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Sibling Species Delimitation in the Aedes communis (Degeer) aggregate
(Diptera, Culicidae)

by
Roy Arthur Ellis

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ABSTRACT

A. communis (Deg.) sens. str. from Canada and the United States, A. nevadensis Chapman and Barr n. status from the northwestern United States, and A. churchillensis sp. n. from western Canada are described. The distribution and keys to the larvae, female imagos and male genitalia of the 3 species are presented. The size and chorionic markings of the eggs of A. communis and A. churchillensis are described and illustrated. Variation in the anatomy and chaetotaxy of the fourth-instar larvae, the anatomy of the salivary glands and the chaetotaxy of the thorax of female imagos, and the ungues of the imagos is described and illustrated. An autogeny survey revealed that the female imagos of A. communis and A. nevadensis are normally obligatorily anautogenous or rarely facultatively autogenous whereas those of A. churchillensis are normally obligatorily autogenous. Differences in the size and general anatomy of the salivary glands of A. churchillensis and their possible association with autogeny are discussed. Mating success of caged imagos of A. communis and A. churchillensis, caged separately or together, was evaluated; imagos of the former species are eurygamous whereas those of the latter are stenogamous; some mating between caged imagos of the two species is possible. Observations of mating between imagos of A. communis in nature are discussed in relation to swarming. Hybridization in the laboratory revealed a low degree of genetic affinity between A. communis and A. churchillensis.

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INTRODUCTION

Revisional studies of the mosquitoes of Canada are needed. All available identification keys exhibit weaknesses for certain groups of species. Some excellent original descriptions and improved redescrptions have recently been published which were based on a thorough exercise of the traditional taxonomic approach and usually included observations on the anatomical variations, cytology, behavior, physiology, and ecology of the species. Less progress has been made in the recognition of anatomically very similar or sibling species of aedine mosquitoes. Only sibling species of medical, cytological or genetic importance have been critically examined by mosquito taxonomists (e.g., members of the Anopheles maculipennis aggregate). Several Aedes spp common to Canada are inadequately described and may include 2 or more sibling species. Contradictory statements regarding the ecology, behavior, and physiology of certain species suggest that sibling species may be more common than generally supposed.

The taxonomic status of Aedes (Ochlerotatus) communis (Degeer)¹ has long been questioned by researchers. Contradictory reports on the reproductive physiology (181, 184 cf. 14), habitat preferences (171 cf. 123), emergence patterns (82 cf. 8), swarming behavior (211 cf. 124), and dispersal patterns (209 cf. 59) of A. communis sens. auct. have caused some workers to suspect that it is composed of 2 or more sibling species.

Manitoba provides a convenient base for studies of mosquito

^{1/} Coe (72) shows that the correct rendering is 'Degeer', not 'de Geer', 'DeGeer' or 'De Geer' as it usually appears in mosquito literature: the only acceptable abbreviation is 'Deg.'.

variation. Centrally located in the geographical range of A. communis sens. lat., both sympatric and allopatric populations of the formerly recognized autogenous and anautogenous forms are available for study. After both live and preserved material from Alaska, California, Utah, Wyoming, Alberta, Manitoba, Ontario, Wisconsin and Michigan were compared, it became apparent that A. communis sens. lat. was characterized by 3 sibling species in North America.

This study deals with the geographic variation and separation of species of the A. communis aggregate.² Three species, Aedes communis (Deg.) sens. str., Aedes churchillensis sp. n. and Aedes nevadensis Chapman and Barr n. status are recognized on the basis of differences in their internal and external anatomy, reproductive physiology, behavior, and general ecology.

^{2/} 'Aggregate' refers to an assemblage of species. Cain (43) suggested the use of the term 'aggregate' in museum work when labelling specimens of inseparable species until diagnostic characters are discovered. The expression 'aggregate' has been used in the zoological literature (e.g., 238).

GENERAL METHODS

A brief outline of the collection and handling procedures for live material used in this study follows. Special materials, methods and terminology are described in their appropriate sections.

Collection.

Most of the taxonomic material was personally collected by the author between April 1970 and June 1972 from northeastern U.S.A. and north, central and western Canada. In addition, live material was generously collected and shipped to this laboratory by L.T. Nielsen (LTN, Wyoming and Utah), R.K. Washino (RKW, California) and J.R. Gorham (JRG, Alaska). Museum specimens were kindly loaned by the persons and institutions mentioned in the acknowledgments.

To minimize handling and rearing and to facilitate identification, 4th instars were usually collected. However, when this was not possible or when other life stages were required, eggs, earlier larval instars, pupae and female imagos were also collected from the field. The procedures followed were: Female imagos — These were collected only from the immediate area of known larval developmental sites. Mosquitoes attempting to blood-feed were captured with an aspirator and transferred to small acrylic holding cages (25x25x150 mm) which had fine mesh nylon screen on 2 sides. Caged female imagos were transported to the laboratory in insulated chests maintained at 10-15°C and 70-85% R.H. by ice and moist towelling, respectively. Larvae — These were collected from their developmental sites by dipping and then transferred to styrofoam food containers (300 ml) for transport to the laboratory in insulated chests maintained at 10-15°C. Pupae — These were also collected by dipping.

To minimize possible injury and mortality of pupae, a special container was used. Up to 50 pupae were placed in a styrofoam food container (300 ml) half-filled with pool water. A similar, but empty, container was inverted over and sealed to the pupal container with masking tape. This container also provided a convenient resting place for adults which emerged in transit. Pupal containers were transported to the laboratory in insulated chests maintained at 10-15°C. Eggs — Field-collected eggs were obtained from sod samples removed from the margins of known oviposition sites. The samples (ca. 1x15x15 cm) were sealed in clear plastic bags for transport to the laboratory in insulated chests maintained at ca. 15°C.

Egg Conditioning and Hatching.

Embryonated eggs of A. communis sens. auct. enter an obligate diapause of 7-9 mth duration under natural conditions (40). However, most eggs, properly conditioned in the laboratory, will hatch in 5 months. Following the recommendations of Horsfall and Fowler (193) and Brust and Horsfall (40), eggs were conditioned by storing them at 20±1°C and 16L:8D for 2 months and then at 5±1°C, without light, for 3 months. Field-collected eggs were stored, in situ, on sod samples sealed in plastic bags. Eggs from female imagos which had oviposited in the laboratory were stored on moist nylon pads in sealed petri dishes. The above procedure proved quite satisfactory for eggs of A. communis from southern Manitoba but gave relatively poor results for eggs of A. churchillensis from Churchill, Man. Eggs of A. nevadensis were unavailable for study.

Eggs on pads were hatched in a nutrient broth solution (1:1000 w/w, powder in tap water) which was maintained at 10±1°C and 16L:8D. Eggs in soil samples were hatched simply by immersing the samples in dechlorinated

tap water maintained at the above temperature and photoperiod.

Mass Rearings.

Mass rearings, i.e., large groups of identified larvae, pupae and imagos from individual sites, were conducted in a humidity-, temperature- and photoperiod-regulated room maintained at 70-85% R.H., $20 \pm 1^\circ\text{C}$ and 16L:8D, respectively. Larvae — Covered plastic pans (6x22x30 cm) containing ca. 1000 ml of distilled water were used to hold larvae. Larval density was kept low (75-100 larvae per pan) to minimize crowding and its inherent detrimental effects. Larvae were initially fed a suspension of powdered TetraMin Staple[®] fish food but this was discontinued when TetraMin Tube Food 60[®] became commercially available. The latter diet, when present in excess of larval requirements, did not tend to foul the pan water as much as the former. Pupae — These were removed from the larval pans daily and transferred to styrofoam food containers (50 pupae per 300 ml container) half-filled with distilled water. The pupal containers were then placed in acrylic cube cages. Cage size (4.9, 15.6 or 216 dm³) and number of pupae per cage was dependent on experimental design and will be noted, where pertinent, below. Adults — Emerging adults were provided with a carbohydrate-water source, rehydrated apples or raisins, on which they were able to feed ad lib. Moist paper-wicks, placed inside the cages, helped to maintain the relative humidity at 75-85%.

Individual Rearings.

Much of the material used for taxonomic study was obtained from individual rearings. Each imago would have associated with it a coded larval and pupal exuvia. The main purposes of this method were to have a means of verifying the identification of a dissected or otherwise damaged imago and of relating larval and imaginal anatomical features.

Individual 4th instars were isolated in coded vials (23x85 mm) half-filled with distilled water. A small amount of larval food was placed in each vial. However, if late 4th instars are used, food is not necessary. After pupation, the larval exuvia was removed and preserved in 80% ethanol in a small, coded vial. The pupa was then transferred to a clean vial, three-quarters-filled with distilled water. A small screen cup was placed over the vial to contain the imago. The screen cup was a 15 mm length of acrylic tubing (25 mm I.D.) to one end of which was glued a circle of fine mesh nylon screen (100 squares per cm²). On top of the screen cup, a moistened raisin was placed to serve as food for the imago. The pupal exuvia was removed after the emergence of the imago and was stored with the larval exuvia. Imagos to be used for pinning were freeze-killed within 24-48 hr after emergence.

SPECIES DESCRIPTIONS

The genus Aedes Meigen of the family Culicidae is the largest and one of the most important mosquito genera. The genus is divided into 24 subgenera, including Ochlerotatus Lynch Arribalzaga with about 150 species. Members of the A. O. communis aggregate belong to group G, the communis group of Edwards (112), which probably originated from the Palaearctic region (298). In North America, group G consists of 28 species, including the present additions.

Aedes (Ochlerotatus) communis (Degeer) sens. str.

Culex communis Degeer, 1776, Mem. des Ins. 6, pl. 17, figs. 2,5.

Culex nemorosus Meigen, 1818, Syst. Besch. Zweifl. Ins. 1:4.

Culex obscurus Meigen, 1830, Abb. Zweifl. Ins. pl. 2, fig. 2.

Culex lazarensis Felt and Young, 1904, Science, n.s., 20:312.

Culex borealis Ludlow, 1911, Can. Ent. 43:178.

Culicada nemorosa diplolineata Schneider, 1913, Verh. Nat. Ver. Bonn. 70:37.

Aedes tahoensis Dyar, 1916, Insecutor Inscit. menstr. 4:82.

Aedes altiusculus Dyar, 1917, Insecutor Inscit. menstr. 5:100.

Aedes masamae Dyar, 1920, Insecutor Inscit. menstr. 8:166.

Ochlerotatus palmeni Edwards, 1921, Ent. Tidskr. 42:52.

Aedes prolixus Dyar, 1922, Insecutor Inscit. menstr. 10:2.

Most of the taxonomic material used in the study of this species will be divided between the Canadian National (CNC) and University of Manitoba (UMC) Collections of Insects.

FEMALE IMAGO. Medium-sized mosquito (length, 5-6 mm). Head: Clypeus dark-brown. Proboscis dark-brown-scaled, occasionally with a few pale scales on basal ventral surface. Palpi short (ca. 0.2 times as

long as proboscis), dark-brown-scaled, occasionally sprinkled with pale scales. Vertex with narrow, curved, decumbent, yellow scales. Occiput with narrow, curved or straight, erect, forked, yellow scales in a broad median patch; similar dark-brown or yellow-brown scales intermixed. Postgena with decumbent, broad, pale-yellow scales. Pedicel usually brown, occasionally yellow or black; usually bearing short, broad, white scales and small setae, especially on mesal surfaces. Thorax: Scutum with dark integument and a variable pattern of pale-yellow to golden-yellow and coppery-brown to dark-brown scales; the latter usually confined to a pair of narrow, longitudinal, submedian stripes and a pair of posterior, supra-alar half-stripes; rarely, the former stripes merge together to form one broad median stripe or are subdivided in the anterior half to form 2 pairs of stripes; also rarely, the latter stripes are absent or have a small dark patch of scales anterior of them. Posterior median bare space surrounded by narrow, pale-yellow scales. Postpronotum with narrow, brown and yellow scales dorsally, scales becoming broader and paler ventrally. Scutellar lobes each with a small patch of narrow, pale-yellow scales. Pleuron with extensive poorly-defined patches of decumbent, broad, white scales. Mesepisternal scale patch extending to anterior angle, narrowly separate from prealar scale patch. Mesepimeral scale patch extending to lower margin. Mesomeron, hypostigma, and postprocoxal membrane bare. Scutal setae: SaS, 73-106 (62-139); SFS, 21-34 (14-40); AcS, 16-26 (10-36); PMSS, 4-6 (4-6); DS, 45-62 (35-70); and SS, 26-38 (21-45). Pleural setae: PpS, 7-10 (6-11); PS, 5-9 (5-10); PaS, 17-22 (14-24); MeSU, 14-24 (12-29); MeSL, 1-3 (0-4); MStU, 4-6 (4-7); and MStL, 5-8 (4-10). Abdomen: Tergite 1 with median patch of white scales, remaining tergites dark-brown-scaled with a moderately-broad basal band of white scales; basal bands widened

laterally, especially on posterior tergites. Sternites mostly white-scaled with indistinct apical bands of dark-brown scales. Legs: Femur: anterior surface dark-brown-scaled, with sprinkling of pale-brown and white scales; posterior surface yellow- and white-scaled with sprinkling of dark-brown scales. Tibia dark-brown-scaled with sprinkling of white scales. Tarsi dark-brown-scaled; first tarsal segment with a few pale-brown scales. Uniserrate ungues as drawn (Fig. 7b,c). Wing: Veins with coppery-brown scales; a few pale-yellow scales usually present dorsally at bases of costa, subcosta, and radius. Length variable, ca. 5.0 mm.

MALE IMAGO. Coloration very similar to that of female imago. Palpi as long as or slightly longer than proboscis; apical segment slightly enlarged. Ninth tergal lobe flattened, tapered, sclerous and as long as or slightly longer than wide (Fig. 4b). Each lobe bears 4-7 (3-8) stout setae which are 0.8-2.5 times as long as the lobe. Gonocoxite clothed with scales and numerous short and long setae; length, ca. 4.5 times width at middle (Fig. 4a). Apical lobe of gonocoxite broadly rounded or bluntly pointed and bears 9-14 setae, each ca. 0.1 times as long as the gonocoxite. Basal lobe of gonocoxite somewhat triangular and conical and bears, dorsally, a stout, recurved parabasal seta which is ca. 0.2 times as long as the gonocoxite and, mesally, a circular row of 12-22 slender, curved setae. Gonostylus slender, arciform and sparsely pilose; length, ca. 0.3 times as long as the gonocoxite; laterally and distally, bears 3 short spine-like setae. Gonostylar claw slightly recurved near apex; length, ca. 0.2 times as long as the gonostylus. Claspette stem is long, slender and strongly arched beyond basal extensions (Fig. 4c); proximal one-third pilose and bears 3-5 short spine-like setae. Claspette filament is 0.5-0.9 times as long as claspette stem; proximal portion narrowly-expanded;

distal portion gradually tapered to a blunt, recurved point; bears 2-5 small longitudinal ridges. Uniserrate ungues as drawn (Fig. 7b,c).

FOURTH INSTAR LARVA. Head: Rounded, broader than long (Fig. 3a) head capsule width, 1.1-1.4 mm. Antenna slender, slightly curved, sparsely spiculate, and shorter than head. Antennal seta 1-A, usually 6-7 (3-10) branched; inserted proximal to middle of antenna; not reaching to apex (Fig. 3c). Head Setae: 7-C, 5-7 (3-11) branched; 5-C and 6-C, usually single, occasionally 1 is 2 branched; 10-C usually 2 (1-3) branched. Submentum with 27-31 (26-31) teeth (Fig. 3d). Prothoracic Setae: 1-P, long, 2 (1-2) branched; 2-P, short, usually single (1-2); 3-P, short, usually single (1-2); 4-P, short, usually single (1-2); 5-P, long 3 (2-4) branched; 6-P, long, single; and 7-P, long, 3 (2-5) branched. Abdomen: Setae 6-I to 6-V, usually 2 (1-3) branched; seta 6-VI, usually single (1-2). Comb segment VIII with 46-70 (38-73) scales arranged in an irregular triangular patch (Fig. 3b); individual scales broad with rounded apex and many moderately-stout, subequal spinules (Fig. 3f). Pentad seta 3-VIII, 7-12 (5-15) branched. Siphonal index, 2.7-2.8 (2.3-3.5). Attached acus present. Pecten with 18-24 (16-26) evenly-spaced, acutely-tapered teeth, confined to proximal half of siphon; first 3-4 teeth basally rudimentary, remainder with 1-5 denticles at base. Siphonal seta 1-S, 5-9 (4-10) branched, barbed, and inserted beyond pecten near middle of siphon. Siphonal seta 2-S single, stout, shorter than apical pecten tooth, and inserted at least its length before apex of siphon. Anal segment longer than broad. Saddle extends 0.5-0.7 down sides of segment X. Seta 1-X, single, rarely 2 branched, and shorter than saddle. Seta 2-X, 5-8 branched. Seta 3-X, single, stout and long. Seta 4-X consists of 16-21 cratal and 1-4 precratal tufts; each tuft 2-8 branched.

Anal papillae elongate and gradually tapered; length, ca. 1.5-3.0 times as long as saddle.

DIAGNOSIS. Fourth instar larvae of A. communis are separated readily from those of A. nevadensis by the shape of the comb scale (Fig. 3e,f) but with difficulty from those of A. churchillensis. Width of head capsule and length and width of siphon are greater in A. communis (Table 2). Male and female imagos of this species can usually be separated from those of A. nevadensis and A. churchillensis by the shapes of the ungues, particularly those of the hindlegs (Tables 5-12; Fig. 7). Male imagos of the 3 species are also separable by differences in the size of certain genitalic structures (Table 3); female imagos are also separable by the chaetotaxy of the thorax (Table 4).

BIONOMICS. One of the commonest forest mosquitoes in North America. A univoltine species most abundant in the spring and early summer. Eggs: Shape, size, color and chorion described (79, 80, 216, 262). Found at air-soil interface, in vegetation or detritus, at margins of temporary and semi-permanent forest, alpine and tundra pools (18, 199, 359). Enter embryonic diapause soon after oviposited and usually hatch the following spring in near-freezing snow-melt water as the oxygen concentration decreases (8, 58, 359). Larvae: External anatomy of 1st and 4th instars described (8, 25, 58, 89, 116, 126, 149, 150, 197, 222, 267, 277, 290, 291, 294, 315, 317, 327, 329, 366). Duration of the 4 larval instars variable (8, 35, 129, 172, 175, 200, 201, 215, 359); but, in southern Manitoba, ca. 10, 7, 7, and 10 d, respectively. First instars may be present even if pool surface or bottom frozen (200). Associated mosquitoes frequently include Aedes canadensis (Theobald), Aedes cinereus Meigen, Aedes diantaeus Howard, Dyar and Knab, Aedes excrucians (Walker),

Aedes fitchii (Felt and Young), Aedes implicatus Vockeroth, Aedes pionips Dyar, and Aedes punctor (Kirby) and infrequently include Aedes barri Rueger, Aedes cataphylla Dyar, A. churchillensis, Aedes dorsalis (Meigen), Aedes impiger (Walker), Aedes intrudens Dyar, Aedes pullatus (Coquillett), Aedes rempeli Vockeroth, Aedes trichurus (Dyar), Aedes vexans (Meigen), Culex restuans Theobald, Culiseta morsitans (Theobald) and Mansonia perturbans (Walker) (41, 164, 192, 215, 267, 292, 318, 331). Have been found in brackish water (123, 267) but usually occur in acidic water having a brown color (171, 200, 210, 250, 267). Aggregations, probably in response to temperature and light, frequently observed (173, 182, 200). Food and functional anatomy of larval mouthparts have been studied (135, 290, 291). Predators include dipteran, coleopteran and trichopteran larvae (68, 69, 164, 202, 203, 204, 210, 305). Parasites include protozoans, microsporidians, fungi, and nematodes (171, 192, 211, 212, 342, 357, 358).

Pupae: External anatomy described (86). Duration of pupal stage variable, about 10 d in southern Manitoba. Imagos: External anatomy well-described (8, 40, 58, 89, 116, 146, 150, 197, 222, 245, 246, 247, 267, 295, 313, 321, 327, 329, 366). Internal anatomy poorly known (40). Intersexes not uncommon (4, 36, 37, 38, 40, 109). Male imagos emerge before female imagos (188, 201, 359). Although both sexes usually found in immediate area of larval development sites (84, 85, 158, 165, 171, 174, 207, 208), they may disperse up to 23 km (59, 183, 185, 272, 283). Both sexes nectar-feeders and may aid in pollination of some flowering plants (94, 128, 210, 334, 335, 336, 360). Female imagos usually obligatorily anautogenous or, rarely, facultatively autogenous (see below); obtain blood from birds and mammals (91, 92, 94, 191, 267) whenever available, but most active in morning and evening (153, 156, 165); attraction to host studied (30,

31, 148). Complete up to 6 ovarian cycles (44, 297, 311). Oviposit eggs singly at bases of plants and in moist detritus at pool margins (359). Fecundity discussed below. Disease vector potential uncertain but may aid in transmission of California encephalitis in North America (88, 189, 339) and tularemia in Russia (162). Predators include dipterans and hemipterans (131, 200). Parasitized by immature hydrachnid mites (156).

DISTRIBUTION (Fig. 1). A. communis is widely distributed in the Holarctic Region. It occurs in Canada and the United States in North America and in Austria (4, 110); Belgium (152); Bulgaria (29); Denmark (266, 267, 359); England (110, 113, 251); Finland (267); France (179, 284, 308); Germany (137, 252, 284, 307, 352, 356); Hungary (259); Italy (117); Yugoslavia (253); Lithuania (304); Norway (265, 267); Poland (68, 69, 84, 85, 308, 332, 333, 363); Rumania (251); Sweden (244, 267, 337, 338, 355); Switzerland (5, 134); Syria (308); Turkey (282); U.S.S.R. (111, 155, 217, 218, 219, 244, 266, 267, 307, 310, 311, 320, 324, 353, 361) in Eurasia. In North America, A. communis occurs throughout much of the northern, western and eastern regions. It is most common in the Boreal, Great Lakes-St. Lawrence, and Subalpine Forest Regions but also occurs, to a limited extent, in the Arctic and Alpine Tundra Regions.³

CANADA. Alberta (289) — Banff (100, 101, RAE), Beaverlodge (RAE), Demmitt (RAE), Edmonton (221, 354), Flatbush (164, 165), George Lake (156, 157, 158), Jasper (139, RAE), Laggan (100, 101), Lake Louise (CNC), Lamoral (100, 101), Lochearn (100, 101), McMurray (CNC), Red Deer (100, 101), Rochester (189), Whitecourt (RAE). British Columbia (83, 176) —

^{3/} Vegetation formation given according to Munroe (260).

Atlin (101, 103), Chezacut (CNC), Cold Creek (CNC), Coquitlam (CNC), Davis Lake (176, 177), Eagle Valley (between Malaka and Craigellachie) (138), Fort Nelson (82, 120), Fort St. John (RAE), Glacier (101, 103), Hatzic (176, 177), Kamloops (CNC), Kaslo (100, 103), Kwinitza (100, 103), Lac le Jeune (CNC), Lower Post (CNC), Muncho Lake (120), Nicomen Island (176), Pass Lake (CNC), Prince George (101, 103), Salvus (101), Skeena Valley (176, 177), Terrace (101, 103), Vancouver (CNC), Vavenby (CNC), Vernon (CNC). Manitoba — Aweme (CNC), Baker's Narrows (RAE), Bird's Hill Park (RAB), Churchill (11, 12, 13, 14, 15, 16, 18, 19, 20, 21, 93, 94, 120, 172, 173, 174, 175, 181, 182, 183, 184, 186, 188, 202, 204, 209, 212, 214, 215, 216, 347, 357, 358, 360, RAE), Dorothy Lake (RAE), E. Braintree (RAE), Falcon Lake (RAE), Flin Flon (36, 37, 39, 40, 214, 216), Gillam (120, 350), Glenlea (RAE), Le Pas (120), McMunn (RAE), Oak Bluff (41), Onanole (RAE), Pinawa (341), Red Rock Lake (RAE), Sandilands Prov. For. (39, 41, 214, 216, RAE), Spruce Siding (RAE), Spruce Woods Prov. For. (RAE), St. Anne (RAE), Telford (RAE), Thompson (RAB), Westhawk Lake (RAE). Newfoundland — Cartwright (CNC), Goose Bay (30, 31, 34, 120, 350), Harmon Field (350). New Brunswick (345). Northwest Territory — Baker Lake (318, RAB), Fort McPherson (CNC), Fort Smith (120, 350), Hay River (288), Norman Wells (120, 350), Padlei (120, 350, 351), Reindeer Depot (120, 350), Sawmill Bay (120), Yellowknife (120, 350). Nova Scotia — Pictou (142), Weymouth (CNC). Ontario — Aberfoyle (329), Arnprior (CNC), Algonquin Park (139, 329), Almonte (91), Ashton (91), Camp Borden (138, 329), Cannifton (205), Carleton Place (91), Chatterton (203, 205), Coral Rapids (211), Cordova Mines (203, 205), Dryden (100, 103, 329), Eramosa (329), Fitzroy Harbour (141), Ghost River (100), Height of Land (100, 103, 329), Kenora (100, 103, 329), Minaki (142, 143, 144), Moose Factory (120, 210, 329, 350),

Nipigon (100, 103, 329), Osnaburg (100, 103), Ottawa (100, 103, 140, 329, 344, 362), Pearl (RAE), Petawawa (33), Port Hope (100, 103, 329), Prospect (91), Roebuck (142), Rossmore (205), Toronto (329), South March (CNC), Vermilion Bay (RAE), White River (100, 103, 329, RAE). Prince Edward Island (346) — Brackley Beach, Rustico Bay (142). Quebec (94) — Eardley (CNC), Fort Chimo (120, 350), Gaspé Peninsula (140), Gaspé County (138), Great Whale River (210, 350, 351), Knob Lake (120, 350), Laurentian Hills (N. of Ottawa) (362), Montebello (138), Old Chelsea (CNC), Rupert House (120). Saskatchewan (294, 295) — Amish (295), Cypress Hills (RAE), Lac La Ronge (295), Waskesiu (143, 295). Yukon — Big Salmon (101), Byer's Camp (101), Carcross (101, 103, 106), Carmacks (101), Dawson (101, 103, 106, 120, 350), 'Halfway to Big Salmon' (101), Hootalinqua (101), Horse Falls (101), Kluané Lake (120), Marsh Lake (120), Selkirk (101), Tahkenna R. (101), Tantalus Mine (101), Whitehorse (101, 120, 178, 350).

