

TAXONOMIC REVISION OF THE *AEDES (OCHLEROTATUS) PUNCTOR* SUBGROUP BASED
ON SPECIMENS COLLECTED IN BRITISH COLUMBIA.

by

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Taxonomic revision of the Aedes (Ochlerotatus) punctor subgroup based
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ABSTRACT

This is a taxonomic thesis which examines the status of six closely related species in the *Aedes (Ochlerotatus) punctor* subgroup. Three of these species were collected in British Columbia and reared to give samples of all their life stages. Anatomical characteristics used to identify egg, larvae, pupae, males and females were examined with light and scanning electron microscopes. The results demonstrate sufficient differences to consider these as good morphospecies. Geographical, reproductive and ecological groupings are considered and they suggest that these are true biospecies. The discussion defines the unit of similarity to which individuals morphologically conform. These species units are typified by anatomical descriptions and a dichotomous key is presented so that individuals can be separated into appropriate species.

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PART A
GENERAL INTRODUCTION

CHAPTER I

INTRODUCTION

The taxonomy of mosquitoes (Diptera: Culicidae) over the last 50 years has been stable enough to indicate that little work remains to be completed. However, the variation present in some groups suggests that our common widespread species may be complexes of siblings. The genus *Aedes* Meigen has 24 subgenera, of which 5 are represented north of Mexico on the North American continent. The black-legged *Aedes* are a natural division characterized by adults with uniformly dark-colored legs which are difficult to identify even by experts. All species of this natural division belong to the subgenus *Ochlerotatus* Lynch Arribalzaga and are well represented in the Canadian mosquito fauna. A revision of the Canadian fauna (Wood et al. 1979) has updated the status of many species. A recent detailed anatomical study has revealed a new species from Canada, *A. nevadensis* Chapman and Barr (Belton 1982). It is a member of the *communis* group, in the black-legged complex and has probably been misidentified by taxonomists in British Columbia. This example illustrates the need for more detailed examination of mosquitoes if our knowledge of the Canadian fauna is to become complete.

The species to be discussed belong to the *Aedes (Ochlerotatus) punctor* (Kirby) subgroup, a division of the *communis* group, whose taxonomic status has long been questioned by researchers. The original descriptions and improved redescriptions are based on anatomical characters and ecology and this thesis will involve all these characteristics. This research will concentrate on specimens collected from along the west coast of Canada because *A. aboriginis* Dyar, a member of this subgroup, has been found only in the rain forest of the

northern Pacific and is endemic to the region. Another member which has been collected from the coastal salt marshes of Alaska is *A. punctodes* Dyar. This species has recently been described from Fennoscandia (Dahl 1974). *A. punctor* (Kirby) and *A. hexodontus* Dyar are two species of the subgroup that are morphologically very similar to *A. aboriginis* but they have circumpolar distributions. The former is a common species of the boreal forest while the latter is often responsible for the biting reputation of tundra mosquitoes. The range of *A. hexodontus* extends southerly along the west coast to montane California and all three species can be collected in British Columbia.

The life history of all species in the *punctor* subgroup is the same. They are univoltine and their eggs hatch with snow melt conditions accompanying spring. The eggs enter an obligatory diapause after being laid in places that will flood the following year. This over-wintering condition requires a sequence of stimuli for the completion of embryonic development and hatching. These cues are exposure to near-freezing or freezing conditions followed by exposure to increasing temperatures in anaerobic pools. In Britain, the hatching of *A. punctor* eggs is triggered by deoxygenation of the growth medium (Fallis and Snow 1983). The succeeding four larval instars filter-feed on algae and microbial organisms in temporary or semipermanent pools. The obtect pupa undergoes complete metamorphosis to yield the adult insect. The males, which usually emerge first, form mating swarms that are evidently attractive to females. If she enters the swarm a male will clasp and fertilize her. This female will then seek a blood meal to initiate egg development. To my knowledge, no member of the *punctor* subgroup is autogenous, that is, does not require a blood meal for egg development.

The swarming and mating flight of Diptera was discussed by Downes (1969). *A. hexodontus* is one of the species Downes used as an example in that paper. When males form mating swarms, these adults use many cues to identify and mate with members of their own species. One of the cues probably used in mating and not discussed by Downes, is contact pheromone. A recent review (Howard and Blomquist 1982) discussed the hydrocarbons that have been found on the cuticle of Diptera. Lang's (1977) behavioural experiments indicated that such attractants may be used by adult *Culiseta inornata* (Williston) (Diptera: Culicidae).

Carlson et al. (1971) isolated the hydrocarbon Z-9-tricoscene from other Diptera. This 23 chained carbon compound is available commercially (Muscalure®) for fly traps. Linley (1983) has shown that these compounds are active in *Culicoides melleus* (Coquillett) but they are so general that Ceratopogonidae males would try to mate with female *Aedes* mosquito abdomens.

In this thesis the methodology for extracting and measuring hydrocarbons from the surfaces of females was investigated. It involved the injection of solvent washes into a gas chromatograph (GC). As these compounds changed from liquid to gas phase it was possible to separate them on a GC column by characteristic retention times. By comparing blanks and standards it is possible to identify peaks that correspond to known hydrocarbons. The resulting information is presented to fulfil criteria for an operational approach to the species concept for the members of the *punctator* subgroup.

CHAPTER II

OBJECTIVE

The retreat of the last glacial sheet has left Canada with a wealth of standing water that has been exploited by mosquitoes as a larval habitat. *A. punctor* is primarily restricted to the coniferous boreal forest and *A. hexodontus* is associated with muskeg in the tundra or at high elevations in the southerly part of the range. These species will live together in the same pools when sympatric populations occur in the muskeg-like conditions of the boreal forest of the northern hemisphere (Knight 1951; Dahl 1974; Enfield 1977; Wood et al. 1979). My own collections from Alberta and British Columbia have confirmed this fact. In British Columbia *A. hexodontus* is found in the same pools as *A. aboriginis*. The early record of this was when Dyar (1920) discussed the conditions of this region and described two *hexodontus* synonyms, *A. leuconotips* Dyar and *A. cyclocerculus* Dyar. The study of these species in this zone of habitat overlap is overdue, especially because there are few adults reared from identified larvae in collections from this region.

Adults of these three British Columbia members of the *punctor* subgroup are similar morphologically, but larvae are distinct enough to separate most specimens to a species. At present the identification of specimens should be based on adults reared from larvae, especially where their range overlaps. Complicating the interpretation of the coastal distribution of these species, *A. hexodontus* is divided into tundra and cordilleran forms but the differences between them have not been investigated in detail. In the past, *A. punctor* has also been divided into a type specimen and a tundra form. Close examination of larval skins in the Canadian National Collection (C.N.C.) revealed that this

tundra form was actually a specimen of *A. hexodontus* (Wood 1977). Wood could not confirm the status of these species with the few specimens he had from northern British Columbia. The lack of larval-reared material from the west coast leaves the status of the *punctor* subgroup uncertain. This thesis will pursue the identification of the *punctor* subgroup in British Columbia by answering the following questions:

1. Are there morphological differences between these three species (*aboriginis*, *hexodontus* and *punctor*) in larval, pupal and adult instars?
2. Are these true or "good" morphospecies in British Columbia where their ranges overlap?
3. Is there a tundra variety of *A. hexodontus* that is distinct from the cordilleran "type" specimen?

CHAPTER III

HISTORICAL REVIEW

A better understanding of the species in the *punctor* subgroup may be gained by reviewing their recorded history. In the eighteenth and nineteenth centuries many voyages were made to explore the North American continent and often naturalists accompanied these trips to collect and observe the wildlife. Naturalists in the tradition of that time sought to find and record every possible species according to the Linnaean approach to taxonomy. It was a voyage exploring Northern Canada that resulted in Kirby (1837) describing a pungent (piercing) mosquito which would become a complex of species of uncertain status.

The description of *Culex punctor* by Kirby is listed in Appendix A. By present taxonomic standards it is extremely vague. Our knowledge about mosquito taxonomy has changed considerably since this record. To complicate the vague description it seems that the original specimens have been lost. It is possible, however, to find redescriptions of the holotype by other authors.

Giles (1900) published a monograph on mosquitoes which included *Culex punctor*. He stated that the type specimens were in the British Museum and were in "very fair" condition. These specimens were two males with brilliant white markings on a very dark ground. Part of the description Giles gave for these specimens was: "the proboscis, palpi and antennae are uniformly dark brown, the last densely plumose with dark haired verticils which show a silvery lustre in certain lights". In the preceding paragraphs he included Kirby's description that stated the antennae were wanting (in both specimens). It seems uncertain for which specimens the antennae were described. The record ended

with a note on habitat which reads "St. Martin Falls, Albany River Hudson's Bay. Two specimens taken in Latitude 65 degrees north". The Albany River does not cross this northern latitude according to current Canadian maps. Giles further clouded the issue in his 1902 edition of the Handbook to Gnats or Mosquitoes. In this treatise he described the unguis (tarsal claw) of both a male and a female from Hudson's Bay, St. Martin Falls. It would seem these were not the true type specimens since these were just two males, according to Kirby's description of the valvules (valvulae internae) or gonocoxites.

Another monograph on mosquitoes was published by the British Museum of Natural History in 1901. In this work Theobald stated that the type specimens were two males and one female. Vockeroth (1954a) felt that Theobald had confused the type specimens with those which Walker (1848) listed under the name *C. punctor*. These specimens were collected from along the Albany River (about 52 degrees Latitude north). The holotype *punctor* was probably collected at Fort Norman, N.W.T., as pointed out by Vockeroth and the original specimens were either lost or mislabeled by the early 1900's.

It is not possible to name all those who have been involved with these mosquito species but within the *punctor* subgroup no other stands out above Dyar. In a series of three papers he attempted to establish the larval identity of *C. punctor* in 1904. In the first of these, Dyar (1904a) described the larva as having the comb of the eighth abdominal segment composed of four or five large thorn-shaped teeth. In a second paper Dyar (1904b) included a larval diagram with a comb composed of six teeth and a magnified picture of a five tooth comb along with an even larger picture of a single comb scale. The single larva was collected from a boggy portion of the woods in the Kootenay District of British Columbia. This specimen more closely resembles *A.*

hexodontus, which I have collected in British Columbia, in having 5 or 7 comb scales. The specific name is derived from the larval character of having a six (hexo) tooth (dontus) comb on each side of the eighth abdominal segment. Dyar did not describe *A. hexodontus* until 1916, so this description remained with *punctor* for several years. In the third paper Dyar (1904c) stated that *C. abserratus* Felt and Young should become a synonym of Kirby's *punctor*. This species was later resurrected as *A. abserratus* (Felt and Young) by Vockeroth (1954a). In 1906 Dyar and Knab completed a larval key for mosquitoes which partially separated *A. punctor* from other larvae on the character of the comb having a single or irregular row of six teeth. The authors admitted that this species might not be the same as that described by Kirby. They stated "We have little idea that this is the species actually intended by Kirby, but just what that was will probably never be known, and this species will do as well as another to represent the name."

Later papers by Dyar described some of the other members of the *punctor* subgroup. In 1916, *A. hexodontus* was described from Fallen Leaf Lake in the mountains of California (Appendix B). Dyar (1917) described *A. aboriginis* (Appendix C) from Longmire Springs, Mount Rainier National Park, Washington. In 1919 he presented the most detailed account to that date for *A. punctor*, *A. hexodontus* and *A. aboriginis*. All three species have similar male genitalia and the mesonotal color pattern became one of the most important characters for identifying adults. Dyar relied upon Theobald's redescription of Kirby's specimens which probably were not the true types, as previously mentioned. He did admit that *punctor* was variable in adults and larvae so he divided the species into two forms. At this time, *abserratus* and *centrotus* Howard, Dyar and Knab were included as synonyms of *punctor* (the former would later be elevated to specific

status).

The 1920 publication by Dyar created confusion about taxonomy in the *punctor* subgroup. It began by discussing the peculiar conditions created by the continual rains of the Pacific coastal region. "The conditions produce an entire change in the aedine species, the whole Canadian (mosquito) fauna is cut off with not a species surviving. Three endemic species take its place and all being derivatives of *punctor*. The region from north to south includes the narrow Skeena River valley, all of Vancouver Island, western Washington and Oregon where it broadens out from the Cascades to the ocean". *A. cyclocerculus* Dyar (Appendix D) and *A. leuconotips* Dyar (Appendix E), both now synonyms of *hexodontus*, were two newly described species from the Skeena River valley, and the third endemic species is *A. aboriginis* (hence the specific name meaning native to the region). The larval specimen of *A. aboriginis* from the Skeena River valley was noted as being slightly different from those of the type locality in Mt. Rainier National Park. These differences were: the head hairs were more branched and the central spine of the comb scales were sharply differentiated from the spinules. Dyar felt that all these species, along with *hexodontus* and *punctor* formed a closely allied group. A major difference between these species was habitat preference. The two new species typically inhabited muskeg pools whereas *aboriginis* was found in drainage or casual pools and *hexodontus* in open marshy pools often of subalpine muskeg in California. *A. punctor* extends from coast to coast across Canada.

The descriptions of many new species resulted in Dyar (1921) publishing a revision to what he called the *punctor* group. It consisted of a *spencerii* and a *punctor* series. The latter was composed of seven species, five of which had a similar male hypopygium (genitalia). These species all live in the same faunal

region often flying together and he felt they could be subspecies except that they were of different larval form and habitat. "The subspecific concept cannot apply to such forms".

The dedicated work of Hearle (1926, 1927) produced two papers dealing with a major mosquito survey in the lower Fraser River valley of British Columbia. In his key to species Hearle (1926) indicated there were only two *punctor* members, *A. punctor* and *A. aboriginis*. In the revised list of British Columbia mosquitoes Hearle (1927) included *A. leuconotips* and *A. cyclocerculus* as possible species but did not include *hexodontus* because it was recorded only from California.

Dyar's (1928) treatise on North American mosquitoes was not the only major taxonomic work at this time. Matheson's (1929) monograph, which was revised in 1944, was used as a standard for North American mosquito taxonomy for about 20 years. Most of Dyar's species were considered of doubtful validity and only *A. aboriginis*, *A. abserratus* and *A. punctor* survived as species in Matheson's key. It was succeeded by Carpenter and LaCasse (1955). These authors followed the general systematic scheme presented by Edwards (1932) for the mosquitoes of the world. He placed the *punctor* species under the holarctic Group G, of the *Ochlerotatus* subgenus which now is referred to as the *communis* group.

An important revision of the *punctor* subgroup by Knight (1951) is currently referred to as the standard in North American taxonomy. He included the two groupings of Dyar based on male genitalia but gave them superspecies status. One group included *A. implacabilis* (Walker) (now *punctor*) and *A. punctodes* Dyar, the latter having been recorded from Alaska. The former is a native of the

eastern half of the continent and has been renamed *A. abserratus* (Vockeroth 1954a). The other superspecies included *A. aboriginis*, *A. hexodontus* and *A. punctor*. The larvae were distinct enough in these five species (a slight overlap occurring in *punctor-hexodontus* and *punctor-punctodes*), to present a key to fourth instar larvae. The similarity of females made writing a single key to species for this stage impossible. It should be mentioned that both *punctor* and *hexodontus* were divided into a type specimen and a tundra variety. Knight felt that larval-associated adults should be used to identify specimens in a particular locality. These words echo the feelings of most authors who have dealt with these species.

I will use Knight's work as the starting point and present detailed morphological descriptions of larvae, pupae and the adults reared individually from them.

PART B
MATERIALS AND METHODS

In this study I collected most of the specimens between March 1983 and May 1985 from British Columbia. Some larvae and adults were donated by the City of Edmonton, Technical Services Laboratory, Parks and Recreation. Dr R. A. Brust, Department of Entomology, University of Manitoba generously donated *A. punctor* adults from Manitoba and Quebec. I have also examined specimens from Dr. P. Belton's collection.

The procedure for collecting larvae from the field was as follows; a 500 ml long-handled dipper was used to scoop larvae from suitable habitats. These specimens were transferred to bottles and returned as soon as possible to the laboratory where they were placed in large glass dishes containing aerated water. Some of the larvae were reared individually but as the technique was not successful most larvae were reared together.

The laboratory that was used to rear the larvae was usually at 22.0° centigrade. The temperature occasionally varied about 1° except on hot summer days when the thermometer would rise as high as 26.5°. The larvae were kept at a 12 hour photo period and fed on finely ground Tetramin® fish food.

When the larvae reached the pupal stage the cast larval skin was placed in a vial with 80% alcohol. The dishes were examined on a regular basis so that an individual pupa would be associated with a specific cast skin. The associated pupa was placed in a small vial that was filled to overflowing. A small emergence cage that fitted over the opening of the vial used for the pupa kept the adult from escaping. This adult was allowed 24 hours for the cuticle to harden and the cast pupal skin was placed in the same vial with alcohol as the larval skin. The live adult was placed in a freezer for about 30 minutes and then treated with acetone as described by Truman (1968).

Each specimen was labelled according to the associated cast skins. The adult was placed in a separate vial with a tight-fitting cap. All specimens were kept in a dark drawer. Not all the larvae were treated in this manner. Some were killed in their fourth larval instar and frozen or preserved in alcohol. A few adults were not treated with acetone. These specimens were killed by placing the emergence cage, with the adult, into the freezer for about 12 hours. The dead adult was transferred to a vial with a tight-fitting cap.

A. hexodontus were successfully reared from the first instar at 2 different temperatures. This was the only species of the *punctor* subgroup with known breeding sites that were readily accessible for sampling. All of these larvae were collected from the same pool. In the laboratory, some were reared at 14° centigrade and the others at room temperature ($22.0 \pm 1.0^\circ$). The cast skins of fourth instar larvae and pupae were treated as described for other specimens.

Attempts were made to obtain eggs from *A. aboriginis* and *A. hexodontus*. Confirmed pupal specimens of these species were placed in a 100 by 45 by 45 cm cage and allowed to emerge at room temperature. The cage had water, finely ground sugar and sugar solution for the adults. Several days after emergence the females were caught, placed in a dish resting upon the forearm and then returned to the cage. After several days this procedure was repeated.

The cast larval and pupal skins were later removed from alcohol and placed on a slide with polyvinyl lacto-phenol medium (Martin 1977). The skins were partially dissected and spread to display all the characters to be measured. The slide was gently heated and a coverslip was placed on the skins. These slides were later examined under a compound microscope with 25 to 400 times magnification. The adult specimens were examined with 10, 47 and 94 times

magnification under a dissecting microscope. All eye-piece units on the microscope were converted to millimeters or micrometers.

Some larvae and adults were prepared for scanning Electron Microscope examination. The larvae that were previously frozen were placed in a freeze drying apparatus for 24 hours. The specimens were then mounted on Cambridge specimen mounts with conducting silver paint. Adults were dissected into smaller pieces and mounted on similar stubs. These mounts were then coated with a fine layer of gold before scanning with an ETEC corporation, Autoscan U-1.

Hexane extracts from females not treated with acetone, were analyzed by capillary column gas chromatography (GC). These females were killed 60 to 90 days before treatment. This adult insect was placed in a small conical based tube and ten microliters of hexane was dripped over the body. This procedure was repeated with another 10 microliters. The insect was placed within the tube so that the body did not rest in the solvent. This 20 microliters of solvent was transferred into a new tube and concentrated to 2 microliters by gently heating. This solvent was then injected into the GC by splitless injection.

In preliminary tests, the first specimen was washed with 20 microliters and 2 were injected into the GC. This method failed to register any hydrocarbon peaks on the column. This specimen was allowed to soak in the hexane for about 30 minutes while the previous run was underway. Two microliters of this solution was injected into the GC after the initial run was completed. The second run from this specimen had many peaks corresponding with fatty acids, masking many of the hydrocarbon peaks. The technique initially described was successful with the next specimen. All subsequent specimens were treated in

that manner.

A non-polar methyl-silicone-coated 20 meter capillary column was used (Durabond-1®). The oven initially began at 80.0° C for 2 minutes then increased at 20.0° per minute to 240.0°. A 2 microliter blank was run in a similar fashion. The linear alkane compounds of the insect extract were identified by their retention times compared with those of known standards using identical GC conditions.

All calculations were performed using a Hewlett-Packard HP-41C®. The analysis of variance program was part of the "Stat Pac" application module that is available from Hewlett-Packard for the HP-41C.

PART C

GENERAL AND SPECIFIC TAXONOMIC CHARACTERISTICS

CHAPTER I

GENERAL TAXONOMIC CHARACTERS

The Canadian insect fauna has recently been discussed (Danks 1979) and the order Diptera (true flies) contains many species, exceeded only by Coleoptera (beetles). A primitive sister group to the true flies is the Mecoptera. North American authors usually follow the general Dipteran classification given by Stone et al. (1965) that recognized 105 families, 1,971 genera and 16,130 species from Canada and the United States north of Mexico. A classical treatment of North American Diptera to families and genera was offered by Curran (1934); this monograph has since been updated (Curran 1965). A more recent revision of the families and genera of nearctic Diptera by members of the Biosystematic Research Institute in Ottawa (McAlpine et al. 1981) is incomplete at the time of writing this thesis. This first volume covers the suborder Nematocera to which the Culicidae (mosquitoes) belong.

Diptera are characterized by having one pair of wings. The second pair associated with the metathorax of other insects is modified into halteres in Diptera. These organs have a gyroscopic function that is used to correct any tendency to yaw from side to side during flight. The identification of Diptera is based primarily on antennal, leg, wing and chaetotaxy (setal arrangement) characters.

There have been two points of view on the division of Diptera into suborders. The first system, based on antennal morphology, has existed since the early nineteenth century. The groupings are; the long-horned flies (Nematocera) and the short-horned flies (Brachycera). The second system of classification is based on the false cocoon (skin of the last larval instar) in

which the pupa completes metamorphosis. The two suborders (Orthorrhapha and Cyclorrhapha) are determined by the type of slit in the puparium that the emerging adult creates. A detailed description of these classifications is presented by Rohdendorf (1974).

The suborders Nematocera, Brachycera-Orthorrhapha and Brachycera-Cyclorrhapha are widely accepted by most taxonomists. This classification is used by Stone et al. (1965) and more recent works like Borror et al. (1981). A new classification of Diptera is emerging that is founded on the principle of phylogenetic systematics (Steyskal, 1974). The traditional approach places too much importance upon single features of the sense organs and nature of metamorphosis. This approach has led to instability in the classification of higher families. The new phylogenetic approach resolves the problem by weighting apomorphic characters less in the development of subordinate taxa. This classification is reflected in "The manual of Nearctic Diptera" (McAlpine et al., 1981). The second volume of this manual will contain a chapter outlining the evolution and phylogeny of Diptera which should clarify the systematic approach.

The Diptera are easily divided into two natural suborders based on antennae, as previously mentioned. Families of the Nematocera are considered to contain the most primitive Diptera. The larval head is well developed and the mandibles move in a lateral direction. The advanced families of Diptera have a reduced larval head with mouth hooks that move in a vertical plane. Pupae of many Nematocera are able to move around actively in suitable habitat while the other Diptera are immobile and complete the pupal stage inside the last larval skin (puparium). Antennae of adult Nematocera have many (6 or more), similar segments (except maybe the basal two) and palps with 3 to 5 segments. The

higher families of Diptera have 3 segmented antennae (the third segment may be annulated) and palps that are reduced to 2 segments.

The nearctic Nematocera are divided into 7 infraorders (McAlpine et al. 1981). One of them, the Culicomorpha contains mosquitoes, blackflies and biting midges. These make up most of the so-called "biting flies" of the world. The group is characterized by lack of ocelli in the adults and the tendency to form mating swarms.

The Culicomorpha is divided into 2 superfamilies, the Culicoidea and Chironomoidea. The former contains 3 families: the Dixidae, Culicidae and Chaoboridae. Some authors still feel the dixids and chaoborids are subfamilies of the Culicidae. The reasoning for this is worth noting. Larvae and pupae of these three families are adapted to air-breathing aquatic life in a freshwater habitat. In an evolutionary perspective, insects are adapted to a terrestrial environment and returning to the aquatic environment was a secondary adaptation. The more primitive Odonata (dragonflies), Plecoptera (stoneflies) and Ephemeroptera (mayflies) have nymphal stages with gills and use dissolved oxygen for aquatic respiration. Most larval Culicoidea have respiratory spiracles on the end of an elongated abdominal siphon. Having only posterior spiracles is defined as metapneustic but one chaoborid genus, *Chaoborus* Lichtenstein, lacks spiracles and is called apneustic. The respiratory siphon brings the spiracles in contact with the atmosphere. This feature along with a highly developed sclerotized head capsule and differentiated thorax makes these larvae distinct from other Diptera. The similarity of mating behaviour together with larval form indicates that the Culicoidea have a common ancestor. Within the Culicoidea only some species have an elongated proboscis (fascicle of mouthparts) and scales on the wing veins in the adult. Those authors who divide the Culicoidea

into three families feel that these characters make the Culicidae unique from the other 2 families. This convention will be followed in this thesis.

Apart from butterflies (Lepidoptera), the mosquitoes are considered the best-known group of insects (Laird et al. 1982). The extent of this knowledge is apparent from the catalog to the mosquitoes of the world (Knight and Stone 1977) and its supplements (Knight 1978, Ward 1984). It replaced the synoptic catalog of the world mosquitoes (Stone et al. 1959) and its supplements (Stone 1961, 1963). Even the terminology for anatomical characters has grown with the more detailed descriptions by present-day culicid taxonomists. Many of the older terms have been replaced with more precise ones and the interpretation of older descriptions can be confusing if there is no standardization. Harbach and Knight (1980) have published a glossary of mosquito anatomy; this work is becoming the standard and its terminology will be used in the present work.

The nearctic Culicidae are divided into 3 subfamilies: Anophelinae, Toxorhynchitinae and Culicinae, the last being relevant to this discussion. The adult Culicinae are distinct from the other subfamilies in having a scutellum with a trilobate posterior margin, with each lobe bearing a group of setae (bristles). The larvae of this subfamily have an elongated siphon on abdominal segment 8 and a labral brush composed of 30 or more hairs. Within the nearctic Culicinae Stone (1981) lists 11 genera: *Wyeomyia* (*Wyeomyia* Theobald), *Uranotaenia* Lynch Arribalzaga, *Psorophora* Robineau-Desvoidy, *Culiseta* Felt, *Mansonia* Blanchard, *Aedes* Meigen, *Haemagogus* Williston, *Deinocerites* Theobald, *Orthopodomyia* Theobald, *Coquillettidia* Dyar and *Culex* Linnaeus. *Culex* is a Linnaean genus that included most mosquitoes until the 1900's. Even *punctor* was given that name when first described by Kirby but more detailed examination and a greater knowledge of mosquitoes has placed it in the genus *Aedes*. The genus *Aedes* has no single

distinct feature that separates it from the others in the Culicinae but may be distinguished by using a combination of characters. North American taxonomists have used Matheson's (1929, 1944) treatises as a standard reference for many years, but they were succeeded by that of Carpenter and LaCasse (1955). This key was brought up to date by a series of supplements (Carpenter 1968, 1970, 1974) and these changes are summarized in the recent publication by Darsie and Ward (1981). Recent keys to families and genera can be found: Newson published a chapter in "Introduction to Aquatic Invertebrates of North America" (Merritt and Cummins 1978) and Stone in the "Manual of Nearctic Diptera" (McAlpine et al. 1981).

Adult *Aedes* can be separated easily from *Culex* by the presence of postspiracular setae; these are located behind the spiracle of the large mesothorax. The female abdomen is evenly tapered at the apex, unlike *Culex*, *Culiseta* and *Mansonia* in which it is rounded. *Psorophora* is similar to *Aedes* in having postspiracular bristles except that the former also has spiracular bristles and *Aedes* does not. Newson (1978) estimates that there are 60 species from North America within this genus. Stone (1981) divides the nearctic *Aedes* mosquitoes into 6 subgenera, 5 of which are found in Canada. Most subgenera are based on details of male terminalia and are not well differentiated in the larvae or in females.

Ochlerotatus Lynch Arribalzaga is one of the two largest subgenera of *Aedes* with about 150 species. Edwards (1932) arranged this subgenus into a number of well-marked groups as follows: Group A (*taeniorhynchus*-group : *Culicelsa*), Group B (*annulipes*-group : *Lepidoplatus*), Group C (*fulvus*-group : *Chrysoconops*), Group D (*albofasciatus* group), Group E (*dorsalis*-group : *Acartomyia*), Group F (*scapularis*-group : *Ochlerotatus*), Group G (*communis*-group : *Pseudoculex* and

Hyparcticus) and Group H (*rusticus*-group : *Feltianus*). These groupings are for the most part characteristic of definite geographical areas. Of these subgenera, Groups F, G and H are characterized by the absence of white bands on the legs (tarsal bands). A common name used for these mosquitoes is the black or dark-legged *Aedes*.

Of the black-legged *Aedes*, Group F includes all the South American species and a few North American ones that are evidently of southern origin. These species are distinct from Group G in having median or submedian longitudinal pale-scaled areas on the scutum (dorsal portion of the thorax). There is an exception to this character - *A. thelcter* Dyar has the scutum uniformly golden-brown. Unlike Group G these species lack scales on the paratergite (mid-ventral sclerite ventral to the scutum) and on the metameron (vertically narrow sclerite above the hind coxa) of the females (Knight 1951). *A. trivittatus* (Coquillett) is the only northern Nearctic species of Group F.

The dark-legged Group H is distinct from the others with certainty only in larvae. They are an unusual group, anatomically, for most of the *Aedes* have only a single pair of siphonal tufts (branched seta with a single insertion). Group H have numerous pairs of branched setae on the siphon. This group is represented in North America by one species, *A. provocans* (Walker). Wood (1977) has recently shown this name to be a senior synonym of *A. trichurus* (Dyar).

