FRONTISPIECE

Chaoborus trivittatus adult male.

SYSTEMATICS AND BIONOMICS OF THE SPECIES OF THE SUBGENUS *SCHADONOPHASMA* DYAR AND SHANNON (*CHAOBORUS*, CHAOBORIDAE, DIPTERA)[1]

ART BORKENT[2]
Department of Entomology
University of Alberta
Edmonton, Alberta, Canada
T6G 2E3

Quaestiones Entomologicae
15: 122-255 1979

Study of structure, intraspecific variation, life cycles and bionomic features suggests the presence of three species of the subgenus Schadonophasma. Chaoborus trivittatus *(Loew) and* Chaoborus cooki *Saether are restricted to North America while* Chaoborus nyblaei *(Zetterstedt) is known only from Fennoscandia.* Chaoborus brunskilli *Saether and* Chaoborus knabi *(Dyar) are conspecific with* C. trivittatus

All stages of each species were studied except first, second and third larval instars of C. nyblaei *which are unknown. Eggs of* C. cooki *and* C. nyblaei, *unlike those of* C. trivittatus, *exhibit a thickened exochorion.* C. cooki *eggs are laid in a spherical mass with little gelatinous matrix while those of* C. trivittatus *are laid in a spiral arrangement in a disc of gelatinous matrix. First instar larvae of* C. cooki *possess a more pronounced egg burster than do those of* C. trivittatus. *All other stages can be distinguished only by using a combination of characters. A compound character index is provided for separation of fourth instar larvae of* C. trivittatus *and* C. cooki *and was used to test possibilities of conspecificity of these two species. Male adults can be identified by the shape of the penis valves and a ratio of the length of two wing veins.*

The thickened exochorion of eggs of C. cooki, *and probably* C. nyblaei, *is an adaptation to overwintering as eggs in temporary ponds.* C. cooki *is univoltine.* C. trivittatus *immatures occur mostly in permanent lentic habitats where this species overwinters as a fourth instar larva. This species may be uni- or multivoltine or have a two year life cycle.*

Behavioural differences are evident between C. trivittatus *and* C. cooki. *Only* C. cooki *larvae are capable of ingesting ostracods. Male adults of* C. trivittatus *form large swarms. Adult females are the main dispersing agent of* C. trivittatus *while limited evidence for* C. cooki *suggests that both sexes of this species disperse. Under laboratory conditions* C. trivittatus *male adults live up to seven to eight days and female adults up to twelve days.*

The pattern of intraspecific variation indicates that some of the variation of fourth instar larvae is due to sex-associated, age-related and geographical variation. Geographical variation of characters of fourth instar larvae and geographical distribution of C. trivittatus *indicates that this species was present in the Beringian refugium and those refugia south of the continental ice sheet during the Wisconsin glaciation.*

A reconstructed phylogeny of some Chaoborus *species is provided. The subgenera* Schadonophasma *and* Chaoborus s. str. *are both monophyletic and are sister groups. An upper Oligocene* Chaoborus *fossil indicates the minimum age of the speciation events which gave rise to the ancestor of these two groups, to be 25 million years.*

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[1] Based on a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at the University of Alberta, Edmonton, Canada.

[2] Present address: c/o D.M. Wood, Biosystematics Research Institute, Research Branch, Agriculture Canada, Ottawa, Ontario, Canada K1A 0C6

A reconstructed phylogeny of Schadonophasma *species indicates that* C. cooki *and* C. nyblaei *are more closely related to each other than either is to* C. trivittatus. *Zoogeographic considerations suggest two possible hypotheses for the origin of these species. The first invokes allopatric speciation between the Nearctic and Palaearctic regions producing* C. trivittatus *and the ancestor of* C. cooki *and* C. nyblaei. *Subsequent geographical isolation of populations of the latter lineage produced* C. cooki *and* C. nyblaei. *The second hypothesis differs in proposing that the* C. cooki-nyblaei *lineage arose in sympatry with* C. trivittatus *from individuals of a* C. trivittatus*-like ancestor that involved an overwintering egg stage which allowed exploitation of temporary habitats. A model for the development of reproductive isolation in sympatry suggests the occurrence of a mutation resulting in a diapausing egg in the ancestral population. Through temporal disjunction of mating periods, homogamic mating, complete selection against overwintering larvae in temporary ponds and overwintering eggs in permanent ponds, the two lineages which gave rise to* C. trivittatus *and the ancestor of* C. cooki-nyblaei *became genetically isolated.*

L'étude de la morphologie, des variations intraspécifiques, des cycles vitaux et de l'histoire naturelle suggère que le sous-genre Schadonophasma *consiste en trois espèces.* Chaoborus trivittatus *(Loew) et* Chaoborus cooki *Saether ne se recontrent qu'en Amérique du Nord, alors que* Chaoborus nyblaei *(Zetterstedt) n'est connu que de la Scandinavie. Je considère* Chaoborus brunskilli *Saether et* Chaoborus knabi *(Dyar) comme appartenant à* C. trivittatus.

J'ai étudié tous les stades de chaque espèce, sauf les premier, deuxième et troisième âges larvaires de C. nyblaei, *qui sont inconnus. Les oeufs de* C. cooki *et de* C. nyblaei, *contrairement à ceux de* C. trivittatus, *ont un exochorion épais. Les oeufs de* C. cooki *sont déposés en une masse sphérique entourée d'un peu de matière gélatineuse, alors que ceux de* C. trivittatus *sont déposés en spirale dans un disque de matière gélatineuse. Les larves du premier âge de* C. cooki. *ont un ovorupteur plus prononcé que celles de* C. trivittatus. *Tous les autres stades ne peuvent être distingués que par des combinaisons de caractères. Un index, défini par de telles combinaisons, permet de séparer les larves du quatrième âge de* C. trivittatus *et de* C. cooki, *et a été utilisé pour vérifier que ces deux espèces étaient bien distinctes l'une de l'autre. Les adultes mâles peuvent être identifiés par la forme des valves de l'édéage et par un rapport entre les longueurs de deux des nervures alaires.*

L'exochorion épais des oeufs de C. cooki, *et probablement de* C. nyblaei, *est une adaptation pour l'hibernation au stade d'oeuf dans les étangs temporaires.* C. cooki *n'a qu'une seule génération par année. Les immatures de* C. trivittatus *se rencontrent surtout dans les étangs permanents où les larves du quatrième âge hibernent. Cette espèce peut avoir une ou plusieurs générations par année, ou avoir un cycle vital de deux ans.*

Il y a plusieurs différences entre le comportement de C. trivittatus *et celui de* C. cooki. *Seules les larves de* C. cooki *peuvent se nourrir d'ostracodes. Les adultes mâles de* C. trivittatus *s'assemblent en grands essaims. Les adultes femelles constituent le principal agent de dispersion de* C. trivittatus, *alors que chez* C. cooki, *il semblerait que les deux sexes participent à la dispersion. En laboratoire, les mâles de* C. trivittatus *vivent jusqu'à sept ou huit jours, alors que les femelles vivent jusqu'à douze jours.*

La variabilité intraspécifique chez les larves du quatrième âge serait reliée au sexe et à l'âge, ainsi qu'à des facteurs géographiques. La variation géographique des caractères du quatrième âge larvaire et la répartition géographique de C. trivittatus *indiquent que cette espèce était présente dans le refuge de Béring. ainsi que dans le refuge situé au sud de la calotte glaciaire continentale durant la glaciation du Wisconsin.*

J'ai reconstruit la phylogénie de quelques espèces de Chaoborus. *Les sous-genres* Schadonophasma *et* Chaoborus s. str. *sont monophylétiques et apparentés. Un fossile de* Chaoborus *datant de l'Oligocène supérieur suggère que le processus de spéciation ayant produit l'ancêtre de ces deux sous-genre a eu lieu il y a au moins 25 millions d'années.*

Une reconstruction de la phylogénie des espèces de Schadonophasma *montre que* C. cooki *et* C. nyblaei *sont plus étroitement apparentés l'un à l'autre que chacun d'eux ne l'est à* C. trivittatus. *Une étude biogéographique suggère deux hypothèses quant à l'origine de ces espèces. La première, basée sur le principe d'évolution allopatrique, suggère que* C. trivittatus *et l'ancêtre de* C. cooki-nyblaei *résultèrent d'une séparation de la population de leur ancêtre commun en deux populations, une néarctique et une paléarctique. Une séparation géographique subséquente de la population paléarctique aurait produit* C. cooki *et* C. nyblaei. *Suivant la seconde hypothèse, la lignée* C. cooki-nyblaei *aurait évolué en sympatrie avec* C. trivittatus, *et serait dérivée d'individus semblables à l'ancêtre de* C. trivittatus, *mais hibernant au stade d'oeuf, cette dernière adaptation ayant permis l'exploitation des habitats temporaires. J'explique l'évolution de l'isolement reproducteur entre ces deux lignées sympatriques comme suit: une mutation aurait introduit la diapause au stade d'oeuf dans la population ancestrale; grâce à une séparation temporelle des périodes reproductrices, permettant ainsi des accouplements homogamiques, et grâce à une sélection totale contre l'hibernation à l'état larvaire dans les étangs temporaires d'une part, et contre l'hibernation à l'état d'oeuf dans les étangs permanents d'autre part, les deux lignées qui produisirent* C. trivittatus *et l'ancêtre de* C. cooki-nyblaei *devinrent génétiquement isolées.*

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INTRODUCTION

For systematists interested in understanding the intraspecific and interspecific variation of species, a frequent concern is the investigation of species which do not exhibit discrete morphological characteristics allowing identification of individuals. This study is partially an investigation of such a problem within the genus *Chaoborus* Lichtenstein. I first recognized that it was difficult to separate species of the subgenus *Schadonophasma* Dyar and Shannon, while attempting to identify fourth instar larvae, pupae and adults using Saether's (1972) key. Some specimens exhibited combinations of characters from different species, as delimited by Saether (1970, 1972). I therefore undertook a reinterpretation of variation exhibited by members of this subgenus through examination of the structural and bionomic features of eggs, all stages of larvae, pupae and adults.

Although *Chaoborus* is assigned species that have marked variation and show slight morphological differences between species, few studies have attempted to precisely interpret this variation. Saether (1967) showed that the characters previously thought to separate *Chaoborus flavicans* (Meigen) and *Chaoborus alpinus* Peus feature overlapping variation and consequently he considered these forms to be conspecific. However, overlap of variation alone is not evidence of reproductive unity. Detailed analysis of character variation, distributional data and bionomic information yields superior data from which to decide species status. This study employs all three sources of data.

However recognition of members of different species is only the initial step permitting systematists to investigate species. I therefore further undertook study of intraspecific variation of the species, including analysis of sex-associated, age-related and geographical variation, and differences between larval instars. Sources of variation of individual characters of *Chaoborus* species are not well understood. Sikorowa (1973) showed that some variation of *Chaoborus flavicans* can be considered ecotypic and Cook (1956: 32) suggested the same for *Chaoborus punctipennis* (Say) larvae. Variation in number of mandibular fan bristles, ratio of length to width of prelabral appendages, total length (Smith, 1960a: 398) and air sac length (von Frankenberg, 1915: 514) of fourth instar *Chaoborus crystallinus* (De Geer) larvae is sex-associated. Total length and color of *Chaoborus americanus* (Johannsen) fourth instar larvae is also sex-associated (Bradshaw, 1973: 1249) as well as reflecting a polymorphism. Roth (1967: 66) noted worn prelabral appendages of overwintered fourth instar larvae of *Chaoborus albatus* Johnson. Seasonal differences of total length of mature fourth instar larvae of *Chaoborus punctipennis* was reported by Muttkowski (1918: 407). *Chaoborus punctipennis* adult size (Cook, 1956: 32) and number of mandibular fan bristles of *Chaoborus anomalus* Edwards fourth instar larvae (McGowan, 1972: 365) may vary geographically. All these studies suggest possible sources of variation and I have attempted to provide interpretations of variation of characters of species of *Schadonophasma* in light of these previous studies.

Systematic studies should be based on evolutionary theory and the aforementioned analyses provide a sufficient background from which to hypothesize the evolutionary history of the subgenus *Schadonophasma* and to also propose a possible example of sympatric speciation. An interpretation of the phylogeny of some *Chaoborus* species is provided.

Because of their importance as fish food (Goldspink and Scott, 1971; Green *et al.*, 1973; Kruger, 1973; Lindquist *et al.* 1943; MacDonald, 1956; Pope *et al.*, 1973), as mosquito predators (Montchadsky, 1964; Sailer and Lienk, 1954; Skierska, 1969, 1974), in the prominent role they play in fresh water communities (e.g. Bonomi, 1962; Fedorenko and Swift, 1972; Juday, 1921; Miyadi, 1932; Miyadi and Hazema, 1932; Petr, 1972; Swüste *et al.*, 1973; Woodmansee and Grantham, 1961) and occasionally as pests (Brydon, 1956; Herms, 1937; Hitchcock, 1965; Lindquist and Deonier, 1942a, 1942b; Lindquist *et al.*, 1951; MacDonald, 1953, 1956; Shemanchuk, 1959) many *Chaoborus* populations are better known bionomically than systematically. For example, although *Chaoborus flavicans* has been studied ecologically in detail (e.g. Balvay, 1977d; Parma, 1971b), no thorough distributional study has been done on this species or any other species of the Holarctic region. This situation allows systematists working on *Chaoborus* to take into account a wide array of ecological work and to draw systematic inferences from such studies.

Chaoborus is composed of medium sized flies 2.0–9.3 mm in length. Adults of this genus are not known to bite although the most primitive genus of the family, *Corethrella* Coquillett, includes species with haematophagous adults (McKeever, 1977; Miyagi, 1974, 1975; Williams and Edman, 1968). In the Holarctic region larvae may be commonly found in permanent and temporary lentic waters and occasionally in rivers.

Chaoborus includes 37 described species in six subgenera (*Neochaoborus* Edwards, *Sayomyia* Coquillett, *Edwardsops* Lane, *Peusomyia* Saether, *Schadonophasma*, and *Chaoborus sensu stricto*). The genus has been recorded from most major land masses with the exception of New Zealand, Antarctica, Greenland, and most oceanic islands. Edwards (1932) gave a world list of species and their distribution. The Palaearctic species have been described most recently by Hirvenoja (1961), Martini (1931), Parma (1969), Peus (1934), Prokesova (1959), and Sikorowa (1967a, 1973) and Nearctic species by Dyar and Shannon (1924) and Cook (1956) who also provided a detailed morphological study. Saether (1970) gave the most recent revision of Palaearctic and Nearctic species and was first to compare material of most species from both these regions. Palaearctic and Nearctic samples of *Chaoborus flavicans* were studied by Saether (1967). Saether (1972) presented keys to fourth instar larvae, pupae and adults of species of the Holarctic region and gave a synopsis of their way of life and structure.

Lane (1953) and Saether (1976) have provided descriptions for most known species of *Chaoborus* in South America. African species have been described by Edwards (1930), Green and Young (1976), McGowan (1972, 1976), and Verbeke (1957, 1958) and Oriental and Australian species by Giles (1902, 1904), and Theobald (1901b, 1903). Fossil species have been described by Borkent (1978b), Edwards (1923), von Heyden (1862), Meunier (1904), and Scudder (1890; questionable identification).

The objects of this study were species of the subgenus *Schadonophasma*, whose adults and larvae are the largest of *Chaoborus* species. Species are restricted to northern boreal regions. Larvae of all species sometimes occur in large numbers in permanent and temporary lentic waters. Adults and immatures are poorly represented in museum collections.

Most descriptions are brief and bionomic information anecdotal (Allan, 1973; Anderson and Raasveldt, 1974; Dickenson, 1944; Dodson, 1970; Dyar and Shannon, 1924; Edwards, 1932; Felt, 1904, 1905; Giles, 1902; Hamilton, 1971; James *et al.*, 1969; James and Smith, 1958; Jenkins and Knight, 1950; Johannsen, 1903, 1934; Loew, 1862; Matheson, 1944, 1945; Pope *et al.*, 1973; Smith, 1960b; Theobald, 1901b; Tullock, 1934; Twinn *et al.*, 1948; Zetterstedt, 1838, 1851). The feeding characteristics and vertical migration of the larvae and the life cycle of *Chaoborus trivittatus* (Loew) from Eunice Lake, British Columbia have been described by Fedorenko (1975a, 1975b, 1975c), Federenko and Swift (1972), Swift (1975, 1976), and Swift and Fedorenko (1975).

Schadonophasma was erected as a subgenus by Dyar and Shannon (1924) to contain the North American species *Chaoborus trivittatus*. Edwards (1932), Cook (1956), Matheson (1944), and Peus (1967) considered *Chaoborus nyblaei* (Zetterstedt) to be conspecific with *Chaoborus trivittatus*. Hirvenoja (1961), however, considered these to be two distinct species. Saether (1970) recognized, on morphological grounds, *Chaoborus nyblaei* in Fennoscandia and Baffin Island, Canada, and *Chaoborus trivittatus*, *Chaoborus cooki* Saether and *Chaoborus brunskilli* Saether in North America.

This study clarifies the above confusion concerning species of *Schadonophasma*.

MATERIALS AND METHODS

Materials

This study was based on examination of 293 eggs of *Chaoborus cooki*, more than 50 egg masses of *Chaoborus trivittatus*, and of all species, 49 first instar, 58 second instar, 139 third instar, and 832 fourth instar larvae, 93 male and 80 female pupae or pupal exuviae and 311 male and 248 female adults. Eggs and most adults were preserved in fluid and members of other stages and some adults were mounted on microscope slides. Many more specimens of all stages, preserved in fluid, were studied. All *Schadonophasma* material examined by Saether (1970), except the female pupa of *Chaoborus trivittatus*, was reexamined. I have also examined material collected by Osten Sacken (MCZ) but, because I could not interpret the locality labels, did not include the material in this study.

For comparative purposes (diagnostic and phylogenetic) I also examined various stages of other species of *Chaoborus*, *Mochlonyx* Loew, and *Eucorethra* Underwood. (Table 1).

Because I wanted to sample a wide geographical area and sampling lakes would have taken too much time, I collected immatures only from smaller water bodies and depended on loans for material from lakes. Place names in Alberta referred to in the text are indicated in Figure 1.

Table 1. Material other than *Schadonophasma* examined. ⊗ = undescribed material.

	First Instar	Second Instar	Third Instar	Fourth Instar	Pupae	Adults
Chaoborus americanus		⊗	⊗	x	x	x
Chaoborus crystallinus		⊗	⊗	x	x	x
Chaoborus flavicans	x	⊗	⊗	x	x	x
Chaoborus obscuripes			⊗			
Chaoborus punctipennis				x	x	x
Chaoborus albatus				x		
Chaoborus pallidipes		⊗	⊗	x		
Chaoborus anomalus		⊗	⊗	x		
Chaoborus certapogones		⊗	⊗	x		
Chaoborus fuliginosus	⊗	⊗	⊗	x		
Mochlonyx velutinus			⊗	x	⊗	x
Eucorethra underwoodi	⊗	⊗	⊗	x	x	x

Voucher specimens from this study and some of the material I collected are in the Stickland Museum, Department of Entomology, University of Alberta, Canada. Other material collected is deposited in museums as indicated in the list of localities at the end of species descriptions.

Nearly all immatures and about half of all adults were collected by myself, mostly in Alberta. The remainder were borrowed from the following museums or persons designated in the text by the following abbreviations. Names of curators are also given to facilitate inquiries about their collections.

ABOr	A. Borkent, Department of Entomology, University of Alberta, Edmonton, Alberta, Canada, T6G 2E3.
BMNH	British Museum (Natural History), London, England, SW7 5BD; P.S. Cranston.
CAS	California Academy of Sciences, San Francisco, California, USA, 94118; P.H. Arnaud.
CNC	Biosystematics Research Institute, Research Branch, Agriculture Canada, Ottawa, Ontario, K1A 0C6; D.M. Wood.
CUNY	Department of Entomology, Cornell University, Ithaca, New York, USA, 14850; L.L. Pechuman.
EFCo	E.F. Cook, Department of Entomology, Fisheries and Wildlife, University of Minnesota, St. Paul, Minnesota, USA, 55101.
FWI	Freshwater Institute, 501 University Crescent, Winnipeg, Manitoba, Canada, R3T 2N6; D.M. Rosenberg.
JDAl	J.D. Allan, Department of Zoology, University of Maryland, College Park, Maryland, USA, 20742.
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts, USA, 02138; J.F. Lawrence.
OASa	O.A. Saether, Museum of Zoology, University of Bergen, N-5014 Bergen, Norway.
UASM	Strickland Museum, Department of Entomology, University of Alberta, Edmonton, Alberta, Canada, T6G 2E3; G.E. Ball.
USNM	Systematic Entomology Laboratory, United States Department of Agriculture, c/o United States National Museum, NHB 168, Washington, D.C., USA, 20560; C.F. Thompson.
WSUP	Department of Entomology, Washington State University, Pullman, Washington, USA, 99163; W.J. Turner.
ZMHF	Zoological Museum, Division of Entomology, SF-00100, Helsinki 10, Finland; B. Lindeberg.

ZMLS Zoological Institute, Department of Systematics, Helgonavägen 3, S-223 62 Lund,
Sweden; H. Andersson.

Methods

Collection, preservation and dissection of material. – Egg masses of *Chaoborus trivittatus*, like those of most other *Chaoborus* species, float at the surface of the water body in which they are laid. I collected these by hand picking the floating masses from the water surface with soft-tipped tweezers and dropping them into 70% ethanol. Although egg masses can be scooped from the water surface with a dip net, they stick to the netting and attempts then made to pick them up result in their disintegration. This method should be avoided if determinations of the number of eggs per egg mass are important.

Because *Schadonophasma* larvae concentrate in the shaded portions of ponds such as that provided by *Typha*, surrounding trees, or willows, it is imperative that these areas be sampled. A common method of collecting larvae is to briskly sweep an aquatic net through a water body. Many third and fourth instar larvae are benthic during daylight hours, so stirring up the bottom is important to ensure adequate samples of these stages.

First and second instar larvae, because of their small size, are best collected with a plankton net. In this study, only ponds were sampled so that the plankton net, with a mesh size of 116 μm, was thrown from the shore and hauled in. Contents of either aquatic or plankton net were washed out in a white enamel pan with three to five centimeters of water to insure that all captured specimens were retrieved. The immatures were then picked up with soft-tipped tweezers and dropped into 70% ethanol.

Pupae were collected in the same manner as larvae except that an overly brisk motion of either plankton or aquatic net will result in specimens in which the pupal horns have been lost. Pupal exuviae were commonly found on the leeward side of ponds and were collected by hand or aquatic net.

Adults were sampled by means of an aerial net. Females of *Chaoborus trivittatus* are sedentary and although they can occasionally be collected with an aerial net, are best retrieved with an aspirator from tree trunks and herbaceous plants at the periphery of ponds.

I attempted to collect adult *Schadonophasma* with light traps but with little success. Twenty-two New Jersey light traps in and around Edmonton, Alberta from June 24 to September 4, 1974 yielded only two female *Chaoborus cooki* but did yield 1065 adults of *Chaoborus sensu stricto*. A New Jersey and CDC (Communicable Disease Centre) light trap beside a pond from which *Chaoborus cooki* adults were emerging caught none. This experience corresponds to that found for mosquitoes, in which woodland species are not attracted to lights but other species are (Bidlingmayer, 1971).

Quantitative samples of immatures for life cycle studies were obtained with the plankton net which was thrown out at least six times in the same direction from the shore and dragged at least twice across the bottom, resulting in the bottom being disturbed and thereby ensuring a representative sample. The numbers of immatures in each sample were not meant to be temporally comparable, but were interpreted to reflect only percentages of an instar present at a given time.

Material, with the exception of some pinned adults, was preserved in 70% ethanol. However, retention in alcohol for long periods of time will fade specimens. Pinned specimens are required for determination of adult coloration.

All immatures measured were prepared using the method described by Saether (1972) with the following modifications. Larvae and pupal exuviae were not cleared in KOH as this is not necessary for accurate measuring or examination and clearing has resulted in some faulty observations concerning shape of the dorsal process of larvae. One antenna and both mandibles were removed from each larva while in Canada Balsam to ensure retention of these parts, especially of younger instars whose mouthparts are easily lost. All larvae were mounted laterally and all pupae and pupal exuviae were mounted with their ventral surfaces up. Pupal exuviae should be mounted with glass chips supporting the coverslip to prevent compression of the specimen. An alternative method is to mount the specimen in Canada Balsam, which is allowed to dry for a few hours before application of the coverslip.

Schlee (1966) indicated the advantages of fluid preserved material for the examination of chironomid adults. Mainly, dried material results in distortion of some key characters. As can be expected, this is also true of chaoborid adults. Therefore, adult material which was to be examined in detail was mounted in Canada Balsam. The two antennae, head, thorax, three left legs, wings and abdomen were disarticulated. Heads, thoraces, and abdomens were cleared in hot 8% KOH, transferred to 15% acetic acid for 15 minutes, and all parts treated consecutively for at least ten minutes each with 98% ethanol, 98% ethanol layered over cedarwood oil, cedarwood oil and Canada Balsam. *Chaoborus* adults need not be so treated to be identified. Most adult material examined was pinned.

The abdomen of each pinned male, after clearing in hot 8% KOH, was placed in one of eight arbitrarily numbered wells filled with glycerine on each of a number of 7.6 x 7.6 cm microscope slides. One gonocoxite and gonostylus with the adjoining penis valve were dissected from the rest of the abdomen and examined under both stereoscopic and compound microscopes. This ensured that no *a priori* decisions were made concerning species differences. Maximum lengths of the penis valves were estimated with the aid of a compound microscope at 200X magnification. After examination, abdomens were stored in glycerine in a genitalia vial on the pin. Examination of the genitalia from different orientations is imperative for the determination of interspecific differences of the penis valve.

Abdomens of some pinned females were treated with a weak solution (three to six crystals in three drams of distilled water) of tri-sodium orthophosphate. This treatment restores dried, more or less shrivelled parts to approximately natural size and also restores eggs, if present in the abdomen, to their natural dimensions.

Number of eggs per female was determined using reared specimens killed in 70% ethanol. Eggs were easily removed and counted while in this medium.

Rearing methods and mating experiments. – All live material was reared at 20 C and a long day (18:6, light:dark) photocycle. Field collected cladocerans, copepods and chironomid larvae and laboratory reared larvae of *Culiseta inornata* provided a continual food source for the larvae. Rearings of larvae to pupae were completed with each larva in a separate Dominion Brand 473 ml wide mouthed Mason jar filled with pond water to ensure that no larvae were lost due to cannibalism.

To determine length of pupal peiod, larvae were reared to adulthood in 22.7 liter aquarium filled with pond water and an abundance of food. Pupae were removed on the day they appeared and kept in separate Mason jars.

In general, rearings were completed from field collected fourth instar larvae, although earlier instars were occasionally captured for rearing. Pupae were not used for rearings as capture often resulted in at least one pupal horn being broken off and consequent reduced adult emergence (Parma 1971b: 46; pers. obs.).

Adults could not be made to mate successfully in the laboratory except when decapitated males were brought into contact with CO_2 anaesthetized females, the method used for mating experiments. Adults were reared from fourth instar larvae of *Chaoborus trivittatus* collected 2.4 km west of Edmonton, Alberta, on 13-V-1976, and 16 km west of Jasper, Alberta, on 18-V-1976, *Chaoborus cooki* collected 1.4 km west of George Lake, Alberta, on 13-V-1976. After mating, each female was placed in a three dram vial with wet paper towelling and gauze was placed over the mouth of the vial. Few adults were used in these experiments because of difficulty in synchronizing adult emergence of *Chaoborus cooki* and *Chaoborus trivittatus* in the laboratory. For the purposes of this study only eggs which embryonated were considered fertilized.

Adult feeding experiment. – This experiment had two purposes; first, to see if adult *Chaoborus trivittatus* drink water and second, to determine if water uptake affects longevity. Goff (1972) tested for imbibition of water by adults of *Chironomus riparius* by coloring sucrose water with food coloring and checking excreta for color changes. This method was used with *Chaoborus trivittatus* adults to determine if imbibition of water took place.

Adult *Chaoborus trivittatus* were collected at 1500–1600 hours on May 6, 1976, 2.4 km west of Edmonton, Alberta, with an aerial net and aspirator. They were transported to the laboratory in a screened cage placed in a styrofoam container with wet paper towels. The adults were then anaesthesized with CO_2 and sorted into treatments by 2300 hours on the day of capture. Ten males were placed in each 15 mason jars and four females in each of three jars. All were kept at 20 C with a long day (18:6, L:D) photocycle. Each jar contained a 35x10 mm plastic petri dish containing 5 ml of deionized water which was either: (1) clear and available, (2) 1% blue food coloring solution (Scott Bathgate Ltd., Winnipeg, Toronto, Vancouver) and available, or (3) screened with netting to prevent the flies from drinking. I assumed uniform humidity in all jars. Fifty males and four females were used in each treatment. The low numbers of females used was due to their scarcity in the field. Some specimens were lost during the experiments and are therefore not recorded in Figure 35.

Mortality, and the presence or absence of colored excreta, were recorded every 12 hours.

Measurements and statistics. – All measured specimens are listed at the end of species descriptions. Most measurements were made with an ocular micrometer (120 divisions) through a Wild M20 compound microscope equipped with phase constrast. Total length of larvae and the Y/X wing ratio were measured with an ocular micrometer (120 divisions) through a Wild M5 stereoscopic microscope. Measurements were taken at as high a magnification as was practical to comply as far as possible with Sokal and Rohlf (1969: 15).

Terms for structures follow those used by Cook (1956), Knight (1971a, 1971b) or Laffoon and Knight (1971). It is likely that many structures of *Chaoborus* larvae are homologous to those of culcid larvae. For example, what are termed here "antennal seta" and "antennal blades" are probably homologous to the "antennal setae" of culicid larvae (Knight and Laffoon, 1971). However, until detailed comparative studies are completed, I use traditional terms.

Measurements of larval structures were those recognized as taxonomically useful by Cook (1956), Parma (1969), Saether (1970) and Sikorowa (1973). Although numbers of bristles in both mandibular fans were counted, to reduce the consequences of possibly lost bristles, only the highest number was used for analysis. Total length was measured as length of head capsule plus distance from the anterior edge of the prothorax to the tip of the abdomen exclusive of the anal tubules. Anal fan setae which are broken off at the bases can still be counted by noting the internal portion of the setae. Some anal fan setae of some larvae were reduced as compared to the other setae and these were only counted if they were at least 0.5 times as long as the longest anal fan seta. I attempted to study the chaetotaxy of larvae but found most setae too difficult to see to obtain reliable, comparative results. I did not study the shape of anal tubules. Studies by Wichard (1975) and Wigglesworth (1938) would suggest that these would exhibit too large a degree of variation to be useful in distinguishing the morphologically similar species of *Schadonophasma*.

Measurement of pupal features follows the treatment by Saether (1970). Pupal abdominal length was measured from the anterior margin of abdominal tergite I to the posterior margin of abdominal segment VIII. I found total length to be too difficult to measure accurately from slide mounted material.

Saether (1970) recorded 74 measurements and 20 ratios from males and 67 measurements and 15 ratios from females of adult *Chaoborus cooki* (♂, n=7; ♀, n=4) and *Chaoborus trivittatus* (♂, n=7; ♀, n=5). According to the results of this study these were all correctly identified, with the possible exception of the adult male *Chaoborus trivittatus* from Lac Phillipe, Quebec. Those measurements or ratios judged, on the basis of Saether's study, to be of possible taxonomic use were studied from slide material. Two of the most important characters, penis valve shape and Y/X wing ratio were also studied from pinned material. Terms for structures of the penis valves are shown in Figure 3B. Total length of the penis valve was measured from the base of the penis valve to the tip of the claw. The characterization of penis valves was based on a study of these structures from many orientations. Because it was impossible to standardize these, future comparisons should preferrably be based on orientations in which the penis valves look similar to those illustrated in this work.

All thoracic setae, except scutellar setae, of the adults were counted on one side of the thorax. Setae on tergite IX were counted for only one side.

Searches for additional characters of all stages to separate the species of *Schadonophasma*, except eggs, previously undescribed, were generally fruitless. Features which yielded no criteria for separation of the species were:

Adults. Structure of digestive tract; setal pattern on thorax; extent of coloration; sperm shape.

Male and female pupae. Reticulation of pupal horns; length/width of respiratory horn; chaetotaxy of abdominal segments II-VIII; coloration, including that of the ribs of the anal paddle; anal paddle shape; degree of serration of outer rib of paddles; length of median rib; distance of plumose seta from base of median rib; distance of plumose seta from base of median rib/length of median rib; length, width and length/width of genital lobes.

Four instar larvae. Microsculpture of head capsule; dorsal outline of head capsule; shape of antennae; curvature of long antennal blades; length of postantennal filaments; length of labrum; width of labrum; distance of long seta from anterior base of labrum; ratio of the distance of long seta from anterior base of labrum to the length of labrum; shape of maxillae; length of seta on maxillary palpus; dorsal outline of the dorsal process.

I assumed that characters, with the exception of the length of the postantennal filaments, not useful for identification of fourth instar larvae would not be useful for younger instars.

Ratios were used to describe shapes or proportions statistically and some are complemented by illustrations. Measurements used to construct ratios or ratios themselves are abbreviated as follows:

Adults

X = length of vein Rs between R-M and fork of Rsa and Rs (Fig. 3C)

Y = length of vein Rs between R-M and fork of R_2 and R_3 (Fig. 3C)

Z = length of vein M between R-M and fork of M_1 and M_2 (Fig. 3C)

R_3 = length of vein R_3 (Fig. 3C)

M_1 = length of vein M_1 (Fig. 3C)

Fe = femur length

Ti = tibia length

Ta_1-Ta_5 = length of tarsomeres 1–5

$$\frac{L}{R} = \frac{\text{length of first tarsomere}}{\text{length of tibia}}$$

$$\frac{P}{U} = \frac{\text{length of penultimate antennal article}}{\text{length of ultimate antennal article}}$$

$$\frac{HW}{PL} = \frac{\text{head width}}{\text{prementum length}}$$

$$\underline{HV} = \frac{\text{length of male}}{\text{gonostylus length X 10}}$$

$$\underline{HR} = \frac{\text{gonocoxite length}}{\text{gonostylus length}}$$

Male and Female Pupae

$$\frac{WS}{LS} = \frac{\text{width of seventh abdominal segment(Fig. 3A)}}{\text{length of seventh abdominal segment}}$$

Larvae

$$\frac{AS}{AL} = \frac{\text{distance of antennal seta from base of antenna}}{\text{antennal length}} \text{ (Fig. 2A)}$$

$$\frac{LB}{AL} = \frac{\text{length of long antennal blade}}{\text{antennal length}} \text{ (Fig. 2A)}$$

$$\frac{LB}{SB} = \frac{\text{length of long antennal blade}}{\text{length of short antennal blade}} \text{ (Fig. 2A)}$$

$$\frac{PAL}{PAW} = \frac{\text{prelabral appendage length}}{\text{prelabral appendage width}} \text{ (Fig. 2A)}$$

Legs are referred to by the following abbreviations.
P_1 = foreleg
P_2 = midleg
P_3 = hindleg

Statistical tests were used to compare species, larval instars and sexes, to understand geographical variation and to complement the species descriptions. Descriptive statistics of samples of eight or more individuals are ranges, means, 1.5 standard deviations (SD), and two standard errors (SE) on either side of the mean.These statistics are those graphically presented in the Hubbs diagrams. For samples of less than eight, only range and mean are given. Ranges only are given for samples of two. Total lengths of larvae are expressed only as a range, as length is growth related and for the purposes of this study, further statistics would not give additional information.

Because *Schadonophasma* fourth instar larvae could not be identified on the basis of discrete characters, I employed a compound character index to recognize fourth instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki.* Although this index has been used primarily to recognize hybrids and analyze zones of hybridization (Freitag, 1965, and papers cited therein; Hubbs and Peden, 1969; Rising, 1970) it is also useful to distinguish morphologically similar species. Compound character indices compile an overall measure of difference to test for morphological discontinuity (i.e. reproductive isolation). Kim *et al.* (1966) have given a step by step analysis of how characters are best used in combination to distinguish similar species and I have followed most of their suggestions. However, because I was using the index to test for lack or presence of conspecificity of samples and provide a means of identification, I did not statistically test homogeneity of samples and could not determine, beforehand, the amount of overlap of character variation between species.

Differences between male and female larvae and pupae were estimated using the unpaired t-test.

Illustrations. – Most illustrations were made with the aid of a drawing tube on a Wild M20 compound microscope from slide mounted material. They complement verbal or statistical descriptions of the species and describe the complex shape and depict the various forms of adult penis valves. Shape of the lateral outline of the dorsal process is also characterized with illustrations. Penis valves were drawn with the head in a horizontal plane.

Scanning electron photomicrographs illustrate some characters.

Distribution maps are provided. Dots represent collecting sites of all stages of a species. These localities are a composite of all material examined and therefore may not accurately reflect present distributions. Details of collecting sites and dates, and stage collected of measured specimens are available at the end of each species description.

Criteria for species recognition. – I have accepted for the purposes of this study Mayr's (1969) species definition as 'groups of actually (or potentially) interbreeding populations which are reproductively isolated from such groups'. Reproductive isolation, reflected in discontinuities in variation of characters and especially in circumstances of sympatry may be used to recognize species. However, some discontinuities can be better explained by other interpretations. Circles of races, ecophenotypic or polymorphic variation may be interpreted incorrectly as reflecting barriers to gene flow and the presence of more than one species (Brown, 1959; Mayr, 1969; Ross, 1974).

When I initiated this study I suspected that *Chaoborus trivittatus* and *Chaoborus cooki* might be conspecific. I therefore undertook a study of the structure, bionomics, behavior, and development of both species and used these data as criteria for species recognition. In addition, I carried out mating experiments with adults of *Chaoborus trivittatus* and *Chaoborus cooki.* In light of the resulting concordant evidence I was better able to interpret discontinuities of morphological variation.

Lack of bionomic data and associated adults for several samples of immatures made me uncertain of their specific status. I describe and discuss these under the heading 'populations *incertae sedis*' to better define and encourage further work on the problems posed by these samples.

Although I recognized the subspecies catagory as useful for the recognition of some distinctive populations, the varied uses of this category has led to numerous misunderstandings of variaton within species and I therefore prefer to describe variation of populations without formally classifying them.

Taxonomic Methods. – The structure of fourth instar larvae, pupae and adults of several populations of *Schadonophasma* in Alberta indicate that these were referable to previously described *Chaoborus trivittatus* and *Chaoborus cooki.* Mating experiments and study of behavior and bionomics were used to test interpretation of morphological differences as a result of reproductive discontinuities. Study of such differences was then applied to all available material to determine if these would support indications of lack of conspecificity. A compound character index was used to test for morphological discontinuities of fourth instar larvae of *Schadonophasma* and provided a means of identification of these larvae. Identification of eggs and first, second and third instar larvae was based on either laboratory rearings or association with identified later stages.

The limited material of *Chaoborus nyblaei* available from Europe presented some problems of interpretation and, although the criterion for recognizing this as a sample of a distinct species was mostly morphological, interpretation of functional significance of some morphological features was also used.

Geographical variation was studied for two purposes. One was to test my concepts of biological species and the other, to better understand the extreme variation and evolutionary history of the species.

Paucity of material limited the stages studied for geographical variation of characters, to fourth instar larvae and adults.

For the study of geographical variation of characters the most informative statistic is the mean. To investigate patterns of variation I plotted mean values of a character for all samples which contained eight or more individuals, on a map of North America or Alberta and visually judged if any patterns were present. Samples of less than eight were lumped with the geographically closest sample.

The geographical variation of all characters of the fourth instar larvae used in the compound character index, of the penis valve length, number of setae on tergite IX of the male adults, and for Y/X wing ratio of both male and female adults, was studied in detail. Male and female adults were analyzed separately.

The correct naming of taxa was confirmed by examination of types.

I discuss my approach to the evolutionary history of species of *Schadonophasma* in the section on phylogeny and zoogeography.

Literature. – Using the very complete bibliography dealing with *Chaoborus* compiled by Roth and Parma (1970) as a basis, I attempted to trace every published account of species of *Schadonophasma* up to at least September, 1977.

Because much ecological work is dependent on correct recognition of the species studied, I have attempted to reidentify every published record either by examination of the original material or on the basis of published distributional and ecological information.

CLASSIFICATION

Genus *Chaoborus*

Edwards (1932) gave a complete list of generic synonyms (with the exception of *Edwardsops* Lane) and Cook (1956) and Saether (1972) described the general structure of *Chaoborus* species. Only additions and corrections to those descriptions are given here. The first, second and third instar larvae are fully described as they differ from fourth instar larvae. Within a species, earlier instars differ from later instars in numerous characteristics, such as head capsule length, antennal length, postantennal filament length, number of mandibular fan bristles and number of anal fan setae and these are described for *Schadonophasma* larvae in a later section. Only qualitative or non-varying differences are described here. Descriptions of earlier instars of *Chaoborus* species are given by Deonier (1943), McGowan (1972), Parma (1969, 1971a), Prokesova (1959), Saether (1967, 1970), Sikorowa (1973) and Smith (1960a). Eggs or egg masses have been described by Aitken (1954), Berg (1937), Herms (1937), Lindquist and Deonier (1942b), MacDonald (1956), McGowan (1974, 1975, 1976), Parma (1971b), Sikorowa (1973), Smith (1960a) and von Frankenberg (1937).

Saether's comments on the subgenus *Sayomyia* appear to be based on only the North American species *Chaoborus punctipennis*, *Chaoborus astictopus* Dyar and Shannon, *Chaoborus albatus*, *Chaoborus annulatus* Cook, and *Chaoborus maculipes* Stone, and do not apply to at least some tropical species. Saether's (1970) calculation of HR was incorrect and actually is the inverse of the data he presented.

Some erroneous interpretations of characters differing between larval instars are discussed under the heading 'Characters Varying between Larval Instars'.

Keys to subgenera of *Chaoborus* of the Holarctic region for adults, pupae, and fourth instar larvae have been provided by Saether (1972). More comprehensive keys must await analysis of species of the Neotropical, Oriental, and Australian regions. Some corrections to Saether's (1972) keys are presented below in the key to species.

Diagnosis. – Adults. Second tarsal article shorter than first; male tarsal claws equal; tarsal claws not toothed; females with three seminal capsules; vein R_1 terminated distal to vein Cu_1 apex.

Pupae. Respiratory horns with spiracular openings small, slit-like; paddles free, movable, each supported by one medial, two marginal ribs (Fig. 2C,D).

Larvae (all instars). Head capsule laterally compressed; antennae proximate; pair of air sacs in both thorax and abdominal segment VII; *no respiratory siphon; anal segment with ventral setal fan.*

Description of Chaoborus. – Adults. Females with row of comb-like setae on anterior face of third tarsus of midlegs (Fig. 4A).

Pupae. Respiratory horns spindle-shaped (Saether, 1972: 272) to globular (Verbeke, 1957: 190); terminalia almost parallel

(Fig. 5B; Blanchard, 1905: 39; Deckart, 1958: 269; Prashad, 1918: 19; Senior-White, 1927: 65; Wesenberg-Lund, 1943: 418), to perpendicular (Fig. 5A) to longitudinal axis of body.

Fourth Instar Larvae. Length 4.4–20.3 mm; predaceous; developing adult eye visible (present or absent in *Chaoborus anomalus*); apex of antenna with six terminal setae (Fig. 2A); four long, one noticeably shorter, one much shorter; pair of setae dorso-posterior of antennae dendritic; ten postantennal filaments; prelabral appendages one in front of other, setaceous or laterally flattened; mandibular fan present; maxillae as shown by Parma (1971a: 175), Cook (1956: 76); anal fan setae plumose, not paired; abdominal segment IX dorsal process flat, conical or with short article.

Third Instar Larvae. Most specimens of most species with developing adult eye visible, absent from *Chaoborus anomalus*; antenna with six terminal setae; pair of setae dorso-posterior of antennae simple; ten postantennal filaments; prelabral appendages, one anterior of other, setaceous or flattened; mandibular fan present; maxillae as shown by Parma (1971a: 175); anal fan setae plumose, not paired.

