Vibrissal fasciculus broad at base incompletely fused .................................. *praecisa* Spencer, p. 313
- Vibrissal fasciculus long and compact .......................... *stricklandi* n. sp., p. 315

10(8). Large specimens, wing length 2.5 mm; aedeagus as illustrated by Spencer (1969) .......................... *secunda* Spencer, p. 314
- Smaller specimens, wing length 2.2 mm or less

310
11(10). Squamal fringe brownish, last and penultimate segments of M₃,₄ equal ................................................. undecima Spencer, p. 315
- Squamal fringe black ......................................................................................................................... 12
12(11). Facial keel broad, aedeagus as illustrated by Spencer (1969) ......................................................... 12
  - Facial keel narrow, aedeagus as illustrated by Spencer (1969) ......................................................... 12
13(7). Frons conspicuously projected above eyes in profile, gena deep approximately one-third eye height, 3 Ori. .......................................................... sexta Spencer, p. 314
  - Frons not projected, gena narrower at most one-fifth eye height, 2 Ori .......................... 14
14(13). Gena one-fifth eye height, vibrissal fasciculus with distinct curvature at end ................................................... labiatarum Hering, p. 311
  - Gena narrower one-sixth to one-eight eye height ........................................................................... 15
15(14). Facial keel conspicuously raised below antennae, broader, aedeagus as in Fig. 34 ............................ maura (Meigen), p. 312
  - Facial keel narrower ......................................................................................................................... 16
16(15). Mesonotum mat greyish ................................................................................................................. wabamunensis Spencer, p. 316
  - Mesonotum shining black .................................................................................................................. prima Spencer, p. 313

_Ophiomyia banffensis_ Spencer


_Comparison and diagnostic characters._ — The members of this species resemble closely those of _O. monticola_ Sehgal, but differ in having narrower facial keel, pale squamae and distinctive aedeagus. Spencer (1969) illustrated the aedeagus characteristic of this species.

_Geographical distribution._ — The members of this species are known only from the locality of the type specimens as follows:

CANADA. Alberta: Banff (Spencer, 1969).

_Ophiomyia decima_ Spencer

_Ophiomyia decima_ Spencer, 1969: 85.

_Comparison and diagnostic characters._ — The members of this species resemble those in the _pulicaria_ group in lacking a distinct vibrissa in male and distinct facial keel. The facial keel is only weakly developed. The main distinguishing characters are the conspicuous peristomal hairs and distinctive aedeagus. Spencer (1969) illustrated the distinctive aedeagus.

_Geographical distribution._ — The members of this species are known only from the type locality:

CANADA. Alberta: Cypress Hills (Spencer, 1969).

_Ophiomyia labiatarum_ Hering


_Diagnostic characters._ — The main distinguishing characters of the members of this species are dark squamal fringe, broad gena, reclinate orbital setulae and a distinct curvature in the vibrissal fasciculus. Spencer (1969) illustrated the aedeagus characteristic of this species.

_Biology._ — Not confirmed in Alberta, but larvae are known to mine below the stem epidermis of various genera of Labiatae in Europe and United States (Spencer, 1969).

_Geographical distribution._ — Members of this species are known in Europe, United States and Alberta, Ontario and Quebec in Canada (Spencer, 1969). The Alberta localities are:
CANADA. Alberta: Edmonton, White Mud Creek park; Elk Island park; George Lake near Busby; Wabamun Lake near Sundance.

Two additional Alberta specimens listed below are only provisionally referred here as they are not separable externally, but the aedeagus (Fig. 33) has slight differences in the shape of the distiphallus.


Ophiomyia maura (Meigen)

Agromyza maura Meigen, 1838:399

Comparison and diagnostic characters. — The adults of this species differ from those of a similar species, O. labiatarum Hering, having narrower gena and distinct aedeagus. The aedeagus of this species (Fig. 34) resembles that of O. asterivora Spencer and differs only in very minor details as the central circular area and deeper concavity on dorsal side. O. asterivora Spencer has a different larval mine. Sasakawa (1961) illustrated this species in detail. Spencer (1964c, 1969) also discussed this species and illustrated the aedeagus.

Biology. — The larvae make long, narrow linear mines with widely spaced frass granules on Aster and Solidago, family Compositae. Sasakawa (1961) illustrated the characteristic leaf mine.

Geographical distribution. — The members of this species are Holarctic in distribution, known from Japan (Sasakawa, 1961), Europe, North America and Canada (Spencer, 1964c, 1969). I have examined the following material from Alberta:

CANADA. Alberta: 1 ♂ Edmonton, White Mud Creek park, 16.vii.1966; Leaf mines on Solidago around Edmonton, ix.1968.

Ophiomyia monticola Sehgal

Ophiomyia monticola Sehgal, 1968:60.

Comparison and diagnostic characters. — The members of this species differ from those of a closely related species, O. banffensis Spencer, in having darker squamae and broad facial keel. Sehgal (1968) illustrated the head, wing and male genitalia characteristic of this species. Spencer (1969) also illustrated the aedeagus.

Geographical distribution. — Members of this species are known from numerous localities in western Canada and also from Alaska (Sehgal, 1968). The Alberta localities are:

CANADA. Alberta: Banff; Cypress Hills, Elkwater; Jasper.

Ophiomyia nasuta (Melander)

Agromyza maura var. nasuta Melander, 1913:260.
Agromyza youngi Malloch, 1914a:312.
Ophiomyia madizina Hendel, 1920:130.
Tylomyza madizina (Hendel); Hendel, 1931:185; Frick, 1952:385; Sasakawa, 1961:359.
Siridomyza madizina (Hendel); Enderlein, 1936:179.
Tylomyza nasuta (Melander); Frick, 1957:201, 1959:372.
Ophiomyia nasuta (Melander); Spencer, 1964c:798.

Comparison and diagnostic characters. — The members of this species differ from those of a closely related Palaearctic species, O. pinguis (Fallén), by having three dorsocentrals
and absence of upper orbital bristles in male. The procline orbital setulae are numerous in males, few in females. Frick (1959) illustrated the characteristic head and wing of this species as *Tylomyza nasuta* (Melander). Sasakawa (1961) illustrated this species as *Tylomyza madizina* (Hendel). Spencer (1964c, 1969) illustrated the aedeagus characteristic of this species.

**Biology.** — Not confirmed in Alberta, but larvae are known to mine the leaves of *Taraxacum officinale* Weber, family Compositae, in United States (Frick, 1959).

**Geographical distribution.** — The members of this species are Holarctic in distribution and are known from numerous localities in Europe (Spencer, 1964c), Japan (Sasakawa, 1961), North America (Frick, 1959) and Canada (Spencer, 1969). I examined the following material from Alberta:


**Ophiomyia none** Spencer

*Ophiomyia none* Spencer, 1969:92.

**Diagnostic characters.** — The main distinguishing characters of the members of this species are acute vibrissal fasciculus, narrow gena, dark squamal fringe and broad facial keel. Spencer (1969) illustrated the aedeagus characteristic of this species.

**Geographical distribution.** — The members of this species are known only from the type locality:

**CANADA. Alberta:** Cypress Hills, Elkwater (Spencer, 1969).

**Ophiomyia praecisa** Spencer

*Ophiomyia praecisa* Spencer, 1969:92.

**Comparison and diagnostic characters.** — The members of this species belong to the group having acute vibrassal angle and deeper gena. They differ from those of a similar species, *O. stricklandi* n. sp., in having broad and incompletely fused vibrissal fasciculus. Spencer (1969) illustrated the aedeagus characteristic of this species.

**Geographical distribution.** — The members of this species are known from the localities of their type specimens as below:

**CANADA. Alberta:** Banff-Jasper Highway, 13 miles North of Banff; Cypress Hills, Elkwater.

**Ophiomyia prima** Spencer

*Ophiomyia prima* Spencer, 1969:93.

**Diagnostic characters.** — The main distinguishing characters of the members of this species are the vibrissal angle of about 80°, frons not projected, narrow facial keel and shining black mesonotum. Spencer (1969) illustrated the aedeagus characteristic of this species.

**Geographical distribution** — The members of this species are known only from the type locality:

**CANADA. Alberta:** Elk Island park (Spencer, 1969).
Ophiomyia pulicaria (Meigen)

Agromyza pulicaria Meigen, 1830:170.
Melanagromyza pulicaria (Meigen); Hendel, 1920:127, 1931:171.
Ophiomyia pulicaria (Meigen); Spencer, 1964c:802, 1969:93.

Comparisons and diagnostic characters. — The members of this species resemble externally those of O. decima Spencer and O. pulicarioides Sehgal, and are reliably separated only by characteristics of male genitalia. The aedeagus of an Alberta specimen has been illustrated (Fig. 35). Spencer (1969) also illustrated the aedeagus.

Biology. — Not confirmed in Alberta, but larvae are known to mine along the leaf midrib of various Compositae in Europe (Spencer, 1969).

Geographical distribution. — The members of this species are widespread in Europe and are known from Alberta and British Columbia in Canada (Spencer, 1969). I examined the following further material from Alberta:


Ophiomyia pulicarioides Sehgal


Comparisons and diagnostic characters. — The members of this species resemble externally those of O. decima Spencer and O. pulicaria (Meigen), and are separated reliably only by examination of the characters of the male genitalia. Sehgal (1968) illustrated the head, wing and male genitalia. Spencer (1969) also figured the aedeagus.

Geographical distribution. — The members of this species are known only from the type locality:


Ophiomyia secunda Spencer

Ophiomyia secunda Spencer, 1969:96.

Comparison and diagnostic characters. — The members of this species differ from those of a closely related species, O. septima Spencer, in having larger size, wing length 2.5 mm, and distinct aedeagus. Spencer (1969) illustrated the aedeagus characteristic of this species.

Geographical distribution. — The members of this species are known from type locality:

CANADA. Alberta: Elk Island park (Spencer, 1969).

Ophiomyia septima Spencer

Ophiomyia septima Spencer, 1969:96.

Diagnostic characters. — The main distinguishing characters of the members of this species are acute vibrissal angle of about 45°, narrow gena, wing length about 1.9 mm and narrow facial keel. Spencer (1969) illustrated the aedeagus characteristic of this species.

Geographical distribution. — The members of this species are known from Alberta and Ontario in Canada. The Alberta locality is:

CANADA. Alberta: Jasper (Spencer, 1969).

Ophiomyia sexta Spencer

Ophiomyia sexta Spencer, 1969:98.
**Diagnostic characters.**—The main distinguishing characters of the members of this species are vibrissal angle of about 80°, wing length about 2.3 mm in male, conspicuously projected frons and three lower orbital bristles. Spencer (1969) illustrated the aedeagus characteristic of this species.

**Geographical distribution.**—The members of this species are known from Alberta, North-west Territories, Manitoba and Quebec in Canada (Spencer, 1969). The Alberta locality is: CANADA. Alberta: Cypress Hills (Spencer, 1969).

*Ophiomyia stricklandi* new species

**Comparison.**—The members of this species differ from those of a similar species, *O. praecisa* Spencer, in having long and compact vibrissal fasciculus and distinct aedeagus. They may be included in Spencer’s (1969) key to Canadian species of the genus *Ophiomyia* Braschnikov by extending couplet 10 as below:

10. Lower orbits conspicuously projected above eyes in profile ............... 10a
- Orbits not projected ........................................ 11

10a. Vibrissal fasciculus broad at base, incompletely fused; aedeagus as illustrated (Spencer, 1969) .................................. *praecisa* Spencer

- Vibrissal fasciculus long and compact; aedeagus as in Fig. 37 ... *stricklandi* n. sp.

**Description.**—Head (Fig. 36). Frons approximately 1.5 times width of eye at level of front ocellus; lower orbits strongly projected in front of eye margin in profile; ocellar triangle small; facial keel broad; eyes oval, approximately 1.2 times higher than their length, bare; gena strongly projected anteriorly, approximately one-fourth eye height; vibrissal angle acute; vibrissal fasciculus strong, compact and with normal curvature; two strong Ors directed upwards; two Ori directed inwards and upwards; orbital setulae few, reclinate; third antennal article rounded at tip.

Mesonotum. Two strong postsutural dc; acr numerous, in six rows.

Wing. Length 1.6 mm in male; costa extended strongly to vein $M_{1.2}$; costal segments 2-4 in ratio of 1 : 0.3 : 0.22; wing tip between $R_{4+5}$ and $M_{1+2}$; crossvein r-m beyond middle of discal cell; distal section of $M_{3+4}$ approximately equal to its basal section.

Male genitalia (Fig. 37-39). Hypandrium (Fig. 39) with narrow side arms and short apodeme, darkly sclerotized; surstyli with very small spinules anteriorly; aedeagus (Fig. 37) with basiphallus elongate and more sclerotized towards its base, distiphallus elongate, well sclerotized, with conspicuous bulb below; ejaculatory apodeme (Fig. 38) broad, bulb small and darkly sclerotized.

Colour. Frons mat black; lunule, facial keel and lower orbits dark brown; mesonotum, scutellum and abdomen shining black; legs and halteres black; squamae pale, margin and fringe brown.

**Derivation of the specific name.**—This species is named in honour of the late Professor E. H. Strickland, Department of Entomology, University of Alberta, Edmonton, Canada.

**Geographical distribution.**—I examined one specimen from the following locality: CANADA. Alberta: Holotype $\delta$ Medicine Hat, 8.viii.1939, coll. E. H. Strickland.

*Ophiomyia undecima* Spencer

**Diagnostic characters.**—The main distinguishing characters of the members of this species are acute vibrissal angle of about 60°, narrower gena, wing length about 2.2 mm, last and penultimate sections of $M_{3+4}$ equal and slightly brownish squamal fringe. Spencer (1969)
illustrated the aedeagus characteristic of this species.

**Geographical distribution.** — The members of this species are known from the type locality:

**CANADA.** Alberta: Banff, 20 miles towards Calgary (Spencer, 1969).

**Ophiomyia wabamunensis** Spencer


**Comparisons and diagnostic characters.** — The members of this species differ from those of the similar species, *O. maura* (Meigen) and *O. prima* Spencer, in having mat greyish mesonotum and distinct aedeagus. Spencer (1969) illustrated the distinctive aedeagus.

**Geographical distribution.** — The members of this species are known only from the type locality:

**CANADA.** Alberta: Wabamun Lake (Spencer, 1969).

**Genus Phytobia Lioy**

**Phytobia** Lioy, 1864:1313.

**Dizygomyza (Dendromyza)** Hendel, 1931:22.


**Shizukoa** Sasakawa, 1963:38; Spencer, 1965a:8.

The main distinguishing characters of the members of this genus are: subcost fold-like distally, joined to costa independent of R<sub>1</sub>; orbital setulae erect or reclinate; costa normally extended to apex of vein M<sub>1+2</sub>, if only to R<sub>4+5</sub> (*P. confessa* Spencer) then notopleural areas dark, larger specimens wing length at least 3.0 mm, scutellum dark, concolorous with mesonotum; halteres with knob white or yellow; second crossvein normally present and wing tip near the apex of vein R<sub>4+5</sub>.

Nowakowski (1962) on the basis of his studies on the male genitalia restricted the genus *Phytobia* Lioy to the species placed in the subgenus *Dendromyza* Hendel and in the subgenus *Phytobia* Lioy.

The larvae of various members of this genus bore inside the cambium of many trees. Of the three species known in Alberta information about biology is available of only one, *amelanchieris* (Greene).

**Key to Alberta species of the genus Phytobia Lioy**

1(0). Costa extended to apex of vein R<sub>4+5</sub> .................................. *confessa* Spencer, p. 317

- Costa extended to apex of vein M<sub>1+2</sub> ........................................ 2

2(1). Mesonotum with humeral and notopleural areas partly yellow; four orbital bristles, upper two reclinate ........................................... *flavohumeralis* Sehgal, p. 317

- Sides of thorax black; five or six orbital bristles, only one upper orbital bristle reclinate ........................................... *amelanchieris* (Greene), p. 316

**Phytobia amelanchieris** (Greene)

**Agromyza amelanchieris** Greene, 1917:314.

**Phytobia (Phytobia) amelanchieris** (Greene); Frick, 1952:390, 1959:375.

**Diagnostic characters.** — The main distinguishing characters of the members of this species are mesonotum, scutellum and pleura distinctly mat grey and five or six orbital bristles, only upper one reclinate. Spencer (1969) illustrated the aedeagus characteristic of this species.
Biology. — Not confirmed in Alberta, but larvae are known to mine the cambium of *Amelanchier canadensis* (L.), family Rosaceae (Frick, 1959).

Geographical distribution. — The members of this species are known from United States and British Columbia, Manitoba, Ontario, Quebec and Saskatchewan in Canada (Spencer, 1969). I examined single male from the following locality:

CANADA. Alberta: 1 ♂ Edmonton, White Mud Creek park, 6.v.1969.

*Phytobia confessa* Spencer

*Phytobia confessa* Spencer, 1969:105.

Diagnostic characters. — The main distinguishing characters of the members of this species are costa extended to apex of vein R\textsubscript{4.5}; conspicuously projected frons; shining black gena and orbits; gena deep, about one-third to one-fifth eye height and wing length about 3.3 mm in male. Spencer (1969) illustrated the aedeagus characteristic of this species.

Geographical distribution. — The members of this species are known from Alberta, Manitoba and Saskatchewan in Canada (Spencer, 1969). The Alberta localities are as below:

CANADA. Alberta: Jumping Pond Creek, 20 miles west of Calgary; Medicine Hat.

*Phytobia flavohumeralis* Sehgal


Diagnostic characters. — The main distinguishing characters of the members of this species are yellow ring around humeral areas on mesonotum; mat greyish black mesonotum and four orbital bristles, two upper orbital bristles recline. Sehgal (1968) illustrated the head, wing and male genitalia characteristic of this species. Spencer (1969) also figured the aedeagus.

Geographical distribution. — The members of this species are known from Alberta, British Columbia, Manitoba, Ontario and Saskatchewan in Canada. I examined the following additional material from Alberta:


Genus *Cerodontha* Rondani


This genus was previously restricted to a small group of species having two scutellar bristles and a conspicuous spine on the third antennal segment anterodorsally. Nowakowski (1961) on the basis of his studies of the genitalia discovered marked similarities between the genus *Cerodontha* Rondani *sensu stricto* and Hendel’s subgenera *Dizygomyza*, *Poemyza* and *Icteromyza*. He proposed the enlarged concept for the genus *Cerodontha* Rondani and included above-mentioned subgenera. Spencer (1963, 1969) and other workers in the family Agromyzidae accepted this concept. Nowakowski (1967) in his recent revision of the genus *Cerodontha* Rondani proposed two new subgenera: *Butomomyza* and *Crastemyza*. The characters used to define these subgenera overlap with those in the subgenus *Dizygomyza* Hendel. Spencer (1969) included the species belonging to these subgenera in the subgenus *Dizygomyza* Hendel. The Albertan species falling in Nowakowski’s subgenus *Butomomyza* are *angulata* (Loew), *eucaricus* Nowakowski, *gibbardi* Spencer, *scirpi* (Karl) and in the subgenus *Crastemyza*, *frankensis* Spencer. The above-mentioned species are included here in
the subgenus *Dizygomyza* Hendel, pending further clarification of Nowakowski’s subgenera *Butomomyza* and *Craestemyza*.

The members of this genus feed exclusively on monocotyledons: Gramineae, Cyperaceae, Juncaceae and Iridaceae.

The main distinguishing characters of this genus are: subcosta joined to costa independent of *R*₁; costa normally extended to apex of vein *M₁₂*, if only to *R₄₅* then lunule broad and higher than semicircle (*Cerodontha (Dizygomyza) frankensis* Spencer); vein *M₁₂* usually near wing tip; crossvein *m*m normally present, halteres with knob white or yellow; scutellum dark and concolorous with mesonotum. Either third antennal article with conspicuous spine anterodorsally and scutellum with only two bristles (subgenus *Cerodontha* Rondani); or frons normally yellow and prescutellars absent (subgenus *Icteromyza* Hendel); or lunule broad, in form of semicircle or slightly higher, but still broad, prescutellars usually present, antennal bases widely separated, third antennal article normally greatly enlarged in male (subgenus *Dizygomyza* Hendel); or lunule substantially higher than semicircle, but conspicuously narrow (subgenus *Poemyza* Hendel).

This genus is represented in Alberta by 16 species, two in the subgenus *Cerodontha* Rondani, seven in the subgenus *Dizygomyza* Hendel, five in the subgenus *Icteromyza* Hendel and two in the subgenus *Poemyza* Hendel.

### Key to Alberta species of the genus *Cerodontha* Rondani

<table>
<thead>
<tr>
<th>Code</th>
<th>Description</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>1(0)</td>
<td>Third antennal article with conspicuous spine anterodorsally; scutellum with two bristles (subgenus <em>Cerodontha</em> Rondani)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>- Third antennal article without such spine; scutellum with four bristles</td>
<td>2</td>
</tr>
<tr>
<td>2(1)</td>
<td>Scutellum and adjoining mesonotum with variable yellow spot; aedeagus with distiphallus comparatively short, but with elongated apical bulbs (Fig. 18a, Sehgal, 1968)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>- Scutellum and adjoining mesonotum mat black; aedeagus with long distiphallus, with short apical bulbs (Fig. 18a, Sehgal, 1968)</td>
<td></td>
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<tr>
<td>3(1)</td>
<td>Lunule broad, in form of semicircle, or slightly higher but still broad</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>- Lunule conspicuously higher than semicircle (subgenus <em>Poemyza</em> Hendel)</td>
<td>11</td>
</tr>
<tr>
<td>4(3)</td>
<td>Frons normally yellow; prescutellars absent (subgenus <em>Icteromyza</em> Hendel)</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>- Frons normally dark; prescutellars usually present (subgenus <em>Dizygomyza</em> Hendel)</td>
<td></td>
</tr>
<tr>
<td>5(4)</td>
<td>Lunule broad, in form of semicircle; third antennal article in male enlarged</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>- Lunule broad, but conspicuously higher</td>
<td>7</td>
</tr>
<tr>
<td>6(5)</td>
<td>All femora distally yellow; frons not projected; smaller specimens, wing length about 2.2 mm</td>
<td></td>
</tr>
<tr>
<td></td>
<td>- Only fore femora yellow distally; frons at most slightly projected; orbits and lunule yellowish</td>
<td></td>
</tr>
<tr>
<td>7(5)</td>
<td>Costa extended to apex of vein <em>R₄₅</em></td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>- Costa extended to apex of vein <em>M₁₂</em></td>
<td>9</td>
</tr>
<tr>
<td>8(7)</td>
<td>Frons conspicuously projected above eyes</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>- Frons not projected</td>
<td></td>
</tr>
<tr>
<td>9(8)</td>
<td>Squamal fringe dark; lower <em>Ors</em> incurved</td>
<td></td>
</tr>
<tr>
<td></td>
<td>- Squamal fringe yellow; <em>Ors</em> parallel or lower one directed slightly outwards</td>
<td></td>
</tr>
<tr>
<td>10(9)</td>
<td>Ors parallel; wing length 2.4-3.0 mm; aedeagus with distiphallus short and less sinuate</td>
<td></td>
</tr>
<tr>
<td></td>
<td>- Lower <em>Ors</em> directed slightly outwards; wing length 3.0-3.2 mm; aedeagus with</td>
<td></td>
</tr>
</tbody>
</table>
Subgenus *Dizygomyza* Hendel

*Dizygomyza* Hendel, 1920:130.


This subgenus is represented in Alberta by seven known species. Biology of various species have not been confirmed in Alberta, but some information about host-plants is known for five Albertan species.

*Cerodontha* (*Dizygomyza*) *angulata* (Loew)

*Agromyza angulata* Loew, 1869:47.


*Cerodontha* (*Butomomyza*) *semiposticata* (Hendel), Nowakowski, 1967:634.

*Cerodontha* (*Dizygomyza*) *angulata* (Loew), Spencer, 1969:113.

Comparison and diagnostic characters. – The members of this species differ from those of a closely related species, *eucaricis* Nowakowski, in having upper orbital bristles parallel, and short and less sinuate distiphallus. Spencer (1969) illustrated the aedeagus characteristic of this species.

Biology. – Larvae are known to mine the leaves of *Carex* spp., family Cyperaceae, in Europe. Pupation occurs outside the mine.

Geographical distribution. – The members of this species are known from Europe, United States and Alberta and Ontario in Canada (Spencer, 1969). I examined the following material from Alberta:

CANADA. Alberta: 1 d Végreville, 22.vi.1968.

*Cerodontha* (*Dizygomyza*) *chaixiana* (Groschke)


*Cerodontha* (*Dizygomyza*) *chaixiana* (Hering), Nowakowski, 1967:643.

*Cerodontha* (*Dizygomyza*) *chaixiana* (Groschke), Spencer, 1969:115.

Diagnostic characters. – The main distinguishing characters of the members of this species are the enlarged third antennal articles, yellowish orbits and lunule and distally yellow fore
femora. Spencer (1969) illustrated the aedeagus characteristic of this species. The distiphallus has a characteristic swelling distally.

Biology. — The members of this species are known to mine the leaves of Poa sp., family Gramineae, in Europe. Hering (1956) described the larval morphology.

Geographical distribution. — The members of this species are known from Europe, and Alberta and Ontario in Canada. I examined the following additional material from Alberta:


Cerodontha (Dizygomyza) eucaricis Nowakowski

Cerodontha (Butomomyza) eucaricis Nowakowski, 1967:636.

Cerodontha (Dizygomyza) eucaricis (Nowakowski), Spencer, 1969:116.

Diagnostic characters. — The main distinguishing characters of the members of this species are the larger size, wing length about 3.0 mm; prescutellars present, yellow squamal fringe and lower Ors directed slightly outwards. Spencer (1969) illustrated the aedeagus characteristic of this species.

Biology. — The members of this species are known to mine the leaves of Carex sp., family Cyperaceae, in Europe.

Geographical distribution. — The members of this species are known from Europe, Alaska, and Alberta, Manitoba and Ontario in Canada (Spencer, 1969). The known Alberta locality is as follows:

CANADA. Alberta: Banff (Spencer, 1969).

Cerodontha (Dizygomyza) frankensis Spencer

Cerodontha (Dizygomyza) frankensis Spencer, 1969:119.

Comparison and diagnostic characters. — The members of this species are distinctive in having costa extended to apex of vein R4.5. They resemble externally those of C. (Dizygomyza) flavocingulata (Strobl), but differ in having darker squamal fringe. Spencer (1969) illustrated the aedeagus characteristic of this species.

Geographical distribution. — The members of this species are known from Alberta, British Columbia and Yukon Territory in Canada. I examined the following material from Alberta:


Cerodontha (Dizygomyza) gibbardi Spencer

Cerodontha (Dizygomyza) gibbardi Spencer, 1969:119.

Diagnostic characters. — The main distinguishing characters of the members of this species are broad lunule, distinctly higher than semicircle and conspicuously projected frons. Spencer (1969) illustrated the aedeagus and head characteristic of this species.

Geographical distribution. — The members of this species are known from Alberta, British Columbia, Manitoba and Saskatchewan in Canada. The known Alberta locality is as follows:

CANADA. Alberta: Onefour (Spencer, 1969).

Cerodontha (Dizygomyza) scirpi (Karl)

Dizygomyza scirpi Karl, 1926:137.
Cerodontha (Butomomyza) scirpi (Karl), Nowakowski, 1967:638.
Cerodontha (Dizygomyza) scirpi (Karl), Spencer, 1969:123.

**Diagnostic characters.** — The members of this species are distinctive in having incurved lower Ors, and slightly darker squamal fringe. Spencer (1969) illustrated the aedeagus characteristic of this species. There is no membranous gap between meso- and distiphallus.

**Biology.** — Larvae mine the leaves of Scirpus spp., family Cyperaceae, in Europe. Pupation occurs towards the base of the leaf sheath. Similar mines seen around Edmonton probably were made by members of this species.

**Geographical distribution.** — The members of this species are known from Europe, and British Columbia and Quebec in Canada (Spencer, 1969). I examined the following material from Alberta:

CANADA. Alberta: 2 ♂ Edmonton, Rainbow Valley, 14.vi.1968; 3 ♂ Edmonton, White Mud Creek park, 10.vi.1968.

*Cerodontha (Dizygomyza) ultima* Spencer

Cerodontha (Dizygomyza) ultima Spencer, 1969:125.

**Diagnostic characters.** — The members of this species are distinctive in having enlarged third antennal article and all femora distally yellow. Spencer (1969) illustrated the aedeagus characteristic of this species.

**Biology.** — Larvae mine the leaves of family Cyperaceae, Scirpus or Carex sp. (Spencer, 1969).

**Geographical distribution.** — The members of this species are known from Ontario, Canada. I examined the following material from Alberta.


**Subgenus Poemyza** Hendel

*Dizygomyza (Poemyza)* Hendel, 1931:35.

This subgenus is represented in Alberta by five species.

*Cerodontha (Poemyza) calamagrostidis* Nowakowski


**Comparison and diagnostic characters.** — The members of this species can only be reliably separated from those of *C. (Poemyza) muscina* (Meigen) by examination of the characters of male genitalia. Spencer (1969) illustrated the aedeagus characteristic of this species.

**Biology.** — Larvae mine the leaves of Calamagrostis spp., family Gramineae, in Europe.

**Geographical distribution.** — The members of this species are known from Europe, and Alberta in Canada. I examined the following material from Alberta:

CANADA. Alberta: 1 ♂ Edmonton, White Mud Creek park, 23.vi.1966.

*Cerodontha (Poemyza) incisa* (Meigen)

Agromyza incisa Meigen, 1830:182.
Dizygomyza (Poemyza) incisa (Meigen), Hendel, 1931:38.
Phytobia (Poemyza) incisa (Meigen), Frick, 1959:381.

Cerodontha (Poemyza) incisa (Meigen), Nowakowski, 1967:651.

Comparison and diagnostic characters. — The members of this species differ from those of C. (Poemyza) inconspicua (Malloch) in having slightly higher lunule and only fore femora distally yellow. The distiphallus is long and narrow with apical bulb. Spencer (1969) illustrated the aedeagus.

Biology. — Larvae mine the leaves of plants belonging to various genera in the family Gramineae. The known genera from Canada are Agropyron, Phalaris, Phleum and Zizania. Several larvae mine and pupate together inside the leaf.

Geographical distribution. — The members of this species are Holarctic in distribution, being known from Europe, Asia, United States and Canada. I examined the following material from Alberta:


Cerodontha (Poemyza) inconspicua (Malloch)

Agromyza inconspicua Malloch, 1913a:310.
Phytobia (Poemyza) inconspicua (Malloch), Frick, 1959:381.
Cerodontha (Poemyza) inconspicua (Malloch), Spencer, 1969:129.

Diagnostic characters. — The members of this species are distinctive in having all femora yellow on distal tips, both sections of M3.44 almost equal and dark frons and orbits. Spencer (1969) illustrated the distinctive aedeagus. The distal tips of distiphallus are slightly dilated at apex.

Biology. — Larvae mine the leaves of Agropyron, family Gramineae.

Geographical distribution; — The members of this species are known from United States and Canada. I examined the following material from Alberta:


Cerodontha (Poemyza) muscina (Meigen)

Agromyza muscina Meigen, 1830:177.
Dizygomyza (Poemyza) muscina (Meigen), Hendel, 1931:44.
Phytobia (Poemyza) muscina (Meigen), Frick, 1959:382.
Cerodontha (Poemyza) muscina (Meigen), Nowakowski, 1967:649.

Comparison and diagnostic characters. — The members of this species differ from those of a closely related species, C. (Poemyza) calamagrostidis Nowakowski, only in having short
and twisted distiphallus. Spencer (1969) illustrated the distinctive aedeagus.

**Biology.** — Larvae mine leaves of many Gramineae. Known host genera in North America are *Agropyron*, *Ehrharta* and *Hordeum*.

**Geographical distribution.** — The members of this species are known from Europe, United States and Canada. I examined the following material from Alberta:


*Cerodontha (Poemyza) superciliosa* (Zetterstedt)

*Agromyza superciliosa* Zetterstedt, 1860:6455.
*Cerodontha (Poemyza) superciliosa* (Zetterstedt), Nowakowski, 1967:650.
*Cerodontha (Poemyza) lateralis* (Macquart), Spencer, 1969:131.

**Diagnostic characters.** — The members of this species are distinctive in having yellowish frons, orbits and notopleural areas. All femora are also yellow on distal tips.

**Biology.** — Larvae mine the leaves of various Gramineae. Known host genera are *Agropyron*, *Avena*, *Elymus*, *Hordeum*, *Triticum* and *Zea*.

**Geographical distribution.** — The members of this species are Holarctic in distribution, being known from United States, Europe, Japan, Canada and Alaska. I examined the following material from Alberta.


**Subgenus Icteromyza** Hendel

*Dizygomyza (Icteromyza)* Hendel, 1931:51.

This subgenus is represented in Alberta by only two species discussed below.

*Cerodontha (Icteromyza) capitata* (Zetterstedt)

*Agromyza capitata* Zetterstedt, 1848:2750.
*Dizygomyza (Icteromyza) capitata* (Zetterstedt), Hendel, 1931:52.
*Phytobia (Icteromyza) capitata* (Zetterstedt), Frick, 1959:386.
*Cerodontha (Icteromyza) capitata* (Zetterstedt), Nowakowski, 1967:654.

**Diagnostic characters.** — The members of this species are distinctive in having larger size, wing length 2.5-3.5 mm and black palpi. Spencer (1969) illustrated the distinctive aedeagus.

**Biology.** — Larvae feed inside the stems of *Juncus* spp., family *Juncaceae* (Spencer, 1969).

**Geographical distribution.** — The members of this species are known from Europe, United States, Alaska and Canada. Known Alberta localities are:

CANADA. Alberta, Banff, Jasper, Mount Eisenhower, near Banff, Nordegg (Spencer, 1969).
Phytobia (Icteromyza) longipennis (Loew)

Agromyza longipennis Loew, 1869:48; Shewell, 1953:46.
Phytobia (Icteromyza) longipennis (Loew), Frick, 1959:386

Cerodontha (Icteromyza) longipennis (Loew), Spencer, 1969:140.

Diagnostic characters. — The members of this species are distinctive in having yellow palpi, yellow femora distally and bare eyes. Spencer (1969) illustrated the distinctive aedeagus.

Biology. — Larvae mine the leaves of Juncus spp., family Juncaceae in United States.

Geographical distribution. — The members of this species are known from United States and Canada. The Alberta locality is:

CANADA. Alberta: Lethbridge (Spencer, 1969).

Subgenus Cerodontha Rondani

Cerodontha Rondani, 1861:10.

This subgenus is represented in Alberta by two species, dorsalis (Loew) and occidentalis Sehgal. Sehgal (1968) and Spencer (1969) discussed the male genitalia differences between these two species.

Cerodontha (Cerodontha) dorsalis (Loew)

Odontocera dorsalis Loew, 1863:54.
Cerodontha dorsalis (Loew), Melander, 1913:249; Frick, 1959:396.
Cerodontha (Cerodontha) dorsalis (Loew), Spencer, 1969:143.

Comparison and diagnostic characters. — The main distinguishing characters of the members of this species are scutellum and adjoining mesonotum with variable yellow spot and slightly smaller size. The aedeagus (Fig. 18c, Sehgal, 1968) is two-thirds the size of that of a closely related species, occidentalis Sehgal, and has distinctly elongated apical bulbs.

Biology. — Larvae mine the leaf sheaths of grasses (Gramineae).

Geographical distribution. — The members of this species are known from Mongolia, South America, United States and Canada. Material examined is as follows:


Cerodontha (Cerodontha) occidentalis Sehgal

Cerodontha (Cerodontha) occidentalis Sehgal, 1968:64; Spencer, 1969:144.

Comparison and diagnostic characters. — The members of this species can be reliably separated from those of a similar species, dorsalis (Loew), only by examination of the characters of male genitalia. The aedeagus (Fig. 18a, Sehgal, 1968) is about 1.5 times as long as in dorsalis (Loew). The apical bulbs on distiphallus are relatively short.

Three males collected from Banff, Alberta on June 28, 1966, are only tentatively referred here, as these most likely represent a further species. They are not separable externally from those of occidentalis, but the aedeagus (Fig. 40) shows conspicuous differences
in the shape of mesophallus. Since these specimens are collected from the same locality as for \textit{occidentalis}, I prefer not to treat them as distinct species, until the range of variation in the aedeagus is more clearly defined for \textit{occidentalis}.

\textbf{Biology.} — Larvae probably mine the leaves of Gramineae.

\textbf{Geographical distribution.} — The members of this species are known from United States, Alaska and Canada. Known Alberta localities (Sehgal, 1968) are as below:

\textit{CANADA.} Alberta: Canmore, near Banff; Blairmore (Sehgal, 1968).

\textbf{Genus \textit{Calycomyza} Hendel}


The main distinguishing characters of this genus are subcosta joined to costa independent of R\textsubscript{1}; costa extended to apex of vein M\textsubscript{1,2}; vein M\textsubscript{1,2} near wing tip; cross vein m-m present, halteres with knob white or yellow; scutellum dark and concolorous with mesonotum; lunule and antennae normal; orbital setulae erect or reclinate; orbits in same plane as frons; frons yellow; notopleural areas yellow; presutural dorsocentral absent and mid-tibia in some members with a lateral bristle.