The Group G (*communis* group) as defined by Edwards (1932) includes most of the North American and European *Aedes* with dark legs. He included many Australian species which do not differ conspicuously from their northern counterparts, in Group G. Apart from black-scaled tarsi these species were

described as follows: lower mesepimeral bristles present (rather numerous), posterior pronotum scales mostly narrow, mesonotum without conspicuous pale patches or stripes, pleurae rather densely scaled and the male coxite with distinct apical lobe, basal lobe various but without flattened hairs. Edwards said that subgroups were defined by the characters of the basal lobe of the coxite. In his list of Group G species, the "[?=punctor]" subgroup included; *A. aboriginis* Dyar, *A. cyclocerculus* Dyar (=hexodontus), *A. hexodontus* Dyar, *A. leuconotips* Dyar (=hexodontus) and *A. punctor* (Kirby).

This discussion was presented to help the reader become familiar with this family. The characters important in separating the *punctor* species is contained in the following discussion.

CHAPTER II

SPECIFIC TAXONOMIC CHARACTERS

Many contributions have been made to establish the identity of the *punctor* subgroup species since Knight's (1951) revision. The characters that have become important to identify the *punctor* subgroup will be discussed in chronological order of the papers. This ordering is important in establishing which are the most relevant records with accurate accounts of the anatomy of these species. The authenticity of other records may be disputed.

Knight's description of the *punctor* subgroup is based on the distinct characters of the male genitalia. The combination of characters is as follows: basal lobe (basal dorsomesal lobe) of the gonocoxite (basistyle) expanded, setose and tubercular in appearance, with stout elongate seta or spine at the tergal margin; apical lobe (apicodorsal lobe) with short clinging setae, some or many of the most sternal-lying of these being flattened and striated (scale-like); and claspette appendage (claspette filament) curved bladelike in lateral view, broadest at the curved portion, apically elongate-tapering.

In 1954, Beckel discussed the black-legged *Aedes* of Churchill, Manitoba. This paper established certain new adult characters including the presence of pale scales at the base of primarily dark-scaled wings, scaling on the postprocoxal membrane and probasisternum. He felt that these characters were useful in identifying *A. hexodontus* in Canada. All of these characters were useful in separating the British Columbia members of the *punctor* subgroup. Knight (1951) separated *A. punctor* into two forms but Beckel could not distinguish the tundra *punctor* from *A. hexodontus*. It has been shown in recent works that the tundra holotype of *A. punctor* in the Canadian National Collection was actually *A.*

hexodontus (Wood 1977). Another interesting observation by Beckel was the change in mesonotal color pattern in female *A. hexodontus* over the season. In early spring this species had two median laterodorsal dark brown stripes that were separated by a median pale scaled stripe. Towards the end of the spring season these stripes became a single median stripe of dark brown scales.

Two of Vockeroth's papers from 1954 are relevant. One of them (1954a) resurrected the name *A. abserratus* (Felt and Young) which was Knight's *A. implacabilis* Walker. This change was accepted in Carpenter and LaCasse's (1955) treatise for North American mosquito taxonomy. In the other paper (Vockeroth 1954b) larvae of *A. punctor* were described as having 10 to 21 comb scales on one or the other side of abdominal segment eight (excepting one specimen which had 7 scales on one side, 11 on the other). *A. hexodontus* larvae were described as having 5 to 9 comb scales. The comb scales were 0.066–0.077 mm in length for *punctor* and 0.111–0.133 mm in *hexodontus*. Vockeroth felt that length of the comb scales was useful in separating these two species. This character was examined in detail in this thesis. Vockeroth also noted the usefulness of examining the color of setae (bristles) on the mesonotum. In *A. punctor* he observed that these setae were a bronzy or pale color while *A. hexodontus* had black setae. Color of setae on several parts of the body was examined in this thesis. Some specimens of *A. hexodontus* from California were examined by Vockeroth (1954b). The larvae were similar but the adults had a lighter ground color and distinct median sublateral dark brown stripes of scales on the mesonotum that was divided by a mid-dorsal pale stripe. These specimens were different enough for Vockeroth to suggest that they might be two subspecies.

The members of the *punctor* complex from Naknek, Alaska, were discussed by Frohne (1955a) who examined 274 larval specimens. Unfortunately the length

of the comb scales was not considered although Vockeroth had found this to be an important character in the northern members of the subgroup. The number of comb scales formed a bimodal distribution with *A. hexodontus* having between 5-9 scales (with a peak at 7) and *A. punctor* having between 10-19 (with a peak at 12). His subsequent paper (Frohne 1955b) included a key to northern mosquito larvae and stressed the importance of "saddle spines" as a potential character for determining species. By comparing the size and shape of these spines in several areas on the saddle the three species, *A. aboriginis*, *A. hexodontus* and *A. punctor*, could be separated. There was overlap in range of this character so Frohne felt that these findings were tentative for the *punctor* subgroup and needed further investigation.

An important treatise for North American taxonomists was published in 1955 by Carpenter and LaCasse. These authors followed Knight's (1951) revision to the *punctor* subgroup except for elevating *A. abserratus* (Felt and Young) to specific status from *A. implacabilis* Walker [= *punctor* (Kirby)]. The latter became a synonym of *A. punctor*. It is unfortunate that neither the information in the paper by Vockeroth (1954b) nor that in Beckel's (1954) paper were included in their key to species, thus female identification did not use such characters as scaling of the probasisternum and postprocoxal membrane. Adults of the *punctor* subgroup were not differentiated by Carpenter and LaCasse. Larvae were separated mainly on the number of comb scales. These authors stated that "at present the identification of these species (*punctor* subgroup) should be based, for the most part, on larvae or larval-associated specimens, particularly where their range overlaps".

A complete key to pupae was published by Darsie (1957) for the *punctor* subgroup along with a key to known nearctic *Aedes* species. The cast pupal

skins from emerged adults of specimens collected in British Columbia were examined in this thesis.

An important contribution to mosquito taxonomy was the key to eggs of *Aedes* in Manitoba (Kalpage and Brust 1968). It is evident from this paper that shape and markings on the exterior of eggs can be used to identify many species. In this thesis the mating of *hexodontus* and *aboriginis* was attempted. However, the univoltine nature of these species made mating experiments difficult, and of all the adults of the two species that were allowed to emerge into a large cage, only two *A. aboriginis* took a blood meal. One of these females laid eggs and they are described below. This is a new description and it adds to those of *A. abserratus*, *A. hexodontus* and *A. punctor* that are given by Kalpage and Brust.

Wood (1977) made an important contribution to the identity of the *punctor* subgroup by examining specimens in the Canadian National Collection. Using the accumulated knowledge of anatomy, he was able to find several incorrectly identified specimens. The holotype *A. masamae* Dyar and 20 paratypes (synonym of *A. communis* (De Geer)) had scaling on the postprocoxal membrane. These specimens were collected by Dyar from Crater Lake, Oregon. The heavily-scaled probasisternum led Wood to believe these were *A. hexodontus*. They could not be distinguished from the series of *hexodontus* that had been collected at the same place and time. Wood felt that some doubt remains over their identity without clear distinction between *hexodontus* and *aboriginis* (*punctor* is not found in Oregon). Close examination of the specimen Knight deposited in the C.N.C. that was labeled "tundra" *punctor*, showed comb scales between 0.11 and 0.12 mm in length. There were 12 scales on one side of abdominal segment VIII and 14 on the other side. The associated female had a uniformly brown-scaled

scutum and a patch of white scales at the base of the costa. The adult "tundra" variety of *hexodontus* in the C.N.C. share these characters. The holotype *A. labradorensis* Dyar and Shannon (Appendix F) female (synonym of *A. hexodontus*) collected in 1906 has an unbanded, brown-scaled scutum. Wood felt that if the arctic population were recognized as distinct species from *hexodontus*, the name *labradorensis* would be applicable. In conclusion, Wood gave *hexodontus* the following description: "a larger species than *punctor*, usually with an unbanded, median brown-scaled scutum. The larvae have 12 or fewer comb scales which are generally longer than 0.1 mm. *A. punctor* has an undivided median dark-scaled scutal band and the larvae have 5 to 25 comb scales (most with more than 12) that are shorter than 0.08 mm. It should be noted that *hexodontus* consists of a cordilleran population that is similar to the tundra form except the submedian scutal bands are darker".

The "type *hexodontus*" as listed by Knight is difficult to establish because it includes the two species described by Dyar (1920) from the Skeena River valley (*cyclocerculus* and *leuconotips*). These specimens, along with Dyar's type *hexodontus*, are described as having the mesonotum covered with pale yellowish or brownish-yellow scales divided longitudinally by 2 submedial dark-brown stripes. This is in contrast with the indistinct scutal markings of the "tundra" forms of *hexodontus*. The larval exuviae of the Skeena River valley specimens that Dyar collected match the description for *hexodontus* except that the *A. leuconotips* lectotype has comb scales between 0.09 and 0.11 mm. This length of comb scale approaches the 0.08 mm record for *punctor*. Wood (1977) felt that additional collection is necessary to clarify whether the coastal specimens are *hexodontus* as their larvae suggest or *punctor* with abnormally long comb scales.

In 1979 the Biosystematic Research Institute in Ottawa revised the Canadian mosquito fauna (Wood et al. 1979). Female *A. hexodontus* is described as having the postpronotum and scutum covered with yellowish-brown scales that may fade to dull yellow. The scutum usually is without darker markings but occasionally there is a pair of distinct submedian stripes. *A. punctor* is described as having the scutum divided by a longitudinal, middorsal, dark-brown, scaled stripe (median and submedian stripes combined). Sometimes there is a pair of dark brown scaled submedian stripes separated by an indistinct, slightly paler median stripe. The yellowish-brown scaled presutural, sublateral and lateral areas are separated from the submedian stripe by a narrow line of pale scales. These authors remarked that *hexodontus* from the mountains were more like *punctor* in having a similar dark-scaled mid-longitudinal stripe on the scutum. If such females had a heavily-scaled probasisternum then they should tentatively be considered *hexodontus*. A bare probasisternum is indicative of *A. punctor*.

In the 1979 revision of the Canadian mosquito fauna, a new approach was used to key larvae to species. It involved the use of characters that previously had only been included in the general descriptions of species. Unfortunately the original descriptions by Dyar did not mention these characters. Wood et al. (1979) used the seta closest to the mid axis of the dorsal mesothorax (seta 1-M), to separate several species. The dichotomous choice is that seta 1-M is as long as head seta 5-C or less than one-third the length. In the succeeding portions of the key, *abserratus*, *hexodontus* and *punctor* follow the latter dichotomous branch and *aboriginis* the former. Specimens of *A. hexodontus* along the west coast do not conform to this trend. This character was examined on my specimens collected in British Columbia and the results of this observation will be elaborated upon in the discussion.

Bohart and Washino (1978) published a key to species for California. This was the area where Dyar collected the type specimens of *A. hexodontus*. In the key to California species *hexodontus* adults are recorded as having dark tarsi and wings except at the extreme base of the costa. This species can be separated from *A. communis* (De Geer) by the pale supra-alar setae, pale erect scales on the vertex (dorsal region of head) and postprocoxal membrane scaling. All of these characters were examined for specimens collected from British Columbia. The associated larval diagram in Bohart and Washino's (1978) key showed seta 1-M of the mesothorax as being single and equal in length to head seta 5-C. This contradicts Wood et al. (1979) who stress that seta 1-M is minute and multibranching. The range in number of comb scales of California *hexodontus* was from 5 to 9 but most commonly 6.

A recent key to species from the coastal region was published by Belton (1983). In this key to British Columbia mosquitoes, he illustrated the larval seta 1-M as being about the same size as 5-C and having 2 branches. The females are described as having the scutum yellowish-brown, paler at the lateral margins, with a broad, single or double, dark-brown median stripe. There are dark postero-lateral half stripes in some specimens. Belton also made note of the pedicels (basal segment of the antennae) cuticular ground color. This character was examined on females of all my specimens of the *punctor* subgroup from British Columbia.

This discussion of taxonomic papers is a summary of the more important publications. It has outlined the characters selected to identify members of the *punctor* subgroup. There are regional keys that have not been mentioned that are used to identify these species. They will be evaluated later in light of the findings of this thesis.

PART D
RESULTS

CHAPTER I

COLLECTION AND DISTRIBUTION

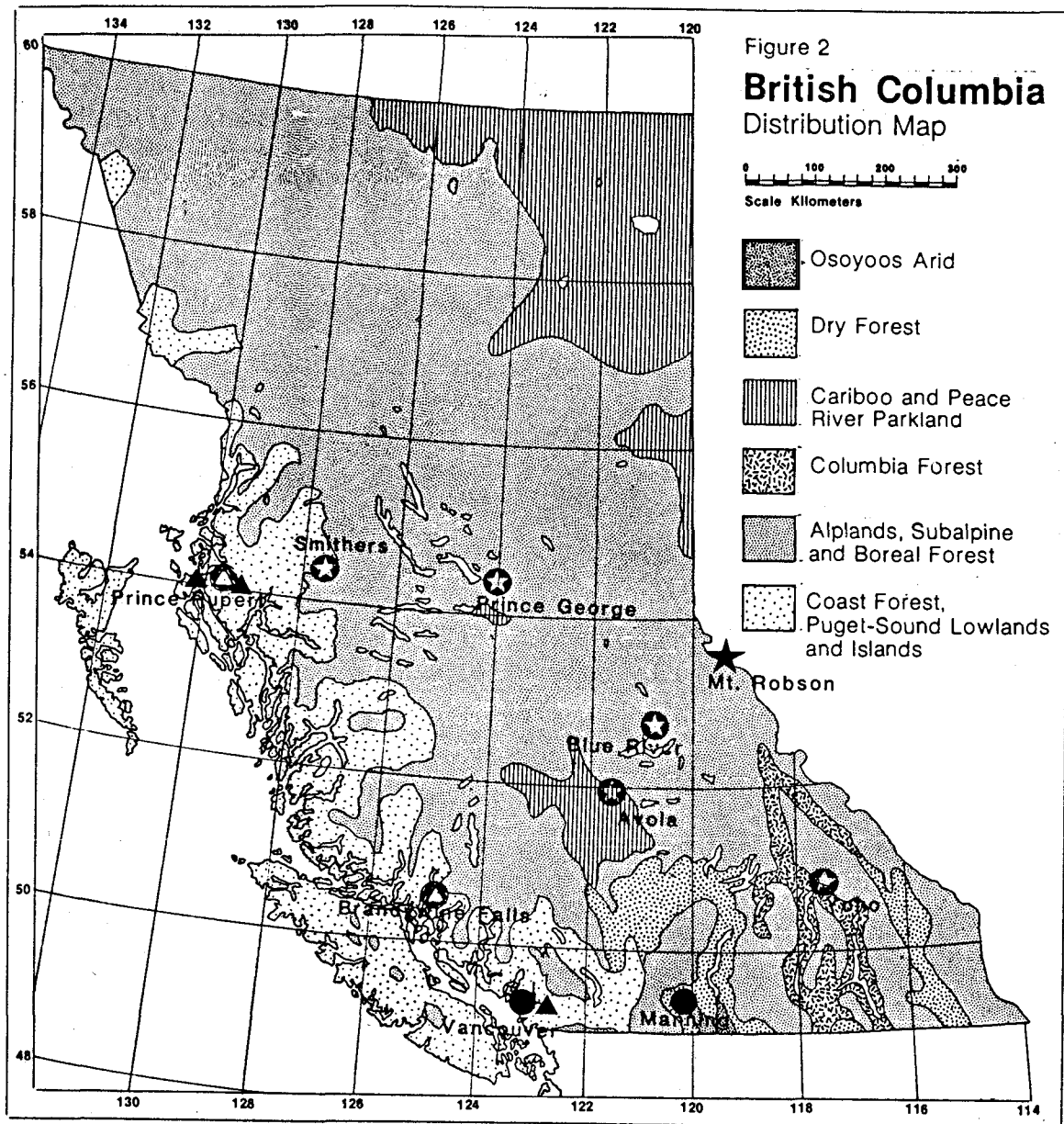
An essential preliminary to this research was the collection of larvae from British Columbia. The reasoning for this decision is a result of the early descriptions of mosquitoes by Dyar from along the west coast. Although work has been done on the *punctor* species since Dyar's time no intensive research on these species has been completed for the coastal region.

At present, larvae seem to be the developmental stage that are needed to be certain about the identity of these species. British Columbia is the only region of North America (except northern Washington) where the ranges of *A. aboriginis* Dyar, *A. hexodontus* Dyar and *A. punctor* (Kirby) overlap. Two other members of the group *A. punctodes* Dyar and *A. schizopinax* Dyar may also occur in the Province. The unique feature in British Columbia is that *A. hexodontus* can be found in the same pools with either *aboriginis* or *punctor*.

The collection of larval specimens for this research was limited by access to suitable habitats. Only a small portion of the coastal region has well developed roads, and collections reflect this.

The intensity of sampling was reduced by the space available in the laboratory and time required for the proper rearing of larvae to adults. The most difficult species to collect was *A. punctor* (Kirby), a common species of the boreal forest. In Figure 1 it can be seen that *punctor* was restricted to the boreal forest region of the Province. No local populations were found within the coastal range of mountains. At the northern site near Smithers, it was associated with *A. hexodontus* Dyar, *A. diantaeus* Howard, Dyar, and Knab, *A.*

Figure 1: Collection sites of British Columbia *punctator* subgroup.



- Aedes aboriginis* Dyar ▲
Aedes hexodontus Dyar ●
Aedes punctor (Kirby) ★
 sympatric *A. aboriginis* and *A. hexodontus* ◐
 sympatric *A. punctor* and *A. hexodontus* ◑

excrucians (Walker) and *Culiseta morsitans* (Theobald). To the east near Prince George it was associated with *A. communis* (De Geer), *A. implicatus* Vockeroth and *A. excrucians*. At sites south of this near Blue River it was found with *A. hexodontus*, *A. communis* and *A. pullatus* (Coquillett). Near Avola, *A. hexodontus* and *A. diantaeus* were associated with *punctor*. To the east of this in Mt. Robson Provincial Park *punctor* was associated with *A. cinereus* Meigen. South of this near Yoho National Park it was sympatric with *A. hexodontus*.

A common species of the coastal rain forest is *A. aboriginis* Dyar. It was found in pools by itself and living sympatrically with *A. hexodontus*. At Prince Rupert it was found near sea level and in the south at 1500 feet near Brandywine Falls Provincial Park. This latter population was also associated with *A. aloponotum* Dyar, *A. cinereus* and *Culiseta morsitans*. Most sites with *aboriginis* were temporary pools with emergent macrophytes and grasses. The specimens of *A. aboriginis* from Burnaby Lake (Belton (1978) and the University of British Columbia Research Forest (U.B.C.R.F.) near Golden Ears Provincial Park were associated with *A. cinereus* and *C. morsitans*. In a roadside ditch in Coquitlam (Lower Mainland region) *aboriginis* was the only species collected.

The most abundant of the *punctor* subgroup around the Vancouver area was *A. hexodontus*. It was found in the muskeg-like habitat of high elevations. It was sympatrically associated with both *punctor* and *aboriginis* that were collected in British Columbia. It was not restricted to high elevations for at Prince Rupert it was collected near sea level. In Mt. Seymour and Cypress Provincial Parks it was associated with *A. pullatus* and *A. pionips* Dyar. To the east at Manning Provincial Park, *A. pullatus* and *A. nevadensis* Chapman and Barr were collected from the same pools as *A. hexodontus*.

The earliest appearance of larvae along the west coast was March 13, 1983 at Brandywine Falls. Early instar larvae were collected as late as May 9 from this site in succeeding years. *A. hexodontus* could be collected as late as June from high elevations in Mt. Seymour Park. Many of the tundra populations of this species do not hatch until mid June in northern Canada.

Larval and female specimens of *A. hexodontus* and *A. punctor* were collected from around Edmonton, Alberta while I was employed by the City of Edmonton mosquito monitoring program (1980, 1981). The samples consisted of larval-associated, adult specimens. Of these two species, *A. punctor* was the most abundant. This is consistent with the findings of Graham (1969) who considered *A. punctor* abundant and *A. hexodontus* rare in Alberta. In 1985 I sampled in Alberta near the Obed summit of the Yellowhead highway where it was hoped that *A. hexodontus* might be collected, but only *punctor* was found.

CHAPTER II

SUMMARY OF SPECIFIC TRAITS

By rearing larvae to adults, ideally the number of cast, fourth-instar skins should be equal to the number of adult specimens. In practice this is seldom true because many specimens die before reaching maturity. Initially the larvae were reared in individual containers but survival was low. Mortality was reduced by rearing the larvae from the same site together in a large dish, then transferring the pupae to separate containers. This method worked well in obtaining many individual specimens but resulted in groups of pupae when the dishes of larvae were not checked during the night or over longer periods of time. Often this did not influence the results because only one species would emerge at that particular time.

Eggs

Attempts at breeding specimens of the *punctor* subgroup was for the most part, unsuccessful. However one *A. aboriginis* laid a total of 18 eggs but 4 of these were not developed and were white with a sack like appearance. The remaining 14 were fully developed with dull black to dark-brown shells. These had a mean length of 601 microns (range 477-678 \pm 18 standard error). The mean width is 260 microns (range 210-307 \pm 8 standard error). The eggs have a distinct bilateral symmetry when viewed dorsally. The outer chorionic tubercles are rounded forming 4 to 5 sided cells. The inner chorionic reticulum forms enclosed cells that correspond with each outer chorionic cell. The shallow ridges of the chorionic reticulum is discontinuous on the outer chorion and continuous on the inner.

Larvae

Table 1 is a summary of the characters which were examined on mounted exuviae. This information is tabulated to correspond with Wood et al. (1979).

Table 1: Observations from larval skins.

CHARACTER	<i>aboriginis</i>	<i>hexodontus</i>	<i>punctor</i>	
HEAD	Seta 5-C no. of branches	2-6	1-3	1-2
	Seta 6-C no. of branches	2-4	1-3	1-3
	Antennal seta 1-A no. of branches	4-12	1-8	2-8
PROTHORAX	Seta 1-P no. of branches	2-3	1-4	1-3
	Seta 2-P no. of branches	1-2	1	1
	Seta 3-P no. of branches	2-4	1-4	1-2
	Seta 2-P & 3-P > 2/3 length of 1-P	+	+	+
	Seta 5-P no. of branches	1-3	1-4	1
	Seta 7-P no. of branches	1-5	1-5	1-4
MESOTHORAX	Seta 1-M no. of branches	1-2	1-7	1-5
	Seta 1-M length = to 5-C	+	+/-	-
	Seta 2-M no. of branches	1-5	1-10	2-4
	Seta 3-M no. of branches	1	1-2	1-2
	Seta 4-M no. of branches	2-4	2-5	2-4
METHEOTARAX	Seta 1-T no. of branches	1-6	1-10	1-10
	Seta 3-T no. of branches	2-12	3-13	3-11

CHARACTER		<i>aboriginis</i>	<i>hexodontus</i>	<i>punctor</i>
A B D O M E N	Seta 1-V at least 1/2 length of 6-IV	+/-	+/-	+/-
	Seta 7-II no. of branches	1-3	1-8	1-2
	Seta 7-II at least 1/2 of 6-II	+	+/-	+
	Seta 7-II about = to 6-II	-	-	+/-
C S O C M A B L - E S	No. of comb scales (on one side)	15-49	3-8	7-16
	Apical spine length > 2X spinules	+/-	+	+
	Comb Scale length (mean in mm)	0.070	0.113	0.084
S I P H O N	Siphon length over siphon width	2.19	2.26	2.22
	Pecten teeth evenly spaced	+/-	+	+
	Apical tooth length (mean in mm)	0.110	0.115	0.123
	Second last tooth length (mean in mm)	0.103	0.106	0.120
	Pecten teeth with one basal cusp	-	-	-
S A D D L E	Saddle encircling anal segment	+/-	+	+
	Seta 1-X length = to saddles	+	+/-	+
	Seta 2-X no. of branches	10-16	9-30	9-16
	Anal papillae length = saddles	+/-	-	+/-

Pupae

There is very little information about pupal anatomy of the *A. punctor* subgroup. Most regional keys to species do not include pupae and Darsie (1957) is the primary source of information. Table 2 is a summary of the characters measured from mounted skins collected from British Columbia. The table uses numbering suggested by Harbach and Knight (1980) and includes data from Darsie (1957) for comparison because not all setal locations were certain.

In Table 2 under the SETA heading, there may be two labels. The first label is Harbach and Knight's and the second, in brackets, is Darsie's. For each principle seta Darsie included a range and a mode for the number of branches. In Table 2 the mode is located directly below the range and is enclosed in brackets. For my specimens from British Columbia, I have included a range for the number of branches and a range or value which fits at least 50% of all specimens that were examined. The latter set of values is located directly below the range and is enclosed in brackets.

Table 2: Observations from pupal skins,
The number of setal branches, the range and mode.

SETA	<i>aboriginis</i>		<i>hexodontus</i>		<i>punctor</i>	
Cephalothorax						
	B.C. pupae	Darsie (1957)	B.C. pupae	Darsie (1957)	B.C. pupae	Darsie (1957)
8	1-5 (2/3)	1-5 (3)	1-5 (2/3)	1-7 (2)	3-9 (4/5)	3-8 (4)
9	1-2 (2)	1-2 (2)	1-6 (1/2)	1-3 (2)	1-4 (1/2)	1-3 (2)
Metathorax						
10	2-8 (4/6)	3-8 (5)	2-8 (3/4)	2-7 (4)	1-7 (5)	3-10 (5)
11	1-4 (2)	1-3 (2)	1-3 (2)	1-2 (1)	1-4 (2)	1-4 (2)
12	1-3 (2)	1-4 (2)	1-6 (2)	1-5 (2)	1-5 (2)	1-4 (2)
Abdominal segment I						
2(H)	1-2 (1)	1 (1)	1-2 (1)	1-3 (1)	1-2 (1)	1-4 (1)
3(K)	1-3 (1)	2-3 (2)	1-3 (2)	1-3 (2)	1-4 (2)	1-4 (1)
5(L)	1-6 (3)	2-6 (3)	1-6 (3/4)	2-6 (4)	2-5 (4)	2-6 (3)
4(M)	3-8 (5)	3-7 (4)	3-8 (5/6)	3-10 (6/7)	4-10 (7)	4-9 (6)
6(S)	1	1-2 (1)	1-2 (1)	1-2 (1)	1-2 (1)	1-2 (1)
7(T)	1-3 (2)	1-3 (2)	1-5 (2)	1-4 (2)	2-4 (2)	1-4 (2)
9(U)	1	1	1	1	1	1

SETA	<i>aboriginis</i>		<i>hexodontus</i>		<i>punctor</i>	
Abdominal segment II						
	B.C. pupae	Darsie (1957)	B.C. pupae	Darsie (1957)	B.C. pupae	Darsie (1957)
3(B)	2-5 (2/3)	2-5 (2)	1-4 (2)	1-5 (2)	2-9 (2/3)	1-5 (2)
1(C)	2-11 (5/6)	3-10 (6)	1-6 (1/2)	1-7 (3)	2-9 (5/6)	2-15 (4)
5(3)	1-2 (1)	1-2 (1)	1-4 (2)	1-7 (2/3)	1-9 (3/4)	1-6 (4)
4(4)	1-7 (4/5)	3-8 (5)	1-11 (4/6)	3-11 (3)	1-10 (6/7)	5-9 (6)
8(8)	stub (1)	1 (1)	stub (1)	1-8 (1)	stub (0)	1 (1)
Abdominal segment III						
3(B)	1-5 (2)	1-3 (2)	1-3 (2)	1-2 (1)	1-4 (1/2)	1-4 (2)
1(C)	1-5 (2)	1-4 (3)	1-3 (2)	1-2 (3)	1-8 (2-5)	2-10 (4)
6(1)	1-3 (1)	1-3 (1)	1-3 (2)	1-6 (2)	2-5 (2/4)	1-5 (3)
4(2)	1-8 (4/5)	1-6 (4)	1-8 (3/5)	4-10 (5)	3-8 (6/7)	3-9 (6)
5(4)	1-4 (2)	1-6 (2)	2-6 (4)	2-9 (6)	3-11 (5/7)	2-9 (6)
Abdominal segment IV						
5(B)	1-3 (2)	2 (2)	1-4 (2)	1-3 (2)	1-2 (2)	1-3 (2)
1(C)	1-4 (2)	1-3 (2)	1-2 (1/2)	1-4 (1)	2-4 (2)	1-4 (2)

SETA	<i>aboriginis</i>		<i>hexodontus</i>		<i>punctor</i>	
Abdominal segment IV						
	B.C. pupae	Darsie (1957)	B.C. pupae	Darsie (1957)	B.C. pupae	Darsie (1957)
6(1)	1-2 (1)	1-2 (1)	1-3 (1/2)	1-5 (2)	1-4 (2)	1-5 (2)
4(2)	1-4 (2)	1-3 (2)	1-5 (2/3)	1-6 (2)	1-6 (3)	1-6 (3)
3(4)	2-5 (4)	2-7 (4)	2-3 (2)	3-7 (4)	2-8 (4/5)	3-7 (4)
Abdominal segment V						
	B.C. pupae	Darsie (1957)	B.C. pupae	Darsie (1957)	B.C. pupae	Darsie (1957)
5(B)	1-2 (2)	2-3 (2)	1-2 (2)	1-3 (2)	1-4 (2)	1-3 (1)
1(C)	1-4 (2)	1-3 (2)	1-2 (1)	1-3 (1)	1-4 (2)	1-3 (2)
6(1)	1-2 (1)	1-3 (1)	1-2 (1)	1-4 (1)	1-3 (2)	1-4 (1)
4(2)	1-5 (3/4)	2-5 (3)	1-6 (2)	2-7 (2)	1-10 (4/6)	3-9 (5)
3(4)	1-3 (2)	1-3 (2)	1-3 (2)	1-2 (2)	1-6 (2)	1-6 (2)
Abdominal segment VI						
	B.C. pupae	Darsie (1957)	B.C. pupae	Darsie (1957)	B.C. pupae	Darsie (1957)
5(B)	1-3 (2)	1-3 (2)	1-3 (1/2)	1-3 (2)	1-2 (1)	1-3 (1)
1(C)	1-3 (2)	1-3 (2)	1-3 (1)	1-3 (1/2)	1-3 (2)	1-4 (2)
6(1)	1-2 (1)	1-6 (1)	1-3 (1)	1-2 (1)	1-4 (1)	1-4 (1)
4(2)	1-3 (2)	1-3 (2)	1-4 (2)	1-5 (2)	1-5 (2/4)	2-4 (3)

SETA	<i>aboriginis</i>		<i>hexodontus</i>		<i>punctor</i>	
Abdominal segment VI						
	B.C. pupae	Darsie (1957)	B.C. pupae	Darsie (1957)	B.C. pupae	Darsie (1957)
3(4)	1-2 (1)	1-2 (1)	1-2 (1)	1-3 (2)	1-2 (1)	1-3 (2)
Abdominal segment VII						
9(A)	1-3 (2)	1-4 (2)	1-3 (2)	1-3 (2)	1-5 (2)	1-3 (1)
5(B)	1-2 (1)	1-3 (1)	1-2 (1)	1-2 (1)	1-2 (1)	1-3 (1)
1(C)	1-2 (1)	1-3 (1)	1-3 (1)	1-2 (1)	1-3 (2)	1-3 (2)
6(1)	2-6 (3/4)	2-6 (3)	2-7 (3/5)	3-9 (4/5)	3-9 (4/6)	2-9 (5)
4(2)	1-2 (1)	1-2 (1)	1-2 (1)	1-3 (1)	1-3 (1/2)	1-3 (1)
3(4)	1-3 (1/2)	1-3 (2)	1-3 (1/2)	1-3 (2)	1-5 (2)	1-4 (2)
Abdominal segment VIII						
9(A)	3-11 (4/5)	2-6 (3)	2-7 (3/5)	2-7 (4)	3-17 (3/5)	1-7 (2)
4(A')	1-2 (1)	1-2 (1)	1-2 (1)	1-3 (1)	1-3 (1)	1-2 (1)
Paddle						
X	1 (1)	1-2 (1)	1-2 (1)	1-2 (1)	1 (1)	1 (1)

Female

The description of adults is difficult to present in tabular form because most of the characters are not simple measurements. To make the information suitable the characters are presented as having a particular condition or not. This is represented as a + or - sign in Table 3. If some specimens had one condition yet other specimens of the same species had the other condition, then it was recorded as +/-.