Second Instar Larvae. Some specimens of some species with developing adult eye visible; antenna with six terminal setae; eight postantennal filaments; prelabral appendages lateral to one another, setaceous; mandibular fan present; maxillae as shown by Parma (1971a: 175); anal fan setae plumose, not paired.

First Instar Larvae. Developing adult eye not visible; egg burster on dorsum of head capsule; antenna with four terminal setae; base of antenna without posterior curve (except *Chaoborus edulis* Edwards; McGowan, 1976: 300); two postantennal filaments; prelabral appendages lateral to one another, setaceous; mandibular fan absent; maxillae as shown by Parma (1971a: 175); anal fan setae simple, in pairs.

Eggs. Outline oval; some species with eggs in jelly-like matrix; white when laid, later light to dark brown; chorion transparent; at least for species of *Chaoborus sensu stricto* egg shell canoe-like in shape (Parma, 1971b: 32; pers. obs.) with dorsal longitudinal slit (see also descriptions of *Schadonophasma* species).

Subgenus *Schadonophasma*

Schadonophasma Dyar and Shannon 1924: 209. TYPE SPECIES (by monotypy) *Corethra trivittata* Loew 1862: 186. Cook 1956: 28. Edwards 1932: 26.

Schadanophasma Saether 1970: 12 (misspelling).

Saether (1970: 14) incorrectly recognized *Chaoborus nyblaei* as type species.

Especially considering the morphological similarity of known stages of *Chaoborus* species, Lane's (1951: 336) suggestion that *Chaoborus* subgenera be raised to generic rank does not seem to be justified and, at least until the world fauna is better understood, subgeneric status should be retained.

Diagnosis. – Adult. Total length 5.2-9.3 mm; general coloration as given by Cook (1956); wings with several spots (Fig. 3C); more darkly pigmented than rest of thorax-anterior pronotum, dorsal portion of posterior pronotum (some specimens not so darkly), ventral half of preepisternum, anterior half of anterior anepisternum 2, pleural apophysis, anterior-dorsal edge of anepimeron, meron, center of anepisternum 3, scutellum, postnotum, two pairs of vittae on scutum; Rsa present, Cu$_{2a}$ faint or absent; wing veins scaled; legs each with apex of femur, apex and base of tibia, apex of first, second and third tarsomeres and, all of fourth and fifth tarsomeres darkly pigmented; pulvilli well developed, at least half as long as claws; ommatidia free, dorsal part of eye at least as long as three ommatidia (Saether, 1970: Fig. 9); no parascutellar setae. Male. Without lobe or stout setae on inner face of gonocoxite; penis valve with apical claw. Female. Inner face of tarsomere three of midlegs and hindlegs with row of comb-like setae (Fig. 4A); segment X not covered by tergite IX in dorsal aspect, neither apically bilobed (Cook, 1956: fig 15A); seminal capsule ovoid with short, slightly curved neck (Cook, 1956: fig. 14J); antenna with 13 flagellar articles.

Pupa. Overall coloration from light to dark brown, females slightly darker than males; mature specimens more darkly pigmented along posterior and anterior margin of each abdominal segment, also bases of some setae, bases of paddles; longitudinal stripes parallel to outer margin of abdominal tergite and sternite; median rib of paddle darker than lateral ribs; in some, outer and middle ribs equally pigmented but darker than inner rib; when pharate adult developed (abdominal setae of pharate adult visible) pigmented wings and legs visible, penis valves of males with apical claw (Fig. 3B); WS/LS of both male and female 1.20–1.89; median rib with plumose seta 0.47–0.79 of its length from base and simple seta near apex; shagreening at base of paddles; outer rib of paddle with only sparse shagreening; median rib almost extended to margin of paddle and curved apically (Fig. 2C,D); respiratory horns spindle-shaped; length of respiratory horn/width of respiratory horn of male 3.30–4.71, of females 3.23–4.80; chaetotaxy as shown on Figure 6, setae present as shown by Belkin *et al.* (1970) except seta 4–II present; male genital sac length 932–1298 μm, width 189–307 μm, length/width 3.24–5.05.

Fourth Instar Larva. Total length 11.4–20.3 mm; head capsule length 1404–2620 μm; seta on anterior face of antenna inconspicuous; AS/AL 0.75–0.93; antenna with curve at posterior base (Fig. 7D); tentorium pigmented, thick, conspicuous (Fig. 2A); dorsal process on abdominal segment IX flat (Fig. 2B, 8C, D); head capsule colorless to dark brown; more pigmented specimens with posterior margin, dorsal surface on head capsule, area around anterior tentorial pit, and line of attachment of mandible conspicuously pigmented; lateral outline of dorsal surface of head capsule as shown by Saether (1970: fig. 11A,B,C) and Figure 2A and 7I; longest mandibular tooth elongate, with curve about 0.75 from base (Fig. 8B; Saether, 1970: fig. 11K; Felt, 1904: fig. 99); head capsule with microsculpture polygonal on posterior edge (Fig. 4B); additional features in key.

Third Instar Larva. As fourth instar larva except following: total length 7.0–13.0 mm; head capsule length 944–1440 μm; lateral outline of dorsal surface of head capsule as in Figure 7H; microsculpture on posterior margin of head capsule not obviously polygonal; antenna with curve at posterior base (Fig. 7c); AS/AL 0.53–0.90; longest mandibular tooth elongate, with or without slight curve about 0.75 from base; additional features in key.

Second Instar Larva. As fourth instar larva except following: total length 4.7–7.3 mm; head capsule length 522–760 μm; lateral outline of dorsal surface of head capsule as in Figure 7G: microsculpture on posterior margin of head capsule not polygonal; antenna with only slight curve at posterior base (Fig. 7B); AS/AL 0.38–0.72; longest mandibular tooth elongate, without curve; additional features in key.

First Instar Larva. As fourth instar larva except following: total length 2.0–4.5 mm; head capsule length 294–494 μm; lateral outline of dorsal surface of head capsule as shown in Figure 7E,F; microsculpture on posterior margin of head capsule not polygonal; antenna without curve at posterior base (Fig. 7A); AS/AL 0.24–0.40; mandible as in Figure 8A; additional features in key.

Description. – Description of the subgenus is provided in the description of *Chaoborus*, the diagnosis of *Schadonophasma*, and the following keys and description of species.

Key to the species of *Schadonophasma*

Species of *Schadonophasma* are morphologically very similar and are therefore difficult to identify. No single character can or should be relied upon to identify larva, pupae or adults to species; thus, to be confident of a correct determination, all characters described should be examined. Because of this overlap of range of variation it is best to identify several individuals from a sample and opposites of the couplet should be compared.

Male adults

The shape of the penis valves is particularly important but difficult to use in identifying males. It is most important that the penis valves be examined from a number of orientations until their shape approximates those illustrated.

1 Penis valve head elongate, with claw mostly parallel to longitudinal axis (Fig. 10A-O); penis valve length 145–232 μm; Y/X wing ratio 1.17–3.22; length of tarsomere five of foreleg 186–273 μm; length of claw of foreleg 53–83 μm; coloration of vittae generally black or very dark brown .... *Chaoborus trivittatus* (Canada, eastern and western U.S.A.)

Penis valve shape not as above (Fig. 11A–N) or if similar (Fig. 11, O,P), specimen from Fennoscandia; penis valve length 191–232 μm; Y/X wing ratio 1.64–3.62; length of tarsomere five of foreleg 220–284 μm; length of claw of foreleg 65–88 μm; coloration of vittae generally brown 2

2 Penis valve head bulbous, with claw mostly perpendicular to longitudinal axis (Fig. 11 A-N); Y/X wing ratio 1.64–3.62; length of claw of foreleg 65–88 μm .... *Chaoborus cooki* (Canada)

Penis valve head elongate with claw mostly perpendicular to longitudinal axis (Fig. 11 O,P); Y/X wing ratio 1.88–2.13; length of claw of foreleg about 85 μm .... *Chaoborus nyblaei* (Fennoscandia)

Female adults

Egg number and type, when present in the abdomen and in good condition, are consistent and reliable characters for species determination.

1 Seminal capsules 71–102 μm in diameter; Y/X wing ratio 1.19–3.22; length of tarsomere

five of foreleg 232–290 μm; length of claw of foreleg 64–81 μm; prementum length 325–510 μm; coloration of vittae generally black or very dark brown; distance from anterior tip of longest ovary to apex of abdomen 0.71–1.11 times total length of abdomen of teneral females; total number of eggs 150–329 in nulliparous individuals; eggs, if present, of parous individuals with no obviously thick exochorion (Fig. 9A)........................ .... *Chaoborus trivittatus* (Canada, eastern and western U.S.A.)

Seminal capsules 65–79 μm in diameter; Y/X wing ratio 2.03–5.83; length of tarsomere five of foreleg 232–325 μm; length of claw of foreleg 64–104 μm; prementum length 458–574 μm; coloration of vittae generally brown; distance from anterior tip of longest ovary to apex of abdomen 0.32–0.62 times total length of abdomen of teneral females (unknown for *Chaoborus nyblaei*); total number of eggs 58–144 in nulliparous individuals; eggs, if present, of parous individuals with obvious thick exochorion (Fig. 9B,C) .... *Chaoborus cooki* (Canada) *Chaoborus nyblaei* (Fennoscandia)

Male and female pupae

Male and female pupae are distinguished from one another by the shape of their genital lobes (Fig. 2C,D), (Deonier, 1943: fig. 1,2).

Saether's (1972) key to pupae should read 'abdominal segment VII' instead of 'abdominal segment VIII' and couplet 7(4) (pg. 271) should read 'Median rib of anal paddle with a minute seta at apex and a single plumose seta medially (Fig. 12 O-Q); greatest width of thoracic organ at or below the middle'.

Male pupae

1 Width of adominal segment VII 1074–1794 μm; respiratory horn length 1.18–1.48 mm; non-teneral live individuals with abdomen nearly vertical (Fig. 5B) .... *Chaoborus trivittatus* (Canada, eastern and western U.S.A.)

Width of abdominal segment VII 1605–1947 μm; respiratory horn length 1.31–1.64 mm; non-teneral live individuals with tip of abdomen nearly horizontal (unknown for *Chaoborus nyblaei* (Fig. 5A) 2

2 WS/LS 1.40–1.69 .... *Chaoborus cooki* (Canada)

WS/LS 1.63–1.74 ....*Chaoborus nyblaei* (Fennoscandia)

Female pupae

1 Width of abominal segment VII 1239–2266 μm; WS/LS 1.25–1.62; mature individuals (pharate adult setae evident) with abdomen full of eggs; non-teneral live individuals with abdomen nearly vertical (Fig. 5B) .... *Chaoborus trivittatus* (Canada, eastern and western U.S.A.)

Width of abdominal segment VII 1605–2382 μm; WS/LS 1.43–1.89; mature individuals (pharate adult setae evident) with ovaries extended to, at most, abdominal segment V (unknown for *Chaoborus nyblaei*); non-teneral live individuals with tip of abdomen nearly horizontal (unknown for *Chaoborus nyblaei*) (Fig. 5A) 2

2 Width of abdominal segment VII 1605–2230 μm; WS/LS 1.43–1.87 .... *Chaoborus cooki* (Canada)

Width of abdominal segment VII 2030–2384 μm; WS/LS 1.71–1.89 ....*Chaoborus nyblaei* (Fennoscandia)

Larvae

Roman numerals refer to larval instars. *Chaoborus nyblaei* I, II, and III are unknown.

1 Prelabral appendages one in front of other 5

Prelabral appendages lateral to one another 2

2 (1) Egg burster on dorsum of head capsule(Fig. 7E,F); antennae each with four terminal setae; two postantennal filaments; mandibular fan absent; most anal fan setae arranged in pairs 3

No egg burster on dorsum of head capsule (Fig. G-I); antennae each with six terminal setae; eight postantennal filaments; mandibular fan present; no anal fan setae arranged in pairs 4

3 (2) Egg burster on dorsum of head capsule not pigmented, shaped as in Figure 7K; head capsule length 294–368 μm; antennal length 79–115 μm; antennal blade length 176–232 μm .... *Chaoborus trivittatus* I (Canada, eastern and western U.S.A.)

Egg burster on dorsum of head capsule pigmented, shaped as in Figure 7J; head capsule length 347–493 μm; antennal length 103–132 μm; antennal blade length 208–288 μm .... *Chaoborus cooki* I (Canada)

4 (2) Head capsule length 522–650 μm; LB/AL 1.02–1.16; 8–14 mandibular fan bristles; 16–21 anal fan setae .... *Chaoborus trivittatus* II (Canada, eastern and western U.S.A.)

Head capsule length 638–760 μm; LB/AL 0.91–1.07; 7–9 mandibular fan bristles; 19–26 anal fan setae .... *Chaoborus cooki* II (Canada)

5 (1) Head capsule length 944–1440 μm; antennal length 423–673 μm; postantennal filament length 354–578 μm 6

Head capsule length 1404–2620 μm; antennal length 623–1235 μm; postantennal filament length 555–1015 μm 7

6 (5) AS/AL 0.58–0.90; PAL/PAW 3.36–15.00; 9–24 mandibular fan bristles; 19–28 anal fan setae .... *Chaoborus trivittatus* III (Canada, eastern and western U.S.A.)

AS/AL 0.53–0.81; PAL/PAW 3.56–6.60; 8–12 mandibular fan bristles; 22–23 anal fan setae .... *Chaoborus cooki* III (Canada)

7 (5) Head capsule length 1404–2384 μm; antennal length 632–1195 μm; LB/SB 1.47–2.92; PAL/PAW 2.63–9.88; 11–36 mandibular fan bristles; 21–33 anal fan setae .... *Chaoborus trivittatus* IV (Canada, eastern and western U.S.A.)

Head capsule length 1707–2620 μm; antennal length 789–1235 μm; LB/SB 1.14–2.13; PAL/PAW 2.00–5.30; 8–17 mandibular fan bristles; 28–40 anal fan setae 8

8 (7) Postantennal filament length 631–944 μm; prelabral appendage length 186–306 μm; PAL/PAW less than 4.16; 28–38 anal fan setae .... *Chaoborus cooki* IV (Canada)

Postantennal filament length 684–1015 μm; prelabral appendage length 300–348 μm for specimens with undamaged tip (tip not coming to flat end (Fig. 15E-H)); PAL/PAW for such specimens 3.58–5.13; 34–40 anal fan setae .... *Chaoborus nyblaei* IV (Fennoscandia)

Eggs

1 Laid in spiral arrangement in flat jelly-like matrix; exochorion thin, without obvious sculpturing (Fig. 9A; 4C); length/width 2.85–3.16 .... *Chaoborus trivittatus* (Canada, eastern and western U.S.A.)

Laid in more or less spherical mass (unknown for *Chaoborus nyblaei*); exochorion thick, with hexagonal sculpturing (Fig. 9B,C; 4D); length/width without exochorion 2.36–2.77 (unknown for *Chaoborus nyblaei*) .... *Chaoborus cooki* (Canada), *Chaoborus nyblaei* (Fennoscandia)

Chaoborus trivittatus (Loew)

Corethra trivittata Loew 1862: 186. Holotype adult male, labelled: 'Me', 'Loew Coll.', 'Type 4050', 'trivittata'; (MCZ). Johannsen 1903: 398. Not Dyar 1902: 201.

Sayomyia trivittata; Felt 1904: 361. Felt 1905: 497.

Sayomyia knabi Dyar 1905: 16. Holotype third instar larva, labelled: 'Sayomyia trivittata (trivittata crossed out), Springfield Mass, F. Knab', '96'. A figure of the prelabral appendage on the label is identical to that drawn by Dyar 1905: 14; (USNM).

Chaoborus trivittatus; Dyar and Shannon 1924: 212. Saether 1970: 23. Johannsen 1934: 44. Dickinson 1944: 351.

Chaoborus trivattus Saether 1970: 23 (misspelling).

Chaoborus nyblaei; Cook 1956: 28 in part (not Zetterstedt). Saether 1970: 14 in part. Matheson 1944: 94.

Chaoborus brunskilli Saether 1970: 21. NEW SYNONOMY. Details of holotype and paratype given by Saether (1970). Label of holotype reads 'L. 244' but this is probably incorrect and should read 'L. 241'; (CNC).

Characters tested to distinguish adults of *Schadonophasma* species are described here to supplement those descriptions by Saether (1970).

Descriptions. – Males. General coloration of most specimens dark grayish brown; specific pigmentation as other members of subgenus; vittae generally black or very dark brown; penis valves as shown in Fig 10A-O. Measurements and proportions: see Table 2.

Females. Coloration as for males. Measurements and proportions: see Table 3.

Male pupae. Non-teneral live individuals with tip of abdomen nearly vertical when at rest (Fig. 5B); coloration as other members of subgenus. Measurements and proportions: see Table 4.

Female pupae. Non-teneral live individuals with tip of abdomen nearly vertical when at rest. (Fig. 5B); mature individuals (pharate adult setae evident) with ovaries extended to at least abdominal segment III; coloration as other members of subgenus. Measurements and proportions: see Table 5.

Cook (1956: 31) reported respiratory horn length of specimens from Green Valley, California to be 1.02–1.13 mm.

Fourth instar larvae. Coloration as other members of subgenus. Measurements and proportions: see Table 6.

Third instar larvae. Coloration as other members of subgenus. Measurements and proportions: see Table 7.

Second instar larvae. Coloration as other members of subgenus. Measurements and proportions: see Table 8.

First instar larvae. Egg burster on dorsum of head capsule not as prominent (Fig. 7F) as that of *Chaoborus cooki* first instar larvae; pigmentation of egg tooth and posterior margin of head capsule not nearly as dark as that of *Chaoborus cooki*; coloration of head capsule very light. Measurements and proportions: see Table 9.

Eggs. Laid in spiral arrangement in disc of jelly-like matrix; egg with thin exochorion (Fig. 9A) with very fine sculpturing (Fig. 4E) restricted to dorsal surface. Measurements and proportions: see Table 10. Egg shell as in Figure 9D.

Bionomics. – Individuals overwinter as fourth instar larvae and are mostly restricted to permanent lentic habitats ranging from small shaded ponds to large deep lakes in woodland. Although some larvae live in temporary waters, they cannot successfully overwinter in these habitats. Adults emerge under spring conditions in Alberta. Records from elsewhere indicate some multivoltine populations (p. 184).

Table 2. Descriptive statistics for male adult *Chaoborus trivittatus*. Measurements in µm unless stated otherwise.

Character	N	Range	Mean	1.5SD	2SE
Total length (mm)	18	6.4–8.6	7.62	0.90	0.28
Number postpronotal setae	24	17–45	30.9	11.2	3.0
Number supraalar setae	26	3–10	6.3	2.5	0.7
Number of supraalar setae	26	22–61	42.2	12.7	3.3
Y/X	156	1.17–3.22	1.810	0.435	0.046
Rsa vein length	21	29–232	120	87	25
P_1Ta_5	20	186–273	235.2	33.4	10.0
P_2Ta_5	20	191–255	228.3	26.1	7.8
P_3Ta_4	17	254–383	334.0	61.6	19.9
P_1 claw length	22	53–83	66.9	12.1	3.4
P_1pulvilli length	22	26–44	39.4	7.4	2.1
Gonocoxite length	20	519–732	653	99	30
Gonostylus length	24	437–637	558	85	23
HV	17	1.26–1.54	1.375	0.104	0.034
Number setae on tergite IX	110	6–21	12.5	4.8	0.6
Penis valve length	112	145–232	194.4	27.1	3.4

Table 3. Descriptive statistics for female adult *Chaoborus trivittatus*. Measurements in µm unless stated otherwise.

Character	N	Range	Mean	1.5SD	2SE
Total length (mm)	21	5.3–8.9	7.00	1.36	0.40
Length of penultimate article	18	162–191	175.9	16.3	5.1
Length of ultimate article	18	168–261	200.4	33.8	10.6
P/U	18	0.75–1.14	0.894	0.152	0.048
Head width	21	838–1132	1025	118	34
Prementum length	21	325–516	445	68	20
HW/PL	21	1.94–3.23	2.325	0.423	0.123
Length fourth palpal article	21	215–307	254	38	11
Number preepisternal setae	21	4–14	9.4	4.2	1.2
Number anepisternal setae	20	14–35	24.0	8.7	2.6
Number upper mesepimeral setae	20	10–40	20.5	11.0	3.2
Number supraalar setae	22	35–72	52.7	17.7	5.0
Y/X	110	1.19–3.22	2.118	0.563	0.072
Claw length of P_1	18	64–87	71.5	9.9	3.1
Pulvilli length of P_1	18	35–58	43.5	8.6	2.7
P_1Ta_5	19	232–290	248.8	22.1	6.7
P_2Ta_5	19	186–319	235.7	41.4	12.5
P_3Ti	20	2077–2844	2375	291	86
P_3Ta_1	19	1204–1829	1404	251	76
P_3Ta_5	19	203–297	257.6	32.3	9.8
P_1L/R	19	0.53–0.66	0.591	0.047	0.014
Number setae in P_2Ta_3 comb	18	13–27	19.5	6.0	1.9
Number setae in P_3Ta_3 comb	14	10–22	16.3	5.1	1.8
Seminal capsule diameter	16	71–103	90.6	12.0	4.0

Table 4. Descriptive statistics for male pupae of *Chaoborus trivittatus*. Measurements in μm unless stated otherwise.

Character	N	Range	Mean	1.5SD	2SE
Total abdomen length (mm)	60	4.6–6.9	5.99	0.73	0.12
Respiratory horn length (mm)	44	1.18–1.48	1.330	0.126	0.025
Respiratory horn width (mm)	43	0.27–0.44	0.352	0.066	0.014
Abdominal segment VII length	65	885–1169	1028	106	17
Abdominal segment VII width	65	1074–1794	1517	272	45
WS/LS	65	1.21–1.89	1.474	0.183	0.030

Table 5. Descriptive statistics for female pupae of *Chaoborus trivittatus*. Measurements in μm unless stated otherwise.

Character	N	Range	Mean	1.5SD	2SE
Total abdomen length (mm)	39	5.1–7.6	6.47	0.87	0.18
Respiratory horn length (mm)	24	1.20–1.77	1.467	0.246	0.067
Respiratory horn width (mm)	24	0.30–0.51	0.398	0.099	0.027
Abdominal segment VII length	37	897–1510	1158	202	44
Abdominal segment VII width	37	1239–2266	1727	381	84
WS/LS	37	1.25–1.62	1.488	0.128	0.028

Table 6. Descriptive statistics for fourth instar larvae of *Chaoborus trivittatus*. Measurements in μm.

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	474	1404–2384	1881	280	17
Antennal length	493	632–1195	858	144	9
LB/SB	482	1.47–2.92	2.14	0.33	0.02
LB/AL	513	0.50–0.92	0.751	0.090	0.005
AS/AL	491	0.80–0.93	0.886	0.035	0.002
Postantennal filament length	500	555–968	743	108	6
PAL/PAW	490	2.63–9.88	5.22	1.44	0.09
Number mandibular fan bristles	517	11–36	21.8	5.9	0.4
Number anal fan setae	513	21–33	28.0	2.2	0.1

Table 7. Descriptive statistics for third instar larvae of *Chaoborus trivittatus*. Measurements in μm.

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	80	944–1357	1127	140	21
Antennal length	83	423–650	509	91	13
LB/SB	77	1.89–2.70	2.26	0.231	0.035
LB/AL	82	0.73–0.96	0.842	0.065	0.010
AS/AL	83	0.58–0.90	0.770	0.097	0.014
Postantennal filament length	88	354–578	440	79	11
PAL/PAW	88	3.36–15.00	6.72	2.68	0.38
Number mandibular fan bristles	82	9–24	13.6	5.9	0.9
Number anal fan setae	87	19–28	23.8	3.3	0.5

Table 8. Descriptive statistics for second instar larvae of *Chaoborus trivittatus*. Measurements in μm.

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	18	522–650	573	44	14
Antennal length	21	215–285	241	21	6
LB/SB	20	1.81–2.38	2.08	0.235	0.070
LB/AL	21	1.02–1.15	1.09	0.058	0.017
AS/AL	20	0.53–0.72	0.605	0.078	0.023
Postantennal filament length	21	203–249	227	20	6
Number mandibular fan bristles	19	8–14	9.9	2.7	0.8
Number anal fan setae	22	16–21	18.9	1.9	0.5

Table 9. Descriptive statistics for first instar larvae of *Chaoborus trivittatus*. Measurements in μm.

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	26	294–368	333	31	8
Antennal length	28	79–115	97.0	11.5	2.9
LB/AL	28	1.85–2.78	2.19	0.26	0.07
AS/AL	27	0.23–0.39	0.301	0.660	0.017
Postantennal filament length	15	73.5–97.0	85.26	11.43	3.87
Number anal fan setae	26	16–23	20.0	2.4	0.6

Table 10. Descriptive statistics for eggs of *Chaoborus trivittatus*. Measurements in μm.

Character	N	Range	Mean	1.5SD	2SE
Length	12	655–684	668	14.3	5.5
Width	12	215–232	224	8.7	3.3
Length/Width	12	2.85–3.16	2.99	0.137	0.053

Derivation of specific epithet. – The name '*trivittatus*' is derived from Latin (tri — three; vitta — stripe) and refers to the three vittae (actually four but two are very proximate) on the scutum of the adult.

Distribution. – Specimens of this species have been collected in woodland areas throughout Canada but are restricted in the United States to California, Oregon, Washington and Montana and to the northeastern States (Fig. 16,17). Lack of records from north central Canada and Alaska probably reflect lack of collecting. *Chaoborus trivittatus* is clearly restricted to woodland. Records from southern Alberta (Fig. 17), for example, are clearly the eastern limit of this species in this area. I attempted to collect east of these localities, but with no success. In the Rocky Mountains, the species has not been found above treeline. The single record from Baffin Island is suspect. No other records of *Schadonophasma* are north of treeline. However, for the sake of completeness, I have included the record on the distribution map.

Records of *Chaoborus trivittatus* from Wisconsin reported by Dickenson (1944) are undoubtedly correct. Cook's (1956) objection to the above report, in that he found one specimen to be culicine, erroneously assumed only one specimen collected. However, Dickenson (1944) also recorded larvae which could only be those of *Chaoborus trivittatus* (length of two centimeters). In addition, I have examined specimens from Vilas County, Wisconsin, which are *Chaoborus trivittatus*.

Even though I have not examined specimens of *Chaoborus trivittatus* from Churchill, Manitoba, the reports by James and Smith (1958) of overwintering larvae (see p. 184), and Twinn *et al.* (1948) of swarming adults (see p. 189) would suggest this species to be present at that locality.

Cleugh and Hauser (1971) give the exact localities for the numbered lakes near Kenora, Ontario, given below.

LOCALITIES

Male Adults

CANADA

ALBERTA: Banff, 24-VII-1918 (1 BMNH, 4 USNM); 10 mi. (16 km) W. Jasper, 4-VI-1976 (5 CNC, 5 USNM, 8 UASM, 20 ABOr); Bigoray River, oxbow lake, 25-V-1971 (1 OASa); 1.5 mi. (2.4 km) W. Edmonton, 3-V-1976 (5 CNC, 5 USNM, 25 ABOr, 7 UASM); Edmonton, 17-V-1974 (1 ABOr); BRITISH COLUMBIA: Kaslo, 13-21-VI-? (7 USNM); Terrace, 18-VI-1960 (5 CNC, 1 ABOr); Prince Rupert, 13-V-1919 (1 CNC); Atlin, 5-VII-1955 (6 CNC, 1 ABOr); Lower Post, 20-VI-1948 (2, CNC) NORTHWEST TERRITORIES: Aklavik, 28-VIII-1932 (1 USNM); Lake Harbour, Baffin Island, 7-VIII-1935 (1 CNC); NOVA SCOTIA: 4-III-1935 (reared) (1 CNC); ONTARIO: North Burgess Twp., 15-20-V-1970, (6 CNC); Black Lk., 44°46′N 76°18′W, 26-IV-1973 (8 CNC, 1 ABOr); Kenora, Lk 241, 13-VI-1968 (reared) (1 CNC); QUEBEC: Lac de Jean Venne (Duncan Lk.), Masham Twp., 20-IV-1973 (3 CNC), 5-14-V-1973 (12 CNC, 2 ABOR); YUKON TERRITORY: Whitehorse, 14-21-V-1949 (5 CNC, 1 ABOr).

UNITED STATES

CALIFORNIA: Alameda Co.,: Oakland, 4-V-1937 (2 CAS); Humboldt Co.: Mad River Beach, 13-VIII-1948 (7 USNM); Monterey Co.: Pacific Grove, 18-VII-1940 (2 USNM); San Luis Obispo Co.: Oceano Beach 20-VIII-1948 (1 USNM); Santa Clara Co.: Stanford University, ?-III-1903 (1 CUNY, 2 USNM), 28-V-1903 (1 USNM); MAINE: (1 MCZ); MASSACHUSETTS: Worcester Co.: Worcester, 23-IV-? (2 MCZ); Audorra (specific locality unknown), (1 USNM); NEW HAMPSHIRE: Belknap Co.: Center Harbor, (7 USNM); Rockingham Co.: Hampton, 21-IV-1906 (1 MCZ); NEW YORK: Essex Co.: Elizabethtown 10-13-VI-1904 (1 CUNY, 1 USNM); OREGON: Multnomah, Clackamas and Washington Co.: Portland, (1 USNM): WASHINGTON: Kitsap Co.: Bremerton, 2-V-1924 (1 USNM); Port Madison, 3-II-1934 (reared) (2 USNM); Hoodsport, 3-9-V-1924 (2 BMNH, 6 USNM).

Female Adults

CANADA

ALBERTA: 10 mi. (16 km) W. Jasper, 4-VI-1975 (8 ABOr, 3 CNC); 1.5 mi. (2.4 km) W. Edmonton, 13-V-1975 (15 ABOr, 8 CNC, 10 UASM); BRITISH COLUMBIA: Kaslo, 13-20-VI-? (7 USNM); Victoria, 4-X-1922 (1 CNC); Canim Lk., 23-VI-1938 (2 CNC); Terrace, 7-18-VI-1960 (8 CNC, 1 ABOr); Atlin, 5-VII-1955 (5 CNC); Lower Post, 20-VI-1948 (1 CNC); NORTHWEST

TERRITORIES: Aklavik, 28-VIII-1932 (1 USNM); ONTARIO: Cordova Mines, 7-IX-1962 (2 CNC); North Burgess Twp., 15-20-V-1970 (1 CNC); Black Lk., 44°46'N 76°18'W, 26-IV-1973 (4 CNC); QUEBEC: Old Chelsea, 20-IX-1961 (12 CNC, 1 ABOr); YUKON TERRITORY: Whitehorse, 15-V-1944 (1 CNC), 16-V-1949 (1 CNC), 15-19-V-1950 (1 CNC).

UNITED STATES

CALIFORNIA: Alameda Co.: Berkeley, 5-VI-1948 (1 USNM); Oakland, 4-V-1937 (1 CAS); Humboldt Co.: Mad River Beach, 13-VIII-1948 (7 USNM); Kings Co.: Hanford, 8-VII-1947 (1 USNM); Madero Co.: Matadero Creek, 24-V-1937 (1 CAS); Mariposa Co.: Yosemite, 15-V-1916 (1 USNM); Mendocino Co.: Garcia River, 30-VII-1948 (1 USNM); Placer Co.: NW of Cisco, Nevada Co., 16-V-1948 (1 USNM) Placer and El Dorado Co.: Lake Tahoe, 17-IX-1915 (1 USNM); San Luis Obispo Co.: Oceano Beach, 20-VIII-1948 (2 USNM); Santa Clara Co.: Stanford University, III-1903 (1 CUNY, 6 USNM); MONTANA: Glacier Co.: North Fork Rangers Station, Glacier National Park, 13-V-1926 (1 USNM), 5-VI-1926 (1 USNM); NEW HAMPSHIRE: Belknap Co.: Center Harbor, (2 USNM); Rockingham Co.: Hampton, 19-VI-1906 (1 MCZ); NEW YORK: Essex Co.: Elizabethtown, 10-11-VI-1904 (2 USNM), 25-VIII-1904 (1 CUNY); Rockland Co.: Bear Mnt., 25-IX-1927 (1 USNM); OREGON: Multnomah, Clackamas and Washington Co.: Portland, 4-VII-1934 (2 USNM); WASHINGTON: Kitsap Co.: Manitou Beach, 13-III-1934 (reared) (1 USNM); Port Madison, 3-II-1934 (1 USNM); Mason Co.: Hoodsport, 5-9-V-1924 (4 USNM).

Male Pupae

CANADA

ALBERTA: 1.5 mi. (2.4 Km.) W. Edmonton, 8-V-1974 (2 ABOr, 1 UASM); BRITISH COLUMBIA: Kaslo (4 USNM); Eunice Lk., 24-V-1971 (3 OASa); Lower Post, 19-20-VI-1948 (20 CNC); NEWFOUNDLAND: 3 mi. (4.8 km) N. St. John's, 4-VI-1975 (1 ABOr); ONTARIO: Kenora, Lk. 241, 13-VI-1968 (1 CNC); QUEBEC: Lac de Jean Venne (Duncan Lk.), Masham Twp., 20-21-IV-1973 (12 CNC, 2 ABOr).

UNITED STATES

CALIFORNIA: Contra Costa Co.: Jewel Lk., 11-V-1948 (5 USNM); Humboldt Co.: Mad River Beach, 13-VIII-1948 (9 USNM); MICHIGAN: Gogebic Co.: Hummingbird Lk., 15-VIII-1971 (1 OASa); WASHINGTON: Snohomish Co.: Everett, 7-IV-1949 (3 WSUP); Hall Lk., 29-VIII-1952 (11 WSUP).

Female Pupae

CANADA

ALBERTA: 53 mi. (85 km) N. Coleman, 3-VIII-1975 (2 ABOr, 2 UASM); 1.5 mi. (2.4 km) W. Edmonton, 8-V-1974 (4 UASM); BRITISH COLUMBIA: Kaslo (4 USNM); Lower Post, 19-20-VI-1948 (8 CNC); NEWFOUNDLAND: 3 mi. (4.8 km) N. St. John's, 4-VI-1975 (1 ABOr); QUEBEC: Lac de Jean Venne (Duncan Lk.), Masham Twp., 20-IV-1973 (1 CNC), 5-6-V-1973 (3 CNC).

UNITED STATES

CALIFORNIA: Contra Costa Co.: Jewel Lk., 11-V-1948 (2 USNM); Humboldt Co.: Mad River Beach, 13-VIII-1948 (8 USNM): Snohomish Co.: Hall Lk., 29-VIII-1952 (4 WSUP).

Fourth Instar Larvae

CANADA

ALBERTA: 2.5 mi. (4.0 km).NW Edmonton, 13-IX-1970 (4 ABOr); 1.5 mi. (2.4 km) W. Edmonton, 26-IV-1975 (25 ABOr, 13 CNC, 5 UASM); 2 mi. (3.2 km) N. Devon, 23-IX-1972 (1 ABOr); 4.7 mi. (7.6 km) NW Mountain Park, 21-IX-1974 (20 ABOr, 7 CNC, 5 UASM); East Henry Pond, Jasper National Park, 12-IX-1968 (1 FWI, 4 CNC); 1.5 mi. (2.4 km) S. Robb, 23-VII-1975 (50 ABOr, 6 UASM); 53 mi. (85 km) N. Coleman, 3-VIII-1975 (10 ABOr, 2 UASM); 43 mi. (69 km) N. Coleman, 3-VIII-1975 (1 ABOr); 33 mi. (53 km) N. Swan Hills, 1-IX-1975 (12 ABOr); 62 mi. (100 km) N. Coleman, 3-VIII-1975 (15 ABOr, 7 UASM); 38 mi. (61 km) N. Swan Hills, I-IX-1975 (11 ABOr); 14 mi. (22 km) E. Fox Creek, 30-VIII-1975 (11 UASM); 1 mi. (1.6 km) N. Swan Hills, 1-IX-1975 (11 ABOr); 23 mi. (37 km) E. Fox Creek, 30-VIII-1975 (11 ABOr); 43 mi. (69 km) E. High Prairie, 1-IX-1975 (11 ABOr); 3 mi. (4.8 km) S. Hinton, 23-VII-1975 (11 ABOr); 32.5 mi. (52 km) N. Banff, 8-XI-1976 (11 ABOr); Pond nr. Kinky Lk., 11-IX-1976 (10 ABOr); 26 mi. (42 km) N. Sundre, 11-X-1976 (11 ABOr); 47 mi. (76 km) N. Nordegg, 7-IX-1976 (11 ABOr); 12 mi. (19 km) S. Seebe, 3-VIII-1975 (11 ABOr); 10 mi. (16 m) W. Jaspeer, 27-IV-1976 (10 ABOr); 58 mi. (93 km) S. Seebe, 3-VIII-1975 (11 ABOr); 28 mi. (45 km) E. Jasper, 27-IV-1976 (11 UASM); 4 mi. (6.4 km) W. Jasper, 20-V-1975 (9 ABOr); 5 mi. (8.0 km) S. Jasper, 18-VI-1975 (12 ABOr); *Pond nr. Cameron Lk., 18-IX-1977 (17 ABOr); *Pond nr. Wabamum Lk., 15-X-1977 (1 ABOr); *Opal, 10-X-1977 (6 ABOr); BRITISH COLUMBIA: 3 mi. (4.8 km) E. Sicamous, 10-VI-1976 (11 ABOr); Prince Rupert, 13-V-1919 (15 USNM); Kaslo, (5 USNM); 4.8 mi. (7.7 km) N. Clearwater, 12-VI-1976 (11 ABOr); Eunice Lk., fall of 1971 (4 OASa, 10 ABOr); Lower Post, 19-VI-1948 (11 CNC); Gwendoline Lk., ?-VIII-1973 (10 ABOr); NEWFOUNDLAND: 3 mi. (4.8 km) N. St. John's, 4-VI-1975 (11 ABOr); 0.4 mi. (0.6 km) W. Logy

Bay, 8-VII-1967 (5 USNM); ONTARIO: Kenora, Lk. 241, 14-V-1969 (3 FWI, 8 CNC); Kenora, Lk. 81, 7-V-1969 (1 FWI, 1 CNC); Kenora, Lk. 230, 14-V-1969 (2 FWI, 2 CNC); Kenora, Lk., 240, 14-V-1969 (1 FWI); *10 mi (16 km) E. Thessalon, 19-IX-1978 (18 ABOr); *Kendel, 15-V-1973 (3 ABOr), 17-VII-1973 (2 ABOr); QUEBEC: Lac de Jean Venne (Duncan Lk.), Masham Twp., 21-IV-1973 (17 CNC); Lk. a la Croix, 26-VI-1971(2 OASa, 10 ABOr); Randin Lk., 19-VI-1974 (10 ABOr); YUKON TERRITORY: Klutlan Glacier moraine, VII-1971 (6 EFCo, 3 ABOr).

UNITED STATES

CALIFORNIA: Contra Costa Co.: Jewel Lk., 11-V-1948 (4 USNM); Humboldt Co.: Mad River Beach, 13-VIII-1948 (12 USNM); Santa Clara Co.: Standford University, ?-II-1945 (3 EFCo, 11 USNM); MAINE: Piscataquis Co.: Milo, 6-I-1906 (1 USNM); MASSACHUSETTS: Hampden Co.: Springfield, ?-VII-1903 (1 USNM); MONTANA: Meagher Co.: *27 mi. (43 km) N. White Sulpher Springs, 27-X-1978; MICHIGAN: Gogebic Co.: Hummingbird Lk., 15-VIII-1971 (3 OASa, 8 JDAl); Ziesnis Bog, 24-VIII-1971 (1 OASa); WASHINGTON: Pacific Co.: 10 mi. (16 km) S. South Bend, 19-VI-1977 (1 ABOr); Snohomis Co.: Hall Lk., 8-V-1953 (10 WSUP); WISCONSIN: Vilas Co.: Forest Service Bog, 24-VIII-1971 (1 OASa).

Third Instar Larvae

CANADA

ALBERTA: 62 mi. (100 km) N. Coleman, 3-VIII-1975 (7 ABOr, 2 UASM); 53 mi. (85 km) N. Coleman, 3-VIII-1975 (1 ABOr); 1.5 mi. (2.4 km) S. Robb, 23-VII-1975 (25 ABOr, 5 CNC); 4.7 mi. (7.6 km) NW Mountain Park, 21-IX-1974 (2 ABOr); BRITISH COLUMBIA: 4.8 mi. (7.7 km) N. Clearwater, 12-VI-1976 (7 ABOr); ONTARIO: Kenora, Lk. 230, 14-V-1969 (2 FWI); Kenora, Lk. 241, 13-VI-1968 (1 FWI, 8 CNC); YUKON TERRITORY: Klutlan Glacier moraine, VII-1971 (22 EFCo).

UNITED STATES

MASSACHUSETTS: Hampden Co.: Springfield, (1 USNM), ?-VIII-1903 (5 USNM).

Second Instar Larvae

ALBERTA: 62 mi (100 km) N. Coleman, 3-VIII-1975 (6 ABOr, 2 CNC, 2 UASM); East Henry Pond, Jasper National Park, 12-IX-1968 (4 FWI); NEWFOUNDLAND: 3 mi. (4.8 km) N. St. John's, 4-VI-1975 (1 ABOr); ONTARIO: Kenora, Lk. 230, 14-V-1969 (5 FWI); Kenora, Lk. 240, 14-V-1969 (1 FWI); QUEBEC: Randin Lk., 19-VI-1974 (2 ABOr).

First Instar Larvae

ALBERTA: 1.5 mi. (2.4 km) mi. W. Edmonton, 26-VI-1975 (10 ABOr, 4 CNC); 10 mi. (16 km) W. Jasper, 18-VI-1975 (8 ABOr, 4 UASM); 20 mi. (32 km) W. Edson 9-IX-1976 (1 ABOr); East Henry Pond, Jasper National Park, 12-IX-1968 (1 CNC); NEWFOUNDLAND: 3 mi. (4.8 km) N. St. John's, 4-VI-1975 (1 ABOr).

Eggs

ALBERTA: 10 mi. (16 km) W. Jasper, 31-V-1976 (12 egg masses ABOr, 2 egg masses CNC, 2 egg masses UASM).

*Material identified but not measured.

Taxonomic notes. – Historically, recognition of specimens of this taxon has presented difficulties. Edwards (1932: 26) incorrectly synonymized *Chaoborus trivittatus* with *Chaoborus nyblaei*. *Chaoborus trivittatus* and *Chaoborus punctipennis* were erroneously considered conspecific by Brunetti (1911: 229), Dyar (1902: 201), Giles (1902: 502) and Theobald (1901b: 296; 1905: 43). Distributional information and/or type of habitat in which larvae were found suggest that Allan (1973; original material examined), Dodson (1970), Main (1953; original material examined), Maleug and Hasler (1967), Myklebust (1966), Stahl (1966) and Teraguchi and Northcote (1966) incorrectly identifed specimens of *Chaoborus trivittatus* as *Chaoborus nyblaei*. Some specimens examined by Smith (1960b) were probably larvae of *Chaoborus trivittatus* as indicated by the number of anal fan setae and PAL/PAW. Similarly, data about overwintering larvae studied by James and Smith (1958) at Churchill, Manitoba indicate that these were individuals of *Chaoborus trivittatus*. I was unable to confirm the identificaion of some specimens from British Columbia collected by Hearle (1928) as *Chaoborus trivittatus*.

Shape of the penis valve of the type specimen (Fig. 10 O) confirmed the naming of this species.

Examination of the type of *Sayomyia knabi* showed that the diagnostically (for that geographical region) thick tentorium of the larvae of *Chaoborus trivittatus* was present. All measurements were within the range of the third instar larvae of *Chaoborus trivittatus*. In addition, the pharate fourth instar larva was evident.

All diagnostic features of *Chaoborus brunskilli* (Saether, 1970: 21) are within range of variation of *Chaoborus trivittatus*. Penis valves of the holotype, when reoriented (Fig. 10M), were inseparable from those of *Chaoborus trivittatus*. Specimens of *Chaoborus brunskilli* mentioned by Anderson and Raasveldt (1974) and Hamilton (1971) are therefore *Chaoborus trivittatus*.