The members of this genus are difficult to separate, because of variations in colour characters. Recent studies by Spencer (1969) have indicated constant differences in male genitalia.

This genus is so far represented in Alberta by two species, \textit{menthae} Spencer and \textit{sonchi} Spencer. I am aware of two further species: one mines the leaves of \textit{Solidago} and the other of \textit{Artemisia}. These probably represent \textit{solidaginis} (Kaltenbach) and \textit{artemisiae} (Kaltenbach) respectively, but this would need confirmation by examination of male genitalia.

\textbf{Key to Alberta species of the genus \textit{Calycomyza} Hendel}

1. Orbits shining black ...................................................... \textit{sonchi} Spencer, p. 325
   - Orbits paler at least in lower areas ................................ \textit{menthae} Spencer, p. 325

\textit{Calycomyza menthae} Spencer

\textit{Calycomyza menthae} Spencer, 1969:152.

\textit{Comparison and diagnostic characters.} — The members of this species resemble closely those of \textit{althaeae} Spencer and \textit{cynoglossi} Frick and can be reliably separated only by examination of characters of male genitalia. Spencer (1969) illustrated the distinctive aedeagus. The colour of squamal fringe is from pale to dark brown.

\textbf{Biology.} — Larvae make brownish blotch mines on the leaves of \textit{Mentha} and \textit{Monarda}, family Labiatae.

\textbf{Geographical distribution.} — The members of this species are known from Ontario and Alberta. I examined the following material from Alberta:

\textit{CANADA.} Alberta: 1 δ, 1 ♀ Edmonton, Fort Road, from leaf mines on \textit{Mentha arvensis} L., coll. 9.viii.1969, emerged 22-25.viii.1969; 1 δ Edmonton, Mayfair park, 17.v.1969.

\textit{Calycomyza sonchi} Spencer


\textit{Diagnostic characters.} — The members of this species are distinctive in having shining
black orbits and pale squamal fringe. Spencer (1969) illustrated the distinctive aedeagus.

**Biology.** — Larvae mine the leaves of *Sonchus* and *Taraxacum*, family Compositae.

**Geographical distribution.** — The members of this species are known from Alberta and Manitoba in Canada. Known Alberta localities are as below:

CANADA. Alberta: Edmonton, University of Alberta campus, Red Deer.

**Genus Amauromyza Hendel**

*Dizygomyza* (*Amauromyza*) Hendel, 1931:59.


*Dizygomyza* (*Cephalomyza*) Hendel; Spencer, 1969:157.

The main distinguishing characters of the members of this genus are subcosta joined to costa independent of R₁; costa extended to apex of vein M₁₂; orbital setulae reclinate; mesonotum and scutellum black; halteres with knob black or partially paler or whitish, if yellow, aedeagus with numerous spinules on distiphallus.

This genus is represented in Alberta by two new species, *riparia* and *shepherdiae*, described below. Three species known from eastern Canada (Spencer, 1969) have not been discovered from the west.

**Key to Alberta species of the genus Amauromyza Hendel**

1. Two lower orbital bristles; gena approximately one-third eye height; aedeagus as in Fig. 43, 44 .......................... *shepherdiae* n. sp., p327
   - Three lower orbital bristles; gena approximately one-fourth eye height; aedeagus as in Fig. 41 .......................... *riparia* n. sp., p. 326

**Amauromyza riparia** new species

**Comparison and diagnostic characters.** — The members of this species differ from those of a similar species, *subinfumata* (Malloch), in having smaller size and distinct male genitalia. They may be included in Spencer’s (1969) key to Canadian species of the genus *Amauromyza* Hendel as shown below at the beginning of the description of *shepherdiae* n. sp.

**Description.** — Head. Frons approximately twice width of eye at level of front ocellus, not projected in front of eye margin in profile. Three strong Ori directed upwards; orbital setulae few, approximately eight, reclinate. Eyes oval, 1.1 times higher than their length. Gena approximately one-fourth eye height. Vibrissa normal. Third antennal article rounded at tip; arista short, thickened at base.

Mesonotum. Three strong dc; acr in about five irregular rows.

Wing. Length 1.5 to 1.6 mm in ßß; costa extended to apex of vein M₁₂; costal segments 2-4 in the ratio of 1.0 : 0.3 : 0.2; crossvein m-m present; last section of M₃₄ approximately twice length of penultimate.

Male genitalia. Hypandrium without apodeme, postgonites elongate; aedeagus and ejaculatory apodeme as illustrated (Fig. 41, 42). Ejaculatory bulb large.

Colour. Frons, gena and face dark brown; orbits and ocellar triangle weakly shining black. Mesonotum, scutellum and pleura mat black, squamae grey, fringe black; halteres with stalk black, and knobby distinctly whitish or paler.

**Derivation of the specific name.** — The members of this species are named *riparia* as the type specimens were caught along the river bank in Edmonton.

**Geographical distribution.** — The members of this species are known only from the type
locality:


*Amauromyza shepherdiae* new species

*Comparisons.* – The members of this species differ from those of *riparia* n. sp. in having only two lower orbital bristles and distinct male genitalia. This species and *riparia* n. sp. are distinguished in Spencer’s (1969) key to Canadian species of the genus *Amauromyza* Hendel, by extending his key as shown below:

2. Halteres entirely black; larger specimens, wing length 2.2 to 3.2 mm ............... *abnormalis* (Malloch)
- Halteres with stalk black, knob whitish or yellowish grey; smaller specimens .......... 3
3. Three lower orbital bristles ............................................. 4
- Two lower orbital bristles; larvae leaf miner on *Shepherdia* ............. *shepherdiae* n. sp.
4. Larger specimens, wing length 1.9-2.2 mm ........................... *subinfumata* (Malloch)
- Smaller specimens, wing length 1.5-1.6 mm in male .................... *riparia* n. sp.

*Description.* – Head. Frons almost equal to width of eye at level of front ocellus, not projected in front of eye margin in profile. Two strong Ors directed upwards, two Ori directed inwards and upwards; orbital setulae few, approximately nine to ten reclinate hairs. Eyes oval, approximately 1.1 times higher than their length. Gena deep, approximately one-third eye height. Vibrissa normal. Third antennal article rounded at tip, arista conspicuously thickened at base, bare.

Mesonotum. Three strong dc; acr in five to six irregular rows.

Wing. Length in male 1.5 mm; costa extended to apex of vein M$_1+2$; costal segments 2-4 in the ratio of 1.0 : 0.3 : 0.3; crossvein m-m present; last section of M$_3+4$ approximately twice penultimate.

Male genitalia. Hypandrium without distinct apodeme; postgonites elongate; aedeagus as illustrated (Fig. 43, 44); ejaculatory apodeme (Fig. 45) with large bulb.

Colour. Frons, gena and face dark brown; orbits and ocellar triangle weakly shining black; mesonotum, scutellum and pleura mat black, weakly shining; antennae black; squamae grey, fringe dark brown; legs black; haltere with stalk black, knob whitish.

*Derivation of the specific name.* – The members of this species are named after the generic name of their food plant *Shepherdia*.

*Biota.* – Larvae make blotch mines (Fig. 46) on the leaves of *Shepherdia canadensis* (L.) Nutt., family Elaeagnaceae. Pupation occurs outside the mine.

*Geographical distribution.* – The members of this species are known from the type locality:

CANADA: Alberta: Holotype ♂ Edmonton, University of Alberta campus, from leaf mines on *Shepherdia canadensis* (L.) Nutt., coll. 5.vii.1968, emerged 25.v.1969; Numerous leaf mines, same data.

Genus *Nemorimyza* Frey

*Nemorimyza* Frey, 1946:42.

*Nemorimyza* Frey was erected as a monotypic subgenus of a large genus *Dizygomyza* Hendel sensu lato. Frick (1952) synonymized *Dizygomyza* Hendel with *Phytobia* Lioy sensu lato. Later (1953, 1959) he treated *Nemorimyza* Frey as a subgenus of *Phytobia*

*Nemorimyza posticata* (Meigen)

*Agromyza posticata* Meigen, 1830:172; Frost, 1924:50.
*Dizygomyza (Dendromyza) posticata* (Meigen); Hendel, 1931:30.
*Dizygomyza (Nemorimyza) posticata* (Meigen); Frey, 1946:42.
*Phytobia (Phytobia) posticata* (Meigen); Frick, 1952:390.

Diagnostic characters. – The members of this species are large shining black flies, wing length approximately 3.0 mm. Other diagnostic characters are: orbits in the same plane as frons; mesonotum shining black; dorsocentra in three rows; prescutellars present; squamal fringe pale whitish; fore-tibial bristle present and abdomen yellowish in male. Sasakawa (1961) and Spencer (1969) illustrated the aedeagus characteristic of this species.

Biology. – The larvae make blotch mines on the leaves of *Solidago* spp. in Alberta. The larvae are also known to mine the leaves of *Aster* spp. in United States (Frick, 1959). Frost (1924) and Sasakawa (1961) illustrated the leaf mine characteristic of this species. The leaf mine is characteristic in having concentric feeding marks. Pupation occurs outside the mine.

Geographical distribution. – The members of this species are Holarctic in distribution and are known from Japan (Sasakawa, 1961), Europe (Hendel, 1931), United States and Canada (Frick, 1959; Spencer, 1969). I examined the following material from Alberta:


**Genus Liriomyza** Mik

*Liriomyza* Mik, 1894:289.

The main distinguishing characters of the genus *Liriomyza* Mik are: subcosta fold-like distally, joined to costa independent of *R*₁; orbital setulæ erect or reclinate; costa extended to vein *M₁₂*; vein *M₁₂* nearest wing tip; scutellum yellow at least centrally; orbits largely in plane of frons; frons usually yellow; crossvein m-m normally present, but absent in *L. singula* Spencer; aedeagus variable in shape, without sclerotized paired tubules as in the genus *Lemurimyza* Spencer.

The genus is represented in Alberta by 27 species. The species in this genus are extremely difficult to separate from external characters alone. The characters of male genitalia are necessary for confirmation of the specific identity of most of the species. Many species very similar in external adult characteristics often belong to very different groups when their male genitalia are studied; e.g., *L. taraxaci* Hering, *L. veluta* Spencer and *L. lathyri* new species are extremely similar in external characters; but the structure of their male genitalia suggests that they belong to entirely different groups.

Six new species described in this treatment are: *L. balearicoides*, *L. bifurcata*, *L. lathyri*, *L. senecionivora*, *L. sinuata* and *L. sylvatica*. Necessary amendments to include these species in Spencer's (1969) key to Canadian species of the genus *Liriomyza* Mik are given.
### Key to Alberta species of the genus Liriomyza Mik

<table>
<thead>
<tr>
<th>Step</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1(0)</td>
<td>Mesonotum with yellow central area adjoining scutellum.</td>
<td>2</td>
</tr>
<tr>
<td>-</td>
<td>Mesonotum without such yellow area</td>
<td>3</td>
</tr>
<tr>
<td>2(1)</td>
<td>Larger specimens, wing length 2.8-3.5 mm; acr in about five irregular rows, scutellum with dark areas laterally.</td>
<td>4</td>
</tr>
<tr>
<td>-</td>
<td>Smaller specimens, wing length approximately 2.0 mm; acr in two rows; scutellum entirely yellow</td>
<td>5</td>
</tr>
<tr>
<td>3(1)</td>
<td>Crossvein m-m present</td>
<td>6</td>
</tr>
<tr>
<td>-</td>
<td>Crossvein m-m absent</td>
<td>7</td>
</tr>
<tr>
<td>4(3)</td>
<td>Femora mostly dark</td>
<td>8</td>
</tr>
<tr>
<td>-</td>
<td>Femora mostly yellow, some specimens with dark spots or streaks</td>
<td>9</td>
</tr>
<tr>
<td>5(4)</td>
<td>Third antennal article black</td>
<td>10</td>
</tr>
<tr>
<td>-</td>
<td>Third antennal article yellow or slightly darkened at base of arista</td>
<td>11</td>
</tr>
<tr>
<td>6(5)</td>
<td>Antennae entirely black; acr in four rows.</td>
<td>12</td>
</tr>
<tr>
<td>-</td>
<td>First and second antennal article yellow; acr in two rows</td>
<td>13</td>
</tr>
<tr>
<td>7(5)</td>
<td>Mesonotum shining black; acr in four rows; femora black with yellow distal tips</td>
<td>14</td>
</tr>
<tr>
<td>-</td>
<td>Mesonotum black grey; acr in two rows; femora with some yellow spots or lines</td>
<td>15</td>
</tr>
<tr>
<td>8(7)</td>
<td>Orbits mostly yellow; aedeagus with ejaculatory duct conspicuously swollen between basiphallus; distiphallus lightly sclerotized</td>
<td>16</td>
</tr>
<tr>
<td>-</td>
<td>Orbits slightly darkened; aedeagus with ejaculatory duct not so swollen, distiphallus darkly sclerotized</td>
<td>17</td>
</tr>
<tr>
<td>9(4)</td>
<td>Third antennal article with conspicuously long pubescence</td>
<td>18</td>
</tr>
<tr>
<td>-</td>
<td>Third antennal article with normal pubescence</td>
<td>19</td>
</tr>
<tr>
<td>10(9)</td>
<td>vte on black and vti on margin of black and yellow areas on vertex</td>
<td>20</td>
</tr>
<tr>
<td>-</td>
<td>vte and vti both on yellow areas</td>
<td>21</td>
</tr>
<tr>
<td>11(10)</td>
<td>Surstyli long and narrow; larva leaf miner on Achillea</td>
<td>22</td>
</tr>
<tr>
<td>-</td>
<td>Surstyli shorter and broader</td>
<td>23</td>
</tr>
<tr>
<td>12(9)</td>
<td>Squamal fringe pale yellow</td>
<td>24</td>
</tr>
<tr>
<td>-</td>
<td>Squamal fringe brown or black</td>
<td>25</td>
</tr>
<tr>
<td>13(12)</td>
<td>Mesonotum brilliantly shining black</td>
<td>26</td>
</tr>
<tr>
<td>-</td>
<td>Mesonotum dull or mat, black or grey</td>
<td>27</td>
</tr>
<tr>
<td>14(13)</td>
<td>vte and vti on yellow areas on vertex, separated by narrow dark band</td>
<td>28</td>
</tr>
<tr>
<td>-</td>
<td>vte on dark and vti on margin of dark and yellow areas; aedeagus as illustrated (Fig. 55, 56)</td>
<td>29</td>
</tr>
<tr>
<td>15(13)</td>
<td>vte on black and vti on margin of dark and yellow areas on vertex</td>
<td>30</td>
</tr>
<tr>
<td>-</td>
<td>vte and vti both on yellow areas</td>
<td>31</td>
</tr>
<tr>
<td>16(15)</td>
<td>Upper orbits partially darkened</td>
<td>32</td>
</tr>
<tr>
<td>-</td>
<td>Orbits yellow</td>
<td>33</td>
</tr>
<tr>
<td>17(16)</td>
<td>Distiphallus with two circular lobes in ventral view</td>
<td>34</td>
</tr>
<tr>
<td>-</td>
<td>Distiphallus as illustrated (Fig. 68, 69)</td>
<td>35</td>
</tr>
<tr>
<td>18(16)</td>
<td>Acrostichals in four rows</td>
<td>36</td>
</tr>
</tbody>
</table>
- Acrostichals in two rows ................................................. 20
  19(18). Femora blackish ................................................. 20
  19a. Femora normal yellow; aedeagus as in Fig. 60, 61 ........ 20
- Aedeagus with distal processes divergent as in Fig. 52, 53 .. 20

- Aedeagus without such distal processes ........................... kenti Spencer, p. 234
  21(15). Acrostichals in two rows .................................... 22
  21a. Acrostichals in three to four irregular rows ............... 23
  22(21). Aedeagus with distiphallus oval, disc-shaped in ventral view .................................................. 23
  22a. Aedeagus as in Fig. 47, 48 ...................................... balcanicoides n. sp., p. 330
  23(21). One Orcs and two to three Ori ............................... 24
  23a. Two Orcs and two Ori ............................................. 25
  24(23). Last section of M₃₄ approximately two times the penultimate; larva leaf miner on Smilacina ......................... 26
- Last section of M₃₄ two and a half to three times the penultimate; aedeagus with 26(25). Mesonotum black, not grey ................................ taraxaci Hering, p. 340
- Mesonotum grey .......................................................... 26
  26a. Frons slightly projected in front of eye margin in profile .................................................. veluta Spencer, p. 341
- Frons not projected in front of eye margin in profile ........... lathyri n. sp., p. 334

Liriomyza balcanicoides new species

Comparisons. — A member of this species resembles that of L. fricki Spencer in external characteristics and can be reliably separated only by examination of male genitalia. The aedeagus (Fig. 47, 48) characteristic of this species is of same general type as that of the Palaeartic species L. balcanica (Strobl) as figured by Spencer (1966c), but is quite distinctive. Besides, the adult differs in having crossvein m-m present. This species may be included in Spencer’s (1969) key to Canadian species of the genus Liriomyza Mik by amending and extending couplet 39 as below:

39. acr in two rows ......................................................... 39a
  - acr in three to four rows ......................................... 40
  39a. Aedeagus as illustrated (Spencer, 1969) ................. fricki Spencer
  - Aedeagus as in Fig. 47, 48 ...................................... balcanicoides n. sp.

Description. — Head. Frons approximately one and a half times width of eye at level of front ocellus, projected in front of eye margin in profile; eyes oval, 1.25 times higher than their length; gena little less than one-third of eye height midway between vibrissal and posterior margins; ocellar triangle small; lunule high; two strong Orcs directed upwards; two Ori, lower one directed inwards, upper one directed upwards; orbital setae few, three to four, reclinate; third antennal article rounded at tip, with normal pubescence; arista pubescent.

Mesonotum. Dorsocentrals 3+1; acr in two rows.

Wing. Length in male approximately 1.5 mm; costa extended to vein M₁₂; costal segments 2-4 in the ratio of 1 : 0.27 : 0.3; crossvein m-m present; last segment of M₃₄ approximately two and a half times the penultimate.

Male genitalia (Fig. 47-50). Hypandrium U-shaped with slender side arms; pregonites broad; postgonites elongated; surstylus (Fig. 50) with characteristic spine placed anteriorly and a small spine dorsally on epandrium; aedeagal apodeme darkly sclerotized; phallopore
small; basiphallus with swollen ejaculatory duct; distiphallus as illustrated with two characteristic processes at distal end; ejaculatory apodeme (Fig. 49) broad, with darkly sclerotized stem, bulb small, sclerotized along lower margin.

Colour. Frons, orbits, lunule, gena and antennae yellow; vte and vti on yellow areas; mesonotum mat greyish black; humeral area yellow, with a dark spot anteriorly; notopleural area yellow; scutellum yellow, with dark areas at its basal corners; mesopleuron yellow with slight dark area anteroventrally; pteropleuron yellow; sternopleuron black, with a narrow yellow band dorsally; femora essentially yellow; tibiae and tarsi brown; squamal fringe dark brown, halteres yellow.

Derivation of the specific name. — The name balcanicoides is given in view of the fact that this species belongs to the same group as L. balcanica (Strobl).

Geographical distribution. — A male of this species is known only from type locality: CANADA. Alberta: Holotype ♂ St. Albert, near Edmonton, 18.vi.1967.

Liriomyza baptisiae (Frost)

Agromyza baptisiae Frost, 1931:275.

Comparisons and diagnostic characters. — The members of this species are small black flies, approximately 1.7 mm in wing length. The adults resemble closely those of L. quadri-setosa (Malloch) in external morphology but differ in having only four orbital bristles. The adults differ from those of another similar species, L. eboni Spencer, in having all three antennal articles black. Spencer (1969) illustrated the distinctive aedeagus.

Biology. — The larvae form linear blotch mines on leaves of Baptisia tinctoria (L.), family Leguminoseae, in Pennsylvania, U. S. A. (Frick, 1959). The larvae probably have some other food plant in Alberta.

Geographical distribution. — The members of this species are known from Pennsylvania, U. S. A. (Frick, 1959) and Canada (Spencer, 1969). I examined the following material from Alberta:


Liriomyza bifurcata new species

Comparisons. — A member of this species resembles closely that of L. kenti Spencer in external characteristics and can be separated reliably only by the examination of male genitalia. It differs from those of similar species, L. nordica Spencer and L. senecionivora new species, in having two rows of acrostichals and distinct male genitalia. L. bifurcata is included in Spencer’s (1969) key to the Canadian species of the genus Liriomyza Mik as shown at the beginning of the description of L. senecionivora new species described later in this treatment.

Description. — Head (Fig 51). Frons wide, approximately two times width of eye at level of front ocellus, slightly projected in front of eye margin in profile; eyes oval, approximately 1.3 times higher than their length; gena approximately one-fifth of eye height midway between vibrissal and posterior margins; ocellar triangle small, lunule almost semicircular above; two strong Ors directed upwards, one Ori directed inwards; orbital setulae three, reclinate; antennal bases approximate; third antennal article rounded at tip, with normal pubescence; arista long and pubescent.

Mesonotum. Dorsocentrals 3+1; acr in two rows.

Wing. Length in male 1.25 mm; costa extended to vein M₁+₂; costal segments 2-4 in the
ratio of 1 : 0.4 : 0.24; wing tip at M₁+2; last segment of M₃+₄ approximately three times penultimate.

Male genitalia (Fig. 52-54). Hypandrium U-shaped with slender side arms, pregonites small; postgonites elongated; surstylus small, with a short spine anteriorly and a cone-like projection dorsally on epandrium; aedeagal apodeme lightly sclerotized; phallobase small; basiphallus with a thick swollen ejaculatory duct; hypophallus small narrow process; distiphallus with two divergent tubules distally and small filamentous hair ventrally; ejaculatory apodeme broad, bulb small and sclerotized along the lower margin.

Colour. Frons, orbits, lunule, gena and antennae yellow; ocellar triangle black; vte and vti on dark areas; mesonotum greyish black; humeral area yellow, with dark spot anteriorly; notopleural area yellow; scutellum yellow with lateral dark areas, mesopleuron yellow with dark dark area anteroventrally; sternopleuron dark, with narrow yellow band along upper margin; femora yellow, slightly brownish at base; tibiae and tarsi brownish; squamal fringe brown, squamae yellow; halteres yellow.

Derivation of the specific name. — The name bifurcata is given in view of two divergent tubular processes on the distiphallus.

Geographical distribution. — A member of this species is known only from the type locality:

CANADA. Alberta: Holotype ♂ Edmonton, White Mud Creek park, 29.vi.1966.

*Liriomyza conspicua* Sehgal


Diagnostic characters. — The members of this species are large flies, wing length 2.8-3.5 mm, with characteristic prescutellar yellow; yellow third antennal segment, scutellum slightly darkened at basal corners and distinct male genitalia. Sehgal (1968) illustrated the head, wing and male genitalia characteristic of this species.

Geographical distribution. — The members of this species are known from various localities in Alberta, Manitoba, Ontario and Saskatchewan in Canada (Sehgal, 1968). I examined the following further material from Alberta:

CANADA. Alberta: 2 ♀♂, 3 ♀ Végreville, 22.vi.1968.

*Liriomyza cordillerana* Sehgal


Comparison and diagnostic characters. — The members of this species resemble closely those of *L. septentrionalis* Sehgal in external morphology and can be reliably separated only by the examination of the characters of the male genitalia. The colour of third antennal article is variable from complete yellow to slightly darkened at base of arista; orbits are usually darkened. Sehgal (1968) illustrated the head, wing and the distinctive aedeagus. Spencer (1969) also figured the aedeagus.

Biology. — Larvae mine the leaves of *Deschampsia caespitosa* (L.) Beauv., family Gramineae.

Geographical distribution. — The members of this species are known from various localities in the Rockies in Alberta, Canada (Sehgal, 1968). I examined the following further material from Alberta:

CANADA. Alberta: 1 ♂ Banff, from leaf mine on grass, 13-23.ix.1966; 1 ♂ Blairmore, 26.vi.1966; 1 ♂ Jasper, from leaf mines on *Deschampsia caespitosa* (L.) Beauv., family Gramineae; 1 ♂ same locality, 1.ix.1966.
Liriomyza eboni Spencer


**Comparison and diagnostic characters.** — The members of this species differ from those of the similar species, *L. baptisiae* (Frost), in having first and second antennal article yellow and acrostichals in two rows. The aedeagus has been illustrated by Spencer (1969).

**Geographical distribution.** — The members of this species are known only from Alberta, from the type locality:

CANADA. Alberta: Blairmore (Spencer, 1969).

Liriomyza edmontonensis Spencer


**Comparison and diagnostic characters.** — The members of this species resemble closely those of *L. sylvatica* new species in external morphology and can be reliably separated only by comparison of the characters of male genitalia. Spencer (1969) illustrated the aedeagus characteristic of this species.

**Geographical distribution.** — The members of this species are known from Alberta and British Columbia in Canada. Known Alberta locality is as follows:

CANADA. Alberta: Edmonton, University of Alberta campus (Spencer, 1969).

Liriomyza eupatorii (Kaltenbach)

Agromyza eupatorii Kaltenbach, 1874:320.

Liriomyza eupatorii (Kaltenbach), Hendel, 1920:143; Spencer, 1969:174.

**Comparison and diagnostic characters.** — The members of this species are very close to those of *L. montana* Sehgal in external characteristics and are reliably separated only by examination of male genitalia. Spencer (1969) figured the distinctive aedeagus of this species. The aedeagus of a caught specimen from Alberta is illustrated in Fig. 55, 56. The distiphallus of this species is very close to that of *L. pictella* (Thompson) and *L. munda* Frick, from which it differs only in minor details. Spencer (1965c) illustrated the aedeagus characteristic of *L. pictella* (Thompson) and of *L. munda* Frick.

**Biology.** — Larvae mine the leaves of members of the genera *Solidago, Helianthus, Eupatorium, Aster,* and *Lampsana,* family Compositae, and *Galeopsis,* family Labiatae, in Europe (Hering, 1957).

**Geographical distribution.** — The members of this species are widespread in Europe and are known from Canada (Spencer, 1969). Frick’s (1953, 1959) description of *L. eupatorii* (Kaltenbach) refers to *L. munda* Frick (Stegmaier, 1966, 1968). I examined the following material from Alberta:


Liriomyza fricki Spencer


Liriomyza fricki Spencer, 1965c:35.

**Comparison and diagnostic characters.** — The members of this species are very close to those of *L. balcanicoides* new species in external characteristics, but the male genitalia are very different. Spencer (1965c, 1969) illustrated the distinctive aedeagus of this species.

**Biology.** — Larvae mine the leaves of various species of the genera *Medicago, Melitotus,*
*Trifolium* and *Vigna*, of the family Leguminosae (Stegmaier, 1968). The flies were also bred from two other genera *Lathyrus* and *Vicia* of the family Leguminosae. The leaf mine is a small blotch with a short linear beginning.

**Geographical distribution.** — *L. fricki* Spencer is a Nearctic species whose members are known from Northern United States and Canada (Spencer, 1969). I examined the following material from Alberta:


**Liriomyza kentii** Spencer


**Comparisons and diagnostic characters.** — The members of this species resemble closely those of *L. bifurcata* new species and are separated reliably only by examination of the characters of male genitalia. The adults differ from those of similar species, *L. senecionivora* new species and *L. nordica* Spencer, in having only two rows of acrostichals. Spencer (1969) illustrated the distinctive aedeagus.

**Geographical distribution.** — The members of this species are known only from the localities of its type series (Spencer, 1969). I examined the following material from Alberta:


**Liriomyza lathyri** new species

**Comparisons.** — The members of this species resemble closely those of *L. veluta* Spencer, *L. trifolii* (Burgess) and *L. taraxaci* Hering in external morphology and can be separated reliably only by examination of the characters of the male genitalia. This species is included in Spencer's (1969) key to Canadian species of the genus *Liriomyza* Mik by amending couplet 43 and adding couplet 44 as below:

43. Aedeagus as in Fig. 57, 58 ................................. *lathyri* n. sp.
   - Aedeagus not so ........................................ 44

44. Aedeagus as illustrated (Spencer, 1969) ................................. *trifolii* (Burgess)
   - Aedeagus as illustrated (Spencer, 1969) ................................. *veluta* Spencer

**Description.** — Frons approximately 1.8 times width of eye at level of front ocellus, not projected in front of eye margin in profile; eyes oval, approximately 1.25 times higher than their length; gena approximately one-fifth of eye height midway between vibrissal and posterior margins; ocellar triangle small; two Ors directed upwards; two Ori directed inwards; orbits narrow; orbital setulae approximately six, reclinate; third antennal article rounded at tip, with normal pubescence; arista pubescent.

Mesonotum. Dorsocentrals 3+1; acr in three irregular rows.

Wing. Length in male approximately 1.7 mm; costa extended to vein M<sub>1,2</sub>; costal segments 2-4 in the ratio of 1 : 0.27 : 0.27; crossvein m-m present; last segment of M<sub>3,4</sub> approximately 2.5 times the penultimate.
Male genitalia (Fig. 57-59). Hypandrium U-shaped with slender side arms; pregonites broad; surstylus typical with a conspicuous spine placed anteriorly; small cone-like projection present on epandrium; phallopore and aedeagus (Fig. 57, 58) as illustrated; ejaculatory apodeme (Fig. 59) broad, darkened at its stem, bulb small, sclerotized along lower margin.

Colour. Frons, orbits, lunule, gena and antennae all yellow or reddish; vte and vti on yellow areas; mesonotum mat greyish black; humeral area yellow, with a dark spot anteriorly; notopleural area yellow; mesopleura essentially yellow, with dark area centrally and along ventral half; sternopleura black, with a narrow yellow band along its dorsal margin, femora essentially yellow; tibiae and tarsi brownish; squamal fringe dark brown; halteres yellow.

Derivation of the specific name. — This species is named *lathyri* after the generic name of its larval food plant.

Biology. — Larvae make large blotch mine with a small linear beginning on the leaflets of *Lathyrus ochroleucus* Hook., family Leguminosae. Pupation occurs outside the mine.

Geographical distribution. — The members of this species are known only from the localities of its type species:


*Liriomyza lima* (Melander)

*A. lima* Melander, 1913:265.


Diagnostic characters. — The main distinguishing characters are: black mesonotum, yellow femora and third antennal article. The pale squamal fringe differentiates this from other species in this group. Spencer (1969) illustrated the distinctive aedeagus.

Geographical distribution. — Members of this species are known from United States and Canada. The Alberta locality is:

CANADA. Alberta: Edmonton (Spencer, 1969).

*Liriomyza millefolii* Hering


Comparison and diagnostic characters. — The members of this species can be easily recognized by the presence of conspicuously long whitish pubescence on the third antennal article and the presence of vertical bristles on yellow areas. The adults resemble closely those of *L. sinuata* new species in external morphology, but the male genitalia are distinct. Spencer (1969) illustrated the aedeagus characteristic of this species.

Biology. — Larvae mine the leaves of *Achillea millefolium* L. and *A. sibirica* Ledeb., family Compositae. Larvae also mine the leaves of *Tanacetum vulgare* L. in the laboratory.

Geographical distribution. — The members of this species are known from Germany (Hendel, 1931) in Europe, and Canada (Spencer, 1969). I examined the following material from Alberta:

same locality, viii.1967

*Liriomyza montana* Sehgal


*Comparison and diagnostic characters.* – The members of this species resemble closely those of *L. eupatorii* (Kaltenbach) in external morphology. The position of vertical bristles on yellow areas used to differentiate the adults of this species from those of *L. eupatorii* (Kaltenbach) is variable as the area of vertical bristles in some specimens is darkened. The male genitalia are, however, quite distinct. Sehgal (1968) illustrated the head, wing and male genitalia characteristic of this species. Spencer (1969) also figured the distinctive aedeagus.

*Biology.* – Larvae probably mine the leaves of grasses (Gramineae).

*Geographical distribution.* – The members of this species are known from various localities in the Rockies in Alberta, Canada (Sehgal, 1968).

*Liriomyza nordica* Spencer


*Comparisons and diagnostic characters.* – The members of this species are very similar to those of *L. senecionivora* new species and differ only in having femora blackish. The male genitalia are, however, very distinct. The adults differ from those of other similar species, *L. bifurcata* new species and *L. kenti* Spencer, in having darker mesopleura and distinct male genitalia. Spencer (1969) illustrated the aedeagus characteristic of this species.

*Geographical distribution.* – The members of this species are known only from the locality of its type series from Canada. I examined the following material from Alberta:


*Liriomyza pilosa* Spencer


*Comparison and diagnostic characters.* – The members of this species resemble closely those of *L. millefolii* Hering in having long pubescence on third antennal article and can be reliably separated only by examination of male genitalia. Surstyli in this species are shorter and broader than in *millefolii* Hering. Spencer (1969) illustrated the aedeagus characteristic of this species.

*Geographical distribution.* – The members of this species are known only from Alberta from the locality of the type specimen as follows:

CANADA. Alberta: Edmonton, University of Alberta campus (Spencer, 1969).

*Liriomyza senecionivora* new species

*Comparisons.* – The adults of this species resemble closely those of *L. nordica* Spencer in external characteristics and can be reliably separated only by the examination of male genitalia. *L. senecionivora* and *L. bifurcata* new species described earlier are included in Spencer’s (1969) key to Canadian species of the genus *Liriomyza* Mik by amending and extending the couplet 38 as below:

38. acr in four rows ............................................. 38a
- acr in two rows ............................................. 38b
38a. Aedeagus as illustrated (Spencer, 1969) .................. *nordica* Spencer

- Aedeagus as in Fig. 60, 61.......................... *senecionivora* n. sp.

38b. Aedeagus as illustrated (Spencer, 1969) .................. *kenti* Spencer

- Aedeagus as in Fig. 52, 53.......................... *bifurcata* n. sp.

**Description.** — Head. Frons wide, approximately 1.8 times width of eye at level of front ocellus, slightly projected in front of eye margin in profile; eyes oval, 1.3 times higher than long; gena approximately one-fifth of eye height midway between vibrissal and posterior margins; ocellar triangle small; lunule high, almost flat above; two strong Ori directed upwards, three Ori directed inwards and upwards; orbital setulae few, approximately seven, reclinate; antennal bases approximate; third antennal article rounded at tip, with normal pubescence; arista long and pubescent.

Mesonotum. Dorsocentrals 3+1; acr in four irregular rows.

Wing. Length in male 2.0 mm; costa extended to vein M₁₂; costal segments 2-4 in the ratio of 1 : 0.23 : 0.26; wing tip at vein M₁₂; crossvein m-m present; last segment of M₃₄ approximately three times penultimate.

Male genitalia (Fig. 60-63). Hypandrium U-shaped with slender side arms; pregonites broad and membranous; postgonites long and narrow; surstyli (Fig. 63) small, with two spines placed anteriorly, small spine on epandrium anteriorly also present; phallophore small and darkly sclerotized; basiphallus and distiphallus lightly sclerotized; ejaculatory duct swollen between basiphallus; distiphallus small; ejaculatory apodeme (Fig. 62) narrow and darkly sclerotized at base, bulb membranous.

Colour. Frons, orbits, lunule, gena and antennae all yellow; ocellar triangle black; vte on black and vti on margin of black and yellow areas; mesonotum mat black; humeral area yellow, with a dark spot anteriorly; notopleural area yellow; scutellum yellow with dark areas at its basal corners; mesopleuron and sternopleuron black with narrow yellow band along upper margins; femora mainly yellow, with slight brownish area towards their base; tibiae and tarsi dark brown; squamae slightly dark; halteres yellow.

**Derivation of the specific name.** — This species is named *senecionivora* after the name of its food plant.

**Biology.** — The larvae make linear mines on the leaves of *Senecio pauciflorus* Pursh. Pupation occurs outside the leaf mine.

**Geographical distribution.** — The members of this species are known only from the type localities:


**Liriomyza septentrionalis** Sehgal

*Liriomyza septentrionalis* Sehgal, 1968:70.

**Comparison and diagnostic characters.** — The members of this species resemble closely those of *L. cordillerana* Sehgal in external morphology, and can be reliably separated only by the examination of the characters of male genitalia.

The third antennal article is variable in colour from complete yellow to slightly darkened at the base of arista; orbits are usually yellow. Sehgal (1968) figured the head, wing and the characteristic aedeagus.

**Biology.** — Larvae mine the leaves of grasses (Gramineae).

**Geographical distribution.** — The members of this species are known from various localities in the Rocky Mountains and Cypress Hills in Alberta and from British Columbia (Sehgal,
Liriomyza singula Spencer


Diagnostic characters. — The members of this species are distinct in the absence of cross-vein m-m; the third antennal article is only lightly darkened at the base of arista. Spencer (1969) figured the distinctive aedeagus.

Geographical distribution. — The members of this species are known only from its type species in Canada (Spencer, 1969). I examined the following material from Alberta:


Liriomyza sinuata new species

Comparisons. — The members of this species resemble those of L. millefolii Hering in having long pubescence on third antennal article but differ in having both vertical bristles on dark areas and distinct male genitalia. This species is included in Spencer’s (1969) key to Canadian species of the genus Liriomyza Mik by amending and extending the couplet 26 as below:

26. Orbits shining black; mesopleura black in lower three-quarters; femora distinctly darkened .................................................. sp. (Constance Bay)

- Orbits yellow; femora yellow .................................. 26a

26a. vte on black and vti on margin of black and yellow ground ...... sinuata n. sp.