Not all the characters were easy to express as a dichotomous choice, in such instances a value was selected that would best qualify the observation. An example of this is the scaling of the probasisternum of the thorax. Some specimens of *A. punctor* have some scales on this sternite but none had 20 or more as in *A. hexodontus*. The value of 20 was selected because it made the latter species distinct from the others that were examined. Many of the characters were presented in such a fashion that distinct differences could be seen in the table. The percent of specimens having the various traits will be discussed later.

Table 3: Observations from female specimens.

CHARACTER		<i>aboriginis</i>	<i>hexodontus</i>	<i>punctor</i>
H E A D	Vertex setae entirely black	+/-	+/-	-
	Pedicel ground color entirely black	-	+/-	-
	Pedicel ground color yellow laterally	+	-	+/-
	Scales on pedicel black	+/-	+/-	-
	Proboscis length (mean in mm)	3.28	3.08	2.90
	Range of proboscis length (in mm)	3.00-4.07	2.50-3.57	2.64-3.07
T H O R A X	Probasisternum bare	+/-	-	+/-
	Probasisternum with > 20 scales	-	+/-	-
	Scutum with dark-brown stripes (some median pale scales)	+/-	+/-	+/-
	Scutum with dark-brown stripe (no median pale scales)	+/-	-	+/-
	Scutum without distinct color pattern	+/-	+/-	+/-
	Scutal setae entirely black	+/-	+/-	-
	Supra-alar setae entirely pale	+	-	+/-
	Supra-alar setae entirely black	-	+/-	-
	Scutellar setae mostly pale (less than 3 black)	+	+/-	+
	Postprocoxal membrane scaled	+	+	+

	CHARACTER	<i>aboriginis</i>	<i>hexodontus</i>	<i>punctor</i>
	Lower mesepimeral setae absent	+/-	-	-
A B D O M E N	Abdomen length (mean in mm)	4.09	3.45	3.52
	Range of length (in mm)	3.57-5.07	2.50-4.79	2.86-4.29
	Sternites with large triangular patch of black scales	+/-	-	+/-
W I N G	Base of costa black scaled	+/-	-	+
	Base of costa > 8 pale scales	-	+	-

Male

The male characters other than genitalia are summarized in Table 4 in the same way as the female characters.

Table 4: Observations from male specimens.

CHARACTER		<i>aboriginis</i>	<i>hexodontus</i>	<i>punctor</i>
H E A D	Vertex setae pale (no dorsal black setae)	+/-	-	+
	Vertex dorsally with more than two black setae	-	+	-
	Proboscis length (mean in mm)	3.63	3.44	3.21
	Range in proboscis length (in mm)	3.29-4.43	2.79-4.07	3.00-3.43
	Palps length (mean in mm)	3.82	3.39	3.39
	Range in palps length (in mm)	3.50-4.57	2.71-4.07	3.21-3.64
T H O R A X	Probasisternum with > 5 scales	-	+/-	-
	Longitudinal dark-brown scutal stripes	+/-	+/-	-
	Longitudinal dark-brown scutal stripe (maybe central pale scales)	+/-	+/-	+
	Scutum without distinct colored scales	-	+/-	-
	Scutal setae entirely black	+/-	+/-	-
	Supra-alar setae pale (< 3 black setae)	+	-	+
	Scutellar setae entirely pale	+/-	-	+
	Scutellar setae entirely black	-	+/-	-
Postprocoxal membrane bare	+/-	+/-	-	
W I N G	Wing primarily dark- scaled (< 4 pale scales at base)	+	-	+

CHAPTER III

TEMPERATURE CONTROLLED REARING OF LARVAE

A total of 51 specimens of *A. hexodontus*, all collected as first instar larvae from the same pool, pupated and 41 adults emerged. Of these, 22 females are from room temperature ($21.0 \pm 1^\circ$ C), 7 from 14° , 8 males are from room temperature and 4 from 14°

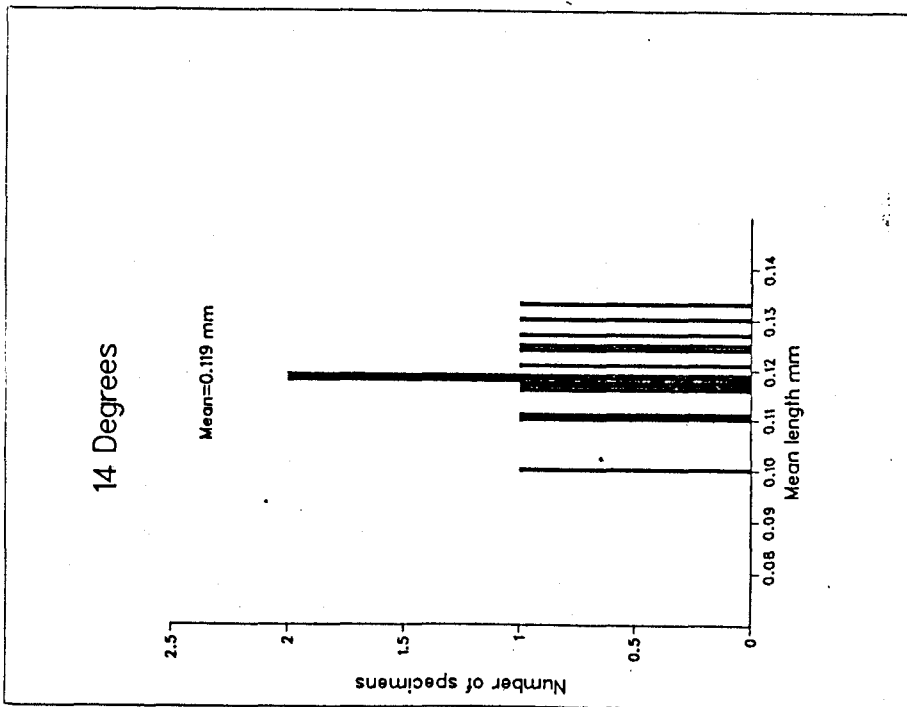
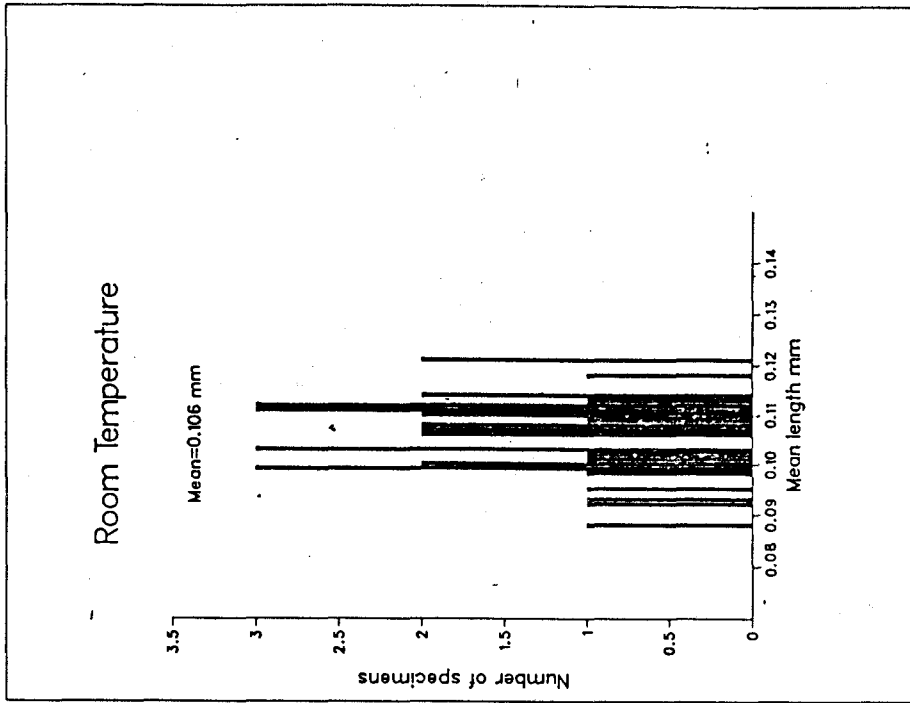
There were no apparent differences in color or color patterns of the adults reared at different temperatures. Measurements determined in Tables 3 and 4 for adults reared at room temperatures had smaller mean lengths than those reared at 14° C. Table 5 shows the differences in measurements of adults from one population that was reared at 2 different temperatures. This is important because *A. punctar* species are separated from *A. hexodontus* according to comb-scale length. Figure 2 is a plot of the mean comb scale length for each specimen (see Appendix G for the raw data). The overall mean for larvae reared at 14° is 0.119 mm and 0.106 mm for the room temperature specimens. The total range from the largest to smallest scales was the same for the different treatments.

An analysis of variance (ANOVA) was used to test the hypothesis that temperature did not change the mean comb scale length. Appendix I is the ANOVA table that resulted from this calculation. The treatments were significantly different so the null hypothesis, that treatment did not change the mean comb scale length, was rejected. Thus, larvae reared at warmer temperatures have a shorter mean comb length (Figure 2) even though the range, from the smallest to the largest, did not change.

Table 5: Characteristics measured from adults reared at different temperature

CHARACTER		ROOM TEMPERATURE	14 DEGREES
Female	Proboscis length (mean in mm)	2.99	3.40
	Range of lengths (in mm)	2.68-3.43	3.21-3.57
	Standard deviation	0.21	0.14
Female	Abdomen length (mean in mm)	3.21	3.69
	Range of lengths (in mm)	2.86-3.79	3.21-4.14
	Standard deviation	0.26	0.33
Male	Proboscis length (mean in mm)	3.31	3.68
	Range of lengths (in mm)	2.86-3.86	3.57-3.79
	Standard deviation	0.30	0.09
Male	Palp length (mean in mm)	3.29	3.61
	Range in lengths (in mm)	2.86-3.79	3.57-3.71
	Standard deviation	0.31	0.07
Male	Third palp segment length (mean in mm)	0.98	1.07
	Range of lengths (in mm)	0.85-1.04	1.04-1.10
	Standard deviation	0.06	0.03

Figure 2: Relationship of rearing temperature to comb scale length for *A. hexodontus* larvae.



CHAPTER IV

SURFACE HYDROCARBONS ON FEMALES

Quantities of hydrocarbons with 21 to 26 carbon atoms were measured for four specimens of each of the three species in the *punctor* subgroup (Appendix H). The units (integrated area) estimate the mass of the compound, about 5 "area counts" per 1 ng of compound. The results were not consistent for all specimens. The second *A. hexodontus* that was run (Appendix H) registered two large peaks. One associated with a 23 carbon compound (C-23) and the other with C-25. The peaks obtained from shorter chained hydrocarbons (from C-18 to C-20) were small and often masked by peaks from unknown compounds. These values are not included in the table of results. The C-23 and C-25 peaks were large for all specimens. These values are expressed as a ratio (C-23 over C-25) and the resulting values are recorded by specimen and localities in Table 6.

Table 6: Ratio of C-23 to C-25 hydrocarbons from female body washes

Species	Site and hydrocarbon ratio				
<i>A. aboriginis</i>	Site:	Brandywine	Brandywine	U.B.C.R.F.	Coquitlam
	C-23/C-25:	0.4500	0.6861	0.7386	0.8942
<i>A. hexodontus</i>	Site:	Brandywine	Brandywine	Avola	Avola
	C-23/C-25:	0.7279	0.7283	0.8268	0.8727
<i>A. punctor</i>	Site:	Avola	Avola	Avola	Yoho
	C-23/C-25:	1.0412	1.0758	1.2526	1.4395

PART E
DISCUSSION

THE INFLUENCE OF ENVIRONMENTAL FACTORS ON PHENETIC EXPRESSION

Influence of temperature on morphology

The temperature at which immature insects develop can influence the expression of morphological traits. Taxonomists should be aware of differences that can be induced by the environment. This variation can explain the wide range of variation in specific traits in some natural populations.

In this study the effect of rearing *A. hexodontus* at different temperatures was investigated. To begin such an experiment, it is critical to start with a genetically uniform population (1 species) of the earliest immature stage preferably from one batch of eggs. This was not possible because breeding these species was not completely possible and eggs from known females were not available. Thus field collected, first-instar larvae of the most accessible species, *A. hexodontus*, were used. Of the several samples of *hexodontus* reared, that from Cypress Provincial Park yielded enough specimens for statistical analysis.

Clements (1963) summarizes the effect of temperature on growth rates of mosquitoes. The temperature controlled rearing of *A. hexodontus* from British Columbia gave the same results to those previously published for this species (Haufe and Burgess 1956). Larvae reared at lower temperatures produce larger adults. This may be important because taxonomists often rear specimens in a warmer laboratory than would be expected under natural conditions.

It has been suggested that *A. aboriginis* is a larger species than *A. punctor* (Wood et al. 1979). This was true for most of the specimens I examined, although a large *A. punctor* can be as big as a small *A. aboriginis* (see Tables 3 and 4). Size alone is not an evidently reliable character to use in separating these two species.

At present species in the *punctor* subgroup can be separated most accurately as larvae. The most important larval characteristics for *A. hexodontus* and *A. punctor* are the size and number of comb scales on the eighth abdominal segment. In general, characteristics of the comb scales are frequently used in mosquito taxonomy because they are easily observed with a low power microscope.

The comb has several attributes that are important. These consist of; the arrangement of the teeth as a group, the number of teeth, length of the teeth (expressed as a mean length) and the size of the apical and lateral spines of individual teeth (spinules). These attributes of the comb scales vary considerably within individuals and between populations.

Within the *punctor* subgroup the length of the comb scales is the most reliable character to separate *A. punctor* from *A. hexodontus* (Wood et al. 1979). The phenotypic variation of the different populations has made establishing the exact value for mean length difficult. An unexpected result of differential temperature rearing of *A. hexodontus* was the phenotypic expression of comb scale length. The size of the comb scales can be significantly affected by temperature.

The smallest mean comb scale length measured in a single specimen from this experiment was 0.088 mm from room temperature. This is well below the

0.10 mm size that Wood (1977) suggested as a mean for *A. punctor*. This indicates that the absolute length of the scales is not as reliable a character as Wood suggested. The size of these scales can evidently reflect the habitat in which the larvae develop. *A. hexodontus* is typically found in the tundra and at high elevations. Dyar collected larvae of this species from sea level at Prince Rupert, British Columbia. Wood (1977) measured the comb scales of Dyar's specimens and found them to fall below the 0.1 mm length. At this point he could not be sure whether these specimens were *A. hexodontus*, as other larval characters indicated, or *A. punctor* with abnormally long comb scales as seemed probable from the habitat. It is likely that the milder climate at this low elevation caused the comb scales to be shorter on these larvae.

The associated adult of the short scaled *A. hexodontus* that was reared at room temperature had a large patch of white scales at the base of the costa and the probasisternum was heavily scaled. No characters in the adults (other than size) were changed by rearing the larvae at high (22.0° C) temperatures. There seems little doubt that *A. hexodontus* and *A. punctor* are true morphospecies.

An alternative to measuring absolute sizes is to measure the ratio of sizes of different parts on the same specimen. In the *punctor* subgroup the length of the last two pecten teeth have been compared with the mean length of the comb scales. Comb scales of *A. hexodontus* are usually longer than the last pecten tooth of the siphon and shorter in *A. punctor*. In British Columbia specimens of both *A. aboriginis* and *A. punctor* had a mean comb scale length that was shorter than either of the last two pecten teeth. This situation was not as clear in specimens of *A. hexodontus*. Only 45.4% of the specimens had the mean comb length longer than the last pecten tooth and 71.3% longer than

the second last tooth. Even for the second last pecten tooth, 28.7% of the specimens of *hexodontus* from British Columbia overlap in this character with *A. punctor*. It seems that the mean comb length does overlap and cannot be used as a single distinct character for separating specimens of these two species. Despite this, mean comb length should not be dismissed as a totally useless character because it does separate most specimens into their respective taxa.

Osmoregulation

Mosquito larvae are secondarily adapted to an aquatic life and these insects have evolved special organs to overcome the problems of living in an aquatic medium. The anal papillae are 2 paired rectal outgrowths that extend through the anus and function in osmoregulation. The length of the anal papillae are usually inversely correlated with the salt content of the larval medium.

The anal papillae have been used as taxonomic characters for members of the *punctor* subgroup. Knight (1951) described *A. aboriginis* as having the anal gills (anal papillae) 2.9X the length of the anal plate (saddle). This description was from a single specimen. Anal papillae of *A. hexodontus* ranged from 1.4 to 3.6X the saddle and *A. punctor* 1.5 to 3.0X (Knight 1951). Carpenter and LaCasse (1955) described *A. aboriginis* as having the anal papillae 1.0 to 2.5X the saddle. *A. hexodontus* and *A. punctor* were the same as recorded by Knight. More recently Wood et al.(1979) described the anal papillae of *A. aboriginis* as longer than the saddle, of *A. hexodontus* as exceptionally long (several times the anal segment) and of *A. punctor* as less than 2X.

My specimens from British Columbia showed considerable variation in the length of the anal papillae. *A. aboriginis* ranged from equal in length to the

saddle, to 3.0X. The shorter anal papillae lengths were recorded from specimens from Prince Rupert and the longer papillae on specimens from Brandywine Falls. For *A. hexodontus* the shorter anal papillae were recorded on specimens from Manning Provincial Park and Oliver Lake near Prince Rupert. The longest papillae were on specimens from Cypress Provincial Park, Brandywine Falls and Diana Lake near Prince Rupert. *A. punctor* had the shortest anal papillae on specimens from Prince George.

The length of the anal papillae is evidently variable from one habitat to another. The collection site at Brandywine Falls is located within the coastal rainforest region. *A. aboriginis* and *A. hexodontus* larvae had the longest anal papillae for these species at this site. This probably indicates that the salt content of the larval medium was low. Within a small geographical area there was considerable variation; *A. aboriginis* collected at the Oliver Lake site near Prince Rupert had small anal papillae but specimens from Diana Lake had large papillae (1.5 to 2.5x the saddle). The length of the anal papillae is apparently not a reliable taxonomic character. However, the length may give useful information about the larval habitat.

Gynadromorphism and intersexes

Another type of morphological variation that occurs in mosquitoes is the expression of characters typical of one sex on a specimen with genitalia of the opposite sex. In some instances there is bilateral expression of male characters on one side of the body and female on the other. Older records have referred to this as gynadromorphism. Marshall (1938) recorded 4 such cases for *A. punctor* in Britain. Gynadromorphism may result from a binucleated egg in which

one of the nuclei is fertilized or when an extra sperm enters the egg and undergoes cleavage to produce haploid (male) tissue in an otherwise female individual. This latter case occurs only in insects where haploidy produces males and diploidy results in females.

Horsfall and Anderson (1961) were the first to show that mosquito intersexes (condition intermediate between maleness and femaleness) can be induced environmentally by short term exposure to abnormally warm temperatures. Continual exposure to warm temperatures causes the determiners of maleness to fail in *A. stimulans* (Walker) and larvae would give rise to females. In *A. (Stegomyia) aegypti* Linnaeus, it has been determined that thermal stress affects a single, autosomal, recessive gene (Craig 1965). Brust (1968) found that 12 univoltine *Ochlerotatus* species show temperature induced intersexes. He felt that a similar genetic mechanism may operate in these univoltine species. Three members of the *punctor* subgroup exhibited an intersex threshold of 24° C (*A. abserratus*, *A. hexodontus* and *A. punctor*). Brust found *A. hexodontus* and *A. punctor* to express intersexes at the same temperatures. It was also shown that different biotypes for *A. hexodontus* would express thermal thresholds for intersex development at different temperatures.

In examining the occurrence of 27 *Aedes* from Manitoba, Brust (1968) found the species that reacted to thermal stress by producing intersexes were univoltine *Ochlerotatus*. The exception was a multivoltine species; *A. (Ochlerotatus) sierrensis* (Ludlow). The presence of a thermal stress trait in the genome of these univoltine *Ochlerotatus* supports the theory that this group of species came to North America from the temperate-arctic interface regions of Eurasia and not from the old world tropics. Even where these species occur in the southerly parts of their range they have selected a habitat that is cooler or shaded from

intense solar radiation. For example *A. hexodontus* occurs only at high elevations in the southerly extension of its range (except Skeena River valley). The univoltine nature of these species precludes any chance of being exposed to high developmental temperatures that would be associated with summer.

One specimen of *A. aboriginis* collected from Diana Lake near Prince Rupert, British Columbia had female palps but on an otherwise male specimen. Subsequent adults from this sample were normal males and females. I have chosen to call this aberrant specimen a gynadromorph rather than an intersex condition which may have been induced by warm laboratory temperatures.

CHARACTERS OF IMPORTANCE

Egg characters

The eggs from one *A. aboriginis* are smaller than those reported for other species in the *punctor* subgroup. Members of the dark-legged *Aedes* have been characterized by Kalpage and Brust (1968) according to adults, habitat and egg type. *A. aboriginis* fit the description of Group IIa given by these authors that includes all the other species of the *punctor* subgroup. Group IIa eggs typically have cell walls (inner and outer chorionic reticulum) that are not raised. *A. aboriginis* has similar shallow cell walls. The large *aboriginis* adult with the small eggs makes this species unique from the others of the *punctor* subgroup.

Larval characters

Aedes aboriginis Dyar

The original description of *aboriginis* by Dyar (1917) is listed in Appendix C. The comb of his specimens had about 20 scales on each side. My specimens ranged from 15 to 47 (Figure 3). Knight (1951) gave a range of 23 to 39 teeth and Wood et al. (1979) estimated between 23 and 40. The specimen I examined with 15 teeth had this portion of the cuticular exoskeleton torn away from the rest. It seems possible that some teeth may have been lost during mounting. Most of my specimens had 20 to 40 teeth. The skins with more than 40 teeth were associated with typical *aboriginis* adults so the identity is presumably correct. Dyar described the teeth as having a row of apical spines (spinules). The spinules on some of my specimens were equal in

Figure 3: Larval comb scale number (one side).
Figure 3A: *A. aboriginis* Dyar
Figure 3B: *A. hexodontus* Dyar
Figure 3C: *A. punctator* (Kirby)

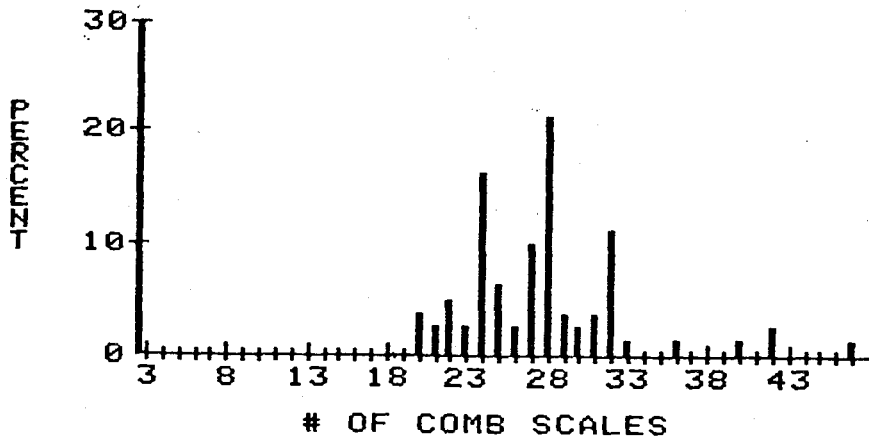


FIGURE 3A

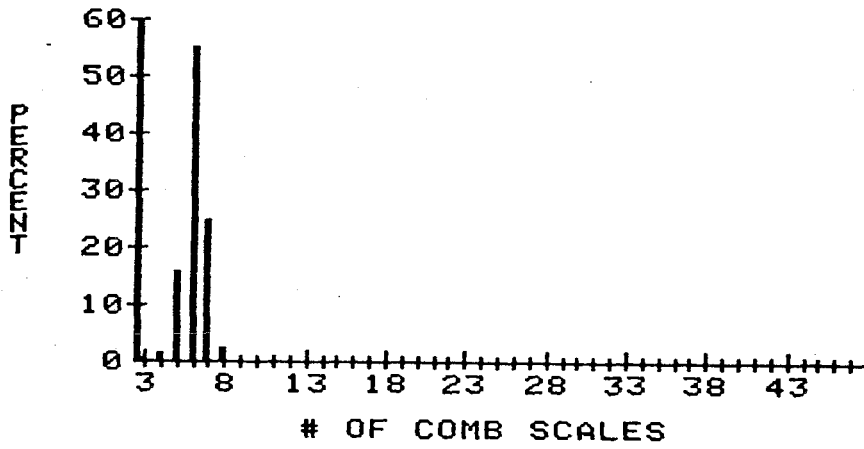


FIGURE 3B

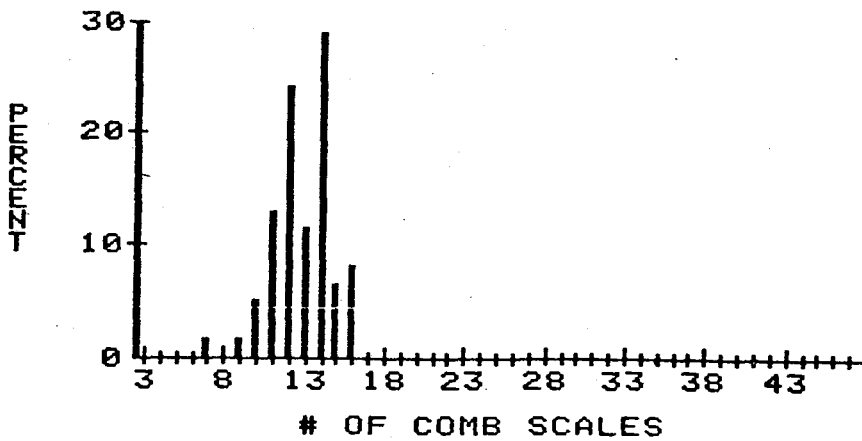


FIGURE 3C

length to the apical spine but in others they were as short as 1/4 its length. In 1920, Dyar noted that the central spines of the comb scales were sharply differentiated from the spinules in the specimens from the Skeena River valley. These were different from his type specimens collected in Washington. The long central spine is usually well differentiated in specimens from British Columbia. There was no obvious central spine in about 15.0% of my specimens. 30.0% of the specimens had spinules that were 1/2 or less than the length of the central spine. Most ranged from 1/2 to 2/3 and considerable variation can exist within a single individual.

In Dyar's original description he stated "the pecten teeth of the respiratory siphon were evenly spaced and followed by a 5 haired tuft" (seta 1-S). In my specimens 5% appear to have even pecten teeth. These specimens are like those described by Wood et al. (1979) who stated that if there are some distal teeth that appear slightly more widely separated, then the spacing increases regularly distally. In their key to species, this type of spacing will still identify *aboriginis* correctly. Seta 1-S in my specimens had 3 to 5 branches (Table 1) and 45 % had a 5-branched seta corresponding to Dyar's description of a 5-haired tuft.

All the descriptions of *aboriginis* that I have seen describe the saddle of the anal segment as encircling to near the ventral edge. One of my specimens appeared to have a saddle that completely encircled the anal segment. This may have been an artifact of the mounting but even after remounting I could not find a visible suture.

The last larval characters discussed by Dyar (1917) were the head setae. He stated that 5-C had 3, rarely 4 branches and 6-C with 3, rarely 2. In my

specimens 5-C had 2 to 6 branches and 6-C had 2 to 4 branches (Table 1). Dyar's specimens from the Skeena River were described as having 5-C with more branches than his type specimens. 50% of my specimens had 5-C with 4 branches (Figure 4) and 60% had 6-C with 3 branches and 30% with 2 (Figure 5). The antennal tuft (seta 1-A) was described by Dyar as having 8 branches. Only 21.5% of my specimens had 1-A with 8 branches (Figure 6).