The identification of the specimen from Lac Phillipe, Quebec, as *Chaoborus trivittatus* by Saether (1970) could not be confirmed as the penis valves were distorted. I have not included the specimen in this description.

Previous descriptions of pupae are given by Saether (1970) (as *Chaoborus trivittatus* and *Chaoborus brunskilli*), by Cook (1956) (as *Chaoborus nyblaei*) and by Felt (1904).

The only useful previous descriptions of fourth instar larvae are those by Saether (1970) (as *Chaoborus trivittatus* and *Chaoborus brunskilli*) and Felt (1904). Cook's (1956) description of larvae of *Chaoborus nyblaei* undoubtedly included specimens of both *Chaoborus trivittatus* And *Chaoborus cooki* (see especially description of head capsule length and PAL/PAW).

Saether (1970) gave the only previous descriptions of first, second and third instar larvae of *Chaoborus trivittatus* (as *Chaoborus brunskilli*).

Chaoborus cooki Saether

Chaoborus cooki Saether 1970:18. Details of holotype, allotype and paratypes given by Saether (1970); (CNC).

Chaoborus nyblaei; Cook 1956: 28, in part (not Zetterstedt).

Characters tested to distinguish between adults of *Schadonophasma* species are described here to supplement the descriptions by Saether (1970).

Description. – Males. General coloration of most specimens light grayish brown; specific pigmentation as other members of subgenus; vittae generally brown; penis valves as shown in Fig. 11A-N. Measurements and proportions: see Table 11.

Females. Coloration as for males. Measurements and proportions: see Table 12.

Male pupae. Non-teneral individuals with tip of abdomen nearly horizontal when at rest (Fig. 5A); coloration as other members of subgenus. Measurements and proportions: see Table 13.

Female pupae. Non-teneral individuals with tip of abdomen nearly horizontal when at rest (Fig. 5A); mature individuals (pharate adult setae evident) with ovaries extended at most to abdominal segment V. Measurements and proportions: see Table 14.

Fourth instar larvae. Coloration as other members of subgenus. Measurements and proportions: see Table 15.

Third instar larvae. Coloratin as other members of subgenus. Measurements and proportions: see Table 16.

Second instar larvae. Coloration as other members of subgenus. Measurements and proportions: see Table 17.

First instar larvae. Egg burster on dorsum of head capsule prominent (Fig. 7E), pigmented; posterior margin of head capsule noticeably pigmented. Measurements and proportions: see Table 18.

Eggs. Laid in spherical mass with slight amount of jelly-lke matrix; egg with thick exochorion (Fig. 9c), with polygonal sculpturing (Fig. 4D). Measurements and proportions: see Table 19. Egg shell as in Fig. 9E.

Bionomics. – Overwinters as egg, immatures restricted to temporary occasionally permanent ponds in woodland. Larvae may be collected only during summer months (Fig. 25B). Adults generally emerge later in season than do those of *Chaoborus trivittatus*.

Derivation of specific epithet. – Named after Dr. E.F. Cook.

Distribution. – Specimens of *Chaoborus cooki* have been collected only from Canada and Alaska (Fig. 18,19). Collecting in Alberta has shown that the species is restricted to woodland. Paucity of records, as compared to *Chaoborus trivittatus* is explained by lack of collecting in the restricted habitat in which the species is found, and the presence of larvae only during the summer months.

Table 11. Descriptive statistics for male adult *Chaoborus cooki*. Measurements in μm unless stated otherwise.

Character	N	Range	Mean	1.5SD	2SE
Total length (mm)	14	6.8–9.3	7.81	1.39	0.50
Number pronotal setae	15	19–51	29.2	13.4	4.6
Number postpronotal setae	15	3–17	6.6	6.2	2.1
Number supraalar setae	15	32–48	40.4	9.1	3.1
Y/X	89	1.64–3.62	2.47	0.578	0.082
Rsa vein length	15	162–377	256	97	33
P_1Ta_5	12	220–284	260.5	31.9	12.3
P_2Ta_5	14	220–284	256.8	31.9	11.4
P_3Ta_4	13	278–435	375.0	69.3	25.6
P_1 claw length	15	65–88	73.6	10.6	3.6
P_1 pulvilli length	15	41–65	49.0	9.8	3.4
Gonocoxite length	15	649–838	755	102	35
Gonostylus length	15	507–732	616	87	20
HV	14	1.05–1.53	1.293	0.260	0.093
Number setae on tergite IX	59	7–17	11.0	3.1	0.5
Penis valve length	49	191–232	211.8	16.7	3.2

Table 12. Descriptive statistics for female adult *Chaoborus cooki*. Measurements in μm unless stated otherwise.

Character	N	Range	Mean	1.5SD	2SE
Total length (mm)	17	5.3–8.5	6.54	1.38	0.45
Length of penultimate article	18	168–226	194.3	21.2	6.6
Length of ultimate article	18	168–237	206.5	33.2	10.4
P/U	18	0.83–1.21	0.953	0.147	0.046
Head width	19	944–1274	1061	120	37
Prementum length	19	441–580	504	56	17
HW/PL	19	1.85–2.44	2.110	0.195	0.060
Length of fourth palpal article	19	191–302	262	38	1
Number anepisternal setae	19	5–13	8.1	3.4	1.0
Number upper mesepimeral	19	8–30	18.6	7.0	2.1
Number upper mespimeral setae	18	9–28	16.6	6.8	2.2
Number supraalar setae	19	38–92	52.4	20.3	6.2
Y/X	100	2.03–5.83	3.741	1.098	0.146
Claw length of P_1	17	64–104	75.4	17.7	5.7
Pulvilli length of P_1	17	35–58	42.3	10.5	3.4
P_1Ta_5	17	232–325	271.9	43.4	14.1
P_2Ta_5	15	220–319	262.5	47.4	16.2
P_3Ti	17	2289–3092	2652	299	97
P_3Ta_1	17	1204–1829	1599	248	80
P_3Ta_5	15	249–348	282.3	39.3	13.5
P_1L/R	16	0.52–0.68	0.599	0.056	0.019
Number setae in P_2Ta_3 comb	15	8–16	12.0	4.0	1.4
Number setae in P_3Ta_3 comb	14	5–14	7.7	3.7	1.3
Seminal capsule diameter	18	65–79	69.8	5.9	1.8

Table 13. Descriptive statistics for male pupae of *Chaoborus cooki*. Measurements in μm unless stated otherwise.

Character	N	Range	Mean	1.5SD	2SE
Total abdomen length (mm)	11	5.6–7.7	6.67	1.01	0.41
Respiratory horn length (mm)	11	1.32–1.64	1.546	0.144	0.058
Repsiratory horn width (mm)	11	0.32–0.45	0.39	0.05	0.02
Abdominal segment VII length	11	968–1227	1145	124	50
Abdominal segment VII width	11	1605–1947	1809	180	72
WS/LS	11	1.40–1.69	1.584	0.148	0.059

Table 14. Descriptive statistics for female pupae of *Chaoborus cooki*. Measurements in μm unless stated otherwise.

Character	N	Range	Mean	1.5SD	2SE
Total abdomen length (mm)	28	5.3–7.6	6.37	1.05	0.26
Respiratory horn length (mm)	25	1.37–1.82	1.631	0.149	0.040
Respiratory horn width (mm)	25	0.34–0.51	0.439	0.072	0.019
Abdominal segment VII length	28	1074–1357	1220	111	28
Abdominal segment VII width	28	1605–2230	2027	223	56
WS/LS	28	1.43–1.87	1.664	0.182	0.046

Table 15. Descriptive statistics for fourth instar larvae of *Chaoborus cooki*. Measurements in μm.

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	210	1707–2620	2150	255	23
Antennal length	210	789–1235	1001	122	11
LB/SB	201	1.14–2.13	1.52	0.22	0.02
LB/AL	201	0.41–0.81	0.628	0.146	0.014
AS/AL	210	0.79–0.93	0.854	0.036	0.003
Postantennal filament length	210	631–944	802	74	7
PAL/PAW	210	2.11–5.18	3.32	0.84	0.08
Number mandibular fan bristles	213	10–17	13.4	1.8	0.2
Number anal fan setae	211	28–38	32.7	2.4	0.2

Table 16. Descriptive statistics for third instar larvae of *Chaoborus cooki*. Measurements in µm.

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	49	1015–1440	1288	158	30
Antennal length	50	464–673	573	75	14
LB/SB	46	1.67–2.30	1.99	0.240	0.047
LB/AL	49	0.64–0.96	0.794	0.146	0.028
AS/AL	50	0.53– 0.81	0.692	0.101	0.019
Postantennal filament length	50	413–543	471	43	8
PAL/PAW	46	3.55–6.60	5.14	1.21	0.24
Number mandibular fan bristles	50	8–12	10.3	1.2	0.2
Number anal fan setae	50	22–33	28.6	3.3	0.6

Table 17. Descriptive statistics for second instar larvae of *Chaoborus cooki*. Measurements in µm.

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	35	638–760	712	51	11
Antennal length	33	273–347	309	23	5
LB/SB	28	2.02–2.97	2.49	0.328	0.083
LB/AL	34	0.91–1.07	0.99	0.058	0.013
AS/AL	33	0.42–0.56	0.479	0.053	0.012
Postantennal filament length	34	215–267	241	19	4
Number mandibular fan bristles	34	7–9	7.9	0.8	0.2
Number anal fan setae	35	19–26	22.0	2.4	0.5

Table 18. Descriptive statistics for first instar larvae of *Chaoborus cooki*. Measurements in µm.

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	20	347–494	432	69	20
Antennal length	20	103–132	117.0	13.5	4.0
LB/AL	20	1.88–2.45	2.15	0.23	0.07
AS/AL	20	0.27–0.38	0.333	0.051	0.015
Postantennal filament length	20	79.4–123.5	93.93	15.24	4.54
Number anal fan setae	19	20–26	23.0	2.4	0.7

Table 19. Descriptive statistics for eggs of *Chaoborus cooki*. Measurements in µm.

Character	N	Range	Mean	1.5SD	2SE
Length with exochorion	13	731–853	804	43.2	17.8
Width with exochorion	13	418–458	431	16.1	6.0
Length/width	13	1.70–2.01	1.86	0.126	0.046
Length without exochorion	13	516–563	530	18.0	6.6
Width without exochorion	13	203–220	214	7.5	2.8
Length/width	13	2.37–2.77	2.47	0.153	0.056

LOCALITIES

Male Adults

ALBERTA: nr. George Lk., 30-VII-1974 (1 ABOr); 0.9 mi. (1.4 km) W. George Lk., 13-V-1976 (reared) (20 ABOr, 15 CNC, 10 UASM); Edmonton, 1-VII-1974 (1 ABOr); MANITOBA: Gillam, 19-VI-1950 (1 OASa), 29-30-VI-1950 (6 CNC); Churchill, 24-VII-1947 (1 CNC), 19-VII-1951 (1 CNC), VII-VIII-1950 (4 CNC); NORTHWEST TERRITORIES: Yellowknife, 6-VII-1949 (2 CNC), 17-VII-1949 (1 CNC); Reindeer Depot, 13-VII-1949 (2 CNC); ONTARIO: Chisholm, 5-VI-1959 (4 CNC), 19-VI-1959 (1 CNC); QUEBEC: Great Whale River, 28-31-VII-1949 (6 CNC); 13-29-VIII-1949 (2 CNC, 1 OASa); YUKON TERRITORY: Whitehorse, 11-24-VII-1950 (7 CNC); Mi. 87 (Km 140), Dempster Hwy., 27-30-VI-1973 (8 CNC), 8-13-VII-1973 (11 CNC), 16-17-VII-1973 (6 CNC), 4-8-VIII-1973 (4 CNC).

Female Adults

ALBERTA: 0.9 mi. (1.4 km) W. George Lk., 13-V-1976 (reared) (10 ABOr, 5 CNC, 3 UASM); MANITOBA: Churchill, 22-30-VII-1948 (14 CNC), VII-VIII-1950 (10 CNC), 17-VIII-1951 (1 CNC); ONTARIO: Chisholm, 19-VI-1957 (6 CNC), 3-VI-1959 (1 CNC); QUEBEC: Great Whale River, 29-VIII-1949 (1 CNC); Indian House Lake, 17-VII-1954 (1 CNC); YUKON TERRITORY: Whitehorse, 3-VII-1919 (1 CNC), 7-22-VII-1950 (5 CNC), 1-VIII-1950 (1 CNC); Mi. 87 (Km 140), Dempster Hwy. 8-13-VII-1973 (15 CNC), 16-17-VII-1973 (17 CNC); 4-8-VIII-1973 (17 CNC).

Male Pupae

ALBERTA: 33 mi. (53 km) S. Jasper, 4-VI-1975 (3 ABOr, 3 UASM); 1.5 mi. (2.4 km) S. Robb, 23-VII-1975 (3 ABOr); NORTHWEST TERRITORIES: Yellowknife, 6-VII-1949 (3 OASa), 14-VII-1949 (1 CNC); YUKON TERRITORY: Mi. 87 (Km 140), Dempster Hwy., 13-VII-1973. (1 CNC).

Female Pupae

ALBERTA: 43 mi. (69 km) N. Coleman, 3-VIII-1975 (5 ABOr, 5 UASM); 20 mi. (32 km) W. Edson, 17-VI-1975 (4 ABOr, 2 CNC, 2 UASM); BRITISH COLUMBIA: 4.8 mi. (7.7 km) N. Clearwater, 12-VI-1976 (4 ABOr); YUKON TERRITORY: Mi. 87 (Km 140), Dempster Hwy., 13-VII-1973 (8 CNC).

Fourth Instar Larvae

ALBERTA: 43 mi. (69 km) N. Coleman, 3-VIII-1975 (13 ABOr); 33 mi. (53 km) S. Jasper, 4-VI-1975, (5 ABOr, 6 UASM); 1 mi. (1.6 km) S. Jasper, 4-VI-1975 (30 ABOr, 15 UASM, 17 CNC); 14.5 mi. (23.3 km) W. Jasper 21-VI-1975 (8 ABOr); 4 mi. (6.4 km) W. Jasper, 20-V-1975 (9 ABOr); 20 mi. (32 km) W. Edson, 5-VI-1975 (15 ABOr, 5 CNC, 4 UASM); 29-V-1976 (3 ABOr); 1.5 mi. (2.4 km) S. Robb, 23-VII-1975 (2 ABOr); 1.5 mi. (2.4 km) W. Edmonton, 12-VI-1975 (5 ABOr, 3 UASM); 0.9 mi. (1.4 km) W. George Lk., 12-V-1975 (5 ABOr, 5 CNC, 3 UASM); BRITISH COLUMBIA: 4.8 mi. (7.7 km) N. Clearwater, 12-VI-1976 (1 ABOr); MANITOBA: Gillam, 10-VI-1950 (1 CNC); Churchill, 1-11-VII-1943 (1 USNM), 29-VI-1950 (1 CNC) *nr. Childs Lk., 27-V-1978 (39 ABOr); NORTHWEST TERRITORIES: Pond nr. Harris River, 2-VI-1973 (1 CNC); ONTARIO: Aberfoyle, 14-V-1974 (1 ABOr); YUKON TERRITORY: Dempster Hwy., 23-30-VI-1972 (13 ABOr); Mi. 87 (Km 140), Dempster Hwy., 13-VII-1973 (11 CNC); Klutlan Glacier moraine, VII-1971 (20 EFCo, 6 ABOr); *Old Crow, 19-VII-1977 (1 ABOr).

UNITED STATES

ALASKA: Mi. 6 (Km 10), McKinley, 14-VI-1954 (1 USNM); Mi. 13.5 (Km 21.7) Cantwell Rd., 17-VI-1954 (1 USNM).

Third Instar Larvae

ALBERTA: 1.5 mi. (2.4 km) W. Edmonton, 26-V-1975 (8 ABOr, 4 UASM); 1 mi. (1.6 km) S. Jasper, 4-VI-1975 (5 ABOr, 5 CNC, 4 UASM); 20 mi. (32 km) W. Edson, 29-V-1976 (3 ABOr, 2 CNC, 2 UASM); 0.9 mi. (1.4 km) W. George Lk., 12-V-1975 (8 ABOr, 3 UASM); NORTHWEST TERRITORIES: Pond nr. Harris River, 2-VI-1973 (1 CNC); YUKON TERRITORY; Klutlan Glacier moraine, VII-1971 (6 EFCo).

Second Instar Larvae

ALBERTA: 1 mi. (1.6 km) S. Jasper 25-VI-1976 (3 ABOr); 7 mi. (11 km) E. Obed, 27-IV-1976 (8 ABOr, 4 UASM); 20 mi. (32 km) W. Edson, 27-IV-1976 (4 ABOr, 4 UASM); 0.9 mi. (1.4 km) W. George Lk., 24-IV-1976 (8 ABOr, 4 UASM).

First Instar Larvae

ALBERTA: 1 mi. (1.6 km) S. Jasper 25-IV-1976 (8 ABOr, 4 UASM); 20 mi. (32 km) W. Edson, 27-IV-1976 (4 ABOr, 4 CNC).

Eggs

From male and female adults collected as fourth instar larvae 0.9 mi. (1.4 km) W. George Lk., Alberta and reared and mated in laboratory (ABor).

*Material identified but not measured.

Taxonomic notes. – Because many specimens of *Chaoborus cooki* key out to *Chaoborus nyblaei* using Saether's (1972) keys, records of *Chaoborus nyblaei* by Anderson and Raasveldt (1974) probably refer to specimens of *Chaoborus cooki.* The numbers of anal fan setae and PAL/PAW recorded by Smith (1960b) suggests that *Chaoborus cooki* larvae were examined. The suggestion by James and Smith (1958) that some of the *Chaoborus nyblaei* population overwinters in the egg stage at Churchill, Manitoba, indicates the presence of *Chaoborus cooki.*

The only previous description of *Chaoborus cooki* is that of the adults, pupae and fourth instar larvae by Saether (1970). Cook (1956) undoubtedly included specimens of *Chaoborus cooki* in his description of *Chaoborus nyblaei.* The larval head capsule length recorded by Cook (1956) as 2.78 mm, larger than any recorded here, probably refers to a specimen of *Chaoborus cooki.* Contrary to Saether's (1970: 26) statement, Cook's (1956) description of the abdomen probably included *Chaoborus cooki.*

Saether (1970: 20) incorrectly states that *Chaoborus cooki* larvae do not have a dorsal process on abdominal segment IX (see page 157).

Chaoborus nyblaei (Zetterstedt)

Erioptera nyblaei Zetterstedt 1838: 830.Three syntypes, all females; LECTOTYPE HERE DESIGNATED, labelled: 'Corethr. nyblaei, Z. ♀, Erioptera, (illegible word), Lapp Dovre'; one syntype with no label and the other labelled 'Corethr. nyblaei, Z.♂, Erioptera, (illegible word) Lapp Dovre.'; (ZMLS).

Corethra nyblaei; Zetterstedt 1851: 3794. Giles 1902: 502. Theobald 1901b: 291.

Chaoborus nyblaei; Edwards 1930: 533. Edwards 1932: 26. Hirvenoja 1961. Saether 1970: 14, in part.

?Corethra pilipes Gimmerthal 1845: 297. Location of male type unknown. Collected at Riga, Latvijskaja S.S.R.

Description. – Males. (n=two, unless otherwise given in parentheses). Total length 7.9–8.5 mm; general body coloration light grayish brown; vittae brown; specific pigmentation as other members of subgenus.

Antennae: pedicel width 302–319 μm; length of flagellar articles 1,2–11,12,13: 244–267 μm, 148–151 μm, 354–371 μm, 261 μm; P/U 1.42–1.56 μm.

Head: width 1096–1125 μm; width between eyes 313–389 μm; clypeus length 447–464 μm; prementum length 470–493 μm; head width/width between eyes 2.90–3.50; head width/clypeus length 2.42–2.45; head width/prementum length 2.22–2.40; number of setae on vertex 106 (1); lengths of palpal articles two to five: 121–139 μm, 249–261 μm, 244–313 μm, 528 μm (1).

Thorax: number of setae: pronotal 24; postpronotal three or four; proepisternal seven or eight; preepisternal four to seven; anepisternals 12 or 13; upper mesepimerals 14 or 15; scutellar 72–88; supraalar 37 or 38.

Wing: length 4.53–4.63 mm; width 1.03 mm; length/width 4.41–4.51; wing length/head width 4.03–4.15; wing length/length of femur of foreleg 1.68 (1); Y/X 1.88–2.13; Y/Z 1.35–1.59; Y/R_3 0.75–0.77; Z/M_1 0.44–0.56; R_3/M_1 0.94–0.99; number of setae on squama 38 (1); length of Rsa 271 μm (1).

Haltere: capitulum nearly spherical; two to three anterior setae; two to three posterior setae.

Legs: Foreleg: Fe 2690 μm (1); Ti 1251 μm (1); Ta_1 590 μm (1); Ta_5 249 μm (1); Hindleg: Fe 2997 μm (1). Length of foreleg claw 85 μm (1); pulvilli length 53 μm (1).

Genitalia. number of setae on tergite IX 10 (1); penis valve length 194–226 μm; penis valve as shown in Fig. 11,0 and P; gonocoxite length 702 μm (1); gonostylus length 609–632 μm; HR 1.15 (1); HV 1.25–1.39.

Females. (n=three, unless otherwise given in parentheses). Total length 8.0 mm (1); general body coloration light grayish brown; vittae brown; specific pigmentation as other members of subgenus.

Antennae: (n=2) pedicel width 162 μm; length of flagellar articles 1,2-11, 12,13: 192–203 μm, 124–138 μm, 180–191 μm, 197-215 μm; P/U 0.89–0.91.

Head. (n=2) head width 1102 μm; width between eyes 360–400 μm;; clypeus length 464–487 μm; prementum length 493–528 μm; head width/width between eyes 2.75–3.06; head width/clypeus length 2.26–2.38; head width/prementum length 2.09–2.24; number of setae on vertex 134–146; length of palpal articles two to five: 151–157 μm, 290–313 μm, 302–331 μm, 586–621 μm.

Thorax. Coloration as in male.

Number of setae: pronotals 24–43; 70.0; postpronotals 3–11, 6.7; proepisternal 8–11, 9.3; preepisternal 8–10, 9.0; anepisternals 13–34, 24.0; upper mesepimerals 17–24, 19.3; scutellar 87–119, 98.3; supraalar 53–66, 59.7.

Wing. ($n=6$, unless otherwise given) coloration as other members of subgenus. length 5.5–6.3, 5.9 mm; width 1.4–1.8, 1.6 mm; length/width 3.55–4.09, 3.84; wing length/head width 5.17–5.25 (2); wing length/length of femur of foreleg 2.22–2.67 (2); Y/X 2.29–3.43, 3.10; Y/Z 1.33–1.67, 1.53; Y/R_3 0.70–0.93, 0.79; ZM_1 0.42–0.56, 0.50; R_3/M_1 0.91–1.01, 0.96; Rsa 126–302, 238 µm.

Halteres: capitulum nearly spherical; two anterior setae (2); two to eight posterior setae (2).

Legs. (2), coloration as other members of the subgenus.

Foreleg: Fe 2608–2631 µm; Ti 2761–2796 µm; T_1 1345–1369 µm; Ta_2 802 µm; Ta_3 625–627 µm; Ta_4 389–401 µm; Ta_1/Ti 0.49.

Midleg: Fe 2395–2537 µm; Ti 2230–2384 µm; Ta_1 1121–1145 µm; Ta_2 637 µm; Ta_3 496 µm; Ta_4 318–342µm; Ta_5 273–296 µm; Ta_1/Ti 0.47–0.51; 7 setae in Ta_3 comb (1).

Hindleg: Fe 2974–3221 µm; Ti 2620–2950 µm; Ta_1 1758–1782 µm; Ta_2 909–944 µm; Ta_3 625–649 µm; Ta_4 366–413 µm; Ta_5 319–325 µm; Ta_1/Ti 0.60–0.67; 7 setae in Ta_3 comb (1).

Length of foreleg claw: 94 µm; pulvilli length 56–61 µm.

Genitalia: seminal capsule diameter 65–76; 71.4 µm; 1.4 (4); cerci length 267–284, 274 µm (4).

Male pupae. Measurements and proportions: see Table 20.

Female pupae. Measurements and proportions: see Table 21.

Fourth instar larvae. Measurements and proportions: see Table 22.

Eggs: only eggs dissected from abdomens of females were examined. Measurements are probably not, therefore, very accurate. Eggs from lectotype with thick exochorionic layer (Fig. 9B); eggs from female from Abisko with exochorionic layer as relatively thick as that shown in Figure 9C. Sculpturing of exochorion not discernable. Measurements and proportions: see Table 23.

Bionomics. – Probably overwinters in egg stage. Larvae have been collected from both permanent and, possibly, temporary lentic habitats (Hirvenoja, 1961). This species may be able to invade temporary ponds. Adults emerge about the end of July.

Derivation of specific epithet. – Named after Olavus Nyblaeus.

Distribution. – The distribution of *Chaoborus nyblaei* is shown in Fig. 20. Although this species is known from certain records only from Fennoscandia, it may, especially if *Chaoborus pilipes* from Riga, Latvijskaja S.S.R. is conspecific with *Chaoborus nyblaei*, be more widely distributed in the boreal region of the Palaearctic region. If this species has requirements similar to those of *Chaoborus trivittatus* and *Chaoborus cooki*, *Chaoborus nyblaei* is restricted to areas of boreal woodland.

LOCALITIES

Male Adults

FINLAND: 2–3 km SW Nuorgam, 24-VII-1960 (1 ZMHF); SWEDEN: Abisko, 1931 (1 BMNH).

Female Adults

FINLAND: 2–3 km SW Nuorgam, 24-VII-1960 (2 ZMHF); SWEDEN: Abisko, 1931 (1 BMNH); NORWAY: Dovre, 30-VII-? (2 ZMLS); unlabelled specimen from type series (1 ZMLS).

Male Pupae

FINLAND: 2-3 km SW Nuogram, 24-25-VII-1960 (2 OASa; 2 ZMHF).

Female Pupae

FINLAND: 2-3 km SW Nuorgam, 24-25-VII-1960 (4 OASa; 3 CNC; 4 ZMHF).

Fourth Instar Larvae

FINLAND: 2-3 km SW Nuorgam, 24-25-VII-1960 (2 OASa, 2 CNC; 20 ZMHF; 2 ABOr).

Eggs

From females collected as follows: SWEDEN: Abisko, 1931 (1 BMNH); NORWAY: Dovre, 30-VII-? (1 ZMLS).

Taxonomic notes. – Considerable confusion has surrounded the name of this species. Edwards (1920: 265), Martini (1931: 58), and Séguy (1942: 169) incorrectly considered *Chaoborus nyblaei* to be conspecific with *Chaoborus pallidus* (Fabricius). Many authors treated *Schadonophasma* as monotypic

Table 20. Descriptive statistics for male pupae of *Chaoborus nyblaei*. Measurements in μm unless stated otherwise.

Character	N	Range	Mean
Total abdomen length (mm)	4	5.5–5.9	5.7
Respiratory horn length (mm)	4	1.31–1.42	1.38
Respiratory horn width (mm)	4	0.30–0.38	0.33
Abdominal segment VII length	4	1003–1109	1056
Abdominal segment VII width	4	1735–1923	1808
WS/LS	4	1.63–1.74	1.71

Table 21. Descriptive statistics for female pupae of *Chaoborus nyblaei*. Measurements in μm unless stated otherwise.

Character	N	Range	Mean	1.5SD	2SE
Total abdomen length (mm)	11	6.4–7.8	7.1	0.74	0.31
Respiratory horn length (mm)	6	1.59–1.73	1.64		
Respiratory horn width (mm)	6	0.37–0.46	0.43		
Abdominal segment VII length	11	1144–1310	1223	77	31
Abdominal segment VII width	11	2030–2383	3315	167	67
WS/LS	11	1.71–1.89	1.81	0.082	0.033

Table 22. Descriptive statistics for fourth instar larvae of *Chaoborus nyblaei*. Measurements in μm.

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	25	1853–2596	2231	306	0.82
Antennal length	26	870–1160	1037	138	36
LB/SB	26	1.24–1.93	1.54	0.206	0.056
LB/AL	26	0.47–0.74	0.650	0.087	0.023
AS/AL	26	0.78–0.91	0.864	0.044	0.012
Postantennal filament length	26	684–1015	845	122	32
PAL/PAW	25	2.00–5.30	3.56	1.142	0.305
Number mandibular fan bristles	25	8–13	12.3	0.95	0.25
Number anal fan setae	24	34–40	36.6	2.90	0.80

Table 23. Descriptive statistics for eggs of *Chaoborus nyblaei*. Measurements in μm.

Character	N	Range	Mean	1.5SD	2SE
Length without exochorion	14	625–778	670	64	23
Width without exochorion	14	236–330	291	42	15
Thickness of exochorion	6	71–106	88		

or have followed Saether's (1970) conclusion that *Chaoborus nyblaei* occurs in North America and, consequently, have incorrectly applied this name to North American specimens of *Schadonophasma* (Allan, 1973; Anderson and Raasveldt, 1974; Cook, 1956; Dodson, 1970; James and Smith, 1958; James *et al.* 1969; Jenkins and Knight, 1950; Main, 1953; Maleug and Hasler, 1967; Matheson, 1944; McCloy, 1950; Myklebust, 1966; Peus, 1967; Smith, 1960b; Stahl, 1966; Teraguchi and Northcote, 1966).

The only previous detailed description of male adult *Chaoborus nyblaei*, by Saether (1970), was based on a specimen of *Chaoborus trivittatus* from Baffin Island, Canada, and the hypopygium of a specimen of *Chaoborus nyblaei* from 2–3 km SW Nuorgam, Finland. The main diagnostic character was shape of the penis valve. Reorientation of the genitalia of these specimens, however, showed that the characterization by Saether (1970) was incorrect. Penis valves of the specimen from Baffin Island are typical of *Chaoborus trivittatus*. Those from the specimen from Finland are similar to, but different from, penis valves of *Chaoborus trivittatus*. I was able to associate the hypopygium from Finland with the rest of the specimen, and the description includes this male.

Adult characters described by Saether (1970), but not given here, were those which could not be measured.

Pupae and fourth instar larvae have been previously described by Hirvenoja (1961) and Saether (1970).

Of the three syntypes of *Chaoborus nyblaei* only measurements of the female genitalia of the lectotype are included in this description. The lectotype and paralectotypes were used only to describe color and wing characters. The features of the pharate female adult prepared from a pupa and described by Saether (1970), are not included in this description.

Saether (1970: 16) incorrectly states that fourth instar larvae of *Chaoborus nyblaei* do not have a noticeable dorsal process on abdominal segment IX (see page 156).

The first, second, and third instar larvae of *Chaoborus nyblaei* are unknown.

ANALYSIS OF MORPHOLOGICAL VARIATION

The following is a discussion of morphological variation of the stages of *Schadonophasma* species. These results describe differences between species of eggs, all larval stages, pupae and adults. Interpretation of some intraspecific morphological variation as the result of age-related, sex-associated and geographical variation, and, as described for *Chaoborus trivittatus*, the result of past distributions, is also provided. Detailed study of structure, especially when combined with bionomic and behavioral observations, can allow interpretation of the functional significance of characters. These data thereby provide an enhanced means of understanding intraspecific variation and phyletic relationships. Comparison of results with studies of other *Chaoborus* species is provided to facilitate further comparison between species of *Chaoborus*, to reinterpret some past results, and to suggest, in some instances, more likely interpretation of data presented here.

Artificial variation

An important source of error in determining intraspecific and interspecific variation of species can result from methods employed in the preservation or preparation of specimens. This factor accounts for some variation previously described.

Cook (1956: 29) noted that thoracic coloration of adult males of *Schadonophasma* was related to age of pinned specimens. Ground color had changed from light grey to yellowish-brown in specimens which had been pinned for more than twenty years. I have not been able to confirm this observaion which may be due, in part, to Cook's (1956) inclusion in his analysis of adults of both *Chaoborus trivittatus* and

Chaoborus cooki, which do differ in thoracic coloration. In addition, glue had seeped unto the thorax of some of the older pinned specimens producing a darker hue.

The color of all material, of any stage, appeared to bleach when preserved in ethanol for more than about four or five years. In addition, clearing with KOH also bleaches the color of specimens. It is uncertain, therefore, whether Saether (1967) adequately described the color variation of KOH-treated larvae of *Chaoborus flavicans*.

Saether (1970: 21) recognized the distinct conical dorsal process of *Chaoborus brunskilli* (=*Chaoborus trivittatus*) fourth instar larvae as diagnostic. Of all material examined, however, only fourth instar larvae preserved in formalin possessed dorsal processes similar to those of *Chaoborus brunskilli* drawn by Saether (1970: fig. 11Q,R) and ethanol-preserved material exhibited flatter dorsal processes (Fig. 2B; 8C,D). Paratype larvae of *Chaoborus brunskilli* came from two localities. Hamilton (1971) states that the specimens from near Kenora, Ontario were preserved in formalin. Anderson and Raasveldt (1974) do not mention the preservative used to kill the specimens from East Henry Pond, Jasper National Park, Alberta. Main (1953: 21) reported reduction in total length of 3.3–11.3% of 23 larvae of *Chaoborus trivittatus* or *Chaoborus flavicans* preserved for 24 hours in formalin. The pronounced dorsal process diagnostic of *Chaoborus brunskilli* is therefore probably a result of shrinkage in formalin.

Saether (1970) erroneously suggested that *Chaoborus cooki* and *Chaoborus nyblaei* fourth instar larvae do not exhibit pronounced dorsal processes. These observations were caused by coverslips compressing cleared specimens and distorting the abdomens. All uncleared fourth instar larvae of *Chaoborus cooki* subsequently examined had a developed dorsal process (Fig. 8D). Additional specimens of *Chaoborus nyblaei*, which had been cleared but preserved in fluid, were available and I mounted these under coverslips supported by glass chips. The abdomens retained their natural dimensions and this allowed observation of the developed dorsal process (Fig. 8C) similar to those of other fourth instar larvae of *Schadonophasma*.

McGowan (1976) reported six or eight postantennal filaments for second instar, and eight or ten postantennal filaments for third instar larvae of *Chaoborus edulis*. However, the larvae of *Chaoborus pallidipes* (Theobald), which are presently indistinguishable from those of *Chaoborus edulis* (compare Green and Young, 1976; McGowan, 1976), have the two posterior postantennal filaments distinctly separated (much more so than described for *Chaoborus flavicans* by Balvay (1977c)) from the rest of the filaments and, if *Chaoborus edulis* also possesses this trait, McGowan's (1976) results reflect the breaking off of this separate pair and the variation is probably an artifact of preparation.

Saether's (1970) misinterpretation of interspecific variation of penis valve shape of adult males because of lack of standard orientation of these is described elsewhere (p. 177).

Characters varying between larval instars

Hennig (1966a) has discussed the importance of making comparisons only between comparable semaphoronts in systematic work. The only difficulty in recognizing semaphorants of *Schadonophasma* concerns the four larval instars; this section describes differences which permit recognition of each of these.

Data on instar differences also allowed comparison of developmental patterns from instar to instar between species and, for some characters, provided important clues for determining the polarity of morphoclines for phyletic studies.

Differences between instars of *Chaoborus* have been described by Balvay (1977a, 1977b, 1977c), Deonier (1943), Fedorenko and Swift (1972), Green (1972), MacDonald (1956), Maleug (1966), McGowan (1972, 1976), Parma (1969, 1971a), Prokesova (1959), Saether (1967, 1970), Sikorowa

(1967b, 1970, 1973), Smith (1960a), Teraguchi and Northcote (1966), von Frankenberg (1915), and Weismann (1866). Few workers have considered geographical variation in their analysis of instar differences (Balvay, 1977a, 1977b, 1977c; Green 1972; Saether, 1967, 1970: 22; Sikorowa, 1973).

Sikorowa (1973) showed that *Chaoborus flavicans* larvae collected from ponds or lakes differed significantly in a number of characteristics, suggesting that ecological factors produce at least some variation. One character, the length of the longest antennal blade, differed significantly between first instar larvae collected from these two habitat types, implying genetic differences.

It was not previously known, therefore, what characters could be used with certainty to distinguish instars of material collected over an extensive geographical area, and an extensive range of habitats. This paper provides that information for larvae of *Chaoborus trivittatus* and *Chaoborus cooki*. Although some mistaken interpretations of characters are discussed here, qualitative differences between instars are given in the description of *Chaoborus* and are not repeated here.

Mensural characters previously found to differ between instars, but not necessarily without some overlap of variation, were total length, distance between anterior and posterior air sacs, head capsule length, antennal length, distance of antennal seta from base of antenna, long antennal blade, short antennal blade length, AS/AL, LB/SB, postantennal filament length, PAL/PAW, number of mandibular fan bristles, and number of anal fan setae. Total length and distance between anterior and posterior air sacs were not measured because they are clearly related to growth and exhibit continuous variation (Balvay, 1977b; Eggleton, 1932; Fedorenko and Swift, 1972; Hongve, 1975; LaRow and Marzolf, 1970; Lewis, 1975; MacDonald, 1956; Main, 1953; Malueg, 1966; McGowan, 1972; Parma, 1971a; Saether, 1967; Sikorowa, 1973; Smith, 1960a; Teraguchi and Northcote, 1966).

Smith's (1960a) report that *Chaoborus crystallinus* first instar larvae have six terminal antennal setae is probably erroneous. Sikorowa (1973: fig. 13) shows only four setae. Further differences between first instar *Chaoborus flavicans* as described by Parma (1971a) and first instar *Chaoborus crystallinus* as described by Smith (1960a) suggest that some second instar larvae contaminated Smith's (1960a) sample of first instar larvae.

Homologous structures in first and later larval instars of Schadonophasma. – To accurately depict differences between larval instars, homologous structures should be compared. Failure to do so has led to nomenclatural misinterpretation of certain structures in the past.

There has been confusion concerning the setae of the mandible of first instar larvae of *Chaoborus*. Parma (1971a: 178) suggests that *Chaoborus flavicans* first instar larvae exhibit a mandibular fan composed of three setae, but Sikorowa (1967b: 88) mentions the presence of four setae. *Chaoborus astictopus* first instars do not have a mandibular fan (Deonier, 1943:385). Saether (1970: 22) states that *Chaoborus brunskilli* (=*Chaoborus trivittatus*) first instar larvae have a mandibular fan of nine bristles. Reexamination of specimen showed a mandible typical of first instars (Fig. 8A) and suggests that the mandibular fan bristles counted were those of the pharate second instar which was present.

All first instar material examined exhibited mandibles similar to that in Figure 8A (also Balvay, 1977c: fig. 4; Weismann, 1866: fig. 22A).

The homologies of mandibular structures of *Chaoborus* larvae, as considered by all authors, are summarized in Table 24.

Balvay (1977c) discusses at length the nomenclature of the mandible of different instars of *Chaoborus flavicans*, and gives new names for all structures except the mandibular fan. He showed that the mandibles of second, third, and fourth instar larvae were structurally similar to each other but were all different from first instar larval mandibles. Balvay (1977c) considered the "mandibular fan" of first instar larvae to be composed of three setae, and to be homologous to the mandibular fan of later instars, but does not give any justification for doing so. A fourth articulated seta between the teeth of the

Table 24. Comparison of studies of homologies of mandibular structure of larvae of *Chaoborus*.

First Instar Larvae			Later Instar Larvae		All Instars
Balvay, 1977c	Parma, 1971a	Sikorowa, 1967b	Knight, 1971b	Balvay, 1977c	This study
Mandibular fan	Mandibular fan	Mandibular fan	Mandibular spurs	Mandibular setae	Mandibular spurs
Mandibular seta	Mandibular tooth				
Spines E_1, E_2	(not reported)	(not reported)	Mandibular spur	Spines E_1,E_2	Seta O–MP unnamed seta
			Mandibular comb and brush	Mandibular fan	Mandibular fan

mandible and the "mandibular fan" was considered homologous to one of the mandibular setae (=mandibular spur of Knight, 1971b) of later instars. Mandibular setae of the second instar developed at the base of the mandibular seta of the first instar larval mandible. In addition, a nerve extends from the mandibular seta base in the first instar to the bases of the two mandibular setae of the second instar. The mandibular seta of the first instar larval mandible identified by Balvay (1977c) is therefore clearly homologous to one of the mandibular setae of later instars.

Although Balvay (1977c) mentions that the mandibular setae of the pharate second instar larva cannot develop inside the first instar mandibular seta because of the basal articulation, the tips of the mandibular fan bristles of pharate second instar larvae of both *Chaoborus trivittatus* and *Chaoborus cooki* do develop inside this mandibular seta.

Mandibles of first instar larvae of *Chaoborus* are similar to those of *Mochlonyx* (James, 1957: fig. 9) which possess four (only three shown by James) setae, three of which are toothed and are very similar and probably homologous to those of later instars of *Mochlonyx* (Cook, 1956: fig. 22E; Johannsen, 1934: fig. 155; Meinert, 1886: 65). However, mandibles of second, third and fourth instar larvae of *Mochlonyx* also bear mandibular fans undoubtedly homologous to the mandibular fans of *Chaoborus*. The three setae on the mandible of first instar *Chaoborus* larvae are therefore not homologous with the mandibular fan of later instars as suggested by Balvay (1977c), Parma (1971a), Sikorowa (1967b, 1973), and Smith (1960a); they are mandibular spurs (Knight, 1971b). Only two of the mandibular spurs, each with a similar pointed mandibular projection at their base, as all four setae of first instars, are retained by later instars. I am not certain that the naming of the mandibular fan as the mandibular brush and comb by Knight (1971b) is justified. I therefore retain the traditional name.

One of two additional setae on the mandible of first instar *Chaoborus* larvae (Fig. 8A), called spines E_1 and E_2 by Balvay (1977c), is probably homologous with seta O-MP (Knight, 1971b) of some culicid larvae. Both setae are retained in later instars of *Chaoborus* (Fig. 8B; Balvay, 1977c: fig. 5,6,7). The setae are undoubtedly homologous to the two setae on the mandible of first instar *Mochlonyx* (James, 1957: fig. 9) and *Eucorethra underwoodi* Underwood (pers. obs.) larvae. Also present in later instars of *Mochlonyx*, these two setae are retained in later instars of *Eucorethra underwoodi* where they are labelled as the pectinate brush by Knight (1971b: fig. 1d). However, their placement, and similarity to those of the mandible of *Chagasia bathana* (Culicidae) (Knight, 1971b: fig. 2f), suggests one of these is seta O-MP. I therefore label the large seta on the mandible of later instars of *Chaoborus* as such, although it is not certain which of the two is actually seta O-MP. Knight (1971b) does not label the second seta. Knight (1971b: fig. 1e,f) incorrectly labelled seta O-MP as one of the mandibular spurs on the mandible of *Chaoborus americanus* (incorrectly identified as *Chaoborus flavicans*).

Sikorowa (1967b: fig. 1a,b) erroneously shows both second and fourth instar larvae of *Chaoborus flavicans* with three mandibular spurs.

Previous authors have misinterpreted changes in the anal fan between first and second instar larvae. Balvay (1977b) considered, without justification, each pair of anal fan setae of first instar larvae to correspond to a single anal fan seta of the second instar. Sikorowa (1970) mentions that these pairs of setae arise from a common base. This is not so in any of the material I have examined, but the sockets for the two setae are placed laterally very close to one another. This paired arrangement of setae is reflected in all later instars in which, although the setae are in an anterior-posterior plane (Fig. 2B), all anal fan setae are placed alternately slightly one side or the other of the sagittal plane. This, and the fact that the number of anal setae for first and second instar larvae is nearly identical for both *Chaoborus trivittatus* and *Chaoborus cooki*, supports the view that each seta in the first instar corresponds to a single seta in the second instar.