UNITED STATES. Alaska (129, 191, 243, 340) — Adak (207), Anaktuvuk Pass (191), Anchorage (124, 150, 151, 207), Auke Bay (131), Big Delta (2), Carlo (Camp 334 A.E.C.) (104), Chitina (131, 132, 150), Circle (207), Copper Center (150), Eagle (101, 105, 150), Eklutna (151), Fairbanks (150, 207, 305, 322, 325, JRG), Fort Wainwright (191), Fort Yukon (150), Galena (180), Golovnin (150), Gulkana (150, 151), Healy (104, 150), Juneau (124, 133, 150), Ketchikan (150), King Salmon (CNC), Kotzebue (150), McKinley Nat. Park. (125, 130, 131, 150, 207), Naknek (126, 150), Nenana (150), Nome (150, 207), Paxton (150), Pitchfork Falls (101, 104), Popof Island (150), Sitka (150), Skagway (101, 103, 104, 150), Slana (150), Summit Lake (322), Tanana (150), Teller (150), Tok (150, 207), Umiat (150, 180, 201, 222), Upper Cook Inlet (122, 123), Valdez (207), Windy (Camp 327 A.E.C.) (104), Wiseman (150), Yakutat (150). California (118,

119) — Alpine Co. (48, 49): Caples Lake (56, RKW), Carson Pass (24, 56), Blue Lakes (24), Woods Lake (56); Amador Co. (48, 49): Carson Spur (56), Oakland Municipal Camp (56), near Silver Lake (56); Calaveras Co. (48, 49, 119); El Dorado Co. (48): Camp Sacramento (24), Echo Summit (65), Fallen Leaf Lake (22, 97); Fresno Co. (51, 240): Kaiser Park (237), Shorthair (237); Inyo Co. (49, 51); Lassen Co. (48, 49); Madera Co. (48, 49); Mariposa Co. (48, 49): Pothole Meadow (54); Mono Co. (48, 49): near Blue Lake (54), Leavitt Meadows Campground (55), Mammoth Lakes (66), Silver Lake (66), Tioga Pass (54); Placer Co. (48, 49): Baxter (24), Cisco Grove (24); Plumas Co. (48, 49): Camp Elwell (102), Mt. Elwell (102) Summit (96, 97, 102, 104), Gold L. Camp (97), Canyon Dam (24); Shasta Co. (119); Sierra Co. (48, 49): Calpine (24), Gold L. (97, 102); Tuolumne Co. (48, 49): near Eagle Meadow (55), Kennedy Meadows (55), Sonora Pass (24), near Tioga Pass (54), Tuolumne Meadows (54), White Wolf Lodge (54); Tulare Co. (51, 240); Tehama Co. (48, 49); County Unknown: Lake Tahoe (97), Sierra Nevada Mtns. (47, 49), Yosemite Nat. Park (66), Yosemite Valley (97), Little Yosemite Valley (97). Colorado (272) — Boulder Co. (167); Chaffee Co. (167); Conejos Co. (167); Clear Creek Co. (167); Custer Co. (167); Grand Co. (167); Gunnison Co. (167); Gothic (316), L. Irwin (316), Floresta (316), Crested Butte (315, 316), Pitkin Campground (316); Jackson Co. (167); Larimer Co. (167); Mesa Co. (167); Park Co. (167); Pitkin Co. (167): Elko Park (274, 316), Galena Mtn. (316); San Miguel Co. (167); Summit Co. (167). Idaho (168) Benewah Co. (327); Bonner Co. (327); Boundary Co. (327); Fremont Co. (327); Kooteni Co. (327); Shoshone Co. (327); Valley Co. (327); County Unknown: Kendrick (149). Maine (115, 213) — Androscoggin Co. (10); Cumberland Co. (10); Franklin Co. (10); Hancock Co. (10); Kennebec Co. (10); Oxford Co. (10); Penobscot Co. (10); Piscataquis Co. (10); Waldo

Co. (10); Washington Co. (10); York Co. (10); County Unknown: Seawall, Mt. Desert Island (309). Massachusetts (115, 213, 343). Michigan (198) — Cheboygan Co.: Mud Lake (199), Bryant's Bog (199); Montmorency Co. (36, 40): Lewiston (RAE), Vienna (RAE); County Unknown: Iron River (CNC). Minnesota (8, 279) — Clearwater Co., Itasca State Park (65, 286, 287), St. Louis, Virginia (8, 65); County Unknown: Tower (8). Montana — County Unknown: Belton (104); Bozeman (250); Glacier Nat. Park (107); Sula (250). Nevada (63, 64, 262) — Douglas Co.: Glenbrook (61, 62, 64, 65), Spooner Summit (61, 62, 64, 65); Ormsby Co.: Lake Tahoe (62, 64), Marlette L. (62, 64); Washoe Co.: Mt. Rose (64), Sundown (61, 62, 64); County Unknown: Sierra Nevada Mtns. (63, 64), Ruby Mtns. (63). New Hampshire (115, 213, 242) — Mt. Washington (104); White Mtns. (100, 104). New Jersey (42, 81) — Passaic Co.: Hanks Pond (46); Sussex Co.: Culvers Lake (46). New York (116, 206, 255) — Albany Co.: Delmar (7); Karner (7); Clifton Co.: Plattsburg (7, 104); Essex Co.: Elizabethtown (7, 22, 104), L. Placid (7); Franklin Co.: Saranac Inn (7); Herkimer Co.: Big Moose (7), Old Forge (7); Rensselaer Co.: Nassau (7); Schuyler Co.: Cayuta L. (7); Tompkins Co.: McLean (7), Ringwood (7); County Unknown: Oneidae (1). Oregon (190, 327, 367) — Clackama Co. (327); Deschutes Co. (327); Douglas Co. (327); Grant Co. (327); Jackson Co. (327); Jefferson Co. (327); Lane Co. (327); Klamath Co.: Crater L. (22, 102, 104, 106, 327); Linn Co. (327); Marion Co. (327); Umatilla Co. (327); Wallowa Co. (327); County Unknown: Chemult (149), Clackamas R. (23), Diamond L. (23, 145), Lost Lake (149), Ollalie L. (23), Prospect (102, 104), Whiskey Creek (104), Windigo Pass (145). Pennsylvania — Luzerne Co.: Bear Cr. Township (45). Utah (179, 272, 275, 276, 292) — Daggett Co. (277); Duchesne Co. (277): Mirror L. (297); Grand Co. (277); Salt Lake Co. (277): Brighton (293,

297); Sandpete Co. (277); Summitt Co. (277, 342); Uintah Co. (277); Utah Co. (277); Wasatch Co. (277); County Unknown: Park City (293). Washington — Chelan Co. (263, 327); Ferry Co. (263, 327); Grant Co. (263, 327); Jefferson Co. (263); Kittitas Co. (263, 327); Lewis Co. (263, 327); Lincoln Co. (263, 327); Okanogan Co. (263, 327); Skamania Co. (263, 327); Whatcom Co. (263, 327); Yakima Co. (263, 327); County Unknown: Cliffdel (149, 327), Columbia Nat. For. (23), Glacier (Mt. Baker region) (98), L. Cushman (Olympics) (98), Mt. Adams (148), Park Rapids (149), Snoqualmie (23). Wisconsin (90, 241) — Crawford Co.: Lynxville (87), Prairie du Chien (87); Dane Co.: Madison (88, 261), Mazomanie (88); Forest Co.: Wabeno (334, 335); Grant Co.: Wyalusing State Park (87, 153); Jackson Co.: Black R. State For. (87); Manitowoc Co.: Two Rivers (153); Vernon Co.: Genoa (87); County Unknown: Land O' Lakes (Palmer L.) (RAE); Meadow Valley, in Sand Hill country (87, 339); Saxeville (100). Wyoming (280) — Albany Co.: Brooklyn Lodge (281), Centennial (281), Keystone (281), Laramie Peak (281), U. of Wyo. Science Camp (281), Towner L. (281); Big Horn Co.: Granite Pass (281), Bear L. Lodge (281), Burgess Jct. (281); Sublette Co.: Bridger Nat. For. (281), S. Fork Fish Cr. (281); Teton Co.: Moran (281), Togwotee Pass (281); Uinta Co.: Mountainview (281), Lone Tree (342, LTN); County Unknown: Yellowstone Nat. Park: Yellowstone L. (108), Mammoth Hot Springs (108), Old Faithful (108), Canyon Stn. (108), Camp Roosevelt (108).

Aedes (Ochlerotatus) nevadensis Chapman and Barr n. status

Aedes communis nevadensis Chapman and Barr, 1964, Mosquito News 24:439.

The holotype and paratype series of Chapman and Barr (65) which were collected 12 June 1962 in Lamoille Canyon, Elko Co., Nevada (U.S. National Museum No. 65968) have been chosen as the type material. In addition, most of the taxonomic material examined in this study will be divided among the Canadian National (CNC) and University of Manitoba Collections (UMC) of Insects.

FEMALE IMAGO. Medium-sized mosquito (length, 5-6 mm). Head: Clypeus dark-brown. Proboscis brown-scaled. Palpi short (ca. 0.2 times as long as proboscis) and dark-brown-scaled; rarely, a few pale scales present. Vertex with narrow, slightly curved, decumbent yellow scales. Occiput with narrow, slightly curved, erect, forked yellow scales in a broad median patch; a few similar brown scales intermixed. Postgena with broad, decumbent, pale-yellow scales. Pedicel usually light-brown or golden-brown, occasionally dark-brown; often bearing short, broad, white scales and small setae, especially on mesal surfaces. Thorax: Scutum with dark-brown integument and a variable pattern of pale-yellow to golden-yellow and coppery-brown to grey-brown scales; the latter usually confined to a pair of narrow, longitudinal submedian stripes and a pair of posterior, supra-alar half-stripes; stripes either diffuse or distinct. Posterior median bare space surrounded by narrow, brown and yellow scales. Postpronotum with narrow, brown and yellow scales dorsally, scales becoming broader and paler ventrally. Scutellar lobes each with a small patch of pale-yellow scales. Pleuron with extensive poorly-defined patches of decumbent, broad, white scales.

Mesepisternal scale patch extending to anterior angle, narrowly separate from prealar scale patch. Mesepimeral scale patch extending to lower margin. Mesomeron, hypostigma, and postprocoxal membrane bare. Tergal setae: SaS, 73-93 (65-106); SFS, 25-33 (21-38); AcS, 19-23 (16-25); PMSS, 5-10 (4-12); DS, 53-69 (48-78); and SS, 30-37 (27-42). Pleural setae: PpS, 8-12 (6-15); PS, 3-6 (3-8); PaS, 14-20 (12-23); MeSU, 17-26 (14-33); MeSL, 3-5 (1-6); MStU, 5-8 (5-8); and MStL, 7-10 (6-13). Abdomen: Tergite 1 with median patch of white scales; remaining tergites dark-brown-scaled with a narrow- to moderately-broad basal band of white scales; basal bands slightly widened laterally, especially on posterior tergites. Sternites mostly white-scaled with indistinct apical bands of dark-brown scales. Legs: Femur: anterior surface dark-brown-scaled, with sprinkling of pale-brown and white scales; posterior surface yellow- and white-scaled, with sprinkling of dark-brown scales. Tibia dark-brown-scaled, with sprinkling of pale-brown and white scales. Tarsi dark-brown-scaled; first tarsal segment with a few pale-brown scales. Uniserrate ungues as drawn (Fig. 7a). Wing: Veins coppery-brown-scaled; a few pale-yellow scales present dorsally at bases of costa, subcosta and radius. Length variable, ca. 5 mm.

MALE IMAGO. Coloration very similar to that of female imago. Palpi as long as or slightly longer than proboscis; apical segment slightly enlarged. Ninth tergal lobe flattened, tapered, sclerous, and as long as or slightly longer than wide (Fig. 4b); each lobe bears 4-5 (3-7) stout setae which are 1.0-2.5 times as long as the lobe. Gonocoxite clothed with scales and numerous short and long setae; length, ca. 3.5 times width at middle (Fig. 4a). Apical lobe of gonocoxite broadly rounded and usually bears 7-14 setae, each ca. 0.2 times as long as the

gonocoxite. Basal lobe of gonocoxite somewhat triangular and conical and bears, dorsally, a stout, recurved parabasal seta which is ca. 0.2 times as long as the gonocoxite and, mesally, a circular row of 12-23 slender, curved setae. Gonostylus slender, arciform, and sparsely pilose; length, ca. 0.4 times as long as the gonocoxite; laterally and distally, bears 3 short, spine-like setae. Gonostylar claw slightly recurved near apex; length, ca. 0.2 times as long as the gonostylus. Claspette stem is long, slender and strongly arched beyond basal extensions (Fig. 4c); proximal one-third pilose and bears 3-5 short, spine-like setae. Claspette filament is 0.5-0.8 times as long as claspette stem; proximal portion moderately expanded, distal portion gradually tapers to a blunt, recurved point; bears 2-4 small longitudinal ridges. Uniserrate unguis as drawn (Fig. 7a).

FOURTH INSTAR LARVA. Head: Rounded, broader than long (Fig. 3a); head capsule width, 1.0-1.4 mm. Antenna slender, slightly curved, sparsely spiculate, and shorter than head. Antennal seta 1-A, usually 4 (2-6) branched; inserted proximal to middle of antenna; usually not reaching to apex (Fig. 3c). Head Setae: 7-C, usually 5 (4-6) branched; 5-C and 6-C, usually single, rarely 1 is 2 branched; 10-C usually single (1-2). Submentum with 25-29 (24-31) teeth (Fig. 3d). Prothoracic Setae: 1-P, long, 2 branches; 2-P, short, single; 3-P, short, single (1-2); 4-P, short, single; 5-P, long, 3 (2-4) branched; 6-P, long, single; and 7-P, long, 3 (3-4) branched. Abdomen: Setae 6-I to 6-V, usually 2 (1-3) branched; seta 6-VI, usually single (1-2). Comb of segment VIII with 44-62 (33-70) scales arranged in an irregular triangular patch (Fig. 3b); individual scales narrow, with strong median spine and weak subapical spinules which are usually less than one-half as long as the median spine

(Fig. 3e). Pentad seta 3-VIII, 7 (6-10) branched. Siphonal index, 2.6 (2.4-2.9). Attached acus present. Pecten with 18 (16-22) evenly-spaced, acutely-tapered teeth, confined to proximal half of siphon; first 3-4 teeth basally rudimentary, remainder with 1-5 denticles at base. Siphonal seta 1-S, 6 (4-9) branched, barbed, and inserted beyond pecten near middle of siphon. Siphonal seta 2-S single, moderately stout, shorter than apical pecten tooth, and inserted at least its length before apex of siphon. Anal segment longer than wide. Saddle extends 0.5-0.7 down sides of segment X. Seta 1-X, single, stout and long. Seta 4-X consists of 12-17 cratal and 2-4 precratal tufts, each tuft 2-6 branched. Anal papillae elongate and gradually tapered; length, ca. 1.5-2.0 times as long as saddle.

DIAGNOSIS. Fourth instar larvae of A. nevadensis are separated from those of A. communis and A. churchillensis by the shape of the comb scale (Fig. 3e,f). Male and female imagos of this species are separated from those of A. communis by the shapes of the ungues, particularly those of the hindlegs (Tables 5-12; Fig. 7) and from those of A. churchillensis by the chaetotaxy of the thorax (Table 4).

BIONOMICS. Locally abundant in certain alpine areas of the northwestern United States. Eggs: Not described but apparently no differences in chorionic markings between this species and A. communis (65). Larvae: Anatomy of 4th instars described (65, 149). Associated mosquitoes include A. pullatus, Aedes increpitus Dyar and A. communis (65, 149). Develop in open overflow meadow pools adjacent to mountain streams and shaded woodland pools (65). Pupae: External anatomy described (65). Imagos: External anatomy described (65). Female imagos usually obligatorily anautogenous, rarely facultatively autogenous (see below).

Fecundity discussed below.

DISTRIBUTION (Fig. 1). Chapman and Barr (65) found only allopatric populations of A. c. nevadensis (= A. nevadensis) in Wyoming, Nevada, and Utah. Gjullin et al. (149) subsequently found sympatric populations of A. c. nevadensis (= A. nevadensis) and A. c. communis (= A. communis) in several areas of Washington, Oregon and Idaho. In this study, several larvae which appeared to be A. nevadensis were collected from sites at Vermilion Bay, Ont., and Spruce Woods Prov. For., Man., with larvae of A. communis. Unfortunately, these specimens were lost and the occurrence of this species in Canada awaits confirmation. This species may also occur in France (see below).

UNITED STATES. Idaho — Kendrick (149), Smith Ferry (149). Nevada — Elko Co.: Lamoille Canyon (64, 65). Oregon — Chemult (149), Lost L. (149). Utah, many areas (65) — Salt L. Co.: Brighton (LTN). Washington — Cliffdel (149), Park Rapids (149). Wyoming — northern and southwestern areas (65).

Aedes (Ochlerotatus) churchillensis sp. n.

A holotype female and paratype series will be deposited in the Canadian National Collection of Insects. The type locality is Churchill, Man. In addition, paratypes will be deposited in the University of Manitoba Collection.

FEMALE IMAGO. Medium-sized mosquito (length, 5-6 mm). Head: Clypeus dark-brown. Proboscis dark-brown-scaled. Palpi short (ca. 0.2 times as long as proboscis), dark-brown-scaled, occasionally with a few pale scales intermixed. Vertex with narrow, curved, decumbent yellow scales along ocular margins and narrow, decumbent brown scales between

ocular margins and occiput. Occiput with narrow, slightly-curved, erect, forked, yellow scales in a median patch; some similar but dark-brown scales surround median patch. Postgena with broad, decumbent, pale-yellow scales. Pedicel usually golden-brown, sometimes dark-brown, and bearing a few white scales and small setae, especially on mesal surfaces. Thorax: Scutum with dark integument and a variable pattern of pale-yellow to golden-yellow and coppery-brown to dark-brown scales; the latter usually confined to a pair of narrow, longitudinal, submedian stripes and a pair of posterior, supra-alar half-stripes; rarely, the former pair merging to form a broad median stripe; both pairs of stripes either diffuse or distinct. Posterior median bare space surrounded by narrow, pale-yellow scales. Postpronotum with narrow, brown and yellow scales dorsally, scales becoming broader and paler ventrally. Scutellar lobes each with a small patch of narrow, pale-yellow or white scales. Pleuron with extensive poorly-defined patches of decumbent, broad, white scales. Mesepisternal scale patch extending to anterior angle, narrowly separate from prealar scale patch. Mesepimeral scale patch extending to lower margin. Mesomeron, hypostigma, and postprocoxal membrane bare. Tergal setae: SaS, 60-91 (50-101); SFS, 21-31 (17-37); AcS, 19-26 (16-37); PMSS, 5-9 (4-12); DS, 45-56 (36-68); and SS, 27-35 (25-40). Pleural setae: PpS, 7-11 (6-13); PS, 4-7 (3-9); PaS, 13-19 (10-20); MeSU, 12-19 (10-22); MeSL, 1-3 (0-4); MStU, 4-5 (3-6); and MStL, 5-8 (4-10). Abdomen: Tergite 1 with median patch of white scales; remaining tergites dark-brown-scaled with a moderately-broad basal band of white scales; basal bands slightly widened laterally on posterior segments. Sternites mostly white-scaled with indistinct apical bands of dark-brown scales. Legs: Femur: anterior surface dark-brown-scaled, with sprinkling of pale-brown and white scales;

posterior surface yellow- and white-scaled, with sprinkling of white scales. Tarsi dark-brown-scaled; first tarsal segment with a few pale-brown scales. Uniserrate ungues as drawn (Fig. 7a). Wing: Veins with coppery-brown scales; a few pale-yellow scales usually present dorsally at bases of costa, subcosta, and radius. Length variable, ca. 5 mm.

MALE IMAGO. Coloration very similar to that of female imago. Palpi as long as or slightly longer than proboscis; apical segment slightly enlarged. Ninth tergal lobe flattened, tapered, sclerous and as long as or slightly longer than wide (Fig. 4b). Each lobe bears 4-8 (4-11) stout setae which are 1.0-2.5 times as long as lobe. Gonocoxite clothed with scales and numerous short and long setae; length, ca. 4.2 times width at middle (Fig. 4a). Apical lobe of gonocoxite broadly-rounded or bluntly-pointed and bears 8-13 setae, each ca. 0.1 times as long as the gonocoxite. Basal lobe of gonocoxite somewhat triangular and conical and bears, dorsally, a stout, recurved parabasal seta which is ca. 0.2 times as long as the gonocoxite and, mesally, a circular row of 12-20 slender, curved setae. Gonostylus slender, arciform and sparsely pilose; length, ca. 0.4 times as long as the gonocoxite; laterally and distally, bears 3 short, spine-like setae. Gonostylar claw slightly recurved near apex; length, ca. 0.2 times as long as the gonostylus. Claspette stem is long, slender and strongly arched beyond basal extensions (Fig. 4c); proximal one-third is pilose and bears 3-5 short, spine-like setae. Claspette filament is 0.5-0.8 times as long as claspette stem; proximal portion narrowly expanded; distal portion gradually tapered to a blunt, recurved point; bears 2-5 small, longitudinal ridges. Uniserrate ungues as drawn (Fig. 7a).

FOURTH INSTAR LARVA. Head: Rounded, broader than long (Fig. 3a); head capsule width, 1.0-1.2 mm. Antenna slender, slightly curved, sparsely spiculate, and shorter than head (Fig. 3a). Antennal seta 1-A, usually 5 (3-7) branched; inserted proximal to middle of antenna, not reaching to apex (Fig. 3c). Head Setae: 7-C, 5-7 (4-8) branched; 5-C and 6-C, usually single, rarely 2 branched; 10-C usually 2 (1-2) branched. Submentum with 27-31 (26-31) teeth (Fig. 3d). Prothoracic Setae: 1-P, long, 2 (1-3) branched; 2-P, short, usually single (1-2); 3-P, short, usually single (1-2); 4-P, short, single; 5-P, long, 3 (2-4) branched; 6-P, long, single; and 7-P, long, 3 (2-4) branched. Abdomen: Setae 6-I to 6-V, usually 2 (1-2) branched; seta 6-VI, usually single (1-2). Comb of segment VIII (Fig. 3b) with 44-64 (32-70) scales arranged in an irregular triangular patch; individual scales broad with rounded apex and many moderately-stout subequal spinules (Fig. 3f). Pentad seta 3-VIII, 7-10 (6-12) branched. Siphonal index, 2.3-3.0 (2.0-3.7). Attached acus present. Pecten with 18-24 (16-25) evenly-spaced teeth confined to proximal half of siphon; first 3-4 teeth basally rudimentary, remainder with 1-5 denticles at base. Siphonal seta 1-S, 6-9 (5-11) branched, barbed, and inserted beyond pecten near middle of siphon. Siphonal seta 2-S single, stout, shorter than apical pecten tooth, and inserted at least its length before apex of siphon. Anal segment longer than broad. Saddle extends 0.5-0.7 down sides of segment X. Seta 1-X, single and shorter than saddle. Seta 2-X, 6-8 branched. Seta 3-X, single, stout and long. Seta 4-X consists of 16-20 cratal and 1-3 precratal tufts; each tuft 2-7 branched. Anal papillae elongate and gradually tapered; length, ca. 1.5-2.0 times as long as saddle.