There were some interesting differences between these species for some of the characteristics that I observed. The prothoracic seta 2-P was two-branched on 98.7% of the *aboriginis* (Figure 7). 2-P was single in all specimens of *hexodontus* and *punctor*. 96.6% of *A. aboriginis* had lower lateral abdominal seta 7-II, at least 1/2 the length of 6-II. This is an important character in separating *aboriginis* from *A. pionips* Dyar and *A. pullatus* (Coquillett). In these latter two species, 7-II is much shorter than seta 6-II according to Wood et al. (1979). Only 3.4% of the *aboriginis* larvae had 7-II a little shorter than 1/2 the length of 6-II. This character seems adequate for separating *pionips* and *pullatus* from specimens of *aboriginis*.

Aedes hexodontus Dyar

Within the *punctor* subgroup this species was not distinguished from *A. punctor*, in North America, until the work of Knight (Wood et al. 1979). The junior synonyms *A. leuconotips* Dyar and *A. cyclocerculus* Dyar remained the northern representatives of this species until Gjullin synonymized these species in 1946. Knight grouped these specimens into a "type" form and created a "tundra" variety based on the dark markings of the adult scutum, for specimens collected from northern Canada.

Figure 4: Larval head seta 5-C.
Figure 4A: *A. aboriginis* Dyar
Figure 4B: *A. hexodontus* Dyar
Figure 4C: *A. punctator* (Kirby)

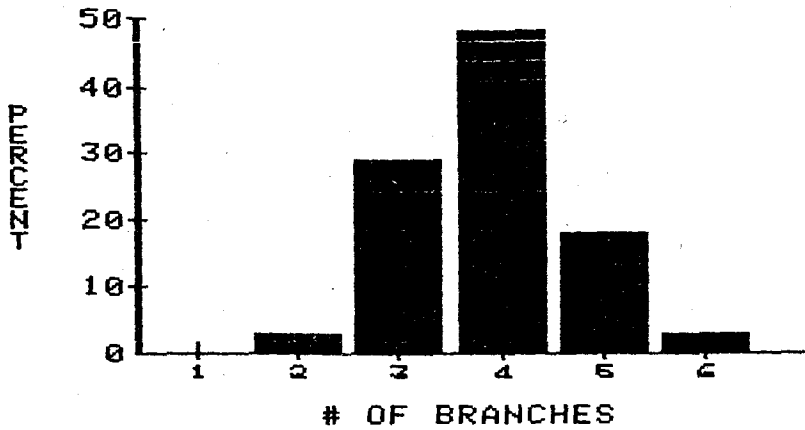


FIGURE 4A

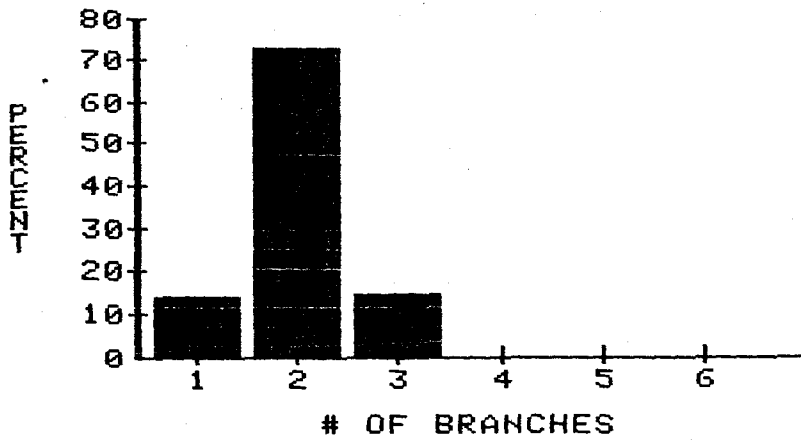


FIGURE 4B

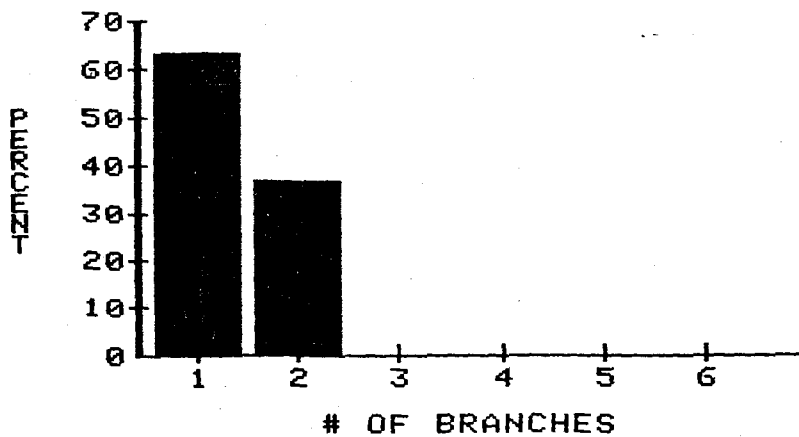


FIGURE 4C

Figure 5: Larval head seta 6-C.
Figure 5A: *A. aboriginis* Dyar
Figure 5B: *A. hexodontus* Dyar
Figure 5C: *A. punctator* (Kirby)

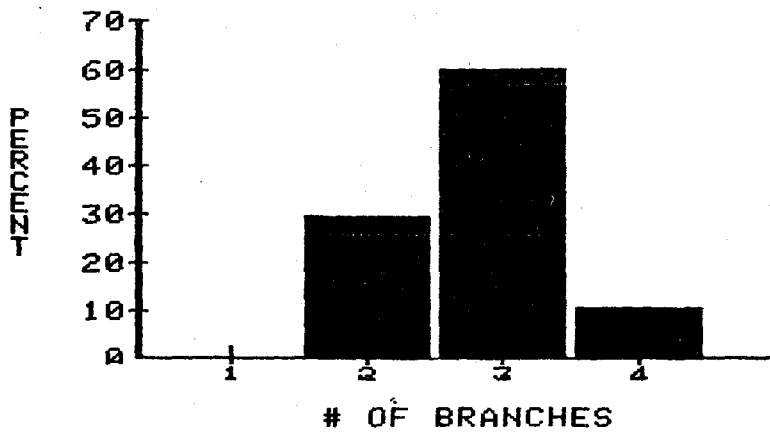


FIGURE 5A

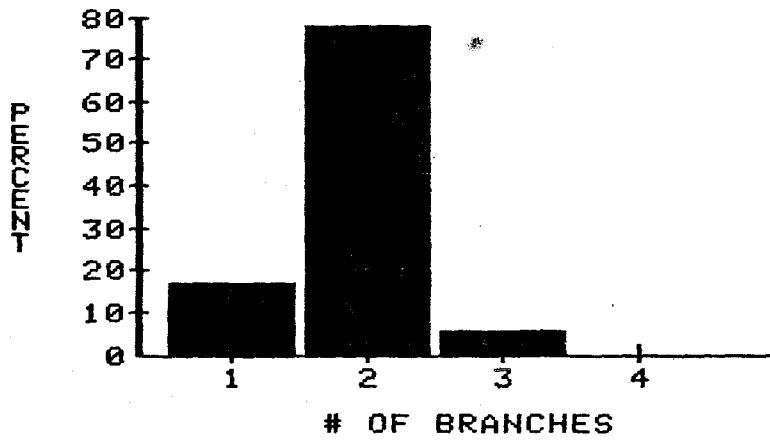


FIGURE 5-B

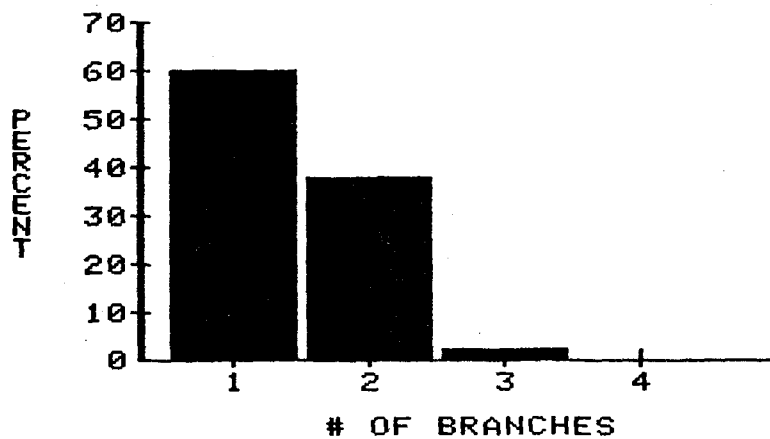


FIGURE 5-C

Figure 6: Larval head seta 1-A.
Figure 6A: *A. aboriginis* Dyar
Figure 6B: *A. hexodontus* Dyar
Figure 6C: *A. punctor* (Kirby)

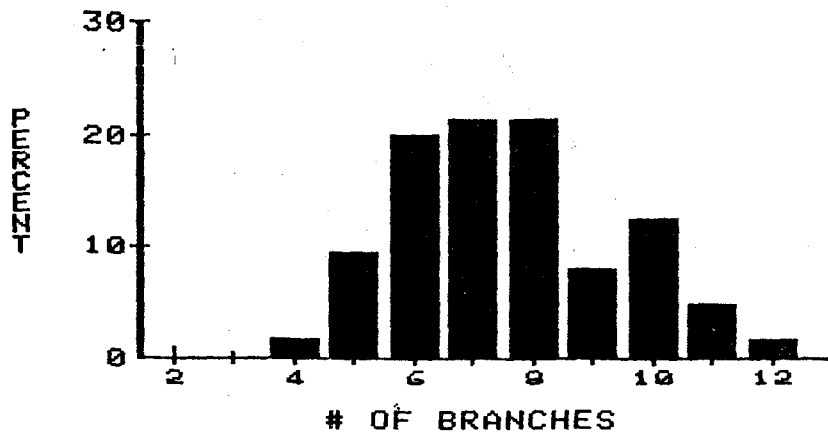


FIGURE 6-A

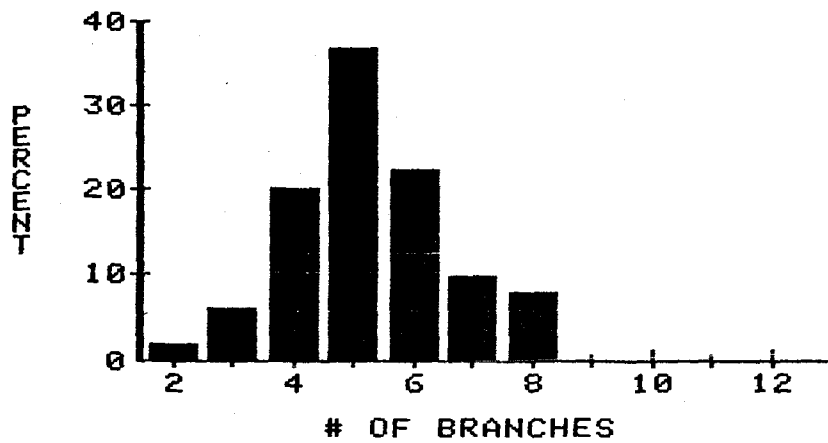


FIGURE 6B

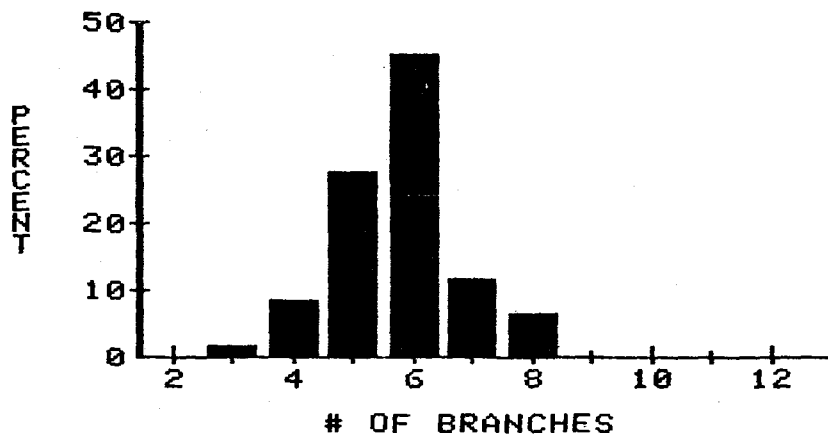


FIGURE 6C

Figure 7: Larval thoracic seta 2-P.
Figure 7A: *A. aboriginis* Dyar
Figure 7B: *A. hexodontus* Dyar
Figure 7C: *A. punctor* (Kirby)

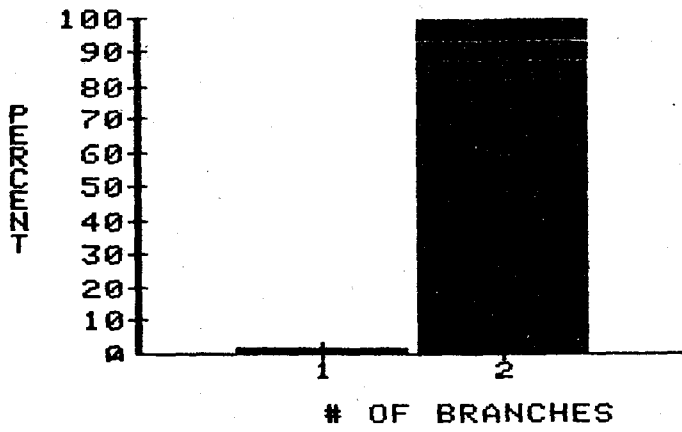


FIGURE 7A

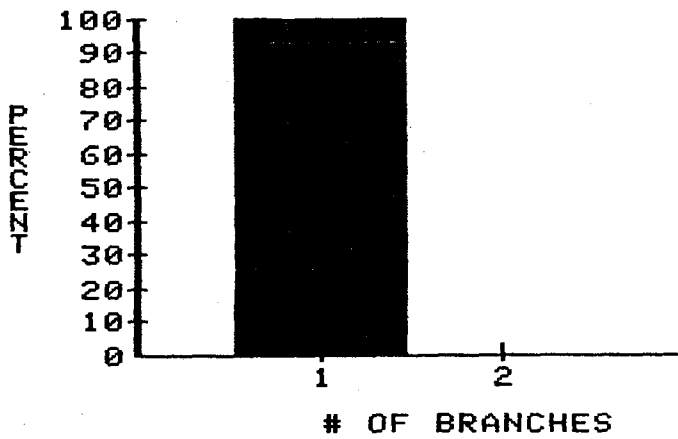


FIGURE 7B

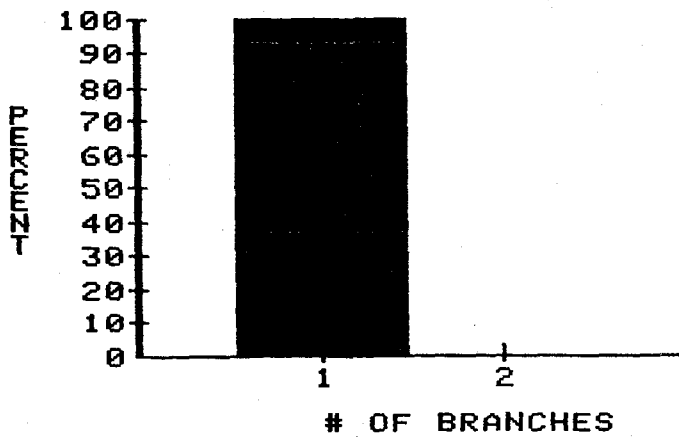


FIGURE 7C

Knight (1951) described head hair 5-C as always double, and 6-C was 78.0 to 100.0% double in the "type" form. The "tundra" variety had 5-C double 0.0 to 17.0% of the time and 6-C double on 0.0 to 7.0% of the specimens. The majority of my specimens had 5-C double in 72.4% and 6-C double in 78.0% (Figure 4 and 5). Dyar described these head hairs as double, although 6-C was sometimes in three's (Appendix B). *A. cyclocerculus* had head hairs double with 5-C occasionally 3 or 1, 6-C rarely 1 (Appendix D). *A. leuconotips* had head hairs double or 6-C single (Appendix E). The major exception to head hairs being double was presented by Wood et al. (1979). They reported these setae as being unbranched on specimens that they examined. Most of the localities were from northern Canada. It seems possible that *hexodontus* may include two varieties. Frohne (1955a) studied the *punctor* in Alaska and felt that the "tundra" variety, as Knight (1951) had discussed, had single head hairs. Of the 33 specimens with intact head hairs, 82.0% were single. Gjullin et al. (1961) in the "Mosquitoes of Alaska" stated that the upper and lower head hairs were single to triple on *hexodontus* from that region.

The thoracic setae were not described originally. Vockeroth (1954a) introduced them as diagnostic characters. He found the prothoracic seta 5-P was double or triple with *A. hexodontus* (single in *punctor*). This character is reliable for most of my specimens, only 4.8% had seta 5-P single (Figure 8B). Vockeroth (1954b) found 5.1% *hexodontus* with this seta single on one or the other side. None of my specimens from British Columbia had 5-P unbranched on both sides.

There seem to be some conflicting views in the literature about the setae of the mesothorax. This is especially true for seta 1-M, as previously mentioned. 1-M in my specimens were single or 2 branched (Figure 9). There

Figure 8: Larval thoracic seta 5-P.
Figure 8A: *A. aboriginis* Dyar
Figure 8B: *A. hexodontus* Dyar
Figure 8C: *A. punctor* (Kirby)

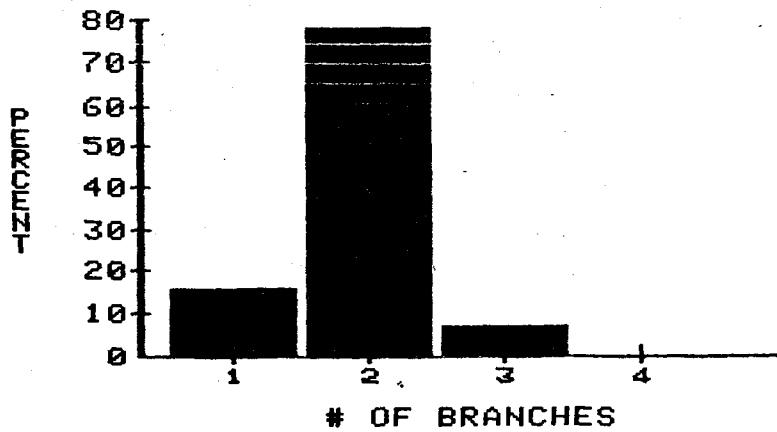


FIGURE 8A

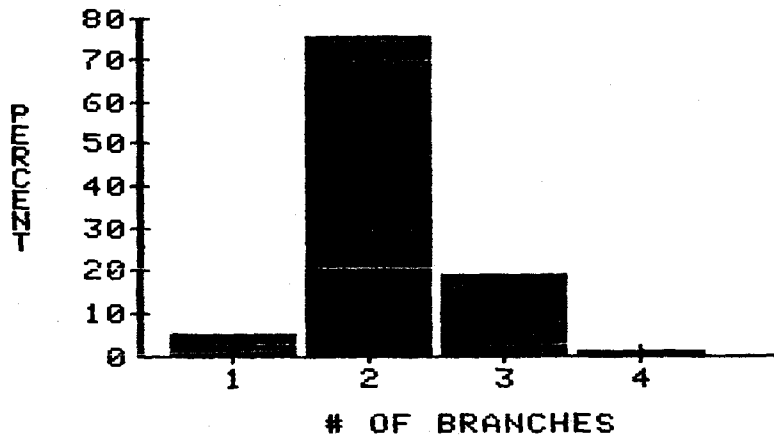


FIGURE 8B

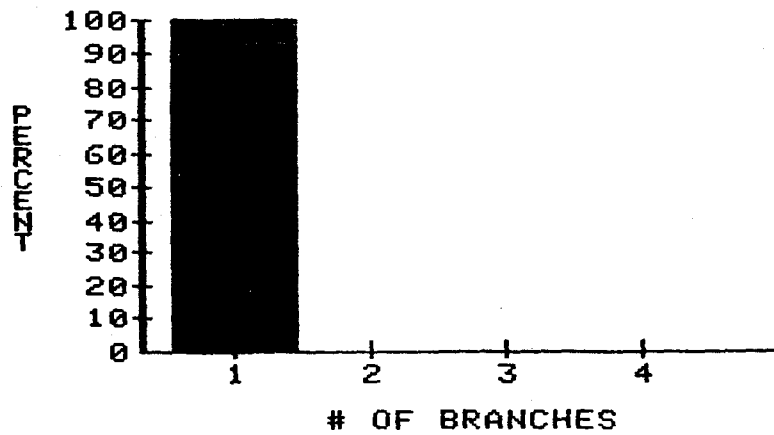


FIGURE 8C

Figure 9: Larval thoracic seta 1-M.
Figure 9A: *A. aboriginis* Dyar
Figure 9B: *A. hexodontus* Dyar
Figure 9C: *A. punctor* (Kirby)

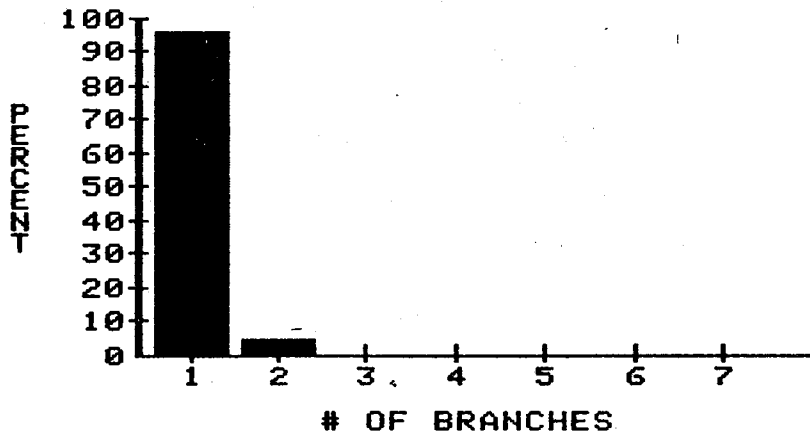


FIGURE 9A

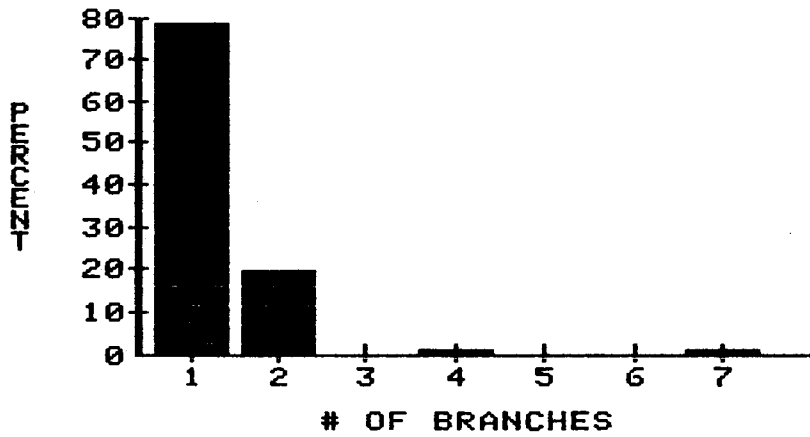


FIGURE 9B

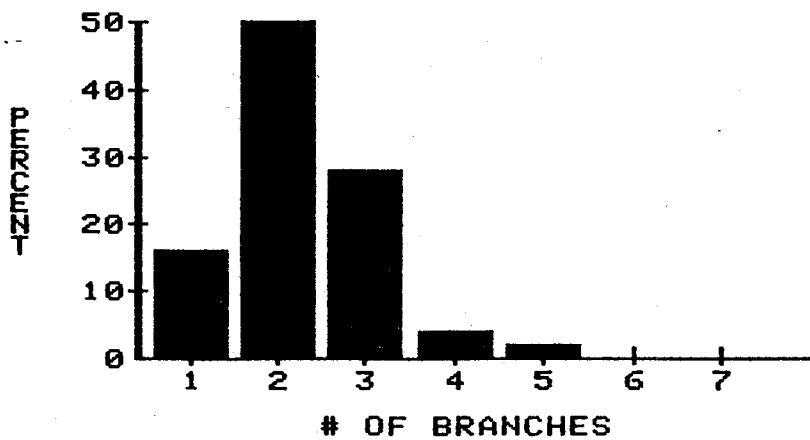


FIGURE 9-C

was an exception to this trend at the Blue River collection site where two specimens had short (less than the length of 5-C) multibranched 1-M. In 82.5% of my specimens seta 1-M was about equal in length to 5-C. This seta (1-M) is not as thick as 5-C and may be difficult to see without high-powered, microscopic examination. All of my specimens were mounted skins and were examined at 120 to 400 times magnification. My results agree with the description of this seta given by Bohart and Washino (1978) and Belton (1983). Interestingly, specimens of *A. hexodontus* from the Edmonton, Alberta, area had seta 1-M short and multibranched. If this seta is short and multibranched on specimens from northern Canada as reported by Wood et al. (1979), there may be two forms of *A. hexodontus*. The "tundra" variety having 1-M short and multibranched and the "type" form having this seta about equal in length to 5-C and being 1 or 2 branched. The specimens of *A. hexodontus* from Blue River area may be an example of differing populations of this species coming together in a suture zone. This area of British Columbia is referred to as the Northern-Cascade suture-zone (Remington 1968). I will elaborate about this in another section of the discussion.

Wood et al. (1979) described the metathoracic setae 1-T and 3-T as minute and multibranched. This was not always true in specimens that I examined. Seta 1-T was 10.3% single and 16.8% double.

The most important characteristics for identifying *A. hexodontus* larvae are the number of comb scales. They range in number from 4-14 on each side of the abdominal segment VIII, and there are usually 6 to 8 in most specimens (Wood et al. 1979). 55.4% of my specimens had 6 comb scales on one or the other side of the abdomen (Figure 3) and 99.0% had these teeth in a single row. The 1.0% that did not have a single row had these teeth organized irregularly.

The spinules on each comb scale ranged from 1/4 to 1/10 the length of the central apical spine.

The length of the comb scales has become important. I examined these scales under 400 times magnification with a compound microscope. If the tip of the central spine was broken off then that tooth was not measured. The mean length was calculated from the total number of scales on the larval skin. I could not determine from the literature whether other authors calculated the mean length from the teeth on both or just one side of the abdomen. The comb scales of *A. hexodontus* in British Columbia have a mean length of 0.113 mm (Table 1). This corresponds with the length measured by Wood (1977).

Aedes punctor (Kirby)

This species is a taxonomic paradox because the original specimens, that have been lost, were adults. Dyar (1904a,b) described what he thought were the larvae for this species but his description could be of *A. hexodontus*. By 1951, Knight was able to offer a more detailed description of the fourth larval instar for members of this subgroup. This is where the paradox arises for Knight could separate the *punctor* species in larval form, only. The true larval form to associate with the original adults of *A. punctor* will never be known.

Knight's (1951) *A. punctor* is divided into two forms and recent work shows the "tundra" variety to be *A. hexodontus* (Wood 1977). For this reason I will concentrate on the larval descriptions of *A. punctor* that are recorded by Wood et al. (1979). Knight based his "type" *punctor* primarily on adult characters and used abdominal setae to distinguish the two larval forms. These characteristics were not measured on my specimens collected in British Columbia as the setae could not be identified with certainty after mounting and often these hairs

became detached with the manipulation of the skins.

In the "Mosquitoes of Canada" (Wood et al. 1979) head hairs on *A. punctor* are described as being usually single. Setae 5-C and 6-C were single in 63.5 and 60.3%, respectively, for the specimens I examined (Figures 4 and 5). The range of branches fall within those recorded for *punctor* by the above mentioned authors.

Thoracic seta 1-P is described as usually double and 89.5% of my specimens agree with this (Figure 10). Wood et al. (1979) described 2-P and 3-P as single. These setae were single in 100.0 and 98.2% of my specimens, respectively (Figure 7 and 11).