Head capsule length. – Variation in this measurement is useful to distinguish *Chaoborus* larval instars (Fedorenko and Swift, 1972; Goldspink and Scott, 1971; LaRow and Marzolf, 1970; Malueg, 1966; MacDonald, 1956; Parma, 1969, 1971a: Prokesova, 1959; Saether, 1967, 1970; Sikorowa, 1973; Teraguchi and Northcote, 1966; von Frankenberg, 1915). However, Balvay (1977c) found that the range of head capsule length overlapped between third and fourth instar larvae of *Chaoborus flavicans*. Variation in lengths of larval head capsules of *Chaoborus trivittatus* and *Chaoborus cooki* (Fig. 21A) shows, consistent with most previous work, no overlap of range between any of the instars within each species, although ranges of third and fourth instar *Chaoborus trivittatus* are proximate. Head capsule length is sex-associated in fourth instar larvae and therefore probably in third instars and any overlap between these instars, as shown by Balvay (1977b), is probably due to a mixture of male fourth instar and female third instar larvae.

Antennal length. – Antennal length is useful to discriminate all instars (or at least 99% of all specimens when authors do not give ranges) collected at a single locality or in a limited geographical region (Green, 1972; McGowan, 1972, 1974, 1976; Parma, 1971a; Saether, 1970; Sikorowa, 1973). Saether (1967) reported a slight overlap between third (330–420 μm) and fourth (420–640 μm) instar antennal lengths of *Chaoborus flavicans* samples from throughout this species' range. Balvay (1977b) reported overlap of antennal lengths only between second and third instars of this species collected in France. Range of variation for *Chaoborus trivittatus* and *Chaoborus cooki* (Fig. 21B) shows that this character can be used to discriminate all instars. Like head capsule length, to which this character is correlated at least in male larvae, antennal length of third and fourth instar *Chaoborus trivittatus* larvae overlap slightly. As this character also exhibits sex-associated variation in fourth instar larvae, the proximity between antennal lengths of third and fourth instar larvae is probably due in part to this source of variation. This, however, could not fully explain Balvay's (1977b) finding of overlap between second and third instars only.

Distance of antennal seta from base of antenna/antennal length (AS/AL). – Parma (1971a: 177) for *Chaoborus flavicans*, and Saether (1970: 22) for *Chaoborus brunskilli* (=*Chaoborus trivittatus*), showed that differences in AS/AL distinguish all instars, although Balvay (1977b) showed overlap for each instar of *Chaoborus flavicans*. *Chaoborus trivittatus* and *Chaoborus cooki* overlap between second and third, and between third and fourth instars (Fig. 22A). Later instars of *Chaoborus trivittatus* exhibit, particularly between second and third instars, a substantial degree of overlap of range of AS/AL. Therefore this character is useful to distinguish all first instar larvae and only some second, third and fourth instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki*. Change in the ratio from instar to instar is more constant in *Chaoborus cooki* than in *Chaoborus trivittatus*, where there is a more pronounced increase from first to second, and a lesser increase from second to third and third to fourth instars.

Length of long antennal blade/antennal length (LB/AL). – This ratio distinguishes all first instar larvae of *Chaoborus cooki* and all first and second instars of *Chaoborus trivittatus* from all later instars (Fig. 22B). The character can also be used to distinguish some fourth from third instar larvae of *Chaoborus trivittatus* and some second, third and fourth instar larvae of *Chaoborus cooki*.

Length of long antennal blade/length of short antennal blade (LB/SB). – First instar larvae do not possess the short antennal blades of later instars. Inequality of length of antennal blades noted by Balvay (1977b) and Parma (1971a: 176) for first instar larvae of *Chaoborus flavicans* is also present in later instars where one of the long antennal blades is slightly shorter than the other three. Both Balvay (1977b) and Parma (1971a: 177) have shown that, although there were statistical differences between LB/SB of second, third and fourth instars of *Chaoborus flavicans*, there was a good deal of overlap of range. Saether (1967: Table 1) showed overlap of variation of this ratio between third (0.43–0.64) and fourth (0.50–0.60) instar larvae of *Chaoborus flavicans*.

Considerable overlap is exhibited between second, third and fourth instars of *Chaoborus brunskilli* (=*Chaoborus trivittatus*) (Saether, 1970: 22). LB/SB overlaps in range between the last three instars of both *Chaoborus trivittatus* and *Chaoborus cooki* (Fig. 23A). There were differences in the pattern of change of LB/SB from instar to instar between *Chaoborus trivittatus* and *Chaoborus cooki*. At least some individuals of *Chaoborus cooki* can be identified to instar using this character where the ratio decreases with each successive instar. The range of ratio for the three later instars of *Chaoborus trivittatus*, however, are nearly identical to each other. There is only a slight increase in the means of the ratio between second and third instars and a slight decrease between third and fourth instars.

As antennal blades are undoubtedly important in capture and ingestion of prey, differences in progression of prey type from instar to instar between *Chaoborus trivittatus* and *Chaoborus cooki* may be suggested. However, detailed interpretation of the adaptive significance of this difference must await further study. *Chaoborus trivittatus* larvae (Fedorenko, 1975a, 1975b; Swift, 1976; Swift and Fedorenko, 1975) probably show closer affinities in prey selection to *Chaoborus flavicans* larvae (Berg, 1937; Dodson, 1970; Parma, 1971b: 43; Sikorowa, 1973: Table 18; Swüste *et al.* 1973) which exhibit allometric change in LB/SB similar to that of *Chaoborus cooki*. However *Chaoborus cooki*, because of the temporary ponds it inhabits, takes quite different types of prey (commonly ostracods, chironomid larvae, culicid larvae). Therefore, an explanation of differing food types does not adequately explain the differences in the pattern of change of LB/SB in *Chaoborus trivittatus* and *Chaoborus cooki*.

Postantennal filaments. – Parma (1971a), Saether (1967, 1970) and Sikorowa (1973) showed no overlap of range between instars in postantennal filament length.

Results for *Chaoborus trivittatus* and *Chaoborus cooki* (Fig. 23B) show that this character is useful to distinguish all individuals of each instar of *Chaoborus cooki* and all, except a few (due to one specimen each) third and fourth *Chaoborus trivittatus*. The smallest antennal filament length of fourth instar larvae is from specimens collected 85 km north of Coleman, Alberta from a high altitude (1975 m) pond which was not shaded. The extreme environmental conditions of this habitat possibly results in smaller individuals.

Prelabral appendages. – Parma (1971a: 176), Saether (1967: Table 1; 1970: 22) and Sikorowa (1973: fig. 9) have shown, in *Chaoborus* species with laterally flattened prelabral appendages in third and fourth instar larvae, that generally prelabral appendages of third instar larvae are more slender than are those of fourth instar larvae. This is also true for these instars of *Chaoborus trivittatus* and *Chaoborus cooki* (Fig. 24A). Amount of overlap of PAL/PAW between third and fourth instar larvae is especially pronounced for *Chaoborus trivittatus.*

Number of mandibular fan bristles. – This character is useful to identify all specimens to instar in only a few species (Balvay, 1977b; Deonier, 1943; Green, 1972; McGowan, 1972, 1976; Parma, 1971a; Saether, 1967; Sikorowa, 1967b; 1973).

There is some overlap of range in number of mandibular fan bristles between second, third, and fourth instar larvae of both *Chaoborus trivittatus* and *Chaoborus cooki* (Fig. 24B) and this character alone can be used only to recognize some second and fourth instars of either *Chaoborus trivittatus* or *Chaoborus cooki.* Range of number of mandibular fan bristles increases in successive instars at a greater rate in *Chaoborus trivittatus* than in *Chaoborus cooki.*

Anal fan setae. – Differences in number of anal fan setae between larval instars have been described for some *Chaoborus* species by Balvay (1977b). Deonier (1943), McGowan (1972, 1976), Parma (1971a), Saether (1967, 1970), Smith (1960a) and Sikorowa (1973).

Variation of this character for *Chaoborus trivittatus* and *Chaoborus cooki* (Fig. 25A) shows that only some fourth instar larvae of either *Chaoborus trivittatus* or *Chaoborus cooki* can be distinguished using the number of anal fan setae. First instar larvae may be distinguished from second instar larvae by their paired arrangement of setae (Balvay, 1977b; Parma, 1971a; Sikorowa, 1970, 1973).

Variation of characters of fourth instar larvae

Age-related variation. – Age-related variation of fourth instar larvae was studied for *Chaoborus cooki* only. These were collected 1.6 km south of Jasper on June 4 (n=29) and June 17, 1975 (n=33) with third instar larvae and pupae, respectively. This ensured a sample of fourth instar larvae which exhibited the total age range. Total length was interpreted as representative of age, and statistical correlation of the following characters with total length was studied to determine age related variation: antennal length, long antennal blade length, short antennal blade length, LB/SB, LB/AL, distance of antennal seta from antennal base, AS/AL, postantennal filament length, prelabral appendage length and width, PAL/PAW, number of mandibular fan bristles and number of anal fan setae. Shape of dorsal process was also studied.

Male and female larvae were distinguished using the index described below in the section about sex-associated variation. Probably because of small sample size, female larvae exhibited no characters significantly correlated with body length. Three characters of male larvae were significantly negatively correlated with growth: long antennal blade length, LB/AL, and prelabral appendage length. Because long antennal blade length and antennal length are not correlated to each other in male larvae, the correlation of LB/AL to total length probably reflects the correlation of the long antennal blades to total length. Therefore only two remaining characters are meaningfully related to age. Relationship to total length of both long antennal blade length (Fig. 26A) and prelabral appendage length (Fig. 26B) indicates wear with age of these two structures. Wear of long antennal blade is probably associated with prey capture. Roth (1967: 66) previously noted wear of prelabral appendages of overwintered *Chaoborus albatus* larvae. Evidence of damage, particularly to the tip of prelabral appendages, producing a blunt tip and therefore a shorter prelabral appendage, is common in fourth instar larvae of *Chaoborus trivittatus* (Fig. 13G), *Chaoborus cooki* and *Chaoborus nyblaei* (Fig. 15A-D). Examination of freshly captured, fluid-preserved material shows that wear of the prelabral appendages is not an artifact of preparation.

Although the drawing of the prelabral appendage of *Chaoborus nyblaei* by Saether (1970: fig. 11G) does not show it, the tip had been broken off and the prelabral appendages of *Chaoborus nyblaei* fourth instar larvae are in fact more elongate (Fig. 15E-H; Hirvenoja, 1961: fig. 2A). The breaking off of the tip of the prelabral appendages of *Chaoborus trivittatus* and *Chaoborus nyblaei* makes them appear similar to those of *Chaoborus cooki* (compare Fig. 15C, 14A-L). However, an undamaged prelabral appendage of *Chaoborus cooki* can be separated from damaged ones of *Chaoborus trivittatus* or *Chaoborus nyblaei* through examination of the form of the tip.

Sex-associated variation. – Inclusion of two different groups of semaphoronts in an analysis of variation of characters can result in an overestimation of the amount of intraspecific variation. Characters which display a large degree of sex-associated variation may therefore be mistakenly interpreted as exhibiting a greater degree of intraspecific variation than is actually present, as shown by the following analysis of some characters of fourth instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki*.

Little has been previously reported about larval sex-associated variation of *Chaoborus* species (Bradshaw, 1973: 1249; Smith, 1960a: 198, von Frankenberg, 1915; 514). Teraguchi and Northcote (1966: fig. 2) give the distribution of head capsule lengths of fourth instar larvae of *Chaoborus flavicans* collected in September which exhibits a bimodality. If this represents male and female larvae, as might be suggested by the results presented below, a comparison of the larvae collected in August and September would suggest that male larvae molt to fourth instar earlier than do females.

Chaoborus trivittatus. Statistical comparison of 14 characters (Table 25) of 23 male and 21 female larvae exuviae from reared fourth instars collected 2.4 km west of Edmonton, Alberta, April 26, 1975, indicated that eight characters differed significantly between male and female fourth instar larvae but none without some overlap.

To sex larvae without rearing, I constructed a compound character index (Table 26) in which range of variation of head capsule length, antennal length, AS/AL, long antennal blade length, LB/SB, and postantennal filament length were divided into numbered units, with typical male larvae given the lowest unit values, and female larvae the highest. Summation of values of each character for each individual showed that male and female larvae can be distinguished if the range of variation of each character in the index is divided into ten units (Fig. 27A). The method, however, depends on a large enough sample to express the bimodality.

Chaoborus cooki. Fourth instar larvae of *Chaoborus cooki* were collected 32 km west of Edson, Alberta on June 5, 1975 and reared to adulthood. Of these, 15 male and nine female larval exuviae were measured for 14 characters and statistically compared (Table 27). Five characters differed significantly between male and female larvae with only postantennal filament length showing no overlap of range. Because of proximity of ranges of postantennal filament length of male and female larvae, this character cannot be used alone to sex larvae which have not been reared. A compound character index, similar to that described above, was used to sex larvae (Table 28). Distance of antennal seta from antennal base was not used in the index because it is so markedly correlated to antennal length (Fig. 29B). Resultant index values for individual larvae (Fig. 27B) show that larvae can be sexed using this method. Fourth instar larvae used to study growth related variation were also sexed using a compound character index (Table 29). Results (Fig. 27C) were tested by examining distribution of characters used to sex larvae. For example, length of postantennal filaments over-lapped only by one specimen between male and female larvae.

It may have been due to smaller sample size used in the analysis of *Chaoborus cooki* that some characters were sex-associated for *Chaoborus trivittatus* larvae, but not for those of *Chaoborus cooki*.

Chaoborus nyblaei. I did not have reared material of *Chaoborus nyblaei* and was, therefore, unable to calculate sex-associated variation from fourth instar larvae of known sex. I attempted to sex the larvae

Table 25. Descriptive statistics for male and female fourth instar larval exuviae of *Chaoborus trivittatus* collected 2.4 km west of Edmonton, Alberta. Measurements in μm.

	MALES					FEMALES				
CHARACTER	N	Range	Mean	1.5SD	2SE	N	Range	Mean	1.5SD	2SE
Antennal Length	23	795–899	836	35	10	21	876–1003	935	44	13
Long Antennal Blade Length	23	609–696	660.9	35.4	9.8	21	673–777	723.1	42.3	12.3
Short Antennal Blade Length	23	278–365	321.8	38.5	10.7	21	290–360	324.8	30.4	8.9
LB/SB	23	1.83–2.45	2.06	0.25	0.07	21	2.04–2.52	2.23	0.19	0.06
LB/AL	23	0.68–0.84	0.791	0.053	0.015	21	0.72–0.84	0.773	0.43	0.012
Antennal Seta from Antennal Base	23	702–813	742	37	10	21	783–922	840	49	14
AS/AL	23	0.87–0.91	0.887	0.019	0.005	21	0.86–0.92	0.899	0.024	0.007
Postantennal Filament Length	23	720–791	759	34	9	21	767–885	816	53	12
Prelabral Appendage Length	23	284–447	376.0	70.5	19.6	21	261–464	367.1	82.6	24.0
Prelabral Appendage Width	23	64–87	75.2	10.6	3.0	21	70–93	81.5	12.4	3.6
PAL/PAW	23	3.27–7.00	5.06	1.34	0.37	21	2.81–6.42	4.56	1.39	0.40
Number Anal Fan Setae	23	25–29	27.4	1.4	0.4	21	25–29	27.6	1.6	0.5
Number Mandibular Fan Bristles	23	20–28	22.5	2.6	0.7	21	19–25	22.7	2.4	0.7
Head Capsule Length	20	1676–2100	1949	156	46	19	1900–2313	2116	188	57

by assuming that those larval characters exhibiting sex-associated variation for both *Chaoborus trivittatus* and *Chaoborus cooki* were also sex-associated for *Chaoborus nyblaei* larvae and constructing a compound character index similar to that for the larvae of *Chaoborus trivittatus* and *Chaoborus cooki*, on the basis of head capsule length, antennal length, long antennal blade length, and postantennal filament length. Presumably because of small sample size (n=24) I could not confidently interpret the slight bimodality present in resultant index values.

Table 26. Compound character index used to sex fourth instar larvae of *Chaoborus trivittatus* collected 2.4 km west of Edmonton, Alberta. Measurements in μm. (– = no data)

	INDEX VALUE									
CHARACTER	1	2	3	4	5	6	7	8	9	10
Antennal length	791- 815	816- 840	841- 865	866- 890	891- 915	916- 940	941- 965	966- 990	991- 1015	1016- 1040
Long antennal blade length	600- 618	619- 636	637- 654	655- 672	673- 690	691- 708	709- 726	727- 744	745- 762	763- 780
LB/SB	1.82- 1.89	1.90- 1.97	1.98- 2.05	2.06- 2.13	2.14- 2.20	2.21- 2.28	2.29- 2.36	2.37- 2.43	2.44- 2.51	2.52- 2.59
AS/AL	0.86	0.87	–	0.88	–	0.89	0.90	–	0.91	0.92
Postantennal filament length	700- 720	721- 740	741- 760	761- 780	781- 800	801- 820	821- 840	841- 860	861- 880	881- 900
Head capsule length	1676- 1741	1742- 1806	1807- 1871	1872- 1936	1937- 2001	2002- 2066	2067- 2131	2132- 2195	2196- 2261	2262- 2326

Correlation of characters. – Analysis of correlation of characters gives important clues on how best to interpret sources of variation, results of compound character indices, and characters used in phylogenetic analysis. Ratios which are significantly correlated to another ratio with which they share one character, or to one of the characters from which the ratio is composed are presented, but most of these correlations are probably artifacts of analysis (Atchley *et al.*, 1976).

Characters of male and female larvae were analyzed separately; this precluded use of specimens of *Chaoborus nyblaei*. However, characters which were significantly correlated for male and female larvae of both *Chaoborus trivittatus* and *Chaoborus cooki* were studied for *Chaoborus nyblaei* fourth instar larvae. Characters were considered significantly correlated at the 95% confidence limit. Because of low numbers of female *Chaoborus cooki* larvae studied, significance or lack of significance may be fortuitous in some comparisons.

The *Chaoborus cooki* larvae that were studied for age-related variation and *Chaoborus trivittatus* larvae that were used to determine sex-associated variation, were studied in this analysis. In addition, the *Chaoborus cooki* larvae studied for sex-associated variation were used to confirm the results from the aforementioned *Chaoborus cooki* larvae. However, presumably because of their greater numbers, some characters were significantly correlated for the *Chaoborus cooki* larvae used to determine age-related variation but were not so for the larvae used to study sex-associated variation.

Results for male and female fourth instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki* are given in Figure 28A-D. As for *Chaoborus trivittatus* and *Chaoborus cooki* (Fig. 29A,B), distance of

Table 27. Descriptive statistics of male and female fourth instar larval exuviae of *Chaoborus cooki* collected 32 km west of Edson, Alberta. Measurements in µm.

	MALES					FEMALES				
CHARACTER	N	Range	Mean	1.5SD	2SE	N	Range	Mean	1.5SD	2SE
Antennal Length	15	945–1079	1025	67	23	9	1067–1195	1143	66	29
Long Antennal Blade Length	15	487–603	539.4	39.2	13.5	9	551–597	569.0	22.8	10.1
Short Antennal Blade Length	15	354–429	395.6	35.4	12.2	9	377–441	407.9	28.8	12.8
LB/SB	15	1.14–1.51	1.37	0.15	0.05	9	1.36–1.54	1.40	0.09	0.04
LB/AL	15	0.47–0.58	0.527	0.050	0.017	9	0.47–0.56	0.501	0.045	0.020
Antennal Seta from Antennal Base	15	812–951	873	59	20	9	905–1021	907	56	25
AS/AL	15	0.80–0.88	0.851	0.039	0.014	9	0.82–0.88	0.848	0.025	0.011
Postantennal Filament Length	15	649–802	769	61	21	9	826–885	851	29	13
Prelabral Appendage Length	15	206–294	251.2	28.4	9.8	8	229–306	268.2	43.6	20.6
Prelabral Appendage Width	15	59–100	81.9	16.5	5.7	8	71–94	84.5	11.5	5.4
PAL/PAW	15	2.29–4.30	3.13	0.79	0.27	8	2.62–3.43	3.18	0.47	0.22
Number Anal Fan Setae	13	31–36	32.6	2.3	0.9	9	32–35	33.7	1.8	0.8
Number Mandibular Fan Bristles	15	10–15	12.5	1.6	0.5	9	12–14	13.1	1.2	0.5
Head Capsule Length	15	2030–2266	2121	103	36	9	2254–2466	2373	102	45

antennal seta from antennal base is strongly correlated to antennal length of fourth instar larvae of *Chaoborus nyblaei* (Fig. 29C).

Correlation between two characters does not necessarily imply a genetic or functional relationship between those characters. However, lack of correlation suggests little relationship, and I have used only that information in subsequent analyses.

Geographical variation. – Study of geographical variation of characters of fourth instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki* explained some of the large intraspecific variation of some characters, and provided evidence for inferring past distributions. In addition, geographical variation can give supportive evidence of reproductive isolation. Discovery of differences in patterns of geographical variation of head capsule length, AS/AL, and number of mandibular fan bristles supports the conclusion from other analyses, that *Chaoborus trivittatus* and *Chaoborus cooki* are different species.

It is difficult to determine to what extent clines are products of past and present gene flow or environmental gradients. However, analyses of intrapopulational correlation show which characters are associated, and study of patterns of geographical variation in different areas can indicate which characters are selected independently. Characters such as these, which in some locations show common patterns, are most likely to reflect gene flow and, possibly, historic events.

The geographical variation of seven characters was studied. However, because head capsule length is correlated with antennal length, at least in male larvae, and analysis of antennal length variation showed almost exactly the same pattern as head capsule length for both *Chaoborus trivittatus* and *Chaoborus cooki*, only results of variation of head capsule length are discussed here. Other characters are those used in the compound character index (Fig. 43).

Chaoborus trivittatus. I studied 21 samples from Alberta and 14 samples, or grouped samples, from the rest of North America. Within Alberta, only two areas showed geographical patterns of variation for some of the characters. The samples, numbered 1–5 and 6–9 (Fig. 30), were collected from an area near to or east of Jasper and north of Swan Hills, respectively.

The characters which show a common pattern are head capsule length (Table 30), AS/AL (Table 31), PAL/PAW (Table 32) and number of mandibular fan bristles (Table 33). Generally there is a linear increase or decrease in mean values of samples 1–5 or 6–9, corresponding to the generally linearly arranged set of localities from which samples were collected. The PAL/PAW of samples 1 and 6 do not fit the pattern suggested by other samples or other characters. In addition, direction of clines differs between areas for different characters. Mean values for head capsule length and AS/AL decrease in a west-east direction in the Jasper area and in a north-south direction in the Swan Hills area, while mean number of mandibular fan bristles decreases and PAL/PAW increases in a west-east direction in the Jasper area and south-north direction in the Swan Hills area. While reflecting gene flow, this pattern suggests the non-correlation of local selection of these two character pairs. Lack of patterns of variation of these four characters, particularly in southwestern Alberta (6 samples), is probably due to either a complicating factor or lack of resolution.

Study of six samples, or clumped samples, from Ontario, Quebec, Newfoundland, Wisconsin and Michigan indicated no apparent patterns of geographical variation, probably because of the few numbers of samples studied from such a large area.

I could distinguish no patterns of geographical variation of head capsule length for samples from outside of Alberta but, because this character can vary markedly in a relatively small area, as shown above, this was probably due to a small number of samples. Therefore it may be significant that, of all samples studied, specimens from Klutlan Glacier moraine, Yukon exhibited the highest mean head capsule length (2157 μm).

Two characters, LB/SB and number of anal fan setae, did not exhibit geographical patterns within

Alberta but did vary geographically on the west coast of North America. At least for number of anal fan setae this discrepancy is explained by the overall homogeneity of samples from Alberta which exhibit, for example, a total range of means in the Jasper region of 27.5–28.1.

Patterns of geographical variation are apparent along the west coast of North America for AS/AL (Table 34), LB/SB (Table 35), PAL/PAW (Table 36), number of mandibular fan bristles (Table 37), and number of anal fan setae (Table 38). Samples are numbered 1–7 (Fig. 31).

Variation in number of mandibular fan bristles and number of anal fan setae, exhibit a linear north-south cline with mean values increasing in a northerly direction. The number of anal fan setae of sample 6 (Table 38) is unexpectedly high, however. The other three characters, AS/AL, LB/SB, and PAL/PAW, show a different pattern of variation, with the highest mean values near the middle of the cline in the Washington or southwestern British Columbia region. None of these three characters show any intrapopulational correlation. In addition, study of AS/AL and PAL/PAW in Alberta shows that at least these two characters are independently selected for. Thus, concurrent patterns of geographical variation of these three characters probably reflect the historic events discussed below.

It seems likely, considering the present distribution of *Chaoborus trivittatus*, that this species was able to survive in both the Alaskan-Yukon refugium, and refugia south of the continental ice sheet during the Wisconsin glaciation. Because *Chaoborus trivittatus* is now restricted to woodland conditions (p. 140), discovery of woodland in parts of the Beringian refugium (Hopkins, 1972) would also suggest that *Chaoborus trivittatus* could have survived in this region.

This inferred distribution during the Wisconsin glaciation adequately explains some geographic variation. Even if an ice free corridor was present in Alberta (Reeves, 1973) and the Alaskan-Yukon refugial population was not reproductively isolated from some populations south of the continental ice sheet, this would not affect the argument presented here. Geographical patterns of variation along the west coast of North America would be the result of resumed reproduction between northern and southern populations along the west coast as the continental ice retreated (Prest, 1969).

The Yukon sample, from a pond on Klutlan Glacier moraine, exhibits the extreme of clinal variation of five characters (AS/AL, LB/SB, PAL/PAW, number of mandibular fan bristles, number of anal fan setae). These patterns are consistent with an hypothesis suggesting the past isolation of this population (see below).

Johnson (1977) has recently suggested that coastal California had a climate during the last continental glaciation similar to that now prevailing. There is little doubt that *Chaoborus trivittatus* populations were present in the region at that time. It would be reasonable to suggest that clinal variation of AS/AL, LB/SB and PAL/PAW along the west coast of the United States (i.e., south of the area formerly occupied by the continental ice sheet) is similar to that existing during the Wisconsin glaciation. Probably the peak of mean values of AS/AL, LB/SB, and PAL/PAW in Washington or southwestern British Columbia represents the northern end of clinal variation of past populations. Subsequent retreat of the continental ice opened a coastal corridor and allowed contact between populations from the Alaskan-Yukon refugium and those immediately south of the ice sheet, thereby resulting in intermediate clinal values (Prince Rupert sample).

Chaoborus cooki. I studied seven samples, number 1–7 (Fig. 32), of fourth instar larvae of *Chaoborus cooki* in Alberta. Two additional samples from the Yukon, from along the Dempster Highway and from a pond on Klutlan Glacier moraine, were so similar to each other and distant from the Alberta samples, that I did not include them in this description.

A common geographical pattern is evident for four characters: head capsule length (Table 39), AS/AL (Table 40), number of mandibular fan bristles (Table 41), and number of anal fan setae (Table 42). Of the three samples from near Jasper, sample 3 is closest geographically to sample 5. Samples 2, 3, and 4 are, although not in a straight line geographically, probably linearly arranged in terms of dispersal of this species along a continuous valley bordered, except to the eastward side of sample 3, by high mountains.

Table 28. Compound character index used to sex fourth instar larvae of *Chaoborus cooki* collected 32 km west of Edson, Alberta. Measurements in μm.

	INDEX VALUE									
CHARACTER	1	2	3	4	5	6	7	8	9	10
Antennal length	945-970	971-995	996-1020	1021-1045	1046-1070	1071-1095	1096-1120	1121-1145	1146-1170	1171-1195
Long antennal blade length	487-499	500-510	511-522	523-533	534-545	546-557	558-568	569-580	581-591	592-603
Postantennal filament length	649-673	674-696	697-720	721-743	744-767	768-791	792-814	815-838	839-861	862-885
Head capsule length	2030-2074	2075-2117	2118-2161	2162-2204	2205-2248	2249-2292	2293-2335	2336-2379	2380-2422	2423-2466

Table 29. Compound character index used to sex fourth instar larvae of *Chaoborus cooki* collected 1.6 km south of Jasper, Alberta. Measurements in μm.

	INDEX VALUE									
CHARACTER	1	2	3	4	5	6	7	8	9	10
Antennal length	870-906	907-943	944-979	980-1016	1017-1052	1053-1089	1090-1125	1126-1162	1163-1198	1199-1235
Long antennal blade length	539-555	556-572	573-588	589-604	605-620	621-637	638-653	654-669	670-686	687-702
Postantennal filament length	731-748	749-764	765-781	782-797	798-814	815-831	832-847	848-864	865-880	881-897
Head capsule length	1841-1907	1908-1973	1974-2039	2040-2105	2106-2172	2173-2238	2239-2304	2305-2370	2371-2436	2437-2502

Table 30. Variation in head capsule length (in μm) of fourth instar larvae of *Chaoborus trivittatus* in Alberta. See Figure 30 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	10	1888–2289	2083	236	99
2	11	1699–2207	1985	184	74
3	10	1546–1959	1785	198	83
4	11	1522–2065	1789	276	111
5	25	1487–2077	1702	215	57
6	11	1982–2266	2091	140	56
7	11	1794–2183	1985	200	81
8	12	1746–2199	1946	211	81
9	11	1687–2112	1885	202	82

Table 31. Variation in AS/AL of fourth instar larvae of *Chaoborus trivittatus* in Alberta. See Figure 30 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	9	0.86–0.92	0.901	0.026	0.012
2	11	0.85–0.92	0.888	0.031	0.012
3	10	0.86–0.91	0.884	0.024	0.010
4	11	0.84–0.91	0.878	0.031	0.012
5	26	0.82–0.92	0.878	0.041	0.011
6	10	0.86–0.92	0.901	0.026	0.011
7	11	0.88–0.92	0.905	0.021	0.008
8	12	0.86–0.92	0.894	0.032	0.012
9	11	0.86–0.91	0.887	0.030	0.012

Table 32. Variation in PAL/PAW of fourth instar larvae of *Chaoborus trivittatus* in Alberta. See Figure 30 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	10	4.50–7.00	5.263	1.094	0.461
2	11	4.29–5.50	4.983	0.470	0.189
3	10	4.54–5.42	5.002	0.472	0.199
4	11	4.33–6.62	5.288	0.874	0.351
5	26	3.79–6.77	5.442	0.830	0.217
6	11	4.15–6.18	5.075	1.010	0.406
7	11	4.54–7.33	5.847	1.184	0.476
8	12	4.75–9.14	5.656	1.875	0.722
9	11	4.54–7.30	5.558	1.267	0.509

Table 33. Variation in numbers of mandibular fan bristles of fourth instar larvae of *Chaoborus trivittatus* in Alberta. See Figure 30 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	10	23–29	25.9	2.9	1.2
2	11	16–23	20.0	3.4	1.4
3	10	17–23	19.7	3.7	1.6
4	11	14–21	17.4	3.6	1.4
5	26	12–24	17.2	4.7	1.2
6	11	18–24	21.4	2.7	1.1
7	11	19–25	22.2	3.0	1.2
8	12	18–30	23.0	5.3	2.0
9	11	18–26	22.5	3.2	1.3

Table 34. Variation in AS/AL of fourth instar larvae of *Chaoborus trivittatus* from the west coast of North America. See Figure 31 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	9	0.83–0.90	0.863	0.033	0.015
2	15	0.86–0.92	0.891	0.027	0.009
3	10	0.89–0.93	0.911	0.019	0.008
4	14	0.89–0.92	0.908	0.018	0.006
5	10	0.85–0.91	0.887	0.025	0.010
6	12	0.87–0.92	0.890	0.023	0.009
7	13	0.84–0.92	0.890	0.035	0.013

Table 35. Variation in LB/SB of fourth instar larvae of *Chaoborus trivittatus* from the west coast of North America. See Figure 31 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	8	1.76–2.18	2.040	0.200	0.094
2	15	1.80–2.49	2.110	0.280	0.097
3	10	2.39–2.81	2.510	0.222	0.094
4	14	2.12–2.92	2.530	0.272	0.097
5	10	1.95–2.44	2.240	0.249	0.105
6	12	1.47–2.34	2.040	0.334	0.129
7	12	1.85–2.37	2.080	0.236	0.091

Table 36. Variation in PAL/PAW of fourth instar larvae of *Chaoborus trivittatus* from the west coast of North America. See Figure 31 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	9	2.63–6.36	4.739	1.717	0.763
2	14	4.14–6.09	5.060	0.702	0.250
3	10	4.18–6.25	5.172	0.953	0.402
4	14	3.82–5.83	4.477	0.847	0.302
5	10	3.27–6.80	5.553	1.496	0.631
6	12	4.25–6.67	4.992	1.199	0.462
7	13	3.30–6.25	4.832	1.482	0.548

Table 37. Variation in numbers of mandibular fan bristles of fourth instar larvae of *Chaoborus trivittatus* from the west coast of North America. See Figure 31 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	11	18–33	27.7	6.6	2.6
2	15	21–36	26.2	6.1	2.1
3	10	22–29	24.7	4.2	1.8
4	14	20–32	25.5	4.2	1.5
5	10	20–29	24.0	3.9	1.7
6	12	21–30	23.8	3.7	1.4
7	16	18–31	22.3	5.8	1.9

Table 38. Variation in numbers of anal fan setae of fourth instar larvae of *Chaoborus trivittatus* from the west coast of North America. See Figure 31 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	9	31–33	32.0	1.3	0.6
2	15	27–31	28.6	2.0	0.7
3	10	26–38	27.4	1.0	0.4
4	14	26–29	27.9	1.3	0.5
5	10	25–29	27.0	1.9	0.8
6	12	27–30	28.4	1.4	0.5
7	12	25–30	27.1	2.1	0.8

Table 39. Variation in head capsule length (in µm) of fourth instar larvae of *Chaoborus cooki*. See Figure 32 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	12	2148–2620	2396	204	79
2	10	1888–2360	2153	228	96
3	63	1841–2502	2153	217	37
4	17	1841–2325	2027	223	72
5	27	1770–2466	2178	260	67
6	13	2030–2443	2216	230	85
7	8	2065–2466	2304	236	111

Table 40. Variation in AS/AL of fourth instar larvae of *Chaoborus cooki*. See Figure 32 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	12	0.81–0.89	0.856	0.038	0.014
2	11	0.81–0.89	0.850	0.035	0.014
3	62	0.80–0.89	0.851	0.031	0.005
4	17	0.81–0.87	0.832	0.023	0.007
5	27	0.80–0.90	0.854	0.038	0.010
6	13	0.80–0.93	0.866	0.046	0.017
7	8	0.83–0.88	0.864	0.025	0.012

Table 41. Variation in numbers of mandibular fan bristles of fourth instar larvae of *Chaoborus cooki*. See Figure 32 for location of sample numbers

Sample	N	Range	Mean	1.5SD	2SE
1	14	13–21	15.4	2.9	1.0
2	11	11–14	12.9	1.4	0.6
3	62	11–15	13.5	1.5	0.3
4	17	12–17	13.9	2.0	0.7
5	27	10–15	12.9	1.6	0.4
6	13	12–16	13.8	1.6	0.6
7	8	13–17	14.5	2.1	1.0

Table 42. Variation in numbers of anal fan setae of fourth instar larvae of *Chaoborus cooki*. See Figure 32 for location of sample numbers.

Sample	N	Range	Mean	1.5SD	2SE
1	13	31–36	33.3	2.1	0.8
2	11	32–38	33.8	2.7	1.1
3	61	28–36	32.8	2.4	0.4
4	17	30–34	31.9	1.6	0.5
5	25	31–36	32.9	2.2	0.6
6	14	31–34	33.0	1.4	0.5
7	8	30–35	32.2	3.1	1.5

The pattern of geographical variation for the characters is similar. Sample 1 exhibits the highest average for all four characters with the exception of AS/AL. The three Jasper samples 2, 3 and 4, show a successive increase and decrease in mean value of number of mandibular fan bristles and number of anal fan setae, respectively. There is, generally, a successive increase of mean values of head capsule length, AS/AL, number of mandibular fan bristles and number of anal fan setae for samples 3, 5, 6 and 7. However, the following are exceptions to this pattern. Sample 5 mean number of mandibular fan bristles is less than that of sample 3. For AS/AL, the mean value of sample 6 is nearly identical to that of sample 7. For number of anal fan setae, the mean values of samples 5, 6 and 7 show no significant change.

Nevertheless, these overall patterns show that some of the greater differences among means may be attributable to this source. In addition, variation of number of anal fan setae of samples 2, 3 and 4 shows that characters vary significantly in a small geographic area and therefore, suggests either strong local selection or restricted gene flow between populations.

Compound character index and characters differing between fourth instar larvae of species of Schadonophasma. – Initially I had difficulty distinguishing between fourth instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki*. Although I could identify some populations using characters described by Saether (1970), I found variation of all individual characters to present a confusing continuum (see Fig. 21-25A) and was uncertain which characters could, in combination, be used to identify members of these two species. I therefore compared reared material of both sexes of *Chaoborus trivittatus* and *Chaoborus cooki*, used in analysis of sex-associated variation, to discover which characters might differ between the two species. Characters examined in the study of sex-associated variation differed significantly, except length of postantennal filaments (see Tables 25, 27) between male larvae and prelabral appendage width between female larvae. Identifications were confirmed through examination of associated adults.

For the purpose of this study I treated these two samples as if they were sympatric. Testing for species differences through initial comparison of samples collected from the same locality reduces differences due to geographic and ecotypic variation. However, such samples were not available to me when I initiated this study.

Six characters which differed between both males and females of *Chaoborus trivittatus* and

Chaoborus cooki and not correlated to each other, were chosen in order to construct a compound character index to give single values for individual specimens summarizing their features (Table 43). The correlation between LB/SB and AS/AL for *Chaoborus cooki* females and between PAL/PAW and number of mandibular fan bristles of male *Chaoborus cooki* were considered to be unimportant, especially as the correlation did not appear in the opposite sex of *Chaoborus cooki* or in either sex of *Chaoborus trivittatus*.

Range of each character was divided into 21 equal units numbered 0–20. The number 0 represented the extreme of *Chaoborus cooki* variation of a character and number 20 the opposite extreme of *Chaoborus trivittatus* variation. *Chaoborus cooki* larvae would therefore receive overall lower final index values than those of *Chaoborus trivittatus*. To compare all *Schadonophasma* species, the index, although based on differences between *Chaoborus trivittatus* and *Chaoborus cooki*, included the variation of *Chaoborus nyblaei*. Consequently the lowest index values of the number of mandibular fan bristles and two of the lowest values of number of anal fan setae, represent extremes of *Chaoborus nyblaei* variation.

The values of two specimens of *Chaoborus trivittatus* went beyond the recorded range of LB/SB and one each beyond the range of PAL/PAW and number of mandibular fan bristles. These specimens were given the highest index value for that character. It seems unlikely that these changes in procedure significantly affected the final results.

The distribution of index values for both *Chaoborus trivittatus* and *Chaoborus cooki* fourth instar larvae (Fig. 33) shows that almost all specimens can be identified with confidence. In addition, if more than seven specimens are examined, range of means of compound character values of *Chaoborus cooki* (34.0 – 43.3) and *Chaoborus trivittatus* (63.8 – 81.0) allows identification of all samples. Although one character was sex-associated for *Chaoborus cooki* and three for *Chaoborus trivittatus*, there was no significant difference between index values of male and female *Chaoborus trivittatus*. There was a significant difference between index values of male and female larvae of *Chaoborus cooki* but with a large degree of overlap. I therefore did not consider it important to separate male and female larvae. In addition, most samples were too small to confidently distinguish male and female larvae using a compound character index.

Chaoborus nyblaei fourth instar larvae (n=20) index values had a range of 16–47, mean of 36.4, 1.5SD of 11.6 and 2SE of 3.6. Therefore *Chaoborus nyblaei* fourth instar larvae can be distinguished from those of *Chaoborus trivittatus* but not from those of *Chaoborus cooki* using this index.

Specimens from Russell Lake, Alberta (n=10, range = 43–57, mean = 52.3, 1.5SD = 7.1, 2SE = 3.0), from Mechant Lake, Quebec (n=11, range = 50–62, mean = 57.1, 1.5SD = 6.8, 2SE = 2.7) and from Gallienne Lake, Quebec (n=19, range = 45–66, mean = 55.3, 1.5SD = 8.4, 2SE = 2.6) exhibited intermediate index values and could therefore not be identified. These samples are described and discussed below under 'Populations *incertae sedis*'.

Mean index values did not exhibit geographical patterns of variation. This was, probably, partially the result of independent patterns of geographical variation of individual characters evidenced, for example, by some characters of *Chaoborus trivittatus* larvae in Alberta.

On the basis of the above results I could determine that variation of each character for all samples studied, although with overlap, differed significantly between fourth instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki* (Fig. 21-25A; Table 6, 15). Fourth instar larvae of *Chaoborus nyblaei* were significantly different in all characters from those of *Chaoborus trivittatus* but were only significantly different from those of *Chaoborus cooki* in postantennal filament length, number of mandibular fan bristles and number of anal fan setae. Both second and third instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki* differed significantly for each character studied. First instars differed

Table 43. Compound character index used to recognize fourth instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki*. Measurement in µm. (– = no data)

	INDEX VALUE																				
CHARACTER	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Antennal length	1185-1210	1159-1184	1133-1158	1107-1132	1081-1106	1055-1080	1029-1054	1003-1028	997-1002	951-976	925-950	899-924	873-898	847-872	821-846	795-820	796-794	743-768	717-742	691-716	655-690
LB/SB	1.08-1.15	1.16-1.23	1.24-1.31	1.32-1.39	1.40-1.47	1.48-1.55	1.56-1.63	1.64-1.71	1.72-1.79	1.80-1.87	1.88-1.95	1.96-2.03	2.04-2.11	2.12-2.19	2.20-2.27	2.28-2.35	2.36-2.43	2.44-2.51	2.52-2.59	2.60-2.67	2.68-2.75
AS/AL	.75	.76	.77	.78	.79	–	.80	.81	.82	.83	.84	.85	.86	.87	.88	–	.89	.90	.91	.92	.93
PAL/PAW	1.70-2.05	2.06-2.41	2.42-2.77	2.78-3.13	3.14-3.49	3.50-3.85	3.86-4.21	4.22-4.57	4.58-4.93	4.94-5.29	5.30-5.65	5.66-6.01	6.02-6.37	6.38-6.73	6.74-7.09	7.10-7.45	7.46-7.81	7.82-8.17	8.18-8.53	8.54-8.89	8.90-9.25
No. mandibular fan bristles	8,9	10	11	12	13,14	15	16	17	18,19	20	21	22	23,24	25	26	27	28,29	30	31	32	33,34
No. anal fan setae	40	39	38	37	36	–	35	34	33	32	31	30	29	28	27	–	26	25	24	23	22

in all characters except LB/AL and postantennal filament length.

Saether (1970: 21) recognized number of mandibular fan bristles (23-32), LB/SB (1.8 – 2.3) and LB/AL (0.70 – 0.79) as diagnostic for *Chaoborus brunskilli* fourth instar larvae. However, it is clear from the distribution of these characters of larvae of *Chaoborus trivittatus* (Fig. 34A-C) that these characters do not exhibit any bimodality suggestive of another species, and cannot be used to distinguish the larvae placed in *Chaoborus brunskilli* as members of a separate taxon.

Because some species of *Chaoborus* exhibit a limited range of number of mandibular fan bristles Saether (1970: 18) argued that 'At least it seems very unlikely that a variation of 11–32 setae, the total variation within *Schadanophasma* (*sic*), may be accounted for by the presence of only one or two species'. I can see no justification for such an argument. Determination of a large range of variation of a character, such as the number of mandibular fan bristles of *Chaoborus trivittatus* reported here, is not a valid criterion for suspecting the presence of more than one species.

Variation of characters of pupae

Pupal material was identified on the basis of reared material, of association with known larvae, of geographical distribution of the species or, observations of pharate adult characters.

The most detailed, recent description of pupae of all species of *Schadonophasma* has been provided by Saether (1970). All material was correctly identified with the exception of pupae of *Chaoborus brunskilli* (=*Chaoborus trivittatus*). The pupa from Stanford, California was not reexamined but the locality from which it was collected and its association with larvae of *Chaoborus trivittatus* shows clearly that this specimen was correctly identified.