DIAGNOSIS. Fourth instar larvae of A. churchillensis are

separated readily from those of A. nevadensis by the shape of the comb scale but with difficulty from those of A. communis by their smaller size, i.e., width of head capsule and length and width of siphon (Table 2). Male and female imagos of A. churchillensis are separated from those of A. communis by the shapes of the ungues, particularly those of the hind-legs (Tables 5-12; Fig. 7) and from those of A. nevadensis by the chaetotaxy of the thorax (Table 4).

BIONOMICS. Non-blood-feeding, univoltine mosquito locally abundant in certain transition-zone habitats of the boreal forest and coastal tundra areas of Alberta and Manitoba, Canada. Eggs: Described below. Embryonic diapause occurs. Larvae: Instar duration similar to A. communis. Associated mosquitoes include A. canadensis, A. cinereus, A. communis, A. diantaeus, A. excrucians, A. fitchii, A. impiger, A. pionips and A. punctor. Found only in acidic water having a brown color. Aggregations frequently observed. Predators unknown; parasitized by protozoans and nematodes (357, 358). Pupae: External anatomy undescribed. Pupal stage variable, ca. 10 d in southern Manitoba. Imagos: Where the 2 species are sympatric, the emergence peak of imagos of A. churchillensis tends to occur 4-5 d after that of A. communis. Both sexes usually found in immediate area of emergence site (14, 181). Dispersal is low (209). Female imagos obligatorily autogenous, probably complete only 1 ovarian cycle, and have a low fecundity (see below).

DISTRIBUTION (Fig. 1). A. churchillensis occurs in disjunct, local populations in northeastern and southeastern Manitoba and in western Alberta. It breeds in snow-melt pools within and at the margins of deciduous and coniferous forests and in coastal tundra. It is most abundant in the Boreal Forest-Tundra Transition zone near Churchill, Man.

CANADA. Alberta — Beaverlodge (RAE). Manitoba — Churchill area (39, 215, RAE), Red Rock L. (RAE), Sandilands Prov. For. (39, RAE), St. Anne (RAE), Telford (RAE).

KEY TO THE SPECIES

Not all museum specimens can be identified with certainty due to the variability of external characters and the subtlety of differences; such specimens are best labelled 'A. communis aggregate' until better diagnostic characters are found.

FEMALE IMAGOS

1. Hindleg ungues gradually curved or curved abruptly beyond the long, narrow, secondary tooth (Fig. 7b,c) communis
Hindleg ungues abruptly curved beyond the short, broad, secondary tooth (Fig. 7a) 2
2. Upper mesepimeral setae, 17-27 (14-33); upper mesepisternal setae, 5-8 (5-8) nevadensis
Upper mesepimeral setae, 12-19 (10-22); upper mesepisternal setae, 4-5 (3-6) churchillensis

MALE GENITALIA

1. Gonocoxites long, 530-628 (510-600) μ ; gonostyli long, 190-220 (180-225) μ churchillensis
Gonocoxites short, 487-557 (450-600) μ ; gonostyli short, 181-209 (168-222) μ 2
2. Gonocoxites wide at middle, 130-158 (120-165) μ ; gonostylar claw short, 36-42 (36-45) μ nevadensis

Gonocoxites narrow at middle, 99-133 (90-150) μ ; gonostylar claw
 long, 42-50 (42-54) μ communis

FOURTH INSTAR LARVAE

1. Comb scales usually with weak subapical spinules less than half as
 long as strong median spine; rarely with 2 or 3 subequal spinules
 (Fig. 3e) nevadensis
 Comb scales with apex rounded and fringed with at least 5 subequal
 spinules (Fig. 3f) 2
2. Head narrow, 1.05-1.17 (0.99-1.20) mm; siphon short, 0.89-1.01 (0.88-
 1.07) mm, and narrow, 0.30-0.37 (0.29-0.42) mm . . churchillensis
 Head broad, 1.20-1.33 (1.14-1.41) mm; siphon long, 1.00-1.14 (0.94-
 1.20) mm, and broad, 0.37-0.42 (0.34-0.44) mm communis

VARIATION IN SIZE AND CHORIONIC PATTERN OF EGGS

Anatomical comparisons of mosquito eggs can help to identify species and to gain a understanding of their phylogenetic relationships. The eggs of many North American species of the genus Aedes have been described. Several identification keys, based largely on the anatomical features of eggs (i.e., color, shape, size, chorionic pattern), are available (e.g., 216, 262, 299) and have enabled ecologists to conduct surveys on the distribution and abundance of pest mosquitoes.

Eggs of A. communis sens. auct. have been described (79, 80, 216). In one of his illustrations, Craig (79) noted a difference in the chorionic reticulation in the median region of eggs of A. communis sens. auct. from Churchill, Man., and Matanuska, Alaska, but did not offer any comment on its significance. Kalpage and Brust (216) described 2 types of eggs of A. communis sens. auct. which differed only in size. The short type was most common at Churchill, Man., where both A. communis and A. churchillensis occur but where the latter predominates; the long egg was most common at Flin Flon, Man., from which only A. communis has been collected.

Chapman and Barr (65) found no differences in the chorionic markings of the eggs of A. c. communis (= A. communis) and A. c. nevadensis (= A. nevadensis). In this study, eggs of A. communis and A. churchillensis were examined to determine the extent of variation in chorionic reticulation and size. Eggs of A. nevadensis were not available for study.

Eggs were obtained from females of A. churchillensis from Churchill, Man., and A. communis from Spruce Woods Prov. For., Man., and Vienna, Mich. Measurements of maximum length and dorsoventral diameter

of eggs of A. churchillensis (n=100) and A. communis (n=20, Vienna, Mich.) were made using a Wild M5 Stereomicroscope equipped with an ocular micrometer. Chorionic mounts of eggs of A. churchillensis and A. communis (Spruce Woods Prov. For., Man.) were prepared according to the technique of Craig (79) and Kalpage and Brust (216). Whole eggs of A. churchillensis and A. communis (Spruce Woods Prov. For., Man.) were prepared for scanning electron microscopy by first attaching the eggs to double-sided masking tape and then evaporating a thin film of gold onto them while they were slowly rotated. A Cambridge Stereoscan Mk. II, operated at 20 kv, was used to view and photograph the eggs.

The chorionic patterns of eggs of A. churchillensis and A. communis are very similar and conform to the descriptions of Craig (79) and Kalpage and Brust (216): i.e., reticulation consists of an irregular network of small, rounded cellules each of which is surrounded by a polygonal cellule wall; the cellules increase in size slightly from the median to the micropylar region of the egg (Fig. 2a-f). However, eggs of A. communis do differ slightly from those of A. churchillensis in the shape of the cellule wall in the median region of the egg. The cellule wall of eggs of A. communis usually digresses from an almost regular 6-sided polygon in the micropylar region to an irregular 4- to 6-sided polygon in the median region (Fig. 2f). The cellule wall of eggs of A. churchillensis, on the other hand, forms an almost regular 6-sided polygon in both regions (Fig. 2c,d,e).

Eggs of these 2 species also appear to differ in the thickness of the exochorion: i.e., the eggs of A. communis appear to have a thicker exochorion than those of A. churchillensis (cf. Fig. 2e,f).

Eggs of A. communis and A. churchillensis differ significantly (One-way analysis of variance, 5% level) in length, dorsoventral diameter and ratio of length to dorsoventral diameter (Table 1). Eggs of A. communis are usually longer and wider and have a smaller ratio than eggs of A. churchillensis.

Although differences in either chorionic pattern or size appear adequate to separate most eggs of A. communis and A. churchillensis, both characters should be examined to preclude misidentification.

VARIATION IN ANATOMY OF FOURTH-INSTAR LARVAE

Culicine larvae are commonly identified by reference to their chaetotaxy and the shape and relative size of their body parts. Because the anatomical characters used for species recognition attain their maximum development in the mature larva, diagnostic keys are usually designed for the identification of the 4th instar. In North America, there are at least 63 species of aedine mosquitoes (58); thus, the range of characters used for the identification of larvae is necessarily broad. Certain characters have proven to be invaluable for the recognition of black-legged Aedes spp (Figs. 3a-f).

Species recognition is particularly important for effective mosquito abatement programs because some aedine mosquitoes are not pests. Some mosquitoes prefer non-mammalian hosts (e.g., A. canadensis) whereas others are autogenous (e.g., A. rempeli, Aedes atropalpus Coquillett). The former mosquito probably never seeks blood during its life span (319); the latter rarely do and only after first cycle oviposition. Recognition of such non-pest species, in the larval stage, has both financial and environmental returns and is seldom difficult.

A. churchillensis is a non-pest species: the females are autogenous and do not take blood even after first cycle oviposition. Both A. nevadensis and A. communis, on the other hand, are pest species: the females are anautogenous. At present, the larvae of A. churchillensis are not readily separable from those of A. communis. The larvae of A. nevadensis can be separated from those of both the other species by the shape of the comb scales on abdominal segment VIII. In this study, larvae of the 3 members of the A. communis aggregate were examined to

determine if anatomical differences could be found to facilitate their separation.

Fourth instars (n=36) from the following North American collection sites were compared: (1) Churchill, Man.; (2) Sandilands Prov. For., Man.; (3) Spruce Woods Prov. For., Man.; (4) Vermilion Bay, Ont.; and (5) Palmer Lake, Wisc. Site 1 was a pure source of A. churchillensis; site 2 was a sympatric population of A. churchillensis and A. communis; and sites 3-5 were pure sources of A. communis.

Larvae used were killed in hot, not boiling, water and stored in 80% ethanol. The following anatomical characters were examined using a dissecting microscope equipped with an ocular micrometer: (1) maximum width of head capsule; (2) distance between setae 5-C; (3) length of antenna, base to seta 1-A to apex; (4) length of antenna, base to seta 1-A; (5) number of branches of seta 1-A; (6) length of seta 4-A; (7) number of branches of seta 7-C; (8) number of branches of right seta 5-C; (9) number of branches of left seta 5-C; (10) number of branches of right seta 6-C; (11) number of branches of left seta 6-C; (12) number of branches of seta 10-C; (13) number of branches of seta 1-P; (14) number of branches of seta 2-P; (15) number of branches of seta 3-P; (16) number of branches of seta 4-P; (17) number of branches of seta 5-P; (18) number of branches of seta 6-P; (19) number of branches of seta 7-P; (20) number of branches of seta 6-I; (21) number of branches of seta 6-II; (22) number of branches of seta 6-III; (23) number of branches of seta 6-IV; (24) number of branches of seta 6-V; (25) number of branches of seta 6-VI; (26) length of siphon, measured along pectin; (27) width of siphon, measured across base; (28) distance between insertions of apical pectin tooth and seta 1-S; (29) number of pectin teeth; (30) number of branches of seta 1-S; (31)

length of seta 2-S; (32) number of comb scales; (33) number of branches of seta 3-VIII; (34) length of saddle, measured across centro-lateral area; (35) width of saddle, measured across centro-lateral area; (36) length of segment X, measured across centro-lateral area of saddle; (37) width of segment X, measured across centro-lateral area of saddle; and (38) length of seta 1-X. The chaetotaxal terminology used above follows the recommendations of Knight and Laffoon (227).

In addition, certain other anatomical features of 4th instars from the above and other collection sites were compared. The number of serrations on the submentum of larvae (n=15) of A. communis (Thompson, Man.), A. churchillensis (Churchill, Man.), and A. nevadensis (Brighton, Utah) were counted. Also, the sclerotized dorsal plate or saddle of abdominal segment X of larvae (n=15) of A. communis (Vermilion Bay, Ont.), A. churchillensis (Churchill, Man.), and A. nevadensis (Brighton, Utah) was examined to determine the extent of variation in the pattern of spiculose ornamentation. Lastly, the shape and number of comb scales on abdominal segment VIII of larvae (n=36) of A. nevadensis (Brighton, Utah) were examined and compared with those of A. communis (Sandilands Prov. For., Man.; Spruce Woods Prov. For., Man.; Vermilion Bay, Ont.; and Palmer Lake, Wisc.) and those of A. churchillensis (Churchill, Man.; Sandilands Prov. For. Man.).

Mature larvae of A. communis and A. churchillensis can be separated statistically into either 2 or 3 groups depending on the anatomical characters compared (Figs. 3a-f; Table 2). Characters 1-4, 12, 22, 26-27, 32 and 34-37 separate the larvae from the 5 sites into 2 groups: (1) sites 1 and 2 and (2) sites 3, 4 and 5. Characters 1, 2, 26, 27 and 37, on the other hand, separate the larvae into 3 groups:

(1) site 1, (2) site 2, and (3) sites 3, 4 and 5. Thus, the second set of characters is best for separating larvae of these 2 species. However, none of the characters examined above will always separate larvae of A. communis and A. churchillensis.

Characters 6-8, 13-15, 17, 19, 21, 28-31, 33 and 37 exhibited anomalous patterns of variation between the larvae examined. Most of these characters divide the larvae of A. communis into subgroups. Such phenotypic plasticity is typical of species having such an extensive range as that of A. communis.

Characters 9-11, 16, 18, 20 and 23-25 were remarkably constant for both species, exhibiting little or no variation in the populations examined.

The submentum, a triangular, serrated sclerite which forms part of the labium of the larvae provides a supplementary character for separating A. nevadensis from A. churchillensis and A. communis (Fig. 3d). Larvae of A. nevadensis had significantly fewer serrations on the submentum, 27.0 ± 2.1 (24-31), than A. communis, 29.2 ± 1.7 (26-31), and A. churchillensis, 29.1 ± 1.9 (26-32). However, the shape of the comb scale (see below) appears to be a more reliable diagnostic character.

The size, shape and arrangement of the spiculate projections on the saddle of mature larvae of A. communis, A. churchillensis, and A. nevadensis conformed to the description given by Frohne (126) for A. communis sens. auct.: i.e, the short, spiculate projections, in groups of 5-25 small spines, were arranged in a uniform pattern of short arcs which tended to adjoin each other. Only slight variation in spinule length was observed within and between the 3 members of the A. communis aggregate.

Chapman and Barr (65) compared the chaetotaxy of the larvae of A. c. nevadensis (= A. nevadensis) and A. c. communis (= A. communis) and concluded that the larvae of the subspecies were inseparable except by the shape of their comb scales. Although the anatomy of the larvae of A. nevadensis was not studied in detail here, the key separation character, namely the comb scales, was reexamined. Larvae of A. nevadensis and A. churchillensis had significantly fewer comb scales than larvae of A. communis. Comb scale number separates the 6 populations compared into the following 3 groups: (1) A. nevadensis (Brighton, Utah, 53±9) and A. churchillensis (Churchill, Man., 54±10); (2) A. communis (Vermilion Bay, Ont., 57±9); and (3) mixed A. communis - A. churchillensis (Sandilands Prov. For., Man., 59±9) and A. communis (Spruce Woods Prov. For., Man., 59±8; Palmer Lake, Mich., 62±8).

Mature larvae of A. churchillensis and A. communis have similarly-shaped comb scales: i.e., the apex of the comb scale is rounded and fringed with subequal spinules (Fig. 3f). The comb scales of A. nevadensis, as described by Chapman and Barr (65), have weak subapical spinules which are usually less than half as long as the strong median spine (Fig. 3e). Although both types of comb scale exhibit considerable variation, larvae of A. nevadensis are readily separated from larvae of the other 2 species.

Two earlier references to comb scales inseparable from those of A. nevadensis occur in the literature. Yamaguti and LaCasse (366) presented a drawing (pl. XX) of the posterior segments of a larva and of a single comb scale, labelled A. communis. Chapman and Barr (65) state that this specimen was from Utah. Seguy (308) presented 2 drawings of comb scales: in one (Fig. 55-5), labelled Ochlerotatus communis, he

depicted a comb scale identical to those of A. nevadensis; in another (Fig. 136E), labelled Aedes communis, he depicted a comb scale similar to those of A. churchillensis and A. communis. It is possible, therefore, that A. nevadensis also occurs in France.

VARIATION IN GENITALIC STRUCTURES OF MALE IMAGOS

The genitalia of male mosquitoes collectively include the structures of abdominal segments IX and X. The genitalic structures which assist the male imago to clasp and hold the female imago during mating have been studied in detail by many culicidologists because of their anatomical and taxonomic importance. Genitalic differences not only allow most male imagos to be identified to species but also give some indications of the probable relationships of groups of species and genera. In this study, selected structures of the genitalia of male imagos were examined to elucidate the differences between and the relationships of members of the A. communis aggregate.

Permanent mounts of the genitalia of male imagos of A. communis (Spruce Woods Prov. For., Man.), A. churchillensis (Churchill, Man.) and A. nevadensis (Brighton, Utah) were prepared according to the technique of Barr (8). Measurements were made of the following genitalic structures, right side only, using a Zeiss Photomicroscope: (1) gonocoxite, length from anterior edge of basal apodeme to apex; (2) gonocoxite, width midway between the apodeme and apex; (3) gonostylus, distance between point of articulation and base of apical claw; (4) gonostylar claw, length; and (5) parabasal seta, length. In addition, the setae on the tergal lobe of the ninth segment were counted. Terminology used follows the recommendations of Knight and Laffoon (226).

The genitalia of male imagos of A. communis, A. churchillensis and A. nevadensis were very similar to each other and conformed, in general, to the description given by Brust and Horsfall (40) for A. communis sens. auct. The 2 flattened, tapered and sclerous lobes of the

tergum of the ninth segment are as long as or longer than wide and bear 3-11 stout setae which are 0.8-2.5 times as long as the lobe (Fig. 4b). The 2 subcylindrical gonocoxites are 3.5-4.5 times as long as wide (Fig. 4a). Each bears a prominent apical and basal lobe. Dorsally, 6-10 long, stout setae are inserted in an irregular single row along the length of the gonocoxite. In addition, numerous short setae are scattered throughout its length. Laterally, the gonocoxite bears many long, slender setae. Ventrally, many long, slender setae are inserted in a long, irregular patch between the middle of the gonocoxite and its apical lobe. Mesally, the gonocoxite is concave and membranous. The entire gonocoxite is clothed with microtrichia. Scales are inserted on the dorsal, lateral and ventral surfaces but, because of the preparation technique used, no distribution pattern could be determined. The apical lobe of the gonocoxite, which extends mesally and ventrally, may be either broadly rounded or bluntly pointed. Nine to 13 slender setae, ca. 0.1 times as long as the gonocoxite, are inserted in its entral face. The basal lobe also extends mesally and is somewhat triangular in shape; the posterior side is flattened or slightly concave whereas the anterior side is rounded. The dorsal edge is more sclerous and bears a stout, parbasal seta which projects mesally at right angles to the gonocoxite and which is ca. 0.2 times as long as the latter. The parbasal spine tapers abruptly and recurves ventrally in its distal quarter. The flattened surface of the basal lobe bears a circular row of 12-22 short, curved setae on its inner rim. The gonostylus, a slender, curved and tubular appendage, articulates with the gonocoxite and is ca. 0.3 times as long as the latter. Apically, it bears the gonostylar claw. The dorsal surface of the gonostylus bears many, very short, slender hairs.

Laterally, beyond the slightly swollen median region of the gonostylus, are inserted 3 short, spine-like setae. The gonostylar claw, actually a stout seta, is inserted at the apex of the gonostylus. This slightly curved seta is ca. 0.2 times as long as the gonostylus. The slender and tubular claspette stem curves broadly beyond the 2 extensions of its base (Fig. 4c). On their dorsal surfaces, the basal extensions and proximal one-third of the stem bear many very short and slender setae and 3-5 short, spine-like setae. The claspette filament, attached apically to claspette stem, is 0.5-0.9 times as long as the latter. The proximal portion of the ligulate filament is narrowly expanded; the distal portion tapers to a recurved point. Two to 5 longitudinal ridges are present along the length of the filament.

Although no reliable diagnostic differences were found among the genitalic structures examined which would permit ready separation of the male imagos of the A. communis aggregate, certain statistical differences were found (One-way analysis of variance and Duncan's multiple range test at the 5% level, Table 3). The length of the gonocoxite separates A. churchillensis from A. communis and A. nevadensis; the gonocoxites of the former were significantly longer than those of the latter. The width of the gonocoxite separates A. communis from A. nevadensis and A. churchillensis; the gonocoxites of the former were significantly narrower than those of the latter. The length of the gonostylus also separates A. churchillensis from A. communis and A. nevadensis; the gonostylus of the former was significantly longer than that of the latter. The gonostylar claw separates A. nevadensis from A. communis and A. churchillensis; the claw of the former was significantly shorter than that of the latter. The length of the parabasal seta does

not give good separation of the members of the A. communis aggregate. The number of setae on the lobe of the tergum of the ninth abdominal segment separates A. nevadensis from A. communis and A. churchillensis: the lobes of the former bore significantly fewer setae than those of the latter. These differences, in combination, will separate most, but not all, male imagos of members of the A. communis aggregate.

VARIATION IN THORACIC CHAETOTAXY OF FEMALE IMAGOS

Thoracic characters commonly employed for the identification of female imagos are the color and arrangement of scale patches on the tergum and the pleuron. However, if these scale patterns are partially or totally obliterated during collection and handling or if the specimens are "flight-worn", identification is often uncertain. To provide a supplementary means for the reliable identification of such "rubbed" specimens, several workers (e.g., 13, 112, 312, 351) have used some of the thoracic setal groups to describe or separate closely-related species. However, the only comprehensive study of aedine mosquitoes has been that of Lunt and Nielsen (245, 246, 247) who found that certain subgeneric and specific groups and, in many cases, species could be separated using the number and arrangement of setae on the thorax of the female imago.

In this study, the thoracic setae of female imagos of A. communis, A. churchillensis and A. nevadensis were examined to determine the amount of variation present within and between the 3 species.

The thoracic setae of female imagos (n=20) of A. communis (Spruce Woods Prov. For., Man.), A. churchillensis (Churchill, Man.), and A. nevadensis (Brighton, Utah) were enumerated. Thoraces were severed from the females, macerated in 10% potassium hydroxide at 50°C for 1 hr, rinsed in 10% acetic acid for 10 min to neutralize the base, washed in 95% ethanol for 20 min, cleared in beechwood creosote for 24 hr, transferred to a glycerol-absolute-ethanol mixture (1:1, v/v) for 10 min, and, finally stored in vials of glycerin until examined.

Counts were based on the total number of setae and setal follicles of the thoracic sclerites. Measurements of thoracic length, from the anterior promontory of the scutum to the posterior edge

of the median scutellar lobe, and counts of setae were made using a Zeiss Photomicroscope. Examinations were made by placing the thorax in a glycerine-filled depression slide. The viscosity of glycerine facilitated manipulation of the thorax for counts and measurement. Left pleural setae were counted first, the thoracic length was measured second, and then, after removing the pleuron, the setae on scutum and scutellum were counted.

Setal terminology used in this study follows the recommendations of Knight and Laffoon (224). Pleural setae counted included the postpronotal, postspiracular, prealar, upper and lower mesepimeral and upper and lower mesepisternal groups (Fig. 5a). Counts of antepronotal and propleural setae were omitted when it became obvious that accurate enumeration was almost impossible due to the subcylindrical shapes of the respective sclerites. Scutal setae counted included the supra-alar, scutal fossal, acrostichal, posterior medial scutal, and dorsocentral groups (Fig. 5b). The setae of the tri-lobed scutellum were counted as one group (Fig. 5b).

The female imagos of members of the A. communis aggregate are separable by differences in their thoracic setae. Although the numbers of setae of the tergum and scutellum exhibit little variation between the 3 species, the number of setae on most of the pleural sclerites of the female imagos differ between species (Table 4). Four of the 7 groups of pleural setae examined differ in the number of setae present in them (One-way analysis of variance and Duncan's multiple range test at the 5% level). The postspiracular, prealar, upper mesepimeral and upper mesepisternal setae exhibit an increase in number among the 3 species: i.e., "hairiness" of the pleuron increases from the female imagos of A. churchillensis to

those of A. communis to those of A. nevadensis. Individual female imagos of each species varied in length but there were no significant size differences between the 3 species. Thus, length comparisons show that "hairiness" is independent of the size of the female imago.