The comb of the eighth abdominal segment has 5-25 scales, with usually more than 10. Only 8.1% of my specimens had fewer than 10 scales. The mean length of these scales is 0.084 and the range is from 0.073 to 0.097 mm. The longer scaled specimens approach the 0.10 mm length suggested as normal for *A. hexodontus*. In a plot of the mean length over the total number of comb scales (Figure 12) one specimen falls within the *A. hexodontus* range. This specimen from west of Prince George has 7 teeth on one side and 11 on the other side of the eighth abdominal segment. The mean length of these scales is 0.097 mm. As previously mentioned, I could not determine from the literature whether the mean length was calculated from both or just one side of the abdomen. I calculated the mean length of scales from both sides of the abdomen so it seemed fitting to plot the values accordingly. Figure 13 is the mean length over the total number of comb scales. In this plot the specimen from Prince George no longer overlaps with the *A. hexodontus*. I have included the "tundra" *punctor* of Knight (Wood 1977) that has been shown to be *A.*

Figure 10: Larval thoracic seta 1-P.
Figure 10A: *A. aboriginis* Dyar
Figure 10B: *A. hexodontus* Dyar
Figure 10C: *A. punctor* (Kirby)

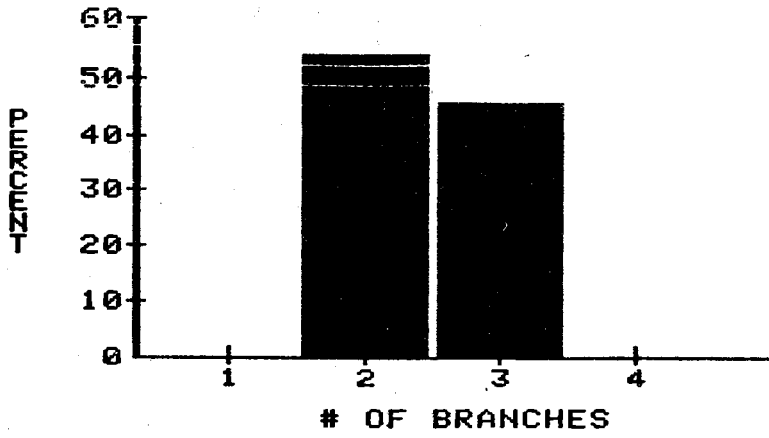


FIGURE 10A

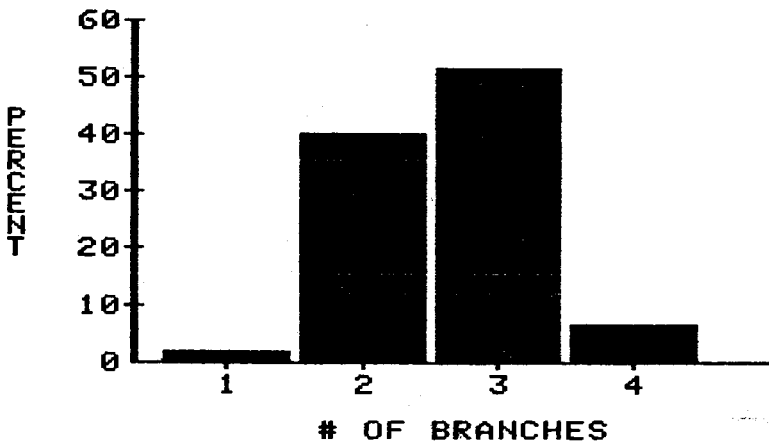


FIGURE 10B

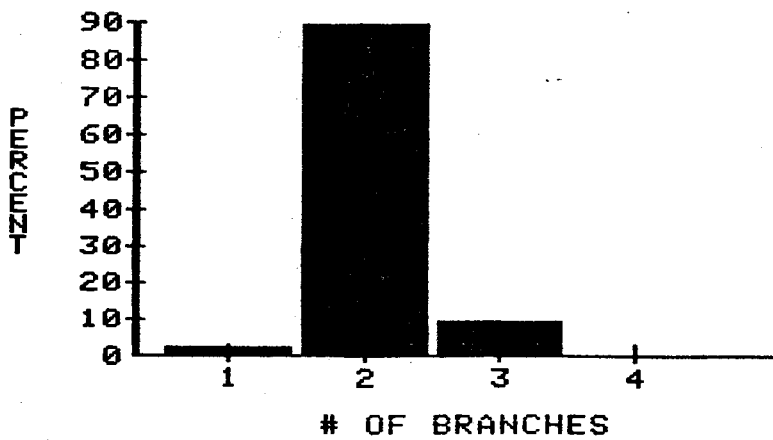


FIGURE 10C

Figure 11: Larval thoracic seta 3-P.
Figure 11A: *A. aboriginis* Dyar
Figure 11B: *A. hexodontus* Dyar
Figure 11C: *A. punctor* (Kirby)

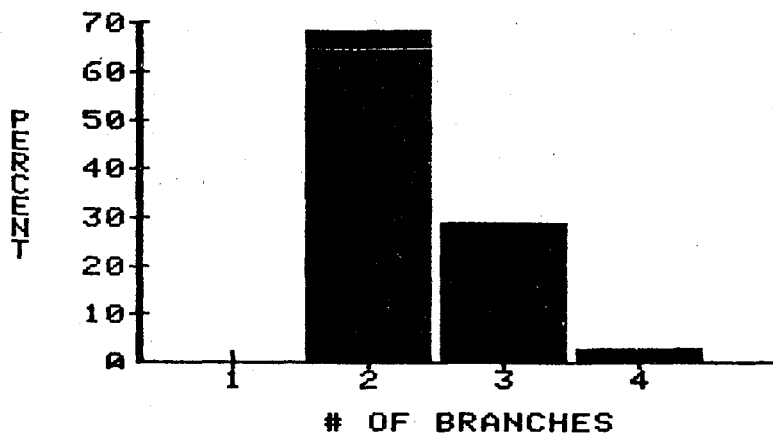


FIGURE 11A

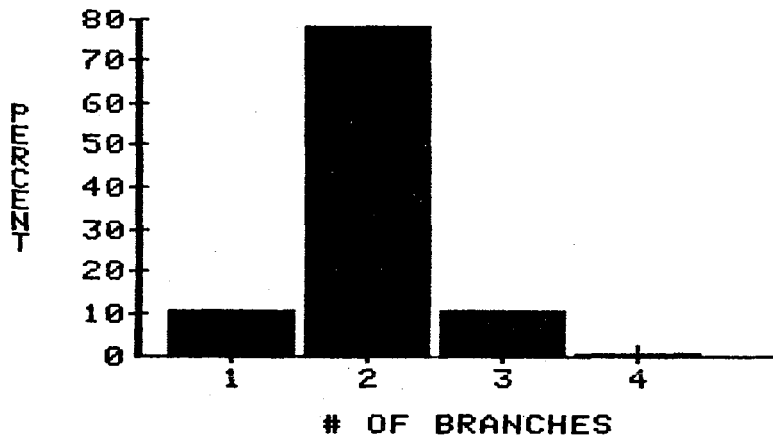


FIGURE 11B

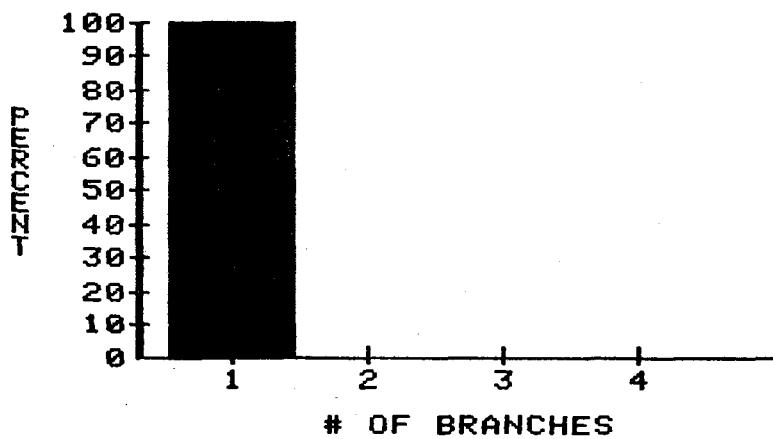


FIGURE 11C

Figure 12: Mean length vs number of comb scales (one side).
for *A. hexodontus* and *A. punctor*.

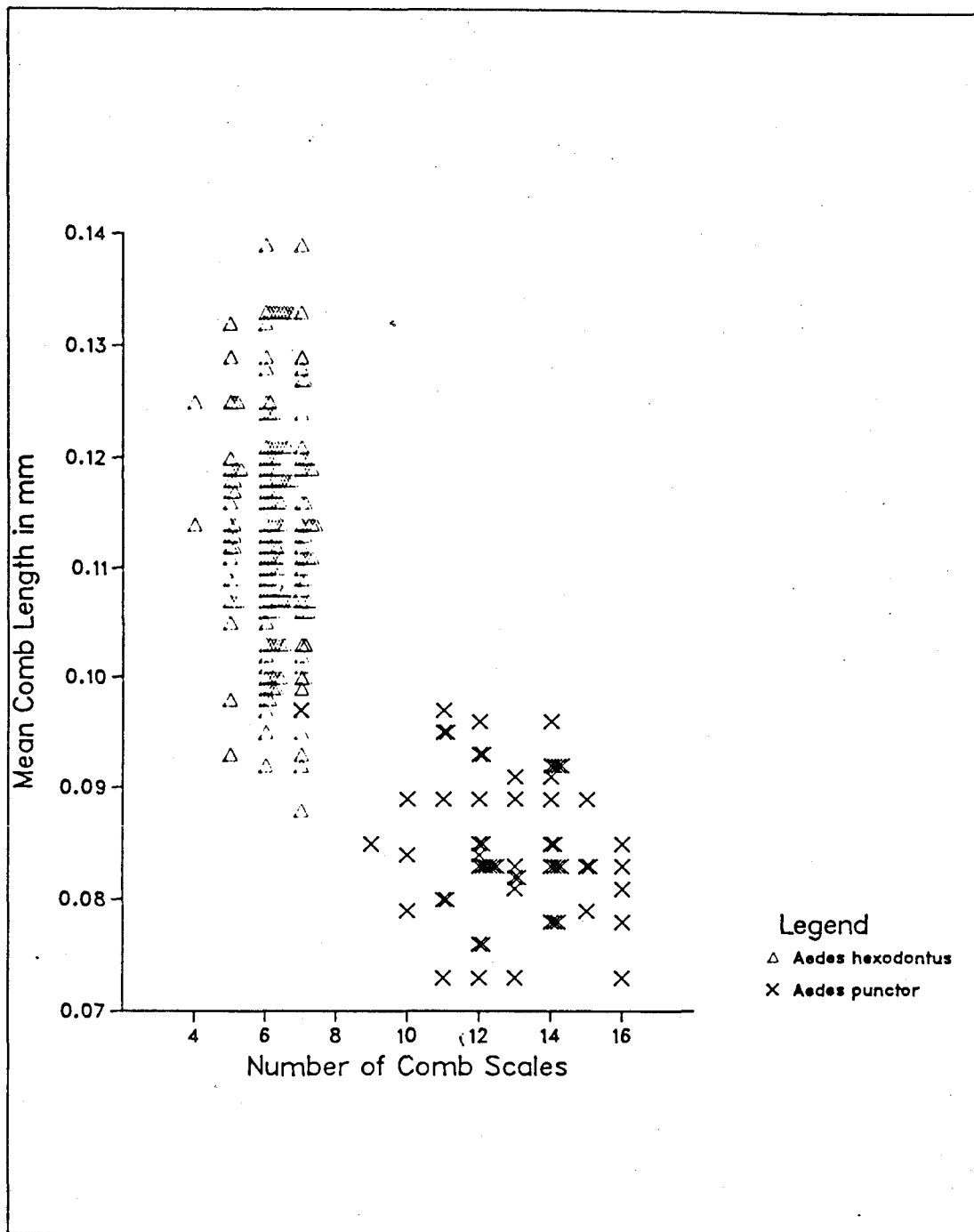
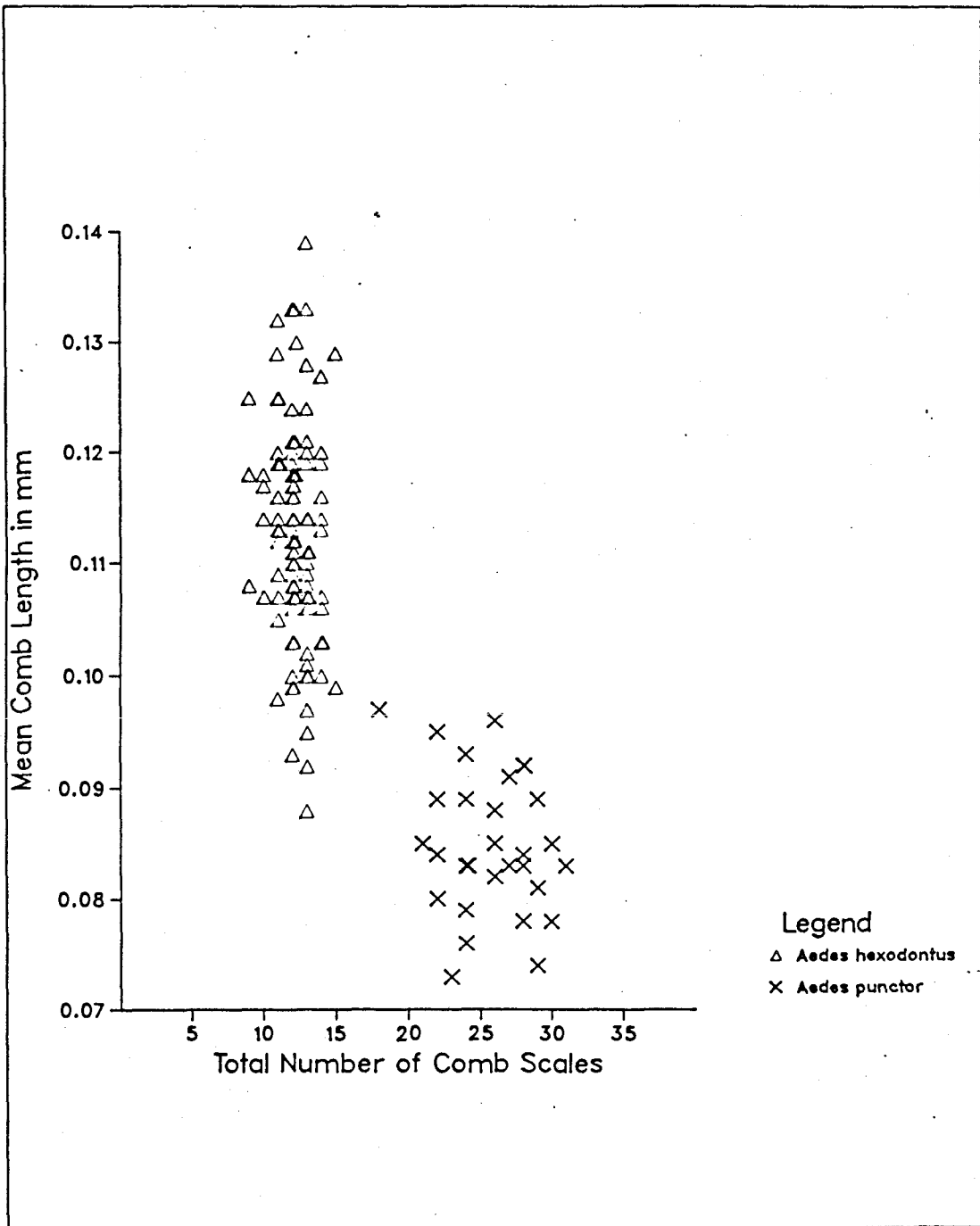


Figure 13: Mean length vs total number of comb scales
for *A. hexodontus* and *A. punctor*.



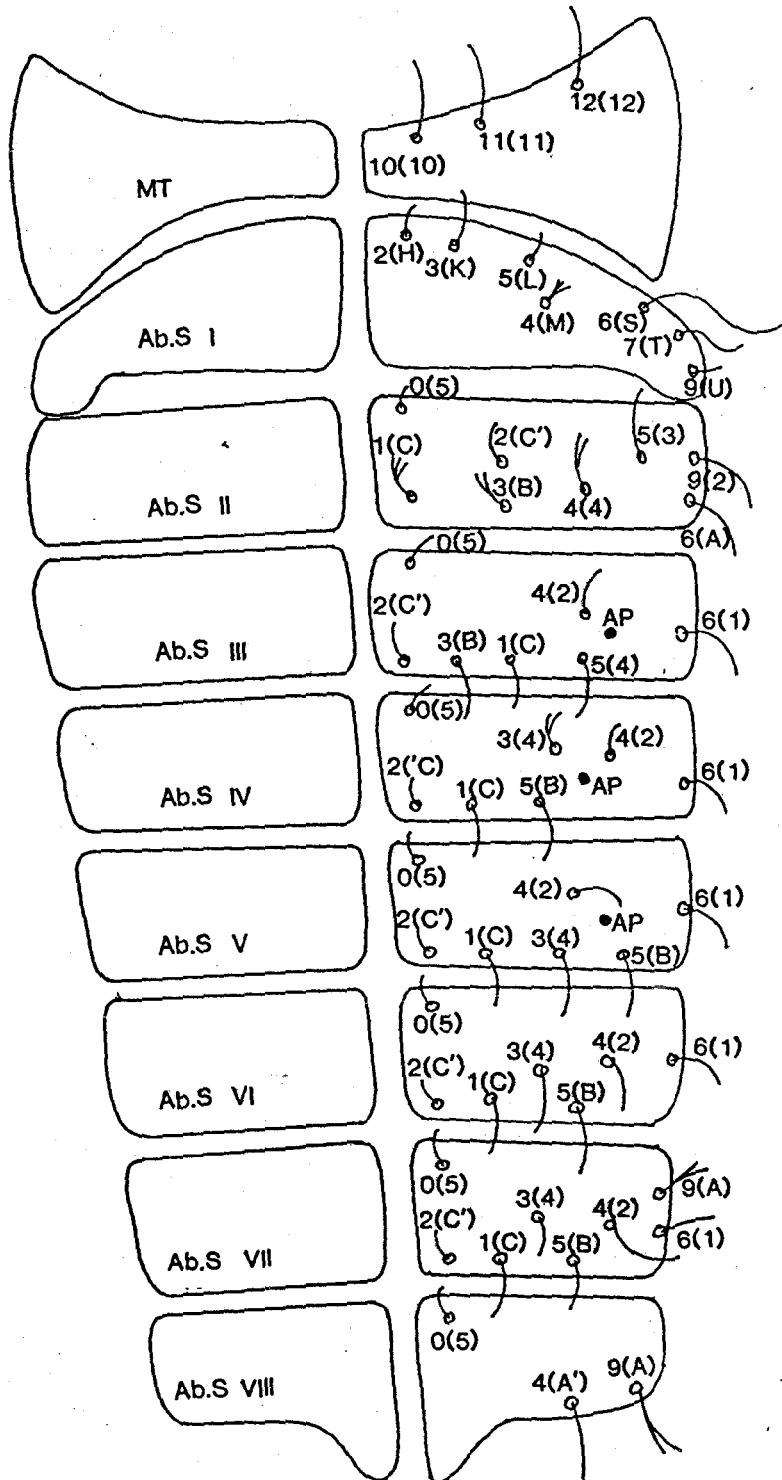
hexodontus. It does not fall within the scattering of points for *A. punctor* in Figure 13. It would be interesting to rear *A. punctor* at low temperatures to see if the comb scale length could be manipulated to overlap with *A. hexodontus* specimens. All adults of my specimens of *A. punctor* with long comb scale lengths conform to the descriptions for this species (lacking the patch of white scales at the base of the wing).

In my specimens of *A. punctor* the mean comb scale length was always less than the length of the the last two pecten teeth. The spinules of the comb scales tended to be longer compared with central spine in *punctor* as opposed to *hexodontus*.

Pupal characters

The information on pupal morphology of the *punctor* subgroup is found in Darsie's (1957) key to known nearctic *Aedes* pupae. He felt it was impossible to characterize accurately Edwards (1932) groups on the basis of pupae. To make this situation worse I found it difficult to determine all the setae that Darsie illustrated. This is the reason for listing Darsie's results with those from my specimens. The location of these setae with Harbach and Knight's (1980) morphological conventions is illustrated in Figure 13. The labeling of these setae according to Darsie is included in brackets. If any of my interpretations are wrong then this information will make them easy to correct.

Figure 14: Generalized *punctor* subgroup pupa.
(after Harbach and Knight (1980) and Darsie (1957))



MT - Metathorax
 Ab.S - Abdominal Segment
 AP - Abdominal puncture

Aedes aboriginis Dyar

Darsie's (1957) key for the *punctor* complex separates *aboriginis* in the first couplet, from all other species in this subgroup. The first character mentioned is seta 5-II (3-II); in this species it should be single, seldom double. Seta 5-II is single on 90.70% of my specimens. *A. hexodontus* and *A. punctor* had 5-II single 9.62% and 6.67% of the specimens, respectively. Seta 5-III (4-III) is said to have 1-3 branches but in his table of summarized data it ranges from 1-6 branches (see Table 2). My specimens of *aboriginis* had 5-III with 1-3 branches on 85.3% of the specimens, although 14.63% were 4 branched. Seta 6-III (1-III) on Darsie's *aboriginis* were generally unbranched as were 79.07% of my specimens (16.28% with 2 branches and 4.65% with 3). The last diagnostic setal character for *aboriginis* that is used by Darsie is 6-IV. This seta is located on the underside of my mounted skins and was not examined.

Aedes hexodontus Dyar

This species is separated from *aboriginis* in the first couplet of the key to *punctor* species, as mentioned above. In *A. hexodontus* seta 3-II is multi-branched on 90.38% of specimens; only 9.62% were single like *aboriginis*. Seta 4-III is 11.76% 2-branched, 23.53% 3-branched and 64.71% with 4 or more branches. Only 14.63% of the *aboriginis* had 4 branches. Seta 1-III is 63.04% branched whereas 20.93% of the *aboriginis* had 1-III branched.

A. hexodontus and *A. punctor* are separated from *A. abserratus* and *A. punctodes* (in part) in the succeeding couplet of Darsie's key. Seta 9-VIII should have 3 or more branches. My *hexodontus* had 4.55% with 9-VIII double and 95.45% were 3 to 7 branched. Seta 6-VII for the *hexodontus-punctor* group according to Darsie should have more than 3 branches. My *hexodontus* were

8.47% double, 22.03% triple and 65.80% with 4 or more branches. As previously mentioned 6-VI was not measured although Darsie noted that this seta was 3 or 4 branched.

The next couplet separates *A. hexodontus* and *A. punctor* from all other examples of *A. punctodes*. The first character states that 6-I should be longer than 7-I. This is true for my specimens of *hexodontus*. Seta 5-IV should be double for *hexodontus* and 64.91% were 2-4 branched on my specimens. Darsie found most specimens to have this seta double; I found 59.65% to have 2 branches.

The last couplet of Darsie's key separates *A. hexodontus* from *A. punctor*. A problem arises at this point because the "tundra" variety of *A. punctor* in the Canadian National Collection has been identified as *hexodontus* (Wood 1977). In light of this fact, I have found problems with Darsie's key, probably because he was using a misidentified specimen. The first character he uses is seta 8-II. On my mounted skins this seta is located on the underside of the specimens. With high power magnification a small trichopore (at least a pore with a small stubby seta) was visible on some specimens. The results of these observations are as follows; 20.65% with no pore or seta, 32.61% with a trichopore (and short seta) and 46.74% with a seta. *A. punctor* shows considerable overlap with *hexodontus* in this character (34.55% with no seta, 54.55% with trichopore and 10.90% with a seta). I feel that this overlap renders this character useless for separating these species.

The second character Darsie uses is seta 1-III (C-III). For *hexodontus* it is described as double or triple. My specimens have 86.44% with 1 to 3 branches and 13.56% with 4 or 5 branches. The situation with *A. punctor*, that is

supposed to have more than three branches, is not as clear because 42.86% had 1 to 3 branches and 57.14% with 4 to 8 branches. As in the first character used by Darsie, the overlap between species makes its use questionable.

The last character used to separate *hexodontus* from *punctor* according to Darsie is the branching of CT-8. This seta should be pedunculate (basal 1/12 unbranched) in *hexodontus* and branched near the base in *punctor*. On my specimens CT-8 appeared to be pedunculate for both species. The number of branches are as follows; 81.70% have 1-3 branches and 18.30% with 4-5 in *hexodontus* and 10.30% with 3 branches and 89.70% with 4-9 branches in *punctor*.

Within the last couplet Darsie divides *A. hexodontus* into a type form and "tundra" variety. If these forms of *hexodontus* are true, then I would expect my specimens to conform to the type description. Darsie describes the type as follows: 5-II (3-II) single to triple, 5-III (4-III) double to quintuple and MT-11 usually double. In my specimens, seta 5-II is 9.62% single, 59.62% 2-branched, 28.84% 3-branched and 1.92% 4 branched. The "tundra" variety as described by Darsie has this seta 4-7 branched. Seta 5-III was 11.76%, 23.53%, 41.18%, 21.57% and 1.96% with 2, 3, 4, 5 and 6 branches, respectively. Darsie's "tundra" variety has 6 or more branches. Mesothoracic seta MT-11 is described as usually double in the type *hexodontus* and in my specimens 36.60%, 53.80% and 9.60% were 1, 2 and 3-branched. The "tundra" variety is described as having MT-11 single. The specimens that I have examined tend to conform to the type *hexodontus* descriptions that are presented by Darsie.

Aedes punctor (Kirby)

This species was separated from *aboriginis* in the first couplet of Darsie's key. *A. punctor* has seta 5-II single in 6.67% of my specimens, 5-III 3-branched on only 4.00% and 6-III (1-III) was never unbranched. These characters should separate *A. punctor* from *A. aboriginis* in most instances.

In the second couplet, where *hexodontus* and *punctor* are separated from *abserratus* and *punctodes* (in part), seta 9-VIII (A-VIII) was described as more than 2 branched in the former species. Seta 9-VIII in my specimens of *A. punctor* was 3-17-branched (Table 2). This seta was usually (72.23%) 3-5-branched. The *hexodontus-punctor* group was described as having 6-VII (1-VII) with more than 3 branches. Only 5.88% of my *punctor* specimens had 3 branches, the others were 4-9-branched (94.12% of specimens).

In the last couplet where *punctor-hexodontus* are separated from *punctodes* (in part), seta 6-I was longer than 7-I on my specimens, as Darsie stated. The second character of the couplet describes 5-IV (B-IV) as being single in *punctodes*. *A. punctor* from my collections was single in 54.55% of the specimens and double in 45.45%. This latter character does not seem reliable for my *punctor* specimens.

The last couplet separating *A. hexodontus* from *A. punctor* does not seem reliable, as previously discussed with *hexodontus*. Within this couplet *A. punctor* is divided into a type and "tundra" variety. My specimens conform to the type *punctor* description. The following seta are described as usually 2-branched but sometimes 3 or 4-branched: 1-IV, 1-V and MT-11. My specimens have seta 1-IV with 50.00% with 2, 40.62% with 3 and 9.38% with 4 branches. Seta 1-V was 2.78%, 58.33%, 30.56% and 8.33% 1, 2, 3 and 4-branched, respectively. Seta

MT-11 was 36.60%, 53.80% and 9.60% 1, 2 and 3-branched, respectively. In all cases at least 50.00% of the setae mentioned were double in my specimens.

Many of my *hexodontus* actually overlap with the "tundra" variety of *punctor* description suggested by Darsie. For seta 1-IV, 54.55% of my *hexodontus* were single and for 1-V, 71.43% were single. The difference was not as distinct for seta MT-11, for only 36.60% were single. If these "tundra" *punctor* are *hexodontus* as indicated by Wood (1977), it seems likely that Darsie was describing *A. hexodontus*.

New pupal characters will be useful to separate *hexodontus* from *punctor* since the characters chosen by Darsie seem to be inadequate. A trend that appears in my results is that most setae on *A. punctor* seem to be more highly branched. Some examples where there is only a small overlap are shown in Table 7. I believe that these characteristics are useful in separating *hexodontus* (type form) from *A. punctor* pupae but should be considered tentative until more of the northern *hexodontus* are examined.

Female characters

Adults of the three species in the *punctor* subgroup that I have collected in British Columbia are exceedingly difficult to separate. The characteristics that will be discussed apply primarily to specimens from this region of North America and should be considered tentative until more northern specimens are examined. All of the adult specimens described below were reared from and identified by examination of larval skins. The adults conformed to the most recent descriptions by Wood et al. (1979) and Darsie and Ward (1981).

Table 7: Important pupal characteristics for *hexodontus* and *punctor*.

Seta	<i>hexodontus</i>		<i>punctor</i>	
	Number of branches	Percent of specimens	Number of branches	Percent of specimens
1-II	1-3	87.70	1-3	16.66
	4-9	12.30	4-6	83.34
3-IV	2-3	100.00	2-3	9.38
			4-8	90.62
1-V	1	71.43	1	2.78
	2	28.57	2-4	97.22
1-VII	1	90.00	1	17.65
	2-3	10.00	2-3	82.35

In Chapter VI of the discussion I have included a generalized description that fits members of this subgroup. Rather than repeating a description of these traits I will concentrate on other characters such as: antennal-pedicle cuticular ground color, setal color and scale color (and patterning). In addition I have included the presence of scales on the postprocoxal membrane, probasisternum and pale scales on the costa of the wing.

Aedes aboriginis Dyar

The color of various characters has been used in separating the adult specimens of the *punctor* subgroup. The cuticular ground color has often been discussed but seldom used as a taxonomic character. A region of the body that is easy to observe is the pedicle of the antennae. The medial margin is the only portion that is covered by a patch of scales. Specimens of *A. aboriginis* have a bright yellow ground color on the pedicle, although some are yellow laterally and light-brown to black medially. One specimen was light-brown laterally and black medially. I have found this to be a useful character; it is helpful with field-collected specimens because it is reliable, unlike scales and setae that may become detached. It is unknown to me if this coloring will change over the season or long periods of time (as in museum specimens). This character was totally reliable in separating specimens of *aboriginis* from *hexodontus*.

The color of setae on the body of adults has been used as a character and although Dyar did not mention setal color he did say the specimens were dark (testaceous). On my specimens of *A. aboriginis* the vertex of the head had pale setae medially and a few black laterally. The scutum had black setae on acrostichal and dorsocentral rows. Posterior to the transverse suture, the setae

became pale in color (from light-brown to yellow). The supra-alar setae were pale on all specimens, at least at the base (some setae had black tips). This was true for the scutellar setae except for a single specimen that had two black setae (all others were pale). Color of setae is useful on reared specimens but of little value on badly rubbed field specimens.

The scale color and patterning is one of the characteristic most widely used by mosquito taxonomists. Scales on the antennal pedicel ranged from black, black and pale, to entirely pale. The scutal scales usually formed patterns dorsally, which are: distinct dark-brown medial stripe or 2 lateral dark-brown stripes that are separated by a pale-scaled stripe medially. Some specimens had postsutural sublateral dark-brown half-stripe in addition to the medial coloration. One specimen had no distinct pattern but the arrangement gave the impression of 2 medial stripes. The abdominal tergites had basal white bands of white scales that were expanded laterally. In some the lateral expansion of scales extended from the basal to the apical edge thus making the apical black band incomplete across the tergite. The abdominal sternites were primarily white-scaled with median black patches on segments 3 to 6.

The presence or absence of scales on some areas of the body is important in distinguishing these species. On *aboriginis* the probasisternum was usually bare although 2 to 8 scales were located dorsally on this segment in some specimens. The postprocoxial membrane was heavily scaled on at least the dorsal half. The wings were primarily dark-scaled but some specimens had a few white scales at the base of the wings. At most there were 4 white scales at the base of the wing in any one specimen.