- Both vt on yellow ground ...................................... 27

Description. — Head. Frons wide, approximately twice width of eye at level of front ocellus, projected in front of eye margin in profile; eyes oval, slightly slanted, 1.25 times higher than their length; gena deep, approximately one-third of eye height midway between vibrissal and posterior margins; ocellar triangle small; lunule high, narrow at top; two strong Ors directed upwards; two Ori, lower one directed inwards and upper one directed upwards; orbital setulae one to two, reclinate; antennal bases approximate; third antennal article rounded at tip, with conspicuous pubescence; arista pubescent.

Mesonotum. Dorsocentrals 3+1; acr in two rows.

Wing. Length in male approximately 1.5 mm; costa extended to vein M₁₂; costal segments 2-4 in the ratio of 1 : 0.35 : 0.25; wing tip at M₁₂; crossovein m-m present; last segment of M₃₄ approximately 2.5 times penultimate.

Male genitalia (Fig. 64-67). Hypandrium U-shaped with slender side arms; pregonites broad; postgonites elongated; surstylus (Fig. 67) small with short spine anteriorly and small spine dorsally on epandrium; aedeagal apodeme darkly sclerotized; phallophore small; ejaculatory duct swollen between basiphallus; distiphallus two long tubular S-shaped processes; ejaculatory apodeme (Fig. 66) broad, bulb small and sclerotized along lower margin.

Colour. Frons, orbits, lunule, gena and antennae all yellow; vte on black and vti on the margin of dark and yellow areas; mesonotum mat black; humeral area yellow, with a dark spot anteriorly; notopleural area yellow; scutellum yellow, with dark area along its basal corners; mesopleuron yellow with slight dark area anteroventrally; sternopleuron black, with a narrow yellow band dorsally; femora mainly yellow; tibiae and tarsi brown, squamal fringe dark brown; halteres yellow.

Derivation of the specific name. — The name sinuata is given in view of the sinuate or wavy distiphallus.

Geographical distribution. — The members of this species are known only from the loca-
ties of its type specimens:


**Liriomyza smilacinae** Spencer


*Comparison and diagnostic characters.* — The members of this species are close to those of *L. undulata* Spencer in external morphology and are separated only by examination of the characters of male genitalia. Spencer (1969) illustrated the characteristic aedeagus.

*Biological.* — Larvae form linear leaf mines on the leaves of *Smilacina stellata* (L.) Desf., family Liliaceae. Spencer (1969) illustrated the leaf mine characteristic of this species.

*Geographical distribution.* — The members of this species are known only from the localities of its type series in Canada (Spencer, 1969). I examined the following material from Alberta:


**Liriomyza socialis** Spencer


*Diagnostic characters.* — The main distinguishing characters of the members of this species are mat grey mesonotum and two rows of acrostichals. The colour of third antennal article varies from pale to dark brown (Spencer, 1969). Spencer (1969) illustrated the distinctive aedeagus.

*Geographical distribution.* — The members of this species are known only from Alberta, Canada. The Alberta localities are as follows:


**Liriomyza sylvatica** new species

*Comparisons.* — A male of this species is very similar to that of *L. edmontonensis* Spencer in external characteristics and is reliably separated only by examination of male genitalia, which, however, are very distinct. This species is included in Spencer’s (1969) key to Canadian *Liriomyza* species by amending and extending the couplet 37 as below:

37. Femora partially darkened ........................................... 37a
- Femora almost entirely bright yellow .......................... arcticola Spencer

37a. Aedeagus as illustrated (Spencer, 1969) ............... edmontonensis Spencer
- Aedeagus as in Fig. 68, 69 ................................. sylvatica n. sp.

*Description.* — Head. Frons approximately 1.3 times wider than the width of eye at level of front ocellus; slightly projected in front of eye margin in profile; eyes oval, 1.4 times higher than their length; gena little less than one-fourth of eye height midway between vibrissal and posterior margins; ocellar triangle small; lunule high; two Ors directed upwards; two Ori directed inwards and upwards; orbital setulae three to four, reclinate; antennal bases approximate; third antennal article with a slight angle anterodorsally, with normal pubescence; arista pubescent.

Mesonotum. Dorsocentrals 3+1; acr in four irregular rows.
Wing. Length in male 1.7 mm; costa extended to vein M_{1,2}; costal segments 2-4 in the ratio of 1 : 0.26 : 0.18; wing tip at vein M_{1,2}; crossvein m-m present; last segment of M_{3,4} approximately three and a half times the penultimate.

Male genitalia. (Fig. 68, 69). Hypandrium U-shaped with slender side arms; pregonites broad; postgonites elongated; surstylus small and lightly sclerotized; aedeagal apodeme darkly sclerotized; phallopore elongate; ejaculatory duct swollen between basiphallus; distiphallus as illustrated; ejaculatory apodeme broad, bulb small and sclerotized along lower margin.

Colour. Frons, gena, lunule and antennae yellow; upper orbits partially darkened up to lower Ors; vte on black and vti on the margin of dark and yellow areas; mesonotum mat greyish black; humeral area yellow, with a dark spot anteriorly; notopleural area yellow; scutellum yellow, with slight dark at its basal corners; mesopleuron black with a narrow yellow band dorsally; sternopleuron black; femora yellow, darkened towards base, tibiae and tarsi dark brown; squamal fringe brownish; halteres yellow.

Derivation of the specific name. — The name *sylvatica* indicates that the species is woodland-inhabiting.

Geographical distribution. — This species is known only from the type locality: CANADA. Alberta: Holotype ♂ St. Albert, near Edmonton, 18.vi.1967.

*Liriomyza taraxaci* Hering

*Liriomyza taraxaci* Hering, 1927:184; Spencer, 1969:188.

Comparisons and diagnostic characters. — The members of this species resemble closely those of *L. velutina* Spencer, *L. trifolii* (Burgess), *L. lathyri* new species, and differ only in having mesonotum black and not grey. The male genitalia are, however, entirely different. Spencer (1969) illustrated the aedeagus distinctive of this species.


Geographical distribution. — The members of this species are known from various localities in Europe (Hendel, 1931) and from Canada (Spencer, 1969). I examined the following material from Alberta:


*Liriomyza undulata* Spencer

*Liriomyza undulata* Spencer, 1969:190

Comparison and diagnostic characters. — The members of this species resemble closely those of *L. smilacinae* Spencer in external morphology, but have distinct male genitalia. Spencer (1969) illustrated the characteristic aedeagus. The distiphallus is distinctive in having a long undulating process distally.

Geographical distribution. — The members of this species are known only from the localities of its type series from Canada (Spencer, 1969). I examined the following material from Alberta:

Liriomyza veluta Spencer


**Comparisons and diagnostic characters.** — The members of this species resemble closely those of *L. lathyri* new species and *L. trifolii* (Burgess) in external morphology and can be separated only by examination of the characters of male genitalia. The adults differ from those of another similar species, *L. taraxaci* Hering, in having mesonotum grey and not black. Spencer (1969) illustrated the distinctive aedeagus.

**Geographical distribution.** — The members of this species are known from various localities of its type series from Canada (Spencer, 1969). I examined the following material from Alberta:


*Liriomyza viciae* Spencer


**Comparison and diagnostic characters.** — The members of this species resemble closely those of *L. melampyga* (Loew) in external morphology and differ only in having acrostichals in two rows and distinctive male genitalia. Spencer (1969) illustrated the aedeagus characteristic of this species as well as that of *L. melampyga* (Loew).

The adults are small flies, wing length approximately 2.0 mm, with characteristic prescutellar yellow and yellow antennae.

**Biology.** — Larvae form blotch mines on the leaflets of *Vicia americana* Muhl., family Leguminosae.

**Geographical distribution.** — The members of this species are known only from the type series from Canada (Spencer, 1969). I examined the following material from Alberta:


**Genus Lemurimyza** Spencer


The main distinguishing characters of the genus *Lemurimyza* Spencer are: subcosta weakly developed distally, joined to costa independent of R₁; costa extended to vein M₁+s; orbital setulae normally erect or slightly proclinate; scutellum yellow; mesonotum with yellow central area adjoining scutellum, epandrium normally with comb-like arrangement of dark spines; aedeagus typical of the genus, with paired sclerotized tubules.

The genus *Lemurimyza* Spencer is represented in Alberta by only one species, *L. pallida* Sehgal. The members of this genus are extremely similar to those of the genus *Liriomyza* Mik in external characteristics, but possess very distinct male genitalia.

*Lemurimyza pallida* Sehgal


**Comparisons and diagnostic characters.** — The members of this species differ from those of two other species, *L. dorsata* (Siebke) and *L. pacifica* (Melander), known from Canada (Spencer, 1969), in having third antennal article yellow and distinctive male genitalia. Sehgal
(1968) illustrated the head, wing and male genitalia characteristic of this species. Spencer (1969) also illustrated the aedeagus.

**Geographical distribution.** — The members of this species are known only from the type locality as follows:

CANADA. Alberta: Banff (Sehgal, 1968).

**Genus Metopomyza Enderlein**


The main distinguishing characters of this genus are subcosta fold-like distally and joined to costa independent of R₁; orbital setulae reclinate; costa extended to apex of vein M₁,₂; scutellum yellow; orbits broad and raised above plane of frons; aedeagus typical of genus.

The members of this genus are very similar to those of the genus *Liriomyza* Mik in external morphology, but the male genitalia are very distinct.

This genus is represented in Alberta by two species, *interfrontalis* (Melander) and *griffithsi* n. sp.

**Key to Alberta species of the genus Metopomyza Enderlein**

1. Squamal fringe yellow; larger specimens, wing length 2.0-2.3 mm ............... *interfrontalis* (Melander), p. 343
   - Squamal fringe brown, smaller specimens, wing length 1.5 mm in male ............... *griffithsi* n. sp., p. 342

**Metopomyza griffithsi** new species

**Comparisons and diagnostic characters.** — A member of this species differs from that of *interfrontalis* (Melander) in having smaller size and brown squamal fringe. It resembles that of a Palaearctic species, *flavonotata* (Haliday), but possesses distinct male genitalia. This species is distinguished in Spencer’s (1969) key to Canadian species of the genus *Metopomyza* Enderlein by amending and extending the couplet 1 as below:

1. Notopleural area black ........................................... 1a
   - Notopleural area yellow ........................................... 2

1a. Larger specimens, wing length 2.0-2.3 mm; squamal fringe yellow ............... *interfrontalis* (Melander)
   - Smaller specimens, wing length 1.5 mm in male; squamal fringe brown ............... *griffithsi* n. sp.

**Description.** — Head. Frons approximately 1.8 times width of eye at level of front ocellus, slightly projected in front of eye margin in profile; orbits broad, slightly raised above the plane of frons; eyes oval, strongly slanted along posteroventral margin, vertical height is almost equal to their length; ocellar triangle small; gena deep, approximately 0.3 times vertical height of eye. Two strong Ors directed upwards; two strong Ori directed inwards; orbital setulae numerous, reclinate; third antennal article slightly angulate antero-dorsally and rounded below, pubescent.

Mesonotum. Dorsocentrals 3+1 decreased in length anteriorly, acr in three to four irregular rows.

Wing. Length in male 1.5 mm; costa extended to vein M₁,₂; costal segments 2-4 in ratio of 1 : 0.33 : 0.26; vein M₁,₂ at the wing tip; crossvein m-m present; last segment of M₃,₄ approximately 0.4 times penultimate.

Male genitalia (Fig. 70-72). Hypandrium with narrow side arms; surstyli (Fig. 10) with
two rows of conspicuous spines as illustrated; phallopore long; aedeagus (Fig. 71) typical of genus; basiphallus broad and sclerotized; mesophallus long and slender; distiphallus as small divergent tubules distally; ejaculatory apodeme (Fig. 72) small and narrow, bulb small, membranous.

Colour. Frons darker below and yellowish above, orbits black; lunule dark; gena greyish black; antennae black; mesonotum mat black, slightly brownish; scutellum almost entirely yellow; mesopleura, sternopleura and pteropleura all black; femora black, with distal tips yellow; tibiae and tarsi brownish black; squamae pale, fringe brownish; halteres yellow.

Derivation of the specific name. — This species is named in honour of G. C. D. Griffiths of the Department of Entomology, University of Alberta, Canada.

Geographical distribution. — A member of this species is known only from the type locality:


Metopomyza interfrontalis (Melander)

Agromyza interfrontalis Melander, 1913:263.
Liriomyza interfrontalis (Melander), Frick, 1952:403.

Comparison and diagnostic characters. — The members of this species differ from those of griffithsi new species in having larger size and pale squamal fringe. Spencer (1969) illustrated the distinctive aedeagus.

Geographical distribution. — The members of this species are known from Canada and United States. The Alberta locality is:

CANADA. Alberta: Elkwater (Spencer, 1969).

Genus Praspedomyza Hendel

Dizygomyza (Praspedomyza) Hendel, 1931:77.
Praspedomyza Hendel, Spencer, 1966b:146.

Nowakowski (1962) on the basis of his studies on male genitalia proposed that this genus should be merged with the genus Liriomyza Mik. Later Spencer (1966b, 1969) in view of the dark colouration, raised orbits and distinct male genitalia justified the retention of Praspedomyza Hendel as a distinct genus.

This genus is represented in Canada by only one species, galiivora Spencer, the common leaf miner on Galium.

Praspedomyza galiivora Spencer

Praspedomyza galiivora Spencer, 1969:199.

Diagnostic characters. — The members of this species are quite distinctive in having yellow third antennal article and distinct male genitalia. Spencer (1969) illustrated the aedeagus characteristic of this species. The colour of third antennal article varies slightly from bright yellow to reddish.

Biology. — Larvae mine the leaves of Galium boreale L., family Rubiaceae.

Geographical distribution. — The members of this species are known from Europe and Canada (Spencer, 1969). I examined the following material from Alberta:

Genus Haplomyza Hendel

Haplomyza Hendel, 1914:73, new name for Antineura Melander, not Osten Sacken 1881.

The members of this genus resemble externally those of the large genus Liriomyza, but possess distinct male genitalia. They are represented in Alberta by only one species, togata (Melander).

Haplomyza togata (Melander)

Antineura togata Melander, 1913:250.
Haplomyza togata (Melander); Frick, 1953:73, 1959:413; Spencer, 1969:201.

Diagnostic characters. — The main distinguishing characters of the members of this species are wing length 1.75-2.2 mm, costa extended to vein M₁,2; crossovein m-m absent; one Ors and three Ori; eyes slanted; frons, gena, face and antennae yellow; mesonotum mat grey, few acrostichals and distinct male genitalia. The ninth sternite is greatly elongate.

Biology. — Larvae are known to make irregular blotch mines on the leaves of Amaranthus spp., family Amaranthaceae, in United States (Frick, 1959).
Geographical distribution. — The members of this species are known from United States, and Alberta and Saskatchewan in Canada (Spencer, 1969). The Alberta locality is:

CANADA. Alberta: Drumheller.

Genus Phytoliriomyza Hendel

Liriomyza (Phytoliriomyza) Hendel, 1921:203.
Phytoliriomyza Hendel; Frey, 1941:19; Frick, 1952:410; Spencer, 1964b:662.
Xyraeomyia Frick, Spencer, 1964b:662.

The members of this genus differ from those of the genus Liriomyza Mik in having dark scutellum and proclinate orbital setulae. They are represented in Alberta by only one species, arctica (Lundbeck).

Phytoliriomyza arctica (Lundbeck)

Agromyza arctica Lundbeck, 1900:304.
Odinia immaculata Coquillett, 1902:185.
Agromyza formosensis Malloch, 1914b:315.
Dizygomyza (Icteromyza) arctica (Lundbeck), Hendel, 1931:57.
Phytoliriomyza arctica (Lundbeck); Shewell, 1953:469; Frick, 1959:414.

Diagnostic characters. — The main distinguishing characters of the members of this species are: eyes oval, slanted, slightly pilose; acrostichals present; wing length approximately 2.0 mm; costa strongly extended to vein M₁,2; crossovein m-m present; and aedeagus with characteristic two long, membranous coiled tubules. Spencer (1963, 1964b, 1969) discussed in detail and illustrated the male genitalia of members of this species.
Agromyzidae of Alberta 345

Biology. – Larvae feed as stem miners on *Sonchus asper* L., family Compositae in Germany (Spencer, 1963). No host plant is yet known in North America.

Geographical distribution. – The members of this species are most widely distributed being known from Europe, Formosa, Canada, United States and South America (Spencer, 1963). I examined the following material from Alberta:


Genus *Pseudonapomyza* Hendel


The members of this genus differ from those in the genus *Phytomyza* Fallén in having crossvein m-m basal to r-m and reclinate orbital setulae. They are represented in Alberta by two species, *atra* (Meigen) and *lacteipennis* (Malloch).

Key to Alberta species of the genus *Pseudonapomyza* Hendel

1. Mesonotum weakly shining black; tarsi dark brown; wings normal ............... *atra* (Meigen), p. 345
   Mesonotum mat grey; tarsi yellow; wings whitish. ...... *lacteipennis* (Malloch), p. 345

*Pseudonapomyza atra* (Meigen)

*Phytomyza atra* Meigen, 1830:191.

*Pseudonapomyza atra* (Meigen); Hendel, 1932:302; Spencer, 1969:209.

Comparison and diagnostic characters. – The members of this species are quite distinctive in having angulate third antennal articles. The adults differ from those of similar species, *P. lacteipennis* (Malloch), in having dark tarsi and weakly shining black mesonotum.

Biology. – Larvae mine the leaves of grasses (Gramineae).

Geographical distribution. – The members of this species are Holarctic in distribution, known from Europe (Hendel, 1932), United States (Frick, 1959) and Canada (Spencer, 1969). I examined the following material from Alberta:


*Pseudonapomyza lacteipennis* (Malloch)

*Phytomyza lacteipennis* Malloch, 1913b:152.


Diagnostic characters. – The main distinguishing characters are mat greyish mesonotum, yellow tarsi and whitish wings.

Biology. – Larvae probably mine the leaves of grasses (Gramineae).

Geographical distribution. – The members of this species are known from United States and Canada. The Alberta localities are as follows:

CANADA. Alberta: Elkwater; Medicine Hat; Orion (Spencer, 1969).

Genus *Paraphytomyza* Enderlein


The name *Phytagromyza* Hendel which has long been used (Hendel, 1920, 1932; Frick,
1952, 1959) for members of this genus, cannot be used now as its type, *P. flavocingulata* (Strobl), is now referred to the genus *Cerodontha* Rondani (Nowakowski, 1962, 1967).

The main distinguishing characters of the genus *Paraphytomyza* Enderlein are: subcosta weakly developed distally, joined to costa independent of R₁; orbital setulae erect or reclinate or absent; costa extended to vein R₄₋₅; crossvein m-m usually absent, if present, always beyond crossvein r-m.

This genus is represented in Alberta by five species. All Alberta species discussed here probably form a single group within the genus *Paraphytomyza* Enderlein, whose members feed on the representatives of the family Caprifoliaceae and other related families of the order Rubiales. Nowakowski (1962) proposed a new genus, *Rubioniomyza*, for this group of flies. The name proved to be synonymous with *Paraphytomyza* Enderlein.

Another group of leaf miners on Salicaceae is probably also represented in Alberta. Linear leaf mines on the under surface of the leaves of *Populus tremuloides* Michx., quite common around Edmonton, are very similar to those of *Paraphytomyza tremulae* (Hering) in Europe on *Populus tremula* L. Since no flies have yet been bred, their identity cannot be confirmed.

**Key to Alberta species of the genus *Paraphytomyza* Enderlein**

1(0). Crossvein m-m present ................................................................. 2
- Crossvein m-m absent ........................................................................... 4

2(1). Dorsocentrals two; mouthparts elongate .................................. nitida (Malloch), p. 347
- Dorsocentrals three or more; mouthparts normal ............................... 3

3(2). Notopleural area yellow ............................................................ plagiata (Melander), p. 347
- Notopleural area brownish black ......................................................... lonicerae (Robineau-Desvoidy), p. 346

4(1). Small specimens, wing length 1.6-1.8 mm in males; aedeagus as illustrated (Fig. 76) ............................................................... spenceri n. sp., p. 348
- Larger specimens, wing length 2.0 to 2.4 mm ................................. orbitalis (Melander), p. 347

*Paraphytomyza lonicerae* (Robineau-Desvoidy)

*Phytomyza lonicerae* Robineau-Desvoidy, 1851:396.

*Phytagromyza lonicerae* (Robineau-Desvoidy); Hering, 1951:36; Frick, 1953:74.


*Comparison and diagnostic characters.* – The members of this species are very close to those of *P. orbitalis* (Melander) in the general shape of aedeagus, but differ in lacking crossvein m-m. Spencer (1969) illustrated the aedeagus characteristic of this species. The posterior spiracles of the puparium are distinctive in having a dark spine in centre.

*Biological.* – Larvae mine the leaves of various members of the genera *Lonicera* and *Symphoricarpos*, family Caprifoliaceae. Frick (1953) reared this species from *Lonicera involucrata* (Richards) Banks and *Symphoricarpos albus* (L.). I observed the leaf mines of this species in Alberta on *Lonicera dioica* L., *L. tartarica* L. and *Symphoricarpos albus* (L.). The leaf mine is whitish, linear with distinct frass granules disposed alternately along the mine. Hering (1951) illustrated the characteristic leaf mine. This species is the first to appear in early spring and there is only one generation a year.

*Geographical distribution.* – The members of this species are known from Europe, United States and Canada (Spencer, 1969). I examined the following material from Alberta:

Paraphytomyza nitida (Malloch)

Agromyza nitida Malloch, 1913a:288; Frick, 1952:373.
Phytagromyza nitida (Malloch); Frick, 1953:74, 1959:417.
Paraphytomyza nitida (Malloch); Spencer, 1969:207.

Diagnostic characters. — The members of this species are distinctive in having elongate mouthparts and absence of crossvein m-m. Spencer (1969) illustrated the distinctive aedegus.

Biology. — Not confirmed. Spencer (1969) noted the similarity between this species and P. orphana (Hendel), a stem miner on Galium in Europe, and has suggested as host one of the Galium species occurring in Alberta.

Geographical distribution. — The members of this species are known from United States (Frick, 1953, 1959) and Canada (Spencer, 1969). I examined the following material from Alberta:


Paraphytomyza orbitalis (Melander)

Phytomyza orbitalis Melander, 1913:271.
Phytagromyza orbitalis (Melander); Frick, 1952:416, 1959:417.
Paraphytomyza orbitalis (Melander); Spencer, 1969:207.

Comparison and diagnostic characters. — The members of this species resemble externally those of a sympatric species, P. spenceri new species, but differ in having a distinct aedegus and larval leaf mine (Fig. 73). The aedegus has been illustrated by Spencer (1969). The females unless represented by bred series cannot be determined definitely.

Biology. — Larvae mine the leaves of Lonicera dioica L. and Symphoricarpos albus (L.), family Caprifoliaceae. The leaf mine (Fig. 73) is broad, linear in shape. Pupation occurs outside the leaf mine.

Geographical distribution. — P. orbitalis (Melander) is a Nearctic species, whose members are known from United States (Frick, 1952, 1959) and Canada (Spencer, 1969). I examined 10 males and one female from Alberta:


Paraphytomyza plagiata (Melander)

Napomyza plagiata Melander, 1913:273.
Agromyza plagiata (Melander); Malloch, 1918:130.
Phytagromyza plagiata (Melander); Frick, 1952:416, 1959:417.
Paraphytomyza plagiata (Melander); Spencer, 1969:208.

Diagnostic characters. — The members of this species can be easily recognised by the characters given in the key.

Biology. — Larvae mine the leaves of Lonicera involucrata (Richards) Banks, family Caprifoliaceae. The leaf mine (Fig. 74) is linear and light greenish in colour.

Geographical distribution. — The members of this species are known from United States
Comparisons and diagnostic characters. — The members of this species resemble externally those of a sympatric species, P. orbitalis (Melander), and can only be reliably differentiated by the examination of the male genitalia. The females unless from bred series are very difficult to determine definitely. The linear leaf mine of this species (Fig. 79) is similar to that of P. luteoscutellata (de Meijere) illustrated by Spencer (1969), but the adults are distinct in having completely black scutellum. This species is distinguished in Spencer’s (1969) key to Canadian species of the genus Paraphytomyza Enderlein by extending the couplet 5 as below:

5. Scutellum yellow, at least between basal scutellar bristles
   luteoscutellata (de Meijere)
5a. Scutellum entirely dark

5a. Wing length up to 2.0 mm; aedeagus as in Fig. 76

Description. — Head (Fig. 75). Frons almost equal to width of eye at level of front ocellus; upper orbits slightly projected in front of eye margin in profile; eyes oval, 1.3 times their width, bare; ocellar triangle small; gena deepest posteriorly, approximately one-sixth of eye height mid-way between vibrissal and posterior margins; two strong Ors directed upwards; two Ori directed inwards; orbital setulae 4-6, reclinate; third antennal article rounded at tip, arista long and pubescent.

Mesonotum. Dorsocentrals 3+1; acr numerous in approximately four rows.

Leg. Mid-tibia without a differentiated bristle medially.

Wing. Length in ♂♂ 1.6-1.8 mm, in ♀♀ approximately 2.0 mm; costa extended to vein R_{4+5}; wing tip between R_{4+5} and M_{1+2}; crossvein m-m absent; costal segments 2-4 in the ratio of 1.0 : 0.23 : 0.28.

Male genitalia (Fig. 76). Hypandrium U-shaped with slender side arms and no apodeme; surstyli broad and rounded, without spines; pregonites broad; postgonites elongate; phallopore short and darkly sclerotized; basiphallus a pair of broad arms; distiphallus removed from basiphallus by a short membranous gap, of two distinctive curved tubes; aedeagal apodeme weakly sclerotized; ejaculatory apodeme small and fan-shaped, bulb small and membranous.

Colour. Frons darker above the lunule; orbits yellow; ocellar triangle black; antennae, gena and lunule yellowish brown; mesonotum and scutellum mat grayish black; humeral and notopleural areas yellow; femora dark brown; tibiae and tarsi mostly yellowish or slightly brownish; squamae yellow, fringe slightly brownish; halteres yellow.

Description of immature stages. — Puparium brownish yellow, oval and deeply segmented, measures approximately 1.5 mm x 0.8 mm.

Larval mouth parts obtained from puparium are illustrated (Fig. 77). Right mandible larger than left, each with two distinct teeth alternate with one another; labial sclerite short and darkly sclerotized; paracylepal phragmata with darkly sclerotized dorsal and weakly sclerotized ventral arms.

Muscle scars on abdominal segments small and oval; tubercles numerous in approximately six to eight rows.

Anterior spiracles small, each with about six to eight bulbs; posterior spiracles (Fig. 78) small and rounded, each with 11-12 bulbs.
Derivation of the specific name. — This species is named in honour of Dr. K. A. Spencer, who has contributed greatly to the knowledge of world Agromyzidae.

Biology. — Larvae mine the leaves of *Lonicera dioica* L. and *Symphoricarpos occidentalis* Hook., family Caprifoliaceae. The leaf mine (Fig. 79) is linear, greenish black, without discrete frass granules. Pupation occurs outside the mine.

Geographical distribution. — I examined the members of this species only from the province of Alberta.


Genus *Napomyza* Westwood

*Napomyza* Westwood, 1840:152

The members of this genus differ from those in the large genus *Phytomyza* Fallén in the presence of crossvein m-m. Male genitalia are, however, distinct. This genus is represented in Alberta by three species.

Key to Alberta species of the genus *Napomyza* Westwood

1(0). Third antennal article with conspicuous pubescence ...... *plumea* Spencer, p. 350
- Third antennal article almost bare .................................. 2

2(1). Smaller specimens, wing length about 2.5-3.1 mm; distiphallus paler ............... *

- Larger specimens, wing length about 3.5-4.5 mm; distiphallus darkly sclerotized

................................................................. *immanis* Spencer, p. 349

*Napomyza immanis* Spencer


Comparison and diagnostic characters. — The members of this species differ from those of a similar species, *nugax* Spencer, in larger size, wing length 3.5-4.5 mm; third antennal article slightly less quadrate and aedeagus with darker distiphallus. Spencer (1969) illustrated the distinctive aedeagus.

Geographical distribution. — Known from Alaska, Alberta, Northwest Territories and Yukon Territory. The Alberta locality is as follows:

CANADA. Alberta: Edmonton, White Mud Creek park (Spencer, 1969).

*Napomyza nugax* Spencer


Comparison and diagnostic characters. — The members of this species differ from those of a similar species, *immanis* Spencer, in having smaller size, wing length 2.5-3.1 mm; quadrate third antennal article and paler distal process on the distiphallus. Spencer (1969) illustrated the distinctive aedeagus. They also differ from *lateralis* (Fallén) in having distinct aedeagus.

Geographical distribution. — Known from Alberta, British Columbia, Ontario and Quebec in Canada (Spencer, 1969). I examined the following material from Alberta:
CANADA. Alberta: 1 δ, 1 ♀ Blairmore, 26.vi.1966.

*Napomyza plumea* Spencer

*Napomyza plumea* Spencer, 1969:217.

**Diagnostic characters.** — The main distinguishing characters are the pubescent third antennal article and distinct male genitalia. The aedeagus has been illustrated by Spencer (1969).

**Geographical distribution.** — Known from Alaska, Alberta, British Columbia, Manitoba and Quebec. The Alberta locality is as follows:

CANADA. Alberta: Banff, Mt. Eisenhower (Spencer, 1969).

**Genus Phytomyza** Fallén


The main distinguishing characters of this genus are subcosta weakly developed distally and joined to costa independent of R₂; orbital setulae proclinate; costa extended to vein R₄₊₅ and crossvein m-m normally absent.

The members of this genus as defined presently on the basis of the direction of orbital setulae and shortened costa, form a very diverse assemblage of many groups. The discovery and use of the characters of male genitalia in agromyzid taxonomy have proved beyond doubt that species extremely similar in external characteristics may have very conspicuous differences in genitalic structures. A close look at any of the recent keys shows that many species and even sometimes genera can be distinguished by examination of characters of male genitalia only. Attempts to divide this genus into various groups have not been successful as characters of male genitalia were not taken into consideration. It is not possible to undertake the full scale revision of this genus as at present the phallic structures of numerous species have not been illustrated.

This is the largest genus of agromyzid flies with about 400 described species in the world. Spencer (1969) reported 83 species for Canada, of which he recorded 41 as occurring in Alberta. Fifteen new species are described in this genus here and four additional species are recorded as new to Alberta. *P. flavicornis* Fallén which has been reported as occurring in Alberta (Spencer, 1969) is not considered here as the Alberta specimens collected from the same locality as those of Spencer’s proved to be a new species *luteiceps* described here, distinguishable from *flavicornis* Fallén in the characters of the male genitalia. This genus is now represented in Alberta by 59 described species and in Canada by 98 species. Necessary amendments to include the further new species in Spencer’s (1969) key to Canadian species are given.

**Key to Alberta species of the genus Phytomyza** Fallén

1(0). Frons basically pale, yellow, orange or reddish ............................................ 2
- Frons basically dark, brown or black .......................................................... 41

2(1). Scutellum all or partially yellow .......................................................... 3
- Scutellum dark, grey or black ........................................................................ 5

3(2). Third antennal article black or dark brown .............................................. 4
- Third antennal article yellow ........................................................................ major Malloch, p. 368

4(3). Upper Ors shorter than lower; aedeagus with up to eight coils .............. ranunculi (Schrank), p. 375
- Two Ors equal .................................................................................................. clematiphaga Spencer, p. 361
5(2). Femora mostly yellow ........................................ 6
- Femora mostly dark, at most with yellow distal tips ........ 7

6(5). Third antennal article black ......................... miranda Spencer, p. 370
- Third antennal article yellow; aedeagus as in Fig. 106 ... luteiceps n. sp., p. 368

7(5). Sides of thorax including humeral and notopleural areas yellow ........ 8
- Sides of thorax dark, at most upper margins of mesopleura with narrow yellow band ......................... 12

8(7). Third antennal article with normal pubescence. ......... 9
- Third antennal article with conspicuously long pubescence ................................ riparia n. sp., p. 376

9(8). Upper Ors shorter than lower or lacking .................. 10
- Two Ors equal; hypopleuron and sternopleuron largely yellow ................................ petasiti Spencer, p. 373

10(9). Second costal segment two and a half to three times length of fourth .......... 11
- Second costal segment longer, approximately four times length of fourth ...................... spondylii R.-D., p. 379

11(10). Second antennal article black; hind margins of eyes black .......... solidaginivora Spencer, p. 378
- Second antennal article yellow; hind margins of eyes yellow ................................ matricariae Hendel, p. 369

12(7). Upper Ors shorter than lower or lacking .................. 13
- Two Ors equal ................................................. 19

13(12). Frons partly darkened .................................. prava Spencer, p. 374
- Frons almost entirely yellow ................................ 14

14(13). Second costal segment more than three and a half times length of fourth .......... 15
- Second costal segment less than three and a half times length of fourth .......... 17

15(14). Upper Ors present; aedeagus as in Fig. 81, 82 .......... aquilegioides n. sp., p. 355
- Upper Ors invariably lacking; larvae leaf miner on Heracleum .......... 16

16(15). Second costal segment three and a half times length of fourth ................... lanati Spencer, p. 367
- Second costal segment four to four and a half times length of fourth .................. spondylii R.-D., p. 379

17(14). Upper Ors normally lacking .............................. 18
- Upper Ors present; aedeagus as in Fig. 93, 94 .......... columbinae n. sp., p. 362

18(17). Second costal segment more than three times length of fourth, approximately 3.3 times; notopleural areas dark; larvae make linear leaf mines on Aster conspicus Lindl .......... asterophaga Spencer, p. 358
- Second costal segment less than three times length of fourth; notopleural areas yellowish; larvae make linear leaf mines on Aster ciliolatus Lindl ................ ciliolati Spencer, p. 360

19(12). Third antennal article with conspicuously long pubescence; aedeagus as in Fig. 104 ................................ lactuca Frost, p. 366
- Third antennal article with normal pubescence. .............. 20

20(19). Broad epistoma present; gena deeply extended .......... 21
- Mouth margin normal ........................................... 24

21(20). Second antennal article black ............................ 22
- Second antennal article yellowish ................................ 23

22(21). Larger specimens, wing length 3.0-3.4 mm ............. illustris Spencer, p. 365
- Smaller specimens, wing length about 2.4 mm in male; aedeagus as in Fig. 88, 89
23(21). Mesonotum light grey ............................................. *blairmorensis* n. sp., p. 358
- Mesonotum darker, blackish grey ................................. *lupini* Sehgal, p. 367

24(20). Acrostichals in three to six rows ........................... 25
- Acrostichals at most in two rows .................................. 28

25(24). Frons slightly darkened above lunule; aedeagus as in Fig. 126
- Frons entirely pale ..................................................... 26

26(25). Gena deep, approximately one-third to one-half eye height
- Gena narrower, one-sixth to one-fifth vertical eye height ........ 29

27(26). Orbits yellow; third antennal article distinctly elongate
- Orbits black; third antennal article not so elongate ............... 28

28(27). Mesonotum paler grey; frons entirely yellow .............. *urbana* Spencer, p. 381
- Mesonotum darker grey; frons slightly brownish yellow ........ 30

29(26). Fore-tibia yellowish; gena approximately one-fifth eye height; aedeagus as in Fig. 133
- Fore-tibia dark; gena approximately one-sixth eye height; larvae blotch-miners on leaves of *Aquilegia* and *Thalictrum* .......... 30

30(29). Aedeagus as in Fig. 81, 82 ....................................... *aquilegioides* n. sp., p. 355
- Aedeagus as figured by Spencer (1969) ......................... *aquilegiana* Frost, p. 354

31(24). Acrostichals lacking or at most three to four isolated hairs present .................................................. 31
- Acrostichals in two rows .............................................. 36

32(31). Squamal fringe dark; second costal segment about twice length of fourth
- Squamal fringe pale; second costal segment one and a half times length of fourth .................................................. 34

33(32). Aedeagus with distiphallus distinctly curved (Fig. 123)
- Aedeagus with distiphallus paler and not so curved, as figured by Spencer (1969) .................................................. 31

34(32). Second antennal article black; larva leaf miner on *Penstemon*
- Second antennal article yellow or slightly brownish .......... 35

35(34). Fore-coxae bright yellow; second antennal article yellow
- Fore-coxae dark; second antennal article brownish; aedeagus as in Fig. 91 .................................................. 36

36(31). Fore-coxae dark ..................................................... 37
- Fore-coxae yellow ....................................................... 39

37(36). Squamal fringe dark ................................................ 38
- Squamal fringe pale; aedeagus as in Fig. 130, 131 ............ *subalpina* n. sp., p. 379

38(37). Aedeagus with distiphallus membranous, as figured by Spencer (1969)
- Aedeagus with distiphallus darkly sclerotized as in Fig. 84; larva leaf miner on *Arnica* .................................................. 36

39(36). Frons distinctly projected above eyes in profile .......... 40
- Frons not so projected; aedeagus as in Fig. 114 ................ *misella* Spencer, p. 371

40(39). Gena deep, about two-third eye height; aedeagus as illustrated (Spencer, 1969) .................................................. 40
- Gena nearly flat; aedeagus as in Fig. 80 ......................... *subtenella* Frost, p. 380
- Gena narrower, about one-third eye height; aedeagus as in Fig. 102

41(1). Upper Ors shorter than lower or absent .................................. jasperensis n. sp., p. 365

- Two Ors equal .............................................. 42

42(41). Upper Ors present ........................................ 43

- Upper Ors absent ........................................ 48

43(42). Second costal segment more than three times length of fourth .................................. 44

- Second costal segment less than three times length of fourth .................................. 45

44(43). Larva leaf miner on Aralia .................................. aralivora Spencer, p. 357

- Larva leaf miner on Angelica .................................. sp. indet. (Angelica), p. 382

45(43). Acrostichals in two rows; larvae leaf miner on Delphinium .................................. delphinivora Spencer, p. 363

- Acrostichals in approximately four irregular rows .................................. 46

46(45). Frons partly yellowish .................................. 47

- Frons darker; aedeagus as in Fig. 110, 111; larvae leaf miner on Mertensia .................................. mertensiae n. sp., p. 369

47(46). Third antennal article small; acrostichals strong .................................. sehgalii Spencer, p. 376

- Third antennal article larger, oval; acrostichals normal; larvae blotch-miners on leaves of Anemone canadensis L. .................................. prava Spencer, p. 374

48(42). Second costal segment more than three times length of fourth; larger specimens, wing length about 2.4 mm; tibiae and tarsi yellowish brown; aedeagus as in Fig. 97 .................................. edmontonensis n. sp., p. 363

- Second costal segment less than three times length of fourth; smaller specimens, wing length about 1.6-1.9 mm; tibiae and tarsi dark .................................. 49

49(48). Frons slightly paler; acrostichals absent; aedeagus with distiphallus straight .................................. aquilegivora Spencer, p. 356

- Frons darker; acrostichals present; aedeagus with distiphallus wavy .................................. thalictrivora Spencer, p. 381

50(41). Tarsi yellowish brown; larva leaf miner on Cornus .................................. agromyzina Meigen, p. 354

- Tarsi dark brown .......................................... 51

51(50). Second costal segment at least three times length of fourth .................................. 52

- Second costal segment less than three times length of fourth .................................. 53

52(51). Larger specimens, wing length 2.8-3.3 mm; mesonotum greyish; third antennal article elongate .................................. involucratae Spencer, p. 365

- Smaller specimens, wing length about 2.7 mm; mesonotum blackish; third antennal article rounded .................................. milii Kaltenbach, p. 370

53(51). Mesonotum brilliantly shining black .................................. 54

- Mesonotum distinctly mat, greyish or black .................................. 55

54(53). Orbits normal in width; only fore-femur with yellow distal tip .................................. canadensis Spencer, p. 359

- Orbits broad; distal tips of femora variable from yellow to almost black; wing base yellow; aedeagus as in Fig. 116 .................................. multifidae n. sp., p. 371

55(53). Third antennal article elongate; frons distinctly projecting above eyes .................................. cineracea Hendel, p. 360

- Third antennal article normal, rounded at tip .................................. 56

56(55). Acrostichals in two rows .................................. 57

- Acrostichals in approximately four irregular rows .................................. 58

57(56). Second costal segment about one and a quarter times length of fourth; orbits dark .................................. lupinivora Sehgal, p. 367

- Second costal segment almost equal to fourth; aedeagus as in Fig. 119
58(56). Mesonotum black ............................................. oxytropis n. sp., p.372
- Mesonotum paler, greyish ................................. 59

59(58). Gena deep, about one-half of eye height; broad rings below eyes formed by orbits
- Gena narrower at most one-fourth eye height; aedeagus as in Fig. 99 ...................... gregaria Frick, p. 364

60(58). Frons distinctly projected; orbits well differentiated ........................................ evanescens Hendel, p. 364
- Frons not projected; orbits normal ........................................ 61

61(60). Frons slightly pale above; distiphallus with distinctly curved distal processes, as
- Frons entirely black ........................................ 62

62(61). Smaller specimens, wing length about 1.75-2.0 mm; aedeagus as figured by Spencer
- Larger specimens, wing length 2.0-2.3 mm; aedeagus with smaller hypophallus
and stouter distiphallus, as figured by Spencer ........................................ caprifoliæ Spencer, p. 360

Phytomyza agromyzina Meigen

Phytomyza agromyzina Meigen, 1830:191.