Beckel (13) used the number of anterolateral (= scutal fossal) and posterolateral (= supra-alar) setae of the scutum to separate female imagos of A. communis sens. auct. and Aedes hexodontus Dyar at Churchill, Man. He stated that the small form of A. communis sens. auct. had an average number of 16.4 anterolateral setae and of 31.6 posterolateral setae. Because A. hexodontus had 45.9 anterolateral and 86.6 posterolateral setae, it could be easily separated from A. communis sens. auct. Beckel also stated that the large form of A. communis sens. auct., rare at Churchill but common in the Padlei district, N.W.T., had numbers of setae which overlapped those of A. hexodontus. This difference in the number of setae between the large and small forms of A. communis sens. auct., Beckel stated, was further evidence of 2 entities within the species. However, in this study, there were no significant size differences between female imagos of A. communis, A. churchillensis and A. nevadensis. Also, the female imagos of A. churchillensis, although having significantly fewer setae in the 2 pertinent areas of the scutum than the female imagos of A. communis, had about twice as many scutal fossal and supra-alar setae as the female imagos examined by Beckel. Until this discrepancy is clarified, separation of "rubbed" female imagos of A. hexodontus from those of members of the A. communis aggregate by setal characters should be avoided.

Lunt and Nielsen (246, 247) presented complete data for the thoracic setae of A. communis sens. auct. based on 42 female imagos

pooled from 11 North American localities. Interestingly, their mean values for the setal groups of the pleuron and scutellum were slightly higher whereas their mean values for setal groups of the scutum were slightly lower than the values observed for the 3 species which I examined. Because the data of Nielsen and Lunt were based on pooled specimens, it is difficult to make population comparisons. Nevertheless, the range of values for each setal group of their female imagos and those studied here do demonstrate the plasticity of these species in North America.

Comparisons of numbers and arrangement of the thoracic setae appear to offer considerable promise in geographical and systematic studies of mosquitoes, particularly of closely-related species. However, there are some problems involved in this approach. First, it is sometimes difficult to ascertain which setal group some of the setae on the anterior promontory of the scutum belong. Second, some of the setal follicles of the supra-alar region are quite small and almost indistinguishable from scale follicles. Lastly, as mentioned above, accurate enumeration of the anteprenotal and propleural setae is often impossible. These limitations may not be applicable to all species but they do place some restrictions on the chaetotactic approach. Nevertheless, setal characters appear adequate to elucidate differences between members of the A. communis aggregate.

VARIATION IN TARSAL UNGUES OF IMAGOS

In the Culicidae, the surfaces of the leg segments, excluding the coxae, are described as though the leg were extended horizontally, perpendicular to the mosquito's longitudinal axis (225), the surfaces being the dorsal, ventral, anterior and posterior. Attached apically to the post-tarsus of each of the 3 pairs of thoracic legs of aedine imagos are a pair of small tarsal claws or unguis (Fig. 6). Thus, the unguis may be termed the anterior unguis and the posterior unguis.

On the imagos of many Aedes spp, the unguis of the fore- and midlegs bear, in addition to the primary tooth, a sub-basal secondary tooth (Fig. 6). The unguis of the hindlegs may or may not bear a secondary tooth. The fore- and midlegs of the male imago bear unguis which differ from each other and from the unguis of the hindleg. The fore- and midlegs of the male imago are used to clasp the female imago during the mating flight; it is generally held that the size and shape of the unguis of the male imago are secondary sexual characteristics. The unguis of the hindlegs of the male imago are much reduced in size and, usually, they closely resemble the shape of the female imago's unguis.

Differences in unguis shape usually occur between genera and species and have been used, to a limited extent, in mosquito identification keys (e.g., 8, 58, 167, 321). Unguis comparisons have been, in some cases, particularly helpful to the taxonomist attempting to separate anatomically similar species and rubbed or damaged specimens.

The earliest illustrations of the unguis of a member of the subgenus Ochlerotatus appear to have been made by Howard (195) for Culex sollicitans (= Aedes sollicitans (Walker)). Howard (196) also

described the unguis of Culex stimulans (= Aedes stimulans (Walker)). Drawings of the foreleg unguis of both sexes were presented as an aid to distinguish this species from several others. However, it was not until Vockeroth (349) used the shape of the unguis of the female imagos to partially separate 5 band-legged species that the value of this character in separating closely related species was fully appreciated. Since Vockeroth's reintroduction of the unguis character, other workers with similar taxonomic problems have used it with considerable success (e.g., 166, 296, 351). Most new descriptions and redescriptions of mosquito species now include a drawing of the unguis.

Several authors have published an outline of the unguis of the foreleg of the female imago of A. communis sens. auct. (8, 58, 167, 321, 351). The unguis pictured are all similar but differences in shape and in the relative length of the secondary tooth are obvious. Unfortunately, none of the authors state which unguis of the foreleg was used, how many unguis were studied before the representative was chosen, or the extent of variation in size and shape observed. In this study, the size and shape of all of the unguis of male and female imagos (n=20) of A. churchillensis, A. communis, and A. nevadensis were compared.

All measurements made were of the unguis of imagos reared in the laboratory from field-collected larvae. The sources of the material used, unless noted otherwise, were as follows: (1) A. nevadensis — Brighton, Utah; (2) A. communis — Sandilands Prov. For., Man., Spruce Woods Prov. For., Man., Vermilion Bay, Ont., and Vienna, Mich. ; and (3) A. churchillensis — Sandilands Prov. For., Man., and Churchill, Man. Three measurements of the anterior and posterior unguis of the right legs of 20 imagos of each sex from each population were made. These

were: (1) total unguis length, from point of attachment to tip of primary tooth; (2) length of the secondary tooth, from base to apex; and (3) length of the primary tooth, from base of secondary tooth to apex of unguis (Fig. 6).

Accurate measurement of the characters described above requires careful preparation of the ungues. Permanent mounts were prepared as follows: the right legs and attached ungues were severed entire from the thorax of the imago; macerated in hot, not boiling, 10% potassium hydroxide for ca. 5 min; transferred to 10% acetic acid for ca. 2 min; rinsed in 95% ethanol for ca. 15 min; cleared in beechwood creosote for ca. 15 min; and mounted, in consecutive order, in natural Canada balsam. To ensure that the ungues were spread apart slightly and lying horizontally in one plane, gentle pressure was put on the coverslip with a blunt instrument.

The ungues of the imagos of A. communis sens. lat. may be briefly described as follows: Male. — (1) foreleg ungues: very large, uniserrate anterior unguis and a large, uniserrate posterior unguis; posterior unguis with unusual 'peg-like' secondary tooth; (2) midleg ungues: very large, uniserrate anterior unguis and large uniserrate posterior unguis; and (3) hindleg ungues: both small and uniserrate, similar in shape to female ungues. Female. — (1) foreleg ungues: both large and uniserrate; (2) midleg ungues: both medium-sized and uniserrate; (3) hindleg ungues: both small and uniserrate. The differences, between the sexes in the size and shape of the anterior and posterior ungues of the fore- and midlegs suggest that the ungues of the male imago have a functional significance absent in the female imago. Because the male imago uses the fore- and midlegs to clasp the female imago during the mating flight, it would appear that differences in size

and shape of the unguis of these legs may have a role, albeit minor, in assuring conspecific matings: i.e., male imagos with ungues "abnormal" for a species might be prevented or inhibited in their attempts to mate with female imagos of that species. The length of the secondary tooth may be the key feature of the unguis; its absence or presence and length may determine where and how the female imago is grasped during mating.

Statistical analyses (One-way analysis of variance and Duncan's multiple range test at the 5% level) of the measurements of the anterior and posterior unguis of the right legs of the imagos of the 3 species reveal some interesting differences within and between the populations examined (Tables 5-12).

Ungues of Male Imagos (Fig. 7)

Overall Length (Table 5). Male imagos of A. communis from Vienna, Mich., had significantly longer anterior and posterior ungues on the fore-, mid-, and hindlegs than those of A. communis, A. churchillensis and A. nevadensis from other sites. In general, statistical analyses split the populations into the following 4 groups: (1) A. communis (Vienna, Mich); (2) A. communis (other allopatric sites); (3) A. churchillensis and A. nevadensis; and (4) mixed A. communis - A. churchillensis.

Length of Primary Tooth (Table 6). The pattern of variation of the lengths of the primary teeth on the ungues of the male imago is similar to that for overall length. Although statistic analysis gave slightly different groupings of populations for each unguis, a basic pattern exists which appears to demonstrate that the ungues of male imagos of A. churchillensis and A. nevadensis are very similar to each

other yet distinct from those of A. communis, the populations of which exhibit some heterogeneity.

Male imagos of A. communis from Vienna, Mich., had longer primary teeth on all ungues than A. communis from other sites and than A. nevadensis and A. churchillensis. Male imagos of A. nevadensis and A. churchillensis had primary teeth which were almost equal in length. Male imagos of A. communis from Vermilion Bay, Ont., and Spruce Woods Prov. For., Man., usually had primary teeth intermediate in length.

Length of Secondary Tooth (Table 7). The pattern of variation of the length of the secondary tooth of the ungues of the male imago was also similar to that for overall length. However, secondary tooth length does appear to give a finer separation of the populations. Notable is the secondary tooth length on the anterior unguis of the hindleg which, statistically, gave the following grouping: (1) A. communis (Vienna, Mich.); (2) A. communis (other allopatric sites); (3) mixed A. communis - A. churchillensis and A. nevadensis; and (4) A. churchillensis.

Ratio of Secondary:Primary Tooth Length (Table 8). Differences between the populations, based on this ratio, were slight. A notable exception was the ratio of the posterior unguis of the hindleg. In this case, 3 groups are apparent: (1) males of A. communis (Spruce Woods Prov. For., Man., and Vermilion Bay, Ont.) and mixed A. communis - A. churchillensis with larger ratios; (2) A. churchillensis and A. nevadensis with intermediate ratios; and (3) A. communis (Vienna, Mich.) with the smallest ratio.

Ungues of Female Imagos (Fig. 7)

Overall Length (Table 9). Female imagos of A. communis from Vienna, Mich., had the longest ungues. Female imagos of A. communis

from Spruce Woods Prov. For., Man., and mixed A. communis - A. churchillensis from Sandilands Prov. For., Man., usually had the shortest unguis. The remaining populations had female imagos with unguis intermediate in length.

Length of Primary Tooth (Table 10). This parameter also exhibited considerable variation within and between populations. Overall, statistical analyses gave the following separation: (1) A. communis (Vienna, Mich.); (2) A. communis (Vermilion Bay, Ont.); (3) A. communis (Spruce Woods Prov. For., Man.) and mixed A. communis - A. churchillensis; and (4) A. churchillensis and A. nevadensis. The anterior unguis of the foreleg gave the most complete separation of the female imagos: i.e., (1) A. communis (Vienna, Mich.); (2) A. communis (Vermilion Bay, Ont.); (3) A. communis (Spruce Woods Prov. For., Man.) and mixed A. communis - A. churchillensis; (4) A. nevadensis; and (5) A. churchillensis.

Length of Secondary Tooth (Table 11). Analysis of the length of the secondary tooth on the unguis of the fore- and midlegs consistently produced the following grouping: (1) A. communis with long secondary teeth; (2) mixed A. communis - A. churchillensis with intermediate-sized teeth; and (3) A. nevadensis and A. churchillensis with short teeth. Analysis of the lengths of the secondary tooth on the unguis of the hindlegs provided a finer distinction between the populations by the following grouping: (1) A. communis (Vienna, Mich.) with very long teeth; (2) A. communis (other allopatric sites) with long teeth; (3) mixed A. communis - A. churchillensis with intermediate-sized teeth; (4) A. nevadensis with short teeth; and (5) A. churchillensis with very short teeth.

Ratio of Secondary to Primary Tooth Length (Table 12). In general, analyses of the ratios of secondary to primary tooth length gave the following grouping: (1) A. communis (Spruce Woods Prov. For., Man.) with a very large ratio; (2) A. communis (Vermilion Bay, Ont.) and mixed A. communis - A. churchillensis with a large ratio; (3) A. churchillensis with an intermediate-sized ratio; (4) A. nevadensis with a small ratio; and (5) A. communis (Vienna, Mich.) with a very small ratio.

Overall, the analysis of the unguis measurements of male and female imagos generated the following grouping: (1) A. communis (Vienna Mich.); (2) A. communis (Spruce Woods Prov. For., Man., and Vermilion Bay, Ont.); (3) mixed A. communis - A. churchillensis (Sandilands Prov. For., Man.); (4) A. churchillensis (Churchill, Man.); and (5) A. nevadensis (Brighton, Utah). Noteworthy are the separation of the 3 species and the position of the Vienna population of A. communis. The latter suggests that this population is either an extreme variant of A. communis or represents yet another sibling species.

Atypical unguis, probably genetic aberrations, were occasionally observed. Only 4 types were noted, each only once, and all involved the secondary tooth. Two female imagos of A. communis had an extra or 'tertiary' tooth on one unguis of the hindleg. Another female imago had very short secondary teeth on both unguis of midleg. A male imago of A. churchillensis had a slender, pointed secondary tooth on one claw of a hindleg. Such abnormalities may be expected whenever large numbers of individuals are examined.

VARIATION IN ANATOMY OF SALIVARY GLANDS OF FEMALE IMAGOS

Comparisons of the general features and the banding patterns of salivary gland chromosomes have aided dipteran taxonomists in the study of closely related species and sibling species aggregates and in the establishment of phyletic lines (e.g., Tabanidae, 27; Simuliidae, 301; Syrphidae, 28). However, certain limitations of available cytological techniques and in the extent of chromosomal configurations have restricted the practical usefulness of salivary gland chromosomes of mosquitoes, in most cases, to studies of the Anophelini (e.g., 74, 75, 121, 159). The salivary gland chromosomes of most Aedes spp so far studied are remarkably similar in configuration, number and size (364). It is odd, therefore, that no extensive studies of the comparative anatomy of mosquito salivary glands have been made in spite of their taxonomic potential. Differences detected in the anatomy of the salivary glands of members of a sibling species aggregate would be invaluable for their differentiation. In this study, the general anatomy of the salivary glands of female imagos of A. communis, A. nevadensis and A. churchillensis was examined to evaluate its usefulness.

Twenty female imagos were reared from each of the following populations: A. communis from Spruce Woods Prov. For., Man., Sandilands Prov. For., Man., St. Anne, Man., Beaverlodge, Alta., and Fairbanks, Alaska; A. churchillensis from Sandilands Prov. For., Man. and St. Anne, Man.; and A. nevadensis from Brighton, Utah. Salivary glands were removed from 6-7 d old females using the dissection technique of Gordon and Lavoipierre (154). The unstained, temporary mounts were examined by phase-contrast microscopy.

The salivary glands of the female imagos of A. communis sens. lat. resemble those of Aedes aegypti(L.) as described by Christophers (70). They are located in the prothorax on either side of the esophagus. Both glands have 3 lobes or acini, 2 lateral and 1 median (Fig. 8) The acini are joined at their anterior ends by the junction of their respective interacinary ducts which unite to form the salivary duct. Each tubular acinus consists of a single layer of cells arranged around the interacinary duct. The lateral acini are always longer than the median acinus. Each of the lateral acini is divided into 2 regions differing in cellular structure: the anterior region is usually broader and has more closely-packed cells than the posterior region (Fig. 8). The median acinus closely resembles the posterior region of the lateral acinus but appears distinct when viewed by phase-contrast microscopy.

Although all of the salivary glands examined exhibited these basic anatomical features, differences between the salivary glands of female imagos of A. communis, A. nevadensis, and A. churchillensis were observed. The salivary glands of A. churchillensis, irrespective of population, were one-half to two-thirds as large as those of A. communis and A. nevadensis (Fig. 9a-d). No significant size differences between female imagos, as determined by thoracic length, were observed. Histochemical studies of mosquito salivary glands (e.g., 278, 365) have shown that the median acinus and the anterior region of the lateral acini are secretory in nature. These secretions may cause agglutination of erythrocytes, inhibit blood coagulation and provoke the typical skin reaction to a mosquito bite (71). Thus, the increased size of salivary glands may be related to the bloodfeeding habit: i.e., the salivary glands of anautogenous mosquitoes, such as A. communis and A. nevadensis, may be

larger because of their function whereas those of autogenous mosquitoes, such as A. churchillensis, may be smaller because they are inactive in this respect. The salivary glands of female imagos of A. churchillensis also differed from those of A. communis and A. nevadensis in the anatomy of the median acinus: the median acinus was shorter, narrower, and exhibited less cellular definition in A. churchillensis (Fig. 9a,b) than in A. nevadensis (Fig. 9c) and A. communis (Fig. 9d).

Another difference between A. churchillensis and the other 2 members of the A. communis aggregate is that the salivary glands of the latter, in situ, were surrounded by a very large, dense, fat body (Fig. 9c,d): the fat body surrounding the salivary glands of the former, on the other hand, was either much reduced or, occasionally, entirely absent.

Female imagos of A. nevadensis had salivary glands which differed from those of A. communis and A. churchillensis. The median acinus was usually more swollen than the lateral acini (Fig. 9c). In addition, bifurcations and, occasionally, trifurcations of the median acinus and of its interacinary duct were common. Both of these features were rare in A. communis and A. churchillensis.

These anatomical differences appear consistent within and between populations of A. communis, A. churchillensis and A. nevadensis and illustrate both the close relation and the uniqueness of each species.

MATURATION OF OVARIAN FOLLICLES

Intensive studies have been made of ovarian development in mosquitoes of biological and epidemiological importance. Excellent reviews of the study of vitellogenesis, i.e., the formation and incorporation of yolk into developing follicles, are available (26, 71, 114). Because information on the nature, synthesis and distribution of follicular yolk is of fundamental importance to studies of the nutritional requirements of female imagos, considerable emphasis has been placed on this aspect of ovarian development.

In mosquitoes, food, in the form of an adequate supply of carbohydrate, is normally required by both male and female imagos soon after emergence. Carbohydrate, essential from an energy standpoint for the continuance of the metabolic activities of the imago, is readily available, as nectar, from the nectaries of many angiosperms (136, 183, 197). The leaf petiole nectaries of some trees and the sweet excretions of many phytophagous insects, e.g., the 'honeydew' of aphids (163), may also be important sources of carbohydrate for some imaginal mosquitoes.

In addition to carbohydrate, the female imagos of most species of mosquitoes require protein. Blood, obtainable from a variety of animals, provides this component of the diet. Without blood, most female mosquitoes are unable to mature their ovarian follicles (Fig. 10a-d). Humoral control of normal vitellogenesis is not fully understood, but, in general, it is believed that gorging on blood by female imagos activates the corpora allata to secrete a gonadotrophic hormone which promotes the incorporation of proteinaceous and lipid yolk material into the growing follicles (71, 114). However, Lea (232) has shown that, in Culex

nigripalpus Theobald, Culex pipiens pipiens L. and A. aegypti, secretion from the corpora allata occurs prior to blood-feeding. He has also shown (231) that the median neurosecretory cells are important to vitellogenesis in Aedes taeniorhynchus Wiedemann. Although blood digestion and follicular maturation are usually synchronous activities, vitellogenesis proceeds uninterrupted by the need for a blood-meal in a few or all female imagos of some species. Although carbohydrate does not appear to be used directly for yolk synthesis in such non-blood-feeding individuals, it may facilitate the mobilization of protein reserves carried over from the larvae.

Two terms have come into general usage to describe the divergent nutritional requirements of mosquitoes. 'Anautogeny' denotes an obligate requirement for protein before vitellogenesis can proceed beyond an early resting stage whereas 'autogeny' denotes the absence of such a requirement (323). To describe individual female imagos of A. impiger and Aedes nigripes (Zetterstedt) which normally seek blood to mature their follicles but which, if unable to obtain blood, are able to mature a few of their follicles, Corbet (78) introduced the term 'facultative autogeny'. This phenomenon is associated with a progressive resorption of most and maturation of a few follicles; facultatively autogenous mosquitoes usually produce very few eggs. Female imagos exhibiting 'obligate autogeny', on the other hand, are those that do not normally seek blood but rather use protein reserves ab intra for follicular maturation. Either expression of autogeny has survival value for a species. Facultative autogeny enables a species to remain locally extant during periods of host scarcity or absence. It would have most adaptive significance in areas where hosts are subject to wide fluctuations in number. Obligat autogeny enables a

species to be completely independent of host availability.

Autogeny, in one form or the other, has been observed in several genera of mosquitoes including Aedes, Anopheles, Culex, Culiseta, Deinocerites, Malaya, Mansonia, Opifex, Orthopodomyia, Toxorhynchites, Tripteroides, Uranotaenia, and Wyeomyia (71, 256, 318). Autogeny has been reported in 17 species of the genus Aedes, subgenus Ochlerotatus (Table 13), including A. communis sens. auct.

Autogeny in A. communis sens. auct. was first reported by Hocking (181). Among female imagos at Churchill, Man., he observed an inverse relationship between flight muscle autolysis and follicular maturation. Hocking (184) confirmed his earlier observations and calculated that flight muscle autolysis could account for the nitrogen requirement of 33% of the eggs hatched. He postulated that only the small form of this species at Churchill was autogenous. However, Beckel (14) found no evidence of flight muscle autolysis in autogenous female imagos of the same size as those examined by Hocking (181, 184). Chapman (63, 64) reported a low level of autogeny in a predominately anaautogenous population of A. communis sens. auct. from the Sierra Nevada Mtns., Nev. At Baker Lake, N.W.T., where A. communis sens. auct. is rare, Smith (318) observed that ca. 2% of a predominantly anaautogenous population were facultatively autogenous. At Churchill, Kalpage (215) observed that ca. 95% of the female imagos of this species were autogenous and found no evidence of flight muscle autolysis in autogenous female imagos. Brust (39) reported that autogeny among this species at Sandilands Prov. For., Man., ranged from 60 to 100%, depending upon the collection and also found no evidence of flight muscle autolysis.

In this study, female imagos of A. communis, A. churchillensis and A. nevadensis from several areas of North America were examined in order to determine their normal mode of follicular maturation.

The survey for autogeny among nulliparous, non-blood-fed mosquitoes of 78 populations of A. communis, A. churchillensis and A. nevadensis involved 6916 ovarian dissections. Female imagos were reared, under conditions already described (see 'General Methods') from field-collected larvae. Allopatric populations of A. communis, A. churchillensis and A. nevadensis were present at 33, 4 and 1 collection sites, respectively; sympatric populations of A. communis and A. churchillensis were present at 20 sites.

Female imagos, aged 5 to 30, usually 7 to 10, days were anesthetized with ether, wetted in 70% ethanol and rinsed in saline before being dissected in a few drops of saline. Intact ovaries were removed, using the technique of Christophers (70), transferred to a drop of saline on a clean slide, covered with a cover slip, and immediately examined by phase-contrast microscopy. Follicular maturation was graded according to the following classification scheme, adapted from Christophers (70) and Clements (71): stage 1a follicles are spheroid, fully separated from the germinal epithelium, consist of 8 undifferentiated cells, and have no yolk (Fig. 11a); stage 1b follicles are spheroid, consist of a definitive oocyte and 7 nurse cells, and have only a trace of yolk (Fig. 11b); stage 2a follicles are spheroid and have yolk around but not obscuring the oocyte (Fig. 11c); stage 2b follicles are slightly ovoid and less than one-third filled with yolk (Fig. 11d); stage 3a follicles are slightly ovoid and one- to two-thirds filled with yolk (Fig. 11e); stage 3b follicles are two-thirds to three-quarters filled

with yolk (Fig. 11f); stage 4a follicles are ovoid and three-quarters to nine-tenths filled with yolk (Fig. 11g); stage 4b follicles are elongate and ovoid and completely filled with yolk but have no chorion (Fig. 11h); and stage 5 follicles, the mature but unlaidd eggs, are egg-shaped and have a chorion (Fig. 11i). Female imagos with the majority of their follicles matured beyond stage 3a were considered obligatorily autogenous. Female imagos with only a few of their follicles matured beyond stage 3a and the remainder of their follicles showing evidence of resorption were considered facultatively autogenous (Fig. 10c). Female imagos with none of their follicles matured beyond stage 2b were considered obligatorily anautogenous (Fig. 10d).

Although a few female imagos (0.3-3.0%) of A. communis and (0.4%) A. nevadensis were found to be facultatively autogenous, an autogeny survey (Table 14) revealed that most female imagos of these species were obligatorily anautogenous whereas all female imagos of A. churchillensis were obligatorily autogenous. Female imagos of A. communis from 53 collection sites were examined for evidence of autogeny. Only a few facultatively autogenous female imagos were reared from some larval populations (Beaverlodge, Alta.; Spruce Woods Prov. For., Man.; St. Anne, Man.; Vermilion Bay, Ont.; Vienna, Mich.; and Palmer L., Wisc.). Female imagos of A. nevadensis from Brighton, Utah, were normally obligatorily anautogenous. Only one facultatively autogenous female imago was found. After 9 d, this female imago had begun to promote several follicles beyond stage 3a.