Saether (1970), however, did not take into account the marked sex-association variation. His description of *Chaoborus cooki* pupae included four males, of *Chaoborus brunskilli* (=*Chaoborus trivittatus*) one male, and of *Chaoborus nyblaei* two males and ten females. The sex of the pupa of *Chaoborus trivittatus* is not known, but as Saether (1970) recorded genital sac length only for male pupae, and did not do so for this specimen, suggests that it was a female.

Descriptive statistics for both sexes of each species for most characters described below are given in the species descriptions and comparison of that data shows only those characters presented in the keys to be useful for species determination.

Because of the small size of individual samples, to estimate sex associated variation of *Chaoborus trivittatus* and *Chaoborus cooki* pupae I compared all males with all females within each species. Compared material of *Chaoborus nyblaei* was from a single locality. Seven characters were studied: abdomen length; length, width and length/width of respiratory horns; .and length, width and width/length of abdominal segment seven. The shape and size of the genital lobes differs markedly between male and female *Chaoborus* pupae (Fig. 2C,D; Deonier, 1943: fig. 1,2). In addition, female pupae are slightly darker in overall coloration than males collected from a single locality.

Five characters were sex associated in pupae of *Chaoborus trivittatus*: length and width of respiratory horns; length and width of abdominal segment seven; and total abdominal length. Length, width and length/width of the respiratory horns; and length and width of abdominal segment seven were sex associated for pupae of *Chaoborus cooki*; for pupae of *Chaoborus nyblaei* length and width of respiratory horns; length, width and width/length of abdominal segment seven; and total abdominal length were sex-associated.

It is reasonable to assume that length and width measurements are sex-associated because of a difference in overall size of male and female pupae. Total abdominal length is sex-associated in pupae of *Chaoborus trivittatus* but not in those of *Chaoborus cooki*. This probably reflects stage of development of eggs, which may distend the abdomen and are more developed in older female pupae of *Chaoborus* *trivittatus* than in *Chaoborus cooki*. Because this character is sex-associated for pupae of *Chaoborus nyblaei* this suggests that ovaries of this species develop in a similar fashion to *Chaoborus trivittatus*.

Saether (1970: 18) noted that width/length of abdominal segment VII (erroneously stated as VIII) is 1.4 for *Chaoborus trivittatus*, 1.5 for *Chaoborus brunskilli* (=*Chaoborus trivittatus*), 1.6 for *Chaoborus cooki*, and 1.7–1.9 for *Chaoborus nyblaei* pupae. Examination of Tables 4, 5, 13, 14, 20 and 21 shows extensive overlap of range of this character between males or females of each species.

Coloration differences noted by Saether (1970) were unreliable when more material was examined. There is little doubt that ethanol preserved specimens lose at least some of their color with time. In addition, Saether (1967) has shown that coloration of the anal paddle ribs varies extensively within pupae of *Chaoborus flavicans*. However, his results may be biased through use of specimens treated with KOH.

Differences of the angle of the abdomen in relation to the longitudinal axis of the body between pupae of *Chaoborus trivittatus* and *Chaoborus cooki* (Fig. 5A,B) were observed from most of the samples as they were collected and/or reared in the laboratory, from localities in Alberta during the course of this study. The character was consistent for identification of pupae examined.

Differences in pupal ovarian development of *Chaoborus trivittatus* and *Chaoborus cooki* were apparent (see key to female pupae) and this trait is also expressed in the stage of ovarian development in teneral female adults (see below). In live female pupae of *Chaoborus trivittatus* at least 48 hours old (at 20 C) ovaries are macroscopically apparent as white elongate organs in the abdomen (see Parma, 1971b: 40). These are not apparent in female pupae of *Chaoborus cooki*.

Variation of characters of male adults

Saether (1970) noted two characters of diagnostic value for determination of adult males to species: shape of penis valves and X/Y wing ratio. These two characters were studied in detail. Other differences between males of the three species of *Schadonophasma* are available by comparison of the descriptions (Table 2, 11). Characters differing significantly between male adults of *Chaoborus trivittatus* and *Chaoborus cooki* are Rsa length, all leg measurements, gonocoxite and gonostylus length, Y/X, number of tergite IX setae and penis valve length.

Differences in coloration of adults of *Chaoborus trivittatus* and *Chaoborus cooki* (see descriptions) may in part be ecophenotypic. Bradshaw (1973: 1256) mentions that male adult *Chaoborus americanus* are a darker color when reared at temperatures below 15 C, and this may also have an effect on color variation of adult *Schadonophasma* (also see Rapoport, 1969; Vernberg, 1962).

Range of variation of Y/X of male adults of *Chaoborus trivittatus* (Table 2) and *Chaoborus cooki* (Table 11), although significantly different, exhibits extensive overlap. Range of variation of Y/X of *Chaoborus nyblaei* male adults (see description) is within the range of Y/X of both *Chaoborus trivittatus* and *Chaoborus cooki*.

I studied geographical variation of this character for *Chaoborus trivittatus* and *Chaoborus cooki* but, possibly because of the small number of samples, recognized no patterns. However, it is clear that the ratio, at least for *Chaoborus trivittatus*, varies markedly in a relatively small geographical area. A sample from 16 km west of Jasper, Alberta, (n=38, range = 1.35 –2.18, mean = 1.705, 1.5SD = 0.310, 2SE = 0.067) differed significantly from a sample from 2.4 km west of Edmonton, Alberta, (n=40, range = 1.54–2.42, mean = 1.915, 1.5SD = 0.309, 2SE = 0.065).

Saether (1970) distinguished four types of penis valves characteristic of each of the four species he described. Apparently because of the similarity of penis valves of the male from Baffin Island with those of the specimen from Finland, he identified the former specimen as *Chaoborus nyblaei*. In addition, differences in the penis valves of the male from Lk. 241, Kenora, Ontario supported his recognition of the larvae from that area as indicative of the new species of *Chaoborus brunskilli*. However, these penis valves were not examined in a standard orientation. Reorientation of the penis valves of the specimens from Baffin Island and Lk. 241, Kenora resulted in forms indistinguishable from those typical of *Chaoborus trivittatus*. The dark, very short tips of the penis valves of *Chaoborus nyblaei*, as drawn by Saether (1970: fig. 7A,B), are actually the claws pointing downward. Outlines of a single penis valve of a male *Chaoborus trivittatus* (Fig. 12A-E), drawn from different aspects, shows that one orientation (Fig. 12D) is very similar to that thought by Saether (1970: fig. 7A,B) to be typical of *Chaoborus nyblaei*, and another (Fig. 12B) typical of *Chaoborus brunskilli* (Saether, 1970: fig. 7C). The effect of changed orientations of a single penis valve of *Chaoborus cooki* (Fig. 12F-J) shows the importance of examining the penis valves from different aspects. For example, one orientation of the valve of a male of *Chaoborus cooki* (Fig. 12F), is extremely similar to one orientation of the penis valve of *Chaoborus trivittatus* (Fig. 12A). For the purposes of this study only Figures 12E and 12H show useful orientations. Of the material I examined, no penis valves of *Chaoborus trivittatus* looked like those of *Chaoborus cooki* when in this orientation.

The two types of penis valves recognized by Saether (1970: 27) to be typical of two forms of *Chaoborus americanus* are also a result of examination of material from different aspects (pers. obs.).

Because of the seemingly impossible prospects of completely standard orientation of penis valves, even though all specimens were drawn with the penis valve head in a horizontal plane, it is not known to what degree this affected the drawings of intraspecific and interspecific variation of penis valves of *Chaoborus trivittatus* (Fig. 10A-O) and *Chaoborus cooki* (Fig. 11A-N). Although a comparison between amount of intrapopulational and interpopulational variation of penis valves of either *Chaoborus trivittatus* or *Chaoborus cooki* do not show very marked differences in these figures, there is actually more interpopulational than intrapopulational variation.

The penis valves of male *Chaoborus nyblaei* are illustrated in Fig. 11 O,P.

Length of penis valves differed significantly between *Chaoborus trivittatus* and *Chaoborus cooki*, even though the entire range of variation of that of *Chaoborus cooki* was contained in the range of variation of length of penis valves of *Chaoborus trivittatus*. Length of penis valves of *Chaoborus nyblaei* was within the range of both *Chaoborus cooki* and *Chaoborus trivittatus*.

The only apparent pattern of geographical variation of the length of penis valves was found in specimens of *Chaoborus trivittatus* from along the west coast of North America (Table 44). Although this linear increase in mean values cannot be confidently interpreted on its own, geographical variation in five larval characters in this region suggests that the pattern is significant (see section on geographical variation of fourth instar larvae).

Number of setae on one side of tergite IX was studied only because it was convenient to do so when examining penis valves. Saether (1970) has already shown a large amount of overlap of variation of this character between *Chaoborus trivittatus* and *Chaoborus cooki*, although analysis here does indicate them to be significantly different. I could detect no patterns of geographical variation of this character for either species.

Variation of characters of female adults

The only diagnostic feature of females given by Saether (1970) was Y/X wing ratio of *Chaoborus trivittatus* and *Chaoborus cooki*. Female adults were not available for *Chaoborus nyblaei*.

I identified females on the basis of their temporal and geographical association with males, geographical distribution or type of ovarian development and egg type. I studied only variation of Y/X wing ratio in detail. Other differences between females of these species are in the descriptions.

Table 44. Variation of penis valve length (in μm) of male adult *Chaoborus trivittatus*.
Sample 1 from Pacific Grove, Stanford, Oakland and Mad River Beach, California. Sample 2 from Hoodsport, Port Madison and Bremerton, Washington, and Kaslo, British Columbia. Sample 3 from Prince Rupert and Terrace, British Columbia.

Sample	N	Range	Mean	1.5SD	2SE
1	9	145–191	167.6	20.6	9.2
2	14	162–209	180.6	17.7	6.3
3	8	168–197	190.0	14.5	6.8

Characters which differed significantly between *Chaoborus trivittatus* and *Chaoborus cooki* were length of penultimate antennal article, prementum length, HW/Pl, number of anepisternal setae, all leg measurements, and seminal capsule diameter. Number of setae on the comb of the third tarsomere of either midleg or hindleg has not been previously recorded but was found to differ significantly between the two species.

Although means of the ratio Y/X of female adult *Chaoborus trivittatus* and *Chaoborus cooki* differ significantly, ranges overlap extensive (Table 3, 12). Mean values did not exhibit geographical patterns of variation. As with males, this character of females can vary markedly in a relatively short distance. A sample from 16 km west of Jasper, Alberta, (n=10, range = 2.03–2.86, mean = 2.414, 1.5SD = 0.425, 2SE = 0.179) differed significantly from a sample 2.4 km west of Edmonton, Alberta, (n=28, range = 1.57–3.22, mean = 2.267, 1.5SD = 0.538, 2SE = 0.136). However, a sample from eight localities in California (n=19, range = 1.19–2.95, mean = 1.919, 1.5SD = 0.653, 2SE = 0.200) did not differ significantly from a sample from Terrace and Atlin, British Columbia and Whitehorse, Yukon, (n=15, range = 1.46–2.56, mean = 2.011, 1.5SD = 0.444, 2SE = 0.153).

Females of *Chaoborus trivittatus* and *Chaoborus cooki* differ in ovarial development. Female *Chaoborus trivittatus* less than one hour old, reared from fourth instar larvae collected 2.4 km west of Edmonton, Alberta, had abdomens full of eggs . Ovaries of some females extended into the thorax. A ratio of distance of the anterior tip of the longest ovary from the end of the abdomen/abdominal length was 0.71–1.11 (mean = 0.967). The ovaries together contained 251–329 (mean = 279) eggs which, at this stage, were each at least 348 μm long. Fedorenko (1975c: 3102) recorded 161 ± 7.4 SE eggs per female pupae from Eunice Lake, British Columbia.

Females of *Chaoborus cooki* less than 12 hours old, collected as early instars 1.6 km south of Jasper, or as fourth instar larvae, 1.4 km west of George Lake, Alberta, had much smaller ovaries with a ratio of the distance of the anterior tip of the longest ovary from the tip of the abdomen/abdominal length of 0.32–0.62 (mean = 0.444). Total number of eggs present was 74–95 (mean = 86). Each egg in a teneral female is no more than 120 μm long. Teneral females of these two species can therefore be distinguished from one another by size of ovaries. A nulliparous female can be identified by number of eggs present. If an individual with at least some eggs present is suspected of being parous, the eggs are developed enough to distinguish the type. A thick exochorion is typical of *Chaoborus cooki* (Fig. 9C) and a thin exochorion of *Chaoborus trivittatus* eggs (Fig. 9A).

I had available only two females of *Chaoborus nyblaei* which still had eggs in their abdomens. One was the lectotype and its abdomen contained eggs with a thick exochorion (Fig. 9B). I could not count the number of eggs present. The other female, from Abisko, Sweden, had the same type of egg and its abdomen contained 58 eggs. Implications of differences in egg type are discussed below in the section on development of eggs.

Descriptions of populations *incertae sedis*

Three samples of larvae and one of pupae could not be identified with certainty. The three larval samples exhibited compound character index values (see p. 174) intermediate between those of *Chaoborus trivittatus* and *Chaoborus cooki*. Although the two samples from Mechant and Gallienne Lakes, Quebec are here described separately, they possibly belong to the same reproductive population, considering the close proximity of the lakes. Pope *et al.* (1973) recognized samples from these two lakes as members of a new species or subspecies of *Schadonophasma* but did not describe them.

Several interpretations of these samples seem equally reasonable. Individuals may belong to one or more new species or they may be hybrids between *Chaoborus trivittatus* and *Chaoborus cooki*, although number of specimens would seem too large to be the product of hybridization (see section on mating experiments). Also, specimens may be members of *Chaoborus cooki*. Data from the sample from Russell Lake, Alberta, shape of prelabral appendages of all larvae of all samples, and shape of penis valves of pupae from Gallienne Lake, Quebec, suggests the likelihood of this (see below for details). None of the specimens in the analysis of *Chaoborus cooki* came from lakes. *Chaoborus cooki* may possibly invade this habitat and resultant individuals may therefore be phenotypically different from individuals of *Chaoborus cooki* described in this study. Sikorowa (1973) has shown that habitat influences variation of characters of larvae of *Chaoborus flavicans*. Examination of adults, study of geographical variation once more material is available, especially from eastern Canada, study of the life cycle, and developmental studies could be used to test this possibility.

Sample from Russell Lake, Alberta. – All specimens collected (1-VIII-1969) were fourth instar larvae. The population from which this sample was taken is within the geographical range of both *Chaoborus trivittatus* and *Chaoborus cooki*. Coloration is as other members of the subgenus. Measurements and proportions are given in Table 45.

Table 45. Descriptive statistics for fourth instar larvae of *Schadonophasma* from Russell Lake, Alberta. Measurements in μm.

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	13	1884–2060	1975	94	35
Antennal length	12	835–947	913	52	20
LB/SB	10	1.71–2.12	1.91	0.18	0.07
LB/AL	12	0.74–0.91	0.800	0.075	0.029
AS/AL	12	0.79–0.90	0.847	0.053	0.020
Postantennal filament length	13	761–882	829	55	21
PAL/PAW	13	1.76–2.44	2.09	0.29	0.11
Number mandibular fan bristles	13	15–19	17.5	1.8	0.7
Number anal fan setae	13	27–30	28.9	1.6	0.6

Variation of most characters gave no clues as to whether this sample might be composed of larvae of either *Chaoborus trivittatus* or *Chaoborus cooki*, or of a third undescribed species, because the range of these characters was within the range of variation of both *Chaoborus trivittatus* and *Chaoborus cooki*. Low PAL/PAW values would suggest the sample is conspecific with *Chaoborus cooki*. However, some specimens exhibit LB/AL values, number of mandibular fan bristles, and number of anal fan setae which are beyond the range of *Chaoborus cooki* and into the range of variation of *Chaoborus trivittatus*.

All characters were examined in relation to clinal variation of these characters of both *Chaoborus trivittatus* and *Chaoborus cooki* for clues of conspecificity. Only mean number of mandibular fan bristles may possibly be explained by clinal variation of this character of *Chaoborus cooki* fourth instar larvae.

All material deposited with ABOr.

Sample from Mechant Lake, Quebec. – All specimens were collected (14-VII-1975) as fourth instar larvae. Although Pope *et al.* (1973) report that a population represented by this sample coexisted with larvae of *Chaoborus trivittatus*, I did not examine any material of *Chaoborus trivittatus* which would have given better clues concerning possibilities of the two being conspecific. However the recognition of two forms in a single lake does not negate possibilities of them being conspecific. Fedorenko and Swift (1972) described two forms of *Chaoborus trivittatus* which differed in size and color but merely represented two overlapping generations.

Larvae are darker than any other *Chaoborus* larvae I have examined. Head capsules were notably darker. In particular, dorsum of head capsule, area around the anterior tentorial pits and dorsal from each pit to dorsum of head capsule, posterior edge of head capsule including ocular-antennal segment, ventral edge of head capsule between antennae and labrum, antennae, maxillary palpus and seta, and anal fan setae were all more darkly pigmented. All thoracic and abdominal segments were infuscated dorsally. Measurements and proportions are given in Table 46.

Some individuals have AS/AL and PAL/PAW values within the range of *Chaoborus cooki* and beyond the range of *Chaoborus trivittatus.* Conversely, some individuals exhibited head capsule length, antennal length, LB/SB, LB/AL, and number of mandibular fan bristles within the range of variation of those characters of *Chaoborus trivittatus* and beyond the range of those of *Chaoborus cooki.*

All material deposited with ABOr.

Sample from Gallienne Lake, Quebec. – All specimens were collected (13-VIII-1971) as fourth instar larvae. Color of larvae was similar to that of larvae from Mechant Lake, Quebec. For measurements and porportions see Table 47.

Some individuals exhibited LB/SB, LB/AL ratios and number of anal fan setae beyond the range of variation of these characters for *Chaoborus cooki* but within the range of those of *Chaoborus trivittatus.* Prelabral appendages were typical of those of *Chaoborus cooki* larvae. Head capsule, antennal and postantennal filament length, and number of mandibular fan bristles of this sample differed significantly from those of larvae from Mechant Lake. However, this might be explained by geographical variation or differences in habitat. No ratios significantly differed between the two samples.

Pupae were darker than any other *Chaoborus* material examined. Measurements and proportions of male pupae are given in Table 48, and of female pupae in Table 49. Nearly all measurements of both male and female pupae were within, or less than, the range of variation of *Chaoborus trivittatus.* Only the WS/LS of male pupae was within the range of WS/LS of both *Chaoborus trivittatus* and *Chaoborus cooki.*

Penis valves were developed in three male pupae but, because these could not be removed to study from different orientations without destroying the rest of the specimen, they were difficult to interpret. Penis valves of one of these individuals were most similar to those of *Chaoborus cooki* adults. However, length of penis valves ranged from 156.6–162.4 μm. Because material had been previously cleared I could not determine the degree of ovarian development of two pharate female adults. One specimen had well developed seminal capsules with a diameter of 50.0 μm.

All material deposited with OASa.

Table 46. Descriptive statistics for fourth instar larvae of *Schadonophasma* from Mechant Lake, Quebec. Measurements in μm.

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	11	1617–1782	1682	71	29
Antennal length	11	731–777	757	24	10
LB/SB	11	1.71–2.15	1.99	0.13	0.05
LB/AL	11	0.79–0.91	0.843	0.046	0.019
AS/AL	11	0.77–0.89	0.841	0.054	0.022
Postantennal filament length	11	637–708	687	31	12
PAL/PAW	11	2.50–3.08	2.82	0.28	0.11
Number mandibular fan bristles	11	12–15	13.2	1.5	0.6
Number anal fan setae	11	26–29	27.5	1.6	0.6

Table 47. Descriptive statistics for fourth instar larvae of *Schadonophasma* from Gallienne Lake, Quebec. Measurements in μm.

Character	N	Range	Mean	1.5SD	2SE
Head capsule length	19	1876–2183	2029	142	42
Antennal length	19	824–974	908	66	20
LB/SB	19	1.85–2.27	2.08	0.21	0.06
LB/AL	19	0.75–0.86	0.810	0.052	0.016
AS/AL	19	0.75–0.91	0.843	0.059	0.018
Postantennal filament length	19	743–861	809	51	12
PAL/PAW	19	1.71–4.00	2.67	0.68	0.21
Number mandibular fan bristles	20	13–17	15.4	1.5	0.4
Number anal fan setae	20	25–29	27.2	1.9	0.6

Table 48. Descriptive statistics for male pupae of *Schadonophasma* from Galliene Lake, Quebec. Measurements in μm unless stated otherwise.

Character	N	Range	Mean	1.5SD	2SE
Total abdominal length (mm)	4	5.5–5.9	5.72	–	–
Respiratory horn length (mm)	4	1.06–1.23	1.112	–	–
Respiratory horn width (mm)	4	0.30–0.32	0.307	–	–
Abdominal segment VII length	9	767–885	821	62	28
Abdominal segment VII width	4	1133–1263	1192	–	–
WS/LS	4	1.45–1.49	1.48	–	–

Table 49. Descriptive statistics for female pupae of *Schadonophasma* from Gallienne Lake, Quebec. Measurements in μm unless stated otherwise.

Character	N	Range	Mean	1.5SD	2SE
Total abdominal length (mm)	8	4.3–5.6	4.81	0.61	0.29
Respiratory horn length (mm)	3	1.07–1.17	1.117	–	–
Respiratory horn width (mm)	4	0.27–0.31	0.289	–	–
Abdominal segment VII length	9	814–885	852	40	18
Abdominal segment VII width	8	979–1227	1136	116	55
WS/LS	8	1.20–1.42	1.32	0.098	0.046

BIONOMICS

Studies of life histories, developmental characteristics, and behavior give important information on questions of conspecificity, and suggest how species closely related retain their reproductive unity, such studies are also important in interpretation of characters used to infer the evolutionary history of such species and the events pertaining thereto. In this section I present observations made on *Chaoborus trivittatus* and *Chaoborus cooki* in Alberta. These are used to infer some probable bionomic features of *Chaoborus nyblaei* in Fennoscandia. For the following analysis observations were made of events which I had the opportunity and time to deal with and which I believed to be most informative to elucidate species differences and their evolution. A more complete, general account of such bionomic information has been presented by Parma (1971b).

Life cycle

All temperate *Chaoborus* species previously studied exhibit a life cycle in which fourth instar larvae overwinter, pupate in spring, emerge as adults which lay eggs and develop to fourth instar larvae by winter (Balvay, 1977d; Bradshaw, 1973; Fedorenko and Swift, 1972; Parma, 1971b; Sikorowa, 1973). In multivoltine populations these fourth instar larvae result in another adult emergence and subsequent larvae but, regardless of number of generations per year, every temperate species studied overwinters as fourth instar larvae. For this reason, immatures of these species are usually present only in permanent waters. Studies of tropical species (Corbet, 1958; Lewis, 1975; MacDonald, 1956; McGowan, 1974, 1975; Tjønneland, 1958; Verbeke, 1957) suggest that these are also restricted to permanent waters. Records of *Chaoborus* larvae in temporary waters in the tropics (Belkin and Heinemann, 1975, 1976; Heinemann and Belkin, 1977a, 1977b; Panday, 1975) can be explained as incidental as McGowan (1974: 498) observed adult females of *Chaoborus anomalus* and *Chaoborus ceratopogones* (Theobald), species restricted to permanent waters in Africa, laying eggs in dishes of water in which the larvae undoubtedly would not survive.

Records of larvae of temperate *Chaoborus* species from temporary waters (e.g. Anderson and Raasveldt, 1974: 16) are likely from either a single generation of a multivoltine population which overwintered elsewhere in permanent waters, a population which eventually became extinct (see p. 186), or are larvae which were transferred from over-flowing ponds upstream on a river to downstream inundation pools. Merely the presence of *Chaoborus* larvae in an aquatic habitat is not sufficient evidence to suppose survival of the population in this habitat. Records of *Chaoborus americanus* and *Chaoborus flavicans* fourth instar larvae from the Red Deer river, near Innisfail, Alberta, when the river still had ice on its edge, showed all specimens with empty guts, suggestive of their inability to successfully survive to adulthood in this habitat. These larvae probably were washed into this permanent river from ponds further upstream. Records of *Chaoborus* larvae from the Hudson River, New York (Beck *et al.*, 1975) are undoubtedly larvae from impoundments further upstream. Peus's (1934) often cited record of *Chaoborus flavicans* from inundation pools along rivers in Germany and Reisen's (1973) observation of a single specimen of *Chaoborus punctipennis* from an inundation pool near a river in Oklahoma are therefore probably from larvae washed downstream from flooded ponds. Retreat of an over-flowing river in inundation areas can leave intact a population of *Chaoborus* larvae (Heinemann and Belkin, 1977a: 272, Roback, 1966; see p. 185).

Chaoborus trivittatus. Fedorenko and Swift (1972) found a population of *Chaoborus trivittatus* in an oligotrophic lake in southwestern British Columbia to be composed of two overlapping generations. Fourth instar larvae overwintered for two consecutive winters before pupating. Although adults emerged every spring, larvae which had overwintered only one winter did not pupate. Continual presence of fourth instar larvae throughout and after the pupal emergence period is therefore indicative of this two year life cycle.

I studied the life cycle of *Chaoborus trivittatus* in a pond 2.4 km west of Edmonton which measured approximately 18 by 85 meters, had a maximum depth of about two to three meters, and was densely shaded by mature stands of *Populus balsamifera* and *Picea mariana.* Sampling during 1975 (Table 50) produced a few fourth instar larvae on May 13, all of which pupated by May 26. These data indicate a univoltine population of *Chaoborus trivittatus.* Changes in pupal and pupal exuvial sex ratios is explained by earlier pupation of male larvae (Table 51) and less time for development of male pupae (p. 193). Emergence of adults was restricted to later in May. Eggs hatched in three to four days under laboratory conditions.

Table 50. Number of *Chaoborus trivittatus* immatures collected 2.4 km west of Edmonton, Alberta.

	LARVAL INSTARS				PUPAE		PUPAL EXUVIAE	
DATE	1	2	3	4	Male	Female	Male	Female
26–IV–1975	–	–	–	234	–	–	–	–
8–V–1975	–	–	–	5	218	156	–	–
13–V–1975	–	–	–	2	186	274	195	134
26–V–1975	106	11	40	–	–	3	–	1
12–VI–1975	25	22	144	–	–	–	–	–
13–VIII–1975	–	–	–	72	–	–	–	–

Table 51. Numbers of pupae resulting from 45 individually reared fourth instar larvae of *Chaoborus trivittatus* collected 2.4 km west of Edmonton, Alberta, 25-IV-1975.

Date	Male	Female
28–IV	18	4
29–IV	5	14
30–IV	–	3
4–V	–	1
Total:	23	22

Overwintering of fourth instar larvae as a feature of *Chaoborus trivittatus* is reflected in the range of collection dates of material examined (Fig. 25B). Gaps in the record undoubtedly reflect lack of collected material (Fedorenko and Swift, 1972; Main, 1953). James and Smith (1958) also observed overwintering of some *Chaoborus trivittatus* larvae (as *Chaoborus nyblaei*).

Parma (1971b) has discussed how univoltine or multivoltine *Chaoborus* populations are a result of environmental factors and vary in response to type of habitat and geographical area. These observations explain the differences between the bivoltine life cycle of *Chaoborus trivittatus* described by Fedorenko and Swift (1972) and the univoltine life cycle described here. In addition, temporal bimodality of records of field collected adults in southern Ontario and Quebec and northeastern United States (Table 52) suggest that some populations of the species are multivoltine in this region (see Balvay, 1977c; Hirvenoja, 1960, 1965; Parma, 1971b).

Table 52. Records of field collected adult *Chaoborus trivittatus* from southern Ontario and Quebec and northeastern United States. Roman numerals represent months and Arabic numerals are: 1=Days 1–10, 2=Days 11–20; 3=Days 21–30(31).

	1–IV	2–IV	3–IV	1–V	2–V	3–V	1–VI	2–VI	3–VI	1–VII	2–VII	3–VII	1–VIII	2–VIII	3–VIII	1–IX	2–IX	3–IX
North Burgess Twp., Ontario					x													
Black Lake., Ontario			x															
Cordova Mines, Ontario																x		
Lac de Jean Venne, P.Q.		x		x	x													
Old Chelsea, P.Q.																	x	
Worcester, Massachusetts			x															
Hampton, New Hampshire			x					x										
Elizabethtown, New York							x	x							x			
Bear Mountain, New York																		x

Chaoborus cooki. The only previous allusion to the life cycle of *Chaoborus cooki* has been by James and Smith (1958) who mention that some of the populations of *Chaoborus nyblaei* (probably = *Chaoborus trivittatus* and *Chaoborus cooki*) at Churchill, Manitoba, overwintered as eggs.

The life cycle of *Chaoborus cooki* was studied at three locations. A pond 1.6 km south of Jasper measured 10 by 41 meters with a maximum depth of 0.9 m during most of its existence. Shading on the north, south and west sides of the pond was provided by *Salix* sp. and *Picea mariana*. The pond was located about 40 m from the south bank of the Miette River and, although it did not initially receive its water from the river, I observed overflow of its banks and flooding of the pond to about six times its normal surface area on two occasions, on 19-VI-1976 and 30-VI-1976. Retreat of the river from this inundation zone seemed to leave most of the population of *Chaoborus cooki* intact. However, I did collect several larvae stranded in isolated pools which drained within one day after retreat of the river. This pond was dry by October 8, 1976.

A pond 32 km west of Edson measured 11 by 29 meters, with a maximum depth of 0.7 m during most of its existence and was well shaded by dense brush and trees of *Picea mariana* and *Populus tremuloides*. The pond was dry by October 8, 1976.

A third pond, 1.4 km west of George Lake, measured 15 by 19 meters and had a maximum depth of 0.9 m during most of its existence. Although surrounded by dense brush and trees of *Picea mariana* and *Populus tremuloides* on its north, east and west sides the pond was often in direct sunlight. However, larvae were almost always located in the shade of numerous *Typha* sp. The pond dried up on two occasions, 23-VII-1976 and 30-X-1976.

Tables 53, 54 and 55 give numbers of animals collected from these three sites. A common type of life cycle is apparent. There is a progression within one growing season, of first through fourth larval instars, pupation, and, observed at 1.4 km west of George Lake and 1.6 km south of Jasper, emergence of adults. Lack of records of larvae after the pupal period until the next spring suggests that *Chaoborus cooki* overwinters in these temporary aquatic habitats as eggs. This conclusion is supported by observed diapause of *Chaoborus cooki* eggs in the laboratory and their resistance to desiccation (p. 191). However, in spite of this adaptation to temporary waters, *Chaoborus cooki* larvae may occasionally live in permanent ponds (e.g. 2.4 km west of Edmonton).

This univoltine life cycle, in which the eggs overwinter, is reflected in the restricted temporal distribution of records of fourth instar larvae of *Chaoborus cooki* (Fig. 25B).

It is clear that this species circumvents the problems presented by temporary habitats to other *Chaoborus* species. Larvae of *Chaoborus americanus* were collected late in the season from each of the three sites studied (Tables 53, 54, 55) and those remaining undoubtedly died when the ponds became dry. Both live and dead *Chaoborus trivittatus* larvae and a live *Chaoborus americanus* fourth instar larva were taken off wet mud at the location 1.4 km west of George Lake on 18-IX-1976.

The unique life cycle of *Chaoborus cooki* in temporary ponds allows this species to avoid competition with other sympatric *Chaoborus* species, except when some of these occasionally inhabit the same temporary ponds. Even so, these would be as younger instars than those of *Chaoborus cooki.*

Chaoborus nyblaei. There is no direct evidence of the type of life cycle of *Chaoborus nyblaei.* However, a thick exochorion, similar to that of *Chaoborus cooki* would suggest that the egg is similarly adapted to resist desiccation and that this species also overwinters as eggs. *Chaoborus nyblaei* larvae have been collected from both a large permanent pond, and a small pool a few meters in diameter, in northern Fennoscandia (Hirvenoja, 1961).

Low number of eggs per female would support the conclusion that *Chaoborus nyblaei* immatures inhabit temporary ponds. Collection of adults only in the later part of July agrees with this interpretation of the type of life cycle.

Table 53. Numbers of *Chaoborus cooki* immatures collected 1.6 km south of Jasper, Alberta. ## symbolizes dry conditions.

	LARVAL INSTARS				PUPAE		PUPAL EXUVIAE	
DATE	1	2	3	4	Male	Female	Male	Female
20–V–1975	–	3	27	–	–	–	–	–
4–VI–1975	–	–	2	34	–	–	–	–
17–VI–1975	–	–	1	33	20	1	–	–
*13–VII –1975	–	–	–	–	–	–	–	1
25–IV–1976	93	7	–	–	–	–	–	–
18–V–1976	–	10	48	–	–	–	–	–
31–V–1976	–	–	53	20	–	–	–	–
13–VI–1976	–	–	2	18	–	–	–	–
30–VI–1976	–	–	–	14	5	–	–	–
*9–IX–1976	–	–	–	–	–	–	–	–
8–X–1976	########	########	########	########	########	########	########	########
28–IV–1977	91	32	–	–	–	–	–	–
12–VII–1977	–	–	–	31	7	3	–	–

**Chaoborus americanus* larvae also present.

Table 54. Numbers of *Chaoborus cooki* immatures collected 32 km west of Edson, Alberta. # symbolizes dry conditions.

DATE	LARVAL INSTARS 1	2	3	4	PUPAE Male	Female	PUPAL EXUVIAE Male	Female
3–VI–1975	1	–	26	31	1	–	–	–
17–VI–1975	–	–	–	4	1	–	–	–
27–IV–1976	8	11	–	–	–	–	–	–
18–V–1976	–	2	16	7	–	–	–	–
29–V–1976	–	1	5	3	1	3	–	–
9–IX–1976	–	–	–	–	–	–	–	–
8–X–1976	################################							
11–XI–1976	################################							
1–I–1977	################################							
27–IV–1977	–	1	–	–	–	–	–	–
*8–VII–1977	–	–	–	–	–	–	–	–
*29–VII–1977	–	–	–	–	–	–	–	–

**Chaoborus americanus* larvae also present.

Table 55. Numbers of *Chaoborus cooki* immatures collected 1.4 km west of George Lake, Alberta. # symbolizes dry conditions.

DATE	LARVAL INSTARS 1	2	3	4	PUPAE Male	Female	PUPAL EXUVIAE Male	Female
12–V–1975	–	–	18	20	–	–	–	–
24–IV–1976	–	12	8	–	–	–	–	–
6–V–1976	–	1	19	29	–	–	–	–
13–V–1976	–	1	2	57	1	–	–	–
25–V–1976	–	–	–	–	6	8	–	–
23–VII–1976	################################							
*18–IX–1976	–	–	–	–	–	–	–	–
30–X–1976	################################							

*Seven *Chaoborus trivittatus* and one *Chaoborus americanus* fourth instar larvae collected.

Development and behavior

Adults. – Parma (1971b: 45) described the emergence of adult *Chaoborus flavicans* and *Chaoborus crystallinus*. Most observations of *Chaoborus trivittatus* and *Chaoborus cooki* agree with that description, but the following are additions or differences. Wings are released from the exuviae after the antennae but before the legs become free. Each of the forelegs and midlegs are released one after the other, but the hindlegs are pulled out together. While the hindlegs are being freed, the wings are folded over the abdomen. Emergence, from the time of the dorsal split to complete release from the exuviae is, under laboratory conditions, 44–95 seconds (n=28) for male and 47–92 seconds (n=25) for female *Chaoborus trivittatus* and 39–70 seconds (n=30) for male and 38–51 seconds (n=13) for female

Chaoborus cooki. All adult *Chaoborus trivittatus* emergences in the laboratory occurred during daylight conditions, and those of *Chaoborus cooki* only took place during night. Myconial fluid was released in 5–21 drops. Males and females flew readily after release of at least some of the myconial fluid but, while females flew only a short distance before landing again, males would fly much further. At 20 C both *Chaoborus trivittatus* and *Chaoborus cooki* males completed rotation of their genitalia within four hours.

Males of both species possess at least some mature sperm upon emergence. Differences in ovarial development between teneral females of *Chaoborus trivittatus* and *Chaoborus cooki* are described elsewhere (p. 179).

Chaoboridae are commonly designated as non-biting mosquitoes. However, Cook (1956:6) states that "Chaoborinae (=Chaoboridae) have all structures necessary for piercing and for feeding on fluids". Felt (1904), Pucat (1965) and Theobald (1901a: 62) suggested that adult Chaoboridae feed on plants but these claims were unsupported. Martini (1931) also recognized adults to be capable of feeding but gave no actual observations.

Both mammalian and avian blood have been found in the guts of female *Corethrella brakeleyi* (Coquillett) and *Corethrella wirthi* Stone (Williams and Edman, 1968). Miyagi (1974) reported the presence of a blood meal of unknown origin in the gut of a female *Corethrella japonica* Miyagi. Its mandibles and hypopharynx are serrated, as are those of female *Corethrella brakeleyi*, *Corethrella wirthi* and *Corethrella appendiculata* Grabham (Miyagi, 1975). McKeever (1977) has recorded *Corethrella* females feeding on *Hyla* tree frogs and was able to attract adult *Corethrella brakeleyi* to a tape recording of frog calls.

Jenkins and Knight (1950) reported an adult male *Eucorethra underwoodi* probing or feeding at pistillate flowers of willow.

Adult *Mochlonyx cinctipes* (Coquillett) did not feed on proffered prunes, raisins, honey-water, or wild flowers, although imbibition of water was observed in the field (O'Conner, 1959). *Mochlonyx velutinus* (Ruthe) took diluted honey (James, 1957).

Some workers have reported on adult life span of chaoborids (summarized by Borkent 1978a: 162) but most, unfortunately, do not report their experimental conditions.

While collecting adult *Chaoborus trivittatus* 2.4 km west of Edmonton, Alberta, on May 13, 1975, I observed that male and female adults often alighted on the pond surface and applied their mouthparts to the water for about 30 seconds, rested for a short period, and then flew away. Air temperature was 17 C. In addition, two males alighted on the ground and walked with their front legs moving alternately in sweeping motions similar to that described by Downes (1974) for adult chironomids searching for honeydew. At this time of year no aphids were present to provide this source of nutrition. Adults commonly exhibit this searching behavior under laboratory conditions if kept in sealed mason jars for at least 24 hours without water.

These observations led me to suspect that adults drink water and that this may be an important factor in prolonging adult life span, consequently influencing adult dispersal capabilities.

I carried out a feeding experiment to see if adults drink water and to determine if water uptake affects longevity.

Blue excreta from adults in jars supplied with dyed water showed that both males and females imbibe water. Longevity results are shown in Figures 35A,B. These results were compared statistically using a Duncan's Multiple Range test ($p<0.05$) and it was found that: 1) there is no significant difference in longevity between males or females given either clear or dyed water; 2) males which could not drink lived for a significantly shorter period than males which could drink; 3) females which could not drink lived for a significantly shorter period than females with dyed water; and 4) although there was no significant difference between females without access to water and those with clear water, this is explained by the low numbers in each treatment. Comparison of females without access to water to combined results of females with dyed or undyed water available, using a T-test, revealed them to be significantly different at the 98% level.

These results show that *Chaoborus trivittatus* adults can imbibe water and that this significantly increases their life span. Longevity of adults of most other species may have been seriously underestimated.

During the springs of 1974–1977 I made daytime observations of behavior of *Chaoborus trivittatus* adults 2.4 km west of Edmonton, and 16 km west of Jasper, Alberta. Males were more often seen throughout the emergence periods. They formed columnar swarms (n=8) of 1–132 individuals at the periphery of ponds at heights of about 0.3–1.8 m. Females were sedentary on surrounding vegetation, particularly on tree trunks. When disturbed, they flew and were easily seen. However, on May 13, 1975, after 1.5 hours of collecting with an aspirator and aerial net from tree trunks and low vegetation at 2.4 km west of Edmonton, only 32 females were procured. Concurrently, males in swarms were extremely numerous. Similarly, 25 females and 218 males were collected with an aspirator from tree trunks at this locality on May 7, 1977. Female pupae and exuviae, collected May 13, 1975, composed 59.6% (n=460) and 40.7% (n=329) of a sample respectively. The possibility that the over-abundance of males was due to their earlier emergence, as might be suggested from laboratory rearings, is therefore unlikely.

When females made one of their occasional flights through a male swarm, they were invariably seized front to front by a male. The pair interlocked genitalia and fell immediately to the ground or water surface, where they assumed an end to end position. Matings lasted 51–64 seconds (x=58.7, n=5). Nine other matings observed required a similar period of time but were not measured exactly.

These data suggest the following pattern. Most adult males emerge earlier than females and form large swarms at the periphery of the ponds from which they emerged. Females, after emergence and an unknown period of time, fly through this 'barrier' of males and are mated. Because the sex ratio of emerging adults is nearly 1:1 (Table 51), the far greater proportion of male adults at pond peripheries suggests that females are the main dispersing agent of this species. Well developed ovaries at emergence are probably correlated to the stable habitat which this species inhabits and suggests that *Chaoborus trivittatus* female adults cannot disperse as far with their fully developed eggs as can *Chaoborus cooki* female adults (see below).

If a sex ratio of nearly 1:1, and observations of concentrated male swarms at the periphery of water bodies are alone indicative of this type of adult behavior (i.e., females mated at the pond or lake periphery and subsequently dispersing), observations of adults of the species *Chaoborus sensu stricto* suggest that these exhibit similar behavior. Bradshaw (1973) reported males to compose 57% of populations of *Chaoborus americanus*. I have observed large male swarms of this species at the periphery of numerous ponds near Edmonton, Alberta. Males make up 43–45% of *Chaoborus flavicans* populations (Parma, 1971b) and swarms have been observed at a number of localities (Berg, 1937). Parma (1971b) noted the concentration of male *Chaoborus flavicans* at the periphery of the water bodies he studied. Parma (1971b) reported males to comprise 39–60% of *Chaoborus crystallinus* populations and both he and Nielsen and Greve (1950) have observed male swarms of this species. Neither sex ratio or swarming behavior have been reported for *Chaoborus obscuripes* (van der Wulp). These data suggest that at least three of the four species of *Chaoborus sensu stricto* share a common type of adult reproductive behavior and dispersal with *Chaoborus trivittatus*. The significance of this is discussed in the section on zoogeography and speciation.

I have little data on adult behavior of *Chaoborus cooki* in the field. In 1975 and 1976, at the pond 1.4 km west of George Lake, and in 1976, at the pond 1.6 km south of Jasper, Alberta, emergence of adult

Chaoborus cooki was observed only during the night. Although both New Jersey and CDC light traps were present at the edges of the ponds, adults that emerged were not trapped. Upon emergence, adults flew upward out of the field of vision. On the day after each of the nights I observed emergence, I swept, with an aerial net, all surrounding vegetation for a least 100 m in all directions of both ponds, but with no captures. I also visually examined the immediate area and climbed the trees surrounding the ponds but neither collected nor saw any adults.

Timing of laboratory matings of *Chaoborus trivittatus* adults (45–65 seconds, n=6) approximated those observed in the field (see above). This would suggest that timings of matings of *Chaoborus cooki* adults in the laboratory (91–122 seconds, n=8) also approximates those under field conditions.

These data, a sex ratio of males to females of about 3–5 to 1 (see p. 193) and retarded ovarial development, indicate that *Chaoborus cooki* adult behavior differs substantially from that of *Chaoborus trivittatus*. This suggests that *Chaoborus cooki* adults do not remain near the pond from which they emerge and both males and females disperse. This behavior would ensure the survival of at least part of the total population. Temporary ponds which became dry before adult emergence would undoubtedly kill the immatures present.

Female adults probably exhibit underdeveloped ovaries on emergence so that fat body can be used as energy for flight should a suitable habitat not be located and would guarantee at least the production of a few eggs once a suitable habitat is found (Roff, 1977).

Lack of records of adults in the area from which they just emerged suggests that the adults mate after a period of dispersal. Greater numbers of males than females would be more conducive to successful mating after dispersal and might explain the inequality in numbers of males and females.