The presence of lower mesepimeral setae was one character that Edwards (1932) used to describe Group G (*communis*) in the *Ochlerotatus* subgenus. He felt these setae should be present and rather numerous. On my specimens of *A. aboriginis* 40.0% had no lower mesepimeral setae on either side of the thorax. There is a possibility that these setae became detached although no visible insertion point was visible. Neither *A. hexodontus* nor *A. punctor* specimens lacked these lower mesepimeral setae.

Aedes hexodontus Dyar

Of the three species collected from British Columbia, *hexodontus* was the most distinct. Ground color of the antennal pedicel was especially distinct. 68.42% had an entirely black pedicel, 29.83% were black medially and dark-brown laterally. One specimen was entirely dark-brown. This contrasts with *aboriginis* which has a yellow to light-brown color.

The setae on this species were usually black but light (pale yellow) on *aboriginis* and *punctor*. The vertex of the head was usually covered with black setae (72.73%). Only 23.63% had equal numbers of pale and black setae while 3.64% had lost most of these setae. This is in contrast with *aboriginis* that has pale setae, at least medially, whereas *hexodontus* has predominately black setae. Dorsally on the scutum all three *punctor* species were covered with black setae that would become mostly pale toward the posterior of the scutum. In 45.45% of the *hexodontus* specimens the dorsal scutal setae were entirely black (without pale posterior setae). The supra-alar region of the scutum was black dorsally and pale ventrally unlike the other two species that were primarily covered with pale setae. *A. aboriginis* had pale supra-alar setae although some specimens did have black-tipped setae. The scutellar setal color was variable with *hexodontus*

and ranged from entirely pale to black with a few pale setae.

The most commonly used characters used to separate females of these three species are scale color and patterning. I observed three general patterns on the scutum; median dark-brown scales that formed a stripe with scattered medial pale scales, distinct dark-brown sublateral stripes that was divided by a median pale-scaled stripe, and no distinct color pattern although the arrangement suggested sublateral stripes. The abdominal tergites II to VII had basal transverse bands of pale scales. These bands were not usually expanded laterally to cut off the black (81.8% of the specimens). This contrasts with the observations on *A. aboriginis* and *A. punctator* that were 40.0% and 13.6% with the lateral expansion cutting off the black on one or more segments. The scale pattern on the abdominal sternites of *A. hexodontus* were primarily pale on segments II to VII. Segment VIII was bare or had a few scattered scales, and segment I was bare. There were some basal-lateral black patches that joined to form a band on segments III to VI. This contrasts with *A. aboriginis* which had a median patch, giving the impression of a black line running from the anterior of III to posterior segment VI.

The probasisternum of *hexodontus* had more than 20 scales on 87.1% of the specimens and 1.8% had fewer than 10 scales on this sternite. This contrasts with *aboriginis* that had fewer than 10 scales. The postprocoxal membrane was heavily scaled on the dorsal 1/2 in 84.1% of the specimens and had only a few scales on the dorsal 1/2 in 15.9% of the specimens. The number of pale scales at the base of the wing was high on most *hexodontus*. 41.8% had a large patch (too many to count), 54.6% had 10 or more scales and 3.6% had only 8 pale scales at the base of the costa.

A. punctor (Kirby)

The cuticular ground color of the antennal pedicel was observed on female *punctor*. 86.4% had a yellow color, either entirely yellow or dark medially and yellow laterally. 13.6% were light-brown and black medially. This contrasts with *hexodontus* that was black, black medially and dark-brown laterally, or entirely dark-brown. Although color is a subjective observation, the yellow, as opposed to black (in *hexodontus*), is quite distinct. A problem may arise in separating a light-brown pedicel from a dark-brown one (rather than black or yellow). An alternative character should be used to distinguish these species in such instances.

The setae on *punctor* were primarily pale in color. The vertex of the head was pale with a few lateral black setae. This contrasts with *hexodontus* (in which the setae are primarily black). The scutal setae were black on the anterior and medial portions but pale laterally and on the posterior edges. The scutellum usually had pale setae with only 1 or 2 black on 4.5% of the specimens. The supraalar setae were entirely pale on 63.6% of the specimens. If there were any black setae then they were located dorsally on the supraalar region of the thorax.

The scales on the pedicel were pale or white scales on 42.1% of specimens and the other 57.9% were pale but mixed with black. The scutum had a single, median, dark-brown stripe of scales in 86.5%, 4.5% appeared to have a pair of medial, dark-brown stripes and 9.0% had no distinct color pattern. This latter group had the scales arranged in a manner that suggested a median stripe. The abdominal tergites had a pale basal band of white scales which became expanded laterally to cut off the black apical band of scales. 13.6% were not expanded

laterally as previously described. The abdominal sternites were usually bare on 1, white scaled on segment II, apical triangular patch of black on segment III to VII and a few scattered pale scales on VIII. 8.3% had a medial, black patch of scales on III to VI with otherwise white-scaled sternites.

The probasisternum was bare on 18.5% of the specimens, 66.7% had less than 10 scales and 14.8% had 10 to 20 scales. The postprocoxal membrane had only a few scales on the dorsal half in 40.6% of specimens and the other 57.4% were heavily scaled on the dorsal half to three-quarters of the membrane. The wings were entirely black scaled in 47.6% of specimens. All others had fewer than 7 pale scales at the base of the costa.

Male characters

Males are often the most difficult stages to identify although the structures of the genitalia usually show the most distinct differences between species. The genitalia of *A. aboriginis*, *A. hexodontus* and *A. punctor* are exceedingly similar. By treating specimens with acetone (Truman 1968) the genitalia remain expanded as they are in live insects. I found no differences except for the single, enlarged seta of the basal dorsomesal lobe of the gonocoxite. In specimens of *A. punctor* this seta was straight for the basal 2/3 and the apical segment of this seta formed a gradual curl. In *A. aboriginis* this seta was straight for the basal 2/3 then it bent at a 90° angle. This bend was followed by a straight portion and the very tip was gradually curled. *A. hexodontus* had 90.6% of the specimens with this seta of the basal lobe as described for *A. punctor* and 9.4% were like those described for *A. aboriginis*. This seta is often difficult to see and could not be observed on many of the specimens. An illustration of the

Fennoscandian *punctor* species by Dahl (1974) shows three species (*A. hexodontus*, *A. punctodes* and *A. punctor*) with the enlarged seta as I have just described for *aboriginis*. Before any assessment can be made of this character more specimens from different regions must be examined.

Many of the characteristics used for females can be used for males but scales and setae are often reduced or absent. The genitalia of these species are so similar that I resorted to other characteristics to establish differences between the *punctor* species in the subgroup. For each of the species I collected in British Columbia, setal color, scale color and patterning, and presence of scales on the probasisternum, postprocoxal membrane and the wing bases, were observed.

A. aboriginis Dyar

The setae on the vertex of the head were primarily pale (95.5%) and seldom accompanied by any that were black. 4.5% had a single black seta on the vertex. The scutal setae were variable, 23.8% having pale, 4.8% entirely black and 71.4% black anteriorly and dorsally but pale posteriorly and ventrally. Supraalar setae were primarily pale (90.9%), and when present there were never more than 3 black. Scutellar setae were primarily pale (90.5%) and 9.5% had a single black seta.

The scales on the vertex of the head were pale-yellowish or yellow (85.7%) but often specimens had some black scales on the posterior margins. The scutal scale patterning was quite variable. 18.2% were bare, the others ranged from an indistinct color pattern (9.1%), distinct median, dark-brown stripe (40.9%) to distinct dark-brown, sublateral stripes separated by a pale-scaled, median stripe (31.8%).

The probasisternum usually lacked scales (65.0%) but some had 1 to 5 dorsally placed scales. The postprocoxal membrane was scaled on 95.0% and 5.0% were bare. The base of the wing was entirely black at the base in 91.0% of specimens and 9.0% had 1 to 3 pale scales.

A. hexodontus Dyar

The setae on the vertex of the head were entirely black in 68.0% of specimens, 12.8% had less than 5 pale setae and 19.2% had a mix of black and pale setae. Scutal setae were entirely black on 63.8% and black with a few posterior setae pale on 86.2% of the specimens. The supraalar region had a few pale setae on 47.7% of specimens and the rest were entirely black. The scutellum had entirely black setae on 10.9%, mostly black with a few setae pale on 47.8%, mostly pale with a few black on 30.4% and entirely pale on 10.9%.

The scales on the vertex of the head were mostly yellow on the anterior and black towards the posterior with only 11.6% entirely yellow. The scutum was often bare (32.1%) but usually there were sublateral stripes of dark-brown scales (50.0%). 1.8% of the specimens had a single, median, dark-brown stripe with no central pale scales, while the other 16.1% were uniformly colored.

The probasisternum was often bare (28.3%) but those with scales ranged from 2 to a large patch. A patch is a dense association of scales, too numerous to count. Only 8.7% of the specimens had 10 or more scales on the probasisternum. The postprocoxal membrane was bare on 11.6% of specimens but usually (88.4%) there were 2 or more dorsally placed scales. All specimens had pale scales at the base of the wing: 6.5% had 4 pale scales the other 93.5% had 8 or more.

A. punctor (Kirby)

The setal color on *punctor* specimens was primarily pale in color as opposed to the black setae on *A. hexodontus*. The vertex of the head had only pale setae on all specimens which is similar to *aboriginis*. The scutum of *punctor* had a mixture of pale and black setae on 55.6% of specimens and pale setae on 44.7%. *A. hexodontus* was never entirely pale and *aboriginis* exhibited all of these conditions. The setae of the supraalar region and scutellum were always pale on *A. punctor*.

The scales on the body were a variety of colors on *punctor* from white, to pale-yellow, to bronzy. The vertex of the head was primarily yellow on 89.9% of specimens, the other 11.1% had a few posterior black scales. The scutum was bronzy to yellow laterally with a distinct, median stripe of dark-brown scales. 22.2% of these had a few median-pale scales but not enough to give the impression of a median stripe of pale scales.

The probasisternum was bare on most specimens (77.8%), others had 1 or 2 dorsally placed scales on the sternite. This is similar to the other *punctor* species although *A. hexodontus* had only 8.7% with 10 or more scales on this sternite. The postprocoxal membrane was scaled on all of the specimens. The base of the wing was entirely dark-scaled on 88.9% of the specimens, the other 11.1% had a single, pale scale. This is similar to *A. aboriginis* but different from *A. hexodontus* that had 8 or more pale scales on most specimens (93.5%).

EVALUATION OF TAXONOMIC KEYS

The information presented thus far is useful in evaluating keys to *A. aboriginis*, *A. hexodontus* and *A. punctor* from British Columbia. I will start with Knight's (1951) key to larvae and continue with major North American mosquito treatises from 1951 to date. This will be followed by the regional keys of the west coast of North America.

Knight (1951)

In Knight's larval key, *A. aboriginis* is separated from the other species by the comb scale number, branching of head hairs 5-C and 1-A and a non-encircling saddle. Most of these characteristics are satisfactory in separating this species from *hexodontus* and *punctor*, except that one of my specimens had the saddle encircling the anal segment. This does not present a major problem because the branching of the head hairs is always much greater in *aboriginis* than the other *punctor* species.

A. hexodontus is separated from *punctor* and *punctodes* by the comb having a row of 5-9 (rarely 10) large teeth on either side of the abdomen. This description fits the *hexodontus* I have recorded. A problem arises with *A. punctor* having 7, 9 or 10 comb scales (Figures 3C and 12). These specimens could be misidentified using this key.

Vockeroth (1954)

In 1954 Vockeroth (1954b) presented a key for female *Aedes* of northern Canada. He included three members of the *punctor* subgroup; *A. abserratus*, *A. hexodontus* and *A. punctor*. Before this, *A. hexodontus* was recorded only from the southern United States. Rempel (1950) had included *A. cyclocerculus* Dyar (= *hexodontus*) as the Canadian equivalent for this species. Vockeroth separated *A. punctor* on the basis of the scale pattern of the scutum. His description is: "mesonotum with sharply defined dark-brown, median line or lines; lateral margins of the mesonotum yellow-white to yellow-brown." The alternative that leads to *hexodontus* and *abserratus* is; "mesonotum almost uniformly brown, sometimes with indications of a median line due more to the arrangement of scales." *A. hexodontus* has considerable variation in scutal scale coloration and fits Vockeroth's description of *A. punctor* (Table 3). *A. hexodontus* was separated from *A. abserratus* by the patch of pale scales at the base of the wing.

Carpenter and LaCasse (1955)

The work by Carpenter and LaCasse was the first major taxonomic treatise since Knight's (1951) revision of the *punctor* subgroup. These authors did not make use of the characters suggested by Beckel (1954) and Vockeroth (1954b). Both *A. hexodontus* and *A. punctor* were divided into type and "tundra" forms based on adult characters. The *A. punctor* "tundra" variety is of doubtful validity (Wood 1977). For this reason I will examine the larval key in detail and briefly discuss the adult keys.

An important character used at the beginning of the larval key (Carpenter and LaCasse 1955) is the saddle encircling the anal segment. This separates *A. aboriginis* from *A. hexodontus* and *A. punctor*. This character is good for all but

one of my specimens. *A. aboriginis* is similar to *A. pullatus* (Coquillett) in larval form. These authors use a character of the comb scales to separate these species. *A. aboriginis* is stated to have spinules less than 1/2 the length of the central spine. Table 1 shows that some specimens of *aboriginis* have large spinules that are greater than one-half the length of the central spine. Some spinules were equal in length to the central spine in my specimens. In these cases it would be difficult to separate these species.

A. hexodontus is separated from *A. punctor* in the larval key on the basis of comb scale number. *A. hexodontus* is identified by a 4-9 scaled comb in a single row. 99.0% of the *A. hexodontus* I examined would be identified correctly in having a single row of comb scales. 8.1% of my *A. punctor* could be incorrectly identified because they had 7-9 comb scales in an irregular or double row. 1.0% of my *hexodontus* had an irregular row of comb scales and 11.8% of my *punctor*. As you can see there is a possibility of misidentifying some specimens of *A. punctor* as *A. hexodontus* using these characteristics.

The female key in Carpenter and LaCasse is of limited value in separating specimens of the *punctor* subgroup. It relies heavily upon the scale patterning on the scutum. I found this character to be extremely variable for *A. aboriginis*, *A. hexodontus* and *A. punctor* (Table 3). The key for males does not even attempt to separate these species. Specimens are so indistinct that all the *punctor* species are grouped into the last couplet of the key.

Darsie and Ward (1981)

This work is a supplement to the "Mosquitoes of North America" by Carpenter and LaCasse (1955). It identifies larvae and females to species and gives distribution maps based on the most recent literature records.

The larval key uses many of the same characteristics as Carpenter and LaCasse (1955). In the couplet that separates *A. hexodontus* from *A. punctor*, they have added the words large and small to describe the comb scales of the VIII abdominal segment. Although the additional description is an improvement, it should be qualified.

In succeeding couplets that separate *hexodontus* and *punctor* from other species, seta 1-X is used as a character. For *hexodontus* 1-X is described as equal in length or longer than the saddle. I found 79.0% to be equal or longer, 19.8% almost equal and 1.2% were shorter. Darsie and Ward describe seta 1-X on *A. punctor* as subequal in length to the saddle. I found 96.7% were equal and 3.3% almost equal.

The larvae of *A. aboriginis* key to a couplet shared with *A. schizopinax* Dyar. The couplet reads: "posterior border of the saddle without aciculae and seta 1-M single (*aboriginis*) or posterior border of the saddle aciculated and seta 1-M with 3-6 branches (*schizopinax*)." Illustrations of an aciculated saddle is presented with the couplet. Frohne (1955b) was the first to use saddle spines in keying out *Aedes* species. The branching of seta 1-M is easier to observe than the saddle spines, at least with a dissecting microscope. I examined the number of branches of 1-M and found 4.5% of the *aboriginis* to be double (Figure 9A).

A. pullatus (Coquillett) has larvae similar to *A. aboriginis*. This species has a short seta 1-X, much shorter than the saddle. All of my specimens of *aboriginis* have seta 1-X equal to or longer than the saddle. This seems to be a useful character in separating these two species.

The key to females is an improvement over its predecessor (Carpenter and LaCasse 1955). The use of scutal markings is replaced with other characteristics.

These include the scaling of the postprocoxial membrane and probasisternum. The presence of lower mesepimeral setae is still used. Some of my *aboriginis* specimens lack these setae, which are used as part of the couplet that leads to this species.

Scaling of the proepisternum (probasisternum) is used to separate *A. aboriginis* and some specimens of *A. punctor* from the rest of the *punctor* subgroup. The couplet chooses between "without scales on the anterior face, at least in the ventral 1/2 and fully scaled." My specimens of *aboriginis* had some dorsal scales on this sternite. In these instances it was difficult to determine whether the scales were attached to the sclerite or just overlapping from surrounding areas. I did not find scales on the ventral portion of this sternite in *aboriginis*. *A. punctor* was variable in this respect, 20.0% of my specimens entirely bare and 15.4% with more than 10 scales on the probasisternum. I think my observations reflect the indecisiveness of this character where *punctor* may split either way at this couplet. *A. aboriginis* may have few if any scales (on probasisternum), while *A. hexodontus* may have primarily heavy scaling and *A. punctor* none to many scales.

In the portion of the key that includes *A. aboriginis* and *A. punctor* (in part), these species are separated from *A. implacatus* Vockeroth. The distinction is based partly on the number of scales at the base of the costa. They describe the *punctor* members as having fewer than 7 pale scales at the base of vein C. All of my *aboriginis* had fewer than 4 pale scales at the base of the wing. *A. punctor* had 90.5% of the specimens with 4 or fewer pale scales at the base of the costa and 9.5% had 6 pale scales. My specimens of *A. hexodontus* had 10 or more pale scales on 94.4% of the specimens and 3.6% had 8 scales. I found this to be a useful character in separating *hexodontus* from *aboriginis* and

punctor. In the last couplet of the key *A. hexodontus* is separated from *A. abserratus*, *A. punctodes* and *A. punctor* (in part) by this character of the wing-base scaling. They also describe the abdominal sternites III to VII as being pale-scaled apically (rarely with few dark scales) for *hexodontus*. An illustration shows *hexodontus* as entirely pale and *punctor* as having a large, basal triangular-patch of black scales. I examined the scale patterns on the abdominal sternites and found them comparable but not as clearly different as in their illustration. Most of the *hexodontus* had lateral black patches of scales on segments III to VII but none had a large basal, triangular patch of black. *A. aboriginis* that I examined usually (80.0%) had a few medial, black scales that gave the impression of a dark central stripe. This is different from the basal triangle on *A. punctor* and lateral black patches on *A. hexodontus*.

Wood, Dang and Ellis (1979)

"The mosquitoes of Canada" has keys for larvae, females and males with elaborate illustrations and species descriptions. The keys are practical as they use an easily observed character or characters in each couplet. The latter is helpful when a single character is not apparent.

The larval key relies heavily upon setal branching and length whereas previous authors relied mostly on characteristics of the comb scales. Use of the character of the saddle encircling the anal segment has been removed from the beginning of the key (unlike Darsie and Ward (1981)). This eliminates the possibility of misidentifying an *A. aboriginis* with an encircling saddle, early in the key.

One couplet for *hexodontus* uses seta 1-M. The couplet reads "mesothoracic seta 1-M as long as head hair 5-C" or "1-M less than 1/3 the

length of 5-C." 82.5% of my specimens had seta 1-M as long as 5-C and 1.6% had seta 1-M $\frac{1}{3}$ the length. All other characteristics they give for *hexodontus* are true for my specimens. These authors examined specimens from only one site in British Columbia and these were probably all adults.

Other larvae in the *punctor* subgroup key out in "The mosquitoes of Canada". I have mentioned that *A. pullatus* (Coquillett) is similar in form to *A. aboriginis*. In the larval key these species are separated by the length and branching of abdominal seta 7-II. The first couplet reads; "lower lateral seta 7-II of second abdominal single or double, half as long as 6-II immediately dorsal" (*aboriginis*) or "lower lateral seta 7-II with 3 or more branches, shorter than $\frac{1}{2}$ the length of 6-II" (*pullatus-pionips*). The second character in this couplet compares the length of seta 1-X with that of the saddle. These characteristics work well in separating these species.

The key to females separates most members of the *punctor* subgroup from one another. *A. aboriginis* and *A. abserratus* are the only two species that key out together but they are separated according to their distributions. *A. aboriginis* is found in coastal British Columbia and *A. abserratus* from Manitoba and east.

The scutal setal and scale coloration is used to separate *A. pionips* Dyar from the *punctor* species. The scutal setae are described as black for *pionips* and yellow or bronzy color for the *punctor* subgroup. My examination of *A. hexodontus* revealed that many females (45.5%) have entirely black scutal setae. A second character in the couplet that separates *pionips* is: submedian stripes broad, dark-brown, separated by a narrow median stripe of yellow scales and contrasting with the yellow-scaled sublateral and lateral areas. The authors feel that species in the *punctor* subgroup may have sublateral stripes but this is

caused by narrowing of the scales and exposure of the darker ground color. I found that the sublateral stripes were less densely covered by scales but these scales are a darker-brown in the species that have sublateral stripes. There is a possibility of mistaking an *A. pionips* for one of the *punctor* subgroup although more detailed examination of *pionips* may reveal some other distinct differences between these species. Darsie and Ward (1981) used the scaling of the postmetasternum to separate the *punctor* species from *pionips*.

The couplets that separate the *punctor* subgroup uses the scaling of the probasisternum to split *A. hexodontus* and *A. schizopinax* from *A. aboriginis*, *A. abserratus* and *A. punctor*. The latter group are described as having a few scales on this sternite. I found 14.8% of the *A. punctor* to have between 10 and 20 scales on this sternite but the majority (85.2%) had less than 10 scales. *A. hexodontus* usually (87.1%) had more than 20 scales on the probasisternum. The second character in this couplet uses the pale scaling at the base of the wing. The *hexodontus-schizopinax* group are described as having a patch of pale scales as opposed to usually dark-scaled wing base. Most (96.4%) of the *A. hexodontus* females that I examined had 10 or more pale scales at the base of the wing. Both *A. aboriginis* and *A. punctor* had less than 7 pale scales at the base of the wing. It would appear that most of the coastal specimens of *A. hexodontus* can be separated from *A. punctor* by the characteristics used by Wood, Dang and Ellis. *A. punctor* females are distinguished from *aboriginis* and *abserratus* by the presence of a median, dark-brown stripe on the scutum as opposed to median-stripes of dark-brown scales or uniform coloration. My *A. aboriginis*, however, did have some specimens with a single, median, dark-brown stripe and some *A. punctor* had median stripes or no color pattern on the scutum. I found these two species extremely difficult to separate from one another. The

abdominal sternite scale pattern was more useful in splitting these species than scutal scale patterning although this latter character was not completely satisfactory.

The key to males separates only part of the *punctor* subgroup. *A. aboriginis*, *A. hexodontus*, *A. punctor* and *A. schizopinax* are separated from *A. abserratus* based on the shape of the basal dorsomesal lobe of the gonocoxite. The former group are not separated from one another. All my specimens did conform to the characteristics used by these authors to identify this subgroup.

Gjullin, Sailer, Stone and Travis (1961)

"The mosquitoes of Alaska" keys larvae, females and males to species. The authors include *A. aboriginis*, *A. hexodontus* and *A. punctor* from this State. They treated *A. punctodes* Dyar as a synonym of *A. punctor*.

The key to larvae relies on the number of comb scales to separate *A. hexodontus* from *A. punctor*. This key is structured like that of Carpenter and LaCasse (1955). *A. aboriginis* is found in the last couplet of the key. This couplet reads: "anal segment about as long as wide; mesothoracic hair No. 1 (1-M) single". I found 1-M to be occasionally double on some specimens (Figure 9C), but there is no problem separating this species from *A. stimulans* (Walker) that shares this couplet. These two species are quite different.

The key to females includes *A. aboriginis*, *A. hexodontus* ("tundra" variety), *A. punctor* and *A. punctor* ("tundra" variety). It relies on the mesonotal scale pattern to separate these species. As previously mentioned this is variable with these species in British Columbia (Table 4).

The key to males uses characteristics of the genitalia and does not separate the species of the *punctor* subgroup. I could not find any reliable differences between these species using the same characteristics.

Gjullin and Eddy (1972)

This version of "The mosquitoes of the northwestern United States" updates the work of Stage et al. (1952). This work keys larvae, females and males to species. They include *A. aboriginis*, *A. hexodontus* and *A. punctor*.

The key for larvae is similar to that of Carpenter and LaCasse (1955). *A. hexodontus* and *A. punctor* are separated on the number of comb scales on the eighth abdominal segment. *A. aboriginis* keys out to a couplet that is shared with *A. schizopinax* Dyar. These species are separated by the length of the spinules on the apical edge of the saddle on the anal segment. This is similar to Darsie and Ward (1981) who discuss the saddle as being aciculated on *schizopinax*.

The key for females separates the species into groups. These include: *aboriginis-punctor* (in part) and *hexodontus-punctor* (in part). The latter group is distinguished from *A. pionips* Dyar on the mesonotal scale color pattern. This is not a satisfactory character for separating these species. The *hexodontus-punctor* grouping is separated by the scaling of the probasisternum. My specimens of *A. punctor* will fit in either group using this character (Table 3) and *A. aboriginis* and *A. hexodontus* would be identified correctly.

The key for males relies on characteristics of the male genitalia. A result of this is that *A. aboriginis*, *A. hexodontus* and *A. punctor* are grouped together. *A. schizopinax* shares this couplet with the three *punctor* species. It is separated by being setose (having minute setae) on the apical portion of the claspette

stem.

Bohart and Washino (1978)

The *A. hexodontus* described in this book were collected in California. This is the earliest record that I could find showing seta 1-M being equal in length to 5-C, and unbranched. These authors describe the comb scales as commonly 6 in number but vary from 5 to 9. Head setae 5-C and 6-C are unbranched to 3-branched in different combinations, 2-2 to 2-1 being the most frequent. These descriptions fit the specimens that I examined from British Columbia. The female *hexodontus* from California are described as having pale supraalar bristles and mostly pale, erect, forked scales on the vertex. I have found the supraalar setae and scales of the vertex entirely black in some of my specimens (Table 3).

British Columbia

There have been four major contributors to the identification of mosquitoes in British Columbia. It includes Dyar from 1904 to 1928, Hearle in 1926 and 1927, Curtis in 1967 and Belton from 1978 to 1983. Hearle (1926) gave a key to species for the Lower Mainland region that included *A. aboriginis* and *A. punctor*. His larval descriptions fit either *hexodontus* or *punctor*. The couplet from his key reads: "anal segment ringed by dorsal plate; comb scales stout, thorn-like in an irregular row six to seventeen." The adults are separated on the mesonotal scale color and patterning. These characteristics are unsatisfactory in separating the species in the *punctor* subgroup.

Curtis (1967) gives a key to species for larvae and females. The larval key relies on the comb scale number to separate *hexodontus* from *punctor*. This

is unsatisfactory in separating these species as previously mentioned. The adults are primarily separated on the mesonotal scale-color and patterning. *A. hexodontus* (in part) is separated from *A. pionips* Dyar by the scutellar and mesonotal setae being yellow or bronzy. I have found many *hexodontus* to have entirely black setae on the scutum.

The latest edition of "The mosquitoes of British Columbia" (Belton 1983) contains keys to larvae and females. The larval key divides *A. hexodontus* and *A. punctor* on the character of the comb scale number and length. The length of the comb scales is compared to the length of the apical pecten tooth of the siphon. *A. punctor* mean comb length is always less than the length of the apical 2 pecten teeth but *A. hexodontus* was not always longer. I found the comb scales to be longer than the last pecten tooth in 45.4% of specimens and longer than the second last tooth in 71.3% of the specimens. In most instances the comb scales are longer than the last two pecten teeth but not completely so with all specimens. The length of the comb scales is given in the larval description of *A. hexodontus* where this species is described as .1 mm in length. *A. punctor* is described as having a mean comb length of .08 mm. As previously discussed this is a relatively reliable character except when *hexodontus* develops in warmer habitats and the comb scale length falls below its usual range. Along with Wood et al. (1979), this key offers the most satisfactory description for these two species. The larval illustration of *A. hexodontus* shows thoracic seta 1-M as long and single (longer than head seta 5-C). This is the second coastal larval-key that shows this seta as long and single, unlike the short multibranching illustration by Wood et al. (1979) and Carpenter and LaCasse (1955).

The first couplet of the larval key uses the character of the saddle encircling the anal segment. As previously discussed, the occasional *A. aboriginis* may be misidentified early in the key. *A. aboriginis* is separated from *A. pionips* Dyar and *A. pullatus* (Coquillett) by the head-hairs having less than 5 branches. 20.5% of my specimens had head hair 5-C with 5 or more branches (Figure 4A). The couplet that separates *aboriginis* also depends upon 5-C having 2 to 4 branches. I found 79.5% of the specimens with 2-4 branches for seta 5-C. The larval description for *A. aboriginis* states that 5-C is 3-to 5-branched, contradicting the larval key that states 5-C has 2-4 branches.

The key for females leaves the *punctor* subgroup to the last few couplets. Just prior to this grouping, *A. pionips* Dyar is separated by the setal color of the scutum and scutellum being dark-brown or black. The *punctor* species are described as having yellow or bronze colored scutal and scutellar setae. As previously mentioned, most of the *hexodontus* I examined had entirely black scutal setae. The alternate character for the couplet states that the fore femora are black with a distinct line of pale scales on the anterior surface in *pionips*. All of my *punctor* specimens fit Belton's description of having entirely dark scales on the anterior surfaces of the fore femora.