Although the actual fecundity of the female imago, i.e., the total eggs oviposited, provides a reasonable estimate of the reproductive capacity of a species, this value is subject to several variables,

including nutrition, light, temperature, humidity, and mating and oviposition stimuli. The potential fecundity, i.e., the total number of ovarian follicles present, may provide a more reliable estimate of reproductive capacity, especially under laboratory conditions. Knowledge of the potential fecundity in each ovarian cycle is critical.

Some observations of the potential fecundity of members of the A. communis aggregate were made during the autogeny survey. Blood-fed nullipars (n=6) of A. communis, collected coming-to-bite at Spruce Woods Prov. For., Man., matured 50.5 ± 14.1 (34-70) follicles to stage 5. One non-blood-fed nullipar of A. nevadensis, reared from a field-collected larva, had 57 follicles at stage 1b. Some comparable data were recorded for autogenous nullipars of A. churchillensis from 3 kinds of habitats at Churchill, Man. Female imagos obtained from coastal-tundra, boreal-tundra and boreal habitats matured 31.1 ± 9.5 (18-55), 30.5 ± 10.0 (18-58) and 49.1 ± 8.6 (35-64) stage 5 follicles, respectively. The potential fecundity of female imagos with stage 5 follicles varied according to habitat. Female imagos from boreal habitats matured significantly more follicles than those from coastal-tundra or boreal-tundra habitats.

Other observations on the potential and actual fecundity of A. communis sens. auct. have been reported. Hocking (181, 184) observed that autogenous female imagos at Churchill, Man., matured, on the average, 64 follicles. Beckel (16) observed that autogenous female imagos at Churchill, oviposited, on the average, 11 eggs but based this value on total eggs produced divided by total female imagos initially alive: assuming that one-half lived to oviposit, a value of 22 eggs per female imago would probably be more realistic. Working with 2 Alaskan populations, Sommerman (322) observed that anaautogenous female imagos oviposited, on

the average, 45 eggs. At Churchill, Man., Kalpage (215) observed that autogenous female imagos, oviposited, on the average, 33 eggs. Kalpage noted that these eggs represented only ca. one-third of follicles in newly-emerged female imagos and that yolk may be resorbed from ca. two-thirds of the stage 2 follicles in order to promote the remaining follicles to stage 5. Brust (39) observed that autogenous female imagos from Sandilands Prov. For., Man., and Churchill, Man., oviposited, on the average, 35 and 42 eggs, respectively. Assuming that all of the autogenous female imagos involved in the above studies were A. churchillensis and that the anautogenous female imagos involved in Sommerman's (322) study were A. communis it would appear that the fecundities of these 2 species are very similar.

Female imagos of members of the A. communis aggregate have polytrophic ovarioles consisting of an anterior germarium, a posterior vitellarium and 2 sheaths, the tunica propria and the ovariole sheath. The vitellarium consist of 2 interconnected follicles; yolk deposition is initiated in the smaller anterior follicle only after the posterior follicle is fully developed. Photomicrographs of the ovarioles of female imagos of A. communis and A. churchillensis revealed that the anterior follicles of the former tend to be much larger than those of the latter, relative to the size of the posterior follicle (Fig. 11d cf. Fig. 11e). The relatively small anterior follicles of A. churchillensis suggest that the female imagos may normally only mature their first follicular complement. The relatively larger anterior follicles of A. communis on the other hand, suggest that the female imagos of this species normally mature 2 or more follicular complements.

Some observations on the number of ovarian cycles of A. communis sens. auct. have been reported. Shlenova and Bey-Bienko (311) reported that some female imagos from Vitebsk, U.S.S.R., completed 6 ovarian cycles but that most completed only 1 or 2. Carpenter and Nielsen (44) reported that some female imagos from the western U.S.A. completed 3 cycles but that most completed only 1 or 2. Rosay and Nielsen (297) reported that some female imagos from Brighton, Utah, completed 3 cycles, but that most completed only 2, and that one female imago from Mirror Lake, Utah, completed 5 cycles, but that most completed only 3 or 4. Probably all of these observations pertain to female imagos of A. communis with possible exception of the female imagos from Brighton, Utah, which may have been A. nevadensis. No observations on the number of ovarian cycles of A. churchillensis have been reported.

MATING BEHAVIOR IN NATURE

Little is known of the actual circumstances surrounding copulation in most aedine mosquitoes. From the limited observations made of swarming and copulation, two hypotheses have been generated. The generally-accepted hypothesis, as set forth by Downes (95), is that copulation normally takes place at a visually determined assembly station, the male swarm. One to many thousand male imagos constitute the quasi-stationary swarm to which female imagos are attracted. A female is captured as she enters the swarm and mating ensues as the pair exit the swarm. Low light intensity seems to be the main stimulus for swarm formation: temperature and humidity probably determine its location and duration. The opposing hypothesis, proposed by Nielsen and Haeger (270), is that swarming and copulation are independent but, occasionally, coincident activities. The latter authors maintain that most mosquitoes mate in casual flights in the emergence area and that swarming is a behavior ritual of unknown function. To determine which, if either, hypothesis is true, more elaborate observations and experiments involving many species are necessary.

In spite of the widespread distribution and usual abundance of A. communis sens. lat., very few observations of swarming and copulation have been made. Wesenberg-Lund (359) observed a small, diurnal swarm of A. communis sens. auct. and A. cataphylla, in shaded clearings of a birch forest, 1-2 m above the ground: some mating pairs were observed. Owen (279) observed a small, crepuscular swarm beside a water tower, ca. 15 m above the ground: mating was not reported. Hocking et al. (188) observed an enormous swarm of A. punctor together with A. communis sens.

auct., 1-3 m above a railway track situated in an open spruce-larch forest: mating was not reported. Nielsen and Greve (260) observed spontaneous matutinal and crepuscular swarming in clearings of a birch forest: the former swarms began in the forest canopy and slowly descended with increasing light whereas the latter began near the ground and slowly ascended with decreasing light. Jenkins and Knight (211) observed crepuscular swarms in an open meadow and at the edge of a cottonwood forest, 1.5-2.5 and 2-3 m above the ground, respectively: mating was not reported. Frohne and Frohne (132) observed small crepuscular swarms 'in a secluded recess of the margin of a glade among alders, willows, and a high spruce', 2-3 m above the ground: several copulating pairs were seen falling from some of the swarms. Frohne (125, 127) observed small crepuscular swarms, 1-2 m above large boulders, in an exposed alpine tundra area: mating was not observed.

The paucity of records suggest that swarming in A. communis sens. lat. may be a rare phenomenon. I have searched for swarms on several occasions at various potential swarming sites during the course of this study but have found none: of course, suboptimal conditions for swarming may have been coincident with my visits or the swarms may have been poorly visible. On the other hand, I have observed copulating pairs of A. communis on two separate occasions. In each case, mating pairs were observed while I was collecting female imagos in a black spruce-willow forest in Spruce Woods Prov. For., Man. Just before noon on 21 June 1971, 12 mating pairs were seen in a 15 min period, while I and 2 assistants were collecting female imagos attempting to feed on us. In each case, the pairs were coupled in flight at 1-2 m above the ground and within 2 m of our group. A brief rain shower occurred about 1 hr before

we began to collect. The sky was heavily overcast and the air temperature was 20.5°C. Two hundred nulliparous females, 80% of which were A. communis, were captured in 15 minutes. Only one mating pair was captured; the imagos were later identified as A. communis. One week later, under almost identical conditions, 2 copulating imagos were observed but could not be captured. On no occasion were males observed performing solo or group flights characteristic of swarms. These observations suggest that mating probably occurs most often in the vicinity of hosts intruding in emergence areas. Somewhat similar observations have been made of Aedes albopictus Skuse by Gubler and Blattacharya (161) who postulated that mating in the vicinity of the host in nature is probably an adaptation which ensures a high insemination rate among feeding female imagos.

MATING SUCCESS OF A. communis AND A. churchillensis IN THE LABORATORY

The mating success of mosquitoes in captivity varies with their sexual maturity, nutritional background and environment. Under conditions considered optimal for a species, the mating success of caged mosquitoes may be either high or low. The mating of stenogamous cage populations is relatively uninhibited whereas that of eurygamous cage populations is extremely low. The terms 'stenogamy' and 'eurygamy' are, like the conditions they describe, admittedly artificial. A species may be eurygamous only because the conditions optimal for mating are poorly known. Similarly, a species may be stenogamous only because it tolerates artificial manipulation. However, if 2 populations, treated under identical cage conditions, differ significantly in their mating success, this may be a reflection of behavioral dissimilarities between the populations. In nature, such dissimilarities could tend to inhibit matings between the 2 populations.

Laboratory studies of mating can provide some clues as to the extent of sexual isolation between populations. Incomplete or complete sexual isolation has been demonstrated between Anopheles quadrimaculatus Say and other Anopheles spp (302, 328), between populations of A. aegypti and A. albopictus (236), between A. aegypti and Aedes mascarensis MacGregor (170) and between Aedes simpsoni (Theobald) and Aedes woodi Edwards (169). Some observations of mating success in caged populations of A. communis and A. churchillensis are reported here.

The observations are based on the mating success of imagos of A. communis and A. churchillensis, either caged together or separate, at various sex ratios, in cages of various sizes and shapes, and for varying

periods of time. Mating success, i.e., insemination, was scored by spermathecal examination. The conditions of light, temperature and photoperiod were as described for imagos (see 'General Methods'). The observations are not, nor were they intended to be, strictly comparable: however, they do provide some indications of the optimal cage conditions for mating in these 2 species and the possible extent of sexual isolation in nature.

Imagos of A. communis are eurygamous. No mating occurred in 10 of 11 cage setups: mating success was only slight in one cage (Table 15). Cage size did not appear to be the determining factor for this success because mating was nil in both smaller and larger cages. The only variable which may possibly explain this success is the longer confinement period, 15-16 d.

Imagos of A. churchillensis, on the other hand, are stenogamous. Mating success of reproductively mature imagos ranged from 10 to 83% in 10 different cage setups. Percentage insemination increased with time (e.g., setup 21). With the possible exception of the largest cage (120x120x210 cm), mating success appeared to be independent of cage size. Sex ratio and density of imagos, within limits, do not appear important to mating success.

When imagos of A. communis and A. churchillensis reared from sympatric larval populations were caged together, mating success was higher, overall, for each species. The observations are difficult to evaluate because only the total number of male imagos, not the number of each respective species, was known (Table 15). However, mating success ranged from 50-90% for A. churchillensis and from 0-14% for

A. communis. Two possible causes for the higher success among imagos of A. communis are, first, that some stimulus for mating was provided by the presence of A. churchillensis; and, second, that male imagos of A. churchillensis mated with some or all of the female imagos of A. communis. When 50 female imagos of A. communis from Thompson, Man., were caged with 50 male imagos of A. churchillensis from Churchill, Man., in a small cube cage (25x25x25 cm), 11% of the female imagos were inseminated after 9 d. However, when male imagos of A. communis and female imagos of A. churchillensis were caged under identical conditions, no mating occurred. These cage trials indicate that eurygamy and stenogamy are more a reflection of male than female sexual behavior and suggest that, if hybridization occurs in nature between sympatric populations of these species, crosses between female imagos of A. communis and male imagos of A. churchillensis may be most likely.

In general the observations indicate the eurygamous and stenogamous nature of A. communis and A. churchillensis, respectively, and suggest that limited hybridization between these 2 species in nature is possible. Information obtained from a series of controlled mating experiments, designed to test the importance of cage size and shape, imaginal age and density, and sex ratio, and studies of natural hybridization between imagos of sympatric populations, using radioisotope-marked individuals, would provide a better understanding of sexual isolation between these species.

GENETIC AFFINITY OF A. communis AND A. churchillensis

Many laboratory studies of hybridization in mosquitoes of epidemiological importance have been conducted and are summarized by Kitzmiller (22), Mattingly (256), Rozeboom and Kitzmiller (303), McClelland (248), Coluzzi and Sabatini (74, 75), Knipling et al. (228) and Coluzzi (73). Such studies are possible, even of species whose imagos exhibit eurygamic behavior, by using the induced copulation technique described by Horsfall and Taylor (197) which circumvents at least 3 prezygotic barriers to fertilization, namely temporal, spatial and behavioral isolation.

Although the genetic affinities of species may be estimated from hybridization studies (264), such studies cannot predictably provide proof of species isolation. Although non-viable or sterile hybrids usually indicate postmating isolation, the production of fertile hybrids is inconclusive: i.e., the absence of sterility barriers does not necessarily indicate conspecificity between crossed populations (239). In this study, hybridization was attempted to evaluate the genetic affinity of A. communis and A. churchillensis.

Because my laboratory cultures of A. communis (Spruce Woods Prov. For., Man.) and A. churchillensis (Churchill, Man.) were slightly asynchronous, only one cross, A. communis ♂♂ x A. churchillensis ♀♀, was possible. Male imagos, 5 d old, and female imagos, 7-8 d old, were mated by induced copulation. Insemination success was evaluated in 2 ways: (1) the spermathecae of a small sample of female imagos (n=5) were removed and examined for the presence of sperm, and (2) the spermathecae of the remaining female imagos were examined immediately after the imagos died.

Eggs oviposited by individual female imagos in screen cup cages were subjected to the egg conditioning and hatching procedures already described. Whole eggs which failed to hatch, after 2 attempts, were inspected for embryos by dissection.

Hybridization provides one of the best means for evaluating the degree of relationship between 2 species. Species incapable of crossing or of producing viable hybrids may be considered reproductively isolated; gene flow is improbable in nature. Although, in this study, no obvious difficulty was encountered in mating the imagos by induced copulation, only 14 of the 17 female imagos able to mature their eggs were inseminated (Table 16). Twelve of the 14 inseminated female imagos oviposited at least part of their egg complement. A few of the eggs oviposited by females 15, 16 and 17 subsequently became fully embryonated. Only 3 of the 5 embryonated eggs of female 17 eventually hatched; however, the larvae died as they moulted to the 2nd instar. Most unembryonated eggs ruptured during the conditioning period. Normally, at least 60% of the eggs of A. churchillensis and 80% of the eggs of A. communis are fully embryonated.

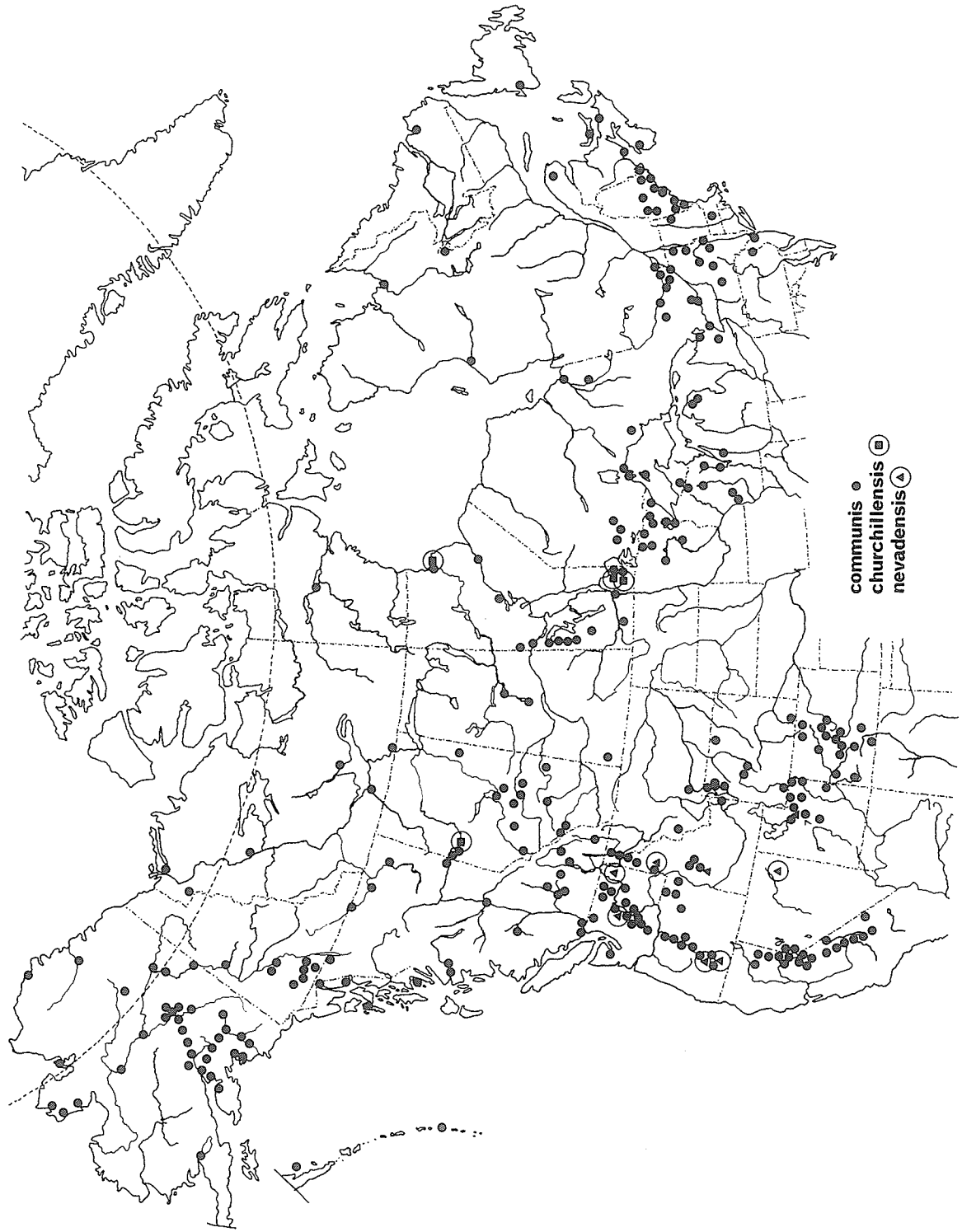
Because most eggs produced by this cross were not embryonated, or, if embryonated, did not yield viable larvae, there appears to be a low degree of genetic affinity between A. communis and A. churchillensis. Gametic isolation and hybrid inviability would be expected to restrict gene flow between sympatric populations of these species. However, before definite conclusions can be drawn, male imagos of A. churchillensis and female imagos of A. communis should be crossed to determine if fertile hybrids are produced.

SUMMARY

In this study, I have dealt with the separation of 3 mosquito species which exhibit rather subtle anatomical differences. The suspicion that A. communis (Deg.) sens. auct. might include more than one species arose from reports in the literature of obviously discontinuous physiological and ecological features between some populations. To test the hypothesis that A. communis sens. auct. was composed of two or more biological species, an autogeny survey was made of representative North American populations. A study of variation of pure populations of the anautogenous and autogenous forms of A. communis sens. auct. revealed anatomical, physiological, behavioral and ecological differences. To replace the former species, 3 species have been established. These species are: A. communis (Deg.) sens. str., A. churchillensis sp. n. and A. nevadensis Chapman and Barr n. status. A. churchillensis alone is characterized by obligate autogeny, by stenogamy, and by a reduction in the size of the salivary glands of the female.

Fig. 1.

Geographical distribution of A. communis, A. churchillensis and A. nevadensis in North America.



● *communis*
◻ *churchillensis*
▲ *nevadensis*

Fig. 2a-f.

Chorionic patterns of eggs of A. churchillensis, and A. communis: (a) churchillensis, from Sandilands Prov. For., Man., ca. 360X; (b) same, ca. 780X; (c) same, ca. 1560X; (d) same, ca. 2040X; (e) churchillensis, from Churchill, Man., ca. 1020X; (f) communis from Spruce Woods Prov. For., Man., ca. 1020X.

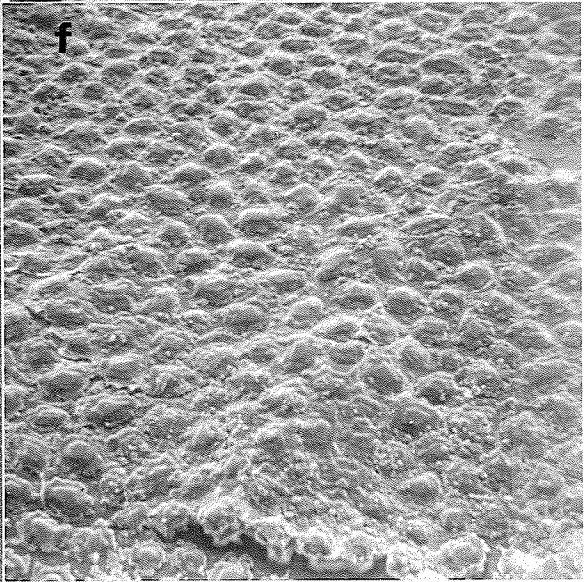
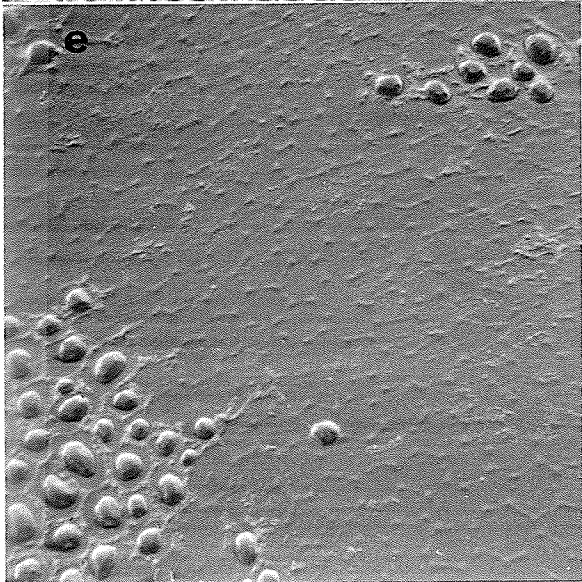
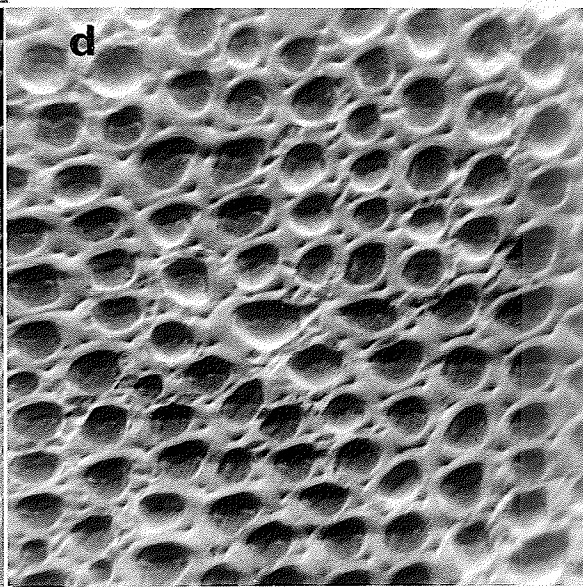
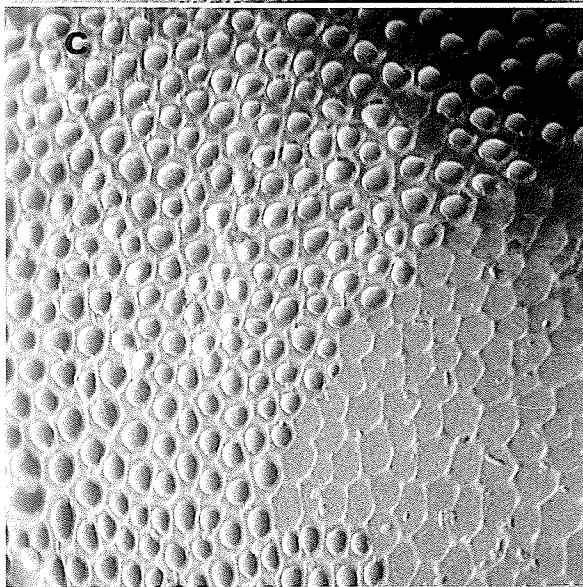
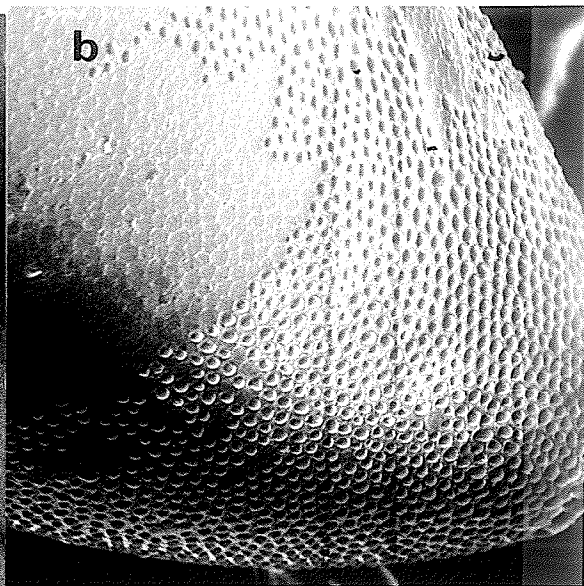
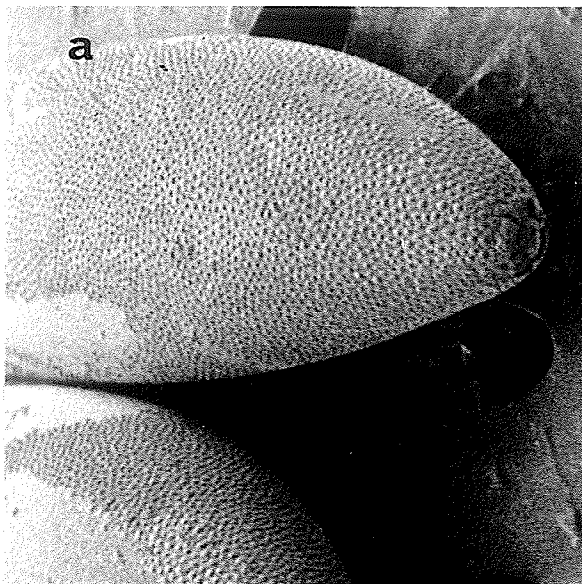


Fig. 3a-f.