Comparison and diagnostic characters. — The members of this species belong to the group
having dark frons and two Ors equal. The adults are quite distinctive in having brownish
yellow tibiae and tarsi. They resemble those of P. notopleuralis Spencer from which they
may be separated by having predominantly dark pleura and distinct male genitalia. Spencer
(1969) illustrated the distinctive aedeagus. Other distinguishing characters of the adults are:
wing length approximately 2.0 mm; mesonotum with slight yellow on humeral and noto-
pleural areas; antennae dark; third antennal article rounded apically, with normal pubes-
cence; and dark femora.

Biology. — Larvae make linear mines in the leaves of Cornus stolonifera Michx. and C.
canadensis L., family Cornaceae.

Geographical distribution. — Known from Europe (Hendel, 1935) and in the United
States from California and Washington (Frick, 1959) and Canada (Spencer, 1969). I examined
the following material from Alberta:

CANADA. Alberta: 1 ♂ Edmonton, White Mud Creek park, 19.v.1968; 2 ♀♀ same locality,
mines around Edmonton on Cornus stolonifera Michx.

Phytomyza aquilegiana Frost

Phytomyza aquilegiana Frost, 1930:459.

Comparison and diagnostic characters. — The members of this species belong to the group
having yellow frons; dark scutellum and pleura; third antennal article black, with normal
pubescence; two Ors equal. The adults resemble those of a sympatric species, P. aquilegi-
oides new species, in external characteristics and can be reliably separated only by examina-
tion of male genitalia. Spencer (1969) illustrated the distinctive aedeagus.

Biology. — Larvae make blotch mines in the leaves of Aquilegia spp. and Thalictrum spp.,
family Ranunculaceae.
Geographical distribution. — Known from United States (Frick, 1959) and Canada (Spencer, 1969). I examined the following material from Alberta:


Phytomyza aquilegioides new species

Comparisons and diagnostic characters. — The members of this species belong to the group characterized by yellow frons; normal mouth margin; dark scutellum; mostly dark femora and pleura; and three to six rows of acrostichals. The upper orbital bristles vary in length from almost equal to two-thirds the length of lower. Therefore, this species has been included in two couples in Spencer’s (1969) key to Canadian species of the genus Phytomyza Fallén as amended below:

19. Only 1 Ors present; second costal section at most three and one-third times length of fourth ........................................... asterophaga Spencer
- Both Ors present; second costal section three and one-half to four times length of fourth .................................................. 19a
19a. Lower Ors only slightly weaker than upper; aedeagus as in Fig. 81, 82 ............ aquilegioides n. sp.
- Invariably small upper Ors present; aedeagus not so ........................................... 20
36. Jowls deep, almost one-half eye height; third antennal segment distinctly elongate; aedeagus as illustrated (Spencer, 1969). .................. banfensis Spencer
- Jowls narrower, about one-sixth eye height; third antennal segment rounded ............... 36a
36a. Aedeagus as illustrated (Spencer, 1969) ........................................... aquilegiana Frost
- Aedeagus as in Fig. 81, 82 ........................................... aquilegioides n. sp.

Description. — Head. Frons approximately 1.5 times width of eye at level of front ocellus, not projected in front of eye margin in profile. Mouth margin normal; lunule high. Two Ors, directed upwards, length of upper Ors varies from equal to two-thirds length of lower; two Ori, directed inwards and upwards, almost equal in size; orbital setulae six to seven, proclinate. Eyes oval, approximately 1.35 times higher than their length, bare; ocellar triangle small. Gena approximately one-sixth vertical eye height. Third antennal article rounded at tip, with normal pubescence; arista normal, with long pubescence.

Mesonotum. Dorsocentrals 3+1 strong bristles; acr four to five irregular rows.

Wing. Length approximately 2.1-2.5 mm; costa extended to vein R_{4+5}; costal segments 2-4 in the ratio of 1 : 0.28 : 0.27; crossovein m-m absent.

Male genitalia (Fig. 80-82). Hypandrium (Fig. 80) V-shaped, with narrow side arms and short, broad apodeme; pregonites broad, postgonites elongate; surstylus normal; aedeagus (Fig. 81, 82) as illustrated; ejaculatory apodeme small, fan-shaped, with small bulb.

Colour. Frons varies from bright yellow to orange; orbits and gena yellow; ocellar triangle weakly shining black; both vertical bristles on dark ground; antennae black; mesonotum, scutellum and pleura mat greyish black; humeral areas with slight yellow; coxae black; femora dark, with yellow on distal tips; tibiae and tarsi yellowish brown; squamae and fringe pale; halteres yellow.

Derivation of the specific name. — The name aquilegioides indicates that the members of this species have similar biology to those of P. aquilegiae Hardy.

Biology. — Larvae make blotch mines on the leaves of Aquilegia formosa Fisch. and
Thalictrum venulosum Trel., family Ranunculaceae. Pupation takes place outside the mine. The dark brown puparia measure approximately 1.75 mm x 0.8 mm, and are covered all over with conspicuous tubercles and spines, as in the palaearctic species P. thalictricola Hendel.

Geographical distribution. – The members of this species are known only from the localities of their type specimens as below:

CANADA. Alberta: Holotype ♂ Edmonton, White Mud Creek park, from leaf mines on Thalictrum venulosum Trel., coll. 5.ix.1968. em. 5.xii.1968; paratypes 1 ♂ same data, emerged 29.xi.1968.


Phytomyza aquilegiophaga Spencer


Comparisons and diagnostic characters. – The members of this species belong to the group characterized by yellow frons; dark scutellum; mostly dark pleura and femora; third antennal article black, with normal pubescence and broad epistoma. The adults resemble those of P. lupini Sehgal but differ in having darker or blackish grey mesonotum and distinct male genitalia. They differ from other related species, P. affinalis Frost, P. blairmorensis new species and P. illistris Spencer, in having second antennal article yellowish brown. Spencer (1969) illustrated the distinctive aedeagus.

Biology. – Larvae bore inside the stems of Aquilegia sp. (cultivated), family Ranunculaceae, and pupate at the stem base. The dark brown pupae can be found during late summer.

Geographical distribution. – The members of this species are known from Canada (Spencer, 1969). I examined the following material from Alberta:


Phytomyza aquilegivora Spencer


Comparisons and diagnostic characters. – The members of this species belong to the group characterized by dark frons, mesonotum and scutellum; upper Ors lacking; essentially dark femora and pleura and second costal segment less than three times length of fourth. The adults resemble those of P. thalictrivora Spencer but differ in having yellowish frons and lacking acrostichals. They also differ from the similar species, P. minuscula Goureau, in having very different male genitalia. Spencer (1969) illustrated the aedeagus characteristic of the species.

Biology. – Larvae make linear mines on the leaves of Aquilegia sp. (cultivated), family Ranunculaceae. Pupation takes place outside the mine.

Geographical distribution. – The members of this species are known only from the locality of its type series from Canada (Spencer, 1969). I examined the following material from Alberta:

CANADA. Alberta: 5 ♂ Edmonton, Aberhart Hospital, University of Alberta campus, swept over Aquilegia sp. (cultivated), 25.vi.1969; 1 ♀ same locality, 1.vi.1967; 3 ♂♂ same

*Phytomyza aralivora* Spencer


**Comparison and diagnostic characters.** — The members of this species belong to the group characterized by dark frons, mesonotum and scutellum; upper Ors shorter than lower; and second costal segment more than three times fourth. The adults resemble those of *P. osmorocephalae* Spencer but differ in having yellow tarsi and distinct male genitalia. Spencer (1969) illustrated the aedeagus characteristic of this species.

**Biology.** — Larvae make linear mines on the leaves of *Aralia nudicaulis* L., family Araliaceae. Pupation takes place inside the mine.

**Geographical distribution.** — The members of this species are known only from Canada (Spencer, 1969). I examined the following material from Alberta:

CANADA. Alberta: 1 ♂ Edmonton, river bed near University of Alberta campus, 14.vi.1969; Numerous leaf mines around Edmonton and in Elk Island park on *Aralia nudicaulis* L.

*Phytomyza arnicivora* new species

**Comparison and diagnostic characters.** — The main distinguishing characters of the members of this species are pale frons; two equal Ors; third antennal article normal; mouth margin normal; mesonotum, pleura and scutellum all mat greyish black; femora black, with slight yellow on distal tips and squamae fringe dark. The adults resemble those of *P. fuscula* Zetterstedt and can be reliably distinguished only by examination of male genitalia. The members of this species are included in Spencer’s (1969) key to Canadian species of the genus *Phytomyza* Fallén by extending the couplet 50 as below:

50. Mesopleura entirely grey ............................................. 50a
- Mesopleura with upper margins narrowly yellow .................. 51

50a. Aedeagus with distiphallus membranous, as illustrated (Spencer, 1969) ...........

.......................................................... *fuscula* Zetterstedt
- Aedeagus with distiphallus sclerotized, as in Fig. 84. .......... *arnicivora* n. sp.

**Description.** — Head. Frons approximately twice width of eye at level of front ocellus, not projected in front of eye margin in profile. Mouth margin normal. Two Ors, equal in size, directed upwards; one large Ori and a small hair below, directed inwards and upwards; orbital setulae few, approximately eight to nine, procline. Eyes oval, almost equal in height to their length; ocellar triangle small. Gena approximately one-fourth vertical eye height. Third antennal article rounded at tip, with normal pubescence, arista normal, pubescent.

Mesonotum. Dorsocentrals 3+1 strong bristles; acr in two rows.

Wing. Length in male 2.4 mm; costa extended to vein R*4+5*; costal segments 2-4 in the ratio of 1 : 0.3 : 0.5; crossvein m-m absent.

Male genitalia (Fig. 83-85). Hypandrium (Fig. 83) small, side arms broad, no apodeme; pregonites broad; postgonites elongate; surstyl normal; aedeagus complex as illustrated in Fig. 84; ejaculatory apodeme (Fig. 85) small, bulb small and membranous.

Colour. Frons pale whitish, slightly darkened at centre; orbits pale; gena yellowish; ocellar triangle weakly shining black; vte on black and vti on margin of dark and yellow grounds; antennae black; mesonotum, scutellum and pleura mat greyish black; coxae black; femora black, with slight yellow on distal tips; tibiae and tarsi black; squamae pale, fringe dark;
halteres pale.

*Derivation of the specific name.* — This species is named after the generic name of its food plant.

*Biology.* — Larvae make linear leaf mines on *Arnica cordifolia* Hook., family Compositae. Pupation occurs inside the leaf mine and the whitish puparia can be collected during July and August.

*Geographical distribution.* — The members of this species are known only from the type locality:


*Phytophyma asterophaga* Spencer


*Comparison and diagnostic characters.* — The members of this species belong to the group characterized by yellow frons; dark scutellum; essentially dark femora and pleura and upper Ors lacking. The adults resemble those of *P. ciliolatii* Spencer and differ in having a darker notopleural area and different biology. Spencer (1969) illustrated the aedeagus and leaf mine distinctive of this species.

*Biology.* — Larvae make linear mines on the leaves of *Aster conspicuus* Lindl., family Compositae. The leaf mines are distinctive in having frass disposed in the form of discrete granules alternately in the mine. Pupation occurs outside the mine.

*Geographical distribution.* — The members of this species were previously known only from the locality of type series from Western Canada (Spencer, 1969). I examined the following material from Alberta:


*Phytophyma banffensis* Spencer

*Phytophyma banffensis* Spencer, 1969:231.

*Comparisons and diagnostic characters.* — The members of this species belong to the group characterized by yellow frons; essentially dark scutellum, pleura and femora; acrostichals in three to six rows and third antennal article with normal pubescence. The adults resemble those of *P. aquilegiana* Frost and *P. aquilegioides* new species but differ in having deeper gena, approximately one-half of vertical eye height, elongate third antennal article and distinct male genitalia. Spencer (1969) illustrated the distinctive aedeagus.

*Geographical distribution.* — The members of this species were previously known only from the locality of its type series from western Canada (Spencer, 1969). I examined the following material from Alberta:


*Phytophyma blairmorensis* new species

*Comparison and diagnostic characters.* — A member of this species belongs to the group characterized by yellow frons; two equal Ors: broad epistoma; normal third antennal segment; dark scutellum and mostly dark femora and pleura. The adult resembles those of
P. lupi\text{"} Sehgal and P. aquilegiophaga Spencer but differs in having second antennal article black and distinct male genitalia. It also resembles other similar species, P. ill\text{"}ustris Spencer and P. aff\text{"}inalis Frost, and may be separated from them as shown below in extension to Spencer's (1969) key to Canadian species of the genus Phytomyza Fallén.

29a. Large specimens, wing length 3.0-3.4 mm; normally one Ors \ldots \ldots . illustris Spencer
29b. Smaller specimens, wing length at most 2.4 mm in male; two Ors \ldots \ldots \ldots \ldots .

29b. Frons entirely yellow; aedeagus as illustrated (Spencer, 1969). . . . . . aff\text{"}inalis Frost
Frons slightly darkened; aedeagus as in Fig. 88, 89 . . . . . . . . . . blairmorensis n. sp.

Description. — Head. Frons approximately 2.5 times width of eye at level of front ocellus; orbits broad, distinctly projected in front of eye margin in profile; broad epistoma. Two equal Ors, directed upwards; two Ori, directed inwards and upwards, lower one weaker than upper; orbital setulae few, six to seven, proclinate. Eyes oval, slightly slanted, their vertical height being approximately 1.25 times their length; ocellar triangle small. Gena approximately one-third vertical eye height. Third antennal article large, circular, with normal pubescence; arista normal, pubescent.

Mesonotum. Dorsocentrals 3+1 strong bristles; acr approximately eight to nine, in two rows.

Wing. Length in male approximately 1.75 mm; costa extended to vein R_{4,5}; costal segments 2-4 in ratio of 1 : 0.35 : 0.65; crossvein m-m absent.

Male genitalia (Fig. 86-90). Hypandrium (Fig. 86) V-shaped, narrow side arms, no distinct apodeme; pregonites broad; postgonites (Fig. 87) long, with hook-like process anteriorly; aedeagus (Fig. 88, 89) as illustrated; ejaculatory apodeme (Fig. 90) small, well sclerotized, bulb small, membranous.

Colour. Frons yellow, very slightly darkened above; orbits yellow, darkened slightly near upper Ors; gena and lunule yellow; ocellar triangle weakly shining black; both Vt’s on dark ground; antennae black; mesonotum, scutellum and pleura mat grey; legs black, only distal tips of femora with slight yellow; squamae pale, fringe brown; halteres yellow.

Derivation of the specific name. — This species is named after the locality of its type specimen.

Geographical distribution. — A member of this species is known only from the type locality:


Phytomyza canadensis Spencer

Phytomyza canadensis Spencer, 1969:231.

Comparison and diagnostic characters. — The main distinguishing characters of the members of this species are: dark frons; two equal Ors; brilliantly shining black mesonotum and scutellum; acrostichals in approximately two rows; dark tarsi and second costal segment less than three times length of fourth. The adults resemble those of the very similar species, P. mult\text{"}ifidae new species, but differ in having narrower orbits and different puparia.

Biology. — The larvae were stated by Spencer (1969) to make linear mines in the leaves of Anemone canadensis L., family Ranunculaceae. The characteristic leaf mines have been illustrated by Spencer (1969). However, a confusion seems to have arisen, since the leaf figured by Spencer is clearly not of this species. Mr. Griffiths and I have found similar leaf mines only on Anemone riparia Fern., never on A. canadensis L. The mined leaf figured by Spencer was probably also of A. riparia Fern.

Geographical distribution. — The members of this species are known only from Canada
from the type locality (Spencer, 1969). I examined the following material from Alberta:

CANADA. Alberta: Numerous empty leaf mines on *Anemone riparia* Fern., Edmonton, White Mud Creek park, 5-6.ix.1968, and in Elk Island park.

*Phytomyza caprifoliae* Spencer


**Comparison and diagnostic characters.** — The main distinguishing characters of the members of this species are: frons black, not projected; two equal Ors; normal third antennal article; mat grey mesonotum, scutellum and pleura; approximately four rows of acr; black tarsi and second costal segment less than three times length of fourth. The adults resemble those of *P. pericymeni* de Meijere and can be reliably separated only by examination of male genitalia. Spencer (1969) illustrated the distinctive aedeagus.

**Biology.** — Larvae mine the leaves of *Symphoricarpos* sp., family Caprifoliceae.

**Geographical distribution.** — The members of this species are known only from the locality of its type series from Canada (Spencer, 1969). I examined the following material from Alberta:


*Phytomyza ciliolati* Spencer

*Phytomyza ciliolati* Spencer, 1969:234.

**Comparison and diagnostic characters.** — The members of this species belong to the group characterized by yellow frons; dark scutellum; essentially dark femora and pleura and upper Ors absent. The adults resemble those of *P. asterophaga* Spencer but differ in having yellow on notopleural areas and different biology.

**Biology.** — Larvae make linear mines on the leaves of *Aster ciliolatus* Lindl., family Compositae. The leaf mines are distinctive in having frass disposed in continuous streaks. Pupation occurs outside the mine. Spencer (1969) illustrated the characteristic leaf mine.

**Geographical distribution.** — The members of this species are known only from the type locality (Spencer, 1969). I examined the following material from Alberta:

CANADA. Alberta: Numerous leaf mines on *Aster ciliolatus* Lindl. around Edmonton during July and August.

*Phytomyza cineracea* Hendel


**Comparison and diagnostic characters.** — The main diagnostic characters of the members of this species are: yellowish brown frons; mat grey mesonotum and scutellum; black tarsi and second costal segment approximately two times the length of the fourth. The adults are distinctive in having an elongate third antennal article. They differ from those of the similar species, *P. erigerontophaga* Spencer, in having frons distinctly projected above eyes and distinct male genitalia. Griffiths (1968) and Spencer (1969) illustrated the aedeagus characteristic of this species.

**Biology.** — Larvae of this species feed inside the stems of *Ranunculus* spp., Ranunculaceae (Griffiths, 1968).

**Geographical distribution.** — The members of this species are known from Europe, Ice-
Phytomyza clematiphaga Spencer

Phytomyza clematiphaga Spencer, 1969:236.

Comparison and diagnostic characters. — The members of this species belong to the group characterized by yellow frons and partially yellow scutellum. The adults differ from those of P. major Malloch in having their body darker and third antennal article black. They differ from those of P. ranunculi (Schrank) in having both Ors of equal length and distinct male genitalia. Spencer (1969) illustrated the distinctive aedeagus.

Biology. — Larvae make linear mines on the leaves of Clematis verticillaris DC. family Ranunculaceae. Pupation occurs inside the leaf mine.

Geographical distribution. — The members of this species are known from Canada only from the type locality. I examined the following material from Alberta:


Phytomyza colemanensis new species

Comparison and diagnostic characters. — A member of this species belongs to the group characterized by yellow frons; two equal Ors; mouth margin normal; third antennal article with normal pubescence; dark scutellum; mostly dark femora and pleura; and acrostichals approximately three to four scattered hairs. The adult resembles those of P. penstemonis Spencer and P. plantaginis R.-D. from which it may be separated as shown below in the extension to Spencer's (1969) key to Canadian species of the genus Phytomyza Fallén:

41. Fore-coxae essentially dark ........................................ 41a.
   - Fore-coxae conspicuously yellow .................. plantaginis R.-D.

41a. First and second antennal segment black; aedeagus as illustrated (Spencer, 1969) ........................................ penstemonis Spencer
   - First and second antennal segment yellowish brown; aedeagus as in Fig. 91........................................ colemanensis n. sp.

Description. — Head. Frons almost twice width of eye at level of front ocellus, slightly projected in front of eye margin in profile. Mouth margin normal. Two equal Ors directed upwards; one strong Ori incurred, one small hair present below Ori; orbital setulae only two, procline. Eyes slightly slanted, their vertical height 1.2 times their length, bare; ocellar triangle small. Gena approximately one-third vertical eye height. Third antennal article with slight angle anterodorsally, with normal pubescence; arista normal, pubescent.

Mesonotum. Dorsocentral 3+1 strong bristles; acr few, three to four scattered hairs.

Wing. Length in male 1.6 mm; costa extended to vein R₄₅; costal segments 2-4 in the ratio of 1 : 0.3 : 0.7; crossvein m-m absent.

Male genitalia (Fig. 91). Hypandrium U-shaped, with broad side arms; pregonites broad;
postgonites elongate, with curved process anteriorly; surstyl normal; aedeagus (Fig. 91) with distinctive hypophallus; ejaculatory apodeme broad, bulb small and membranous.

Colour. Frons, orbits and gena yellow; ocellar triangle weakly shining black; Vte on black and Vti on margin of dark and yellow ground; first and second antennal articles yellowish brown; third antennal article black; legs black; mesonotum, scutellum and pleura mat greyish; squamae and fringe pale.

*Derivation of the specific name.* — This species is named *colemansenis* after the name of the type locality.

*Geographical distribution.* — A member of this species is known only from the type locality:


*Phytomyza columbinae* new species

*Comparison and diagnostic characters.* — The members of this species belong to the group characterized by yellow frons; upper Ors shorter than lower; dark scutellum; essentially dark femora and pleura. The adults differ from those of the similar species, *P. timida* Spencer, and may be separated as shown below in extension to Spencer's (1969) key to Canadian species of the genus *Phytomyza* Fallén:

24. Jowls narrow, one-fifth to one-fourth vertical eye height. ................. 24a
24a. Fore-tibia yellowish; aedeagus as illustrated (Spencer, 1969) .... *timida* Spencer
- Fore-tibia dark; aedeagus as in Fig. 93, 94 ................. *columbinae* n. sp.

*Description.* — Head. Frons approximately twice width of eye at level of front ocellus, not projected in front of eye margin in profile. Mouth margin normal; lunule high. Two Ors, directed upwards, upper one shorter than lower; two Ori, directed inwards and upwards; orbital setulae few to five, procline. Eyes oval, approximately 1.2 times higher than their length, bare; ocellar triangle small. Gena approximately 0.22 times vertical eye height. Third antennal article rounded at tip, with normal pubescence; arista normal, pubescent.

Mesonotum. Dorsoventrals 3+1 strong bristles; acr in four to five irregular rows.

Wing. Length 1.5-1.8 mm; costa extended to vein R₄₊₅; costal segments 2-4 in the ratio of 1 : 0.33 : 0.4; crossvein m-m absent; wing tip at M₃₊₄.

Male genitalia (Fig. 92-95). Hypandrium (Fig. 92) V-shaped, with small apodeme; pregonites broad; postgonites elongate; surstyl normal; aedeagus (Fig. 93, 94) as illustrated; ejaculatory apodeme (Fig. 95) small, fan-shaped, bulb small, membranous.

Colour. Frons and gena pale; orbits slightly darkened, lunule dark; ocellar triangle shining black; antennae black; both Vt's on dark ground; mesonotum, scutellum and pleura mat greyish black; legs black; squamae pale, fringe brown; halteres yellow.

*Derivation of the specific name.* — This species is named *columbinae* after the common name of its food plant, columbine (*Aquilegia*).

*Biology.* — Larvae make blotch mines in the leaves of *Aquilegia* sp. (cultivated) and *Thalictrum venulosum* Trel., family Ranunculaceae. Pupation occurs outside the mine. The dark brown puparium measures approximately 1.5 mm x 0.75 mm and is densely covered with small spinules.

*Geographical distribution.* — The members of this species are known only from the type locality:

CANADA: Alberta: Holotype ♂ Edmonton, White Mud Creek park, from blotch mines on *Thalictrum venulosum* Trel., coll. 6.ix.1968, emerged 19.x.1968; paratypes 2 ♂♂ Edmonton, Aberhart Hospital, University of Alberta campus, from leaf mines on *Aquilegia* sp.

Phytomyza delphinivora Spencer

Phytomyza delphinivora Spencer, 1969:238.

Comparisons and diagnostic characters. — The members of this species belong to the group characterized by dark frons, mesonotum and scutellum; essentially dark femora and pleura; upper Ors shorter than lower and second costal segment less than three times length of fourth. The adults differ from those of the similar species, P. mertensiae new species and P. prava Spencer, in having only two rows of acrostichals and distinct male genitalia, Spencer (1969) illustrated the aedeagus characteristic of this species.

Biology. — Larvae mine the leaves of Delphinium sp. (cultivated), family Ranunculaceae. Spencer (1969) illustrated the characteristic linear mine. Pupation occurs outside the mine.

Geographical distribution. — The members of this species are known only from the type locality (Spencer, 1969). I examined the following material from Alberta:

CANADA. Alberta: 2 η Edmonton, White Mud Creek park, 28.v.1967; Numerous leaf mines around Edmonton on Delphinium sp. (cultivated).

Phytomyza edmontonensis new species

Comparisons and diagnostic characters. — A member of this species belongs to the group characterized by dark frons; upper Ors absent; essentially dark femora and pleura; mat greyish black mesonotum and scutellum; and second costal segment more than three times length of fourth. The adult resembles that of P. modica Spencer from which it may be separated as shown below in an extension to Spencer’s (1969) key to Canadian species of the genus Phytomyza Fallén:

78. Second costal section long, five times length of fourth. ........... pallipes Spencer
- Second costal section shorter, up to 3.5 times length of fourth ............... 78a

78a. Second costal section slightly over three times length of fourth; veins pale; aedeagus as illustrated (Spencer, 1969). ............... modica Spencer
- Second costal section 3.5 times length of fourth; veins brownish; aedeagus as in Fig. 97. ....................... edmontonensis n. sp.

Description. — Head. Frons approximately twice width of eye at level of front ocellus, not projected in front of eye margin in profile. One Ors, curved upwards; three strong Ori directed inwards; orbital setulae numerous, proclineate. Eyes almost circular, their vertical height being 1.1 times their length; ocellar triangle small. Gena narrow, approximately 0.3 times eye height midway between vibrissal and posterior margins. Third antennal article slightly enlarged, rounded at tip, with normal pubescence; arista normal, pubescent.

Mesonotum. Dorsoventrals 3+1 strong bristles; acr in three irregular rows.

Wing. Length in male 2.4 mm; costa extended to vein R₄+₅; costal segments 2-4 in the ratio of 1 : 0.26 : 0.3; crossovein m-m absent.

Male genitalia (Fig. 96-98). Hypandrium (Fig. 96) U-shaped, with broad side arms, pregonites elongate; postgonites broad anteriorly and with a small hook; surstyli small; aedeagus (Fig. 97) darkly sclerotized and as illustrated; ejaculatory apodeme (Fig. 99) very broad, bulb small and membranous, latter with darkly sclerotized areas.

Colour. Frons, orbits and gena brown; ocellar triangle black; mesonotum, scutellum and
pleura mat black; femora black, tibiae and tarsi yellowish brown; wing veins brownish; squamae and fringe pale; halteres yellow.

**Derivation of the specific name.** – This species is named after the type locality.

**Geographical distribution.** – A member of this species is known only from the type locality:


**Phytomyza evanescens** Hendel


**Comparisons and diagnostic characters.** – The diagnostic characters of the members of this species are: dark frons; two equal Ors; normal third antennal article; mat grey mesonotum, scutellum and pleura; dark tarsi; second costal segment less than three times length of fourth and acrostichals in approximately four rows. The adults differ from those of the similar species, *P. caprifoliæ* Spencer, *P. pericylmeni* de Meijere and *P. queribunda* Spencer in having frons distinctly projected and characteristic male genitalia. The surstyli have long wing-like processes. Griffiths (1964) illustrated the male genitalia characteristic of this species. Spencer (1969) also figured the aedeagus.

**Biology.** – Larvae feed inside the stems of *Ranunculus* spp., family Ranunculaceae (Griffiths, 1969).

**Geographical distribution.** – The members of this species are known from Europe, Iceland, Faroes (Griffiths, 1968) and Canada (Spencer, 1969). I examined the following material from Alberta:


**Phytomyza fuscula** Zetterstedt


**Comparison and diagnostic characters.** – The members of this species belong to the group characterized by yellow frons; dark scutellum; essentially dark femora and pleura; mouth margin normal; third antennal article black, with normal pubescence; two Ors equal; acr in two well-defined rows and dark fore-coxæ.

Spencer (1969) groups this species both under yellow frons and dark frons. The Alberta specimens correspond to the colour form having yellow frons. The aedeagus of Alberta specimens corresponds exactly to that figured by Spencer (1969) including the weakly sclerotized membranous processes in the distiphallus. Griffiths' (1969) description of *fuscula* Zett. from Greenland refers to *puccinelliae* Spencer (see Spencer, 1969).

**Biology.** – Larvae of this species mine the leaves of grasses (Gramineæ) in Canada (Spencer, 1969).

**Geographical distribution.** – The members of this species are known from Europe (Hendel, 1935) and Canada (Spencer, 1969). I examined the following material from Alberta:


**Phytomyza gregaria** Frick


**Comparison and diagnostic characters.** – The distinguishing characters of the members of
this species are: dark frons; two equal Ors; normal third antennal article; mat black mesonotum, scutellum and pleura; acrostandals in approximately four rows; dark tarsi and second costal segment less than three times length of fourth. The adults resemble those of the similar species, *P. pericylmeni* de Mejere, but differ in having darker mesonotum; narrower gena, approximately one-fourth eye height and distinct male genitalia. The aedeagus of an Alberta specimen is illustrated in Fig. 99. Spencer (1969) also illustrated the aedeagus.

**Biology.** — The larvae mine the leaves of *Lonicera involucrata* (Richards) Banks, family Caprifoliaceae.

**Geographical distribution.** — The members of this species are known from United States (Frick, 1959) and Canada (Spencer, 1969). I examined the following material from Alberta:

**CANADA.** Alberta: 1 ♂ St. Albert, near Edmonton, 18.vi.1967; Numerous leaf mines on *Lonicera involucrata* (Richards) Banks around Edmonton

*Phyto myza illustris* Spencer


**Comparison and diagnostic characters.** — The members of this species differ from those of similar species, *blairmorensis* new species and *affinalis* Frost, in larger size, wing length 3.0-3.4 mm and normally only one Ors. Spencer (1969) illustrated the aedeagus characteristic of this species.

**Geographical distribution.** — Known from Alberta, British Columbia and Yukon Territory. The Alberta locality is:

**CANADA.** Alberta: Blairmore (Spencer, 1969).

*Phyto myza involucratae* Spencer

*Phyto myza involucratae* Spencer, 1969:249.

**Comparison and diagnostic characters.** — The members of this species differ from those of a similar species, *mili* Kaltenbach, in having larger size, wing length 2.8-3.3 mm, grey mesonotum and third antennal article large and elongate. Spencer (1969) illustrated the distinctive aedeagus.

**Geographical distribution.** — Known from Alberta and British Columbia. The Alberta locality is:

**CANADA.** Alberta: Frank; St. Albert.

The following type specimen was examined:


*Phyto myza jasperensis* new species

**Comparisons and diagnostic characters.** — A member of this species belongs to the group characterized by yellow frons; normal mouth margin and third antennal article; two equal Ors; dark scutellum; mostly dark femora and pleura and acrostichals in two rows. The adult resembles that of *P. pedicularicaulis* Spencer and can be reliably separated only by examination of male genitalia. This species may be included in Spencer’s (1969) key to Canadian species of the genus *Phyto myza* Fallén by amending couplet 43 and extending 44 as below:

43. Frons strongly projected above eyes; jowls conspicuously deep, two-thirds eye height ............................................. *subtenella* Frost
44. Frons less projected; jowls at most one-half eye height. ............................................. 44a
44a. Aedeagus as illustrated (Spencer, 1969) ............... pedalicularicaulis Spencer
- Aedeagus as in Fig. 102. ................................... jasperensis n. sp.

Description. — Head. Frons approximately 2.5 times width of eye at level of front ocellus, projected in front of eye margin in profile. Mouth margin normal. Two equal Ors directed upwards; two Ori, lower one smaller than upper, incurved; orbital setulae few, approximately eight, proclinate. Eyes oval, their vertical height being 1.3 times their length, bare; ocellar triangle small. Gena approximately one-third eye height. Third antennal article rounded at tip, with normal pubescence; arista slightly thickened at base, pubescent.

Mesonotum. Dorsocentrals 3+1 strong bristles; acr in two rows.

Wing. Length in male 2.6 mm; costa extended to vein R_{4.5}; costal segments 2-4 in ratio of 1 : 0.27 : 0.45; crossvein m-m absent.

Male genitalia (Fig. 100-103). Hypandrium (Fig. 100) V-shaped, with narrow side arms; pregonites broad; postgonites (Fig. 101) long, with hook-like process anteriorly, surstyli normal; aedeagal apodeme exceptionally long; aedeagus (Fig. 102) relatively short and as illustrated; ejaculatory apodeme (Fig. 103) broad, bulb small and membranous.