The separation of the *punctor* females into species relies on the scaling of the probasisternum and pale scale-patch at the base of the wing. This is one of the more reliable sets of characters used to separate females of *hexodontus* from *aboriginis* and *punctor*. *A. punctor* is separated from *A. aboriginis* by the wing base having a few pale scales versus none in *aboriginis*. This was true for most of the specimens that I examined. It does mention in the female key that these two species are hardly distinguishable from one another.

In the species descriptions Belton (1983) mentions that most localities for *A. punctor* are cited from Hearle (1926). This is unsatisfactory because *A. hexodontus* was not separated from *punctor* in Hearle's key to species. Belton points out that many of the Provincial records for *punctor* may actually refer to *hexodontus*.

USE OF MORPHOLOGICAL TECHNIQUE AND HOLISTIC BIOLOGICAL APPROACH IN SPECIES CLASSIFICATION

Morphological approach

Most extant species are described purely on morphological characters, hence they should be called morphospecies (Scudder 1979). This form of taxonomic system is a relatively rigid device which does not describe phenetic, genetic, phylogenetic and ecological relationships adequately. At a practical level the traditional approach of using morphospecies is of particular value to pest control agencies and others who need to identify field-collected specimens.

Zavortink (1974) has discussed the status of taxonomy by the use of morphological characters with mosquitoes. The techniques for observing and our knowledge about anatomy has become more precise since the early descriptions of type specimens by taxonomists. Larval rearing has aided in accurate determination of subtle setal variations and the amount of variation. The result is an accurate description upon which keys to species are based. Zavortink (1974) believes there is a movement from "alpha" to "beta" taxonomy in mosquitoes. This means that the emphasis on finding and describing species (alpha taxonomy) is being replaced by the arrangement of species into good natural classifications (beta taxonomy). These classifications consist of revisions and monographs to species groups. This thesis is an example of a revision to species for the *punctor* subgroup that is needed to consolidate our knowledge of the Canadian fauna. Larval rearing of these species to adults is a good test for the morphological technique. If all individuals conform to the descriptions in

each instar then there can be no doubt about validity of describing these species through morphology. British Columbia offers a unique opportunity to test the morphological technique for three of the species in the *punctor* subgroup because their ranges overlap and instances of sympatry can be tested.

At the evolutionary level biologists have to deal with species as the basic units of classification. Trying to understand the point in evolution where reproductive isolation has occurred between similar populations has brought the definition of a species under question. The assumption is that at the time of divergence of two populations from a common ancestor, speciation has occurred. Biochemical, cytological and numerical taxonomy are fields of biosystematics which use refined techniques to aid in clustering variants of similar individuals into groups which the evolutionist may define as distinct units. At a practical level the traditional approach to identify morphospecies often fails to distinguish very similar individuals of different species.

In applying this reasoning to the *punctor* subgroup, there are two important points to make. Firstly, these species are known primarily from the anatomical descriptions and that information is incomplete in several parts of their range. Recent examination of museum specimens with current knowledge has revealed improper identifications and some confusion over their identities (Wood 1977). My research should help to fill this gap and resolve the conflicts uncovered in the literature. Secondly, my research will be useful in guiding the collection of specimens from along the west coast. It presents detailed descriptions from larval-reared adults with an emphasis on the most important characteristics in all instars. These descriptions are supplemented with Scanning Electron Microscope examination of specimens.

Holistic biological approach

Another common approach to defining species groupings is through reproductive (or biological) groupings. Neither morphological nor biological approach has been entirely satisfactory in defining taxonomic species so Doyen and Slobodchikoff (1974) proposed an operational approach to species classification. Through a series of steps they approached species classification by phenetic, geographic, reproductive and ecological groupings of populations. I will explore the use of this approach to clarify the relationships of species in the *punctor* subgroup.

The populations of species I examined form good phenetic groupings. The larval stages have the most distinct differences. The pupae also show differences although these are not so distinct. Adults are even less distinct than the immature stages. *A. hexodontus* females are more easily recognized than *A. aboriginis* and *A. punctor*. The latter two species can usually be separated but not with certainty. The males are the least distinct stage of development but *A. hexodontus* does seem to retain the greatest differences. According to Doyen and Slobodchikoff (1974), if populations are similar then a geographical grouping should be considered.

A. aboriginis is restricted to the coastal and Columbian rainforests of North America. *A. punctor* is a common species of the boreal forest, seldom being found north or south of this zone. *A. hexodontus* has a circumpolar, tundra distribution with a southerly montane extension down along the Coastal, Cascade-Sierra and Rocky Mountain ranges. Over vast stretches of habitat *A. hexodontus* or *A. punctor* (at least individuals that conform to specific descriptions) do not occur together (allopatry). Over most of their range *A.*

aboriginis, *A. hexodontus* and *A. punctator* form good geographic groupings with no overlap. There is only a small portion of their range that overlaps and larvae occur in the same pools (sympatry).

A. hexodontus has the most difficult distribution to interpret. My sampling has been restricted to British Columbia (larval reared specimens) and these do not conform to descriptions by Wood et al. (1979). Univariate techniques provide a superior means of analyzing geographic variation in a single character (Doyen and Slobodchikoff 1974). This would involve a test of larval thoracic seta 1-M from specimens all across North America. The "tundra" type is typified by the descriptions of Wood et al. (1979) and the type form is typified by the descriptions of Belton (1983) and Bohart and Washino (1978). If *A. hexodontus* has two forms and the difference is typified by thoracic setae 1-M then the collection site at Blue River is of particular interest. Presumably isolation has caused the differentiation of the two forms and this may have occurred during continental glaciation. The "tundra" variety of *A. hexodontus* was probably isolated in the arctic steppe refugia and the type form in the southern conifer refugia. Remington (1968) has discussed the many possible suture-zones of hybrid interaction between recently joined biotas after glaciation. The Northern-Cascade suture zone is the area of contact between biotas of the vast northern transcontinental woodland and northern extension of the far west mountain chain. The Blue River site falls within these central valleys of British Columbia. Remington (1968) points out that the Cascade residents have recently been invaded by the biota from the north with the receded glacial barrier. The prominence of the "coastal" type of *hexodontus* (with larval seta 1-M long and simple) at the Blue River site might support this statement by Remington. The "tundra" variety (with short multibranching 1-M) appears to be the rare *hexodontus*

invader into the Northern-Cascade suture zone. It is interesting to note that the "tundra" form extends across Canada to the southeastern edge of the continent (Remington 1969). I would assume that the Alberta and eastern habitats with *hexodontus* have typically northern forms. I was not able to confirm this with reared specimens during my research but this certainly seems true for all the reared specimens in the Canadian National Collection (Wood et al. 1979).

If geographic groupings are allopatric then their genetic compatibility should be tested. I was not successful in rearing specimens of the *punctor* subgroup. Only one *A. aboriginis* took a blood meal and laid eggs. In instances of sympatry, Doyen and Slobodchikoff (1974) suggested looking for some form of reproductive isolation. With the *punctor* subgroup this involves examination of the role of swarming.

The importance of mating swarms is mentioned in the introduction but needs further clarification. Downes (1969) has discussed the development of swarms over environmental markers. *A. hexodontus* apparently use visual clues to orient by light colored markers on a dark background. The swarm, with this species, is the response of the individual and is independent of responses between the insects themselves. Female *hexodontus* will orient to the same environmental markers as the males but often below the male swarm and in a less distinct pattern. Swarms of *A. aboriginis* and *A. punctor* have been observed (Wood et al. 1979; Belton 1983). All of these swarms seem to be in response to specific environmental markers.

The antennae of Culicidae are conspicuous and elaborate organs. The Diptera have 3 basic parts to the antennae; the basal segment or scape, the second segment (pedicel) that encloses the Johnson's organ and the remaining

part called the flagellum. In the Culicidae the scape is rudimentary. The pedicel has an array of scolopophores (tension receptors) that are attached medially around the basal plate of the flagellum. Each segment of the flagellum (13 segments) carries a whorl of long stiff setae which can stand at a 90° angle to the shaft or fold according to changes in blood pressure in the flagellum. The male flagellum is specialized and acts as a collector of sound energy and is tuned to the wing beat frequency of the female of its own species. The female antenna is similar to that of the male but is less specialized. It does not respond to sound but probably monitors air currents during flight. It has been shown that the differences between wing beat frequencies of different species can be large enough that a large species could be discriminated from a smaller one. Also there is a frequency difference between sexes so that during mating, males could avoid mating attempts with other males (Belton and Costello 1979). These authors showed that *A. aboriginis* had a distinct wing beat frequency from 9 other species and this was inversely related to size on a logarithmic scale. The wing beat frequency recorded for *A. punctor* is greater than that of *A. aboriginis* (Belton and Costello 1979). These authors felt that sound plays only an occasional role in preventing mating between species. It is possible that sound may act as a trigger for the mating behaviour of males.

Hartberg (1975) discussed the possible reproductive isolating mechanisms that are used by different species of *Aedes*. He mentioned evidence for the role of contact chemoreception as a possible isolating mechanism. More recent evidence tends to support the hypothesis that contact chemoreception is operational in mosquitoes (Lang 1977; Linley 1983). By measuring the surface hydrocarbons from hexane washes of females, I found physiological differences between

aboriginis, *hexodontus* and *punctor* specimens. If one accepts that the 23 chained hydrocarbons are active contact pheromones (as Muscalure® may be for the housefly) then the differences in these compounds on different species may be significant (Table 6).

In instances where similar populations of organisms occur in sympatry, Doyen and Slobodchikoff (1974) suggested looking for some form of reproductive isolation. In all instances where larvae were collected in sympatry the female body washes showed no overlap in C-23/C-25 hydrocarbon ratios. *A. punctor* never overlapped with *aboriginis* or *hexodontus*. This may be evidence of a possible reproductive isolation in instances of sympatry of these species.

If partial reproductive isolation is not shown (or no information is available) then ecological groupings should be considered (Doyen and Slobodchikoff 1974). In British Columbia I found *A. aboriginis* only in the coastal rainforest zone (Figure 1) which is dominated by Western Hemlock, Western Red Cedar, Sitka Spruce and Douglas-fir. It was always collected in temporary or casual pools. *A. hexodontus* is found in the Arctic tundra, Alpine tundra and Subalpine forest vegetation zones. The bog-like conditions at sea-level is the usual habitat for collection of *hexodontus* near Prince Rupert. Otherwise it was found in Alpine tundra or Subalpine forests. The Subalpine forest is similar to the boreal forest where *A. punctor* is found. The boreal forest vegetation zone is characterized by White Spruce and Black Spruce in the wetter areas. In Alberta I collected *A. hexodontus* and *A. punctor* where coniferous trees were the dominant forest cover. Maire (1983) studied the larval distributions of 6 snow-melt species in the high subarctic region of Quebec. The results of reciprocal averaging analysis indicated that the vegetation of bog ridges was highly correlated with species associations. He found *A. hexodontus* highly correlated with the vegetation unit

dominated by *Carex limosa* and *A. punctor* with the *Picea mariana* and *Carex oligosperma* units. These three mosquito species in British Columbia form good ecological groupings. Instances of larval sympatry occur when adults use the same pools for breeding in zones of habitat overlap.

There is need to test the genetic compatibility of *A. aboriginis* and *A. punctor* to see if they are good reproductive groupings. There is an urgent need to test the geographic grouping of *A. hexodontus* to determine the status of the "tundra" variety and the southerly, montane form.

REVISION AND KEY OF THE *PUNCTOR* SUBGROUP

To begin a revision of the *punctor* subgroup it is necessary to understand their relationship with other members of the *Ochlerotatus* subgenus. Edwards (1932) presented the Group G in the *Ochlerotatus* subgenus as follows:

<i>Aedes</i>	<i>aboriginis</i>	Dyar
A.	<i>alpinus</i>	Linnaeus
A.	<i>aurifer</i>	Coquillett
A.	<i>cacothius</i>	Dyar
A.	<i>cataphylla</i>	Dyar
A.	<i>communis</i>	Degeer
A.	<i>cyclocerculus</i>	Dyar
A.	<i>detritus</i>	Haliday
A.	<i>diantaeus</i>	Howard, Dyar and Knab
A.	<i>gonimus</i>	Dyar and Knab
A.	<i>hexodontus</i>	Dyar
A.	<i>idahoensis</i>	Dyar
A.	<i>impiger</i>	Walker
A.	<i>implacabilis</i>	Walker
A.	<i>intrudens</i>	Dyar
A.	<i>lateralis</i>	Meigen
A.	<i>leucomeles</i>	Meigen (?)
A.	<i>leuconotips</i>	Dyar
A.	<i>meulleri</i>	Dyar
A.	<i>nearcticus</i>	Dyar
A.	<i>nigripes</i>	Zetterstedt
A.	<i>niphadopsis</i>	Dyar and Knab
A.	<i>pacificensis</i>	Hearle
A.	<i>parvulus</i>	Edwards
A.	<i>pionips</i>	Dyar
A.	<i>pullatus</i>	Coquillett
A.	<i>punctor</i>	Kirby
A.	<i>schizopinax</i>	Dyar
A.	<i>schtakelbergi</i>	Schingarew
A.	<i>spencerii</i>	Theobald
A.	<i>sticticus</i>	Meigen
A.	<i>thibaulti</i>	Dyar and Knab
A.	<i>ventrovittis</i>	Dyar

The status of many species has changed since the work of Edwards (1932). The number of species in the northern holarctic *Ochlerotatus* Group G has been reduced even though many new species have been added. Knight and Stone

(1977) is the most recent catalog for mosquitoes but these authors do not include subgeneric groupings. According to my own interpretation, Group G is as follows (important synonyms from Edwards and others follow the appropriate names):

A.	<i>aboriginis</i>	Dyar
A.	<i>abserratus</i>	(Felt and Young)
A.	<i>aurifer</i>	(Coquillett)
A.	<i>cataphylla</i>	Dyar
	- <i>pacificensis</i>	Hearle, subspecies status
A.	<i>churchillensis</i>	Ellis and Brust
A.	<i>communis</i>	(DeGeer)
A.	<i>detritus</i>	(Haliday)
A.	<i>diantaeus</i>	Howard, Dyar and Knab
A.	<i>hexodontus</i>	Dyar
	- <i>cyclocerculus</i>	Dyar
	- <i>laboradorensis</i>	Dyar and Shannon
	- <i>leuconotips</i>	Dyar
	- <i>masamae</i>	Dyar
A.	<i>impiger</i>	(Walker)
	- <i>nearcticus</i>	Dyar
	- <i>parvulus</i>	Edwards
A.	<i>implacatus</i>	Vockeroth
	- <i>impiger</i>	authors prior 1954, not Walker 1848
A.	<i>intrudens</i>	Dyar
A.	<i>leucomelas</i>	(Meigen)
A.	<i>meulleri</i>	Dyar
A.	<i>nevadensis</i>	Chapman and Barr
A.	<i>nigripes</i>	(Zetterstedt)
	- <i>alpinus</i>	authors not Linnaeus
A.	<i>niphadopsis</i>	Dyar and Knab
A.	<i>pionips</i>	Dyar
A.	<i>pullatus</i>	(Coquillett)
A.	<i>punctodes</i>	Dyar
A.	<i>punctor</i>	(Kirby)
	- <i>implacabilis</i>	Dyar
A.	<i>schizopinax</i>	Dyar
A.	<i>schtakebergi</i>	Schingarew
A.	<i>spencerii</i>	(Theobald)
	- <i>idahoensis</i>	(Theobald) subspecies status
A.	<i>sticticus</i>	(Meigen)
	- <i>gonimus</i>	Dyar and Knab
	- <i>lateralis</i>	authors, not Meigen
A.	<i>thibaulti</i>	Dyar and Knab
A.	<i>ventrovittis</i>	Dyar
	- <i>calcothius</i>	Dyar

Numerical techniques to classify *Aedes* have been attempted several times (Steward 1968; Lunt and Nielsen 1971a, b; Rohlf 1977). Steward (1968) tried to classify the Canadian *Aedes* using 76 morphological (adult, male terminalia and larval characteristics), three ecological, two physiological and one geographical characters. The results indicated that *aboriginis*, *hexodontus*, *punctor* and *punctodes* deserve no more than subspecific rank. The reliability of characters selected for this study and the weighting of plesiomorphic (primitive) as opposed to apomorphic (specialized) traits was questioned by Nielsen (1969). A more open evaluation of the numerical techniques used by mosquito taxonomists was offered by Crovello (1969). This attitude towards the numerical technique evolved into the more critical work of Rohlf (1977).

Based on larval chaetotaxy, Rohlf (1977) presented a phylogeny and classification for *Aedes* mosquitoes. The results of this analysis yielded a grouping somewhat different from that which I have presented for Group G. *A. aurifer* (Coquillett) and *A. thibaulti* Dyar and Knab was moved to Group 7 (= Group F), the *scapularis* group and *A. spencerii* (Theobald) was elevated to a new group (Group 10) along with *A. idahoensis* (Theobald). *A. decticus* Howard, Dyar and Knab and *A. rempeli* Vockeroth were added to Group G. The American species, *A. churchillensis* Ellis and Brust, *A. meulleri* Dyar and *A. nevadensis* Chapman and Barr were not included in Rohlf's (1977) classification. As well, the old-world species *A. detritus* (Haliday), *A. leucomelas* (Meigen) and *A. schtakebergi* Schingarew were not included in the analysis. Whether the groupings of Edwards (1932) will remain as more information becomes known about *Aedes* is beyond the scope of this thesis. The following is the status of Group 8 (Group G), the *communis* group according to Rohlf's analysis.

<i>A.</i>	<i>aboriginis</i>	Dyar
<i>A.</i>	<i>abserratus</i>	(Felt and Young)

A.	<i>cataphylla</i>	Dyar
A.	<i>communis</i>	(DeGeer)
A.	<i>decticus</i>	Howard, Dyar and Knab
A.	<i>diantaeus</i>	Howard, Dyar and Knab
A.	<i>hexodontus</i>	Dyar
A.	<i>impiger</i>	(Walker)
A.	<i>implacatus</i>	Vockeroth
A.	<i>intrudens</i>	Dyar
A.	<i>nigripes</i>	(Zetterstedt)
A.	<i>niphadopsis</i>	Dyar and Knab
A.	<i>pionips</i>	Dyar
A.	<i>pullatus</i>	(Coquillett)
A.	<i>punctodes</i>	Dyar
A.	<i>punctor</i>	(Kirby)
A.	<i>rempeli</i>	Vockeroth
A.	<i>schizopinax</i>	Dyar
A.	<i>sticticus</i>	(Meigen)
A.	<i>ventrovittis</i>	Dyar

The preceding has outlined the basic premise on which to establish a revision. The following is a generalized description to identify members of the *punctor* subgroup.

Generalized description of the *A. punctor* subgroup

Males

Legs - Legs primarily dark-scaled, hind and mid femora and tibia may be pale scaled anteriorly and ventrally. Head - Palps slightly shorter to equal or longer than proboscis; apical 1/4 to 1/3 of the third palp segment enlarged, bearing a tuft or fringe of 50 or more long setae that arise from the ventrolateral surface. Thorax - Paratergite with a patch of scales. Scutal scales normal, coloration similar to the female but may be reduced or absent. Postprocoxal membrane scaled or bare. Abdomen - Genitalia with basal lobe on the gonocoxite conical or triangular and broadest at the basal attachment, setose with an enlarged seta arising lateral to a tuft of setae (rather than having a row of setae like *communis*). Apex of the gonocoxite with expanded apicodorsal

lobe, medial edge with short, thick, curved (ventrally directed) setae. Claspette narrowing at apex, setose; claspette filament broadest at curved portion and blade-like or inflated, droplet shaped in section, tapering evenly at base, four times longer than wide, without flange or keel on convex side. Lateral abdominal setae pale, yellow or with a yellowish tinge.

Females

Legs - Primarily dark-scaled except some anterior and ventral pale scales, some have a small ring of pale scales at the union of the femora and tibia; tarsomeres dark-scaled, without bands of paler scales. Postprocoxal membrane scaled, at least on the dorsal half. Head - Dorsal vertex and lateral edges with yellow or pale scales; lateral scales oppressed, anterior dorsal scales narrow and curved downward, posterior scales erect and forked (some may be black). Antennal pedicel medially covered with scales and short setae. Palps dark-scaled; proboscis mostly dark scaled. Thorax - Scutal setae color primarily yellow or bronze or dorsally black and pale at lateral edge of scutum (some *hexodontus* all black); scutal scale color variable, it may be any combination of the proceeding conditions: 1) without distinct markings, range in color from yellow, bronzy to dark-brown, 2) broad longitudinal single or divided dark stripe medially, 3) posterior pair of dark submedian half-stripes. Supra-alar setae usually yellow or black dorsally and pale ventrally (some *hexodontus* are entirely black). Posterior pronotum with yellow or brownish, narrow scales, broadening ventrally with 7-16 setae present posteriorly (specimens from British Columbia with 5-9 setae), occasionally 1 or 2 detached ventrally (some specimens have 4-5 setae on dorsal margin). Upper 1/2 of subspiracular area, hypostigmal and anterior postspiracular areas bare (Anepisternum); subspiracular scale patch separate from posterior pronotum. Mesepimerion scaled to the ventral edge; 1-6

lower mesepimeral setae (*A. aboriginis* often without lower mesepimeral setae). Dorsal katepisternum scaled to the anterior dorsal corner. Meteusternum (metameron and metapostnotum) with scale patches; (Knight (1951) referred to the last three conditions as almost continuous scale patch from proepisternum to metamerion). Probasisternum scaled or bare. Wings - Primarily dark-scaled except at the base where there may be numerous pale scales. Abdomen - Tergites with transverse basal white scaled bands, without additional scattered pale scales. Sternites primarily white-scaled with varying degrees of black bands. Segment VIII with considerable scattered scales (bare in some specimens).

Pupae

The information pertaining to pupal taxonomy is sparse. Wood et al. (1979) refers to Darsie (1957) for a pupal key to species. In this key about half of the species from Group G of the *Ochlerotatus* are used and even fewer from Group F and H. Many of the setae have been renumbered since Darsie's key was written. The new numbering system is based upon ontogenetic homologies between larval and pupal setae where the location is determined by linked common neurons that develop within the larval cuticle (Belkin 1960; Barr and Myers 1962). Figure 14 shows the numbering of setae by Darsie (1957) and that by Harbach and Knight (1981) in the mosquito taxonomy glossary. With the lack of information available I felt it was not possible to complete a generalized description to the pupae of the *punctor* subgroup. I can not be sure if my description would fit other species not of this subgroup.

Larvae

Head - Antennae spiculate, expanded at base and shorter than the maximum head width; setae A-1 inserted before the middle with 2-12 branches (never single rarely two branched); setae A-2 with subapical constriction. Head hairs 5, 6 and 7 prominently developed; 6-C anterior to 5-C and with as many or more branches than 5-C; 7-C inserted on a level between 5-C and 6-C; 4-C minute (less than $1/8$ 6-C). Inner mouth-brush hairs with comb-like tips. Thorax - Prothoracic setae 1-P, 2-P and 3-P approximately equal in length and width (3-P at least $3/4$ the length of 1-P). Abdomen - Lateral abdominal setae 6-II usually $1/2$ the length of 7-II (never less than $1/3$), 6-II with 1-5 branches (occasionally more in *hexodontus*). Comb of the eighth segment composed of an even or irregular row of 5-20 teeth per side or a small patch (20-50); central spine of the scales as long as base (except some *aboriginis* where the comb scales are densely fringed with long spicules. Siphon - Siphonal index (length over maximum width) about 3.0, always less than 4 times as long as the width of the base; setae 1-S inserted before the middle of the siphon but beyond the base of the last pecten tooth, with 2-9 branches. Pecten teeth evenly spaced although spacing may increase regularly dorsally; each tooth with 1-5 cusps at base. Setae 9-S not thickened or strongly curved. Anal segment - Saddle with complete or narrowly incomplete sclerite (except *schizopinax* where saddle encircles about $2/3$ of the anal segment); 1-X usually single, about equal in length to saddle and inserted from within the margin near the posterior edge. Setae 2-X with 3-10 branches (single in *abserratus*). Ventral brush with 16-24 tufts, 0-4 precratal setae. Anal papillae equal to or longer than saddle.

Keys to species

Based on general morphological descriptions, the following can be considered members of the *punctor* subgroup; *A. abserratus*, *A. aboriginis*, *A. hexodontus*, *A. punctodes*, *A. punctor* and *A. schizopinax*.

There is little information about *A. punctodes* in the literature. It seems to be similar to *A. punctor* except the saddle does not completely encircle the anal segment. The male *A. punctodes* is supposed to have similar genitalia to *A. implacabilis* (Walker). Knight (1951) placed these two species into a separate superspecies from the other members of the *punctor* subgroup based on the unusual male genitalia. *A. implacabilis* is now considered to be a synonym of *A. punctor* and *A. abserratus* is elevated to specific status in replacement for *implacabilis*.

Dahl (1974) recently described *A. punctodes* from Northern Fennoscandia. She found the male genitalia of *A. punctodes* was not profoundly different from *A. hexodontus* and *A. punctor* that she collected from this region. Dahl also pointed out that a figure of *A. punctodes* genitalia was not available in the literature. I did not collect this species and was unable to make any assessment as to the status of *A. punctodes*. For this reason I have left it out of the adult keys to species for the *punctor* subgroup.

A. schizopinax was not described or included in Darsie's (1957) work on pupae. Dyar (1929) did not describe the pupae of this species. Knight and Stone (1977) made no reference to pupal descriptions for *A. schizopinax*. The absence of information has forced me to leave this species out of the pupal key to species.

Larval key to species

1. Anal seta 2-X single, as long as 3-X; dorsolateral setae 1-IV and 1-V minute, less than half the length 6-IV and 6-V.....*abserratus*

Anal seta 2-X multiple, much shorter than 3-X; dorsolateral setae 1-IV and 1-V longer than 2/3 length of 6-IV and 6-V..... 2

2. Comb scale number usually 20 or more, in a patch; seta 1-M as great in diameter as 5-C or 6-C, greater in diameter than 2-M, 3-M and 4-M; head seta 5-C and 6-C usually 3 or more branched..... 3

Comb scale number usually less than 20, in a single regular or irregular row; 1-M thin or minute, never as thick as 5-C or 6-C, the same diameter as 2-M, 3-M and 4-M; head setae 5-C and 6-C usually single or double..... 4

3. 1-M 1-2-branched; saddle almost completely encircling the anal segment, short saddle spines, with dissecting scope not visibly extending beyond saddles edge; more than 1 basal cusp on pecten teeth.....*aboriginis*

1-M 3 or more branched; saddle encircling only 2/3 of anal segment, long saddle spines, extending beyond the posterior edge of the saddle; usually a single basal cusp on the pecten teeth.....*schizopinax*

4. 5-P single; 3-P single; mean comb scale length less than that of last two pecten teeth (about 2/3 its length), total comb scales (both sides of VIII) with 20 or more teeth (occasionally less); abdominal seta 7-II usually 1/2 or more the length of 6-II..... 5

5-P double (always on at least one side); 3-P double (occasionally single); mean comb scale length equal or longer than apical pecten teeth (greater than 2/3), total comb scales (both sides) less than 15; 7-II 1/2 or less than length of 6-II..... 6

5. Saddle encircling the anal segment.....*punctor*

Saddle not completely encircling the anal segment.....*punctodes*

6. 1-M long, equal to or longer than head seta 5-C, usually single, occasionally double.....*hexodontus*
"cordilleran" form

1-M short, less than 1/3 length of 5-C, with 3 or more branches.....*hexodontus*
"tundra" form

Pupal key to species

1. Seta 5-II single, seldom double; 5-III 1-3 branches, occasionally 4; 6-III usually single; seta 3-I usually single.....*aboriginis*
 Seta 5-II 2 or more branches; 5-III 4 or more branched (some *hexodontus* 2-3-branched); 6-III usually 2 or more branched (some *hexodontus* single); seta 3-I 2 or more branched..... 2
2. Seta 9-II 1-2-branched; seta 6-VII mostly double or triple..... 3
 Seta 9-II 3 or more branched (if 2-branched then seta 6-I is longer than 7-I); seta 6-VII usually 4 or more branched..... 4
3. Seta 5-IV single; MT-11 and 1-V usually single.....*punctodes* (in part)
 Seta 5-IV double; MT-11 and 1-V usually double.....*abserratus*
4. Seta 6-I longer (by 1.5X length) than 7-I..... 5
 Seta 6-I equal in length to 7-I.....*punctodes* (in part)
5. Seta 3-IV single; 1-II usually 1-3-branched; setae 1-V and 1-VII usually single; CT-8 usually 3 or fewer branches..... *hexodontus*
 Setae 3-IV and 1-II usually 4 or more branched; seta 1-V 2-4-branched; 1-VII usually 2 or 3 branched; CT-8 usually 4 or more branches.....*punctor*

Female key to species

1. Ventral surface of the proboscis mostly pale-scaled; abdominal tergite VII extensively pale-scaled *schizopinax*
Ventral surface of proboscis dark-scaled; abdominal tergite VII dark-scaled, with pale basal band 2
2. Vein C with patch of pale scales at base (always > 8 pale scales); pedicel ground color black or dark-brown; heavily scaled probasisternum (rarely < 10 scales), scales attached ventrally on sternite *hexodontus*
Vein C entirely black-scaled (at most 6 pale scales); pedicel ground color yellow or light-brown laterally, often black medial surface (unknown for *abserratus*); probasisternum bare, at most 10 scales, restricted to dorsal surface 3
3. Abdominal sternites III to VI with large apical triangle of black scales; wing base often with a few pale scales *punctor*
Abdominal sternites III to VI primarily white-scaled, a few median black scales, giving the impression of anterior-posterior stripe; wing base black, rarely a few pale scales *aboriginis*
(West coast)
abserratus
(Manitoba and east)

Male key to species

1. Basal lobe of gonocoxite thumb-like; its tuft of setae occupying apex of lobe; enlarged seta of the basal lobe shorter than most of the other setae *abserratus*
Basal lobe relatively large and triangular; enlarged seta of the basal lobe longer than other setae 2
2. Second and third palpomeres extensively pale-scaled; claspette stem setose to the apex *schizopinax*
Second and third palpomeres entirely dark-scaled; claspette stem setose on the basal 2/3, never to the apex 3
3. Wing base dark-scaled, occasionally 1-3 pale scales; vertex of head with < 2 black setae, other pale; supraalar setae mostly pale, < 3 black setae; palps always longer than proboscis 4
Wing base with 8 or more pale-scales; setae on the vertex with > 2 black; supraalar region with > 3 black setae; palps usually equal or less than length of proboscis *hexodontus*
4. Enlarged seta of basal lobe straight on the basal 2/3 followed by 90° bend and straight portion, tip curled; Pacific rainforest region *aboriginis*
Enlarged seta of basal lobe straight for the basal 2/3, followed by curled tip (no distinct 90° bend) - this character applies to specimens from British Columbia; Boreal forest *punctor*

PART F
CONCLUSIONS

It is appropriate at this point to answer the questions presented in the general introduction based on the information presented. The first question asked was if there are morphological differences between *aboriginis*, *hexodontus* and *punctor* in larval, pupal and adult instars. The dichotomous keys for these instars reflect the differences that I found between these species. *A. aboriginis* showed no overlap with *hexodontus* and *punctor* in the thoracic setal character used in the larval key. A few *A. punctor* overlapped with *A. hexodontus* with respect to comb scale number and size but none of my *A. punctor* had thoracic seta 5-P double. This latter character seems reliable. Pupal chaetotaxy is not as well known as the larval chaetotaxy for *Aedes*. I found considerable overlap in the branching of the setae of pupae with the three species that I examined. There are some differences between these species but no single, distinct character was evident. Differences in the females of these species are recorded in the most recent literature and I examined these characteristics. I found *A. hexodontus* to be distinct from *A. aboriginis* and *A. punctor* adults. These differences may be indicative of the coastal region and not applicable in northern and eastern Canada. *A. punctor* adults are exceedingly similar to *A. aboriginis*, although I found size and surface hydrocarbon differences. Wingbeat frequency is related to size and probably plays an important role in mating swarms. The males are as difficult to separate as the females, although *A. hexodontus* specimens are the most distinct of these species. It is interesting to note the differences of *A. aboriginis* eggs from the descriptions offered by Kalpage and Brust (1968) for other members of the *punctor* subgroup. The small symmetrical shape of *aboriginis* eggs is quite unique for the subgroup. In general terms these eggs are similar to other dark-legged *Aedes*.