Anatomical features of 4th instar larvae of members of the A. communis aggregate: (a) Head and pro-thorax, (b) Terminal abdominal segments, (c) Antenna, and (d) Submentum, of A. communis; (e) Comb scales of A. nevadensis; and (f) Comb scales of both A. communis and A. churchillensis. C, head. 5-C, upper frontal seta. 6-C, lower frontal seta. 7-C, preantennal seta. 10-C, suprarorbital seta. A, antenna. 1 to 6-A, antennal setae. Segment VIII: CS, comb scales; and 1 to 5-VIII, pentad setae. Segment X: Sa, saddle; AP, anal papillae; 1-X, lateral setae; 2-X, upper caudal seta and; 4-X, precratal and cratal setae. Siphon (Si); P, Pectin; 1-Si, siphonal setal tuft; 2-Si, dorsal preapical seta; and 8-Si, ventral apical seta.

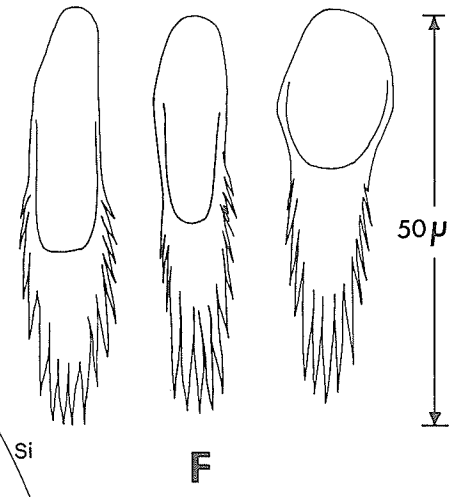
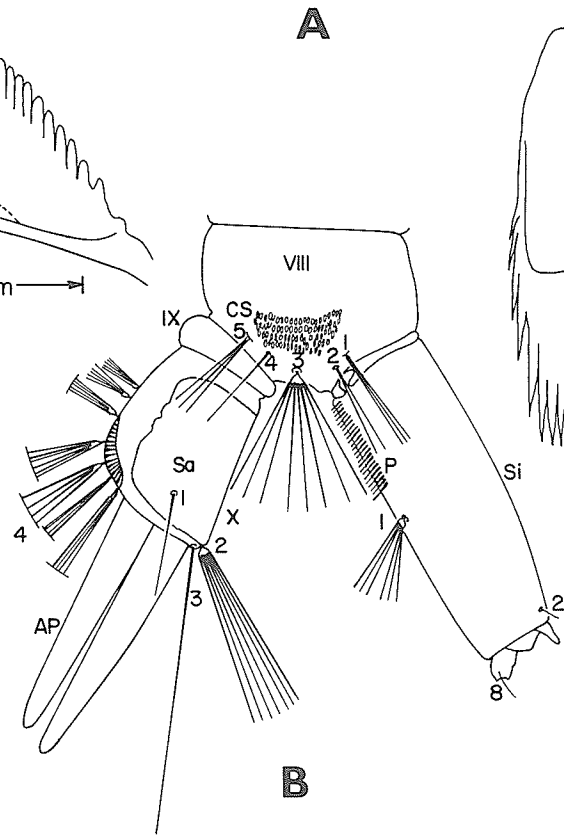
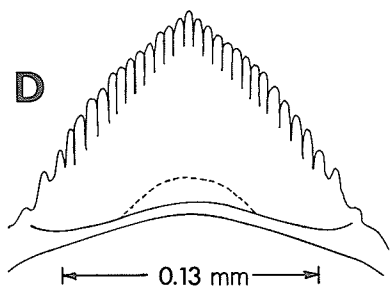
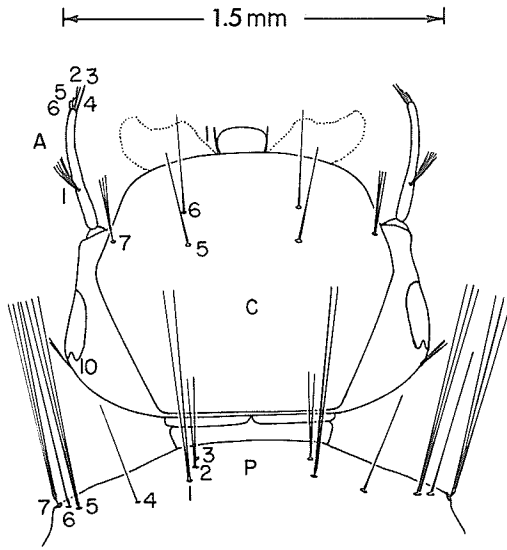
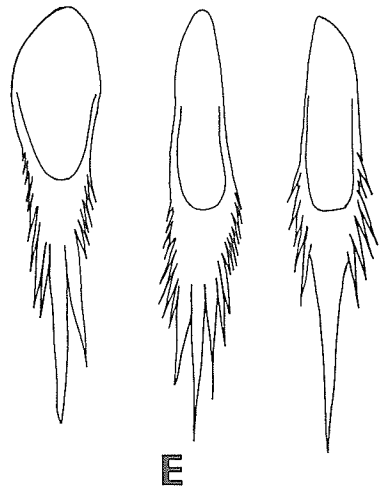
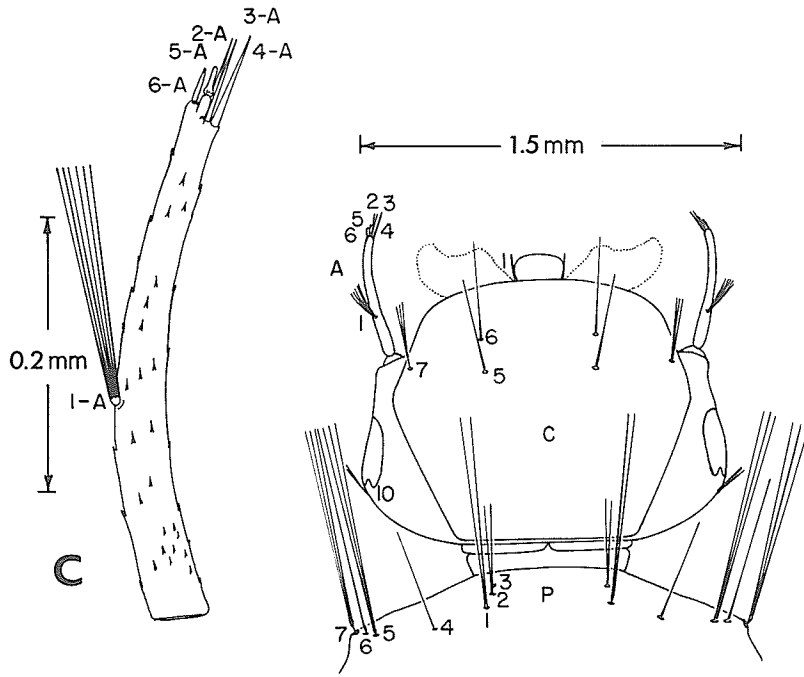


Fig. 4a-c.

Diagram of gonocoxite (A), ninth tergal lobes (B), and claspettes (C) of male genitalia of members of the A. communis aggregate. AG, apodeme of gonocoxite. AML, apical mesal lobe. BML, basal mesal lobe. CF, claspette filament. CSt, claspette stem. Gc, gonocoxite. GC, gonostylar claw. Gs, gonostylus. MM, mesal membrane. PSp, parabasal spine. IX-Br, bridge of ninth tergite. IX-TL, tergal lobes of ninth tergite.

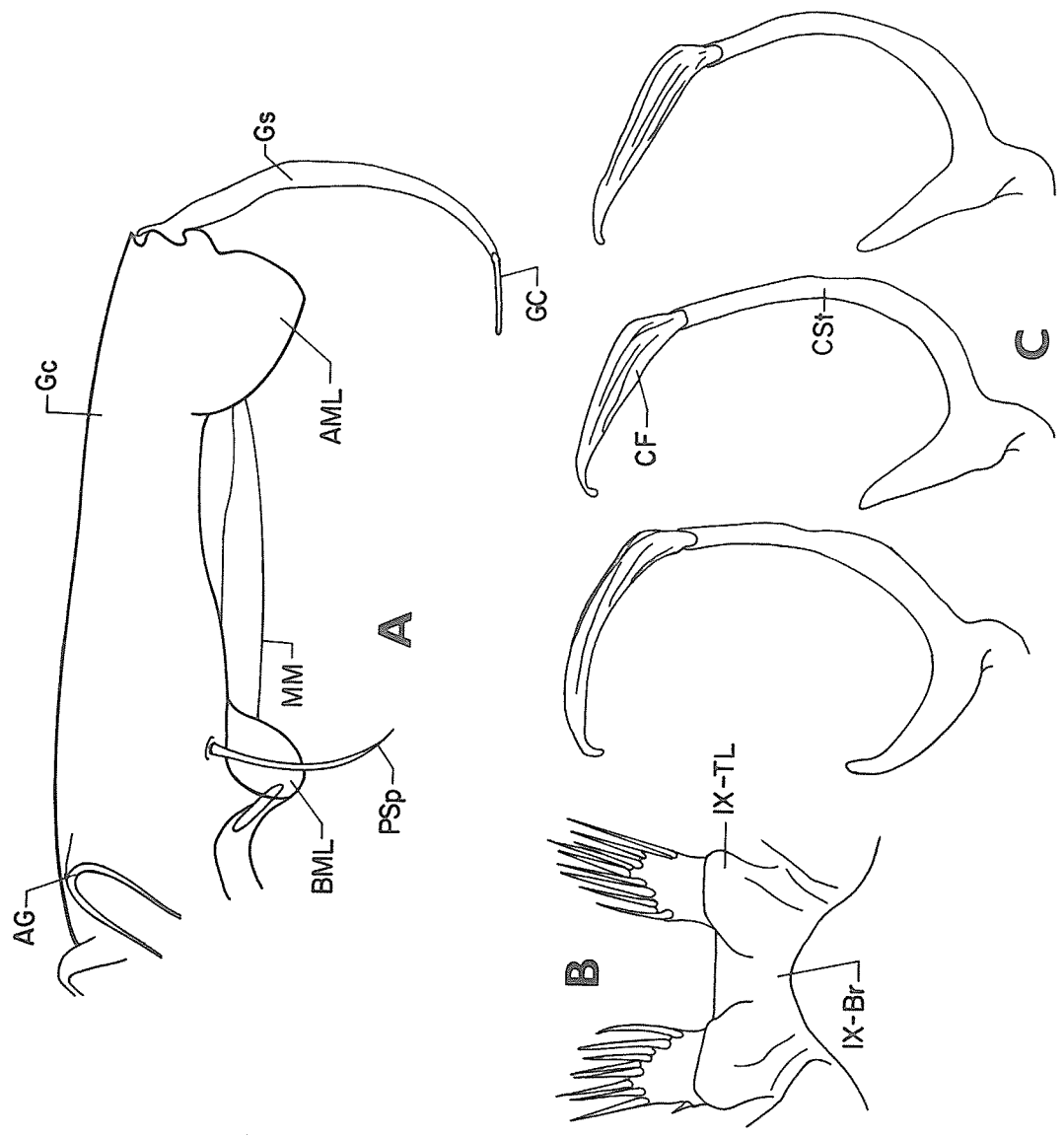


Fig. 5a,b.

Chaetotaxy of female imagos of members of the A. communis aggregate; lateral (A) and dorsal (B) views of the thorax showing location of pleural, scutal, and scutellar setae. AA, acrostichal area. Ap, anteprenotum. AcS, acrostichal setae. AnP, anterior promontory. ApS, anteprenotal setae. C-I, forecoxa. C-II, midcoxa. C-III, hindcoxa. DS, dorsolateral setae. H, halter. Hy, hypostigium. MP, mesepimeron. MS, mesothoracic spiracle. Men, mesepisternum. Msm, meron. MtS, metathoracic spiracle. MeSL, lower mesepimeral setae. MeSU, upper mesepimeral setae. MStL, lower mesepisternal setae. MStU, upper mesepisternal setae. Pa, paratergite. PA, postspiracular setae. PaS, prealar setae. PMSS, posterior medial scutal setae. Sa, supra-alar area. SA, subspiracular area. SF, scutal fossa. SS, scutellar setae, SaS, supra-alar setae, SCA, scutal angle. Scu, scutum. SFS, scutal fossa area. Stm, scutellum. W, wing.

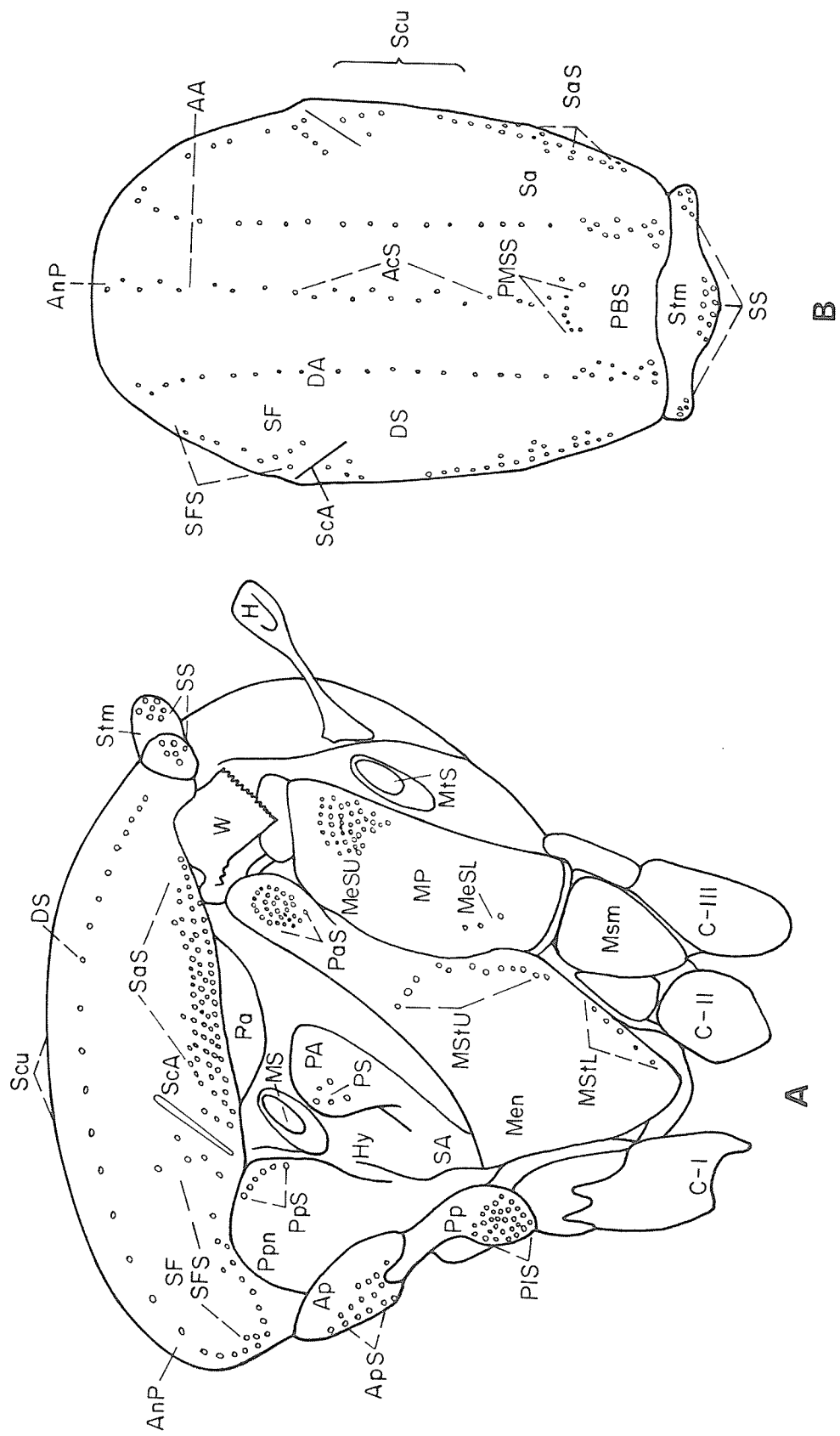


Fig. 6.

Diagrams of lateral view of ungues of foreleg and of the measurements made of an individual ungue of a female imago. Em, empodium. L₁, overall length of ungue. L₂, length of the secondary tooth. L₃, length of the primary tooth. Pt, post-tarsus. PT, primary tooth. ST, secondary tooth. Ta-1₅, 5th tarsal segment of foreleg.

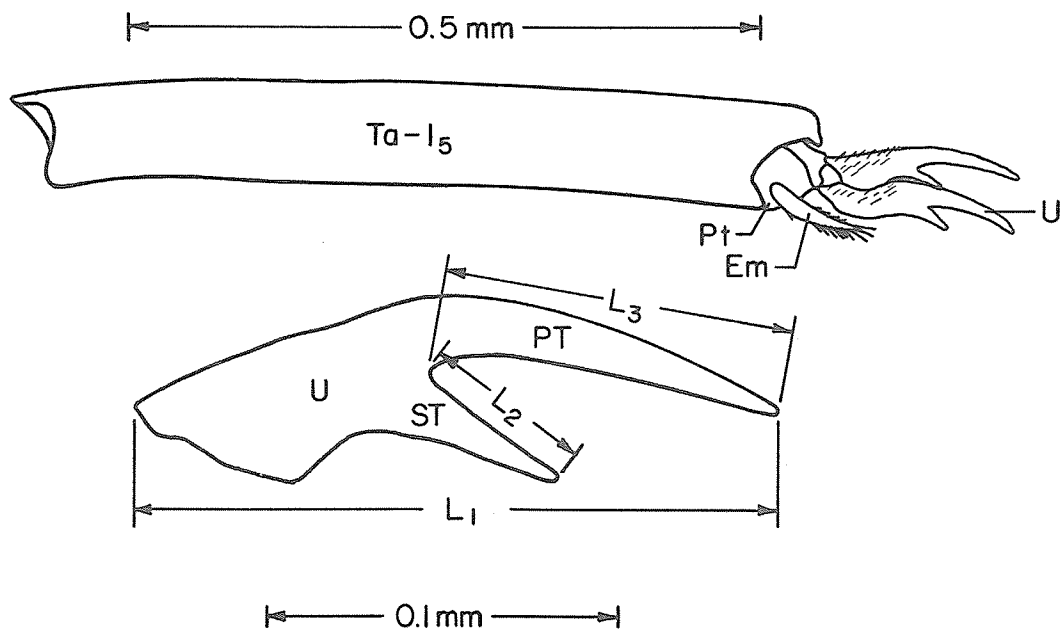


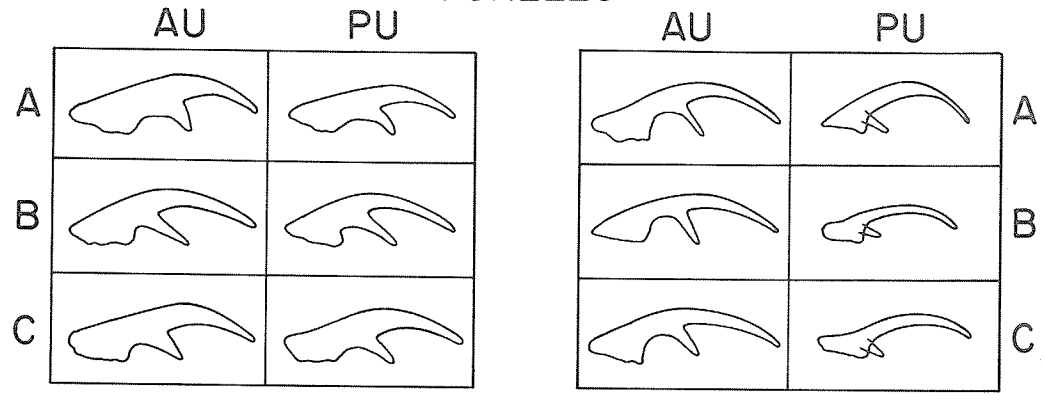
Fig. 7.

Shapes of anterior and posterior unguis (AU and PU, respectively) of female and male imagos of A. churchillensis (A), A. nevadensis (A) and A. communis (B, typical; C, atypical). Each pair of unguis drawn to scale.

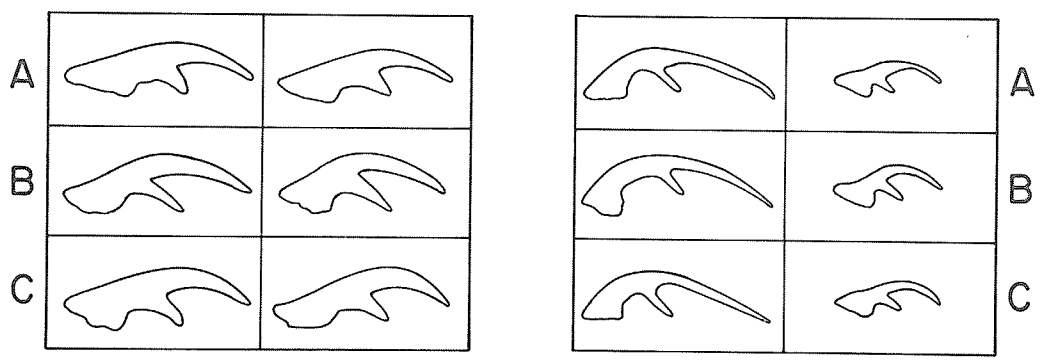
♀

♂

FORELEG



MIDLEG



HINDLEG

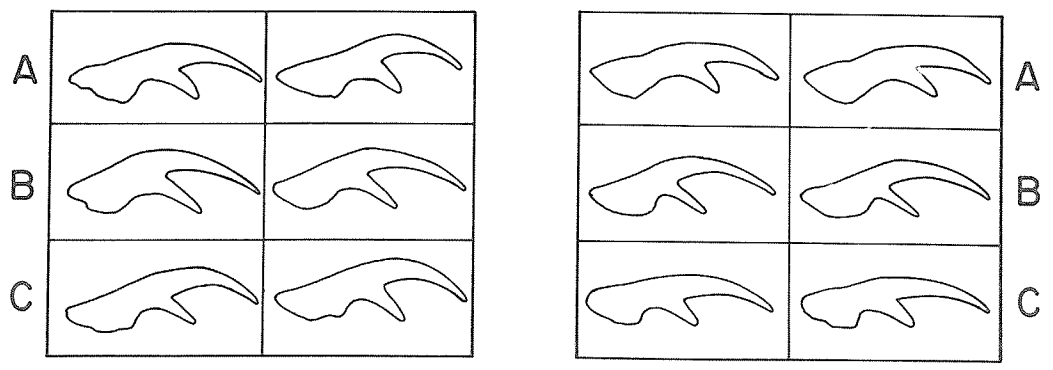


Fig. 8.

Diagram of a salivary gland of A. communis sens. lat. Ba, bifurcation of lateral acinus. Biad, bifurcation of interacinary duct. Iad, interacinary duct. La, lateral acinus. Ma, median acinus. Sd, salivary duct.