Colour. Frons, orbits and gena bright yellow; maxillary palpi black; ocellar triangle weakly shining black; lunule yellow; both Vt's on dark ground; first antennal article yellowish, second and third articles black; mesonotum, scutellum and pleura mat grey; only mesopleura with narrow yellow band along upper margin; legs with fore-coxae yellowish, femora dark with yellow on distal tips, tibiae and tarsi black; squamae yellow, fringe brownish; halteres yellow.

Derivation of the specific name. — The species is named jasperensis after the name of the type locality.

Geographical distribution. — This species is known only from the following locality: CANADA. Alberta: Holotype ♂ Jasper, 17.vi.1966.

Phytomyza lactuca Frost

Phytomyza lactuca Frost, 1924:85.

Comparison and diagnostic characters. — The members of this species belong to the group characterized by yellow frons; dark scutellum; essentially dark pleura and femora; and two Ors equal. The adults differ from all other species in this group by having conspicuously long pubescence on the third antennal article and distinct male genitalia. The aedeagus of an Alberta specimen bred from Crepis tectorum L. is illustrated in Fig. 104. Spencer (1969) illustrated the aedeagus characteristic of this species.

Biology. — Larvae make long linear mines, usually on under surface of the leaves of Taraxacum officinale Weber, Crepis tectorum L. and Sonchus uliginosus Bieb., family Compositae. Larvae are also known to mine the leaves of Lactuca scariola var. integrifolia (Bogenh.) G. Beck in Pennsylvania, U. S. A. (Frost, 1924).

Geographical distribution. — The members of this species are known from United States (Frick, 1959) and Canada (Spencer, 1969). I examined the following material from Alberta:

Phytomyza lanati Spencer


Comparison and diagnostic characters. — The members of this species differ from those of a similar species, *spondylii* R.-D., in having second costal segment shorter, about 3.5 times length of fourth. These specimens cannot be satisfactorily separated on the basis of external characteristics alone; however, the male genitalia are distinct. Spencer (1969) illustrated the aedeagus characteristic of this species.


Geographical distribution. — The members of this species are known from California in United States and Alberta in Canada. The Alberta locality is:

CANADA. Alberta: Jasper (Spencer, 1969).

Phytomyza lupini Sehgal

Phytomyza lupini Sehgal, 1968:73.

Comparisons and diagnostic characters. — The members of this species belong to the group characterized by yellow frons; dark scutellum; mostly dark pleura and femora; two oes equal; third antennal article black, with normal pubescence and broad epistoma. The adults resemble those of *P. aquilegiophaga* Spencer and differ in having slightly paler grey mesonotum and distinct male genitalia. They differ from another similar species, *P.blairmorensis* new species, in having the second antennal article yellowish brown and distinct male genitalia. Sehgal (1968) illustrated the head, wing and male genitalia characteristic of this species. Spencer (1969) also illustrated the aedeagus.

Biology. — Larvae bore inside the stems of *Lupinus sericeus* Pursh, family Leguminosae. The pale whitish puparia are found inside the stems. The puparia are characteristic in having a small horn in the posterior spiracles.

Geographical distribution. — The members of this species are known only from western Canada: Alberta and British Columbia (Sehgal, 1968). The material examined remain the same as reported earlier (Sehgal, 1968).

Phytomyza lupinivora Sehgal


Comparison and diagnostic characters. — The main distinguishing characters of the members of this species are: dark frons; distinctly mat greyish mesonotum and scutellum; dark tarsi; normal third antennal article and acrostichals in two rows. The adult resembles that of *P. oxytrupidis* new species from which it is separated by having slightly longer second costal segment, approximately one and a quarter times the length of the fourth, and darker orbits. Sehgal (1968) illustrated the head and wing characteristic of this species.

Biology. — Larvae make linear mines on the leaves of *Lupinus sericeus* Pursh, family Leguminosae. Pupation occurs outside the mine.

Geographical distribution. — A member of this species is known only from the type locality:

CANADA. Alberta: Blairmore (Sehgal, 1968).
**Phytomyza luteiceps** new species

**Comparisons and diagnostic characters.** — The members of this species belong to the group characterized by yellow frons; dark scutellum and yellow femora. The adults resemble those of *P. flavicornis* Fallén and can be separated reliably only by examination of characters of the male genitalia. Spencer (1965d, 1969) illustrated the aedeagus of *P. flavicornis* Fallén. It is doubtful at present if the true *P. flavicornis* Fallén occurs in Alberta. This species is included in Spencer's (1969) key to Canadian species of the genus *Phytomyza* Fallén, by amending and extending the couplet 10 as below:

10. All coxae yellow; jowls exceptionally deep at rear, at least two-thirds of eye height ........................................ 10a

- Mid- and hind-coxae black ........................................ *rufipes* Meigen

10a. Mesonotum black, weakly shining; aedeagus as illustrated (Spencer, 1969) ........

- Mesonotum mat greyish black; aedeagus as in Fig. 106 ............ *luteiceps* n. sp.

**Description.** — Head. Frons wide, little more than three times width of eye at level of front ocellus, conspicuously projected in front of eye margin in profile. Broad epistoma present; lunule low. One strong Ors and three strong Ori; orbital setulae 10-11, procline. Eyes oval and slanting; their vertical height being almost equal to their length, bare; ocellar triangle small. Gena deep, approximately 0.7 times vertical eye height. Third antennal article rounded at tip, with short upcurved pubescence; arista normal and pubescent.

Mesonotum. Dorsocentra 3+1 strong bristles; acr in approximately two rows.

Wing. Length 2.5 to 2.8 mm; costa extended to vein R₄₊ₛ; costal segments 2-4 in the ratio of 1 : 0.3 : 0.4; crossvein m-m absent.

Male genitalia (Fig. 105-107). Hypandrium (Fig. 105) almost circular below, with broad arms as illustrated; pregonites broad; postgonites long with small process anteriorly; aedeagus (Fig. 106) as illustrated; ejaculatory apodeme (Fig. 107) short, bulb small.

Colour. Frons bright yellow; orbits and gena yellow; Vte on black and Vti on yellow ground; ocellar triangle shining black; lunule yellow; antennae completely yellow; arista brown; mesonotum and scutellum mat grey; humeral and notopleural areas yellow; sternopleura slightly brownish at base; meso- and pteropleura yellow; legs with coxae, femora and tibiae yellow, tarsi slightly brownish; squamae yellow, fringe brown; halteres yellow.

**Derivation of the specific name.** — This species is named *luteiceps* because of the mostly yellow head.

**Biology.** — Not confirmed, but the larvae will probably prove to feed in stems of *Urtica.*

**Geographical distribution.** — The members of this species are known only from the localities of its type series as below:


**Phytomyza major** Malloch

*Phytomyza major* Malloch, 1913b:150.

**Comparisons and diagnostic characters.** — The members of this species belong to the group characterized by yellow frons and yellow scutellum. The adults differ from those of other species in this group, *P. elemapathaga* Spencer and *P. ranunculi* (Schrank), in having a mostly yellow body, yellow third antennal article and distinct male genitalia. The adults are largely yellow flies, wing length approximately 4.0 mm. Spencer (1969) illustrated the distinctive aedeagus. The aedeagus of an Alberta specimen is as in the Fig. 108.
Geographical distribution. – The members of this species are known from Labrador (Frick, 1959) and western Canada (Spencer, 1969). I examined the following material from Alberta:


Phytomyza matricariae Hendel


Comparison and diagnostic characters. – The members of this species belong to the group characterized by yellow frons; dark scutellum; essentially dark femora; upper Ors shorter than lower; and with slight yellow on upper parts of mesopleura, humeral and notopleural areas. The adults resemble those of P. spongyllii R.-D. but differ in having the second costal segment shorter, approximately three times the length of the fourth and distinct male genitalia. Spencer (1969) illustrated the aedeagus characteristic of this species.

Bioglogy. – In Alberta the larvae make linear mines in the leaves of Achillea millefolium L., A. sibirica Ledeb., Chrysanthemum sp. (cultivated), Matricaria matricarioide (Less.) Porter, and Tanacetum vulgare L., belonging to the family Compositae. Pupation occurs outside the mine. Detailed biology and host-plant relationships are discussed in a separate paper (Sehgal, 1971).

Geographical distribution. – The members of this species are known from Europe (Hendel, 1935) and Canada (Spencer, 1969). I examined numerous specimens bred from all hosts listed above from various localities around Edmonton.

Phytomyza mertensiae new species

Comparison and diagnostic characters. – The members of this species belong to the group characterized by dark frons; upper Ors shorter than lower; dark mesonotum and scutellum; essentially dark femora and pleura; and second costal segment less than three times length of fourth. The adults differ from those of the similar species, P. prava Spencer and P. sehali Spencer, in having darker frons and distinct male genitalia. This species is included in Spencer’s (1969) key to Canadian species of the genus Phytomyza Fallén by amending and extending couplet 88 as below:

88. Third antennal article distinctly enlarged ................. nepetae Hendel
     - Third antennal article small .......................... 88a

88a. Frons paler, brownish above; acr strong ...................... sehali Spencer
     - Frons dark brown; acr normal; aedeagus as in Fig. 110, 111 .... mertensiae n. sp.

Description. – Head. Frons approximately two and a half times width of eye level of front ocellus, slightly projected in front of eye margin in profile. Mouth margin normal; lunule high. Two Ors, directed upwards, upper smaller than lower; two Ori, directed inwards and upwards, lower one weaker than upper; orbital setulae few, approximately six to seven, procline. Eyes oval, approximately 1.17 times higher than their length, bare; ocellar triangle small. Gena approximately 0.22 times vertical eye height. Third antennal article normal, rounded at tip; arista normal, pubescent.

Mesonotum. Dorsocentrals 3+1 strong bristles; acr in four irregular rows.

Wing. Length approximately 2.0 mm; costa extended to vein R_{4+5}; costal segments 2-4 in the ratio of 1 : 0.32 : 0.35; crossvein m-m absent.

Male genitalia (Fig. 109-112). Hypandrium (Fig. 109) small, V-shaped, with broad side
arms; pregonites broad; postgonites elongate; surstyli normal; aedeagus (Fig. 110, 111) complex as illustrated; ejaculatory apodeme (Fig. 112) broad, bulb small and membranous.

Colour. Frons, orbits, gena and lunule dark brown; ocellar triangle weakly shining black; antennae black; mesonotum, scutellum and pleura mat greyish black; coxae black; femora black, with yellow on distal tips; tibiae and tarsi dark brown; squamae yellow, fringe brown; halteres pale.

Derivation of the specific name. — This species is named after the generic name of its food plant.

Biology. — Larvae make linear mines in the leaves of Mertensia paniculata (Ait.) G. Don, family Boraginaceae. Pupation occurs outside the mine.

Geographical distribution. — The members of this species are known only from the type locality:

CANADA. Alberta: Holotype δ Edmonton, White Mud Creek park, from leaf mines on Mertensia paniculata (Ait.) G. Don, coll. 10.ix.1966, emerged 10.iii.1967; paratypes 1 ♀ same data; 1 δ same locality, 8.vi.1967.

Phytomyza merula Spencer


Comparison and diagnostic characters. — The members of this species differ from those of a very similar species, gregaria Frick, in having deeper gena, about one-half eye height and orbits in form of a broad ring below eyes. Spencer (1969) illustrated the distinctive aedeagus.

Geographical distribution. — Known only from Alberta, Canada from the following locality:

CANADA. Alberta: Jasper (Spencer, 1969).

Phytomyza milii Kaltenbach

Phytomyza milii Kaltenbach, 1864:248; Spencer, 1969:255.

Phytomyza intermedia Spencer; Griffiths, 1964:405.

Comparison and diagnostic characters. — The members of this species belong to the group characterized by dark frons; mat black mesonotum and scutellum; two equal Ors, black tarsi and second costal segment at least three times the length of the fourth. The adults resemble those of P. involucratae Spencer and can be reliably separated only by examination of male genitalia. The sclerotization of distiphallus varies in this species (Griffiths, 1964). The aedeagus of an Alberta specimen is as illustrated in Fig. 113. Griffiths (1964) illustrated the aedeagus of European and Faeroese specimens. Spencer (1969) also illustrated the aedeagus.

Biology. — Larvae probably mine the leaves of grasses (Gramineae) in Alberta.

Geographical distribution. — The members of this species are known from Europe, Iceland, Faeroes (Griffiths, 1964) and Canada (Spencer, 1969). I examined the following material from Alberta:


Phytomyza miranda Spencer

Phytomyza miranda Spencer, 1969:255.

Comparison and diagnostic characters. — The members of this species differ from those of
a similar species, *luteiceps* new species, in having black third antennal article. The elongate surstyli and aedeagus as figured by Spencer (1969) are quite distinct.

**Geographical distribution.** — The members of this species are known only from Alberta, Canada from the following locality:

CANADA. Alberta: Blairmore (Spencer, 1969).

*Phytomyza misella* Spencer

*Phytomyza misella* Spencer, 1969:256.

**Comparisons and diagnostic characters.** — The members of this species belong to the group characterized by yellow frons; normal mouth margin and third antennal article; two equal Ors; essentially dark femora and pleura; acrostichals in two rows; and yellow fore-coxae. The adults differ from those of the similar species, *P. subtenella* Frost, by having frons less projected, narrower gena and distinct aedeagus. They also resemble those of *P. pedicularicaulis* Spencer and *P. jasperensis* new species but have entirely different male genitalia. The aedeagus of an Alberta specimen is illustrated (Fig. 114). Spencer (1969) also illustrated the aedeagus.

**Geographical distribution.** — The members of this species are known only from western Canada from the type locality (Spencer, 1969). I examined the following material from Alberta:


*Phytomyza multifidae* new species

**Comparisons and diagnostic characters.** — The members of the species belong to the group characterized by dark frons; two equal Ors; brilliantly shining black mesonotum, scutellum and pleura; and second costal segment less than three times length of fourth. The members of this species were included in Spencer’s (1969) key to Canadian species of the genus *Phytomyza* Fallén at couplet 61 as *Phytomyza* sp. (Sehgal). This couplet is amended as below:

61. Orbits normal in width; only fore knees yellowish ............. *canadensis* Spencer
   - Orbits broad; knees variable from yellow to almost dark; wing base yellow; aedeagus as in Fig. 116 .................................. *multifidae* n. sp.

**Description.** — Head. Frons approximately 1.6 times width of eye at level of front ocellus, not projected in front of eye margin in profile. Mouth margin normal; lunule low. Two Ors, directed upwards, equal in size; two Ori, directed inwards, the lower one smaller than upper; orbital setulae few, approximately seven to eight, procline. Eyes almost circular, approximately 1.1 times higher than their length, bare; ocellar triangle small. Gena approximately one-third vertical eye height. Third antennal article rounded at tip, with normal pubescence; arista normal, pubescent.

Mesonotum. Dorsocentrales 3+1 strong bristles; acr in three to four irregular rows.

Wing. Length 1.5-1.7 mm; costa extended to vein R_{4+5}; costal segments 2-4 in the ratio of 1 : 0.33 : 0.66; crossvein m-m absent; M_{3,4} at wing tip.

Male genitalia (Fig. 115-117). Hypandrium (Fig. 115) small, V-shaped; pregonites broad; postgonites elongate; surstyli normal; aedeagus (Fig. 116) complex, as illustrated; ejaculatory apodeme (Fig. 117) small, fan-shaped, bulb small, membranous.

Colour. Frons, orbits, gena and lunule dark; ocellar triangle shining black; antennae black; mesonotum, scutellum and pleura shining black; legs black; distal tips of femora in females bright yellow, but in male dark; wing base yellow; squamae and fringe pale; halteres bright
yellow.

*Derivation of the specific name.* — This species is named after the specific epithet of its food plant *Anemone multifida* Poir.

*Biology.* — Larvae make linear mines in the leaves of *Anemone multifida* Poir., family Ranunculaceae. Pupation occurs outside the mine.

*Geographical distribution.* — The members of this species are known only from the type locality:


*Phytomyza oxytropidis* new species

*Comparison and diagnostic characters.* — The members of this species belong to the group characterized by dark frons; two equal Ors; normal third antennal article; mat greyish black mesonotum and scutellum; two rows of acrostichals; and dark tarsi. The adults resemble the member of *P. lupinivora* Sehgal from which they may be separated as shown below in extension to Spencer's (1969) key to Canadian species of the genus *Phytomyza* Fallén.

65. Second costal section short; less than 1.25 times length of fourth 65a
   - Second costal section longer, at least 1.5 times length of fourth 66
65a. Second costal section approximately 1.25 times length of fourth; orbits dark
   - Second costal section almost equal to fourth; orbits yellowish *

*Description.* — Head. Frons approximately twice width of eye at level of front ocellus, slightly projected in front of eye margin in profile. Two Ors equal in size, directed upwards; two Ori, lower one smaller than upper, directed inwards; orbital setulae few, six to seven, procinate. Eyes oval, approximately 1.2 times higher than their length; ocellar triangle small. Third antennal article rounded at tip, with normal pubescence; arista normal, pubescent.

Mesonotum. Dorsocentrals 3+1 strong bristles; acr few, three to six scattered hairs.

Wing. Length in male 1.6 mm; costa extended to vein R$_{4.5}$; costal segments 2-4 in the ratio of 1:0.5:0.93; crossvein m-m absent; M$_{3.4}$ at wing tip.

Male genitalia (Fig. 118-120). Hypandrium (Fig. 118) with broad side arms and conspicuously long apodeme; pregonites broad; postgonites elongate and broad anteriorly; surstyli small, without any big spines; aedeagus (Fig. 119) with characteristic long spines between two long, darkly sclerotized arms of basiphallus; distiphallus separated by a small membranous section; ejaculatory apodeme (Fig. 120) broad, bulb small.

Colour. Frons, gena, lunule and antennae all black; orbits slightly yellowish in most specimens; ocellar triangle weakly shining black; legs black; mesonotum, scutellum and pleura mat greyish black.

*Derivation of the specific name.* — This species is named *oxytropidis* after the generic name of its food plant.

*Biology.* — Larvae make linear mines on the leaflets of *Oxytropis splendens* Dougl. and *O. campestris gracilis* (A. Nels), family Leguminosae. Pupation occurs inside the leaf mine.

*Geographical distribution.* — The members of this species are known only from the localities of its type specimens as below:

**CANADA.** Alberta: Holotype ♂ Jasper, 5 miles south of Athabasca Falls, from leaf mines on *Oxytropis splendens* Dougl., coll. 15.x.1967, emerged iv.1968; paratypes 1 ♂, 2 ♀♀ same

*Phytomyza penstemonis* Spencer

*Phytomyza penstemonis* Spencer, 1969:265.

**Comparisons and diagnostic characters.** — The members of this species belong to the group characterized by yellow frons; dark scutellum; essentially dark femora and pleura; two equal Ors; acrostichals approximately three to four scattered hairs; and pale squamous fringe. The adults resemble those of *P. plantaginis* R.-D. and *P. colemannensis* new species but differ in having second antennal article black and distinct male genitalia. Spencer (1969) illustrated the aedeagus characteristic of this species.

**Biography.** — Larvae make linear mines on the leaves of *Penstemon confertus* Dougl. and *P. procerus* Dougl., family Scrophulariaceae. Larvae pupate inside the leaf mine.

**Geographical distribution.** — The members of this species were previously known only from the locality of its type series from western Canada (Spencer, 1969). I examined the following material from Alberta:


*Phytomyza periclymeni* de Meijere

*Phytomyza periclymeni* de Meijere, 1924:145.

**Comparison and diagnostic characters.** — The main distinguishing characters of the members of this species are: dark frons; normal third antennal article; two equal Ors; mat grey mesonotum, scutellum and pleura; dark tarsi; second costal segment less than three times the length of the fourth; and acrostichals in approximately four rows. The adults resemble those of *P. caprifolae* Spencer and can be reliably separated only by examination of male genitalia. Spencer (1969) illustrated the aedeagus characteristic of this species.

**Biography.** — In Alberta the larvae mine the leaves of *Lonicera involucrata* (Richards) Banks, family Caprifoliaceae.

**Geographical distribution.** — The members of this species are known from Europe (Hendel, 1935) and Canada (Spencer, 1969). I examined the following material from Alberta:


*Phytomyza petasiti* Spencer

*Phytomyza petasiti* Spencer, 1969:266.

**Comparisons and diagnostic characters.** — The members of this species belong to the group characterized by yellow frons; dark scutellum; essentially dark femora; and mostly yellow pleura. The adults resemble those of *P. spondylii* R.-D. and *P. matricariae* Hendel and differ in having both Ors equal and distinct male genitalia. The aedeagus of this species has been illustrated by Spencer.

**Biography.** — Larvae make linear mines on the leaves of *Petasites sagittatus* (Pursh) A. Gray, family Compositae. Pupation occurs outside the mine.
Geographical distribution. – The members of this species are known only from Canada (Spencer, 1969). I examined the following material from Alberta:


Phytomyza plantaginis R.-D.

Phytomyza plantaginis Robineau-Desvoidy, 1851:404.

Comparisons and diagnostic characters. – The members of this species belong to the group characterized by yellow frons; two equal Ors; third antennal article elongate and with normal pubescence; essentially dark femora and pleura; and acrostichals usually few isolated hairs. The adults differ from those of the similar species, P. syngenesiae (Hardy), by having pale squamal fringe; shorter second costal segment, approximately 1.5 times length of fourth, and conspicuously yellow fore-coxae. They differ from those of other similar species, P. penstemonis Spencer and P. colemannensis new species, by having yellow second antennal article and distinct male genitalia. Spencer (1969) illustrated the aedeagus characteristic of this species.

Biology. – In Alberta the larvae make linear mines in the leaves of Plantago major L., family Plantaginaceae. Pupation occurs inside the leaf mine.

Geographical distribution. – The members of this species are Holarctic in distribution, known from Europe, Australia, Japan, U. S. A. and Canada. I examined the following material from Alberta:


Phytomyza prava Spencer


Comparison and diagnostic characters. – The members of this species are distinctive in having frons which is basically yellow, but is conspicuously darkened. This species has therefore been included in both parts of the key having yellow frons and dark frons. Other diagnostic characters of the members of this species are: dark scutellum; dark femora and pleura and only one Ors. The adults resemble those of P. mertensiae new species, but differ in having yellowish frons and gena, and distinct male genitalia. Spencer (1969) illustrated the aedeagus characteristic of this species.

Biology. – Larvae make dark blotch mines on the leaves of Anemone canadensis L., family Ranunculaceae. The leaf mine of this species was illustrated among undetermined mines in Fig. 531 (Spencer, 1969). Pupation occurs outside the mine.

Geographical distribution. – The members of this species were previously known from Canada only from the locality of its type series (Spencer, 1969). I examined the following material from Alberta:

Phytomyza queribunda Spencer


Comparison and diagnostic characters. – The members of this species belong to the group characterized by dark frons; mat greyish mesonotum and scutellum; two Ors equal; dark tarsi; second costal segment less than three times length of fourth; and acrostichals in four rows. The adults resemble those of \textit{P. caprifoliæ} Spencer and \textit{P. periclymeni} de Meijere but differ in having frons slightly paler above and entirely different male genitalia. Spencer (1969) illustrated the characteristic aedeagus of this species.

Geographical distribution. – The members of this species are known only from the type locality in Canada (Spencer, 1969). I examined the following material from Alberta:


Phytomyza ranunculi (Schrank)

\textit{Musca ranunculi} Schrank, 1803:140.
\textit{Phytomyza flavoscutellata} Fallén, 1823b:4.
\textit{Phytomyza albitpes} Meigen, 1830:195.

Comparisons and diagnostic characters. – The members of this species belong to the group characterized by yellow frons; dark third antennal article and yellow scutellum. They differ from another species in this group, \textit{P. clematiphaga} Spencer, by having the upper orbital bristle shorter than lower and distinct male genitalia.

The Alberta specimens from Elk Island park, bred from leaf mines on \textit{Ranunculus abortivus} L., correspond in colour to the form \textit{albitpes} Meigen having yellow on mesonotum. One specimen from George Lake corresponds in colour to the form \textit{flavoscutellata} Fallén having darker mesonotum.

The number of coils in the distiphallus vary from one coil in a Faeroes specimen (Griffiths, 1964) to eight coils in Alberta specimens. There are five coils in the European specimens illustrated by Nowakowski (1962). Besides, there is variation in the direction of coils, which in some specimens are coiled upwards, while in others downwards. The number of coils and their direction does not seem to be related to their external colour variations in this species as was pointed out by Griffiths (1964). However, it is possible that more than one species is involved in its entire range.

The male genitalia of this species are also very close to that of \textit{P. vbeana} Griffiths, but the latter differs in having 11 coils in the distiphallus and dark mesonotum and scutellum.

Biology. – In Alberta the larvae make linear mines in the leaves of \textit{Ranunculus abortivus} L., family Ranunculaceae. Pupation occurs outside the mine.

Geographical distribution. – The members of this species are Holarctic in distribution, known from Europe (Hendel, 1935), United States (Frick, 1959), Faeroes, Iceland and Greenland (Griffiths, 1966), Japan (Sasakaw, 1961) and Canada (Spencer, 1969). I examined the following material from Alberta:

Phytomyza riparia new species

Comparisons and diagnostic characters. — A member of this species belongs to the group characterized by yellow frons; upper Ors shorter than lower; mouth margin normal; mat greyish mesonotum and scutellum; upper margins of mesopleura, humeral and notopleural areas yellow; essentially dark femora; and second costal segment approximately three and a half times length of fourth. The adult resembles that of P. spondylii R.-D., from which it may be separated as shown below in extension to Spencer's (1969) key to Canadian species of the genus Phytomyza Fallén:

13. Two Ors equal ................................................................. 14
   - Upper Ors shorter than lower or lacking ................................ 13a
13a. Third antennal segment with normal pubescence; upper Ors sometimes lacking; aedeagus as illustrated (Spencer, 1969) ....................... spondylii R.-D.
   - Third antennal segment with conspicuously long pubescence; upper Ors present; aedeagus as in Fig. 121 ............................... riparia n. sp.

Description. — Head. Frons almost twice width of eye at level of front ocellus, only slightly projected in front of eye margin in profile. Mouth margin normal. Two Ors, upper shorter than lower, one side of holotype has only one Ors, directed upwards; two strong Ori, directed inwards; orbital setulae few, six to seven, procline. Eyes oval, approximately 1.2 times higher than their length, bare; ocellar triangle small. Gena approximately one-fourth of vertical eye height. Third antennal article rounded at tip, with conspicuously long pubescence; ariata normal, pubescent.

Mesonotum. Dorsocecntals 3+1 strong bristles; acr in almost five irregular rows.

Wing. Length in male 2.0 mm; costa extended to vein R₄,₅; costal segments 2-4 in the ratio of 1 : 0.3 : 0.3; crossvein m-m absent.

Male genitalia (Fig. 121-122). Hypandrium with broad side arms and inconspicuous or small apodeme; pregonites broad; postgonites elongate; surstyli normal; aedeagus (Fig. 121) as illustrated with two long characteristic processes in the distiphallus; ejaculatory apodeme (Fig. 122) broad, bulb small.

Colour. Frons, orbits and gena yellow; both Vt's on dark ground; third antennal article dark brown; upper parts of mesopleura, humeral and notopleural areas yellow; mesonotum and scutellum mat greyish, slightly paler; coxae black; femora dark brown, with yellow on distal tips; tibiae and tarsi yellowish brown; squamae yellow, fringe brown; halteres yellow.

Derivation of the specific name. — This species is named riparia as its holotype was collected along the Saskatchewan River bank.

Geographical distribution. — The members of this species are known only from the type locality:


Phytomyza sehgalii Spencer

Phytomyza sehgalii Spencer, 1969:274.

Comparisons and diagnostic characters. — The members of this species differ from those of mertensiae new species in having paler frons and from prava Spencer in having strong acrostichals, small third antennal article and distinct male genitalia. Spencer (1969) illustrated the aedeagus characteristic of this species.

Geographical distribution. — Known only from Alberta, Canada from the following locality:
Phytomyza senecionella new species

Comparison and diagnostic characters. — The members of this species belong to the group characterized by yellow frons; two Ors equal; dark scutellum; essentially dark femora and pleura; normal mouth margin and third antennal article; acrostichals only two to three scattered hairs; dark squamal fringe and fore-coxae. The adults resemble those of the similar species, P. syngenesiae (Hardy), and males of the two can be separated reliably only by examination of the genitalia. This species is included in Spencer’s (1969) key to Canadian species of the genus Phytomyza Fallén as below:

40. Second costal section short; 1.5 times length of fourth; third antennal segment enlarged; squamal fringe pale ........................................... 41
40a. Second costal section longer, approximately twice length of fourth; third antennal segment normal; squamal fringe dark ........................................... 40a

40a. Aedeagus as illustrated (Spencer, 1969) .................. syngenesiae (Hardy)
- Aedeagus as in Fig. 123. ........................................... senecionella n. sp.

Description. — Head. Frons wider than width of eye at level of front ocellus (1:0.55), very slightly projected in front of eye margin in profile. Two Ors equal, directed upwards; one strong Ori and one small hair present below directed inwards; orbital setulae few, six to seven, procline. Eyes almost circular, their vertical height being almost equal to their length, bare; ocellar triangle small. Gena deep, approximately two-fifths of eye height. Antennal bases approximate; third antennal article rounded at tip, with normal pubescence; arista normal and pubescent.

Mesonotum. Dorsocentrals 3+1 strong bristles; acr two to three scattered hairs.
Wing. Length in male 2.75 mm; costa extended to vein R_{4+5}; costal segments 2-4 in ratio of 1:0.3:0.56; crossovein m-m absent; vein M_{3+4} at wing tip.

Male genitalia. (Fig. 123-124). Hypandrium with side arms broad and no conspicuous apodeme; pregonites broad; postgonite with small hook anteriorly; surstyiil small and normal; aedeagus (Fig. 123) as illustrated; ejaculatory apodeme (Fig. 124) slightly broad, bulb small and membranous.

Colour. Frons, orbits and gena yellow; both Vt’s on dark grounds; all antennal articles black; ocellar triangle shining black; mesonotum, scutellum and pleura mat grey; legs black, only tips of femora with slight yellow, coxae black; squamae yellow, fringe dark; halteres yellow.

Derivation of the specific name. — This species is named after the generic name of its food plant.

Biology. — Larvae make broad linear mines on the leaves of Senecio congestus var. palustris (L.), family Compositae. The leaf mines were more or less communal with more than one larva feeding in them. Pupation occurs usually at the leaf bases or sometimes on the stem.

Geographical distribution. — The members of this species are known only from the type locality:

Phytomyza solidaginivora Spencer

Phytomyza solidaginivora Spencer, 1969: 274.

Comparison and diagnostic characters. — The members of this species differ from those of similar species, matricariae Hendel, in having dark second antennal article and distinct male genitalia. Spencer (1969) illustrated the aedeagus characteristic of this species.

Biology. — Larvae make linear leaf mines on Solidago, family Compositae.

Geographical distribution. — Known only from Alberta, Canada from the following locality: CANADA. Alberta: Edmonton, University of Alberta campus (Spencer, 1969).

Phytomyza solidaginophaga new species

Comparisons and diagnostic characters. — The members of this species belong to the group characterized by yellow frons; two equal Ors; normal third antennal article; dark scutellum; mostly dark femora and pleura; and three to six rows of acrostichals. The adults resemble those of P. aquilegiana Frost and P. aquilegioides new species but differ in having the frons slightly darkened below and distinct male genitalia. They also resemble those of another similar species, P. ilicis Curtis, and may be separated as shown below in extension to Spencer’s (1969) key to Canadian species of the genus Phytomyza Fallén:

32. Frons distinctly darkened, either above or below.................. 32a
- Frons entirely pale, yellow or orange, at most orbits dark ............. 33

32a. Aedeagus as illustrated (Spencer, 1969); larva leaf-miner in Ilex ... ilicis Curtis
- Aedeagus as in Fig. 126; larva leaf-miner in Solidago ...... solidaginophaga n. sp.

Description. — Head. Frons approximately twice eye width at level of front ocellus, slightly projected in front of eye margin in profile. Mouth margin normal; lunule low. Two equal Ors, directed upwards (one specimen has only one Ors, but has two bristles in the same socket as upper Ori; two Ori have therefore been considered as normal for the members of this species). Two Ori, directed inwards, lower one weaker than upper; orbital setulae few, approximately seven, procinate. Eyes oval, approximately 1.2 times higher than their length, bare; ocellar triangle small. Gena approximately 0.28 times vertical height of eye. Third antennal article rounded at tip, with normal pubescence; arista normal, pubescent. Mesonotum. Dorsoventral 3+1 strong bristles; acr in approximately four irregular rows.

Wing. Length in male approximately 2.1 mm; costa extended to vein R₄₅; costal segments 2-4 in ratio of 1:0.26:0.3; crossvein mm absent.

Male genitalia (Fig. 125-127). Hypandrium (Fig. 125) V-shaped, with broad side arms; pregonites broad; postgonites elongate; surstyli normal; aedeagus (Fig. 126) with characteristic row of small spines between two long arms of basiphallus, as illustrated; ejaculatory apodeme (Fig. 127) small, bulb small and membranous.

Colour. Frons yellow, slightly darkened just above lunule; orbits slightly darkened along eye margins; lunule and gena darkened; ocellar triangle weakly shining black; both Vt’s on dark ground; antennae black; mesonotum, scutellum and pleura mat greyish black; femora black, with yellow distal tips; tibiae and tarsi dark brown; squamae yellow, fringe brown; halteres yellow.

Derivation of the specific name. — This species has been named after the generic name of its food plant.

Biology. — Larvae make linear mines in the leaves of Solidago lepida DC, family Compositae. Pupation occurs outside the mine.

Geographical distribution. — The members of this species are only known from the type
locality:

CANADA. Alberta: Holotype ♂ George Lake near Busby, University of Alberta field station, from mines on the leaves of Solidago lepida DC, coll. 7.vi.1968, emerged 30.iv.1969, coll. G. C. D. Griffiths; paratype 1 ♂ same data.

Phytomyza spondylii R.-D.

Phytomyza spondylii Robineau-Desvoidy, 1851:147.

Comparisons and diagnostic characters. – The members of this species belong to the group characterized by yellow frons; dark scutellum; and essentially dark femora. The colour of the upper margins of the mesopleura, humeral and notopleural areas is variable from yellow to almost dark. A small upper Ors is usually present. The adults having yellow on the sides resemble those of P. matricariae Hendel and differ in having the second costal section longer, approximately 3.5 times the fourth and dark second antennal article. The darker forms resemble those of P. asterophaga Spencer but differ in having entirely different male genitalia. Spencer (1969) illustrated the aedeagus characteristic of this species.

Biology. – Larvae make linear mines in the leaves of Heracleum lanatum Michx., family Umbelliferae. Pupation occurs outside the mine.

Geographical distribution. – The members of this species are known from Europe (Hendel, 1935) and Canada (Spencer, 1969). I examined the following material from Alberta:

CANADA. Alberta: 2 ♂♂, 2 ♀♀ Edmonton, White Mud Creek park, from leaf mines on Heracleum lanatum Michx., emerged 18-19.vii.1966.

Phytomyza subalpina new species

Comparisons and diagnostic characters. – A member of this species belongs to the group characterized by yellow frons; normal mouth margin and third antennal article; two Ors equal; dark scutellum; essentially dark femora and pleura; acrostichals in two rows; and dark fore-coxae. The adult resembles that of P. fuscula Zetterstedt but differs in having a pale squamal fringe and distinct male genitalia. It differs from another similar species, P. atripalpis Aldrich, as shown below in extension to Spencer’s (1969) key to Canadian species of the genus Phytomyza Fallén:

53. Second costal section short, less than twice length of fourth ............... 53a - Second costal section longer, twice length of fourth. ............... gelida Spencer

53a. Gena two-fifths eye height ........................................ atripalpis Aldrich - Gena one-fifth eye height ............................................ subalpina n. sp.

Description. – Head. Frons approximately twice width of eye at level of front ocellus; mouth margin normal; lunule low. Two equal Ors directed upwards; two Ori, lower one weaker, both directed inwards; orbital setulae four to five, proclineate. Eyes oval, their vertical height being approximately 1.3 times their length, bare; ocellar triangle small. Gena approximately one-fifth vertical eye height. Third antennal article rounded at tip, with normal pubescence; arista normal, pubescent.

Mesonotum. Dorsocentals 3+1 strong bristles; acr approximately nine hairs, in two rows. Wing. Length in male approximately 2.1 mm; costa extended to vein R₄,₅; costal segments 2-4 in ratio of 1 : 0.35 : 0.65; crossvein m-m absent.

Male genitalia (Fig. 128-132). Hypandrium (Fig. 128) U-shaped with broad side arms; pregonites broad; postgonites (Fig. 129) elongate, with hook-like process anteriorly; sirstyli normal; aedeagus (Fig. 130, 131) as illustrated; ejaculatory apodeme (Fig. 132) small, bulb membranous.
Colour. Frons, gena and lunule yellow; orbits yellow, slightly darkened near upper Ors; ocellar triangle weakly shining black; both Vt’s on dark ground; antennae black; mesonotum, scutellum and pleura mat grey; femora, tibiae and tarsi black; squamal fringe dirty pale, squamae pale; halteres yellow.

_Derivation of the specific name._ — This species is named _subalpina_ as its holotype was collected in the subalpine zone of foothills of Rocky Mountains.