These observations lead to the second question: "are these true or "good" morphospecies in British Columbia where their ranges overlap?" I am able to

answer this question because the identification of larval specimens was used to label the associated adult specimens. Even when larval *A. hexodontus* were collected in the same pools as *aboriginis* and *punctor*, the ensuing adult of *hexodontus* had black or dark-brown pedicel, pale-scaled patch at the wing base and scaled probasisternum. The males had the pale-scaled patch at the wing base and more black setae than *aboriginis* and *punctor*. I was not able to find "good" morphological differences between adult *A. aboriginis* and *A. punctor*. There were other differences as mentioned above. The unusual shape of the enlarged seta of the basal dorsolmesal lobe on the gonocoxite of *aboriginis* was significant. Dahl (1974) presented an illustration of *A. punctor* from Fennoscandia with an enlarged seta similar to that I have described for *aboriginis*. The distinct larval differences between these three *punctor* species in British Columbia leads me to answer yes, these are good morphospecies in this zone of habitat overlap. I think that adult specimens of *A. aboriginis* and *A. punctor* from the west coast of North America should be reared from larvae to confirm their identity.

The last question addressed in the introduction asked if *A. hexodontus* has two forms: one associated with the west coast of North America and the other from the tundra with a circumpolar distribution. I found one character that seems to be unique to coastal specimens. Larval seta 1-M is long and single on my specimens and in the records of Bohart and Washino (1978) and Belton (1983). Older records do not mention this seta (Knight 1951; Carpenter and LaCasse 1955; Stage et al. 1952; Gjullin et al. 1961; Gjullin and Eddy 1972; and Curtis 1967). The recent edition to "The mosquitoes of North America" (Darsie and Ward 1981) does not discuss this character. The major Canadian work (Wood et al. 1979) does discuss thoracic seta 1-M. They describe it as short and multibranching. Wood's et al. (1979) larval key to species does not work

for coastal specimens of *hexodontus* because it relies on a short multibranching seta 1-M. This leads me to believe that the coastal specimens of *A. hexodontus* are unique and should be treated as a subspecies. I have constructed my larval key so that *A. hexodontus* may be divided into these subspecies units.

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APPENDIX A

ORDER DIPTERA. Linn.

1. NEMOCERA. (sic) Lat.

Family CULICIDAE. *Culicidans*.

CXCVI. Genus *Culex*. Linn.

1. *Culex punctor*. Pungent *Culex*.

C. (punctor) nigra; pedibus, alaxinque, albarum, neuris, testaceis (sic).

Pungent *Culex*, black with legs, and nervures of the white wings, testaceous.
length of the body 3 1/2 lines.

Two specimens taken in Lat. 65 degrees.

Description.

Black body. Proboscis longer than the trunks; sheath black; valvules and lancets testaceous; palpi somewhat incrassated towards the apex; antennae broken off in both specimens; wings white, iredescent, with testaceous nervures, without scales, hairs, and fringe; legs testaceous.

APPENDIX B

Aedes hexodontus, new species from Dyar, 1916.

Male - Integument black. Head with pale straw-yellow scales, flat and appressed on the sides, narrow curved on the vertex, the black ground showing; vertical bristles pale straw-color, those along the eye margins black; erect forked scales low on the neck, black; median groove bare. Mesonotum with narrow curved pale straw-colored scales; two brown bands about five scales wide, of smaller dark brown scales, separated by three scales wide of normal straw-colored scales on each side of the median bare groove; an angled lateral bare line shows as a thick black mark; no subdorsal brown stripes; scales about antescular space paler. Abdomen with narrow basal segmental white bands; venter white-scaled, apices of segments and median band black. Legs black, femora whitish beneath; tibiae and tarsi largely whitish scaled within. Length of wing, 4.5 mm, the wing-scales black.

Genitalia - Side pieces over three times as long as wide, rounded at tip; apical lobe large, prominent, with short curved setae; basal lobe large, conical, evenly setose. Harpagones long, the basal part of shaft minutely setose, other half smooth; filament sickle-shaped, with an angular membrane at the base outwardly.

Female - Similar, the mesonotum overspread with brown, but showing also subdorsal short posterior brown stripes; venter of the abdomen nearly all pale scaled, showing only traces of black apical bands and median stripe.

Larva with head-hairs double or the lower in threes; pecten of the tube even, followed by a tuft of five hairs; anal segment ringed by the plate; comb scales six, each with a very sharp central spine and slight lateral fringes.

Egg - Narrowly fusiform, smooth, not angled, one side flattened, ends roundedly pointed, the micropylar end blunter, shortly conical at tip, which has small mucilaginous cushion; sculpturing fine and obscure; black, shining, laid singly.

This species is quite distinct. The coloration of the mesonotum is variable, distinctly banded or all dark brown or all golden yellow. The banded form is similar to *tahoensis*, *lazarensis* and *pullatus*, while the suffused brown form resembles *impiger*. Some specimens are very difficult to distinguish from *tahoensis* though in general the coloration is yellower. The venter of the abdomen is commonly all white or with paired apical black marks. The median black band is only very rarely present. The male genitalia resemble *campestris*, while the larva falls close to *abserratus*.

Type Cat. No. 20353, U.S. Nat. Mus.

Bred from early spring pools in muddy hoof-marks in the edge of a marsh, in shallow grassy pools along the lake filled by high waves and in mountain pools with *tahoensis*. All these pools of a temporary character. Fallen Leaf, Lake Tahoe, California, last part of May and first of June, 1916.

APPENDIX C

Aedes aboriginis, new species, Dyar 1917.

Head and mesonotum with dark yellow or brownish yellow narrow curved scales; a double line of small dark brown ones dorsally; traces only of the posterior lateral lines; areas around the antescutellar space golden. Abdomen black with basal segmental narrow white bands, triangularly widened at the sides, narrow posteriorly; venter grayish white scaled, with traces of a median-ventral black stripe. Legs black, femora whitish beneath nearly to tip; tibiae with a sprinkling of gray scales; knee-spot white. Wing-scales black, the scaling uniform, fine outstanding scales on the third vein like the rest.

In the male, the medioventral stripe of the abdomen is distinct, crossed by apical segmental black bands.

Genitalia - (See plate II). Apical lobe of the side-piece small, with slightly curved, partly oppressed setae; basal lobe large, expanded, tubercular, setose, the setae very long and dense on the lower edge, concealing a moderately stout curved spine, not longer than setae. A thickened area between basal lobe and base, punctured by the insertions of small setae. Stem of harpago moderate, the filament rather short, fusiform, with pointed curved tip.

Larva (See plate II). Scales of the lateral comb about 20, each with a row of apical spines. Air-tube with pecten teeth evenly spaced, followed by a five haired tuft. Anal segment not ringed by plate, the plate reaching near the ventral line and evenly margined. Head-hairs: upper in threes, rarely fours; lower in threes, rarely in twos. Ante-antennal tuft of eight.

Types, male and female, No. 21544, U.S. Nat. Mus.; bred from larvae found the middle of June, in the last stage, but with few pupae, in temporary puddles on the marsh and in wood-pools near the marsh. Longmire Springs, Mount Rainier National Park, Washington, issued June 17 to July 1, 1917 (H. G. Dyar).

Adult females, Glacier, Washington, June 3, 1917 (H. G. Dyar), and females and males, Lake Cushman, Washington, June 26, 27, 28, 1917 (H. G. Dyar); Hoquiam, Washington, May 27, 1904 (H. E. Burke) the latter erroneously recorded under *hexodontus* by me (Ins. Insc. Mens., 14, 1917); old specimens of this, the larger species, Ashford, Washington, August 1, 1906 (Dyar and Caudell).

The males were observed swarming at Lake Cushman in small groups in the forest in the forenoon, bright sunlight shining through the trees, but well screened by the dense foliage. The swarms were on the back side of the trunks of enormous cedar trees, in one case growing upon a rocky bank, which added to the shadow. The swarms were from 6 to 10 feet from the ground, varying from a few to 50 individuals.

APPENDIX D

Aedes cyclocerculus, new species from Dyar, 1920.

Female - Head brownish yellow scaled, dull whitish on the sides; mesonotum brownish yellow scaled, whitish around the antescutellar space; two diffused dark brown median bands; posterior-lateral stripes broad, black-brown, distinct. Abdomen with basal segmental white bands, widening at the sides; venter whitish-scaled, the segments black-scaled on the sides. Legs black, femora white below; knee-spots white.

Male - Ground-color scales lighter yellow and sparser than in the female, the dark markings broad. White abdominal bands narrow; ventral scaling mixed with black. Genitalia: side pieces over three times as long as wide, the clasp with long terminal spine; apical lobe low-conical, large, with dense recurved or flattened short setae; basal lobe quadrately expanded, tubercular-setose, the setae longer and denser about the marginal spine, the filament is stout and strongly recurved. Harpago with short hirsute stem, the filament rather broadly fusiform with pointed tip, about one-half as long as the stem. Harpes and unci normal. Basal appendages rather long, with five or six terminal and sublateral spines.

Types, male and female, No. 22617, U.S. Nat. Mus.; Prince Rupert, British Columbia, May 11, 12, 1919 (H. G. Dyar).

Larva - Head-hairs in twos (upper occasionally 3 or 1, lower rarely 1). Lateral comb of the eighth segment of six or seven large scales, each with long pointed tip, shortly and sparsely fringed at the base. Air tube two-and-a-half times as long as wide; pecten of evenly spaced teeth, followed by a 5-haired tuft. Anal segment ringed by the plate, short and quadrate, the ventral brush obliquely posteriorly directed.

Larvae in muskeg-pools early in May. The larvae are small, darkly colored, and occurred in considerable numbers in one pool.

Total, 83 specimens: Prince Rupert, British Columbia, May 11-31, 1919; Ketchikan, Alaska, June 20, August 6, 8, 1919; Cape Fanshaw, Alaska, June 22, 1919; Juneau, Alaska, June 23, 1919.

APPENDIX E

Aedes leuconotips, new species from Dyar, 1920.

Female - Head yellow-brown scaled, with whitish diffuse spots at the sides. Mesonotum yellow-brown, with two diffuse broad median dark brown bands; posterior lateral stripes faint, showing only traces. Abdomen with basal white segmental bands, widening at the sides; venter grayish white scaled. Legs black, femora white beneath; knee-spots white.

Male - Ground-color scales paler than in female and sparser. Posterior lateral bands broad and distinct, similar to the median ones. Venter mixed with black scales, predominating on tips of segment. Genitalia: Side pieces over three times as long as wide, the clasp with long terminal spine; apical lobe low-conical, large, with dense recurved or flattened short setae; basal lobe quadrately expanded, tubercular-setose, the setae longer and denser about the marginal spine, which is very stout and contrasted. Harpago with short hirsute stem, the filament rather broadly fusiform with pointed tip, about one-half as long as stem. Harpes and unci normal. Basal appendages rather long, with five or six terminal and subterminal spines.

Types, males and female, No. 22618, U.S. Nat. Mus.; Prince Rupert, British Columbia, May 26, 30, 1919 (H. G. Dyar).

Larva - Head-hairs in twos, or the lower simple; lateral comb of the eighth segment seven large scales, each with a long pointed tip, shortly and sparsely fringed at base. Air-tube two-and-one-half times as long as wide; pecten evenly spaced teeth, followed by 6-haired tuft. Anal segment ringed by the plate, rather short and broad, the ventral brush obliquely posteriorly directed.

Larvae in muskeg-pools in May. The larvae are pale in color, whitish, and occurred sparsely in the pools, in two cases but one larva in a pool.

Total, 44 specimens: Prince Rupert, British Columbia, May 22 - June 13, 1919; Ketchikan, Alaska, June 20, 1919; Cape Fanshaw, Alaska, June 22, 1919; Juneau, Alaska, June 23, 1919.

APPENDIX F

Aedes labradorensis, new species, Dyar and Shannon, 1925.

Proboscis slightly shorter than the abdomen, black. Palpi about one-fifth the length of proboscis. Head with dark brown narrow curved scales, which shade to whitish on the sides rather than the vertex. Mesonotum black, with narrow curved dark brown scales, shading to yellowish about the antescutellar space, but not gray on the lateral margins; black posterior side stripes often quite distinct and edged within by a line of light scales, sometimes less contrasted. Abdomen black with basal segmental whitish bands, which are narrowed centrally in an arc and are not more than one-third the length of the segment dorsally, widening moderately at the sides; venter whitish scaled, the tips of the segments sometimes shaded. Legs black, the femora whitish beneath and narrowly tipped with white. A few white scales at the base of costa. Length 4.5 to 5 mm.

Type and paratypes - 11 females, no. 27862, U.S. Nat. Mus.; Hawk's Harbor, Labrador, July 20, 1908.

Three females reported by Howard, Dyar and Knab from Cape Charles, St. Lewis Inlet and Rigolet, Labrador, appear to be this species, and have been placed under *labradorensis* instead of under the *provocans* label as the latter has been made a synonym of *punctor* by Dyar. A twelfth female from Hawk's harbor is light gray. We think it to be a badly faded specimen of *labradorensis*, although the date of capture is the same as that of fresh specimens.

APPENDIX G

This section includes a list of the measurements taken from *A. hexodontus* larval skins. It includes specimens that were reared at room temperature and those from 14° C. All of the specimens were from the same pool at Cypress Provincial Park. The character abbreviations used in the table are as follows: 1) C. S. refers to comb scale, 2) L. P. refers to last pecten tooth and 3) SL. P. refers to second last pecten tooth. Comb scales that had broken tips or were at a poor angle for measuring were not included in these results.

Larval measurements (in mm) from Room Temperature reared *A. hexodontus*.

Specimen Character	R11	R21	R22	R23	R24	R31	R32	R33	R34
C. S. 1	0.119	0.119	0.114	0.119	0.122	0.088	0.102	0.119	0.114
C. S. 2	0.119	0.116	0.125	0.122	0.106	0.094	0.103	0.125	0.120
C. S. 3	0.116	0.108	0.125	0.102	0.108	0.094	0.103	0.134	0.125
C. S. 4	0.108	0.105	0.120	0.097	0.113	0.100	0.097	0.122	0.109
C. S. 5	0.117	0.113	0.119	0.111	0.109	0.088	0.111	0.128	
C. S. 6	0.123	0.098	0.109	0.103			0.116	0.122	
C. S. 7							0.105		
C. S. 8									
C. S. 1	0.122	0.119	0.116	0.120	0.100	0.122	0.097	0.120	0.097
C. S. 2	0.122	0.119	0.128	0.103	0.122	0.116	0.091	0.125	0.106
C. S. 3	0.120	0.103	0.128	0.125		0.109	0.086	0.116	0.106
C. S. 4	0.117	0.122	0.122	0.117		0.109	0.109	0.128	0.097
C. S. 5	0.116	0.100	0.125				0.114	0.117	0.109
C. S. 6	0.113	0.116	0.119				0.109	0.113	0.109
C. S. 7							0.094	0.106	0.088
C. S. 8									
mean length	0.118	0.112	0.121	0.112	0.111	0.102	0.103	0.121	0.109
siphon index	2.000	1.724	2.400	2.250	2.545	2.381		2.333	2.292
L. P.	0.116	0.097	0.134	0.122	0.116	0.123	0.113	0.138	0.097
SL. P.	0.114	0.094	0.122	0.111	0.094	0.113	0.094	0.109	0.088
L. P.	0.109	0.116	0.119	0.116	0.116	0.128	0.103	0.131	0.109
SL. P.	0.084	0.114	0.117	0.109	0.089	0.122	0.097	0.113	0.094
Seta S-2	0.059	0.058	0.066	0.063	0.056	0.053	0.059	0.056	0.056

Larval measurements (in mm) from Room Temperature reared *A. hexodontus*.

Specimen Character	R35	R36	R37	R38	R39	R310	R41	R51	R61
C. S. 1	0.103	0.106	0.109	0.100	0.091	0.105	0.109	0.102	0.091
C. S. 2	0.103	0.109	0.103	0.091	0.100	0.109	0.100	0.128	0.103
C. S. 3	0.109	0.106	0.109	0.109	0.097	0.125	0.102	0.125	
C. S. 4	0.103	0.113	0.100	0.119	0.105	0.103	0.094	0.103	
C. S. 5	0.103	0.119	0.100	0.106	0.088		0.097	0.091	
C. S. 6	0.100	0.122			0.098		0.088		
C. S. 7							0.103		
C. S. 8									
C. S. 1	0.100	0.122	0.105	0.116	0.081	0.100	0.102	0.116	0.091
C. S. 2	0.091	0.125	0.106	0.100	0.106	0.116	0.106	0.106	0.103
C. S. 3	0.094	0.109	0.100	0.119	0.094	0.106	0.103	0.119	0.102
C. S. 4	0.094	0.100	0.109	0.119	0.103	0.100	0.106	0.125	
C. S. 5	0.094	0.088	0.094	0.106	0.094	0.128	0.077	0.114	
C. S. 6	0.109		0.097	0.116	0.084	0.106			
C. S. 7			0.100	0.113					
C. S. 8									
mean length	0.100	0.111	0.103	0.110	0.095	0.110	0.099	0.113	0.098
siphon index	2.455	2.174	2.250	2.545		2.545	2.167	2.333	2.000
L. P.	0.109	0.125	0.109	0.106		0.109	0.109	0.113	0.097
SL. P.	0.102	0.109	0.097	0.100		0.100	0.097	0.097	0.078
L. P.	0.097	0.116	0.106	0.084		0.106	0.113	0.113	0.089
SL. P.	0.100	0.103	0.097	0.094		0.097	0.100	0.097	0.063
Seta S-2	0.059	0.061	0.059	0.063		0.034		0.056	0.063

Larval measurements (in mm) from Room Temperature reared *A. hexodontus*.

Specimen Character	R62	R63	R71	R73	R74	R81	R82	R83	R84
C. S. 1	0.103	0.072	0.113	0.089	0.066	0.100	0.106	0.103	0.103
C. S. 2	0.091	0.072	0.116	0.089	0.102	0.119	0.116	0.088	0.114
C. S. 3	0.084	0.084	0.109	0.105	0.088	0.122	0.106	0.100	0.114
C. S. 4	0.094	0.094	0.094	0.106	0.122		0.108	0.097	0.097
C. S. 5	0.078		0.122	0.100	0.116		0.108	0.091	0.109
C. S. 6	0.081		0.094		0.106		0.106	0.092	0.106
C. S. 7							0.084		
C. S. 8									
C. S. 1	0.091	0.103	0.109	0.100	0.133	0.119	0.097	0.091	0.109
C. S. 2	0.088	0.106	0.103	0.103	0.125	0.111	0.102	0.089	0.106
C. S. 3	0.084	0.113	0.113	0.100	0.125	0.092	0.109	0.084	0.116
C. S. 4	0.089	0.084	0.122	0.102	0.113	0.097	0.109	0.077	0.084
C. S. 5	0.088	0.106	0.122	0.105	0.102		0.114	0.084	0.109
C. S. 6		0.097	0.117		0.075		0.108	0.106	0.122
C. S. 7							0.106		0.113
mean length	0.088	0.093	0.111	0.100	0.106	0.108	0.106	0.092	0.108
siphon index	2.167	2.417	2.286	2.238	2.000	2.273	2.286	2.182	2.400
L. P.	0.091	0.109	0.133	0.106	0.109	0.119	0.109	0.109	0.109
SL. P.	0.083	0.069	0.103	0.109	0.113	0.097	0.072	0.084	0.106
L. P.	0.091	0.109	0.106	0.116	0.106	0.113	0.106	0.100	
SL. P.	0.088	0.094	0.098	0.120	0.094	0.103	0.069	0.084	
Seta S-2	0.069	0.056	0.056	0.053	0.056	0.050	0.056	0.047	0.053

Larval measurements (in mm) from Room Temperature reared *A. hexodontus*.

Specimen Character	R85	R86	R87	R88	R91	R92	R93	R94	R95
C. S. 1	0.094	0.103	0.113	0.088	0.091	0.133	0.125	0.078	0.100
C. S. 2	0.088	0.113	0.109	0.103	0.100	0.119	0.113	0.097	0.106
C. S. 3	0.103	0.122	0.122	0.106	0.109	0.117	0.117	0.069	0.108
C. S. 4	0.106	0.119	0.116	0.106	0.102	0.117	0.102	0.094	0.100
C. S. 5	0.103	0.114	0.122	0.109	0.102	0.106		0.106	0.122
C. S. 6	0.116		0.106	0.103	0.109			0.113	
C. S. 7								0.114	
C. S. 1	0.106	0.094	0.113	0.109	0.111	0.097	0.122	0.102	0.097
C. S. 2	0.111	0.106	0.095	0.106	0.097	0.081	0.116	0.103	0.102
C. S. 3	0.114	0.111	0.109	0.100	0.106	0.066	0.119	0.109	0.119
C. S. 4	0.108	0.117	0.109	0.108	0.094	0.088	0.119	0.113	0.103
C. S. 5	0.113	0.120	0.122	0.109	0.094	0.091	0.106	0.111	0.117
C. S. 6	0.117	0.117	0.125	0.084	0.078		0.100	0.102	
C. S. 7			0.120						
C. S. 8									
mean length	0.107	0.112	0.114	0.103	0.099	0.099	0.114	0.101	0.107
siphon index	2.000	2.286	2.381	2.083	2.182	2.364	2.182	2.182	2.500
L. P.	0.113	0.119	0.128	0.100	0.116	0.106	0.119	0.113	0.113
SL. P.	0.106	0.103	0.109	0.097	0.100	0.094	0.103	0.103	0.100
L. P.	0.106	0.117	0.122	0.097	0.131	0.091	0.122	0.119	0.119
SL. P.	0.097	0.114	0.125	0.088	0.109	0.083	0.109	0.119	
seta S-2	0.053	0.053	0.053	0.058	0.055	0.053	0.056	0.048	0.063

Larval measurements (in mm) from 14° C reared *A. hexodontus*.

Specimen Character	F11	F12	F21	F22	F31	F32	F33	F34	F35
C. S. 1	0.106	0.128	0.120	0.128	0.109	0.116	0.128	0.125	0.119
C. S. 2	.0116	0.113	0.133	0.128	0.125	0.094	0.141	0.130	0.119
C. S. 3	0.116	0.114	0.122	0.138	0.125	0.122	0.144	0.131	0.122
C. S. 4	0.125	0.113	0.131	0.138	0.120	0.106	0.142	0.122	0.127
C. S. 5	0.128	0.116	0.138	0.125	0.122	0.122	0.144	0.130	0.116
C. S. 6	0.128		0.136	0.116				0.106	0.106
C. S. 7				0.116					
C. S. 8									
C. S. 1	0.114	0.113	0.127	0.134	0.114	0.125	0.111	0.116	0.117
C. S. 2	0.130	0.125	0.122	0.125	0.119	0.119	0.136	0.120	0.125
C. S. 3	0.125	0.122	0.134	0.125	0.116	0.122	0.128	0.122	0.088
C. S. 4	0.127	0.123	0.138	0.128	0.119	0.125	0.134	0.131	0.084
C. S. 5	0.125		0.138	0.131	0.125	0.117	0.125	0.127	0.094
C. S. 6	0.116		0.131	0.134	0.119	0.105	0.133	0.128	0.102
C. S. 7			0.125	0.116				0.127	
C. S. 8			0.125						
mean length	0.121	0.118	0.130	0.127	0.119	0.116	0.133	0.124	0.110
siphon index	2.455		2.455	2.000	2.071	2.458	2.167	2.240	2.250
L. P.	0.119	0.131	0.131	0.125	0.138	0.113	0.116	0.116	0.106
SL. P.	0.116	0.125	0.113	0.113	0.125	0.100	0.116	0.111	0.094
L. P.	0.123	0.122	0.125	0.134	0.131	0.120	0.098	0.111	0.109
SL. P.	0.125	0.128	0.113	0.122	0.131	0.111	0.094	0.109	0.097
seta S-2	0.058	0.053	0.063	0.063			0.069	0.059	0.056

Larval measurements (in mm) from 14° C reared *A. hexodontus*.

Specimen Character	F36	F41	F43	F51	F52	F53
C. S. 1	0.122	0.094	0.122	0.103	0.100	0.098
C. S. 2	0.128	0.108	0.131	0.119	0.091	0.108
C. S. 3	0.113	0.100	0.130		0.122	0.111
C. S. 4	0.127	0.086	0.128		0.120	0.106
C. S. 5			0.125		0.130	0.119
C. S. 6			0.116		0.131	0.100
C. S. 7						
C. S. 8						
C. S. 1	0.119	0.094	0.094	0.119	0.113	0.117
C. S. 2	0.138	0.113	0.116	0.113	0.119	0.116
C. S. 3	0.122	0.094	0.108	0.123	0.125	0.105
C. S. 4	0.128	0.116	0.106	0.122	0.131	0.128
C. S. 5	0.131	0.097	0.106	0.122	0.109	0.108
C. S. 6		0.100	0.128	0.125	0.128	
C. S. 7				0.116	0.122	
C. S. 8						
mean length	0.125	0.100	0.117	0.118	0.119	0.111
siphon index	2.038	2.154	2.000	2.417	2.375	2.417
L. P.	0.139		0.128	0.128	0.116	0.128
SL. P.	0.125	0.122	0.123	0.125	0.113	0.116
L. P.	0.138	0.116	0.125	0.125	0.116	
SL. P.	0.120	0.116	0.117	0.130	0.114	
seta S-2	0.061		0.056	0.063	0.063	0.063

APPENDIX H

A. aboriginis females.

Specimen Site Hydrocarbon	<i>aboriginis</i> 1 Coquitlam	<i>aboriginis</i> 2 U.B.C.R.F	<i>aboriginis</i> 3 Brandywine	<i>aboriginis</i> 4 Brandywine
C-21	20.34	1.40	1.18	1.24
C-22	3.19	4.40	0.76	0.49
C-23	28.30	16.56	9.77	5.66
C-24	5.43	3.64	2.48	1.44
C-25	31.65	22.42	21.71	8.25
C-26	4.76	3.52	1.41	

A. hexodontus female.

Specimen Site Hydrocarbon	<i>hexodontus</i> 1 Brandywine	<i>hexodontus</i> 2 Brandywine	<i>hexodontus</i> 3 Avola	<i>hexodontus</i> 4 Avola
C-21	2.53		0.51	1.01
C-22	1.31		0.32	0.60
C-23	21.66	8.83	6.30	18.57
C-24	4.58		1.37	4.09
C-25	29.74	12.13	7.62	21.28
C-26	6.31		0.59	2.81

A. punctor females.

Specimen Site Hydrocarbon	<i>punctor</i> 1 Avola	<i>punctor</i> 2 Avola	<i>punctor</i> 3 Avola	<i>punctor</i> 4 Yoho
C-21	3.53	8.56	1.09	4.95
C-22	0.87		1.19	3.67
C-23	18.69	67.15	11.36	46.25
C-24	3.31	7.83	2.98	6.48
C-25	17.95	53.60	10.56	32.13
C-26	4.19	8.63	1.74	3.68

APPENDIX I

Analysis of variance of mean comb length for *A. hexodontus* in the experiment with temperature controlled rearing of larvae.

	sum of squares	degrees of freedom	mean square	F-value
Treatments	.00184	1	.00184	28.86
Error	.00313	49	.0000639	
Total	.00498	50		

I had no reason to suspect that these larvae reared as 2 groups were different from one another so I used a two tailed test. I selected a 99% level of significance to test these means. The probability of accepting the null hypothesis would mean that the F-value would have to fall between 0.26 and 3.81. The F-value from the ANOVA calculation was 28.86, therefore I rejected the null hypothesis that the means were equal.