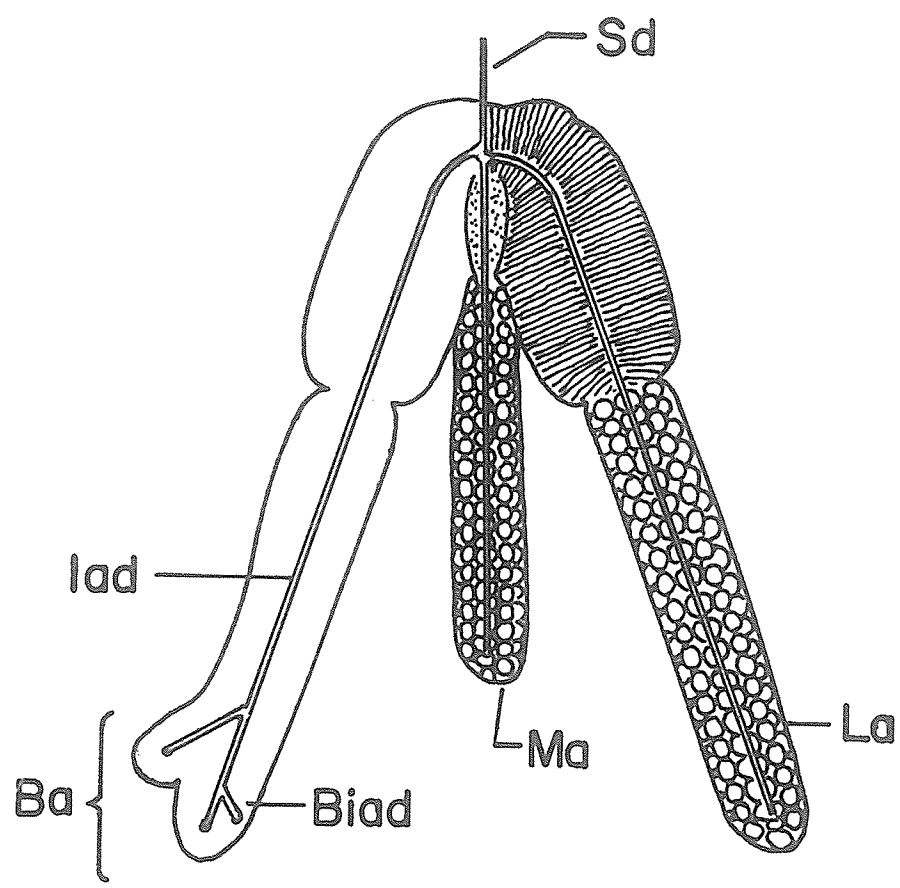


Fig. 9a-d.

Salivary glands of 6 to 7 d old female imagos of members of the A. communis aggregate: (a) A. churchillensis (160X; Sandilands Prov. For., Man.; note size of median acinus and absence of fat body material); (b) A. churchillensis (100X; St. Anne, Man.; note size of median acinus); (c) A. nevadensis (100X; Brighton, Utah; note size and bifurcation of median acinus and presence of fat body material); and (d) A. communis (100X; Fairbanks, Alaska; note size of median acinus and presence of fat body material).

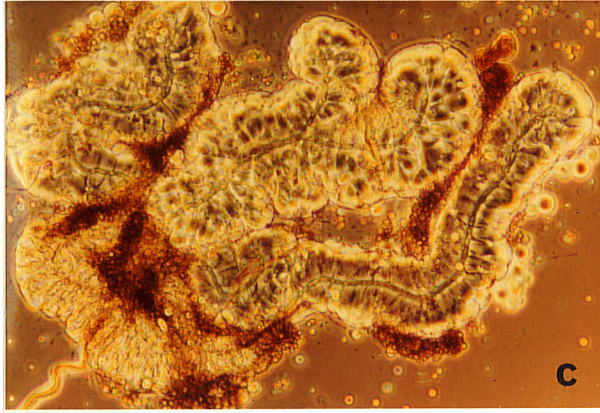
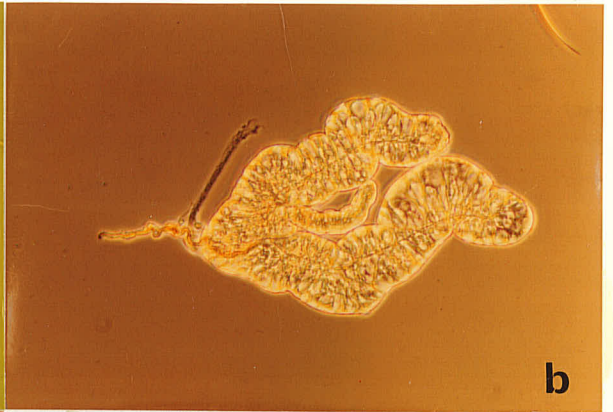


Fig. 10a-d.

Appearance of individual follicles and those of obligatorily anautogenous and facultatively autogenous female imagos of A. communis sens. str.:

(a) follicular epithelium of primary and secondary follicles (Fairbanks, Alaska; 9 d old ♀; 400X); (b) nurse cells and oocyte of a stage 2a follicle (same site and age as above; 250X); (c) group of follicles at normal resting stage, 2a, of an obligatorily anautogenous female imago (Beaverlodge, Alta.; 7 d old ♀; 100X); and (d) group of follicles of a facultatively autogenous female imago with some advanced beyond resting stage (Beaverlodge, Alta.; 10 d old ♀; 125X).

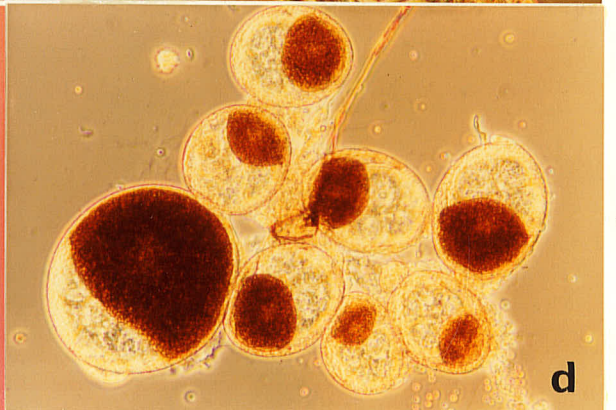


Fig. 11a-i.

Stages of follicular maturation in female imagos of members of the A. communis aggregate: (a) stage 1a (160X; 9 d old ♀, A. communis; Fairbanks, Alaska); (b) stage 1b (160X; 11 d old ♀, A. communis; Spruce Woods Prov. For., Man.); (c) stage 2a (250X; 9 d old ♀, A. communis; Fairbanks, Alaska); (d) stage 2b (250X; 9 d old ♀, A. communis; Fairbanks, Alaska); (e) stage 3a (160X; 7 d old ♀, A. churchillensis; Sandilands Prov. For., Man.); (f) stage 3b, late (160X; 7 d old ♀, A. churchillensis; Sandilands Prov. For., Man.); (g) stage 4a (100X; 7 d old ♀, A. churchillensis; St. Anne, Man.); (h) stage 4b (100X; 7 d old ♀, A. churchillensis; St. Anne, Man.); and (i) stage 5 (100X; 7 d old ♀, A. churchillensis; St. Anne, Man.).

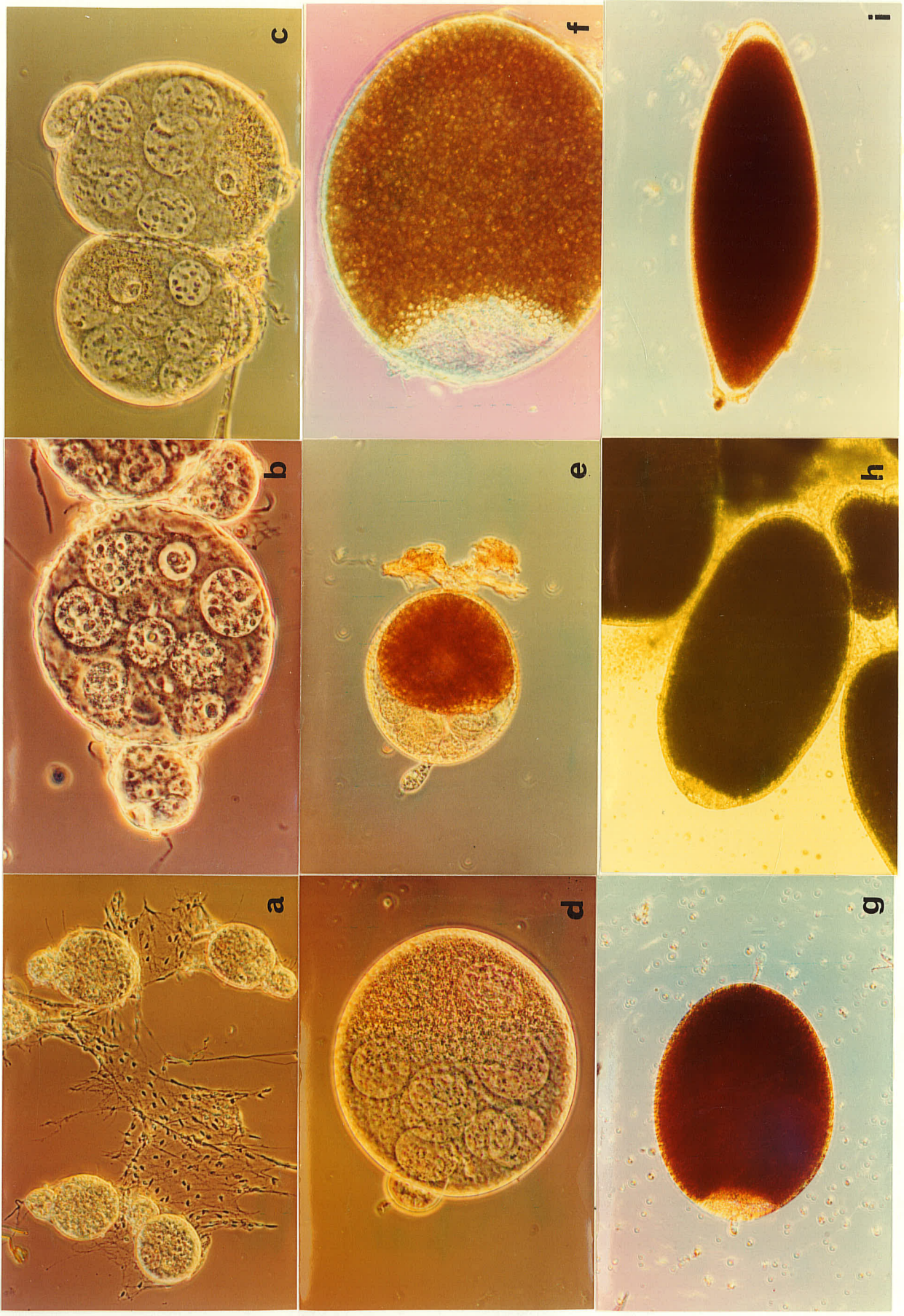


Table 1. Dimensions of eggs of A. churchillensis sp. n. (n=100) and A. communis sens. str. (n=20).

Species	Size, μ					
	Maximum Length		Dorsoventral Diameter		Ratio Length : Diameter	
	Range	$\bar{X} \pm S.E.$	Range	$\bar{X} \pm S.E.$	Range	$\bar{X} \pm S.E.$
<u>churchillensis</u>	760-920	817 \pm 30 a ¹	240-400	284 \pm 21 a	2.1-3.5	2.9 \pm 0.4 a
<u>communis</u>	804-902	863 \pm 27 b	294-353	320 \pm 18 b	2.5-3.0	2.7 \pm 0.1 b

1/ Means within a column followed by the same letter are not significantly different at the 5% level by one-way analysis of variance, unequal replication.

Table 2. Extent of variation ($\bar{x} \pm S.E.; R$) of 38 selected anatomical characters of 4th instars (n=36) of *A. churchillensis* sp. n. (Churchill, Man.), mixed *A. churchillensis* - *A. communis* (Sandilands Prov. For., Man.) and *A. communis* sens. str. (Spruce Woods Prov. For., Man.; Vermilion Bay, Ont.; and Palmer L., Wisc.).

Character ¹	Source of Larvae				
	Churchill	Sandilands	Spruce Woods	Vermilion Bay	Palmer L.
1.	1106±60 ^{2,3} (993-1203) c	1197±46 b (1127-1337)	1243±41 a (1146-1318)	1282±48 a (1184-1413)	1272±46 a (1203-1375)
2.	299±24 c (248-344)	327±25 b (287-382)	331±18 ab (306-363)	339±30 ab (306-439)	342±25 a (306-382)
3.	403±31 b (325-478)	401±33 b (344-497)	424±27 a (363-478)	417±32 a (344-478)	429±21 a (382-458)
4.	149±35 b (57-191)	150±25 b (96-191)	173±17 a (134-210)	161±24 a (96-191)	162±19 a (134-210)
5.	4.5±1.1 a (3-7)	5.4±1.4 a (3-10)	5.9±1.4 a (4-9)	5.8±1.5 a (3-10)	6.2±1.7 a (3-10)
6.	101±13 b (70-130)	107±12 ab (70-130)	105±15 b (60-130)	113±17 a (70-140)	101±15 b (70-120)
7.	6.0±1.3 b (4-8)	6.1±1.4 b (4-10)	6.1±1.1 b (5-9)	5.3±0.8 c (3-7)	6.9±1.6 a (3-11)
8.	1.0±0.2 ab (1-2)	1.0±0.2 ab (1-2)	1.0±0.0 b (1-1)	1.1±0.4 a (1-2)	1.1±0.2 ab (1-2)
9.	1.0±0.2 a (1-2)	1.1±0.2 a (1-2)	1.0±0.2 a (1-2)	1.0±0.0 a (1-1)	1.1±0.2 a (1-2)

Table 2. Cont'd.

Character ¹	Source of Larvae				
	Churchill	Sandilands	Spruce Woods	Vermilion Bay	Palmer L.
10.	1.1±0.4 (1-2) a	1.1±0.2 (1-2) a	1.2±0.4 (1-2) a	1.1±0.2 (1-2) a	1.3±0.4 (0-2) a
11.	1.1±0.2 (1-2) a	1.1±0.2 (1-2) a	1.2±0.4 (1-2) a	1.0±0.2 (1-2) a	1.1±0.3 (1-2) a
12.	1.4±0.5 (1-2) b	1.8±0.6 (1-3) a	2.1±0.6 (1-3) a	1.9±0.7 (1-3) a	1.9±0.5 (1-3) a
13.	2.0±0.4 (1-3) ab	2.0±0.3 (1-3) ab	1.8±0.4 (1-2) bc	1.7±0.5 (1-2) c	2.1±0.4 (2-3) a
14.	1.2±0.4 (1-2) a	1.0±0.2 (1-2) ab	1.1±0.3 (1-2) ab	1.0±0.0 (∅) b	1.2±0.4 (1-2) a
15.	1.1±0.3 (1-2) b	1.0±0.2 (1-2) b	1.1±0.2 (1-2) b	1.0±0.2 (1-2) b	1.3±0.5 (1-2) a
16.	1.0±0.0 (∅) a	1.0±0.0 (∅) a	1.0±0.0 (∅) a	1.0±0.2 (1-2) a	1.0±0.2 (1-2) a
17.	2.9±0.5 (2-4) ab	2.9±0.5 (2-4) b	3.0±0.5 (2-4) ab	2.9±0.5 (2-4) ab	3.1±0.6 (2-4) a
18.	1.0±0.0 (∅) a	1.0±0.0 (∅) a	1.0±0.0 (∅) a	1.0±0.0 (∅) a	1.0±0.0 (∅) a
19.	3.1±0.4 (2-4) b	3.0±0.7 (2-5) b	3.1±0.6 (3-4) b	3.1±0.4 (3-4) a	3.5±0.7 (2-5) b

Table 2. Cont'd.

Character ¹	Source of Larvae				
	Churchill	Sandilands	Spruce Woods	Vermilion Bay	Palmer L.
20.	2.0±0.0 a (∅)	2.0±0.2 a (2-3)	2.0±0.0 a (∅)	2.0±0.3 a (1-3)	2.0±0.3 a (2-3)
21.	2.0±0.2 b (1-2)	2.0±0.0 ab (∅)	2.0±0.0 ab (∅)	2.0±0.3 a (2-3)	2.0±0.0 ab (∅)
22.	1.9±0.2 b (1-2)	2.0±0.0 a (∅)	2.0±0.0 a (∅)	2.0±0.0 a (∅)	2.0±0.0 a (∅)
23.	1.9±0.2 a (1-2)	2.0±0.0 a (∅)	2.0±0.0 a (∅)	2.0±0.4 a (1-4)	2.0±0.0 a (∅)
24.	2.0±0.2 a (1-2)	1.9±0.2 a (1-2)	1.9±0.3 a (1-2)	1.9±0.2 a (1-2)	2.0±0.0 a (∅)
25.	1.0±0.0 a (∅)	1.0±0.0 a (∅)	1.0±0.0 a (∅)	1.0±0.0 a (∅)	1.0±0.0 a (∅)
26.	947±62 c (802-1070)	992±80 b (898-1280)	1083±59 a (955-1203)	1053±51 a (936-1165)	1083±46 a (974-1184)
27.	334±33 c (287-420)	362±24 b (305-420)	392±21 a (344-439)	393±23 a (344-439)	386±16 a (363-420)
28.	51±18 b (10-90)	59±20 b (30-110)	85±24 a (30-130)	64±24 b (30-130)	65±21 b (30-110)
29.	21.0±2.5 b (16-25)	20.0±2.2 bc (16-24)	22.1±2.0 a (18-26)	21.0±2.5 b (16-26)	19.4±1.4 c (17-22)

Table 2. Cont'd.

Character ¹	Source of Larvae				
	Churchill	Sandilands	Spruce Woods	Vermilion Bay	Palmer L.
30.	7.5±1.4 a (5-11)	7.2±1.1 ab (5-9)	6.7±1.1 bc (5-9)	6.4±1.2 c (4-10)	7.6±1.4 a (5-10)
31.	55±17 b (40-100)	56±9 b (40-80)	64±9 a (40-80)	60±10 ab (40-80)	50±12 c (30-60)
32.	54±10 c (32-70)	59±9 ab (42-75)	59±8 ab (38-72)	57±9 bc (38-72)	62±8 a (42-73)
33.	8.5±1.3 b (6-12)	8.6±1.2 b (6-11)	7.9±1.1 bc (6-11)	7.6±1.2 c (5-10)	10.3±1.9 a (6-15)
34.	417±39 c (344-497)	407±33 c (401-535)	488±29 a (439-535)	476±22 a (420-535)	433±27 b (382-516)
35.	230±32 c (153-306)	250±40 b (172-344)	260±33 b (191-344)	290±50 a (210-382)	252±34 b (191-344)
36.	554±96 c (306-649)	646±72 b (439-840)	686±34 a (611-745)	681±79 a (516-802)	632±63 b (478-764)
37.	359±30 c (306-420)	390±24 b (344-478)	408±24 a (363-478)	414±37 a (248-458)	420±33 a (325-478)
38.	212±30 c (153-248)	223±34 bc (153-287)	262±34 a (191-344)	245±86 ab (153-554)	203±39 c (115-287)

Table 2. Cont'd.

- 1/ (1) Maximum width of head capsule. (2) Distance between seta 5-C. (3) Length of antenna (base to seta 1-A to apex). (4) Length of antenna (base to seta 1-A). (5) Number of branches of seta 1-A. (6) Length of seta 4-A. (7) Number of branches of seta 7-C. (8) Number of branches of right seta 5-C. (9) Number of branches of left seta 5-C. (10) Number of branches of right seta 6-C. (11) Number of branches of left seta 6-C. (12) Number of branches of seta 10-C. (13) Number of branches of seta 1-P. (14) Number of branches of seta 2-P. (15) Number of branches of seta 3-P. (16) Number of branches of seta 4-P. (17) Number of branches of seta 5-P. (18) Number of branches of seta 6-P. (19) Number of branches of seta 7-P. (20) Number of branches of seta 6-I. (21) Number of branches of seta 6-II. (22) Number of branches of seta 6-III. (23) Number of branches of seta 6-IV. (24) Number of branches of seta 6-V. (25) Number of branches of seta 6-VI. (26) Length of siphon (measured along pectin). (27) Width of siphon (measured across base). (28) Distance between insertions of apical pectin tooth and seta 1-S. (29) Number of pectin teeth. (30) Number of branches of seta 1-S. (31) Length of seta 2-S. (32) Number of comb scales. (33) Number of branches of seta 3-VIII. (34) Length of saddle (measured across centro-lateral area). (35) Width of saddle (measured across centro-lateral area). (36) Length of segment X (measured across centro-lateral area of saddle). (37) Width of segment X (measured across centro-lateral area of saddle). (38) Length of seta 1-X.
- 2/ Measurable characteristics expressed in micra. ^{3/} Means within a row followed by the same letter are not significant at the 5% level by Duncan's multiple range test.

Table 3. Measurements ($\bar{x} \pm S.E.$, R; n=20) of selected male genitalic structures of A. nevadensis st. n. (Brighton, Utah), A. communis sens. str. (Spruce Woods Prov. For., Man.), and A. churchillensis sp. n. (Churchill, Man.).

	Species		
	<u>nevadensis</u>	<u>communis</u>	<u>churchillensis</u>
Gonocoxite Length, μ .	507 \pm 20 b ¹ (480-540)	524 \pm 33 b (450-600)	579 \pm 49 a (510-600)
Gonocoxite Width, μ .	144 \pm 14 a (120-165)	116 \pm 17 b (90-150)	138 \pm 26 a (105-210)
Gonostylus Length, μ .	192 \pm 6 b (180-201)	195 \pm 14 b (168-222)	205 \pm 15 a (180-225)
Gonostylar Claw Length, μ .	39 \pm 3 b (36-45)	46 \pm 4 a (42-54)	47 \pm 8 a (33-45)
Parabasal Seta Length, μ .	98 \pm 13 a (82-144)	86 \pm 13 b (50-110)	92 \pm 13 ab (76-137)
IX-Tergal Lobe Setae, No.	4.3 \pm 0.7 b (3-6)	5.7 \pm 1.2 a (3-8)	5.9 \pm 1.8 a (4-11)

^{1/} Means within a row followed by the same letter are not significantly different at the 5% level by one-way analysis of variance and Duncan's multiple range test.

Table 4. Numbers of thoracic setae on the pleuron and tergum of female imagos (n=20) of members of the Aedes communis aggregate.

Species	PLEURAL SETAE ¹							
	PpS	PS	PaS	MeSU	MeSL	MSTU	MSTL	
<u>nevadensis</u>	9.7±2.1 a ^{2,3} (6-15)	4.6±1.3 a (3-8)	17.3±2.9 b (12-23)	21.7±4.9 a (14-33)	3.6±1.1 a (1-6)	6.3±1.2 a (5-8)	8.7±1.8 a (6-13)	
<u>communis</u>	8.3±1.3 b (6-11)	6.9±1.6 c (5-10)	19.2±2.5 c (14-24)	18.9±4.7 b (12-29)	2.1±0.9 b (0-4)	5.3±1.0 b (4-7)	6.5±1.3 b (4-10)	
<u>churchillensis</u>	8.8±1.9 ab (6-13)	5.8±1.6 b (3-9)	15.7±3.0 a (10-20)	15.3±3.6 c (10-22)	1.8±1.0 b (0-4)	4.4±0.9 c (3-6)	6.7±1.7 b (4-10)	
TERGAL SETAE ⁴								
	SaS	SFS	AcS	PMSS	DS	SS		
<u>nevadensis</u> 1.4±0.1 a ⁵ (1.2-1.6)	83.2±10.1 ab (65-106)	28.7±3.9 a (21-38)	20.9±2.3 a (16-25)	7.5±2.2 a (4-12)	61.0±8.4 a (48-78)	33.1±3.6 a (27-42)		
<u>communis</u> 1.4±0.3 a (1.2-1.7)	89.7±16.4 a (62-139)	27.4±6.2 ab (14-40)	21.1±5.2 a (10-36)	5.1±0.8 b (4-6)	53.7±9.0 ab (35-70)	32.2±6.0 a (21-45)		
<u>churchillensis</u> 1.4±0.1 a (1.3-1.5)	79.1±11.4 b (50-101)	25.8±5.3 b (17-37)	21.8±2.7 a (16-37)	7.6±1.6 a (4-12)	50.0±6.3 b (36-68)	31.3±4.0 a (25-40)		

Table 4. Cont'd.

1/ Pleural setae: PpS, postpronotal; PS, postspiracular; PaS, prealar; MeSU, upper mesepimeral; MeSL, lower mesepimeral; MStU, upper mesepisternal; and MStL, lower mesepisternal. 2/ $\bar{x} \pm S.E., R.$ 3/ Means within a column followed by the same letter are not significant at the 5% level by one-way analysis of variance and Duncan's multiple range test. 4/ Tergal setae: SaS, supra-alar; SFS, scutal fossal; ACS, acrostichal; PMSS, posterior medial scutal; and SS, scutellar. 5/ Thoracic length, mm.