_Geographical distribution._ — This species is known only from the type locality:


**Phytomyza subtenella** Frost

_Phytomyza subtenella_ Frost, 1924:89.

_Comparison and diagnostic characters._ — The members of this species belong to the group characterized by yellow frons; normal mouth margin and third antennal article; usually two equal Ors (but one specimen has three equal Ors); essentially dark femora and pleura; acrostichals in two well-defined rows and yellow fore-coxae.

The adults, wing length approximately 2.5 mm, differ from those of the similar species, _P. jasperensis_, in having the frons strongly projected in front of eye margin; gena deeper, approximately two-thirds of eye height and distinct male genitalia. The paraphalli in Alberta specimen were independent of the basiphallus and not joined as it appears from Spencer’s (1969) illustration in which they are overlapping.

_Geographical distribution._ — The members of this species are known from the United States (Frick, 1959) and Canada (Spencer, 1969). I examined the following material from Alberta:


**Phytomyza subtilis** Spencer


_Comparison and diagnostic characters._ — The members of this species differ from those of a very similar species, _urbana_ Spencer, in having darker grey mesonotum and slightly brownish frons. The male genitalia as figured by Spencer (1969) are, however, very distinct.

_Biology._ — Larvae make blotch mines on the leaves of _Lathyrus ochroleucus_ Hook., family Leguminosae.

_Geographical distribution._ — Known from Alaska and Alberta. The Alberta locality is as follows:

CANADA. Alberta: Wabamun Lake (Spencer, 1969).

**Phytomyza syngenesiae** (Hardy)

_Chromatomyia syngenesiae_ Hardy, 1849:391.


_Comparisons and diagnostic characters._ — The members of this species belong to the group characterized by yellow frons; dark scutellum; mostly dark femora and pleura; two Ors equal; normal third antennal article; and acrostichals normally lacking or at most three
to four isolated hairs present. The adults resemble closely those of an Old World species, P. horticola Goureau, and can be separated reliably only by examination of the male genitalia. Griffiths (1967) and Spencer (1969) illustrated the aedeagus characteristic of this species.

**Biology.** — Larvae make linear mines in the leaves of numerous Compositae and rarely on non-Compositae hosts (Griffiths, 1967). In Alberta the flies have been bred from only two host-plants of the family Compositae, *Senecio* sp. (Spencer, 1969) and *Crepis gracilis* (D.C. Eat.) Rydb.

**Geographical distribution.** — The members of this species are widespread in Europe, Australia, New Zealand, U. S. A. and Canada (Griffiths, 1967). I examined the following material from Alberta:

**CANADA.** Alberta: 1 ♀, 2 ♂♂ Edmonton, University of Alberta campus, from leaf mines on *Crepis gracilis* (D.C. Eat.) Rydb., coll. 4.vi.1966.

*Phytomyza thalictrivora* Spencer

*Phytomyza thalictrivora* Spencer, 1969:279.

**Comparison and diagnostic characters.** — The members of this species belong to the group characterized by dark frons, mesonotum and scutellum; essentially dark femora and pleura; upper Ors lacking; and second costal segment less than three times length of fourth. The adults resemble those of *P. aquilegivora* Spencer but differ in having darker frons and few acrostichals. They also resemble those of *P. minuscula* Goureau, but possess distinct male genitalia. Spencer (1969) illustrated the aedeagus characteristic of this species.

**Biology.** — Larvae make linear mines on the leaves of *Thalictrum venulosum* Trel., family Ranunculaceae. Pupation occurs outside the mine.

**Geographical distribution.** — The members of this species are known only from Canada (Spencer, 1969). I examined the following material from Alberta:


*Phytomyza timida* Spencer

*Phytomyza timida* Spencer, 1969:279.

**Comparison and diagnostic characters.** — The members of this species belong to the group characterized by yellow frons; dark scutellum; and essentially dark femora and pleura. Spencer (1969) includes this species among those having upper orbital bristle shorter than lower. This character is probably variable as the Alberta specimens examined had both upper orbital bristles almost equal. The aedeagus of a specimen from Banff, Alberta is illustrated (Fig. 133) and agrees with that figured by Spencer (1969).

**Geographical distribution.** — The members of this species are known from Canada only from the locality of its type series (Spencer, 1969). I examined the following material from Alberta:


*Phytomyza urbana* Spencer


**Comparison and diagnostic characters.** — The members of this species differ from those of a similar species, *subtilis* Spencer, in having paler greyish mesonotum and paler frons and
distinct male genitalia. Spencer (1969) illustrated the aedeagus characteristic of this species.

Geographical distribution. – Known only from Alberta, Canada from the following locality:

CANADA. Alberta: Blairmore (Spencer, 1969).

Phytomyza sp. (Angelica arguta Nutt.)

Comparison and diagnostic characters. – The distinguishing characters of the female of this species are: yellowish brown frons; wing length 2.5 mm; second costal segment three times length of fourth; dark squamal fringe; dark mesonotum, scutellum, pleura and femora and acrostichals in two to three rows. It resembles the adults of P. aralivora Spencer but has entirely different biology. This species cannot be definitely determined at present as no males are available for examination.

Biology. – Larvae make linear mines in the leaves of Angelica arguta Nutt., family Umbelliferae.

Geographical distribution. – The members of this species were examined only from southwestern Alberta as below:

CANADA. Alberta: 1 ♀ Blairmore, from leaf mines on Angelica arguta Nutt., coll. 5.ix. 1966, emerged 10.iii.1967; numerous leaf mines, same locality.

INSECT HOST-PLANT RELATIONSHIP IN THE FAMILY AGROMYZIDAE

The members of the family Agromyzidae are exclusively internal plant feeders during their larval stage. Larval feeding results in a definite pattern called the mine, and the study of the mining habits is called minology or hyponomology (Hering, 1951).

The agromyzid mines fall into two general categories. First, the epidermal leaf mines, in which the mining larva feeds only inside the epidermal layer of the leaf. These are restricted mainly to the old world tropics. The second, the parenchymal mine, in which the larva feeds on the parenchymatous tissue inside the leaf or other part of the plant. The majority of mines belong in this category. Leaf mines are usually seen externally and generally are more visible from one side than the other. Surface mines on other parts of a plant can also be detected as whitish or greenish channels with faecal granules distributed in definite tracks. Mines inside the stem or root are not easily detected, however, the injury caused by the mining larva can be seen by breaking the injured plant part. The shape of the larval mine is usually constant within the species, but varies between species. This helps greatly in the separation of closely related species which cannot otherwise be reliably identified by adult morphology. Hering (1951) dealt with shapes of mines made by mining insects and later, in 1957, illustrated the mines of European species in detail.

The relationship between the endophagous larvae of mining insects and their food plants is typically parasitic in nature. However, modern parasitology as a science does not concern itself with the study of such relationships. Nowakowski (1962) commenting on this situation proposed the term “zoophyttoparasitology” for the study of animals as parasites and plants as hosts. The most important features of this relationship in the family Agromyzidae are the active choice of host-plant by the mining insect, the varying degree of host-plant specificity, and the adaptations of the maggot for an endoparasitic life in the semi-liquid environment of the leaf parenchyma. The understanding of this relationship is of great importance in dealing with the systematics of this group as it permits the use of the host-parasite discrimination method. It provides valuable information for identification of similar species, which cannot be separated on adult morphological characteristics alone.
Hering (1951) discussed the distribution of leaf mining species on plants of various families and examined the established phylogenetic relationships between the plant families in a system based on serum diagnosis alone as proposed by Mez (1926). Mez’s system of classification has now been criticized by modern botanists because of similar serum reactions obtained for certain plant families which clearly are not closely related.

Table 2 lists the known local host-plants for the Albertan species. It is realized that the information on host-plants is not adequate for all species, but some useful observations can still be made. The arrangement of plant families is after the supposedly phylogenetic system of Takhtajan (1969). The phylogenetic relationships between plant families and orders is still a matter of controversy. Most plant classifications fall into two groups depending on the supposed nature of the primitive angiosperm flower (Davis and Heywood, 1965). One group is based on the assumption that the earliest angiosperms were wind pollinated and that the monocotyledons and dicotyledons have arisen independently from unknown gymnosperms. According to the second group of systems, dicotyledons and monocotyledons were both derived from primitive angiosperms which were insect-pollinated. Such a view is supported by many recent workers (Eames, 1961; Hutchinson, 1964; Takhtajan, 1969). Hutchinson (1964) in his revised edition of classification of angiosperms maintained a basic division of dicotyledons into woody “Lignosae” and herbaceous “Herbaceae,” a system which allegedly leads to wide separation of certain plant families which are markedly similar in the structure of their flowers. In the absence of established phylogenies of both angiosperms and agromyzid parasites, it is difficult to study the trends in their coevolution.

It is generally accepted that the larvae of Cyclorrhapha were primitively saprophagous from which various specialized feeding habits like phytophagy, carnivory and parasitism have been derived (Hennig, 1952).

The dominance of agromyzids on angiosperm hosts suggest that angiosperms were well established as flowering plants before the agromyzids made their appearance. Although opinions differ as to precisely when angiosperms first appeared on the evolutionary scene, there is a general agreement that they came into prominence suddenly during the late Cretaceous (Eames, 1961). Hennig (1965) reviewed all supposed records of agromyzid fossils and concluded that the family Agromyzidae is not yet known to be represented in the Tertiary Baltic amber. In fact there are so far no fossils which can be definitely referred to the family. The occurrence of a large number of closely related and poorly differentiated species and their abundance on hosts belonging to highly evolved plant families suggests that much of the diversification of the family Agromyzidae is relatively recent. However, the possibility that the group goes back to late Cretaceous as suggested by Nowakowski (1962) must be admitted.

The recent use of male genitalia in agromyzid taxonomy has split many groups originally supposed to be polyphagous or oligophagous species, into species with much narrower host-plant specificity. It is becoming increasingly apparent that the majority of agromyzid species are restricted feeders, being monophagous or oligophagous. Strict monophagy also appears to be rare unless it results from a plant genus being monotypic. Nowakowski (1962) discussed the subject of host-plant specificity among the European species and revealed many examples where the original wide host range was found to be the result of misidentifications or assemblage of many species under the same name. The most polyphagous species, Phyto- myza syngenesiae (Hardy), appears to be a restricted feeder in Alberta and has been bred from only two plant genera Crepis and Senecio of the family Compositae. This species is known from many Compositae and rarely from other host-plants (see Frick, 1959 as Phyto- myza atricornis Meigen; Griffiths, 1967).

Most agromyzid genera occurring on species of monocot families are also represented on
various dicotyledons. The few exceptions are the species of the genus Cerodontha Rondani occurring only on monocot families Graminiae, Cyperaceae, and Juncaceae; and the members of the ambigua/nigripes groups of the genus Agromyza Fallén which feed only on grasses. The species in these groups are uniform in external morphology of adults and in the general shape of the male genitalia, and probably represent early specialization of their feeding habit. Various species of the agromyzid genera Liriomyza Mik and Phytomyza Fallén feeding on grasses will probably prove to be oligophageous. The oligophagy of various grass-mining species has not been investigated because of the problems of identification of grasses at the time the mining larvae are collected.

The family Ranunculaceae is selected by members of the agromyzid genera Melanagromyza Hendel, Ophiomyia Brachnikov and Phytomyza Fallén. Melanagromyza actaeae n. sp. feeding inside the stems of Actaea rubra (Ait.) Willd. and an Ophiomyis sp. making surface mines below the stem epidermis of Thalictrum venulosum Trel. appear to be specialized monophagous species. There are many closely related and poorly differentiated Phytomyza species feeding on the plant genera Aquilegia and Thalictrum, some of which are oligophageous species feeding on both. The species of the genus Phytomyza Fallén feeding on the plant genera Clematis, Delphinium and Ranunculus are specialized monophagous species. Three local species of the plant genus Anemone support three different leaf miners of the genus Phytomyza Fallén. The members of the agromyzid genera Agromyza Fallén, Melanagromyza Hendel and Hexomyza Enderlein feeding on Ulmaceae, Urticaceae and Salicaceae are all specific feeders. Two species known to have rosaceous host-plants in Europe and the United States have not yet been discovered on Alberta hosts. One is a specific cambium miner, Phytobia amelanchieres (Greene), feeding on Amelanchier canadensis (L.) (Frick, 1959), and the other Agromyza spiraceae Kaltenbach, an oligophageous species feeding on various genera of the subfamily Rosoideae in Europe. Members of the family Leguminosae are fed on by the representatives of the agromyzid genera Agromyza Fallén, Liriomyza Mik and Phytomyza Fallén. Most of these species are monophagous in Alberta, with the exception of Liriomyza fricki Spencer which is oligophageous. The plant families Cornaceae, Araliaceae, Umbellifereae and Elaeagnaceae are fed on by specific feeders of the agromyzid genera Melanagromyza Hendel, Phytomyza Fallén and Amauromyza Hendel. Members of the plant family Caprifoliaceae support oligophageous species belonging to the agromyzid genera Paraphytomyza Enderlein and Phytomyza Fallén. The oligophagous species feed on the plant genera Lonicera and Symphoricarpos. The plant families Boraginaceae, Scrophulariaceae; Plantaginaceae and Labiatae have specialized specific feeders. The family Compositae supports a highly specialized agromyzid fauna belonging to the genera Melanagromyza Hendel, Ophiomyia Braschnikov, Liriomyza Mik, Calycomyza Hendel, Nemorimyza Frey and Phytomyza Fallén. Most of these species are specific monophagous feeders. However, some oligophageous species feed on the plant genera Crepis, Taraxacum, and Sonchus; others feed upon members of tribe Anthemideae of the family Compositae, as shown by the host range of Phytomyza matricariae Hendel and Liriomyza millefolii Hering.
Table 2. Albertan host-plant records of Albertan agromyzid species.

DICOTYLEDONS

<table>
<thead>
<tr>
<th>Family Ranunculaceae</th>
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<tbody>
<tr>
<td><em>Actaea rubra</em> (Ait.) Willd</td>
<td><em>Melanagromyza actaeae</em> n. sp.</td>
</tr>
<tr>
<td><em>Anemone canadensis</em> L.</td>
<td><em>Phytomyza prava</em> Spencer</td>
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<tr>
<td><em>Anemone multifida</em> Poir.</td>
<td><em>Phytomyza multifidae</em> n. sp.</td>
</tr>
<tr>
<td><em>Anemone riparia</em> Fern.</td>
<td><em>Phytomyza canadensis</em> Spencer</td>
</tr>
<tr>
<td><em>Aquilegia</em> sp. (cultivated var.)</td>
<td><em>Phytomyza aquilegiana</em> Frost, <em>P. aquilegiophaga</em> Spencer, <em>P. aquilegivora</em> Spencer, <em>P. columbinae</em> n. sp.</td>
</tr>
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</table>

| *Clematis verticillaris* DC | *Phytomyza clematiphaga* Spencer |
| *Delphinium* sp. (cultivated) | *Phytomyza delphinivora* Spencer |
| *Ranunculus abortivus* L. | *Phytomyza ranunculi* (Schrank) |
| *Thalictrum venulosum* Trel. | *Phytomyza aquilegioides* n. sp., *P. columbinae* n. sp., *P. thalictrivora* Spencer, *Ophiomyia* sp. |

| *Thalictrum* sp. | *Phytomyza aquilegiana* Frost |

<table>
<thead>
<tr>
<th>Family Ulmaceae</th>
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<tbody>
<tr>
<td><em>Ulmus americana</em> L.</td>
<td><em>Agromyza aristata</em> Malloch</td>
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<th>Family Urticaceae</th>
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<tr>
<td><em>Urtica gracilis</em> Ait.</td>
<td><em>Melanagromyza martini</em> Spencer, <em>Phytomyza</em> sp., <em>luteiceps</em> n. sp.</td>
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<td><em>Potentilla</em> sp.</td>
<td><em>Agromyza</em> sp.</td>
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<th>Family Leguminosae</th>
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<tbody>
<tr>
<td><em>Lupinus sericeus</em> Pursh</td>
<td><em>Phytomyza lupini</em> Sehgal, <em>P. lupinivora</em> Sehgal</td>
</tr>
<tr>
<td><em>Oxytropis splendens</em> Dougl.</td>
<td><em>Phytomyza oxytropidis</em> n. sp.</td>
</tr>
<tr>
<td><em>Trifolium repens</em> L.</td>
<td><em>Liriomyza fricki</em> Spencer</td>
</tr>
<tr>
<td><em>Vicia americana</em> Muhl.</td>
<td><em>Liriomyza fricki</em> Spencer, <em>L. viciae</em> Spencer</td>
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<th>Family Cornaceae</th>
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<tbody>
<tr>
<td><em>Cornus canadensis</em> L.</td>
<td><em>Phytomyza agromyzina</em> Meigen</td>
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<td><em>Cornus stolonifera</em> Michx.</td>
<td><em>Phytomyza agromyzina</em> Meigen</td>
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<th>Family Araliaceae</th>
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<tr>
<td><em>Aralia nudicaulis</em> L.</td>
<td><em>Phytomyza aralivora</em> Spencer</td>
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</table>
Family Umbelliferae
- *Angelica arguta* Nutt.
- *Heracleum lanatum* Michx.

Phytomyza sp.
Phytomyza spondyliai R.-D.

Family Elaeagnaceae
- *Shepherdia canadensis* (L.)

Amauromyza shepherdiae n. sp.

Family Caprifoliaceae
- *Lonicera dioica* L.
- *Lonicera involucrata* (Richards)
- *Lonicera tartarica* L.
- *Symphoricarpos albus* (L.)
- *Symphoricarpos occidentalis* Hook.
- *Symphoricarpos sp.*

Paraphytomyza lonicerae (R.-D.), *P. orbitalis* (Melander), *P. spenceri* n. sp.
Paraphytomyza plagiata (Melander), Phytomyza gregaria Frick, *P. periclymeni* de Meijere
Paraphytomyza lonicerae (R.-D.), *P. orbitalis* (Melander)
Paraphytomyza spenceri n. sp.
Phytomyza caprifoliae Spencer

Family Rubiaceae
- *Galium boreale* L.

Praspedomyza galiivora Spencer

Family Boraginaceae
- *Mertensia paniculata* (Ait.)

Agromyza canadensis Malloch, Phytomyza mertensiae n. sp.

Family Scrophulariaceae
- *Penstemon confertus* Dougl.
- *Penstemon procerus* Dougl.
- *Veronica* sp. (cultivated)

Phytomyza penstemonis Spencer
Phytomyza penstemonis Spencer
Phytomyza crassiseta Zetterstedt

Family Plantaginaceae
- *Plantago major* L.

Phytomyza plantaginis R.-D.

Family Labiatae
- *Mentha arvensis* L.

Calycomyza menthae Spencer

Family Compositae
- *Achillea millifolium* L.
- *Achillea sibirica* Ledeb.
- *Arnica cordifolia* Hook
- *Aster ciliatus* Lindl.
- *Aster conspicuosus* Lindl.
- *Bidens cernua* L.
- *Chrysanthemum* sp. (cult.)
- *Crepis gracilis* (D.C. Eat.) Rydb.
- *Crepis tectorum* L.

Phytomyza matricariae Hendel
Melanagromyza achileana n. sp., *Liriomyza millefolii* Hering,
Phytomyza matricariae Hendel
Phytomyza arniciuora n. sp.
Phytomyza ciliolati Spencer
Phytomyza asterophaga Spencer
Melanagromyza bidenticola n. sp.
Phytomyza matricariae Hendel
Phytomyza syngenesiae (Hardy)
Phytomyza lactuca Frost
**Agromyzidae of Alberta**

Matricaria matricarioides (Less.) Porter
Petasites sagittatus (Pursh)
Senecio congestus palustris (L.)
Senecio pauciflorus Pursh
Senecio sp.
Solidago lepida DC
Solidago sp.

Sonchus uliginosus Bieb.
Sonchus sp.
Tanacetum vulgare L.
Taraxacum sp.

**MONOCOTYLEDONS**

Family Liliaceae

Smilacina stellata (L.)
Maianthemum canadense Desf.

Liriomyza smilacinae Spencer
Liriomyza sp.

Family Cyperaceae

Scirpus sp.

Cerodontha (Dizygomyza) ? scirpi (Karl)

Family Gramineae

Agropyron repens (L.) Beauv.
Agropyron smithii Rydb.
Deschampsia caespitosa (L.)
Phalaris arundinacea L.
Triticum aestivum L.

Cerodontha (Poemyza) incisa (Meigen)
Cerodontha (Poemyza) incisa (Meigen)
Liriomyza cordillerana Sehgal
Cerodontha (Poemyza) incisa (Meigen)
Cerodontha (Poemyza) superciliosa
(Zetterstedt)

**ACKNOWLEDGEMENTS**

I am grateful to B. Hocking, Department of Entomology, University of Alberta, for providing the opportunity and support for this project in Alberta, Canada. I also express my most sincere thanks to him for his criticism of the manuscript and keen interest throughout this study. I am grateful to G. E. Ball, Department of Entomology, University of Alberta, for his ever available help, supervision and valuable criticism of the manuscript. I am also grateful to K. A. Spencer, London, England and G. C. D. Griffiths, Department of Entomology, University of Alberta, for numerous useful discussions and valuable suggestions during this study. I would like to thank J. G. Packer, Department of Botany, University of Alberta, for help in identification of host-plants; and J. Boliček for help in translating the abstract into German.
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Fig. 1-2. *Agromyza albipennis*. 1. aedeagus, ventral view. 2. ejaculatory apodeme. Fig. 3-5. *A. brevispinata*. 3. aedeagus, ventral view. 4. distiphallus, lateral view. 5. surstylus. Fig. 6. *A. hock ingi*, surstylus. Fig. 7. *A. r hock ingi*, surstylus. Fig. 8-9. *A. kincaidi*. 8. aedeagus, ventral view. 9. aedeagus, lateral view. Fig. 10-12. *A. nearctica*. 10. aedeagus, lateral view. 11. ejaculatory apodeme. 12. hypandrium.
Fig. 23–25. *Melanagromyza actaeae*. 23. muscle scars and tubercle band from lateral portion of first abdominal segment of larva. 24. anterior spiracle. 25. posterior spiracles. Fig. 26–31. *M. bidenticola*. 26. head, lateral view. 27. aedeagus, lateral view. 28. hypandrium. 29. cephalopharyngeal skeleton of larva. 30. anterior spiracle. 31. posterior spiracles. Fig. 32. *Melanagromyza* sp. 32. aedeagus, lateral view.
Fig. 33. *Ophiomyia labiatarum*, aedeagus, lateral view. Fig. 34. *O. maura*, aedeagus, lateral view. Fig. 35. *O. pulicaria*, aedeagus, lateral view. Fig. 36–39. *O. stricklandi*. 36. head, lateral view. 37. aedeagus, lateral view. 38. ejaculatory apodeme. 39. hypandrium. Fig. 40. *Cerodontha ? occidentalis*, aedeagus, lateral view.
Fig. 41–42. *Amauromyza riparia*. 41. aedeagus, lateral view. 42. ejaculatory apodeme. Fig. 43–46. *A. shepherdiae*. 43. aedeagus, lateral view. 44. distiphallus, ventral view. 45. ejaculatory apodeme. 46. leaf mine on *Shepherdia canadensis* (L.) Nutt. Fig. 47–50. *Liriomyza balcanicoides*. 47. aedeagus, lateral view. 48. aedeagus, ventral view. 49. ejaculatory apodeme. 50. surstylus.
Fig. 51–54. *Liriomyza bifurcata*. 51. head, lateral view. 52. aedeagus, lateral view. 53. aedeagus, ventral view. 54. ejaculatory apodeme. Fig. 55–56. *L. eupatori*. 55. aedeagus, lateral view. 56. aedeagus, ventral view. Fig. 57–59. *L. lathyri*. 57. aedeagus, lateral view. 58. aedeagus, ventral view. 59. ejaculatory apodeme.
Fig. 60–63. Liriomyza senecionivora. 60. aedeagus, lateral view. 61. aedeagus, ventral view. 62. ejaculatory apodeme. 63. surstylus. Fig. 64–67. L. sinuata. 64. aedeagus, lateral view. 65. aedeagus, ventral view. 66. ejaculatory apodeme. 67. surstylus. Fig. 68–69. L. sylvatica. 68. aedeagus, lateral view. 69. aedeagus, ventral view.
Fig. 70-72. *Metopomyza griffithsi*. 70. surstylus. 71. aedeagus, lateral view. 72. ejaculatory apodeme. Fig. 73. *Paraphytozya orbitalis*, leaf mine on *Lonicera dioica* L. Fig. 74. *P. plagiata*, leaf mine on *Lonicera involucrata* (Richards) Banks. Fig. 75-79. *P. spencerii*. 75. head, lateral view. 76. aedeagus, lateral view. 77. cephalopharyngeal skeleton of larva. 78. posterior spiracle. 79. leaf mine on *Lonicera dioica* L.
Fig. 80–82. Phytomyza aquilegioides. 80. hypandrium. 81. aedeagus, lateral view. 82. distiphallus, ventral view. Fig. 83–85. P. arnivora. 83. hypandrium. 84. aedeagus, lateral view. 85. ejaculatory apodeme. Fig. 86–90. P. blairmorensis. 86. hypandrium. 87. postgonite. 88. aedeagus, lateral view. 89. aedeagus, ventral view. 90. ejaculatory apodeme.
Fig. 91. *Phytomyza colemanensis*, aedeagus, lateral view. Fig. 92–95. *P. columbinae*. 92. hypandrium. 93. aedeagus, lateral view. 94. distiphallus, ventral view. 95. ejaculatory apodeme. Fig. 96–98. *P. edmontonensis*. 96. hypandrium. 97. aedeagus, lateral view. 98. ejaculatory apodeme. Fig. 99. *P. gregaria*, aedeagus, lateral view.
Fig. 100–103. Phytomyza jasperensis. 100. hypandrium. 101. postgonite. 102. aedeagus, lateral view. 103. aedeagus, ventral view. Fig. 104. P. lactuca, aedeagus, lateral view. Fig. 105–107. P. luteiceps. 105. hypandrium. 106. aedeagus, lateral view. 107. ejaculatory apodeme.
Fig. 108. *Phytomyza major*, aedeagus, lateral view. Fig. 109–112. *P. mertensiae*. 109. hypandrium. 110. aedeagus, lateral view. 111. distiphallus, ventral view. 112. ejaculatory apodeme. Fig. 113. *P. miltii*, aedeagus, lateral view.
Fig. 114. *Phytomyza misella*, aedeagus, lateral view. Fig. 115–117. *P. multifidae*. 115. hypandrium. 116. aedeagus, lateral view. 117. ejaculatory apodeme. Fig. 118–120. *P. oxytropidis*. 118. hypandrium. 119. aedeagus, lateral view. 120. ejaculatory apodeme. Fig. 121–122. *P. riparia*. 121. aedeagus, lateral view. 122. ejaculatory apodeme.
Fig. 123–124. *Phytomyza senecionella*. 123. aedeagus, lateral view. 124. ejaculatory apodeme. Fig. 125–127. *P. solidaginophaga*. 125. hypandrium. 126. aedeagus, lateral view. 127. ejaculatory apodeme. Fig. 128–132. *P. subalpina*. 128. hypandrium. 129. postgonite. 130. aedeagus, lateral view. 131. aedeagus, ventral view. 132. ejaculatory apodeme. Fig. 133. *P. timida*, aedeagus, lateral view.
THE ADULT RHYACOPHILIDAE AND LIMNEPHILIDAE (TRICHOPTERA) OF ALBERTA AND EASTERN BRITISH COLUMBIA AND THEIR POST-GLACIAL ORIGIN

ANDREW PEEBLES NIMMO
Hancock Museum
New Castle-upon-Tyne, England

Quaestiones entomologicae
New Castle-upon-Tyne, England
7: 406 1971

Corrigenda. A. Nimmo 1971, Quaest. ent. 7:3-234.

p. 16 Line 2. ‘Rhyacophilidae Ulmer’ should read ‘Rhyacophilidae Stephens’.

p. 49 Line 44. For: ‘Tergum VIII of male unmodified of variously . . . ’ read ‘Tergum VIII of male unmodified or variously . . . ’.

p. 68 Line 14. ‘Apatania shoshone; Betten, . . . ’ should read ‘Apatania shoshone; Betten, . . . ’.

p. 75 Line 27. For: ‘The holotype, allotype, and three male and 36 paratypes . . . ’ read ‘The holotype, allotype, and three male and 36 female paratypes . . . ’.

p. 77 Line 7. Omit reference to Fig. 605 (N. laloukesi not shown). See Fig. 1b, right side, for Lake Louise locality.


p. 134 Line 19. ‘Limnephilus (Goniotaulius) Pulchellus; . . . ’ should read ‘Limnephilus (Goniotaulius) pulchellus; . . . ’.


p. 178 Fig. 497. Male genitalia, dorsal aspect (partial).

p. 203 In range pattern no. 6, the first species, for: ‘Rhyacophila vemma’ read: ‘Rhyacophila vemma’.

p. 203 In range pattern no. 6, N. laloukesi. Omit Fig. 605. See note to p. 77, line 7 (above).

p. 222 Line 24. For: ‘. . . possible 6%, . . . ’ read ‘. . . possibly 6%, . . . ’.

AN APPARATUS AND METHOD FOR THE FIELD SEPARATION OF TABANID LARVAE (DIPTERA: TABANIDAE) FROM MOSS

ANTHONY W. THOMAS
Department of Entomology
University of Alberta
Edmonton 7, Alberta

Quaestiones entomologicae
7: 407-408 1971

A portable apparatus and its use for the separation of tabanid larvae from moss in the field is described. Thirty-seven hours work yielded 463 larvae in 16 species (Hybomitra 10, Chrysops 3, Atylotus 2, Haematopota 1). Compared with a Berlese funnel drying unit, this apparatus was 80% efficient.

Ce texte donne la description et l'utilisation d'un appareil facilement transportable, construit pour séparer, au champ, les larves de tabanidé de la mousse. Trente-sept heures de travail ont permis de séparer de la mousse 463 larves appartenant à 16 espèces (Hybomitra 10, Chrysops 3, Atylotus 2, Haematopota 1). Si on compare cet appareil à celui de Berlese, soit des entonnoirs séchant, son efficacité est de 80%.

The major habitat of Hybomitra and Atylotus larvae in northern North America is moss (Teskey, 1969). The separation of larvae from moss is tedious and has only been accomplished with any efficiency by drying the moss (Teskey, 1962). Miller (1951) transported moss back to the laboratory and hand sorted it on a table. He considered a yield of 10 to 15 larvae per man per day unusually high. Teskey's (1962) apparatus is efficient but is dependent upon a power supply. It also necessitates the transport of moss from the field to the laboratory and is thus of no use on extended collecting trips. The following apparatus was developed for collecting tabanid larvae from moss when transfer back to the laboratory was not practical.

CONSTRUCTION OF THE PORTABLE SEPARATOR

The frame was built of ½ inch O. D. aluminum alloy tubing having a 1/16 inch wall. It consisted of two six feet long side pieces, two two-feet-nine-inch pieces for the width and four four feet long legs. In use, the legs were pushed one foot down into the moss as an aid to frame stability. The frame was held together by four copper corner pieces, each made of a standard plumbers' tee and 90° elbow and three two-inch long copper pipes. This frame supported two nets. The upper one was four mesh/inch, made of string and manufactured as a base for carpets, and received the moss. The lower one was 20 mesh/inch, made of fiberglass and manufactured as window screening, and was to collect larvae.

METHOD OF USE

The separator is easily portable, either dismantled or assembled when it can be carried upside down on one’s back. When an area was to be searched for larvae it was far easier to take the apparatus to the area than transport the moss to the separator. Excessive water was
removed by hand squeezing and the moss then placed on the top net. Enough moss was collected to cover this to a depth of \( \frac{1}{2} \) inch; about \( \frac{3}{4} \) of a cubic foot of loosely packed moss. Collection of a sample took less than five minutes. The moss was then shredded by hand, the aim being to separate individual moss plants. This shredding process took between 15 and 20 minutes. During shredding the larvae leave the moss and crawl or fall through the mesh and become stranded on the lower net. This lower net was examined about every two minutes and the larvae retrieved. When the moss was thoroughly shredded the upper net was hit from beneath with the hands. This tossed the moss into the air causing any remaining larvae to separate out. The moss was then discarded and another sample was worked. It is important to shred the moss thoroughly and not place too much on the net at a time.

The above method separates pupae as well as larvae but such pupae are almost always crushed. Precautions are necessary if intact pupae are wanted. The sample must be collected with care and without squeezing. The shredding of such saturated moss is difficult.

This apparatus was used in musks where the substratum was all moss and in sloughs where there was a layer of moss and dead horsetails (Equisetum) on a clay substratum.

RESULTS

During May and June 1970, 273 larvae of 15 species (2 Atylotus, 1 Haematopota, 9 Hybomitra, 3 Chrysops) were collected during 25 hr sampling in three localities in Alberta. The smallest return was 27 larvae for five hours work and the maximum yield was 42 larvae for two hours work.

On five other occasions the moss, after being subjected to field sorting, was brought back to the laboratory and placed in extracting units (Teskey, 1962) until dry. In 12 hr of field work 190 larvae of nine species were obtained, 45 others were obtained from the drying units. Assuming the drying units to be 100% efficient at extracting larvae the efficiency of the field separator ranged from 70% to 89% (average, 80%). Eighty-nine small larvae (< 1 cm) were obtained with the drying units. No attempt to identify these beyond the family level was made. No small larvae were seen during field separations.

DISCUSSION

When an absolute quantitative result is required this portable separator is of no use. However, when a power supply is unavailable, or it is not practical to transport moss to the laboratory, it provides an efficient way of sampling moss for tabanid larvae.

REFERENCES


ACKNOWLEDGEMENTS

I wish to thank W. G. Evans for financing the drying units and portable separator.
Announcement — First International Congress of Systematic and Evolutionary Biology

The Society of Systematic Zoology and the International Association for Plant Taxonomy have joined forces to develop this first opportunity for botanical/zoolological interaction at the international level. The University of Colorado (Boulder, Colorado) has extended a gracious invitation to meet on that campus August 4-11, 1973. The diversity of ecological situations in the surrounding countryside makes this one of the most attractive sites in North America, both aesthetically and scientifically. The presence of experienced, enthusiastic biologists on that campus also provides an indispensable ingredient for the success of this Congress.

To begin the planning phase, two committees have been appointed by the sponsoring organizations, a Steering Committee and an International Advisory Committee. The following have been asked to serve on these bodies:

Steering Committee
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J. O. Corliss (Convenor)
J. L. Reveal (Secretary)
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Th. Eckardt (Germany)
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R. B. Freeman (U. K.)
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D. L. Hull (U. S. A.)
* P. D. Hurd, Jr. (U. S. A.)
M. A. Klappenbach (Uruguay)

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Department of Botany, University of Maryland, College Park, Maryland, U. S. A.
National Museum of Natural History, Smithsonian Institution, Washington, D. C., U. S. A.
Department of Vertebrate Zoology, Smithsonian Institution, Washington, D.C., U. S. A.

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Natural History Museum, University of Colorado, Boulder, Colorado, U. S. A.
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A. Takhtajan (U. S. S. R.)  
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E. Mayr (U. S. A.)  
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C. D. Michener (U. S. A.)  
E. C. Olson (U. S. A.)  
* R. W. Pennak (U. S. A.)  
* J. A. Peters (U. S. A.)  
R. A. Ringuet (Argentina)  
C. W. Sabrosky (U. S. A.)

(*Also member of Steering Committee.)

The Steering Committee will be the principal organizing group. The International Committee will provide valuable advice and guidance in the development of the Congress and it is recognized by the International Union of Biological Sciences as the special working group responsible for this event.

Program plans at this point encompass interdisciplinary symposia and contributed paper sessions. The botanists will not convene a nomenclatural section but a zoological one on this subject is anticipated. In the next few months the outline of the program and other activities will begin to take form. All suggestions will be gratefully received, carefully considered, and as many adopted as practical or feasible. Correspondence may be addressed to any member of the Steering Committee but preferably to the Secretary: Dr. James L. Reveal, Department of Botany, University of Maryland, College Park, Maryland 20740.
Publication of *Quaestiones Entomologicae* was started in 1965 as part of a memorial project for Professor E. H. Strickland, the founder of the Department of Entomology at the University of Alberta in Edmonton in 1922.

It is intended to provide prompt low-cost publication for accounts of entomological research of greater than average length, with priority given to work in Professor Strickland’s special fields of interest including entomology in Alberta, systematic work, and other papers based on work done at the University of Alberta.

Copy should conform to the Style Manual for Biological Journals published by the American Institute of Biological Sciences, Second Edition, 1964, except as regards the abbreviations of titles of periodicals which should be those given in the World List of Scientific Periodicals, 1964 Edition. The appropriate abbreviation for this journal is *Quaest. ent.* An abstract of not more than 500 words is required. All manuscripts will be reviewed by referees.

Illustrations and tables must be suitable for reproduction on a page size of $9\frac{3}{4} \times 6\frac{3}{4}$ inches, text and tables not more than $7\frac{3}{4} \times 4\frac{3}{4}$ inches, plates and figures not more than $8\frac{1}{2} \times 5$ inches. Reprints must be ordered when proofs are returned, and will be supplied at cost. Subscription rates are the same for institutions, libraries, and individuals, $4.00 per volume of 4 issues, normally appearing at quarterly intervals; single issues $1.00. An abstract edition is available, printed on one or both sides (according to length) of $3 \times 5$ inch index cards (at $1.00 per volume) or on $5 \times 8$ inch standard single row punched cards ($1.50 per volume).