Differences in dispersal capabilities and behavior of *Chaoborus trivittatus* and *Chaoborus cooki* concurs with the suggestion by Southwood (1962) that, generally, species found in unstable habitats show more intensive dispersal behavior than do those in more stable habitats. For species of *Chaoborus*, degree of ovarial development in teneral adults (Fedorenko, 1975c; Parma, 1971b) and number of eggs per female (Fedorenko, 1975c; McGowan, 1974; Parma, 1971b; Sikorowa, 1973) is also correlated to stability of habitat.

Egg rafts of *Chaoborus trivittatus* are laid in a similar way to those of *Chaoborus flavicans* and *Chaoborus crystallinus* (Parma, 1971b: 28). I have observed oviposition in the field during daylight hours, but did not measure the rate of egg laying.

I have no observations of oviposition by females of *Chaoborus cooki*.

Eggs. – Egg rafts of *Chaoborus trivittatus*, like those of species of *Chaoborus sensu stricto* (McCloy, 1950 (as *Chaoborus crystallinus* = *Chaoborus americanus*); Parma, 1971b; Sikorowa, 1973) are in the form of floating discs with the eggs arranged in a spiral. My observations of egg rafts and egg development are similar to those reported by Parma (1971b: 30). I found many egg rafts stuck to floating debris at the water surface. Eggs in the laboratory turn dark brown after one or two days. The pharate first instar larvae were positioned as shown by Parma (1971b: fig. 12) for *Chaoborus flavicans*. As Parma (1971b: 29) has pointed out, oviposition can be disrupted; thus I did not consider number of eggs per raft to be a significant measurement. I have found an egg mass, for example, of *Chaoborus trivittatus* composed of nine eggs. This clearly does not reflect the number of eggs per female (p. 179) and therefore cannot be used to interpret interspecific or intraspecific variation.

Eggs of *Chaoborus cooki* were obtained only from laboratory mated females. These were laid in a semispherical mass on walls of vials, which were used to retain adults. The eggs were held together by minute amounts of gelatinous matrix. The exochorion of each individual was also sticky. Endochorions of fertilized eggs turned dark brown within two to three days. The endochorion of non-fertilized eggs turned slightly brown in places.

I attempted to collect eggs of *Chaoborus cooki* from the site 1.4 km west of George Lake, after the pond had become dry on October 30, 1976, when the surface soil was frozen to a depth of about one to three centimeters. Soil samples were taken from each of 50 by 50 cm grids on the entire area covered by the high water mark of the temporary pond. When *Typha* sp. stems were present in a grid a sample was taken of these, cut off below the soil surface. In addition, samples of brush that immediately surrounded the pond were taken. In the laboratory soil samples were sieved and vegetation scanned under the binocular microscope. Nine soil samples were treated with floatation techniques using NaCl. I was unable to retreive any eggs or egg shells.

I have observed hatching of eggs only for *Chaoborus trivittatus* from 2.4 km west of Edmonton, and 16 km west of Jasper, Alberta. The events of hatching were similar to those described by Parma (1971b: 32). Eggs of *Chaoborus trivittatus* hatch within three days, usually all of one egg mass hatching within a few hours. A few eggs were sieved from a bottom sample taken from a pond 16 km west of Jasper, Alberta, on June 18, 1976, after the adult emergence period was completed. All eggs were white, suggesting that they were not fertilized, and by June 24, 1976, all had deteriorated in the laboratory. Outer eggs on the egg raft hatch first. Egg shells of *Chaoborus trivittatus* split longitudinally and the posterior part of each larva is freed. A few were caught with their head capsule stuck in the egg shell but most, with violent struggling, freed themselves. Unlike the egg shells of *Chaoborus crystallinus* and *Chaoborus flavicans* (Parma, 1971b: fig. 13), and *Chaoborus americanus* (pers. obs.), in which the egg shell on each side of the longitudinal slit folds inwards, the sides of the egg shell of *Chaoborus trivittatus* fold outward (Fig. 9D). This unique character may have evolved to compensate for the large size of *Chaoborus trivittatus* first instar larvae and therefore allow for fewer numbers of first instar larvae being stuck in the egg shell.

All eggs of *Chaoborus trivittatus* collapsed under atmospheric conditions and therefore are not resistant to desiccation.

Eggs of *Chaoborus cooki* do not hatch within a few days, as do those of other *Chaoborus* species (Deonier, 1943; Herms, 1937; McGowan, 1974: 498; Sikorowa, 1973: 76). Endochorions of these eggs, white when laid, become extremely dark brown within 2–3 days. Larvae develop to at least a stage where head capsule and air sacs are visible, but do not hatch at 20 C. After three months at this temperature, and an L:D photoperiod of 18:6, some eggs were treated with either three successive floodings, three days apart, of deoxygenated water, or one treatment with xylene vapor, but they failed to hatch. Other eggs were treated to 20 C temperatures and an L:D photoperiod of 18:6 for two months, 2 C and total darkness for four months and then returned to former conditions but with no evidence of hatching. A few eggs did hatch after being kept at 20 C and an L:D photoperiod of 18:6 for two months and then total darkness at 2 C for ten months. Study of the egg shell showed that the exochorion was gone (as it was in some unhatched eggs), and the chorion had split to release the larva in a way different (Fig. 9E) to that described for other species.

Eggs of *Chaoborus cooki* were treated to one month of atmospheric conditions without collapse. The thick exochorion is apparently a protective layer against desiccation. The highly sculptured exochorion probably functions as a plastron under alternately dry and wet conditions (Hinton, 1969; Hinton and Service, 1969).

Larvae. – I observed horizontal clumping of second, third, and fourth instar larvae in ponds which were not entirely shaded from direct sunlight. Clumping was related to presence of shade provided either by surrounding vegetation, topographical features, or emergent aquatic vegetation. This is clearly a factor which influences sampling results of *Chaoborus trivittatus* and *Chaoborus cooki* larvae from shallow water bodies. For example, a pond measuring about 5 by 14 m, 7.6 km northwest of Mountain Park, Alberta, was sampled successively with a dip net along the north side and a portion of the south side which were exposed to direct sunlight, without collecting a single larva. A prominent boulder on the south shore provided shade in part of the pond and in this region I collected 109 fourth instar larvae of *Chaoborus trivittatus* in a single sweep of the net.

Similar response to shade is probably exhibited by *Chaoborus pallidus* (Akehurst, 1922: 352; Edwards, 1920; Sikorowa, 1964)

This factor is probably one which influences the restriction of *Schadonophasma* species to woodland conditions. In addition, it is possible that this resonse to shading is a modification of the response to light which is important in vertical migration of some *Chaoborus* species (Chaston, 1969; LaRow, 1968, 1969).

I observed grooming behavior of fourth instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki*. Larvae often lashed at the posterior portions of their bodies with their antennae and mandibles. Occasionally larvae place the posterior portion of the abdomen in their oral cavity, the anal fan completely in the mouth. Even the slightest disturbance resulted in return to a normal position. However, on one occasion I observed a larva of *Chaoborus trivittatus* keep its tail end in its mouth for over 2.5 hours. This behavior is undoubtedly an important adaptation for removal of epibionts.

I did not observe larvae of *Chaoborus trivittatus* or *Chaoborus cooki* bury themselves in the bottom substrate in aquaria, although, when disturbed, they would dart toward the bottom and often cling with mouthparts to bottom debris.

Although differences in prey type were evident between *Chaoborus trivittatus* and *Chaoborus cooki*, I did not quantify this information because of biases produced by preservation techniques (Swift and Fedorenko, 1973). Although Fedorenko (1975a, 1975b) and Swift and Fedorenko (1975) have recorded the diet of *Chaoborus trivittatus* fourth instar larvae, from an oligotrophic lake in southwestern British Columbia, as composed of copepods and cladocerans, it is not known to what extend another habitat, such as a pond, affects prey type. For example, I observed *Chaoborus trivittatus* fourth instar larvae capturing chironomid larvae. I did not find ostracod remains in the gut of *Chaoborus trivittatus* fourth instar larvae and, in the laboratory they lashed out at, but rejected ostracods as food. Contrary to this I found numerous *Chaoborus cooki* larvae with ostracods in their crops. Chironomid and, in *Chaoborus cooki* larvae from some ponds, culicid larvae were also common. To a certain degree, differences of prey type must reflect habitat differences, but these observations of ostracod ingestion suggest species differences in ability to ingest at least this prey type.

Male larvae of both species pupate earlier than do female larvae (Table 51, 56). *Chaoborus cooki* larvae have a more extended pupation period than do those of *Chaoborus trivittatus* under laboratory conditions.

Pupae. – Pupation of individuals of *Chaoborus* species has not previously been observed. The following is derived from observations of a single pupation for each of *Chaoborus trivittatus* and *Chaoborus cooki*. Under laboratory conditions pupation required about two or three seconds. The fourth instar larva suddenly contracted along its entire body length in a quivering motion. The larva turned into a vertical position, the pupal horns popped through the thoracic suture, followed by the thorax and head of the pupa. The larval exuviae slipped down the length of the pupal abdomen and was thrown off the tip by a forward flick of the abdomen.

Parma's (1971b: 38) description of macroscopic color changes during pupal development also apply to pupae of *Chaoborus trivittatus* and *Chaoborus cooki*.

Under laboratory conditions, the pupal period of *Chaoborus trivittatus* is three (n=1) to four (n=85) days for males and four (n=22) to five (n=4) days for females. The pupal period of male *Chaoborus cooki* lasted two to six days (n=1,2,6,28,21 respectively), and of females three to seven days (n=1,13,13,11,4 respectively).

Table 56. Numbers of pupae resulting from 42 individually reared fourth instar larvae of *Chaoborus cooki* collected 32 km west of Edson, Alberta. Pupation recorded only on dates presented.

	NUMBER OF PUPAE	
DATE	Male	Female
5–VI–1975	0	0
6–VI–1975	4	0
9–VI–1975	25	2
13–VI–1975	2	7
16–VI–1975	1	0
20–VI–1975	1	0
Total:	33	9

Differences in development of ovaries between pupae of *Chaoborus trivittatus*, *Chaoborus cooki* and *Chaoborus nyblaei* are described elsewhere (p. 179).

To compare the sex ratio of *Chaoborus trivittatus* and *Chaoborus cooki* I collected fourth instar larvae before any indication of pupation in the field, from 2.4 km west of Edmonton and 32 km west of Edson, Alberta (not the same locality from which the life cycle of *Chaoborus cooki* was studied), respectively. Individual rearings of 44 larvae of *Chaoborus trivittatus* produced 23 male and 21 female pupae and 42 *Chaoborus cooki* larvae produced 33 male and nine female pupae. The use of a compound character index to sex fourth instar larvae of *Chaoborus cooki* (p. 161), from 1.6 km south of Jasper, indicated a sex ratio of 52 males to 10 females.

MATING EXPERIMENTS

Observations of forced matings in the laboratory between members of two populations give indications of their reproductive compatability and, therefore, their conspecificity. I tested my interpretation of morphological, bionomic and temporal discontinuities as indicative of the presence of two species of *Schadonophasma* in North America by attempting to cross individuals of *Chaoborus trivittatus* and *Chaoborus cooki*.

Results of crossing (Table 57) show several important features. Crossings of male *Chaoborus trivittatus* and female *Chaoborus cooki*, as compared to intraspecific crossings, showed reduced number of eggs, number of fertilized eggs, and reduced fertility. Four of the six crosses resulted in no eggs being laid. Reduced fertility and low number of eggs from some of the intraspecific crosses must be the result of experimental conditions.

Crosses between male *Chaoborus cooki* and female *Chaoborus trivittatus* resulted in no eggs. It was apparent during the crossings that male *Chaoborus cooki* had difficulty in coupling with the female genitalia. In an additional six attempted couplings the penis valves of male *Chaoborus cooki* could not insert into the female genitalia of *Chaoborus trivittatus* and copulation did not take place. This may be due to the more bulbous nature of the head of penis valves of *Chaoborus cooki* which may not fit into the proper receptacle of the female genitalia.

These observations indicate that reproductive isolation between *Chaoborus trivittatus* and *Chaoborus cooki* is additionally maintained by mechanical and genetic incompatibilities.

Table 57. Results of intraspecific and interspecific crossings of adult *Chaoborus trivittatus* and *Chaoborus cooki*.

Species crosses (♂ X♀)	Couple No.	No. of Eggs	%Fertile
TRIV. X TRIV.	1	190	98.4
	2	133	71.3
	3	27	77.8
	4	180	60.0
	5	171	97.1
COOKI X COOKI	1	78	61.5
	2	72	86.1
	3	73	88.7
	4	70	70.4
	5	0	0
COOKI X TRIV.	1	0	0
	2	0	0
	3	0	0
TRIV. X COOKI	1	85	11.8
	2	65	0
	3	0	0
	4	0	0
	5	0	0
	6	0	0

PHYLOGENY AND ZOOGEOGRAPHY

Phylogenetic and zoogeographic considerations are logical conclusions to systematic studies. In this section I give my working principles for such considerations, evidence for the recognition of three species of *Schadonophasma*, and hypothesize their evolutionary history. Because the evolution of species of *Schadonophasma* can be best understood in the context of ex-group comparisons I also consider the evolution of the genus *Chaoborus*.

In recent years there has been much debate concerning the principles and methods of cladistic analysis as used to infer phyletic relationships (e.g. Ashlock, 1974; Brundin, 1972; Darlington, 1970; Griffiths, 1972, 1974; Hull, 1970; Mayr, 1974; Schlee, 1975; Sneath and Sokal, 1973; Sokal, 1975; and papers cited in these). Although adherance to methods themselves can blind investigators to more reasonable alternative interpretations (Darlington, 1970), Hennigian principles (see Kavanaugh, 1972) have broad applicability in the determination of evolutionary relationships. I have, therefore, used them to infer the evolutionary history of species of the genus *Chaoborus*.

One potential source of error in the application of cladistic analysis concerns the weighting of characters on a superficial basis. Hecht and Edwards (1977) and Szalay (1977) have discussed the importance of detailed investigation of individual characters used in phylogenetic analysis. Although this may not be possible in many studies, this investigation provided a basis from which to better interpret the evolutionary significance of most characters used and therefore improved the use of cladistic techniques. These data allowed a more probable interpretation of the evolution of some *Chaoborus* species and, in particular, of the species of *Schadonophasma*.

Most systematic studies, some because of a lack of bionomic information, only consider allopatric speciation as the means of evolution of lineages. In a recent study Tauber and Tauber (1977) have proposed a genetic model for sympatric speciation of more general applicability than that proposed by Bush (1975a, 1975b). However, most studies suggesting interpretations of sympatric speciation lack study of the phyletic relationships between the organisms concerned. My interpretation of possible speciation events in the history of *Schadonophasma* species provides an example of how phyletic relationships and zoogeographical considerations may give supportive evidence for inferring an allopatric or sympatric speciation model.

Darlington (1970: 3) has criticized assumptions of dichotomous speciation and described several situations in which branching was possibly polychotomous. I have not found evidence of trichotomous speciation of the three species of *Schadonophasma*. The presence of synapomorphies for two of the species supports only dichotomous speciation in the history of *Schadonophasma* species.

Evidence and Recognition of three species of *Schadonophasma*

The basic taxonomic unit used for inference of phylogenies is the species or species group. A phylogeny therefore depends on correct interpretation of the diversity it attempts to explain. The following is a discussion of evidence for the recognition of three species of *Schadonophasma*.

Morphological, bionomic, developmental and behavioral incongruities, as well as differences in geographic variation and distribution among groups of populations, are logical criteria for recognition of species if the biological species concept is accepted as a testable hypothesis. Only experimental tests of reproductive incompatibilities, however, might provide direct evidence of reproductive isolation. It is the concordance of such indirect and direct evidence of reproductive isolation that allows systematists to interpret the former as the result of such reproductive isolation. The results of this study, as do many others, confirm the validity of this assumption.

From the results of this study I consider discontinuities in the following features to support my conclusion that there are two species of *Schadonophasma* in North America recognizable as *Chaoborus trivittatus* and *Chaoborus cooki*:

1. Structure of eggs, all stages of larvae, pupae and adults
2. Pattern of development of LB/AL from first through fourth instar larvae.
3. Characters of fourth instar larvae which are sex-associated in one species but not the other.
4. Correlations of characters of fourth instar larvae.
5. Patterns of geographical variation of characters of fourth instar larvae in Alberta.
6. Rates of development of eggs, larvae and ovaries of adults.
7. Life cycle and types of habitat commonly occupied.
8. Larval prey type.
9. Adult behavior.
10. Reproductive compatibilities, when adults from different populations were crossed in the laboratory.
11. Lack of sympatry in western and eastern coastal regions of the United States.

I do not have nearly the same amount of evidence to justify recognition of the third species, *Chaoborus nyblaei*, in Fennoscandia. Because of similarity of compared semaphoronts, I assumed that all specimens from Fennoscandia were conspecific. Adult material collected 2–3 km SW of Nuorgam, Finland, on July 24, 1960, was probably conspecific with larval and pupal material collected there.

Most characters of the immatures and color of adults of *Chaoborus nyblaei* are similar to those of *Chaoborus cooki*. However, shape of the adult male penis valve and prelabral appendage of fourth instar larvae are most similar to those of *Chaoborus trivittatus*. This combination of features suggests the presence of a third species, and this is further supported by extremes of variation of certain characters of the fourth instar larvae of *Chaoborus nyblaei* (number of mandibular fan bristles and anal fan setae).

Because of difficulties in interpreting morphologically similar, allopatric populations separated by a geographical area from which specimens are not known (Mayr, 1969), it is impossible to be certain that *Chaoborus nyblaei* is a separate species. Therefore it might be conspecific with either *Chaoborus trivittatus* or *Chaoborus cooki*. Overall morphological similarity would indicate, if this were so, that *Chaoborus nyblaei* and *Chaoborus cooki* are conspecific. However, patterns of geographical variation of *Chaoborus cooki* would not suggest that the higher mean values of number of anal fan setae, and lower mean value of number of anal fan setae of the larvae of *Schadonophasma* in Fennoscandia are the result of variation of those characters of *Chaoborus cooki*. Nevertheless, the possibilities of character displacement producing such features as exhibited by the population in Fennoscandia cannot be presently negated. Further study of *Chaoborus nyblaei* populations to complement the data given in this study for *Chaoborus trivittatus* and *Chaoborus cooki*, further investigation of the range of *Chaoborus nyblaei* and detailed analysis of geographical variation of *Chaoborus nyblaei* and *Chaoborus cooki* once further samples become available, would give further clues to questions of conspecificity. Not withstanding, it is probable that the Bering Strait area is devoid of *Schadonophasma* populations and presents at least a recent barrier between North American, and should they exist, eastern Asian populations of *Schadonophasma*.

Phylogeny of *Chaoborus*

Saether (1970), using cladistic methods, proposed a phylogeny of *Chaoborus* species and chaoborid genera but dealt only with those of the Holarctic region. He used 29 characters to determine relationships among subgenera of *Chaoborus*. However, his interpretation of the polarity of many of these characters is questionable.

A number of characters are used by Saether (1970), for which he gives no criteria for determining the apomorphic and plesiomorphic ends of the morphoclines and for which there are none apparent (Maslin, 1952). For example, the character HW/WBE is considered plesiomorphic if 2.5–4.2 and apomorphic if 1.5–1.8. However, the closest sister group to *Chaoborus* for which these data are available is *Mochlonyx* which, if all species are considered, has a total range of 1.8–2.4 (Cook, 1956). If this feature represents the plesiomorphic condition of *Chaoborus*, both ends of the morphocline recognized by Saether would be apomorphic. However, HB/WBE ratio of male adult *Eucorethra underwoodi* is 8.3–8.5 (Cook, 1956) and this may also reflect plesiomorphy. Until further ex-group comparison has been made, phylogenetic interpretation of this character is conjectural.

It is also not clear how Saether interpreted the polarity of morphoclines of values of Y/R_3 and Y/X of adults (males?), width/length of abdominal segment VII of pupae and AS/AL of larvae, when these data were available only for some species of *Chaoborus*.

It is well known that character states which involve loss of a feature are particularly suspect of convergent or parallel evolution (e.g. it could be as likely for species to independently lose features as for a single ancestor of species to do so). Interpretation of the following character states as synapomorphic provides at best an uncertain basis for reconstructing a phylogeny: loss of parascutellar setae and reduction of number of mesepimeral and pronotal seta of adults; loss of color of the pupal paddle membrane; reduction of the relative length of the median rib of the pupal paddle; and reduction of the larval tentorium.

Shape of the apex of the male adult gonostylus and loss of a pair of larval labral setae are autapomorphies for *Chaoborus pallidus*, and cannot be used to determine relationships between species or groups of species.

Saether (1970: 47, Trend 46) considered the placement of the simple seta toward the apex of the median rib of the pupal paddle to be apomorphic within *Chaoborus*. This condition, however, most closely approximates the condition featured by *Mochlonyx* and *Eucorethra* pupae suggesting that it is more likely to be the plesiomorphic character state.

Following Saether's (1970) publication, larvae of some African species have been well described (Green and Young, 1976; McGowan, 1972, 1976). In addition, Saether (1976) has redescribed adults, pupae and fourth instar larvae of *Chaoborus brasiliensis* (Theobald) and *Chaoborus magnificus* Lane from Venezuela. Using these descriptions and my own observations, I have constructed a phylogeny of those species of *Chaoborus* for which sufficient information is available. The characters used and interpretation of their plesiomorphic and apomorphic states are given in Table 58. All character states were judged plesiomorphic or apomorphic on the basis of ex-group comparisons (especially *Mochlonyx* and *Eucorethra*) with the exception of prelabral appendage shape. The interpretation of several characters requires special comment.

Two characters used are interpreted as apomorphic in their reduced state: relative length of the median rib of the pupal paddle and, relative degree of sclerotization and size of the larval tentorium. These were used because of a shortage of characters in this analysis. As proposed here, reduction of the larval tentorium has occurred twice.

The prelabral appendage of *Chaoborus* larvae is undoubtedly a seta (Balvay, 1977c). Although it is not known which seta of other chaoborids is homologous to this prelabral appendage, it is reasonable to assume that ontogenetic development of the prelabral appendage from a simple seta in the first two instars of all *Chaoborus* species to a laterally flattened appendage in the last two instars of some species, corresponds to the evolution of these setae (Akehurst, 1922: 352).

The only clues for determining the polarity of AS/AL of *Chaoborus* larvae are provided by the larvae of *Mochlonyx velutinus* and *Eucorethra underwoodi*. *Mochlonyx velutinus* fourth instar larvae possess an antennal seta near to the base of the antenna but none were measured exactly. The AS/AL of three fourth instar larvae of *Eucorethra underwoodi* was 0.51–0.59 (mean=0.558). In the construction of the phylogeny I have used this feature only to interpret the extreme values of AS/AL of *Schadonophasma* as apomorphic. Change of this ratio, from a low value in first instar larvae to a high ratio in fourth instars (Fig. 22A), would support such an interpretation.

The polarity of two characters, coloration of adult legs and state of the larval dorsal process, has apparently been misinterpreted by Saether (1970). He suggested that ringed legs of adults is a plesiomorphic state. This is probably only partially true. Although bases and apices of leg segments and articles are dark in a number of ex-groups, and is therefore probably plesiomorphic, spotted femur and tibia of legs of some African spcies of *Chaoborus* (Verbeke, 1958), and some species of the subgenus *Sayomyia* (e.g. *Chaoborus punctipennis*, *Chaoborus astictopus*, (per. obs.) *Chaoborus brasiliensis*), is probably apomorphic.

Saether (1970: 50) also considered the two segmented dorsal process of the fourth instar larvae of some *Chaoborus* species to be the plesiomorphic condition for the genus and implies (Trend 67) that the dorsal process is actually the evolutionary vestige of the respiratory siphon. However, as pointed out by Cook (1956: 14) 'the annulation on which this "siphon vestige" occurs has a musculature which indicates that it is a segment. This then is segment 9, and the siphon occurs on segment 8. Thus, the term "siphon vestige" seems to be inaccurate'. In addition, Parma (1971a) followed the shape of the dorsal

Table 58. Characters and character states within the genus *Chaoborus*.

Character	Plesiomorphic	Apomorphic
Adults.		
1. Leg coloration	Pigmented only at bases and apices of leg segments and tarsal articles	Femur and tibia ringed or spotted along their lengths
2. Wing coloration	Spotted	Not spotted
3. Gonocoxite shape	No protuberance on inner face	Protuberance on inner face
4. Penis valve	No apical claw when head rounded	Apical claw and rounded head
5. Comb-like setae on 3rd metatarsomere of female	Absent	Present
Pupae		
6. Median rib of pupal paddle	Straight at apex	Curved at apex
7. Median rib of pupal paddle	Extended to edge of paddle	Not extended to edge of paddle
Larvae		
8' Prelabral appendage	Setose; covered with spines	Broadened with spines directed anteriorly and posteriorly
8" Prelabral appendage	Broad with spines directed anteriorly and posteriorly	Broad with spines directed only anteriorly
8''' Prelabral appendage	Broad with spines directed anteriorly and posteriorly	Setose but with spines directed only anteriorly and posteriorly
9. Antenna	Not curved at posterior base	Curved at posterior base
10. Dorsal Process	No article present	Single article present
11. Tentorium	Strongly sclerotized and thick	Weakly sclerotized and thin
12. Subordinate Mandibular Tooth	Not spinose	Spinose
13. AS/AL	Lower value	Higher value

process from instar to instar of *Chaoborus flavicans* and found the pointed dorsal process to be present only in the later instars. If this feature represents the siphon vestige, one would expect it also to be present in earlier instars. I further tested this hypothesis by examining the position of the tracheal trunks of fourth instar larvae of *Chaoborus cooki*. I found that thawing previously frozen larvae resulted in the trachea filling with gas, allowing them to be clearly observed. The tracheal trunks showed a notable dorsal bend in the eighth abdominal segment (Fig. 8D) similar to the dorsal bend of the tracheal trunks of *Mochlonyx* larvae into the siphon (Montchadsky, 1953: fig. 1).

These observations indicate that the small dorsal article of the ninth abdominal segment of larvae of some *Chaoborus* species is in fact a newly evolved feature and not the vestige of the respiratory siphon. Absence of such an article is therefore the plesiomorphic condition. The pointed dorsal process exhibited by *Chaoborus flavicans* and *Chaoborus crystallinus* fourth instar larvae is also probably an independently derived characteristic.

The most probable phylogeny of species of *Chaoborus*, using the characters in Table 58, is presented in Figure 36. I accept Saether's (1970) conclusion concerning the phyletic relationships between the four species of *Chaoborus sensu stricto*. This phylogeny differs from that hypothesized by Saether (1970,

1976) primarily in considering *Chaoborus albatus* as possibly the sister species of *Chaoborus magnificus* and these species plus *Chaoborus brasiliensis*, *Chaoborus punctipennis*, and *Chaoborus astictopus* (hereafter designated as 'ambpa') the sister group of *Schadonophasma* plus *Chaoborus sensu stricto*. The placement of *Chaoborus pallidipes* is uncertain. This species could equally well be the sister group of *Schadonophasma* plus *Chaoborus sensu stricto*, or of the species group 'ambpa'.

The grouping of *Chaoborus anomalus*, *Chaoborus ceratopogones*, and *Chaoborus pallidus* is tentative. These are recognized as monophyletic on the basis of leg coloration which, as here hypothesized, shows convergence with the species group *Chaoborus brasiliensis*, *Chaoborus punctipennis*, and *Chaoborus astictopus*. Any of *Chaoborus anomalus*, *Chaoborus ceratopogones* or *Chaoborus pallidus* could be considered a sister group of the species group 'ambpa' if the following events are assumed to have occurred: 1) the basal curvature of the larval antenna was secondarily lost in these species, or the curvature evolved independently in species groups 'ambpa' and *Schadonophasma* plus *Chaoborus sensu stricto*; and 2) *Chaoborus albatus* and *Chaoborus magnificus* secondarily lost the derived coloration of adult legs. However, these events provide a less parsimonious explanation than does the convergence of leg coloration as presented here. Similarly the development of a lobe on the inner face of the gonocoxite of both *Chaoborus anomalus* and the species group *Chaoborus brasiliensis*, *Chaoborus punctipennis*, and *Chaoborus astictopus*, is considered a result of convergent evolution.

A character which may be synapomorphous for *Chaoborus anomalus*, *Chaoborus ceratopogones* and *Chaoborus pallidus*, except for which observations were not available for all other species, is the basally swollen and highly curved postantennal filaments (Saether, 1970: fig. 6C). Verbeke (1958: 43) also considered *Chaoborus ceratopogones* and *Chaoborus pallidus* to be closely related on the basis of similarity of adults, pupae and larvae.

Although the broadening of the prelabral appendage may have evolved independently four times, I here consider it to have occurred only once. The setose appearance of the prelabral appendages of *Chaoborus punctipennis* and *Chaoborus astictopus* is therefore a derived state and is only superficially similar to the primitive condition. This explains why the setaceous prelabral appendages of these two species have spines directly only anteriorly and posteriorly.

Fossil evidence

The study of fossils can give important evidence for the correct interpretation of the evolutionary history of a group of extant organisms. However, few systematists studying arthropods are fortunate to have such fossils available to them.

A number of authors have described or mentioned *Chaoborus* subfossils (Alhonen and Haavisto, 1969; Deevy, 1942; Frey, 1955, 1962, 1976); Goulden, 1966a, 1966b; Hofmann, 1971, 1978; Marland, 1967; Stahl, 1959, 1969) or fossils (Borkent, 1978b; Edwards, 1923; von Heyden, 1862; Hope, 1847; Meunier, 1904; Scudder, 1890 (questionable identification); Serres, 1829: 268). Most of the fossil material is in need of redescription. I examined the fossil pupa and disarticulated pupal parts described by von Heyden (1862) as *Culicites (=Chaoborus) tertiarius* and have published (Borkent, 1978b), a redescription of those fossils and of some larval fragments (mandibles and anal fans) also present on the brown, paper-coal. The pupal paddles exhibit median ribs which extend to the edge of the paddle and are curved apically. In addition the subordinate tooth at the base of the two larger teeth of some of the larval mandible is very similar to that of *Chaoborus flavicans*. It is not certain that the larval fragments are from the same species as the pupa and pupal parts. Nevertheless, mandible structure suggests that they are from a population conspecific with *Chaoborus flavicans* (*Chaoborus sensu stricto*), or from a species which is the sister species of *Chaoborus flavicans*. The apical curvature of the median rib of the pupal paddles is a synapomorphous character which serves to group *Schadonophasma* and *Chaoborus sensu* *stricto*. Although I cannot confidently place the fossil pupa or pupal parts with one of these lineages, it is clear that if convergence has not taken place this species shares a common ancestry with, or within, either of these two subgenera.

According to Mägdefrau (1968), Edwards (1923) correctly determined the age of the fossils as Upper Oligocene. This would indicate that speciation giving rise to *Chaoborus flavicans*, and its sister species *Chaoborus crystallinus*, took place at least 25 million years B.P., and that the speciation event which gave rise to the lineages represented by extant species of *Schadonophasma* and *Chaoborus sensu stricto* took place before that time.

The finding of these fossils at Rott, Siebengebirge, West Germany is consistent with a hypothesis that the species group of *Schadonophasma* plus *Chaoborus sensu stricto* evolved under temperate conditions (Mägdefrau, 1968).

Phylogeny of *Schadonophasma*

Saether (1970) proposed a phylogeny for the species of *Schadonophasma* based on six characters. I have already discussed the difficulties of interpretation of four of these (number of mesepimeral and pronotal setae; ratio of Y/X; WS/LS; shape of dorsal process). Saether's phylogenetic interpretation of variation of the penis valve shape seems to be correct for *Schadonophasma*. The interpretation of body size variation is probably incorrect but is discussed below.

Although the phylogeny I propose for the species of *Schadonophasma* is identical to that of Saether (1970), except for his consideration of *Chaoborus brunskilli* (=*Chaoborus trivittatus*) as the sister species of *Chaoborus trivittatus*, my approach to the problem is substantially different. For the analysis I have chosen seven characters (Table 59), some of which are discussed below.

Table 59. Characters and character states within the subgenus *Schadonophasma*.

Character	Plesiomorphic	Apomorphic
Adults.		
1. Penis valve	Apical claw short	Apical claw elongate
Fourth Instar Larvae		
2. Head capsule length	Smaller	Larger
3. AS/AL	Lower value	Higher value
4. Prelabral appendage	Elongate	Broad
5. Number of mandibular bristles	Lower	Higher
6. Number of anal fan setae	Lower	Higher
Eggs		
7. General structure	Thin exochorion; no pattern on surface of exochorion	Thick exochorion; polygonal pattern on surface of exochorion.

Saether (1970: 43) in Trend 2, recognized the largest chaoborid, *Eucorethra underwoodi* to represent the plesiomorphic condition and the smallest, the apomorphic condition. He therefore considers the large size of *Schadonophasma* spp. and within the subgenus *Chaoborus cooki* and *Chaoborus nyblaei*, to be plesiomorphic. However, his determination of polarity of this morphocline is almost certainly incorrect.

Schadonophasma species are the largest of all described *Chaoborus*, and are larger than all species of *Cryophila* Edwards, *Mochlonyx*, *Promochlonyx* Edwards, and *Australomochlonyx* Freeman; genera to which *Chaoborus* is more closely related than to *Eucorethra*. It is almost certain therefore that the large size of *Schadonophasma* members as a group, and those of *Chaoborus cooki* and *Chaoborus nyblaei* in particular, represents an apomorphic condition. In this presentation I have used larval head capsule length to represent the overall size of the species.

I have already discussed above the interpretation of AS/AL and prelabral appendage shape.

The high number of mandibular fan bristles of some members of *Chaoborus trivittatus* probably represents the apomorphic end of a morphocline. *Mochlonyx* fourth instar larvae have six to seven bristles in the mandibular fan (Cook, 1956; O'Conner, 1959), and no other *Chaoborus* species have members exhibiting such large numbers of mandibular fan bristles.

Some fourth instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki* and all those of *Chaoborus nyblaei* have a larger number of anal fan setae than other *Chaoborus* species. *Mochlonyx* fourth instar larvae have 28–30 anal fan setae, *Eucorethra underwoodi* has 32 (Cook, 1956). These ex-group comparisons would suggest that only the high number of anal fan setae of *Chaoborus cooki* and *Chaoborus nyblaei* are apomorphic. However, some evidence suggests that the evolution of changes in number of anal fan setae is more complex. From observations of the swimming behavior of *Chaoborus* larvae it is clear that the anal fan functions as a fulcrum against which the larvae can produce a forward motion. It would seem reasonable therefore to suggest that if there are developmental restrictions on the size of individual anal fan setae, the number of anal fan setae may be related to the size of the species and that these two characters coevolved. Distribution of number of anal fan setae, relative to range of head capsule length for species of *Chaoborus* for which these data are available (Fig. 37), would support this hypothesis. These two characters would generally, therefore, not give independent evidence of phyletic relationships. However, it is also apparent from Figure 37 that the relationship is not a constant one. Although this may be due to inadequate sampling for some species, it is probable that other factors are important in the evolution of number of anal fan setae. For example, even though there is no significant difference in head capsule length of *Chaoborus cooki* and *Chaoborus nyblaei* fourth instar larvae, number of anal fan setae does significantly differ. I have therefore interpreted the large number of anal fan setae as autapomorphic for *Chaoborus nyblaei*.

The egg structure and type of egg mass of *Chaoborus trivittatus* is extremely similar to those of species of *Chaoborus sensu stricto*. Because *Chaoborus sensu stricto* is the sister group of *Schadonophasma* it is probable that the condition found in *Chaoborus trivittatus* represents the plesiomorphic state within *Schadonophasma*. However, it is possible that the character state of *Chaoborus trivittatus* represents a convergence with species of *Chaoborus sensu stricto*. A 'layer of jelly-like substance' or 'thin gelatinous sheath' around individual eggs (= thick exochorion?) of some species has been described (MacDonald, 1956; McGowan, 1976; Sikorowa, 1973) and, if these features are homologous with those of *Chaoborus cooki* and *Chaoborus nyblaei*, they might be considered plesiomorphic within *Schadonophasma*. However, the eggs of these other species of *Chaoborus* need to be better studied before such inferences can be made.

The proposed phylogeny of the species of *Schadonophasma* is given in Figure 38.

Zoogeography and speciation events

Hennig (1966b) has shown that zoogeographic inferences are dependent upon accurate interpretation of the evolutionary relationships of organisms. Because it seems likely that detailed study of *Chaoborus* species, both extant and fossil, will alter the phylogeny of *Chaoborus* as proposed here, I will not discuss the zoogeography of the genus. However, the inferred sister group relationship between

Schadonophasma and *Chaoborus sensu stricto* is probably correct.

Because all extant species of *Schadonophasma* and *Chaoborus sensu stricto* are found only in north temperate regions it would be reasonable to assume that the ancestor which gave rise to extant species of *Schadonophasma* was present in the north temperate region. Distributions of species of *Chaoborus sensu stricto* give no clues as to where specifically this ancestor may have arisen.

In the following discussion of the speciation event giving rise to *Chaoborus cooki* and *Chaoborus nyblaei*, I have assumed that *Chaoborus nyblaei* has had or does have a continuous Palaearctic distribution. However, future work may indicate that *Chaoborus nyblaei* has been, and is presently, restricted to Fennoscandia. A more likely explanation of the speciation event giving rise to *Chaoborus cooki* and *Chaoborus nyblaei* would suggest that dispersal of adults (or possibly desiccation resistent eggs on the feet of migrating shorebirds) took place over the North Atlantic during a period of climatic amelioration.

There are two equally probable zoogeographic interpretations of the history of *Schadonophasma* species (Figure 39).

The first suggests that the ancestor of extant *Schadonophasma* species was Holarctic in distribution. A split of its populations into Nearctic and Palaearctic elements resulted in the lineage giving rise to *Chaoborus trivittatus* and to the ancestor of *Chaoborus cooki* and *Chaoborus nyblaei* (hereafter referred to as *Chaoborus cooki-nyblaei*). The Palaearctic species then reinvaded North America and subsequently was split into Palaearctic and Nearctic populations which gave rise to *Chaoborus nyblaei* and *Chaoborus cooki* respectively. The model only requires allopatric speciation and dispersal to have taken place. A land bridge between Asia and North America is known to have appeared and disappeared a number of times during the Tertiary and Quaternary (Hopkins, 1967, 1972) which could have provided, during certain periods, a barrier to contact between Asian and North American populations.

The second zoogeographic hypothesis suggests that the ancestor of extant *Schadonophasma* species arose in North America and speciated there to give rise to the lineages resulting in *Chaoborus trivittatus* and *Chaoborus cooki-nyblaei*. Although an allopatric speciation model might explain the speciation event in North America resulting in the lineages which gave rise to *Chaoborus trivittatus* and *Chaoborus cooki-nyblaei*, it seems most likely that the invasion into temporary waters by *Chaoborus cooki-nyblaei* was not the result of geographical isolation. Although the lineage might have invaded temporary ponds because of competition with other *Chaoborus* species as a geographic isolate, it seems more likely that, especially considering the degree to which *Chaoborus trivittatus* and other *Chaoborus* species can coexist (Stahl, 1966), this would not result in a speciation event. It is also difficult to imagine two isolated geographical areas which contained populations of the ancestral species, one of which contained only temporary waters conducive to the evolution of a temporary pond species.

The available data for *Schadonophasma* species allow for a hypothesis of sympatric speciation. The following are hypothesized events, as indicated by this study, for *Schadonophasma* species and features of species of *Chaoborus sensu stricto*.

The Nearctic species ancestral to extant *Schadonophasma* species inhabited permanent waters with fourth instar larvae as the over-wintering stage. Upon emergence of adults in spring, the males formed swarms on the periphery of the permanent water body and mated with females after these emerged. These are features of *Chaoborus trivittatus* and those species of *Chaoborus sensu stricto* for which information is available, and are therefore, probably plesiomorphic characteristics of *Schadonophasma*. As previously shown for the two species of *Chaoborus trivittatus* and *Chaoborus americanus*, which overwinter as fourth instar larvae in permanent ponds (p. 186), the dispersing females occasionally laid eggs in temporary ponds. Eggs which hatched resulted in larvae which could not survive overwintering in this habitat. This type of egg was strongly selected against, as all larvae which hatched from them in temporary ponds would die. Tauber *et al.* (1977) have shown that mutation of a single allele can result in the appearance of diapause in individuals of a population. If this feature is controlled by a single gene in *Schadonophasma* species, crosses of male *Chaoborus trivittatus* and female *Chaoborus cooki* resulting in diapausing eggs would suggest that the allele for diapausing eggs is dominant. I have assumed this to be the situation in the following discussion. The primitive non-diapausing egg is represented by autosomal recessive alleles *aa*. Mutation resulted in the production of a dominant *Aa*, producing diapausing eggs. A female carrying these genes laid her eggs in a temporary pond, which then diapaused in this habitat. Resistance to complete desiccation might not have evolved at this stage because, at least for the temporary ponds I investigated, the bottoms were quite moist; probably, in some ponds, moist enough to prevent desiccation of eggs. Larvae which hatched out in spring from these overwintered eggs would mature to adulthood at a later time than would those in permanent ponds, which emerge as adults early in spring. This might give at least a certain degree of temporal isolation. However, as discussed above (p. 184), *Chaoborus trivittatus* might be multivoltine in certain regions and this may have provided some temporal overlap between two populations of the ancestral species.

The adults which emerged from the temporary pond would, as did the parent population in permanent ponds or lakes, have swarmed and mated at the pond periphery. This homogamic behavior led to further segregation of populations and ensured an increase in numbers of individuals carrying this gene. The resultant adults would carry the alleles *AA* or *Aa*. Any *aa* eggs laid in temporary ponds would be eliminated as larvae. *AA* or *Aa* eggs subsequently laid in permanent ponds would survive and hatch in the spring as first instars, but any other *Chaoborus* larvae, if present, would be fourth instar and these first instars would probably be cannibalized. To hypothesize the removal of heterozygotes from the temporary pond lineage (and therefore the continued production of *aa*), I suggest that the allele *A* became associated with co-dominant or recessive features conducive to temporary pond existence and therefore, as the temporary pond populations adapted to the temporary pond environment, heterozygotes were selected against. Adult behavior and comparatively reduced ovarian development of extant *Chaoborus cooki*, may be examples of such adaptations, but these also may have evolved after the speciation had occurred.

Through temporal disjunction of mating periods, homogamic mating, complete selection against overwintering larvae in temporary ponds, and partial selection against heterozygotes in temporary ponds and overwintering eggs in permanent ponds, the two lineages giving rise to *Chaoborus trivittatus* and *Chaoborus cooki-nyblaei* became genetically isolated. These suggested events are summarized in Figure 40.

Chaoborus cooki-nyblaei invaded the Palaearctic region, and subsequent barriers to reproduction, as described for the first zoogeographic hypothesis, resulted in isolated populations which gave rise to *Chaoborus cooki* and *Chaoborus nyblaei.*

The sympatric speciation model is dependent at least on the assumption that *Chaoborus nyblaei* does in fact overwinter as an egg. Although this was inferred from available data, I have no direct evidence that this is so. Study of the life cycle of *Chaoborus nyblaei* would therefore provide a test of this hypothesis. If study of the populations I have described as 'populations *incertae sedis*' show these to be one or more species, this may provide additional evidence for testing this proposal of sympatric speciation.

CONCLUDING REMARKS

On the basis of their work, taxonomists should indicate particularly fruitful areas for future research: those concerned primarily with the group studied in particular, and those concerned with systematic problems in general.

Because of the paucity of museum material of specimens of *Schadonophasma*, future endeavors relating to the systematics of the subgenus must await further collecting. Some details concerning the bionomics of species may bear further investigation, as indicated in the text. In particular, investigation of the life cycle of *Chaoborus nyblaei* and the specific affinities of the 'populations *incertae sedis'* may provide additional insights into the systematics of species of *Schadonophasma.* The phyletic relationships of species of *Chaoborus* are yet poorly known. Fossil species and extant species from the tropics, are particularly in need of study and the entire genus is worthy of a complete revision.