Table 5. Variation ($\bar{x} \pm s, E, R$) in overall length of anterior and posterior ungues of the right legs of male imagos ($n=20$) of A. communis sens. str., A. churchillensis sp. n. and A. nevadensis st. n.

Population ¹	Foreleg Ungues		Midleg Ungues		Hindleg Ungues	
	Ant.	Post.	Ant.	Post.	Ant.	Post.
A	140±8 ^{2,3} (114-154)	179±8 ^a (172-193)	116±7 ^a (104-135)	209±17 ^a (172-258)	97±5 ^a (86-104)	103±4 ^a (94-109)
B	114±4 ^b (78-91)	149±5 ^{bc} (109-182)	89±4 ^b (47-109)	167±5 ^b (141-208)	72±4 ^{bc} (47-96)	80±3 ^b (50-104)
C	114±8 ^b (91-125)	150±9 ^b (135-167)	94±7 ^b (78-104)	167±12 ^b (146-187)	77±8 ^b (55-89)	80±6 ^b (70-91)
D	110±11 ^b (94-135)	139±16 ^d (125-177)	88±13 ^b (63-104)	140±18 ^d (115-185)	71±10 ^{bc} (44-83)	75±11 ^b (50-94)
E	112±3 ^b (78-130)	146±3 ^{bcd} (130-138)	87±3 ^b (63-104)	157±3 ^c (133-174)	69±2 ^c (50-81)	78±2 ^b (65-89)
F	108±3 ^b (102-115)	141±4 ^{bcd} (135-148)	88±4 ^b (81-96)	151±5 ^c (141-156)	75±4 ^{bc} (70-86)	75±4 ^b (68-81)

1/ Populations A, B, and C are A. communis from Vienna, Mich., Spruce Woods Prov. For., Man., and Vermilion Bay, Ontario, respectively; D is mixed A. communis - A. churchillensis from Sandilands Prov. For., Man.; E is A. churchillensis from Churchill, Man.; and F is A. nevadensis from Brighton, Utah. 2/ Means within a column followed by the same letter are not significantly different at the 5% level by one-way analysis of variance and Duncan's multiple range test. 3/ All values expressed in micra.

Table 6. Variation ($\bar{x} \pm S.E., R.$) in length of primary tooth of anterior and posterior ungues of the right legs of male imagos ($n=20$) of A. communis sens. str., A. churchillensis sp. n. and A. nevadensis st. n.

Population ¹	Foreleg Ungues		Midleg Ungues		Hindleg Ungues	
	Ant.	Post.	Ant.	Post.	Ant.	Post.
A	89±5 ^{2,3} (78-96)	93±10 a (86-102)	60±3 a (55-65)	128±15 a (107-177)	47±5 a (34-52)	51±3 a (44-57)
B	76±2 b (57-89)	80±3 b (65-96)	49±2 b (26-63)	100±3 bc (78-125)	40±3 b (26-63)	44±2 b (29-57)
C	73±7 b (57-83)	76±5 bc (68-83)	51±3 b (44-57)	101±12 b (65-115)	42±5 b (31-50)	43±5 b (34-50)
D	72±10 b (60-94)	72±11 c (57-94)	42±7 c (31-50)	85±16 d (55-112)	38±4 cd (26-42)	36±5 c (26-47)
E	72±2 b (57-81)	72±2 c (60-83)	44±2 c (26-52)	94±3 bc (63-125)	31±3 d (24-27)	35±1 c (26-42)
F	65±3 c (55-78)	77±4 bc (70-83)	44±3 c (39-52)	92±5 cd (83-99)	36±2 c (31-39)	36±3 c (31-39)

1,2,3/ See respective footnotes, Table 5.

Table 7. Variation ($\bar{x} \pm S.E., R.$) in length of secondary tooth of anterior and posterior ungues of the right legs of male imagos ($n=20$) of A. communis sens. str., A. churchillensis sp. n. and A. nevadensis st. n.

Population ¹	Foreleg Ungues		Midleg Ungues		Hindleg Ungues	
	Ant.	Post.	Ant.	Post.	Ant.	Post.
A	22±2 ^{2,3} (18-26)	32±3 ^a (26-37)	25±3 ^a (21-29)	31±6 ^a (24-39)	21±3 ^a (18-26)	21±2 ^a (18-26)
B	19±1 ^b (16-50)	30±1 ^b (16-37)	23±1 ^b (16-29)	28±2 ^{ab} (13-39)	19±1 ^b (11-26)	20±1 ^a (11-29)
C	19±4 ^b (13-26)	27±4 ^c (21-31)	25±4 ^a (16-29)	27±5 ^b (18-34)	20±3 ^{ab} (13-24)	21±3 ^a (16-26)
D	19±4 ^b (13-24)	24±4 ^d (18-29)	21±4 ^{bc} (13-26)	23±5 ^c (16-37)	16±3 ^c (11-21)	17±3 ^b (11-21)
E	18±1 ^b (13-21)	25±1 ^{cd} (18-31)	19±1 ^c (13-29)	25±1 ^{bc} (16-34)	14±1 ^d (11-16)	16±2 ^b (13-21)
F	19±3 ^b (16-26)	25±2 ^{cd} (21-29)	20±4 ^c (11-26)	26±3 ^{bc} (24-31)	15±1 ^c (13-16)	15±1 ^b (13-16)

1,2,3/ See respective footnotes, Table 5.

Table 8. Variation ($\bar{x} \pm S.E., R.$) in ratio of secondary to primary tooth length of anterior and posterior ungues of the right legs of male imagos (n=20) of A. communis sens. str., A. churchillensis sp. n. and A. nevadensis st. n.

Population ¹	Foreleg Ungues		Midleg Ungues		Hindleg Ungues	
	Ant.	Post.	Ant.	Post.	Ant.	Post.
A	0.24±0.03 b ² (0.14-0.30)	0.34±0.03 b (0.29-0.39)	0.43±0.03 b (0.33-0.48)	0.24±0.04 b (0.18-0.29)	0.45±0.07 ab (0.35-0.64)	0.41±0.05 c (0.35-0.53)
B	0.25±0.01 b (0.18-0.32)	0.37±0.01 a (0.24-0.41)	0.47±0.02 ab (0.30-0.70)	0.27±0.01 a (0.13-0.36)	0.48±0.02 a (0.33-0.63)	0.46±0.02 ab (0.33-0.61)
C	0.26±0.04 b (0.18-0.33)	0.35±0.04 ab (0.28-0.41)	0.49±0.05 a (0.33-0.56)	0.27±0.04 a (0.19-0.33)	0.48±0.06 a (0.31-0.58)	0.47±0.07 a (0.32-0.63)
D	0.26±0.04 b (0.19-0.33)	0.34±0.03 b (0.27-0.39)	0.46±0.04 ab (0.39-0.59)	0.27±0.03 a (0.20-0.33)	0.48±0.09 a (0.31-0.62)	0.47±0.08 a (0.31-0.60)
E	0.26±0.01 b (0.17-0.36)	0.35±0.01 a (0.28-0.48)	0.44±0.02 b (0.28-0.61)	0.26±0.01 ab (0.20-0.37)	0.48±0.02 b (0.31-0.67)	0.45±0.01 abc (0.33-0.57)
F	0.29±0.05 a (0.23-0.42)	0.33±0.02 b (0.30-0.37)	0.44±0.07 b (0.27-0.56)	0.28±0.02 a (0.25-0.33)	0.42±0.03 b (0.39-0.50)	0.42±0.03 bc (0.39-0.50)

1,2/ See respective footnotes, Table 5.

Table 9. Variation ($\bar{x} \pm S.E., R.$) in overall length of anterior and posterior ungues of the right legs of female imagos (n=20) of A. communis sens. str., A. churchillensis sp. n. and A. nevadensis st. n.

Population ¹	Foreleg Ungues		Midleg Ungues		Hindleg Ungues	
	Ant.	Post.	Ant.	Post.	Ant.	Post.
A	115±10 a ^{2,3} (99-135)	120±9 a (104-138)	109±8 a (96-127)	127±10 a (101-136)	101±10 a (83-128)	104±10 a (87-148)
B	80±1 cd (73-89)	85±1 d (77-90)	72±1 d (68-89)	82±1 d (73-89)	68±2 c (28-73)	73±1 d (65-79)
C	85±7 bc (76-96)	90±7 bc (79-102)	80±7 bc (67-92)	84±7 cd (67-99)	74±6 b (63-88)	77±6 bc (71-92)
D	79±9 d (64-97)	86±8 cd (74-102)	77±8 c (64-92)	82±8 d (68-94)	72±7 b (60-85)	76±7 cd (65-87)
E	83±2 bcd (56-95)	92±1 b (78-97)	81±2 b (60-90)	88±1 b (72-97)	76±1 b (60-82)	81±1 b (72-88)
F	88±5 b (82-97)	91±5 b (84-100)	84±5 b (74-90)	87±6 bc (76-94)	77±4 b (72-85)	79±4 b (72-86)

1,2,3/ See respective footnotes, Table 5.

Table 10. Variation ($\bar{x} \pm S.E., R.$) in length of primary tooth of anterior and posterior ungues of the right legs of female imagos (n=20) of A. communis sens. str., A. churchillensis sp. n. and A. nevadensis st. n.

Population ¹	Foreleg Ungues		Midleg Ungues		Hindleg Ungues	
	Ant.	Post.	Ant.	Post.	Ant.	Post.
A	57±4 ^{2,3} a (51-64)	62±7 a (55-77)	52±4 a (45-59)	57±6 a (48-72)	47±5 a (42-58)	49±6 a (42-63)
B	43±1 c (36-49)	45±1 c (40-52)	41±1 b (30-48)	43±1 b (34-50)	34±1 c (22-39)	36±1 c (31-40)
C	46±4 b (41-52)	49±4 b (44-54)	42±3 b (34-47)	45±5 b (36-58)	37±4 b (29-44)	39±5 b (31-50)
D	41±6 cd (32-52)	43±6 d (34-56)	37±6 c (29-48)	39±6 c (31-52)	34±5 c (27-46)	36±6 c (30-46)
E	32±1 e (26-45)	44±1 cd (37-50)	35±1 d (26-42)	39±1 c (30-46)	31±1 d (20-36)	33±1 d (20-38)
F	40±3 d (34-46)	42±4 d (34-47)	39±3 c (32-42)	39±3 c (32-46)	34±3 c (28-37)	35±3 cd (28-38)

1,2,3/ See respective footnotes, Table 5.

Table 11. Variation ($\bar{x} \pm s$, E., R.) in length of secondary tooth of anterior and posterior ungues of the right legs of female imagos (n=20) of A. communis sens. str., A. churchillensis sp. n. and A. nevadensis sp. n.

Population ¹	Foreleg Ungues		Midleg Ungues		Hindleg Ungues	
	Ant.	Post.	Ant.	Post.	Ant.	Post.
A	21±2 a ^{2,3} (19-24)	21±2 a (19-26)	22±3 a (18-26)	22±2 a (18-24)	21±2 a (18-24)	21±3 a (16-24)
B	21±2 a (12-24)	22±1 a (12-26)	21±1 a (15-25)	22±1 a (15-26)	19±1 b (8-22)	20±1 b (11-23)
C	20±3 a (10-23)	22±2 a (18-26)	21±4 a (8-25)	21±2 a (15-26)	19±2 b (14-22)	20±2 ab (16-25)
D	18±4 b (13-24)	19±4 b (13-25)	19±5 b (11-26)	19±5 b (11-26)	17±4 c (10-26)	17±4 c (11-26)
E	16±1 c (13-20)	16±1 c (14-21)	16±1 c (9-18)	17±1 c (12-21)	15±1 d (8-20)	15±1 d (11-19)
F	16±2 c (13-18)	16±1 c (13-18)	16±2 c (12-19)	16±2 c (11-19)	16±2 cd (13-25)	16±2 cd (13-18)

1,2,3/ See respective footnotes, Table 5.

Table 12. Variation ($\bar{x} \pm s$, E., R.) in ratio of secondary to primary tooth length of anterior and posterior unguis of the right legs of female imagos (n=20) of A. communis sens. str., A. churchillensis sp. n. and A. nevadensis st. n.

Population ¹	Foreleg Ungues		Midleg Ungues		Hindleg Ungues	
	Ant.	Post.	Ant.	Post.	Ant.	Post.
A	0.37±0.03 e ² (0.32-0.44)	0.35±0.04 d (0.25-0.44)	0.42±0.03 b (0.36-0.47)	0.39±0.03 d (0.33-0.44)	0.44±0.04 d (0.34-0.50)	0.43±0.06 c (0.34-0.54)
B	0.50±0.01 a (0.32-0.64)	0.49±0.02 a (0.30-0.65)	0.51±0.02 a (0.34-0.60)	0.53±0.02 a (0.32-0.60)	0.55±0.02 a (0.36-0.67)	0.54±0.02 a (0.34-0.68)
C	0.44±0.06 bc (0.22-0.51)	0.44±0.04 b (0.38-0.52)	0.49±0.08 a (0.20-0.56)	0.48±0.04 b (0.39-0.55)	0.51±0.04 b (0.43-0.60)	0.51±0.03 a (0.46-0.57)
D	0.45±0.05 b (0.37-0.58)	0.42±0.05 b (0.31-0.50)	0.49±0.06 a (0.34-0.57)	0.49±0.07 b (0.34-0.61)	0.49±0.08 bc (0.33-0.63)	0.47±0.07 b (0.34-0.59)
E	0.41±0.01 cd (0.30-0.56)	0.38±0.08 c (0.33-0.49)	0.44±0.02 b (0.25-0.56)	0.44±0.01 c (0.36-0.53)	0.47±0.02 bcd (0.33-0.60)	0.46±0.01 bc (0.38-0.65)
F	0.38±0.04 de (0.33-0.47)	0.37±0.04 cd (0.25-0.44)	0.42±0.05 b (0.31-0.50)	0.41±0.05 cd (0.31-0.50)	0.46±0.04 cd (0.36-0.54)	0.46±0.05 bc (0.36-0.55)

1,2/ See respective footnotes, Table 5.

Table 13. List of species of the genus Aedes, subgenus Ochlerotatus in which autogenous female imagos have been reported.

Species	References
<u>campestris</u> Dyar & Knab	63, 215.
<u>caspius</u> (Pallas)	60, 67 <u>In</u> 318, 256, 258.
<u>communis</u> (Degeer)	11, 12, 13, 14, 16, 39, 63, 64, 181, 184, 215, 318.
<u>detritus</u> (Haliday)	67 and 348 <u>In</u> 318.
<u>dorsalis</u> (Meigen)	63, 160.
<u>flavescens</u> (Muller)	3, 63.
<u>hexodontus</u> Dyar	6, 318.
<u>impiger</u> (Walker)	76, 77, 78, 215, 318.
<u>melanimon</u> Dyar	63.
<u>nigripes</u> (Zetterstedt)	76, 77, 78, 215, 318.
<u>nigromaculis</u> (Ludlow)	63.
<u>niphadopsis</u> Dyar & Knab	63.
<u>punctor</u> Kirby	3, 63.
<u>rempeli</u> Vockeroth	318, 319.
<u>schizopinax</u> Dyar	63.
<u>sollicitans</u> (Walker)	229.
<u>taeniorhynchus</u> (Wiedemann)	229, 230, 231, 234, 235, 268.

Table 14. The occurrence of obligate anautogeny, facultative autogeny and obligate autogeny in populations of A. communis sens. str., A. churchillensis sp. n. and A. nevadensis st. n.

Species	Locality	Year	No. ♀♀ Dissected	Autogeny	
				Anautogeny % Oblig.	Autogeny % Fac. % Oblig.
<u>communis</u>	Banff Nat. Park, Alta.	1970	17	100	
	Beaverlodge, Alta.	1972	172	97.1	2.9
	Demmitt, Alta.	1972	80	100	
	Elk Island Prov. Park, Alta.	1970	20	100	
	Obed, Alta.	1970	62	100	
	Whitecourt, Alta.	1972	316	100	
	Fort St. John, B.C.	1972	200	100	
	Baker's Narrows, Man.	1971	54	100	
	Churchill(C1), Man.	1970	24	100	
	Churchill(c2), Man.	1970 1971	11 40	100 100	
	Churchill(C9), Man.	1971	16	100	
	Churchill(C10), Man.	1971	8	100	
	Churchill(C10A), Man.	1970	10	100	
	Churchill(C17), Man.	1970	40	100	
	Churchill(C36), Man.	1971	4	100	

Table 14. Cont'd.

Species	Locality	Year	No. ♀♀ Dissected	Anautogeny		Autogeny	
				% Oblig.	% Fac.	% Oblig.	
<u>communis</u>	Churchill(C38), Man.	1971	2	100			
	Churchill(C40), Man.	1971	6	100			
	Churchill(C42), Man.	1971	2	100			
	Dawson L., Man.	1971	151	100			
	Duck Mtn. Prov. Park, Man.	1971	23	100			
	Falcon L., Man.	1971	10	100			
	Glenlea, Man.	1970	6	100			
	McMunn, Man.	1971	55	100			
	Red Rock L., Man.	1971	76	100			
	Riding Mtn. Nat. Park, Man.	1971	40	100			
	Sandilands(S2) Prov. For., Man.	1971	5	100			
	Sandilands(S3) Prov. For., Man.	1971	5	100			
	Sandilands(S6) Prov. For., Man.	1971	6	100			
	Sandilands(S7) Prov. For., Man.	1971 1972	50 78	98 100		2.0	
	Sandilands(S17A) Prov. For., Man.	1971 1972	71 22	100 100			
	Sandilands(S17) Prov. For., Man.	1971 1972	9 20	100 100			
Sandilands(S18) Prov. For., Man.	1971 1972	39 28	100 100				

Table 14. Cont'd.

Species	Locality	Year	No. ♀♀ Dissected	Anautogeny		Autogeny	
				% Oblig.	% Fac.	% Oblig.	
<u>communis</u>	Sandilands(S19) Prov. For., Man.	1972	23	100			
	Sandilands(S30) Prov. For., Man.	1971	7	100			
	Sandilands(S37) Prov. For., Man.	1971	2	100			
	Sandilands(S101) Prov. For., Man.	1971	1	100			
	Sandilands(S112) Prov. For., Man.	1971	35	100			
	Spruce Siding, Man.	1971	3	100			
	Spruce Woods Prov. For., Man.	1970 1971	210 206	100 99.5		0.5	
	St. Anne, Man.	1971 1972	106 50	100 98		2.0	
	Telford, Man.	1971	173	100			
	Thompson, Man.	1971	437	100			
	Pearl, Ont.	1970	9	100			
	Vermilion Bay, Ont.	1970 1971	329 225	99.7 100		0.3	
	Fairbanks, Alaska.	1972	61	100			
	Caples L., Calif.	1972	30	100			
	Echo Summit, Calif.	1972	25	100			
	Lewiston, Mich.	1970	15	100			
	Vienna(V15), Mich.	1970	82	98.8		1.2	
	Vienna(V491), Mich.	1970	33	97		3.0	

Table 14. Cont'd.

Species	Locality	Year	No. ♀♀ Dissected	Anautogeny		Autogeny	
				% Oblig.	% Fac.	% Oblig.	
<u>communis</u>	Land O'Lakes, Wisc.	1970	113	100			
	Palmer L., Wisc.	1970	120	99.2	0.8		
	Lone Tree, Wyo.	1971	25	100			
<u>nevadensis</u>	Brighton, Utah	1972	240	99.6	0.4		
<u>churchillensis</u>	Beaverlodge, Alta.	1972	69				100
	Churchill(C0), Man.	1971	32				100
	Churchill(C1), Man.	1970	1				100
	Churchill(C2), Man.	1971	50				100
	Churchill(C10), Man.	1971	21				100
	Churchill(C10A), Man.	1970	1				100
	Churchill(C17), Man.	1970 1971	1555 386				100 100
	Churchill(35), Man.	1971	7				100
	Churchill(C36), Man.	1971	9				100
	Churchill(C37), Man.	1971	7				100
	Churchill(C38), Man.	1971	27				100
	Churchill(C40), Man.	1971	21				100
	Churchill(C41), Man.	1971	20				100

Table 14. Cont'd.

Species	Locality	Year	No. ♀♀ Dissected	Anautogeny		Autogeny	
				% Oblig.	% Fac.	% Oblig.	
<u>churchillensis</u>	Churchill(C42) Man.	1971	26				100
	Red Rock L., Man.	1971	5				100
	Sandilands(S2) Prov. For., Man.	1971	5				100
	Sandilands(S6) Prov. For., Man.	1971	14				100
	Sandilands(S7) Prov. For., Man.	1971	83				100
		1972	74				100
	Sandilands(S30) Prov. For., Man.	1971	17				100
	Sandilands(S37) Prov. For., Man.	1971	10				100
	Sandilands(S101) Prov. For., Man.	1971	1				100
	Sandilands(S112) Prov. For., Man.	1971	9				100
	St. Anne, Man.	1971	112				100
		1972	14				100
Telford, Man.	1971	2				100	

Table 15. Mating success of A. communis sens. str. and A. churchillensis sp. n. in various combinations of sex ratio, cage size, and period of confinement.

Set-up	Species	Source	Sex Ratio (♂:♀)	Cage Size (cm)	Confinement Period (d)	Females Mated (%)
1.	<u>communis</u>	Beaverlodge, Alta.	100:100	25x25x25	6	0
2.	"	Whitecourt, Alta.	"	"	"	0
3.	"	"	"	"	6-7	0
4.	"	Fort St. John, B.C.	50:50	"	5	0
5.	"	"	"	"	8	0
6.	"	Dorothy L., Man.	70:63	"	7	0
7.	"	Spruce Woods Prov. For., Man.	12:20	"	10	0
8.	"	Thompson, Man.	100:100	"	11	0
9.	"	"	"	50x50x50	15-16	4
10.	"	"	"	25x25x50	12-15	0
11.	"	Palmer L., Wisc.	ca. 2500:2500	120x120x210	7-13	0
12.	<u>churchillensis</u>	Churchill, Man.	24:17	15x15x15	11	15
13.	"	"	50:50	"	8-9	36
14.	"	"	18:4	"	"	66
15.	"	"	100:100	25x25x25	"	54
16.	"	"	27:50	"	14	50
17.	"	"	101:67	"	10-11	30
18.	"	"	80:56	"	7	50

Table 15. Cont'd.

Set-up	Species	Source	Sex Ratio (♂:♀)	Cage Size (cm)	Confinement Period (d)	Females Mated (%)
19.	<u>churchillensis</u>	Churchill, Man.	291:127	50x50x50	8-9	60
20.	"	"	440:175	"	10-11	10
21.	"	"	ca. 2500; 2500	120x120x210	1-2 3-4 8-9	0 28 83
22.	<u>communis</u> / <u>churchillensis</u>	Thompson♀♀/ Churchill♂♂	50:50	25x25x25	9	11
23.	"	Thompson♂♂/ Churchill♀♀	"	"	9	0
24.	<u>communis</u> / <u>churchillensis</u> ₁	St. Anne, Man.	50:50 ²	15x15x15	9	14/50 ³
25.	"	"	21:23	"	7	0/90
26.	"	"	100:75	25x25x25	12	11/78
27.	"	"	42:29	"	12	0/89

1/ communis ♂♂ and ♀♀ x churchillensis ♂♂ and ♀♀. 2/ total communis and churchillensis ♂♂ : total communis and churchillensis ♀♀.

3/ Percentage communis ♀♀/churchillensis ♀♀ inseminated; species separation based on autogeny and anatomy.

Table 16. Mating success, egg production, and viability of hybrids resulting from the cross between male imagos of A. communis sens. str. and female imagos of A. churchillensis sp. n.

Female	Inseminated ¹	Number of Eggs				Mature Larvae
		Retained	Laid	Embryonated	Hatched	
1	-	15	18	-	-	-
2	-	1	31	-	-	-
3	-	42	0	-	-	-
4	+	45	0	-	-	-
5	+	26	0	-	-	-
6	+	21	4	0	-	-
7	+	1	18	0	-	-
8	+	0	41	0	-	-
9	+	0	30	0	-	-
10	+	0	56	0	-	-
11	+	1	28	0	-	-
12	+	7	13	0	-	-
13	+	18	7	0	-	-
14	+	4	33	0	-	-
15	+	3	19	2	0	-
16	+	0	39	4	0	-
17	+	0	27	5	3	0

^{1/} Scoring for insemination based on the presence (+) or absence (-) of sperm in at least 1 of the 3 spermathecae.

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