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Department of Entomology,
University of Alberta, Edmonton, Canada.
Quaestiones entomologicae

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CONTENTS

Editorial – Four Men and a Moth ........................................... 411
Jacobson – The pale western cutworm, *Agrotis orthogonia* Morrison
  (Lepidoptera: Noctuidae): a review of research .......................... 414
Cheung – Purification and properties of arginine phosphokinase
  from honeybees *Apis mellifera* L. (Hymenoptera, Apidae) ............. 437

Editorial – Four Men and a Moth

Of the 4000 or so species of Noctuidae occurring in North America, few are of any great economic importance. Most are unknown to the man in the street and even to the farmers they are most likely to influence directly. Yet we know a lot today in comparison with what we knew in 1911 when it first became apparent that the interests of the white man in North America were also the interests of one of these species, the pale western cutworm, then known as *Porosagrotis orthogonia* (Morrison). Most of what we know was discovered by as grand a quartet of entomologists as a single insect species could ever hope to attract: E. H. Strickland, William C. Cook, H. L. Seamans, and Larry A. Jacobson: the sequence is chronological; to distinguish between these men on any other basis would be improper. How little we knew of the pale western cutworm was exemplified by the disastrous recommendation to farmers by the Canadian government, to cultivate out all weeds before moth flight. This cutworm lays its eggs in loose soil, not, like some other noctuids, on the leaves of plants. But all this, and more, comes out in Jacobson’s able, though modest review.

All these four men were primarily interested in the whole life-cycle of the whole insect; in its relationship to its environment, and in the problems it set for the farmer. In pursuit of these interests they, like the pale western cutworm, ignored the forty-ninth parallel. All four were men of strong views, given to speaking their minds. None who knew them would expect them all to agree on anything, let alone on such complex problems as this insect presented. Yet this very diligence in disagreement was the source of their strength as a group, for each sometimes proved another right; sometimes one suspects, by trying to prove him wrong.

Strickland, working from a Canada Department of Agriculture Field Station at Lethbridge, Alberta, when the trouble first started was quick to provide interim recommendations to farmers for control with insecticides. At the same time he was busy accumulating data on predators and parasites with a view to a more basic solution to the problem. Cook, assistant state entomologist for Minnesota, worked from there and at the Montana Agricultural Experiment Station. His major interest in the effects of weather and climate on insects conferred upon us the ability to predict outbreaks from weather data. Back in Lethbridge, Seamans applied Cook’s findings in forecasting, developed practical methods for cultural control, and laid the foundations of our knowledge of feeding habits, rearing methods and nutrition. Jacobson, following Seamans at Lethbridge, took Cook’s interest in the influence of weather into the laboratory and quantified the influence of several factors to yield a more definitive life history. He also developed the first effective chemical control, followed up on the work of Seamans on rearing, and contributed much on the behaviour of adults in the field and the laboratory. Jacobson, in this review, assesses the considerable contributions of others.
There have been times when superficial consideration of problems like that presented by the pale western cutworm has seemed to suggest that studies of the kind conducted by these four men are outmoded and redundant. The development of new and superior insecticides and technology for their application, of radio-sterilisation and plant breeding techniques seem to encourage such thoughts. But time has shown and will continue to show that there is no substitute for a knowledge of the biology of the insect and of the plant or animal on which it feeds. There will always be a place in applied entomology for the naturalist, for the man with a flair for revealing those features of the life of an insect which permit some finesse in our attempts to control it. Indeed I see this as the central function of an applied entomologist; as that which distinguishes him from a chemist and an engineer.

Despite what has been accomplished, it cannot be said, sixty years later in 1971, that the pale western cutworm problem has been solved. Though the value of crops saved exceeds by many times the cost of research done (none of these men made fortunes or even drew large salaries), the problem is still with us. And so it must be, for just as we select strains of insects resistant to our insecticides merely by using them, we also select strains of insects which damage our crops merely by growing them. And insects evolve so much faster than we do.

No better example of the dependence of applied entomology on basic entomology could be found than the pale western cutworm. The mistakes of 1911-1912 could be repeated at any time should our use of land change in favour of any of the other 3999 species of noctuid moths. We are very nearly as ignorant about the lives of most of them today as we were about the pale western cutworm in 1911; it would pay us to study them now.

It is a pleasure and a priviledge to publish, on the eve of the 50th anniversary of the Department of Entomology at the University of Alberta, a paper which reflects so much credit on the founder of the department and on one of his students.

Brian Hocking
Frontispiece: Life stages of *Agrotis orthogonia* Morrison. (A and B) ♂ and ♀ moth; (C and D) ventral views of ♂ and ♀ pupa; (E) larva; (F) egg with fully developed embryo (25x).
THE PALE WESTERN CUTWORM, AGROTIS ORTHOGONIA MORRISON
(LEPIDOPTERA: NOCTUIDAE): A REVIEW OF RESEARCH

L. A. JACOBSON
Canada Department of Agriculture
Research Station
Lethbridge, Alberta

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The pale western cutworm, Agrotis orthogonia Morrison, has been one of the major insect pests of grain production in the open plains of western Canada and the United States at frequent intervals since 1911. The history of occurrence and known distribution is described. The generic combinations and synonymy are brought up to date. Life history data in the various areas of occurrence are compared. Research on biology of the various stages is reviewed. Known parasites and predators are recorded and their role in natural control is discussed. The relationships of infestations and weather and the factors used in forecasting outbreaks are reviewed. Various methods of control in the field in the past, and their present status, are included with suggestions of possible methods for the future.


The pale western cutworm, Agrotis orthogonia Morrison, has been one of the major economic pests of grain production in the open plains of western Canada and the United States for many years.

This publication is a review of research on this insect and deals with biology, ecology, and control. References do not include publications on local distribution and control unless they include research data not available elsewhere.

History

The history of the pale western cutworm as a pest in western Canada has been described (Gibson, 1912, 1914, 1915; Seamans, 1926, 1931, 1952). In the United States the first occurrence and subsequent infestations and outbreaks are recorded: Montana (Parker, Strand, and Seamans, 1921; Cook, 1930); North Dakota (Webster, 1924); Oklahoma (Eshbaugh, 1933); Utah (Sorenson and Thornley, 1941); New Mexico (Eyer, 1957); Nebraska (Pruess and Roselle, 1969).

The pale western cutworm was virtually unknown before 1911 and apparently did not become a pest until after the cultivation of range lands and the growing of grain became widespread in the prairies of the United States and Canada. Seamans (1934a, 1934b) described how numbers increased because of the change from native prairie, where grasses
predominated, to extensive areas of cultivated land with susceptible crops and with cultural procedures favorable to cutworms.

Some research on the biology and control of the pale western cutworm was conducted in most of the areas where the cutworms occurred, particularly when it was first found and during subsequent outbreaks. Because of the importance of the insect as a destructive pest and the devastating losses that occurred, research in western Canada has continued since 1913. Most of the Canadian investigations were centered at Lethbridge, Alberta, and involved personnel throughout the Prairie Provinces.

**Synonymy**

The generic combinations and synonymy of the pale western cutworm follow:

*Agrotis orthogonia* Morrison


1926. *Porosagrotis orthogonia duae* Barnes and Benjamin, Canad. Ent. 58:303; described from Inyo Co., Calif.

**DISTRIBUTION**

Walkden (1950) describes the pale western cutworm as a typical dryland cutworm in semi-arid areas. He states that outbreaks have occurred in western Kansas, northeastern New Mexico, the Panhandle sections of Texas and Oklahoma, eastern Colorado, western South Dakota and North Dakota, Montana, Utah, and Wyoming in the United States. In Canada the pale western cutworm is generally confined to the prairie region (Bowman, 1951). Under severe drought conditions it may be found in the outer fringes of the park belt or Savanna region. Seamans (1938) outlined the outbreak area in Canada as extending from Cowley in the foothills of Alberta to Broadview in eastern Saskatchewan and from the International Boundary northward to Turtleford and Lloydminster, Saskatchewan.

The areas where infestations have occurred in Canada and the United States are shown in Figure 1. The map is based on information obtained from various publications and from the USDA Co-operative Economic Insect Reports for the period 1952-1970. There are localities within the area, such as local mountain ranges or deserts, where the pale western cutworm has not been found.

**LIFE HISTORY**

The pale western cutworm has only a single generation annually throughout its area of occurrence. The eggs are laid in the soil in early autumn and hatch the following spring. The larvae first feed on early growth such as volunteer cereals or weeds; later they also feed on seeded crops until early summer. As they mature they become less active and form an earthen cell in the soil 2 to 3 inches below the surface. Here they remain dormant until they pupate. The moths emerge from the cell during the late summer, mate, and lay eggs soon after.
The life history of this cutworm varies considerably from one geographical area to another. Crumb (1929) points out that single-brooded species of the Noctuidae tend to be of northern distribution and that in the southern part of the range, where hatching is earlier, the quiescent periods of prepupae and pupae are longer so that a single generation occupies a full year. Table 1 shows the variation in life cycle between northern, southern, and intermediate areas of occurrence in selected areas of the United States and Canada.
Table 1. Dates of various periods in the life history* of *A. orthogonia* at various locations of the United States and Canada.

<table>
<thead>
<tr>
<th></th>
<th>Lethbridge, Alberta</th>
<th>Cedar City, Utah</th>
<th>Clovis, New Mexico</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>49°43’N - 112°48’W</td>
<td>37°40’N - 113°4’W</td>
<td>34°14’N - 103°13’W</td>
</tr>
<tr>
<td>First hatching</td>
<td>April 1</td>
<td>March 1</td>
<td>February 1</td>
</tr>
<tr>
<td>Larval period</td>
<td>to June 20</td>
<td>to June 10</td>
<td>to June 1</td>
</tr>
<tr>
<td>Moth period</td>
<td>Aug. 12 - Sept. 15</td>
<td>Sept. 5 - Oct. 10</td>
<td>Sept. 15 - Oct. 25</td>
</tr>
</tbody>
</table>

*Mean times after Seamans (1931), Sorenson and Thornley (1941), and Eyer (1957).

Egg

Description. — The egg was first described by Parker *et al.* (1921). When laid, the egg is a glistening milk-white, which later becomes dull grey; it is spheroidal, flattened dorso-ventrally, 1 mm in diameter, and 0.8 mm in height.

When an egg is completely incubated the fully formed embryo can be seen under magnification through the chorion, imparting to the egg a bluish color (frontis. F).

Eggs of noctuid species commonly occurring in Alberta, including *A. orthogonia*, were identified by differences in the pattern of reticulations or ridges on the chorion in the micropyle area (Seamans, 1933).

Incubation and hatching. — The eggs are laid in the early fall and hatch the following spring. Incubation in the field, determined by placing eggs after oviposition in simulated sites in soil, required from 30 to 50 days (Jacobson and Blakeley, 1958a). Lindsay (1954) showed that development rate of the embryo varied directly with temperature. Development took 11, 14, 21, and 33 days at 30°, 25°, 20°, and 15°C, respectively; no development was apparent at 5°C.

In the field the eggs do not usually hatch until the soil is warmed above freezing. In western Canada hatching usually occurs about April 1, although occasionally when the ground is clear of snow earlier than this date some hatching may occur. Instances have been recorded of hatching in the fall (Cook, 1930) but such occurrences are rare. Table 1 shows the approximate date of hatch of the pale western cutworm in various areas.

Contact moisture or high relative humidity is required for hatching. In the laboratory this requirement is provided by adding water directly to the eggs or to the substrate. Under field conditions soil moisture is usually adequate.

Laboratory studies showed that the rate of hatching of fully developed eggs increases with temperature and relative humidity, that prolonged exposure to temperatures from -5° to -15°C does not affect ultimate hatch, and that desiccation, particularly in the range 20° to 30°C, may cause considerable mortality. Findings in the laboratory, corroborated by studies outdoors, show that eggs are admirably adapted to develop, withstand climatic factors, and hatch at a time when their survival is ensured (Jacobson and Blakeley, 1958a).

Diapause. — Early authors noted that development of the embryo was completed during the fall but the eggs would not hatch readily until a further treatment near 0°C intervened (Cook, 1930). They apparently presumed that only the advent of cold weather prevented the eggs from hatching. Andrewartha and Birch (1954) postulated that a weak diapause was involved.
Jacobson (1962a, 1962b) showed that fully developed embryos immediately begin to feed and continue development when dissected from eggs but when left in the egg hatch slowly and unevenly. This is considered as a weak diapause, the intensity of which is reflected by the rate at which they hatch. Investigations showed the rate of hatching is influenced by the temperature of incubation and by the duration and temperature of the post-incubation treatment. When diapause is firmly established, temperatures above 15°C are required to break diapause and to produce a complete hatch whereas at lower temperatures only partial hatching occurs. As diapause is eliminated hatching occurs at progressively lower temperatures.

Intensity of diapause varies in eggs laid at the same time. Some eggs will hatch at suitable temperatures with moisture when embryonic development is complete. Others will require exposure to temperatures from 0° to 10°C before diapause is eliminated. The weak diapause in eggs of the pale western cutworm in its natural habitat is sufficient to prevent hatching in the fall and to ensure that most eggs will hatch in the spring when food is available for larvae.

Larvae

Description. — The larvae of *A. orthogonia* were described by Parker *et al.* (1921). Walkden (1950) described some of the morphological characters that identify cutworms, including the pale western cutworm, that attack cereal and forage crops in the central great plains. The internal morphology of larvae was described by Hocking and Depner (1961). When fully grown the larvae are from 30 to 40 mm long and 5 to 7 mm thick and the general color is usually grey with no definite stripes or markings. The only readily distinguishable characteristic is in the head; the capsule is yellow-brown with two distinct vertical black dashes that form an imperfect H or inverted V (frontis. E).

Larval feeding. — On hatching the larvae are small, about 2 to 3 mm long, and difficult to find. During early instars the larvae feed on available young seedlings, such as weeds and volunteer grains. All instars of larvae are subterranean in habit, attacking the plant below the surface of the ground. Occasionally they are forced to the surface during heavy rains and sometimes at night after extremely warm days.

Early workers believed that early instars fed above ground since the leaves of grain showed notches or holes. It was later demonstrated that these punctures were made by larvae feeding beneath the soil on the coleoptile and the furled leaves of the wheat plant (Jacobson, Farstad, and Blakeley, 1950). When the larvae become older and larger, and as the host plant grows, the cutworm continues to feed below the surface either cutting off the plant and leaving it to wither and die on the surface or, sometimes, pulling it into the soil there to consume it. A key to the insects, including cutworms, damaging grain plants, based on damage observed was prepared by Strickland (1948). More recently another type of feeding was observed. Plants of almost mature winter wheat were found that had been cut near the soil surface. Fully grown larvae, apparently to satisfy a requirement for fibrous material when green food is unavailable, girdle the stem by peripheral feeding. When the stem becomes brittle it falls over. It was estimated that such damage could exceed 10 per cent (Jacobson, 1967).

Number of instars. — The number of instars of *A. orthogonia* Morrison is usually six, although in some situations may be more (Parker *et al.*, 1921). Hardwick (1965), commenting on supernumerary molts in another noctuid, noted that the number may vary from species to species and from individual to individual depending on the nutritive value of the food and varying with temperature. In the laboratory, pale western cutworm larvae starved during instars III or IV more often had seven instars than those that were not
starved (Jacobson and Blakeley, 1960). In an insectary Parker et al. (1921) found that most larvae of this species had seven instars, some had eight, a few individuals passed through nine, and one was noted with 10. No instances are known of the pale western cutworm having fewer than six instars. The exact number of instars that occur in the field is not known. Undoubtedly, it varies from six to eight, or even more, depending upon the temperature, quality and quantity of available food, and the extent of starvation that may occur when a crop is destroyed and food is unavailable.

**Duration of larval period.** — The duration of the entire larval period can also vary even under controlled conditions of food and temperature. Developmental times of larvae reared in the laboratory and hatched on the same day ranged from 40 to 76 days. The duration of development of larvae varies inversely with temperature (Table 2).

Table 2. Durations (days) of development of larvae, prepupae, and pupae of *A. orthogonia* at various constant temperatures.

<table>
<thead>
<tr>
<th>Instar</th>
<th>30°C</th>
<th>25°C</th>
<th>20°C</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>3</td>
<td>4</td>
<td>8</td>
</tr>
<tr>
<td>II</td>
<td>3</td>
<td>3</td>
<td>6</td>
</tr>
<tr>
<td>III</td>
<td>3</td>
<td>4</td>
<td>7</td>
</tr>
<tr>
<td>IV</td>
<td>3</td>
<td>5</td>
<td>7</td>
</tr>
<tr>
<td>V</td>
<td>5</td>
<td>5</td>
<td>8</td>
</tr>
<tr>
<td>VI</td>
<td>7</td>
<td>8</td>
<td>14</td>
</tr>
<tr>
<td>Larvae total</td>
<td>24</td>
<td>29</td>
<td>50</td>
</tr>
<tr>
<td>Prepupae</td>
<td>32</td>
<td>19</td>
<td>13</td>
</tr>
<tr>
<td>Pupae</td>
<td>25</td>
<td>26</td>
<td>28</td>
</tr>
<tr>
<td>Hatch to adults, total</td>
<td>81</td>
<td>74</td>
<td>91</td>
</tr>
</tbody>
</table>

When the larvae were fed Thatcher wheat, Marquis wheat, Compana barley, and Exeter oats, the mean durations from hatching to pupation at 25°C were 45.6, 45.7, 51.8, and 52.7 days, respectively, the latter two periods being significantly different at the 1 per cent level from the first two (Jacobson and Blakeley, 1958b).

Seamans and McMillan (1935) noted differences in development and other effects when larvae were fed various foods, and Hocking (1953) found differences when different parts of the wheat plant were used.

Development in the field obviously must vary greatly since larvae probably hatch at various times and are subjected to varying degrees of food deprivation and have access to various kinds of food plants.

**Damage to crops.** — In the field, feeding by early instars is not readily discernible. As the larvae become larger they are able to cut off and consume more plants. Damage becomes evident when the larvae are in instar III or IV. It is characterized by the appearance of bare
areas, usually at first in sandy areas or on knolls, later these areas may enlarge encompassing many acres; sometimes entire fields may become bare (Parker et al., 1921; Cook, 1930; Seamans, 1938; Walkden, 1940). Moths apparently select hilly areas because they are more favorable for oviposition. Descriptions of the extent of areas infested and the occurrence of severe crop losses have been noted (Gibson, 1914; Cook, 1930; Seamans, 1926, 1938, 1952; Sorenson and Thornley, 1941; Eyer, 1957).

The density and distribution of larvae in the field as well as such other factors as weather and stage and condition of host plants may influence the damage that may occur. Seamans (1938) found that 15 or more larvae per square yard (18/m²) will destroy a crop. Previously Seamans (1931) had stated that in some seasons an infestation of about 1/ft² (11/m²) is sufficient to completely destroy a crop whereas the next year the same infestation will not be noticed. In 1965 the mean numbers of larvae/ft² (m²) from 25 samples in various portions of an infested field of wheat were:

<table>
<thead>
<tr>
<th></th>
<th>Range</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Damaged area (100% loss)</td>
<td>0-7</td>
<td>3.04 (33)</td>
</tr>
<tr>
<td>Margin (50% loss)</td>
<td>0-5</td>
<td>2.44 (26)</td>
</tr>
<tr>
<td>Part crop (25% loss)</td>
<td>0-3</td>
<td>0.84 (9)</td>
</tr>
</tbody>
</table>

These counts indicate that variation in population can occur in a relatively short distance as these counts were made in three lines parallel to each other and about 6 feet apart. The counts also indicate relationships between density and the degree of crop damage (Jacobson, unpublished). The interrelations between cutworms and the host plant have been investigated (Jacobson and Peterson, 1965). Wheat can withstand feeding by instar I and instar II since the larvae cannot cut off wheat plants. The larvae damage the plants by cutting holes in the leaves as they elongate through the coleoptile. The number of plants affected increases with increased larval population (Jacobson et al., 1950). Other experiments in the laboratory, in the greenhouse, and on field plots with pale western cutworm at various stages of larval development and wheat at various stages of growth showed that larvae did not completely sever the plants until instar III; the rate and amount of damage varied directly with size and densities of larvae, temperatures above 15°C, and soil moisture; and damage varied inversely with the age and size of the wheat plant (Jacobson and Peterson, 1965). Damage to wheat by the pale western cutworm is indicative of a dynamic situation where both the insect and the host plant are actively developing and the advantage to one or the other is constantly changing.

**Effects of starvation.** — Experiments showed that, if weeds in fields containing first-instar larvae were allowed to grow for a short period and then were destroyed by cultivation, the young larvae would starve in 10 days to 2 weeks, after which it would be safe to seed the intended crop. Surveys of infested fields along with history of timing of pre-crop cultivation and seeding showed that delayed seeding resulted in less damage than in those fields where the cultivation and seeding were done simultaneously (Seamans, 1937). Greenhouse studies showed that larvae that had fed were more susceptible to starvation than larvae that had not fed (Seamans and Rock, 1945). In the laboratory this was reconfirmed along with the observation that a digestive disturbance occurred in larvae that were fed after starvation (Salt and Seamans, 1945).

Other effects of starvation were studied with all instars. Larvae survived starvation longer when they were larger or when temperatures were lower. When food was made available to larvae that had been starved for some time some of them were unable to resume feeding (Jacobson, 1952). Desiccation is another factor involved in mortality from starvation. Instar IV larvae were more resistant to desiccation than starved instar II larvae. The rate of mortality was lowest at RH50. At RH0 and RH100 the rate was almost the same, indicating that
desiccation and excessive moisture were equally harmful to larvae (Jacobson and Blakeley, 1957b).

The kind of food affected mortality of larvae when they were starved. Larvae were fed Marquis wheat, Thatcher wheat, Compana barley, or Exeter oats until instar V and then starved. Larvae that were fed the oats were least resistant to starvation whereas those fed the wheat varieties showed the greatest resistance to starvation (Jacobson and Blakeley, 1958b). The rate of mortality was associated in each case with the amount of weight gain and hence was a reflection of better utilization of food. Larvae at all stages were fed on wheat and starved. When larvae were starved for various periods before instar V and then fed, the larval period was prolonged, supernumerary moults occurred, and the pupae weighed less. When larvae were starved in their ultimate instar their development accelerated, the pupae weighed less, and fecundity was reduced (Jacobson and Blakeley, 1960).

**Host plants of larvae.** — Lists of plants attacked by larvae of the pale western cutworm have been published (Sorenson and Thornley, 1941; Cook, 1930; Webster and Ainslie, 1924). These include a variety of crops grown in the areas where this cutworm has been known to occur. Generally, however, the larvae prefer cereals and the greatest losses have occurred to crops of wheat, oats, and barley. In gardens and in areas where vegetable crops are grown, the pale western cutworm often appears along with other cutworm species.

**Nutrition of larvae.** — Before 1950, studies on the pale western cutworm primarily involved field ecology and the information obtained was directly concerned with life history and field control. Many questions about the biology and behaviour of the insect went unanswered. Over a period of about 15 years McGinnis and Kasting carried out a series of nutritional and biochemical investigations aimed at providing some of the answers. Their first reports showed that the rate of growth and development depended on both quality and quantity of the food consumed. They found that larvae with free access to Thatcher wheat sprouts were larger and developed more rapidly than larvae allowed the same food for only 2 hours each day (McGinnis and Kasting, 1959). They also found that the variety of wheat sprouts upon which the larvae fed affected growth (Kasting and McGinnis, 1959).

The amino acids essential in the diet of this insect were determined using a radioactive tracer technique (Kasting and McGinnis, 1966). Results indicated that it had the same general requirements as other animals; no abnormal amino acid requirements were evident (Kasting and McGinnis, 1962). The amino acids in the normal diet of these larvae are largely bound in the protein form. It was necessary, therefore, to determine whether the larvae could utilize dietary protein. Results of a study with protein-U-\(^{14}\)C showed that the larvae readily digested the protein (McGinnis and Kasting, 1962). The presence of proteolytic enzymes was confirmed in a subsequent study with gut homogenates (Khan and Kasting, 1961). Other enzymes, including various carbohydrases, peptidases, and lipases, were also shown to be present.

A synthetic diet for the pale western cutworm was described in 1967 and growth factor requirements were determined by the classical deletion procedure (Kasting and McGinnis, 1967). Results indicated that niacinamide, choline, pantothenic acid, pyridoxine, riboflavin, folic acid, and thiamin are essential. No requirement for biotin, inositol, or vitamin B\(_{12}\) was demonstrated.

Because this insect grows fast and is large in the later instars, it has been used effectively as a laboratory animal. Several techniques connected with the nutrition of the species have been developed and tested, as for example, the use of lyophilized plant tissue in diets (McGinnis and Kasting, 1960) and measurement of consumption and digestibility of food (McGinnis and Kasting, 1964a, 1964b, 1969; Kasting and McGinnis, 1965).
Prepupae and pupae

Prepupae. — The prepupal stage has been described as a quiescent or non-feeding period between the end of the larval period and the pupal period. When feeding ceases, the body becomes shrivelled and assumes a yellowish color. In laboratory rearing the exact date on which larvae become prepupae is difficult to establish. Sometimes the larvae may stop feeding for several days only to resume. A more accurate measure of the prepupal period was obtained by daily weighings after the fifth moult until feeding ceased and until weights had decreased about 25 per cent. The duration of the prepupal period is considered to be the time from the date of maximum weight to the date of pupation (Blakeley and Jacobson, 1960).

In the field the larva, after completing its feeding, burrows 2 to 6 inches (5 to 15 cm) into the soil and constructs an earthen cell enclosing itself. Each larva forms its cell by injecting fluid through its mouthparts into the surrounding earth and compacting this with head and body movements until a smooth lining is formed. In the laboratory where this was observed in glass tubes the process was completed in a few days (Blakeley, 1954).

The mean durations of the prepupal stage of insects that had been reared through the larval stage under similar conditions of food and temperature and assigned to 20°, 25°, and 30°C at the beginning of the prepupal stage were 12.5, 19.8, and 31.8 days, respectively. The longer prepupal interval at 30°C was considered to be a form of diapause that enabled the pale western cutworm to survive as a single-brooded species in the wide variation of climate from the prairies of Canada to Texas in the United States (Blakeley and Jacobson, 1960). This relationship with temperature will also allow for a compensatory effect to ensure eclosion at the normal time of year if larval development is accelerated because of increased temperatures.

Pupae. — In the field, the change from the prepupal stage to pupae occurs inside the earthen cell. In the laboratory where soil is not used this change occurs normally without a cell. The pupae has been described (Parker et al., 1921).

In the field it is difficult to determine when prepupae change to pupae except by periodic collections. The progress of development in 1965 is shown in Table 3. No feeding larvae were found after July 5. These data, which are for one year only, show that pupation was complete about August 1 but experience has shown considerable variation from year to year related to weather and moisture conditions. Density decreased as the season progressed as a result of natural mortality factors such as parasitism, predation, and inclement weather.

Table 3. Numbers of larvae, prepupae, and pupae of A. orthogonia collected from 25 square-foot samples from a field near Lethbridge, Alberta, in 1965.

<table>
<thead>
<tr>
<th>Date</th>
<th>Larvae</th>
<th>Prepupae</th>
<th>Pupae</th>
<th>Total</th>
<th>Number/ft²</th>
</tr>
</thead>
<tbody>
<tr>
<td>June</td>
<td>18</td>
<td>76</td>
<td>0</td>
<td>76</td>
<td>3.0</td>
</tr>
<tr>
<td></td>
<td>23</td>
<td>66</td>
<td>2</td>
<td>68</td>
<td>2.7</td>
</tr>
<tr>
<td></td>
<td>29</td>
<td>52</td>
<td>3</td>
<td>55</td>
<td>2.2</td>
</tr>
<tr>
<td>July</td>
<td>2</td>
<td>29</td>
<td>13</td>
<td>42</td>
<td>1.8</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>3</td>
<td>33</td>
<td>36</td>
<td>1.4</td>
</tr>
<tr>
<td></td>
<td>16</td>
<td>0</td>
<td>19</td>
<td>20</td>
<td>0.8</td>
</tr>
<tr>
<td></td>
<td>27</td>
<td>0</td>
<td>8</td>
<td>10</td>
<td>0.3</td>
</tr>
<tr>
<td>August</td>
<td>4</td>
<td>0</td>
<td>1</td>
<td>9</td>
<td>0.3</td>
</tr>
</tbody>
</table>
In the laboratory the duration of the pupal stage varied inversely with temperature and directly with weight. An increase of 10 mg in the pupae was associated with an increase of 0.12 days in the duration of the pupal stage (Blakeley and Jacobson, 1960). Since larvae may vary in vigour and not all may have an equal opportunity to feed, they vary in weight. This, and other causes of individual variation, accounts for the variation in time of change to prepupae, to pupae, and finally to emergence of the moths. At 25°C duration of the pupal stage of 48 pupae ranged from 21 to 46 days and averaged 27 days (Blakeley and Jacobson, 1960).

Toward the end of the pupal period the adult can be seen inside the pupal case. Eclosion from the pupal case, the subsequent escape from the earthen cell, and the ascent through the soil using spines on the middle and hind legs has been described (Blakeley, 1954). Sex of the pupae is easily determined (Butt and Cantu, 1962) and the method used is invaluable in laboratory investigations to determine sex ratio before adults emerge. The pupae of each sex are shown in frontis. C and D.

_Mortality of prepupae and pupae._ — The pupal cell and surrounding soil protect the prepupa and pupa from desiccation. However, the insect is not completely safe as the population density decreases during these stages (Table 3). Of 50 non-feeding larvae placed outdoors in early July and examined at regular intervals until September 13, eight died of undetermined causes, eight were killed by parasites and four by predators, and 12 were recorded as missing. Only eight of the original 50 emerged as moths. The category missing is used to describe prepupa and pupae that died from predation by insects or animals or other causes and soon disintegrated (Jacobson, unpublished).

**Adult stage**

_Moth._ — The description of the adult male by Morrison (1876) has been repeated in the literature (Parker _et al._, 1921; Blakeley, 1954). Both sexes are easily identifiable in the field and usually are readily distinguished from other species that appear coincidently. Moths are readily sexed. The antennae of the males, described originally as strongly serrate, are pectinate; those of the females are filiform (frontis. E and F).

Eclosion of moths appears to conform to a diurnal rhythm; 90.7 per cent emerged in the laboratory between noon and midnight and 49.5 per cent between 1400 and 1600 hours (Jacobson, 1965). In the field and laboratory, male moths emerge earlier in the flight period than females (Cook, 1930).

_Flight._ — In western Canada, the moths first appear on flowers or around lights during the first two weeks in August. Their numbers increase until the end of the month and gradually decline in September. The flight period varies from one area to another and reflects differences in latitude (Table 1). At Saskatoon, Saskatchewan, moths appear and the flight terminates earlier than at Lethbridge. The duration of the flight varies from year to year according to the weather. In 1950, in the immediate Lethbridge area the flight was terminated in early September by unseasonably high maximum temperatures that completely dried the flowers upon which the moths were feeding. Flights usually terminate during periods of cool weather, marked by snow and freezing temperatures. Cooley (1922) recorded the end of the flight in 1921 after a severe snowstorm in early September. In years when conditions remain favourable moths can be found in low numbers until late September. Duration of flight undoubtedly influences the numbers of eggs that are laid.

Moths of the pale western cutworm are crepuscular and exhibit a distinctive diurnal pattern of activity. Only rarely during the day are moths found before noon except when they are unusually abundant and the weather is warm. During the early afternoon males and a few females begin to appear on flowers and numbers of both sexes increase gradually
until sunset. In the late afternoon females become more abundant. Counts of moths on flowers show that the preponderance of one sex over the other changes. Until 1600 hours males outnumber the females about eight to one; after that time until sunset the proportion is reversed. The change in ratio is probably due to differences in feeding habits between the sexes and to the oviposition behaviour of the females.

Activity is related to temperature. At 22°C and above, moths are very active and difficult to capture, but as the temperature drops below 22°C, the moths become more passive; below 10°C the moths stop flying and seek shelter at ground level, usually around patches of flowers. As the season progresses the daily interval of activity lessens.

The moths feed on flowers and are readily attracted to light as evidenced by capture in light traps. The numbers of moths caught each hour in a light trap designed to capture moths for hourly periods (Seamans and Gray, 1934) were similar until midnight but became less after that time until about 0300 hours. The decline in numbers is apparently associated with decrease in temperature during the night. Similar data were recorded by Cook (1930) over a four-year period when numbers were counted on flowers during the dark period commencing at 2000 hours.

A study of activity of both sexes was made using electrophysiological apparatus described by Edwards (1964) wherein the flying activity of males and walking of females were recorded electronically. Peaks of female activity occurred after sunset, near midnight, and at sunrise. Male activity was centered mainly at midnight. It was assumed that activity at that time was associated with mating since it coincided with a similar activity time of females. The crepuscular times were interpreted as times of feeding or oviposition.

Laboratory studies showed that the maximum distance flown on a flight mill was 14.7 miles (23.7 km) for males and 3.5 miles (5.6 km) for females, that speed varied from less than 1 to 3 m.p.h. (1.6 to 4.8 km/hr), that total flight times were usually marked by a series of repeated flights, and that flying ceased with exhaustion but would resume after rest or feeding (Jacobson, 1965). Chance (1971) has measured the drag-speed relationship of the flight mill I used and calculated the compensation for this which gives values for the insects in free flight about 20 per cent higher than these.

Preliminary investigations in the field using marked-capture techniques appeared to indicate that movement of moths was local, confined to adjacent fields and patches of flowers. Other observations showed that during the daily flight period movement in and out of the flowers was almost constant except that the proportions of males to females were reversed between one part of the day and another. No definite records of mass migrations of moths of the pale western cutworm have been observed or recorded. Known data indicate that the moth is not as strong a flier as other noctuid species that are known to be capable of migrating considerable distances.

The duration of the flight period and daily activity is associated with availability of suitable flowers from which the moths obtain nectar. In western Canada the favoured flowers are sunflowers (Helianthus sp.) and goldenrods (Solidago spp.), both of which occur throughout the prairie region along roads and field margins. In some areas of Montana and Utah the moths are attracted to rabbitbrush (Chrysothamnus sp.) (Cook, 1930; Sorenson and Thornley, 1941), a plant that occurs on the Canadian prairies in eroded and arid areas but is not utilized by the moths of the pale western cutworm since this cutworm does not usually occur in these areas. Moths have been observed feeding on the blossoms of broomweed (Gutierrezia sp.), Russian thistle (Salsola pestifer A. Nels.), Canada thistle (Cirsium arvense (L.) Scop.), perennial sow-thistle (Sonchus spp.), gumweed (Grindelia squarrose (Pursh) Dunal), and several species of fleabane (Erigeron spp.). Moths are energetic feeders. They crawl about on the flowers, quickly uncoil their long sucking tubes,
and insert them into blossoms after blossoms.

The length of life of moths varies inversely with temperature, at constant temperatures in the laboratory ranging from a mean of 38 days at 0°C to 7.4 days at 35°C. At room temperature, 22°C, there was no difference between sexes, the mean life span being 12 days. Longevity of females at room temperatures was influenced by food; those fed honey and water had a mean length of life of 14 days; those fed with water, 8 days; and those not fed, 5 days. The length of life in the field cannot be determined but must be very variable as it is dependent on temperatures, available food, prevailing weather, and presence of predators. Females collected from flowers in the field usually die in 1 to 5 days after capture.

*Mating and oviposition.* — Mating is rarely observed in the field. A few instances are recorded of copulating pairs being found on flowers during the early evening or at night (Cook, 1930; Seaman, 1931). In the laboratory copulation usually occurs during the night as attested by the numbers of pairs attached together in the morning. Vigils at night showed that most matings occurred from 0100 hours to daylight (Jacobson, unpublished). Evidence of mating determined by dissecting females for the presence of spermatophores showed that mating usually occurred during the first 2 nights after emergence. Most of the females mated only once; multiple matings occurred in less than 20 per cent of the females examined. The most spermatophores found in one female was three. In several instances a male mated with two or three females. Moths mated at all experimental temperatures between 5° and 35°C. High temperatures appeared detrimental for mating as only one out of five females mated at 30° and 35°C, whereas in the range from 5 to 25°C, three or more out of five females usually mated. Continuous lighting deterred mating; at 25°C only one female out of eight was mated whereas in continuous darkness the proportion was 1:2 (Jacobson, 1965).

The duration of copulation of the pale western cutworm is not known with any degree of certainty. Data on other noctuid species (Hardwick, 1965) indicate that the interval could extend from 45 minutes to 3 hours.