In general, this study suggests that investigation of the bionomics of species of some groups may provide additional tests of the sympatric speciation model. Because of domination of evolutionary concepts by the allopatric speciation model, the full implications and requirements of the sympatric speciation model are poorly understood. These aspects of the model can only become clear when additional information on bionomics of organisms which may have speciated sympatrically become available.

As is well illustrated by the work of Bush (1975b) on tephritid fruit flies, a sympatric speciation model can only be justifiably invoked from a solid base of bionomic data. Although allopatric speciation has in the past been the favored hypothesis to explain differentiation of organisms, it is also evident that only morphological and distributional data are available for most organisms. Therefore, until adequate bionomic data are available for a large array of taxonomic groups, it will be difficult to estimate the frequency of occurrence of sympatric speciation. As discussed by Bush (1975a), sympatric speciation occurs under special genetic and environmental conditions. It seems clear that, in certain groups (mammals, birds, and carabid beetles), such conditions are rarely, if ever met. In the genus *Chaoborus*, considering the similarity of the life cycle of most species, it appears that sympatric speciation occurs with less frequency than does allopatric speciation. Nevertheless, some groups, like some species groups of tephritid flies, appear to be more prone to speciate sympatrically. This pattern suggests, therefore, that systematists should not apply the *most common* mode of speciation to all taxonomic groups under investigation. Rather, each speciation model should be based on data available for that group.

An aspect not explicitly clear in previous discussions of sympatric speciation concerns the phyletic relationships and zoogeography of the organisms concerned — essential considerations in any speciation model. This study of *Schadonophasma* provides an example of how zoogeographic considerations may provide additional evidence for elucidation of sympatric speciation.

In conclusion, it is the intensive study of only a few closely related species, as here reported for the subgenus *Schadonophasma*, which can most fruitfully provide the basic information necessary to test hypotheses of sympatric speciation.

ACKNOWLEDGEMENTS

Many individuals have contributed to this study and I extend my thanks to them all. In particular, I express my sincere appreciation to my supervisor G.E. Ball, not only for cultivating my interests in entomology and, particularly, in systematics, since our first encounter when I was yet in high school, but also for his cheerful enthusiasm and thoughtful direction throughout the course of this study. He allowed me to choose and made financially possible this study (including support from National Research Council grant A-1399).

I thank D.A. Craig for many enthusiastic discussions of some of the results of this work.

I also express my appreciation to my wife Annette, who shared numerous field trips and has helped with many of the tasks involved in this study.

To my fellow students with whom I have had numerous discussions about the principles and foundations of systematics and about this work, I express my gratitude: in particular S. Ashe, D. Lafontaine, R. Longair, and R. Roughley.

I thank G. Braybrook for technical assistance with the scanning electron microscope and J. Scott for his helpful suggestions concerning drafting techniques and for completing some of the figures. I acknowledge D.E. Griffiths for her masterful drawing of the frontispiece.

I thank all the individuals and institutions noted in the text for loan of material.

I express my appreciation to Parks Canada for collecting permits for Jasper and Banff National Parks.

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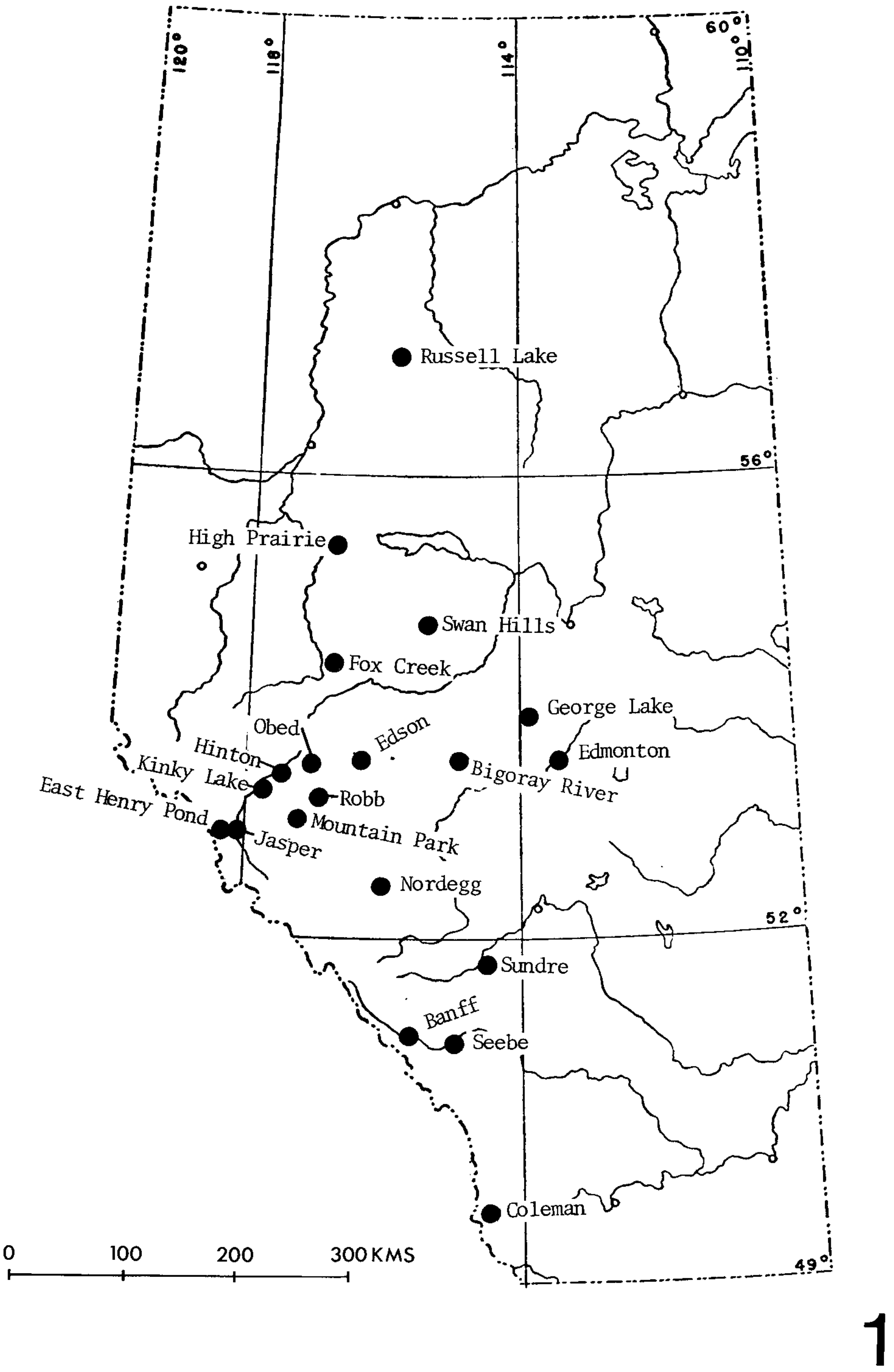

Figure 1. Place names in Alberta cited in text.

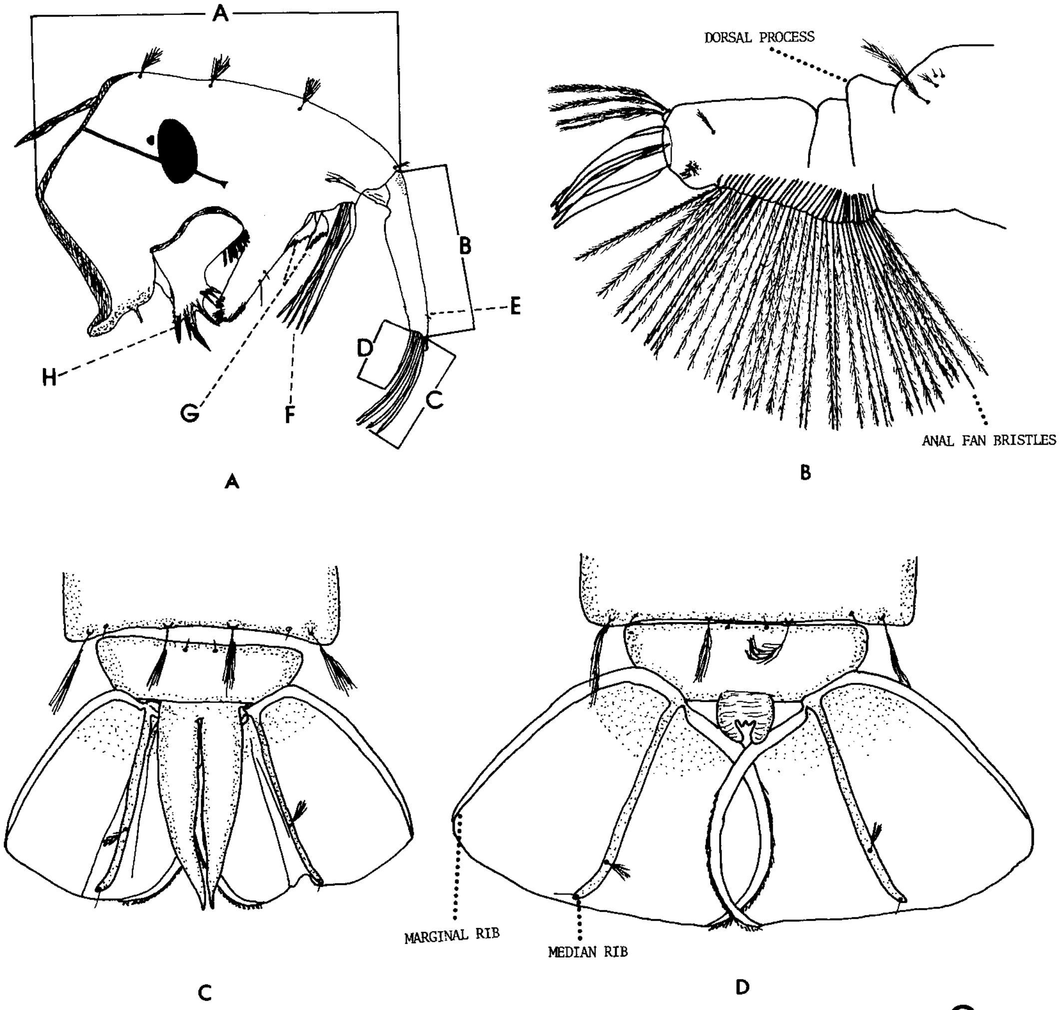

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Figure 2. A. Characters and measurements of head capsule of fourth instar larva: *A*. Head capsule length; *B*. Antennal length; *C*. Long antennal blade length; *D*. Short antennal blade length; *E*. Antennal seta; *F*. Postantennal filaments; *G*. Prelabral appendages; *H*. Mandible; total length of mandibular fan bristles and labral brush setae is not shown; B. Characters of terminal abdominal segments of fourth instar larva. C. Terminalia of male pupa. D. Terminalia of female pupa. All drawings from specimens of *Chaoborus cooki*.

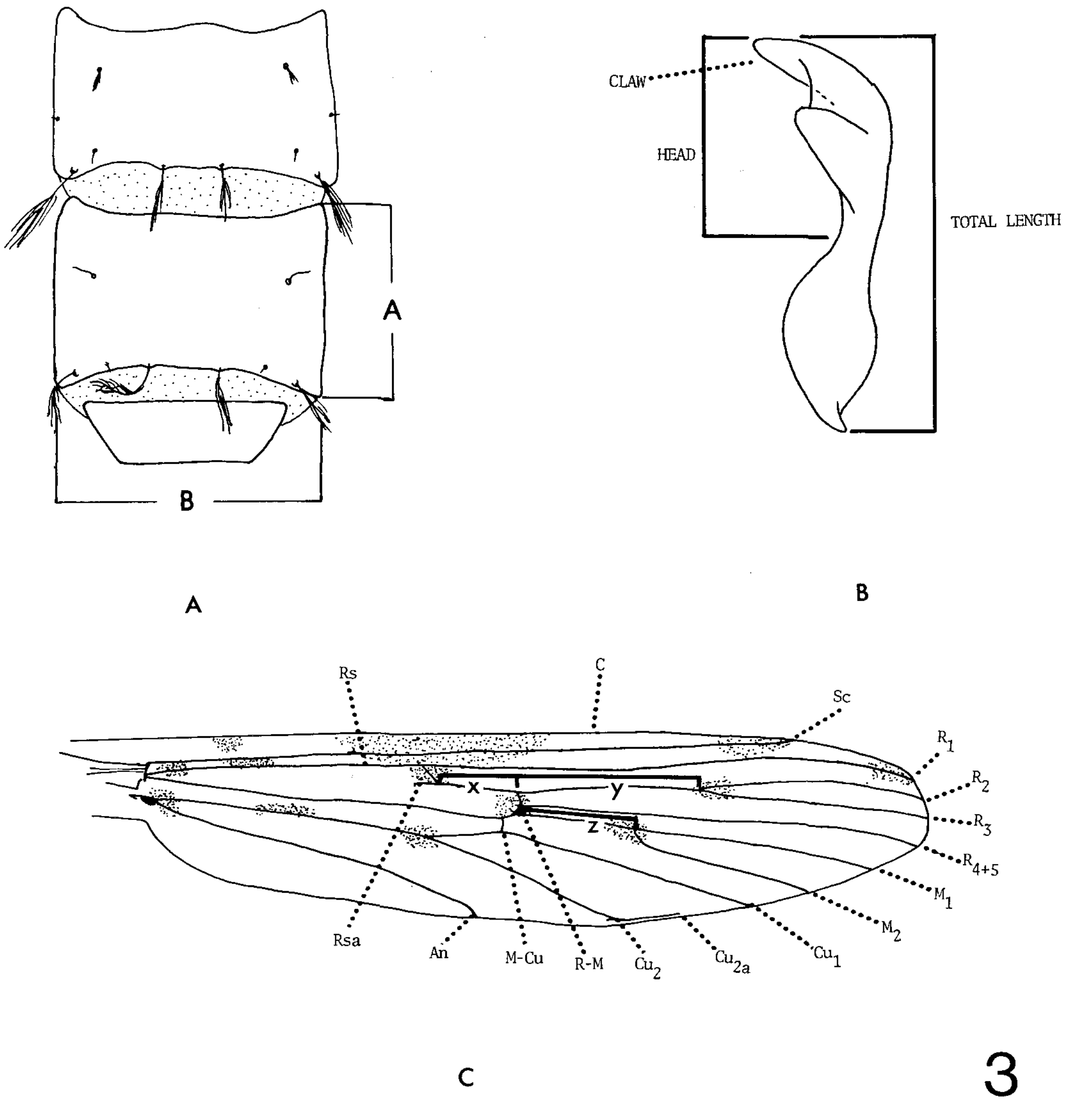

Figure 3. Terms and measurements A. Terminal abdominal segments of pupa: *A*. Length of abdominal segment VII; *B*. Width of abdominal segment VII. B. Male adult penis valve. C. Wing of adult (male).

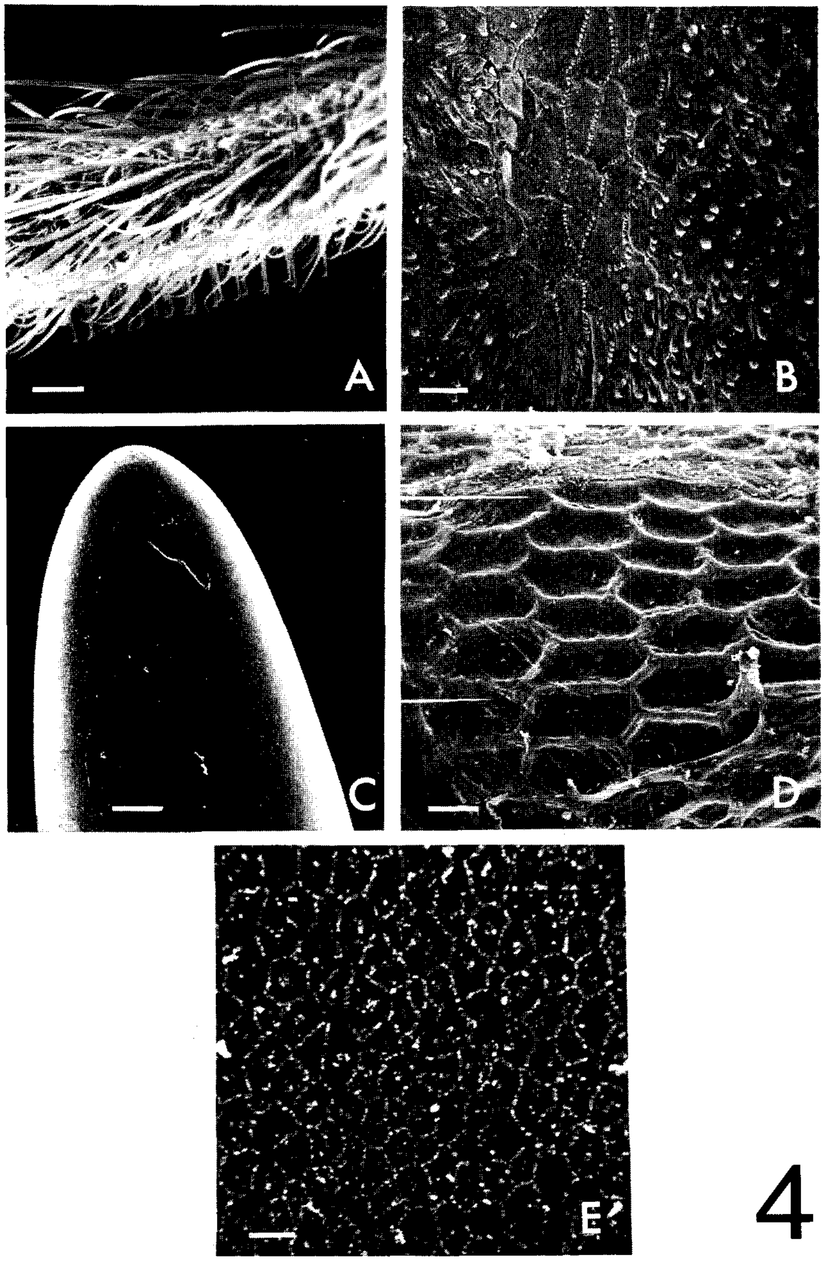

Figure 4. Scale line = 20μm for Figures A–D and 1μm for Figure E. A. Third tarsomere of midleg of female adult. B. Microsculpture of dorsal margin of head capsule of fourth instar larva. C. Exochorion of egg of *Chaoborus trivittatus*. D. Exochorion of egg of *Chaoborus cooki*. E. Sculpturing of dorsum of exochorion of *Chaoborus trivittatus*.

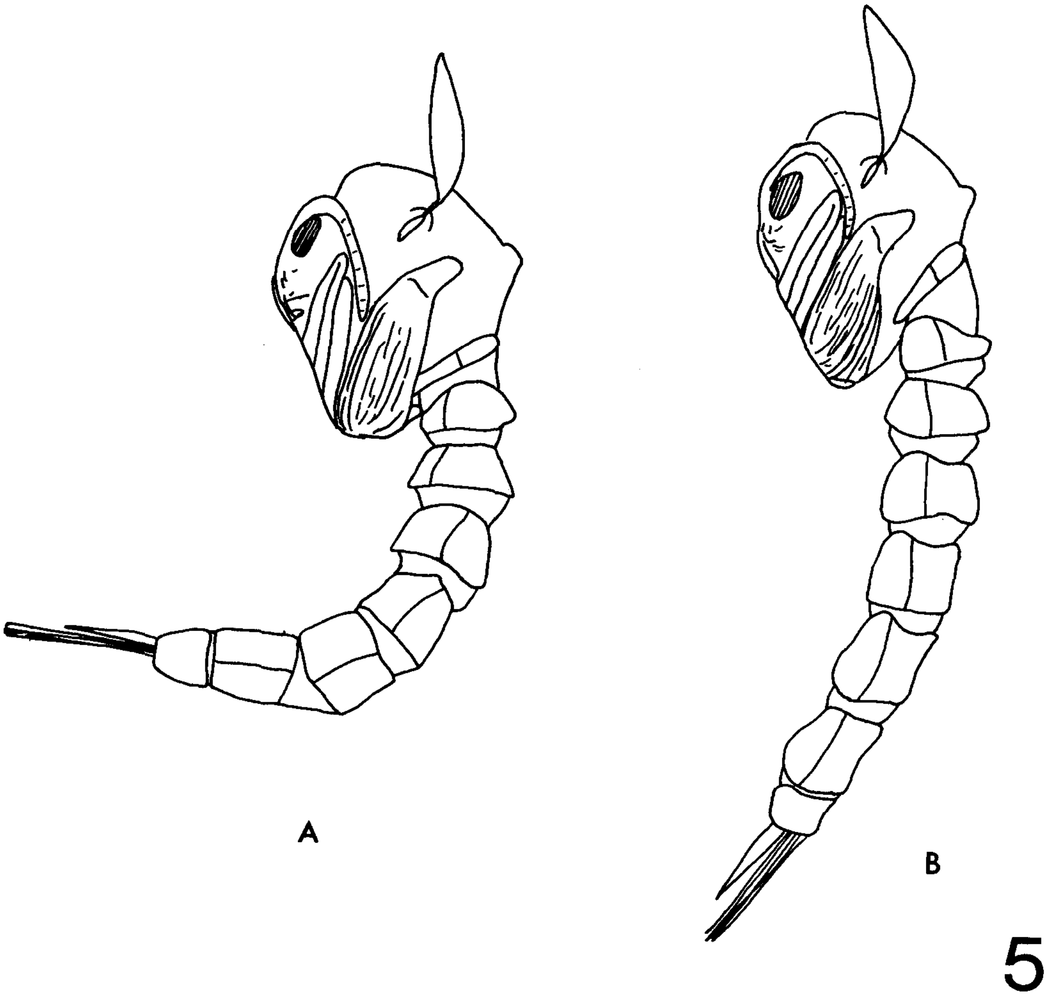

Figure 5. Posture of live pupae. A. *Chaoborus cooki*. B. *Chaoborus trivittatus*. Drawings from photographs of live pupae.

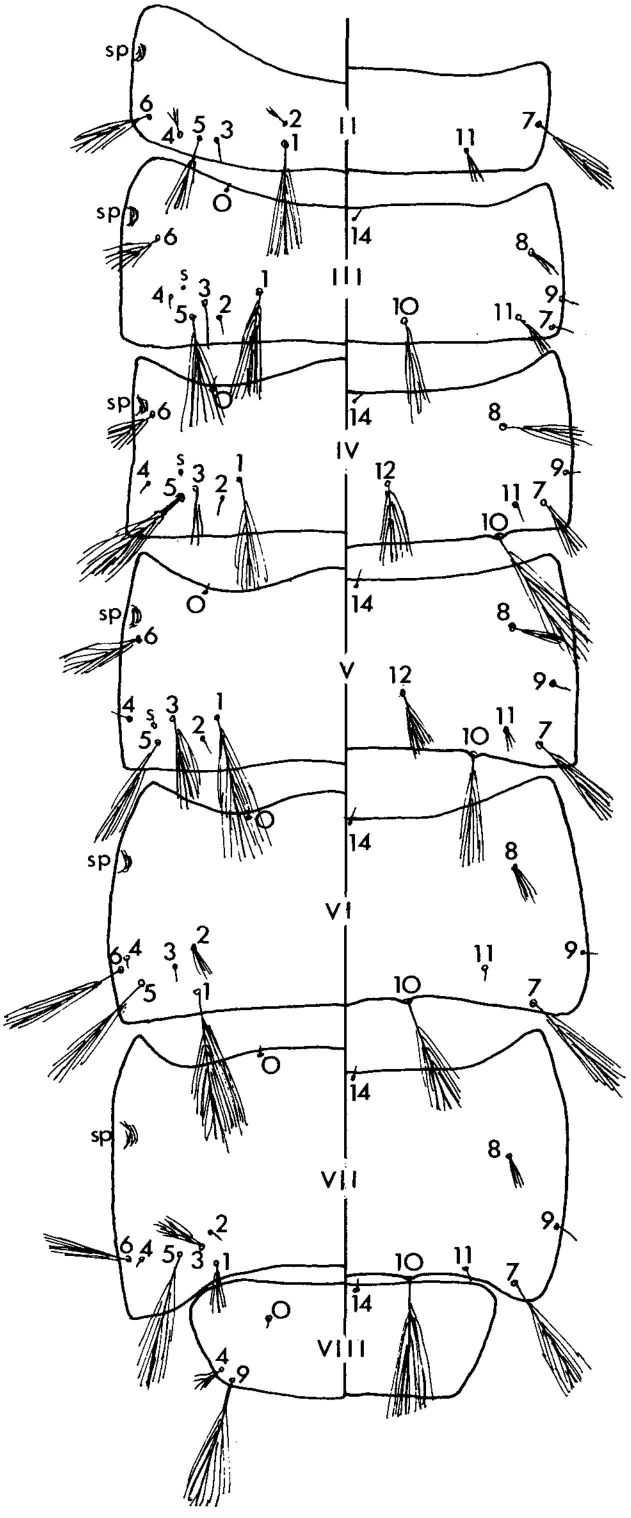

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Figure 6. Abdominal chaetotaxy of pupa of *Schadonophasma*. Setae numbered after Belkin *et al.* (1970). S: sensilla; sp: spiracular scar.

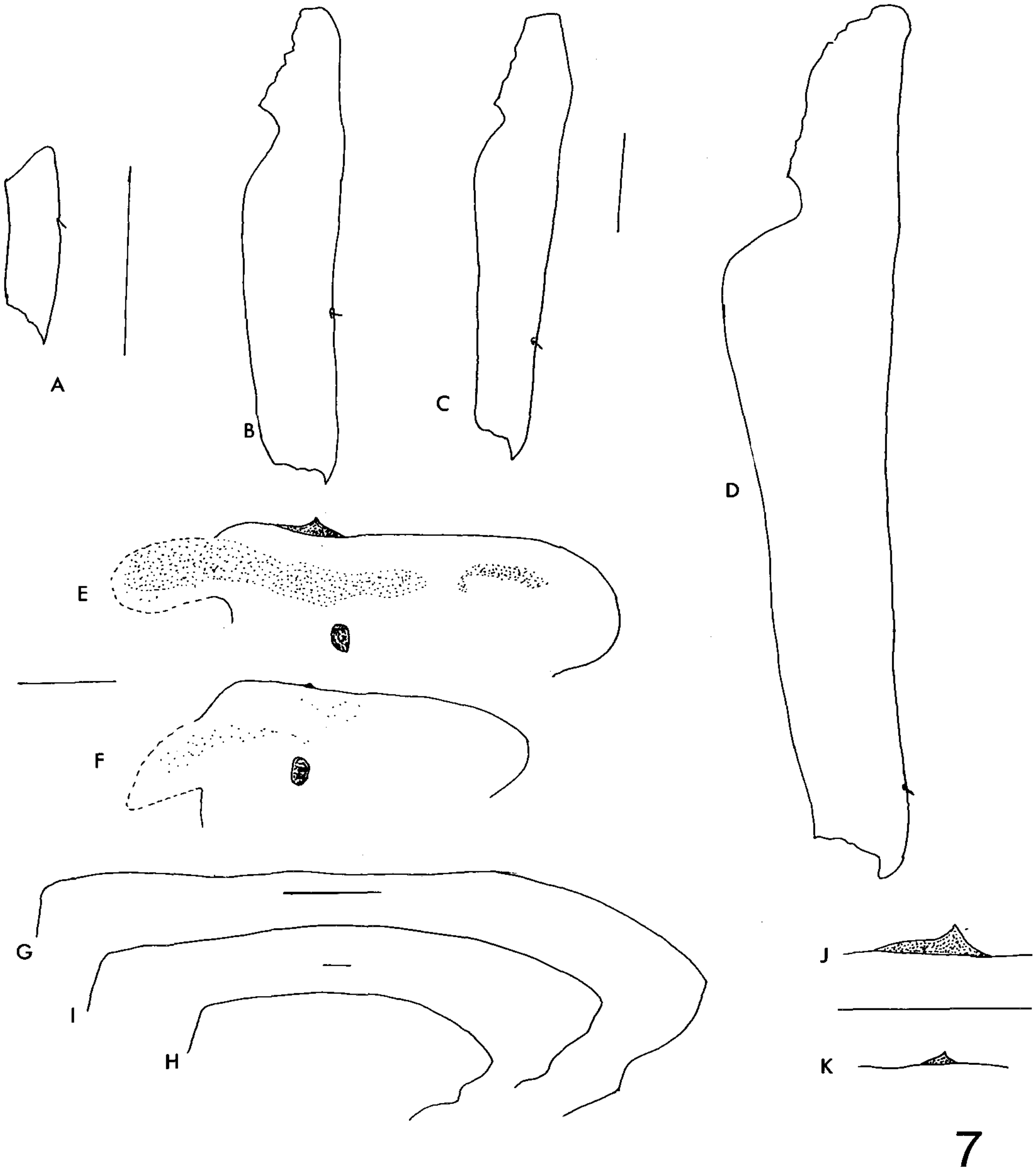

Figure 7. Scale line = 0.1 mm. Antenna and dorsal outline of head capsule of larval instars of *Schadonophasma*. Antennae: A. First instar; B. Second instar; C. Third instar; D. Fourth instar. Dorsal outline of head capsule: E. First instar of *Chaoborus cooki*; F. First instar of *Chaoborus trivittatus*; G. Second instar; H. Third instar; I. Fourth instar. J. Egg burster of first instar of *Chaoborus cooki*. K. Egg burster of first instar of *Chaoborus trivittatus*.

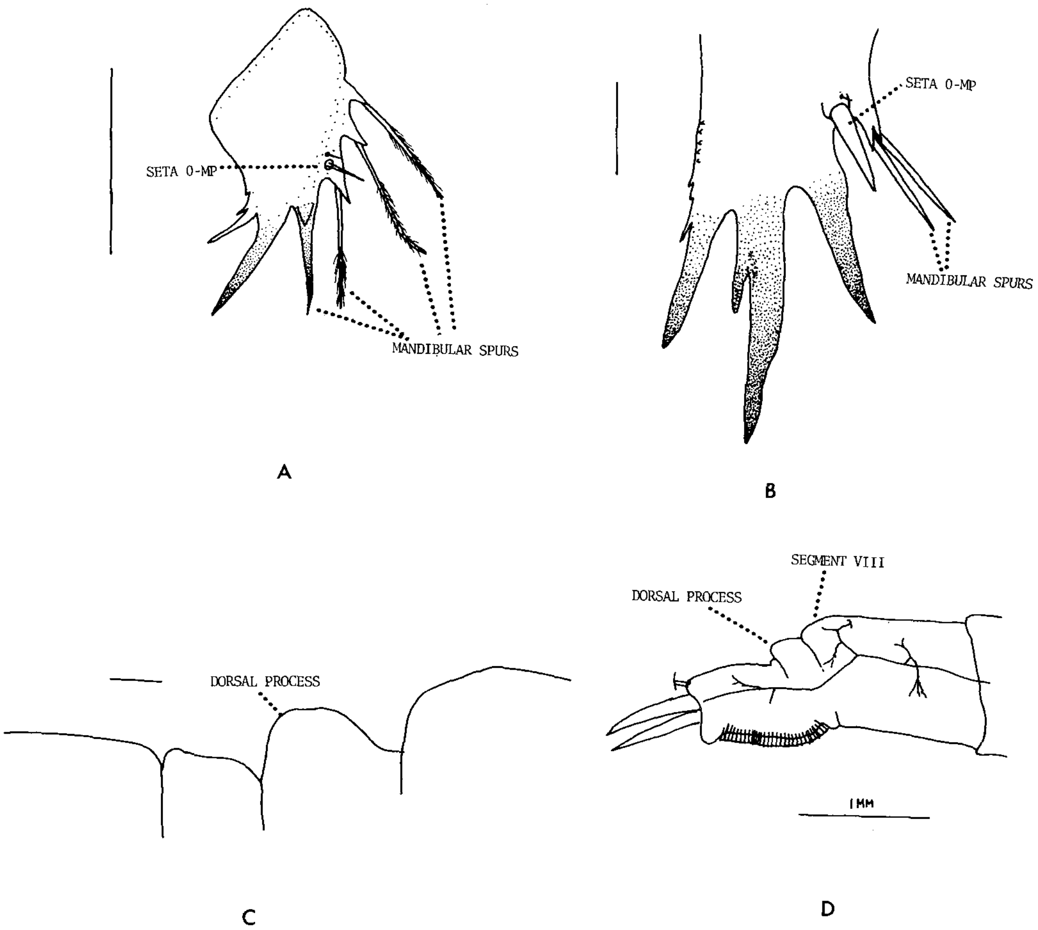

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Figure 8. Except where indicated, scale line = 0.1 mm. A. Mandible of first instar larva. B. Mandible of fourth instar larva (mandibular fan not shown). C. Dorsal process of fourth instar larva of *Chaoborus nyblaei*. D. Terminal abdominal segment of fourth instar larva of *Chaoborus cooki* showing position of tracheae.

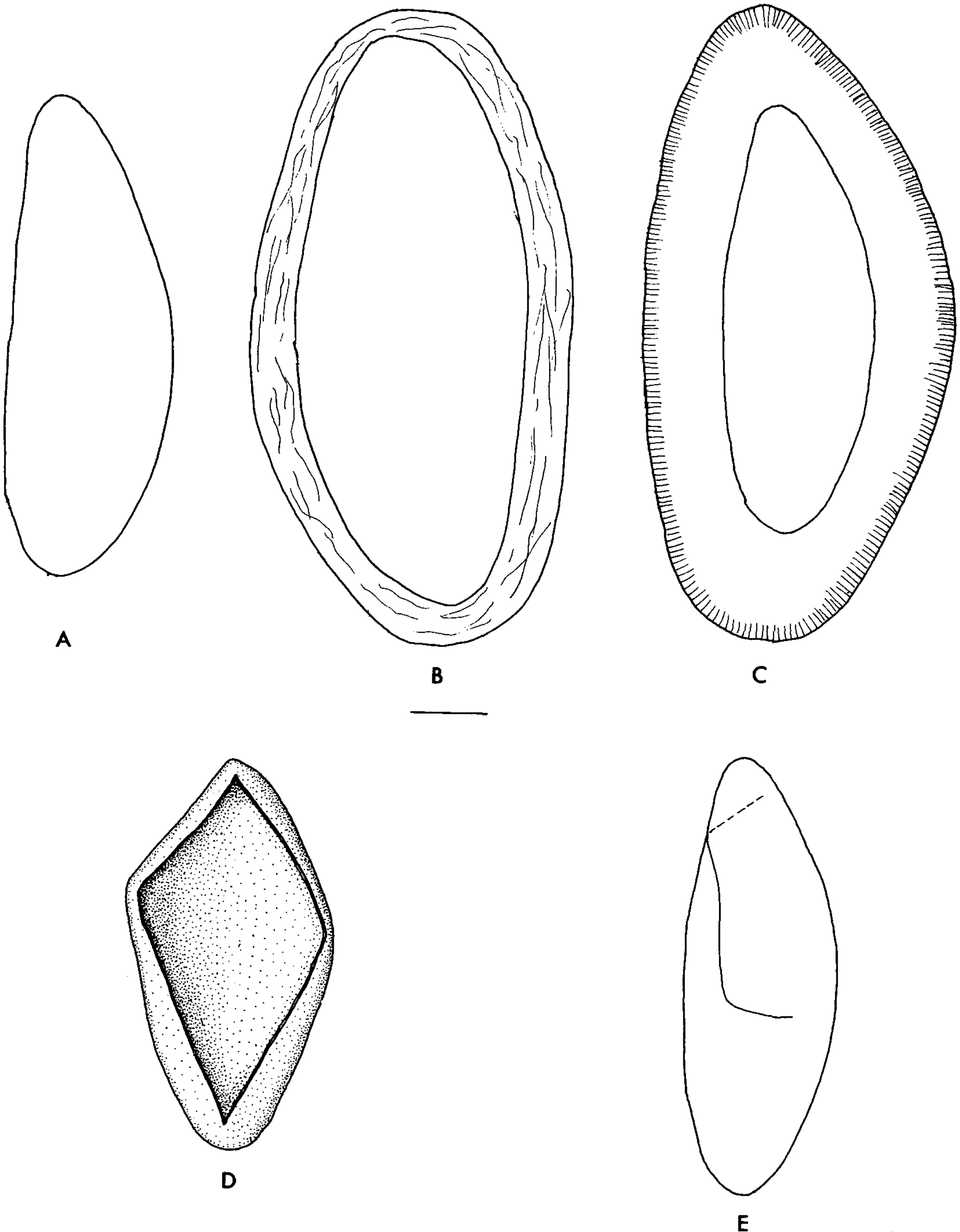

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Figure 9. Scale line = 0.1 mm. Egg structure. A. *Chaoborus trivittatus*. B. *Chaoborus nyblaei*. C. *Chaoborus cooki*. Egg shell. D. *Chaoborus trivittatus*. E. *Chaoborus cooki* (fracture line indicated).

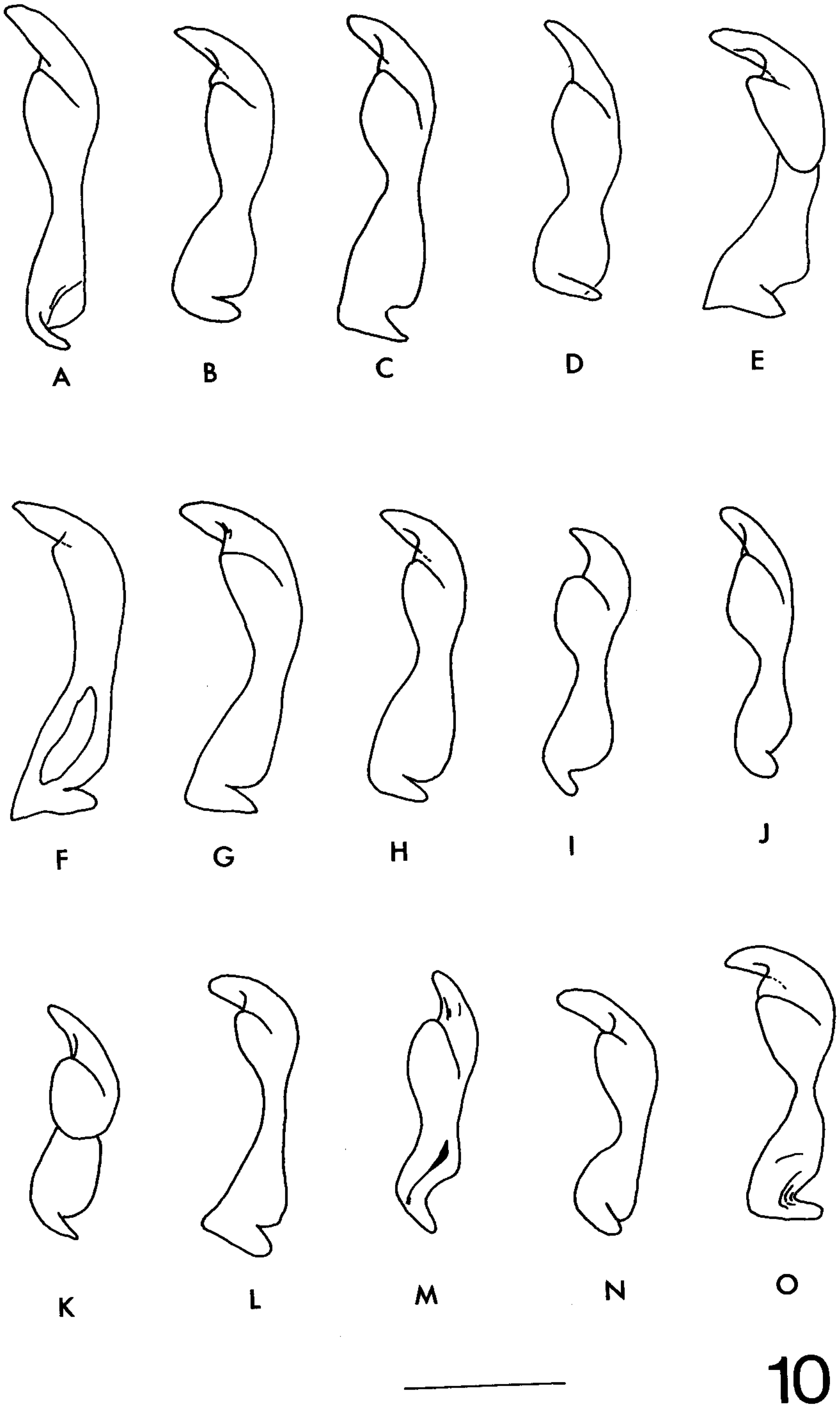

Figure 10. Scale line = 0.1 mm. Penis valves of adult male *Chaoborus trivittatus*. A–G. Intrapopulational variation of specimens from 2.4 km west of Edmonton, Alberta. H–O. Interpopulational variation of specimens from: H. Banff, Alberta; I. Hoodsport, Washington; J. North Burgess Twp., Ontario; K. Whitehorse, Yukon Territory; L. Old Chelsea, Quebec; M. Lake 241, Kenora, Ontario (holotype of *Chaoborus brunskilli*); N. Stanford, California; O. Maine (holotype of *Chaoborus trivittatus*).

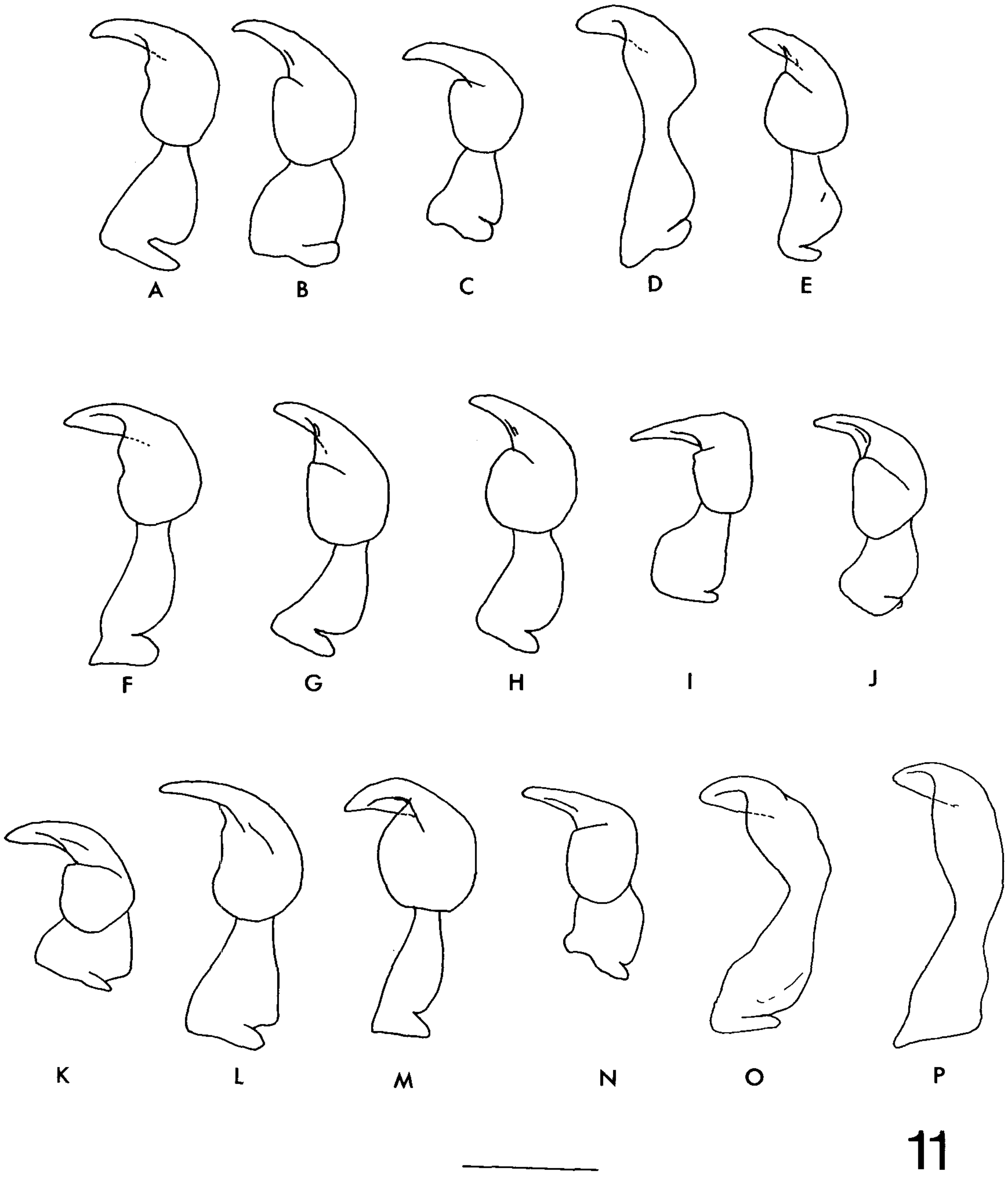

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Figure 11. Scale line = 0.1 mm. Penis valves of adult male *Chaoborus cooki*. A–H. Intrapopulational variation of specimens from 1.4 km west of George Lake, Alberta. I–N. Interpopulational variation of specimens from: I. Km. 140, Dempster Highway, Yukon Territory; J. Churchill, Manitoba; K. Gillam, Manitoba; L. Whitehorse, Yukon Territory; M. Yellowknife, Northwest Territories; N. Chisholm, Ontario. Penis valves of adult male *Chaoborus nyblaei*. Specimens from: O. 2–3 km SW Nuorgam, Finland; P. Abisko, Sweden.