Dissections of females collected from flowers in the field and capture in light traps disclosed that 96 per cent had mated (Jacobson, 1965). Since mating occurs early in the life of a female and over a wide range of environmental conditions, it is concluded that the opportunity for mating is not a factor in oviposition by the pale western cutworm. Oviposition by the pale western cutworm in the field and laboratory has been studied for some time (Parker *et al*., 1921; Cook, 1930; Sorenson and Thornley, 1941). These authors found that oviposition occurred in the late afternoon and early evening, that moths laid the eggs in loose dusty soil, and that each female was capable of laying about 100 eggs. In the field eggs are difficult to find unless the exact site of oviposition is observed. Further knowledge was obtained from laboratory studies using moths that had been reared (Jacobson, 1965). Eggs developed during the pupal stage and were ready for fertilization when the moths emerged. Oviposition began on the first or second day after mating, reached a peak soon after, and continued until just before the females died. Maximum oviposition by one female was 564 eggs. In 19 cages, each containing 4 to 18 females and as many or more males, mean numbers per female ranged from 161 to 488. Oviposition occurred at all temperatures from 5 to 35°C, the optimum temperature being between 10 and 25°C. More eggs were laid in the dark or in subdued light than in continuous bright light. Females when unfed could oviposit but when fed water or sugar solutions they laid more eggs. A diurnal rhythm of oviposition occurred with distinct peaks; 80 per cent or more of the eggs were laid between noon and early evening. Rhythm of oviposition was apparently initiated by light and could be reversed by reciprocal light regimens but was maintained in continuous dark or light (Jacobson, 1965).

*Sex ratio.* — References to sex ratio (Cook, 1930; Eyer, 1957) indicate a preponderance
of males. Cook (1930), who counted the numbers of each sex on flowers over a period of several years determined that the ratio of males to females was three to two. Apparently he was not aware that the ratio may change with the time of day or other factors. Eyer (1957) used the numbers of each sex that were captured in light traps and found the ratio was six or seven males to each female. Light trap records over a number of years has shown that males are more readily attracted to lights, possibly because males are stronger fliers and greater numbers of them may be in flight during hours of darkness. Strickland (1922) found that when pans were baited in the field with a fermented molasses solution nearly 50 per cent of the captured moths were females. Counts of moths reared in the laboratory, both from larvae collected in the field and those reared from eggs in the laboratory, show that both sexes occur in almost equal numbers.

REARING METHODS

Procedures for conducting research on the pale western cutworm in the laboratory have undergone many changes during the course of investigations. Rearing methods were developed that permitted the conduct of research on biology, physiology, nutrition, or insecticide testing with all stages at all times of the year.

General methods for all stages have been described (Parker et al., 1921; Cook, 1930; Jacobson and Blakeley, 1957a). Methods for obtaining eggs and procedures for their use in investigations under various environmental conditions have been outlined (Lindsay, 1954; Jacobson and Blakeley, 1957b; Jacobson, 1962a, 1962b). The rearing of larvae for various purposes has been described by various authors; on various food plants (Seamans and McMillan, 1935; Jacobson and Blakeley, 1958b; Hocking, 1953), on artificial diets (McGinnis and Kasting, 1959, 1960; Kasting and McGinnis, 1967), and for insecticide testing (McDonald, 1969). One of the difficulties of mass rearing is that the larvae are cannibalistic (Dethier, 1939) and must be contained separately in suitable containers. Hence, the number that can be reared at a time is limited. The methods of containing pupae until emergence have been described (Blakeley, 1954; Blakeley and Jacobson, 1960). Moths have been used for various purposes: for oviposition (Jacobson and Blakeley, 1957b); for flight mill studies (Jacobson, 1965), and for light trap captures (Cook, 1930; Seamans and Gray, 1934).

Many species of Noctuidae cannot be reared successfully in the laboratory beyond three generations (Hardwick, 1965) as vigour and viability progressively decline and susceptibility to laboratory disease increases. Similar results have been obtained when successive generations of the pale western cutworm have been reared in the laboratory. It is, therefore, desirable to replace laboratory cultures with eggs obtained from females collected in the field each year if possible.

NATURAL ENEMIES AND DISEASE

Parasites

Internal parasites of the larvae of the pale western cutworm have been recorded in the various areas of occurrence (Strickland, 1921; Parker et al., 1921; Cook, 1930; Seamans, 1931; Sorenson and Thornley, 1941; Walkden, 1950; Brooks, 1952). The biology of parasitism was admirably described by Strickland (1923). Schaaf (1971) studied the parasitoid complex of Euxoa ochrogaster (Guenée) with emphasis on the identification of immature stages and review of biology. Many of the species noted also parasitize larvae of A. orthogonia. Dipterous parasites include the families of Ichneumonidae, Braconidae, and Chalcididae. Table 4 shows the parasites recorded by various authors in their respective areas.
Table 4. Recorded parasites of *A. orthogonia*.

<table>
<thead>
<tr>
<th>Parasite</th>
<th>Record by</th>
<th>Present status, notes</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Diptera: Tachinidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bonnetia compta Fall.</td>
<td>a,b,c,d,e</td>
<td><em>Pseudomeriania nigrocornea</em> Tot.</td>
</tr>
<tr>
<td>Ernestia radicum Fab.</td>
<td>b,d</td>
<td><em>Gonia aldrichi</em> Tot.; perhaps also <em>longiforceps, breviforceps, and longipulvilli</em> (D. M. Wood, correspondence)</td>
</tr>
<tr>
<td>Gonia capitata DeG.</td>
<td>b,d</td>
<td></td>
</tr>
<tr>
<td>G. longiforceps Tot.</td>
<td>c,e</td>
<td></td>
</tr>
<tr>
<td>G. brevipulli Tot.</td>
<td>g</td>
<td></td>
</tr>
<tr>
<td>G. aldrichi Tot.</td>
<td>e</td>
<td></td>
</tr>
<tr>
<td>Metaphyto genalis Coq.</td>
<td>a</td>
<td><em>Peleteria sp.</em>, perhaps <em>anaxias</em> (Wlk) or <em>haemorrhhoa</em> (Wulp) (D. M. Wood, correspondence)</td>
</tr>
<tr>
<td>Peleteria robusta Wied.</td>
<td>a,b,d</td>
<td></td>
</tr>
<tr>
<td>Wagneria rohweri Tnsd.</td>
<td>c</td>
<td><em>Periscepia rohweri</em> Tnsd.</td>
</tr>
<tr>
<td><strong>Diptera: Bombyliidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anthrax molitor Loew.</td>
<td>c</td>
<td></td>
</tr>
<tr>
<td>Villa alternata (Say)</td>
<td>h</td>
<td></td>
</tr>
<tr>
<td>Villa willistoni (Coq.)</td>
<td>g</td>
<td><em>Poecilanthrax willistoni</em> (Coq.)</td>
</tr>
<tr>
<td>Poecilanthrax sackenii (Coq.)</td>
<td>h</td>
<td></td>
</tr>
<tr>
<td><strong>Hymenoptera: Braconidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Meteorus vulgaris Cress.</td>
<td>c,d,f</td>
<td><em>Meteorus leviventris</em> Wesmael</td>
</tr>
<tr>
<td>Chelonus sp.</td>
<td>d</td>
<td></td>
</tr>
<tr>
<td>Zele sp.</td>
<td>d</td>
<td></td>
</tr>
<tr>
<td><strong>Hymenoptera: Ichneumonidae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Paniscus sp.</td>
<td>b</td>
<td></td>
</tr>
<tr>
<td>Apanteles griffini Vier.</td>
<td>f</td>
<td></td>
</tr>
<tr>
<td><strong>Hymenoptera: Chalcididae</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Berecyntus bakeri (Howard)</td>
<td>c</td>
<td><em>Copidosoma bakeri</em> (Howard)</td>
</tr>
</tbody>
</table>

a – Parker *et al*., 1921; b – Strickland, 1923; c – Cook, 1930; d – Seamans, 1931; e – Sorenson and Thornley, 1941; f – Walkden, 1950; g – unpublished records; h – Brooks, 1952.
Predators

Many species of insect predators have been observed attacking larvae and adults of the pale western cutworm. Species of predaceous wasps and larvae of ground beetles prey on cutworms in the field (Cook, 1930; Seamans, 1931). When moths are feeding on flowers they are often attacked by arthropod predators, which include various species of Arachnida, Mantidae, Coreidae, Reduviidae, and Phymatidae (Sorenson and Thornley, 1941; Seamans, 1931). Many native birds including larks, sparrows, buntings, crows, curlews, and Franklin’s gulls have been observed digging cutworms from the soil or carrying them to their nests; some have been seen capturing moths on flowers (Cook, 1930; Seamans, 1931; Sorenson and Thornley, 1941).

Value of natural enemies

The early workers with the exception of Strickland (1923) doubted that parasites and predators were important in the control of the pale western cutworm (Parker et al., 1921; Cook, 1930). Subsequent investigations showed that the incidence of parasites varied from year to year and was influenced by weather (Seamans, 1923, 1935). Rearing records show that parasitism can vary from 20 to 70 per cent. This indicates that when climatic conditions favour their increase, parasites, along with predators, can play an important role in quickly reducing populations of cutworms after years of severe outbreaks.

Disease

The role of disease in reducing populations of the pale western cutworm in the field has not been adequately assessed. Crumb (1929) listed several diseases that caused reductions in populations of tobacco cutworms, but as these are surface-feeding species the diseases that affect them may not affect the pale western cutworm, which spends most of its time in the soil. Steinhaus and March (1962) identified bacteria found in field-collected larvae. Cook (1930) postulated that disease may be a controlling factor. McMillan (unpublished report) recorded a disease found in one field that accounted for 47 per cent mortality, but this may have been the effect of climatic stress during years of a severe outbreak. Outbreaks of disease frequently occur when larvae are reared in the laboratory but some doubt exists that similar outbreaks occur in the field. Walkden (1950) listed several disease organisms and noted that many larvae collected in the field for rearing died in the laboratory of a disease, which he named “the rearing disease”, that turned larvae black similar to dead larvae found in the field after a heavy rain. A disease of pale western cutworms reared in the laboratory was described by Kasting, McGinnis, and Hawn (1971). They called it “black disease” and identified the causative bacterium as Pseudomonas aeruginosa.

RELATIONSHIP OF INFESTATION TO WEATHER

The numbers of many animals are largely determined by weather. Andrewartha and Birch (1954), after reviewing earlier publications (Parker et al., 1921; Seamans, 1923; Cook, 1924, 1926, 1930), used the pale western cutworm as an example of numbers of animals in natural populations. The various effects of precipitation on this insect and other crop insects were reviewed by Beirne (1970).

Weather, distribution, and outbreaks

Confinement of distribution of the pale western cutworm to the semiarid region of the plains in Canada and the United States indicates a relationship to the weather that prevails in these regions. Cook (1923, 1926, 1927a, 1927b, 1928, 1929, 1930) studied the physical
ecology of Noctuidae of the American plains with special reference to *A. orthogonia*. He related distribution to weather by means of climographs for various regions and predicted areas in the United States where the pale western cutworm could be found occasionally and in outbreak numbers. His prediction of economic distribution conforms almost identically to that shown in Figure 1, which includes records to 1970, almost 50 years later. He found a high negative correlation between abundance of the pale western cutworm and years when rainfall in May, June, and July exceeded 5 inches (12.7 cm). Dry weather was favorable to increase. He further indicated that one favorable year may increase the number of cutworms to cause slight damage and local outbreaks but two successive favorable years were necessary to produce a severe and widespread outbreak.

**Forecasting**

The relationship of seasonal rainfall and possible outbreaks of the pale western cutworm led to the development of a method of forecasting. Seamans (1923, 1935) based the forecast on the assumption, confirmed by rearing records, that increased rainfall forced the larvae to feed and move about above ground where they were exposed to attack by parasites. The basis of the prediction was the number of “wet days” — days on which 0.25 inches (0.64 cm) or more of rain fell — in May and June. More than 10 “wet days” resulted in a decrease in the numbers of cutworms, less than 10 were followed by an increase. In western Canada a forecast was prepared each year, delineating areas where a hazard was anticipated. This information was made available through the daily and weekly newspapers, radio and television, and extension agencies of government and industry. Accepted methods of preventing infestations by cultural means were given with the forecast. In Montana, Wall (1932) showed that the method of predicting infestations was accurate.

Seamans (1923, 1935) considered parasites as the main factor in reducing populations during outbreaks when rainfall was above normal, whereas Cook (1930) indicated that fungous and bacterial diseases were equally or more important. In western Canada from 1945 to 1953 counts of moths were made on flowers during the peak of the flight in three selected locations. The mean number of moths per minute decreased in each location with an increase in the number of wet days during the previous May and June ($r = -0.878$).

**CONTROL**

**Cultural**

Early attempts at cultural control involved the use of ploughs, packers, discers, and other available implements. It was found that packing and the use of a press drill limited the movement of larvae in the soil but did not achieve satisfactory results (Strickland, 1915; Parker *et al.*, 1921; Cook, 1930. The observation that moths could not deposit eggs in fields that were crusted because they had not been cultivated for some time before oviposition (Parker, Strand, and Seamans, 1920) led to a recommendation that infestation could be prevented by allowing a crust to form on the surface before the oviposition period. This method of prevention was the only control measure available for many years and was widely followed throughout the areas in the United States and Canada where the pale western cutworm was an economic pest. Surveys during outbreaks showed that damage was less, or none at all, in fields where the method was practised (McMillan, 1935; Seamans, 1952). This method was later augmented by cultural methods to starve early instars in the spring (Seamans, 1937, 1952) which represented the first control measure that could be used after infestations were found in the field. Since the method involved a delay of 10 days to 2 weeks after cultivation of new growth before seeding and an additional operation it was
not readily adopted by farm operators.

Poisoned baits
Another of the early attempts at control in the field made use of poisoned baits (Strickland, 1915). Many of the available poisonous materials were added to various carriers, mainly bran, and spread on the soil (Parker et al., 1921; Cook, 1930; Seamans, 1931). The consensus was that the baits were not effective (Cook, 1930; Seamans, 1931) mainly because of the subterranean feeding habits of the pale western cutworm.

Chemical control
When DDT and related organochlorine compounds came into general use for control of agricultural pests it was felt that sprays and dusts would not be effective, as the pale western cutworm fed almost exclusively below the soil surface. The first successful demonstration of control in the field (Jacobson et al., 1952) showed that chlordane, dieldrin, aldrin, and, to a lesser extent, toxaphene, when applied as sprays to the soil surface could protect crops from damage. These materials were selected from results of laboratory assessment (Brown et al., 1947). Faulkner (1954) found, in laboratory tests, that some of the insecticides killed the embryos in unhatched eggs. Further testing in other areas confirmed these results and led to the general recommendation that dieldrin was the most effective material (Hoerner, 1953; Pfadt, 1956; Eyer, 1957; DePew and Harvey, 1957). Dieldrin was later replaced by endrin because of its effectiveness at low rates. When organochlorine compounds were found to present a residue hazard to livestock and humans other less persistent materials were sought. Field testing showed that several organophosphorus insecticides, including AC-47031 [cyclic ethylene (diethoxyphosphinyl) dithioimidocarbonate] and fen-sulfothion (dasanit) were as effective as endrin (Jacobson and McDonald, 1966). Additional tests in the field showed that AC-47031 and monocrotophos (azodrin) were slightly superior to endrin (DePew, 1970). Laboratory testing further confirmed the effectiveness of AC-47031 and indicated that other organophosphorus insecticides could be used to control the pale western cutworm (McDonald, 1969).

The use of insecticides provides a further advantage to the farmer. When these materials were not used, fields that had been destroyed could not be reseeded until the larvae had ceased feeding. The plantings, delayed until late in June in western Canada, were often damaged by frost or snow before they were ready for harvesting. Damaged fields can be reseeded immediately after treatment with an insecticide.

Future control methods
The impetus in the search for alternative methods for controlling insects is toward the use of methods other than the application of insecticides because of the problems that result from the accumulation of residues, the possibility that insects have become resistant to insecticides, and that insecticides contaminate the environment. Some of the alternatives might include microbial pesticides, natural or synthetic pheromones to attract adults to be killed with poisons or other means, the use of antifeeding compounds, the breeding of resistant crops, chemosterilants, and integrated control embodying several methods.

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I express my gratitude to colleagues, present and past, at the entomological laboratories at Lethbridge, Alberta; Saskatoon, Saskatchewan; and Brandon, Manitoba, who have assisted in the furtherance of knowledge of the pale western cutworm. I especially acknowledge
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A. C. CHEUNG
Department of Entomology
University of Alberta
Quaestiones entomologicae
Edmonton, Alberta
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Arginine phosphokinase was purified from honeybee thoraces. Its molecular weight was estimated by Sephadex gel chromatography at about 36,000. In the direction of arginine phosphate synthesis, the enzyme had a pH optimum around 8.3. The energy of activation for the reaction from 22-45 C was 7,000 cal/mole. Optimum molar ratio of Mg++: ATP appeared to be 1:1. Besides Mg++, the enzyme was activated to various extents by Mn++, Ca++, Co++, and Cu++. UTP, GTP, CTP, and ADP could not substitute for ATP as substrate. The enzyme phosphorylated L-arginine methyl ester and to a much less extent D-arginine, but did not phosphorylate creatine, guanidoacetic acid, nor hippuryl-L-arginine.

L'arginine phosphokinase a été purifiée à partir de thoraces d'abeilles. Son poids moléculaire a été estimé par chromatographie sur gêle Sephadex à environ 36,000. Dans la réaction donnant la synthèse de l'arginine phosphate, l'enzyme a un pH optimum aux environs de 8.3. L'énergie d'activation pour la réaction de 22-45 C était 7,000 cal/mole. Le rapport molaire optimum de Mg++: ATP apparaît être 1:1. En plus de Mg++, l'enzyme a été activée à différents degrés par Mn++, Ca++, Co++, et Cu++. UTP, GTP, CTP, et ADP ne peuvent pas remplacer l'ATP comme substrat. L'enzyme phosphorylante L-arginine methyl ester et à un degré moins élevé, la D-arginine, mais ne phosphorylante pas la créatine, l'acide guanido-acétique, et la hippuryl-L-arginine.

Using crab-muscle extracts, Lohmann (1935) first discovered the enzyme arginine phosphokinase (EC 2.7.3.3) which catalyzed the reaction:

\[
\text{ATP + arginine} \rightarrow \text{ADP + arginine phosphate + H}^+ 
\]

Since then other workers have described the enzyme from various invertebrates. Arginine phosphokinase has been purified or identified from extracts of the following species: freshwater crayfish Potamobius astacus, and P. leptodactylus (Elodi and Szorényi, 1956), sea crayfish Jasus verreauxi (Morrison et al., 1957; Uhr et al., 1966), shrimps Palaemon serratus, P. elegans (Virden and Watts, 1964), crabs Pagurus bernhardus, Callinectus sapidus (Blethen and Dalplan, 1968), Atelecyclus septemdentatus, Cancer pagurus, Portunus depurator, Carcinus maenas, Maia squinado (Virden and Watts, 1964), lobsters Homarus vulgaris (Pradel et al., 1964; Virden et al., 1965), H. americanus (Blethen and Kaplan, 1967; Regnouf et al., 1969), and Nephrops norvegicus (Virden and Watts, 1964), molluscs Pecten maximus, and Chlamys opercularis (Virden and Watts, 1964), the horseshoe crab Limulus polyphemus (Blethen and Kaplan, 1968), echinoderms Centrostephanus rodgersii, Heliocidaris erythrogramma (Griffiths et al., 1957a), and Echinus esculentus, Holothuria forskali, and Asterias rubens (Virden and Watts, 1964), the tunicate Styella mammiculata (Virden and Watts, 1964), the cephalochordate Amphioxus lanceolatus (Virden and Watts, 1964), arachnids Pholcus phalangioides, and Dugesiella hentzi (Blethen and Kaplan, 1968), the annelid Sipunculus nudus (Regnouf et al., 1969), insects Melanoplus bruneri, Apis mellifera, Porthetria dispar, Sympetrum rubicundulum, (Blethen and Kaplan, 1968), and Calliphora erythrocephala (Lewis and Fowler, 1962), protozoans Tetrahymena pyriformis (Robin and Viala, 1966; Watts and Bannister, 1970), and Stentor coerulescens (Watts et al., 1968), and from the bacteria Escherichia coli (Di Jeso, 1967).

In the study of the properties of this enzyme most workers used enzymes extracted from
crustaceans. Little work has been done on the enzyme from insect sources. Recently Carlson et al. (1971) reported the crystallization of arginine kinase from honeybee thoraces. These workers indicated that the physical, chemical, and catalytic properties of the enzyme were being studied. So far there has been no report on the properties of an insect APK. I report a method of purifying arginine phosphokinase from honeybee thoraces and the investigations on some properties of the enzyme in the direction of arginine phosphate synthesis.

The following abbreviations are used: arginine phosphokinase, APK; arginine phosphate, AP; adenosine triphosphate, ATP; uridine triphosphate, UTP; guanosine triphosphate, GTP; cytidine triphosphate, CTP; adenosine diphosphate, ADP; diethyl aminoethyl cellulose, DEAE-cellulose; disodium ethylenediamine-tetraacetate, EDTA; and Tris (Hydroxymethyl) aminomethane, Tris.

MATERIALS AND METHODS

Experimental animals

Honeybee workers (Apis mellifera L.) were obtained from a local apiary and frozen until use.

Sources of chemicals

ATP and L-arginine came from both Sigma Chemical and Calbiochem. UTP, CTP, GTP, ADP, L-arginine methyl ester, hippuryl-L-arginine, guanidoacetic acid, creatine, cytochrome c, Tris, and DEAE-cellulose came from Sigma Chemical. D-arginine, myoglobin, haemoglobin, and bovine albumin came from Nutritional Biochemicals. L-cysteine HCl, 2-mercaptoethanol, reduced glutathion, γ-globulin, and Aquacide I came from Calbiochem. MgSO₄, MnSO₄, CuSO₄, CoCl₂, CaCl₂, ammonium molybdate, 1-amino-2-naphthol-4-sulfonic acid, and EDTA came from Fisher Scientific.

Assay procedure

The activity of the enzyme was estimated by measuring the inorganic phosphate released after acid hydrolysis of arginine phosphate. The assay procedure was modified from that of Morrison et al. (1957). The reaction mixture contained a final concentration of 50 mM Tris, 1 mM 2-mercaptoethanol, 5 mM ATP, and 10 mM each of arginine and MgSO₄, pH 8.3. In a typical assay, 0.9 ml of the stock solution was incubated at 30 C for 5 min, the reaction was started by adding 0.1 ml APK solution. The reaction was stopped after 5 min by adding 0.5 ml 30% acetic acid. The solution was placed in boiling water for exactly 1 min, after which it was immersed in an ice-bath. The colorimetric determination of inorganic phosphate was started by adding 2.0 ml 5% w/v ammonium molybdate in 15% v/v H₂SO₄ followed by 0.5 ml 0.25% aminonapthol sulfonic acid half a minute later. The mixture was diluted with 5 ml glass distilled water. The absorbance of the resulting blue solution was read at 540 nm in a Beckman DU-2 spectrophotometer after 20 min. Controls were run in the same way except that acetic acid was added before adding the enzyme. Enzyme activity was measured as the difference in absorbance between the 5 min assay and the control. When working with the crude extracts and various (NH₄)₂SO₄ fractions, correction for ATPase activity was made by subtracting the change in absorbance without arginine in the stock solution. By using a standard curve prepared with various amounts of inorganic phosphate, enzyme velocity was converted to μmoles arginine phosphate synthesized per min.

For higher temperatures or lower substrate concentrations, the duration of the assay was reduced to ensure that only the linear portion of the reaction velocity was measured.

Protein concentrations were determined spectrophotometrically according to the method of Layne (1957).
RESULTS

Purification of arginine phosphokinase

Purification procedure was carried out at 0-4 C. The buffer used was 10 mM Tris, 5 mM EDTA, pH 7.0, unless stated otherwise.

Extraction. – Bee thoraces weighing 50 g were homogenized in 150 ml Tris buffer with an omni-mixer for 3 min and centrifuged at 10,000 g for 30 min. The supernatant was saved. The above procedure was repeated on the precipitate with 100 ml buffer. The supernatants were combined.

Ammonium sulfate fractionation. – Granular (NH₄)₂SO₄ was added to the combined supernatant until 60% saturated. The precipitate formed after centrifugation at 10,000 g for 30 min was discarded. More (NH₄)₂SO₄ was added to the supernatant until 80% saturated and the precipitate collected after centrifugation at 10,000 g for 30 min was saved. Precipitate from this (NH₄)₂SO₄ fraction gave the highest specific activity reading. The reading was much lower than expected, probably due to the high concentration of SO₄ = ion which was a potent inhibitor of creatine phosphokinase (Noda et al., 1960). Chloride, nitrate, and acetate as the sodium and potassium salts inhibited arginine phosphokinase from lobster (Virden et al., 1965).

Sephadex G-100 chromatography. – The precipitate from 80% (NH₄)₂SO₄ fraction was dissolved in Tris buffer and put through a Sephadex G-100 column (1.4 x 102 cm) equilibrated with 50 mM Tris, 5 mM EDTA, 100 mM KCl, pH 7.0 buffer. The column was eluted with the same buffer. Protein concentration of the eluent was estimated by measuring the absorbance at 280 nm and APK activity was assayed in the direction of AP synthesis as described under assay method.

DEAE-cellulose chromatography. – The solution from Sephadex chromatography was dialyzed against two changes of Tris buffer overnight. The dialyzed solution was pumped through a DEAE-cellulose column (2.5 x 24 cm) equilibrated with Tris buffer. The column was eluted by 0.1, 0.2, 0.4 M NaCl, and 30% (NH₄)₂SO₄ in Tris buffer. The enzyme appeared shortly after 0.1 M NaCl in Tris buffer was pumped into the column. The enzyme solution obtained was free of ATPase activity. A final concentration of 1 mM 2-mercaptoethanol was added to the enzyme solution. A summary of the data is listed in Table 1.

Table 1. Purification of arginine phosphokinase from honeybee thoraces. Weight of thoraces, 50 g.

<table>
<thead>
<tr>
<th>Step</th>
<th>Vol. (ml)</th>
<th>Protein (mg)</th>
<th>Sp. Act. (μmoles/min/mg protein)</th>
<th>Purification</th>
<th>Total Act. (μmoles/min)</th>
<th>Yield (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crude extract</td>
<td>222</td>
<td>910</td>
<td>0.29</td>
<td>1</td>
<td>264</td>
<td>100</td>
</tr>
<tr>
<td>(NH₄)₂SO₄ fractionation</td>
<td>11.4</td>
<td>340</td>
<td>0.08*</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Sephadex G-100</td>
<td>47.5</td>
<td>95</td>
<td>1.83</td>
<td>6.3</td>
<td>174</td>
<td>66</td>
</tr>
<tr>
<td>DEAE-cellulose</td>
<td>125</td>
<td>5</td>
<td>33.7</td>
<td>116</td>
<td>167</td>
<td>63</td>
</tr>
</tbody>
</table>

* See text for the explanation of the exceptionally low specific activity.
Estimation of molecular weight by Sephadex G-100 gel chromatography

A Sephadex G-100 column (1.4 x 102 cm) was calibrated according to the method of Andrews (1964). The proteins used were γ-globulin, bovine albumin, haemoglobin, myoglobin, and cytochrome c. The molecular weight of the enzyme estimated by this method is 36,000 ± 3,000 (Fig. 1).

Electrophoresis of APK

The APK solution was concentrated by Aquacide I to a concentration of 9.6 mg/ml. About 5 µl was applied to each Sepaphore III cellulose polyacrylate strip (1" x 6½") and electrophorezed at a constant current of 1 ma/strip for 65 min. The buffer used was 10 mM Tris, 1 mM EDTA, 1 mM 2-mercaptoethanol, at pH’s 9.0, 7.0, and 4.0. At these three pH’s the enzyme migrated as a single protein band, APK activity coincided with the band. Protein was stained with Ponceau S.

Effect of pH on APK activity

The assays were done in 50 mM Tris, 100 mM bicarbonate buffer. Maximum activity occurred around pH 8.3. At pH’s higher than 9.0, the enzyme activity declined rapidly (Fig. 2).

Effect of enzyme concentration on velocity

The reaction velocity was directly proportional to enzyme concentration over the concentration range studied (Fig. 3). The reaction time used was 5 min for APK concentrations up to 4 µg/ml; above this the reaction time was 2.5 min. This eliminated the chance of measuring the non-linear portion of the reaction velocity.

Temperature stability of the enzyme

Aliquots of the enzyme solution were incubated at various temperatures for 15 min and then assayed at 30 C for 15 min. There was no loss of activity up to 40 C, from 40-45 C activity declined slightly, and beyond 45 C a sharp decline in activity was observed (Fig. 4).

Effect of temperature on velocity

To ensure only the initial velocities were measured, the assays were shortened as the temperature was increased. The durations of the assays for 22, 29, 34, 39, 45, and 50 C were 5', 5', 3', 2', 1', and 1', respectively. Velocity increased from 22-45 C, beyond this temperature range velocity declined (Fig. 5). When the reciprocals of absolute temperatures for the range of 22-45 C were plotted against the logarithm of velocity, a linear Arrhenius plot was obtained (Fig. 6). The activation energy calculated from the slope of the graph was 7,000 cal/mole.

Effect of sulphydryl compounds

Addition of sulphydryl compounds to the assay solution increased the enzyme activity by as much as 33%. Cysteine, 2-mercaptoethanol, and reduced glutathion all had similar effects. The activation by 2-mercaptoethanol is shown in Fig. 7.

Activation by various bivalent cations

The metal salts used were either sulfates or chlorides. No activity was detected without adding bivalent cations. Addition of 10 mM of Mg++, Mn++, Cu++, Ca++, and Co++ activated the enzyme to various extents. The enzyme was more active with Mn++ than with Mg++; Cu++, Ca++, Co++ activated the enzyme to a much less extent. These results are listed in Table 2.
Fig. 1. Estimation of the molecular weight of honeybee APK by Sephadex G-100 gel chromatography. The proteins used and their molecular weights were: 1. γ-globulin, 160,000; 2. bovine albumin (dimer), 134,000; 3. bovine albumin (monomer), 67,000; 4. haemoglobin, 64,500; 5. myoglobin, 17,800; 6. cytochrome c, 12,400. The molecular weight of APK estimated by this method is 36,000 ± 3,000.

Fig. 2. Effect of pH on reaction velocity of honeybee APK. The buffer used was 50 mM Tris, 100 mM bicarbonate at various pH's. Optimum activity occurred around pH 8.3.

Fig. 3. Effect of enzyme concentration on the reaction velocity of honeybee APK. Reaction time was 5 min up to 4 μg APK added, above 4 μg, reaction time was 2.5 min.

Fig. 4. Temperature stability of honeybee APK. Aliquots of the enzyme were incubated at various temperatures for 15 min and then assayed at 30 C for 15 min.
Fig. 5. Effect of temperature on reaction velocity of honeybee APK. Duration of the assays were progressively decreased as temperature was increased so that only the linear portion of the reaction velocity was measured. APK: 1.3 μg/assay.

Fig. 6. The Arrhenius plot of the data from Fig. 5. $T = \text{absolute temperature; } v = \text{μmoles/min. }$ APK: 1.3 μg/assay.

Fig. 7. Effect of 2-mercaptoethanol on reaction velocity of honeybee APK. With sulfhydryl-free APK and reaction solution, addition of 2-mercaptoethanol to the reaction solution increased the enzyme activity up to 33% of its original activity. APK: 1.3 μg/assay.
Table 2. Activation of APK by metal ions. Conditions as described in assay procedure except that 10 mM of the following ions was used in place of Mg++. APK: 1.3 µg/assay.

<table>
<thead>
<tr>
<th>Metal ion</th>
<th>Enzyme activity (µmoles/min)</th>
<th>Percentage activity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mn++</td>
<td>0.082</td>
<td>111</td>
</tr>
<tr>
<td>Mg++</td>
<td>0.074</td>
<td>(100)</td>
</tr>
<tr>
<td>Ca++</td>
<td>0.017</td>
<td>23</td>
</tr>
<tr>
<td>Co++</td>
<td>0.010</td>
<td>13.5</td>
</tr>
<tr>
<td>Cu++</td>
<td>0.006</td>
<td>8.1</td>
</tr>
<tr>
<td>None</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

Effect of varying magnesium concentration on velocity

The effect of increasing magnesium concentration on velocity was studied with three levels of ATP concentration (Fig. 8). The maximum velocity was reached when the molar ratio of Mg++ : ATP was one. Increase in the ratio caused a slight decline in velocity. Similar results were obtained when Mg++ was replaced by Mn++. The Lineweaver-Burk plot of the reaction velocities against ATP concentrations at 5 mM and 10 mM Mg++ indicates that the inhibition by Mg++ was competitive.

Specificity of arginine phosphokinase

When ATP was replaced by the same concentration of UTP, CTP, GTP, or ADP, no activity was observed.

The ability of the enzyme to phosphorylate several guanidino compounds was determined. The final concentration of the guanidines in the reaction mixture was 10 mM. The results of the experiment are shown in Table 3. Both L-arginine methyl ester and D-arginine served as substrates to a limited extent.

![Graph showing the effect of magnesium concentration on reaction velocity of honeybee APK at three ATP concentrations. Reaction time, 5 min; APK: 1.3 µg/assay.](image-url)
Table 3. Specificity of APK: phosphorylation of guanidines. Conditions as described in assay procedure except that 10 mM of the following guanidines was used in place of L-arginine. APK: 2.6 μg/assay.

<table>
<thead>
<tr>
<th>Guanidines</th>
<th>Enzyme activity (μmoles/min)</th>
<th>Percentage activity</th>
</tr>
</thead>
<tbody>
<tr>
<td>L-arginine</td>
<td>0.13</td>
<td>(100)</td>
</tr>
<tr>
<td>L-arginine methyl ester</td>
<td>0.056</td>
<td>43</td>
</tr>
<tr>
<td>D-arginine</td>
<td>0.016</td>
<td>12.3</td>
</tr>
<tr>
<td>Guanidoacetic acid</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Hippuryl-L-arginine</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Creatine</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

DISCUSSION

Using sedimentation and diffusion experiments, Elodi and Szorényi (1956) estimated the molecular weight of APK from *Potamobius astacus* to be 43,000. Virden *et al.* (1966) concluded from estimates obtained with ultracentrifuge analysis, gel filtration, and density-gradient centrifugation, that the molecular weight of the enzyme from *Homarus vulgaris* was 37,000. Bletham and Kaplan (1968) estimated the molecular weights of APK from several arthropods by gel chromatography to range from 35,000 ± 2,000 to 38,000 ± 2,000. Moreland and Watts (1967) discovered the existence of two forms of APK in some molluscs; one with a molecular weight of 40,000 and the other 80,000. From the distribution of the isoenzymes in different muscle tissues, they suggested that the different forms of enzyme were associated with different muscle functions and structures. Regnouf *et al.* (1969) had shown that APK from *Homarus vulgaris* had a molecular weight of 43,000 and consisted of a single polypeptide chain, whereas APK from the annelid *Sipunculus nudus* with molecular weight of 86,000 was a dimer. Oriol *et al.* (1970) again showed that APK’s from lobster and crab with molecular weights of about 40,000 were monomers. Robin *et al.* (1969) identified an APK from the polychaetes *Sabella pavonina* and *Spirographis spallanzanii* with a molecular weight of 160,000. Thus, various workers have shown that there are at least three forms of APK in invertebrates, a monomer with a molecular weight of about 40,000, a dimer, and a tetramer, with corresponding molecular weights. In the present study, both gel chromatography and electrophoresis indicated that only one form of APK was present in honeybee thoraces, and from gel chromatography, the molecular weight of the enzyme was estimated to be 36,000 ± 3,000.

The honeybee enzyme has a pH optimum around 8.3. The activity declines sharply at pH’s higher than the optimum and becomes insignificant beyond pH 9.5. Virden *et al.* (1965) had similar results with APK from *Homarus vulgaris*. However, Morrison *et al.* (1957) reported a pH optimum of 8.4-8.5 with APK from *Jasus verreauxi* with a much broader pH tolerance. Whether this difference in pH tolerance is due to differences between the enzymes or to experimental conditions is still to be investigated.

As in *Homarus vulgaris* (Virden *et al.*, 1965), APK from honeybees is activated by Ca++ and Co++. The enzyme from sea crayfish was not activated by either Ca++ or Co++ (Morrison *et al.*, 1957).
The enzyme is quite specific with respect to the nucleotide substrate. ATP cannot be substituted by UTP, CTP, GTP, or ADP. It is less specific with the guanido substrate. The enzyme is able to phosphorylate L-arginine methyl ester and to a much less extent, D-arginine. APK from *Sabella pavonina* was reported to show significant activity with D-arginine (28% of the activity with L-arginine) and those from *Maia squinado, Eupagurus bernhardus, Pecten maximum, Polycelis cornuta, Myxicola infundibulum, and Holothuria forskali* were also reported to have some activity with D-arginine (1-7% of the activity with L-arginine) (Virden and Watts, 1964).

Without added metal ions, no activity was observed. A similar finding was reported by Virden et al. (1965) with lobster enzyme, and a trace of activity was reported by Morrison et al. (1957) with crayfish enzyme. Optimum molar ratio of Mg**: ATP appeared to be 1:1, similar to the findings of Griffiths et al. (1957b). An increase in the ratio led to a slight decline in activity.

Preliminary studies of initial velocity and product inhibition indicated that the reaction mechanism is random sequential.

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REFERENCES


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