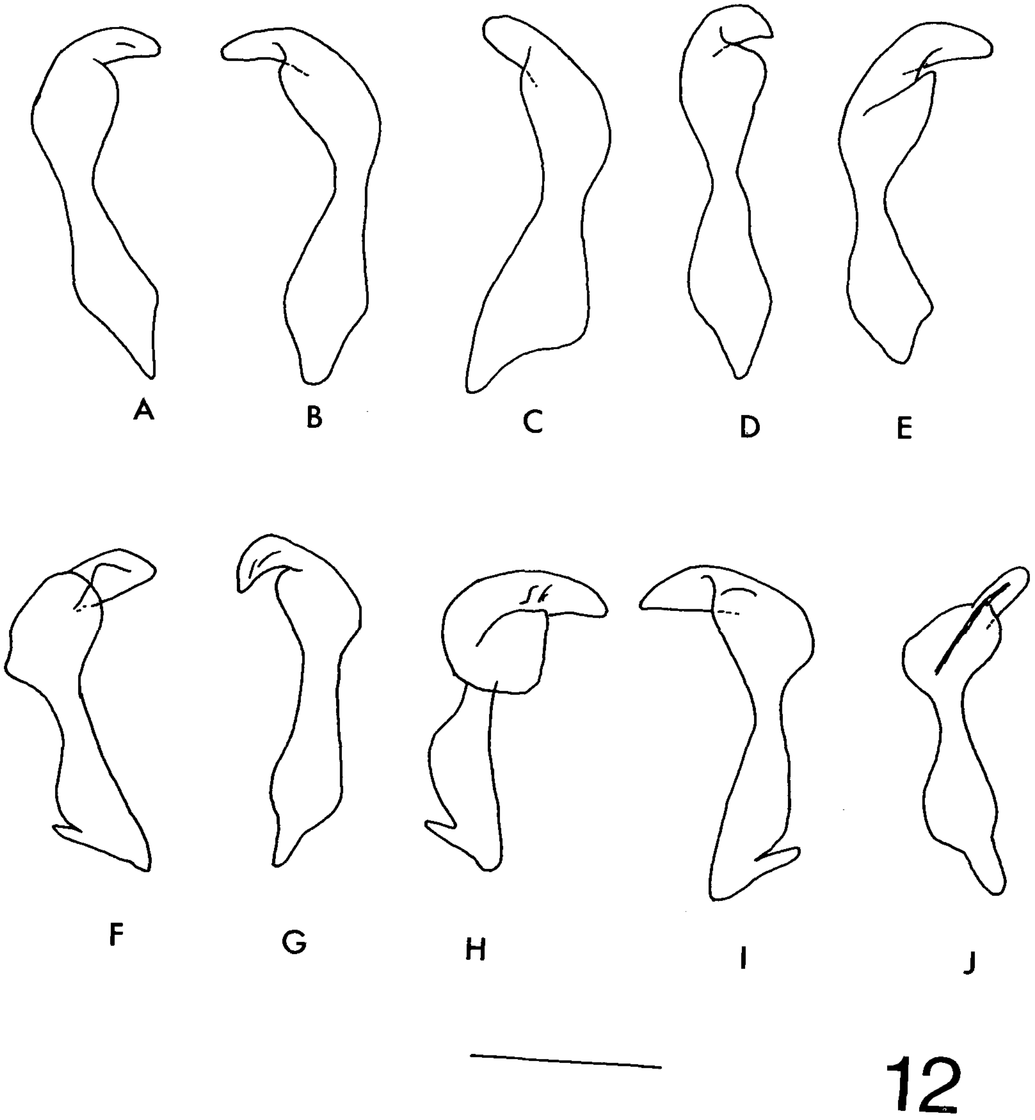

Figure 12. Scale line = 0.1 mm. Variation of penis valves of adult males due to orientation. A–E. *Chaoborus trivittatus* from 2.4 km west of Edmonton, Alberta. F–J. *Chaoborus cooki* from 32 km west of Edson, Alberta.

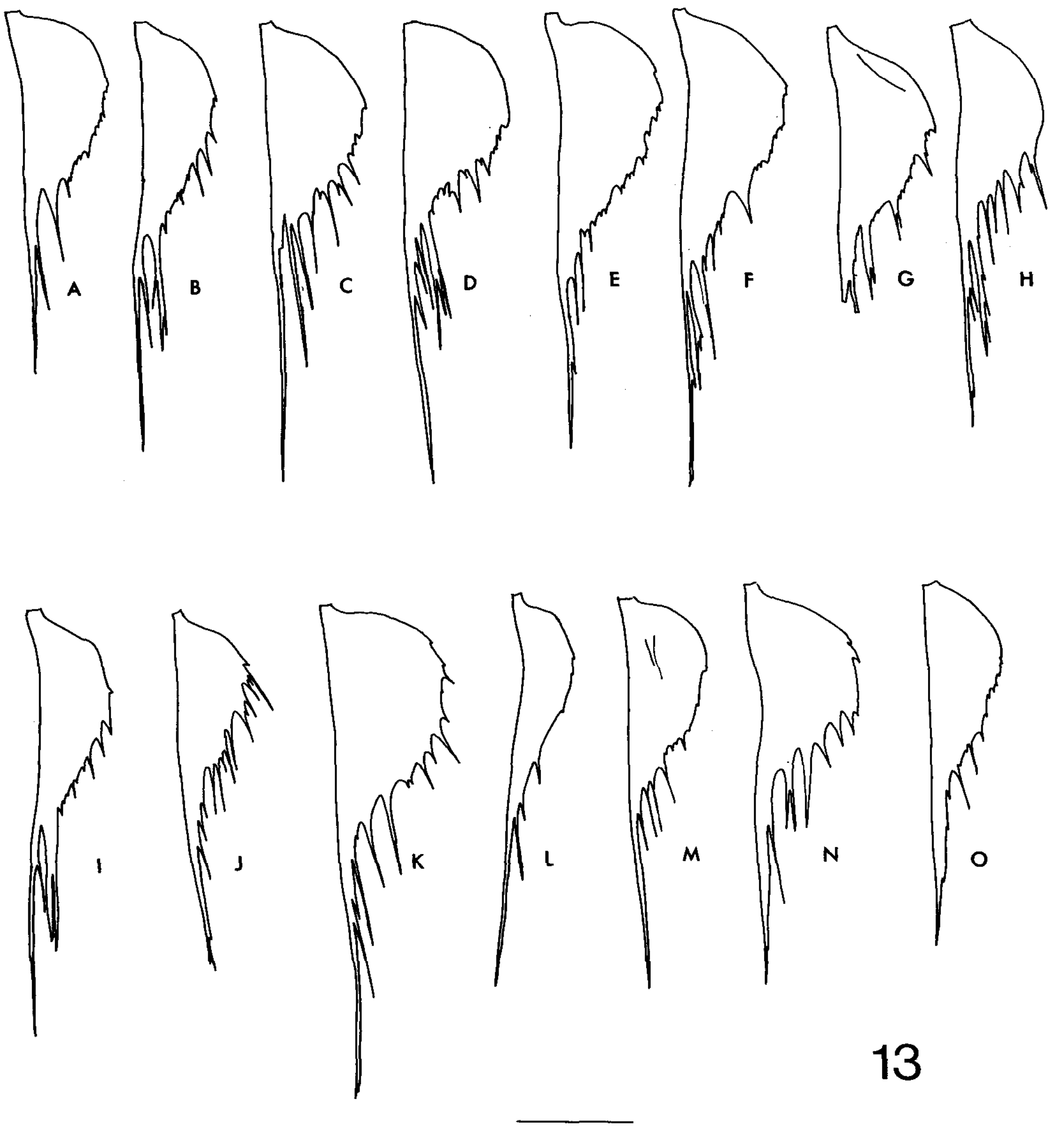

Figure 13. Scale line = 0.1 mm. Prelabral appendages of fourth instar larvae of *Chaoborus trivittatus*. A–G. Intrapopulational variation of specimens from 2.4 km west of Edmonton, Alberta. H–O. Interpopulational variation of specimens from: H. 4.8 km north of St. John's, Newfoundland; I. 2.4 km west of Edmonton, Alberta; J. 2.4 km south of Robb, Alberta; K. Gwendoline Lake, British Columbia; L. 4.8 km east of Sicamous, British Columbia; M. 45 km east of Jasper, Alberta; N. Lake 241, Kenora, Ontario; O. East Henry Pond, Jasper National Park, Alberta.

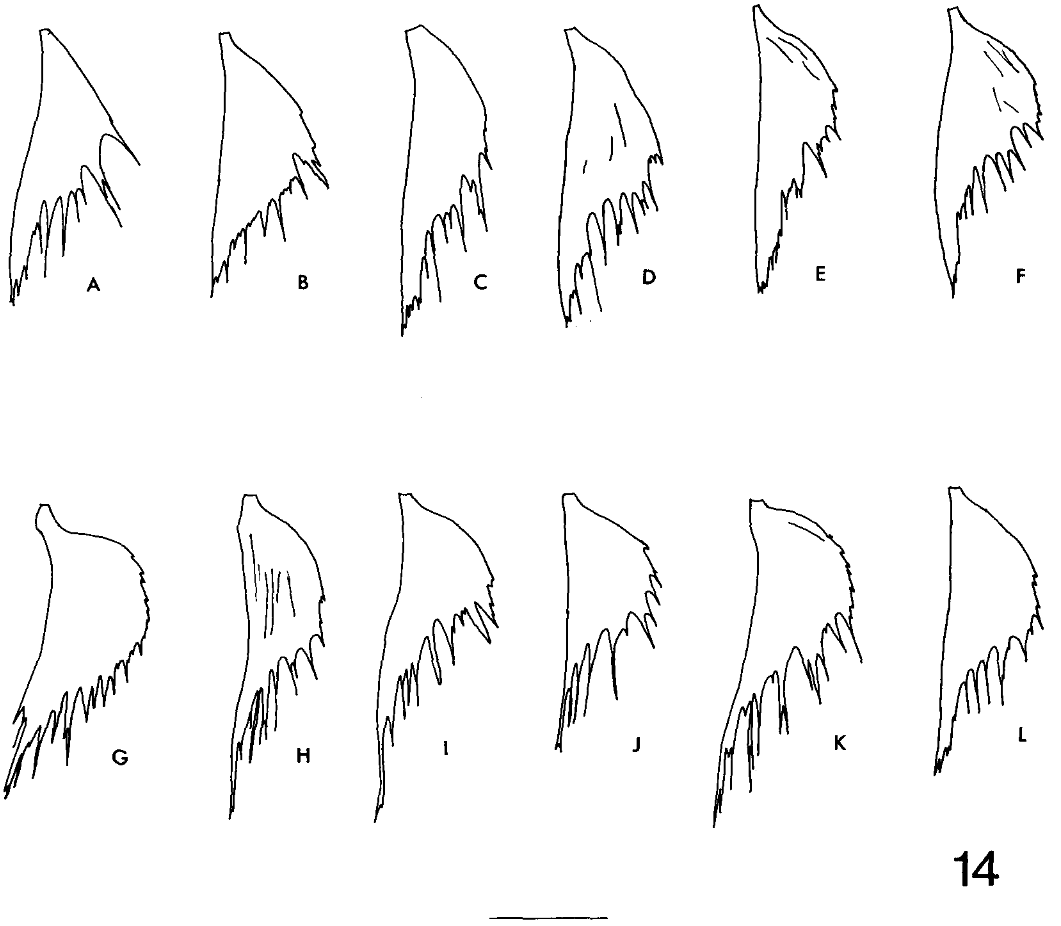

Figure 14. Scale line = 0.1 mm. Prelabral appendages of fourth instar larvae of *Chaoborus cooki*. A–F. Intrapopulational variation of specimens from 1.6 km south of Jasper, Alberta. G–L. Interpopulational variation of specimens from: G. Churchill, Manitoba; H. Pond nr. Harris River, Northwest Territories; I. Dempster Highway, Yukon Territory; J. 1.4 km west of George Lake, Alberta; K. Klutlan Glacier moraine, Yukon Territory; L. 23.3 km west of Jasper, Alberta.

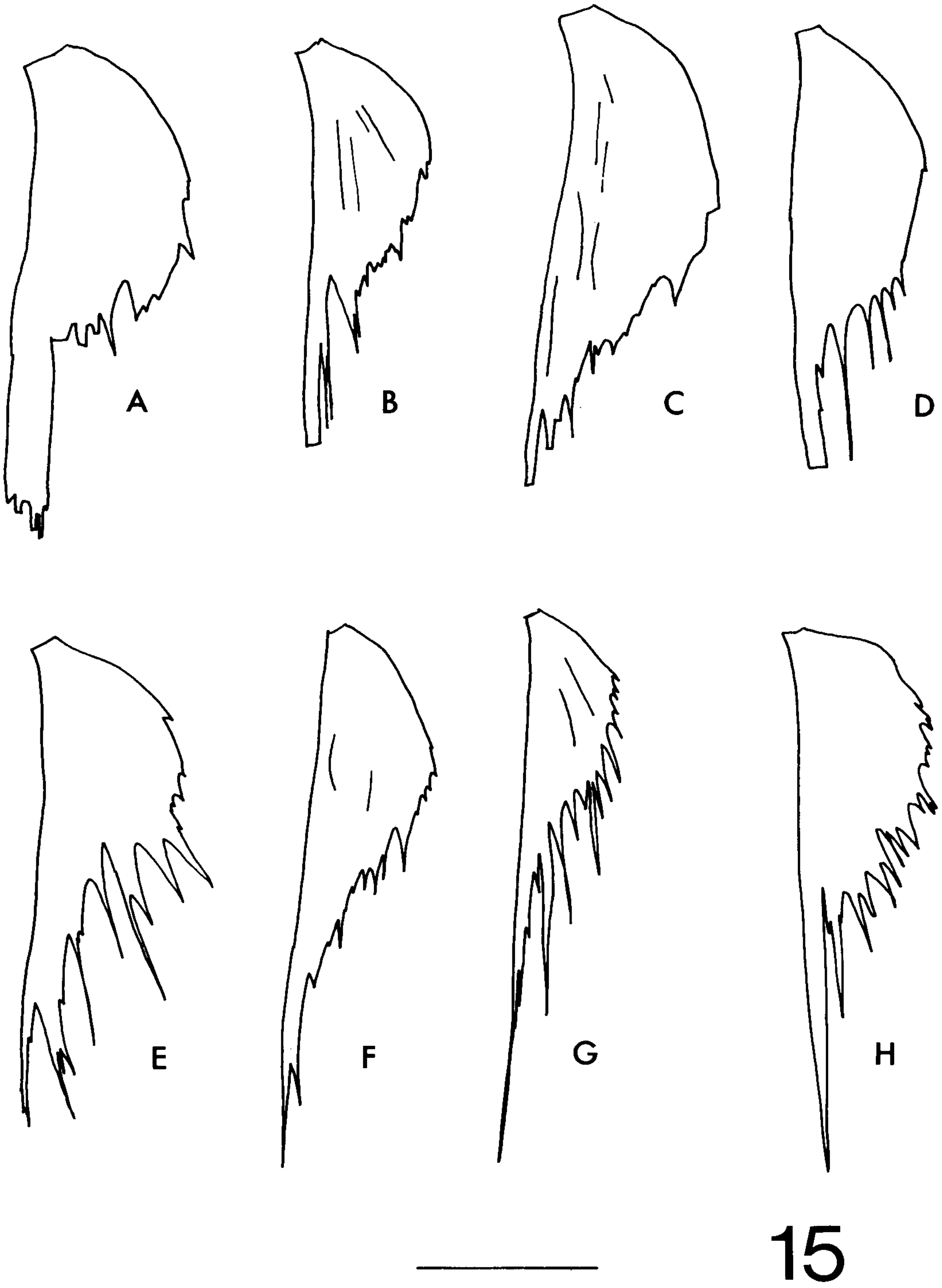

Figure 15. Scale line = 0.1 mm. Prelabral appendages of fourth instar larvae of *Chaoborus nyblaei* from 2-3 km southwest of Nuorgam, Finland.

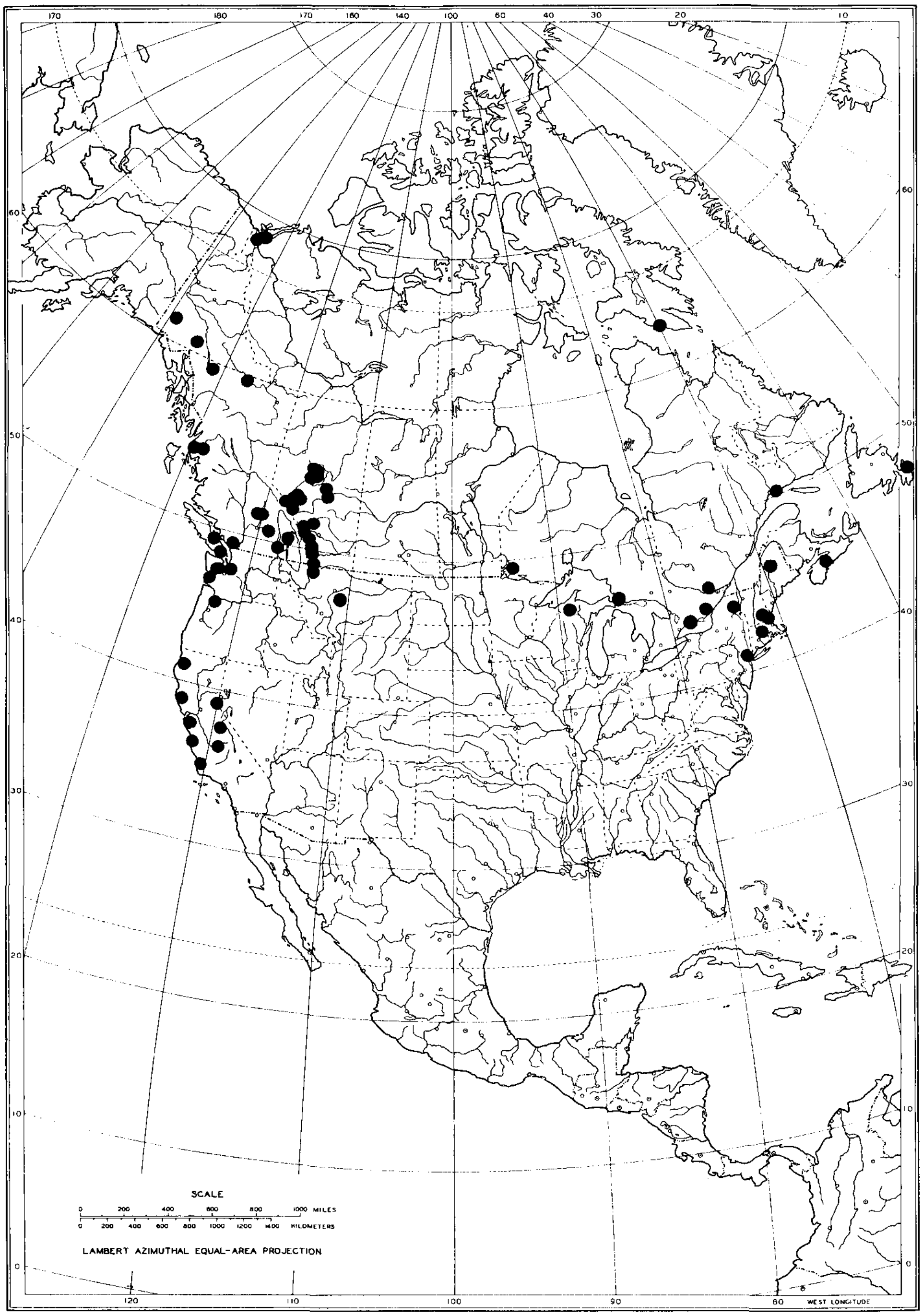

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Figure 16. Known distribution of *Chaoborus trivittatus*.

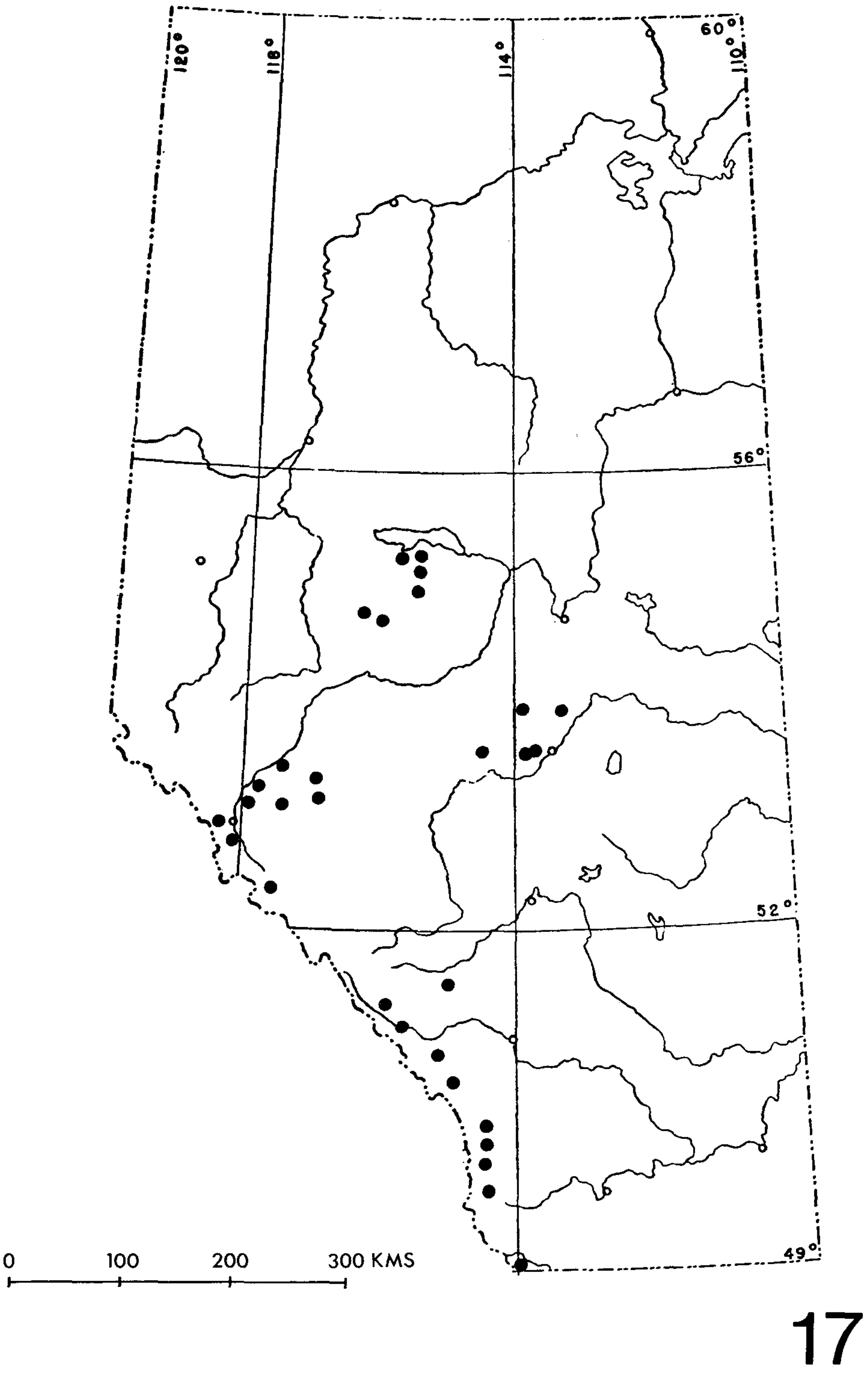

Figure 17. Known distribution of *Chaoborus trivittatus* in Alberta.

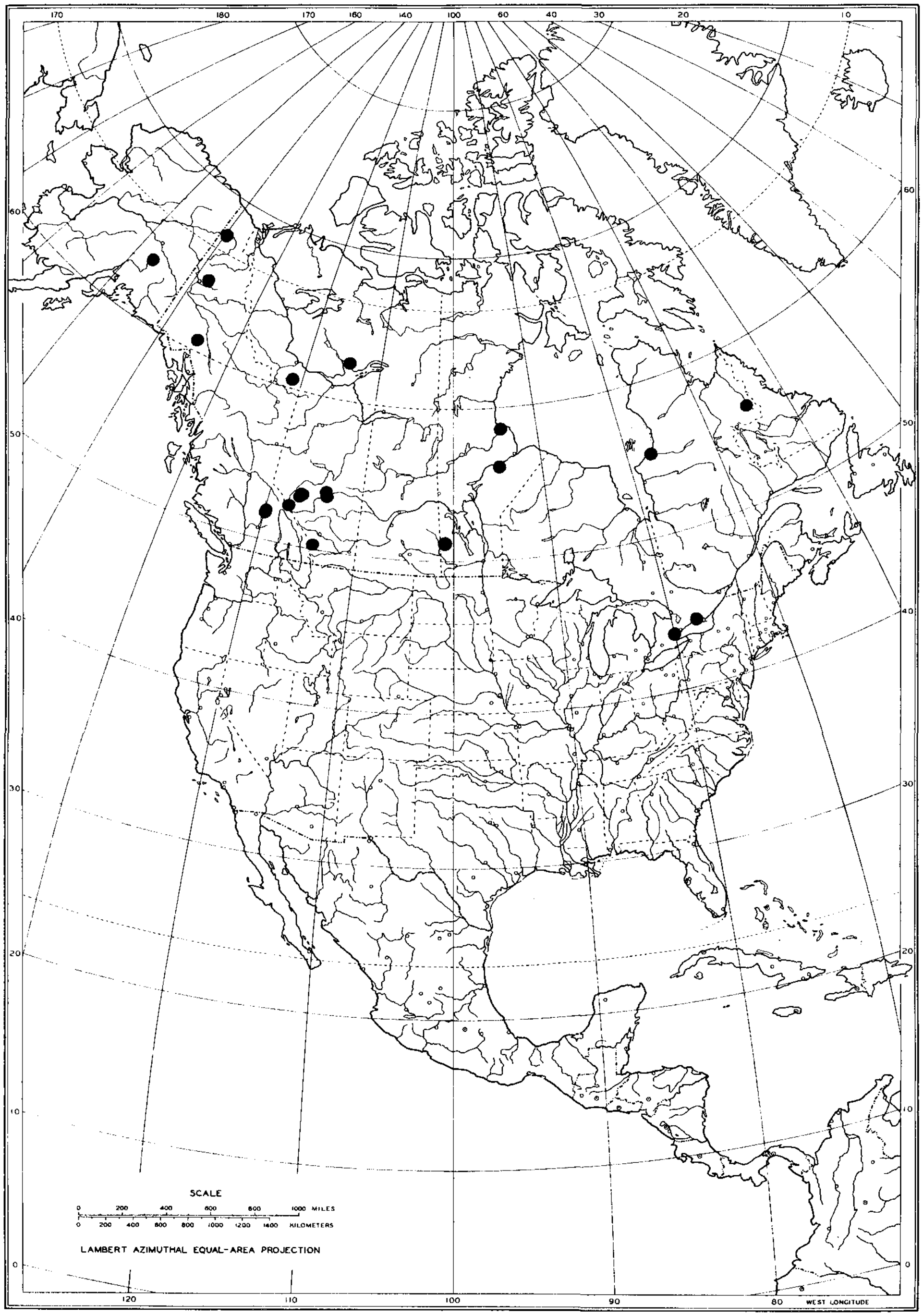

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Figure 18. Known distribution of *Chaoborus cooki*.

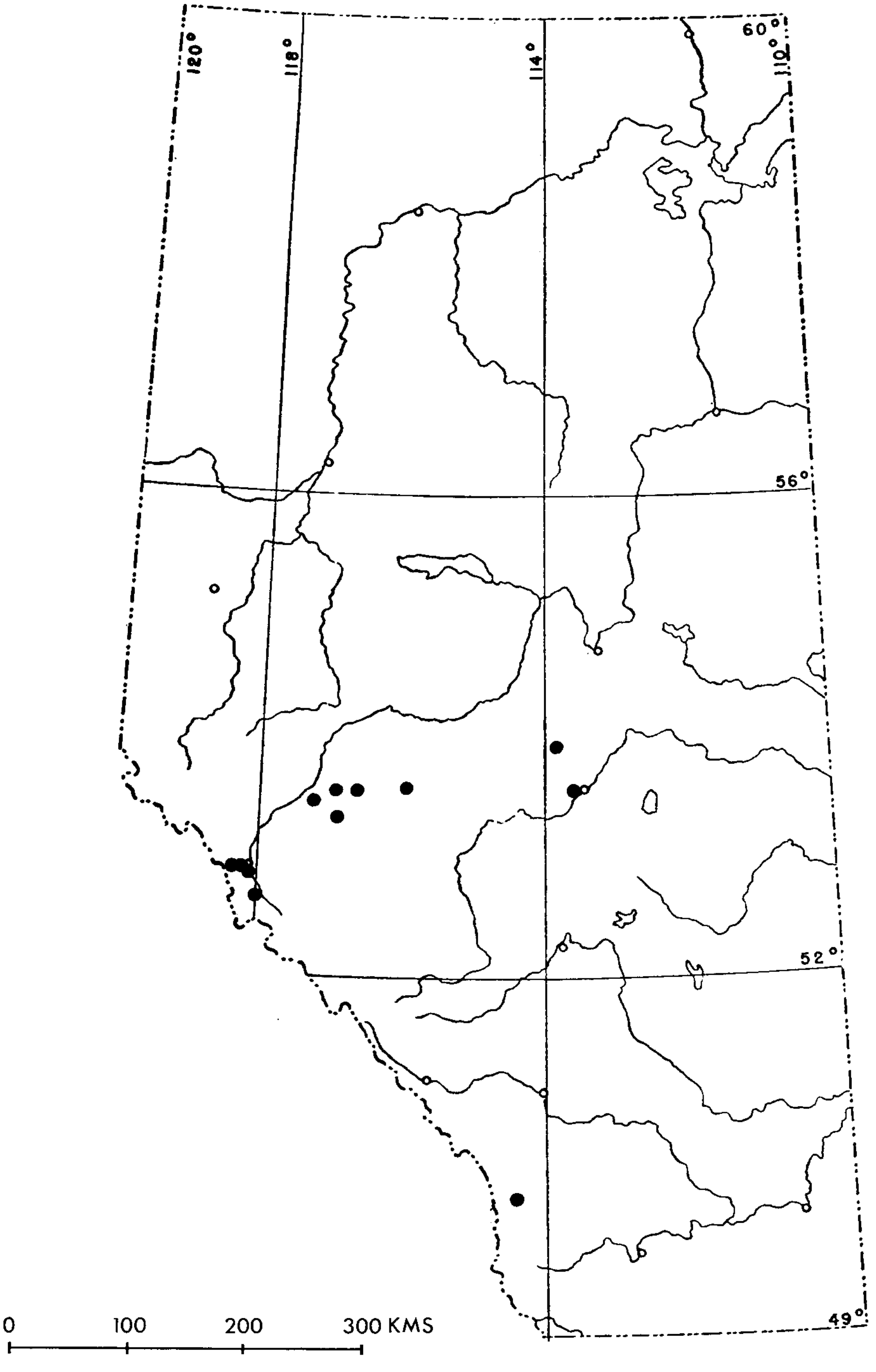

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Figure 19. Known distribution of *Chaoborus cooki* in Alberta.

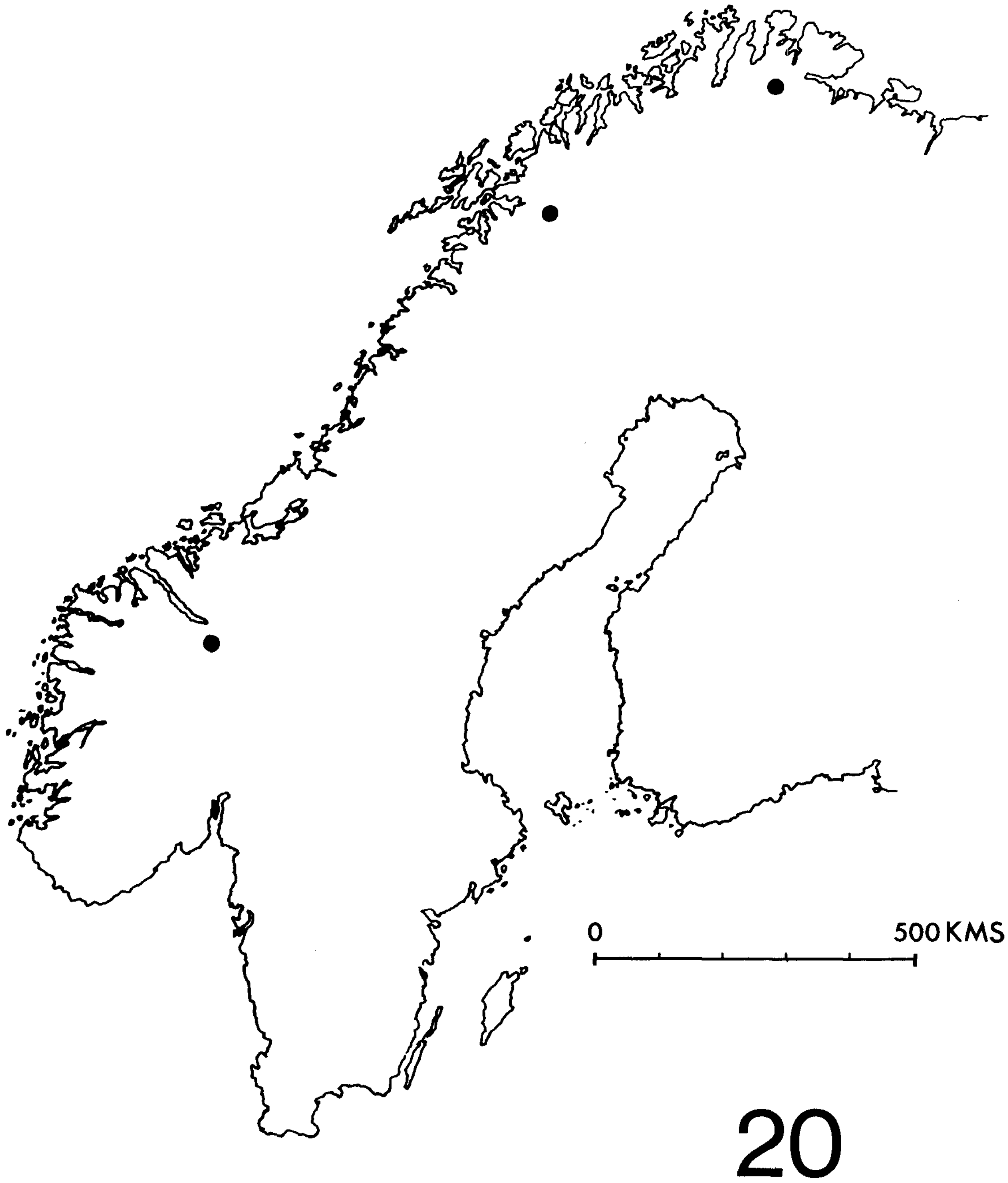

Figure 20. Known distribution of *Chaoborus nyblaei*.

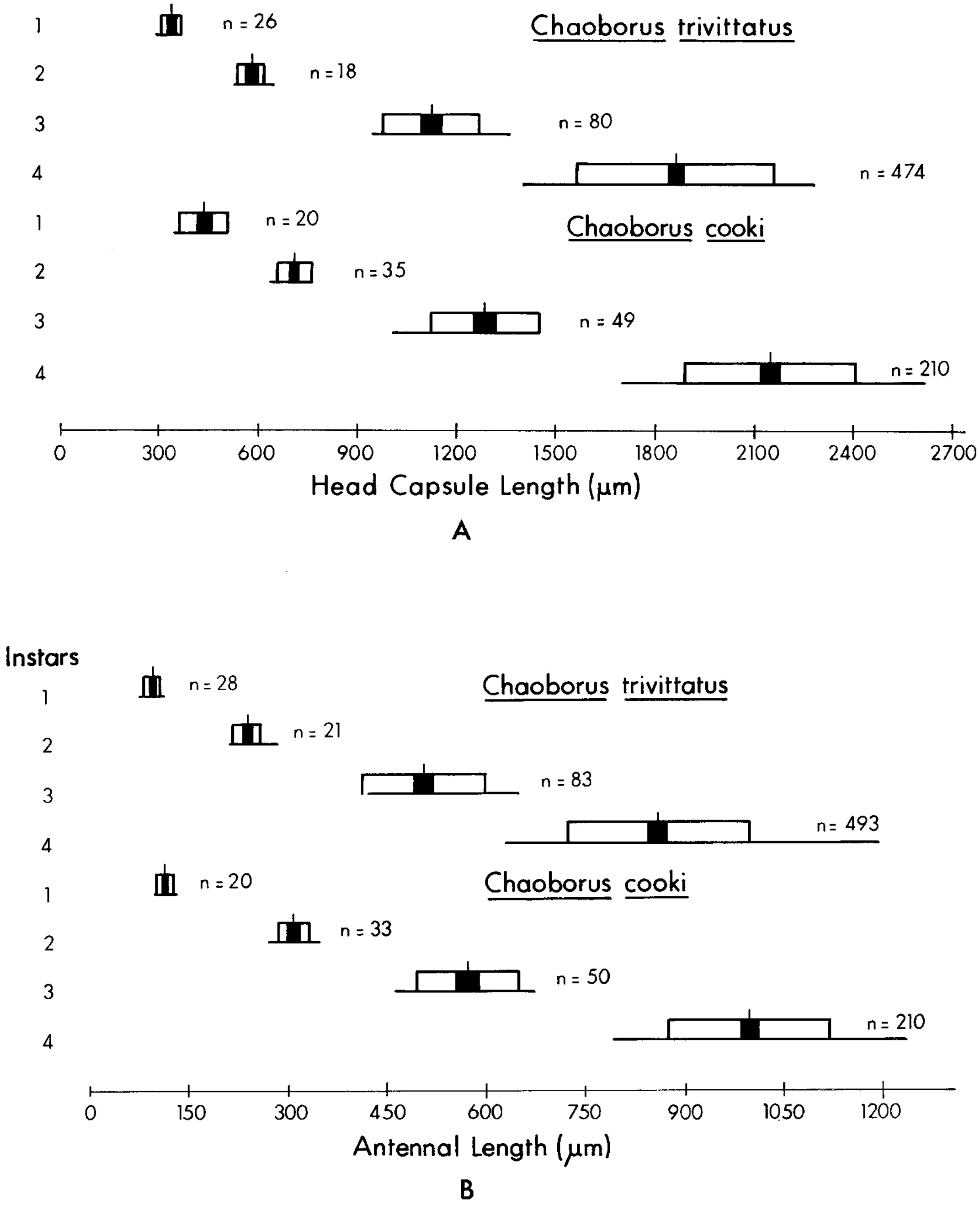

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Figure 21. Variation of characters of larval instars of *Chaoborus trivittatus* and *Chaoborus cooki*. A. Head capsule length. B. Antennal length.

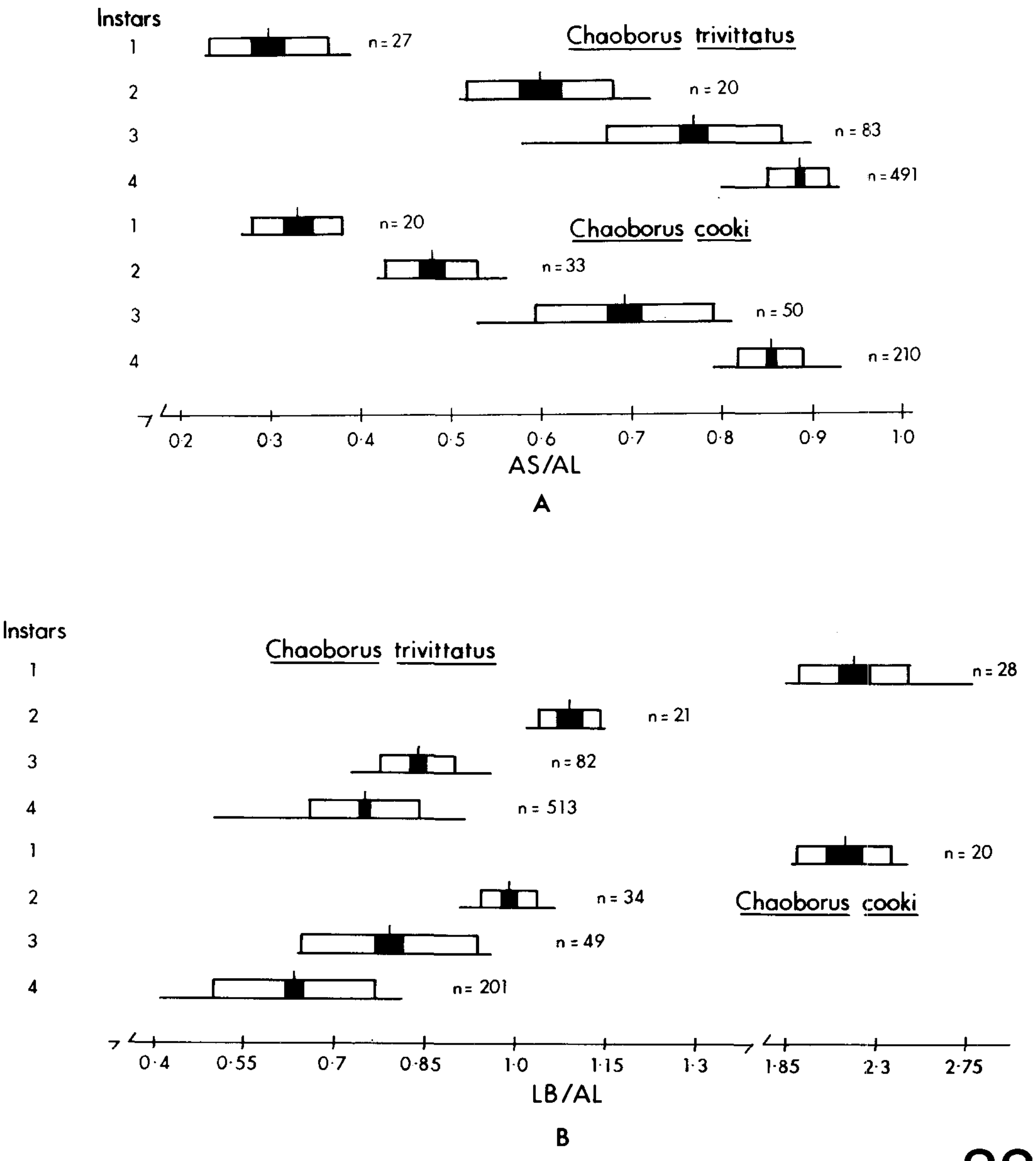

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Figure 22. Variation of characters of larval instars of *Chaoborus trivittatus* and *Chaoborus cooki*. A. AS/AL. B. LB/AL.

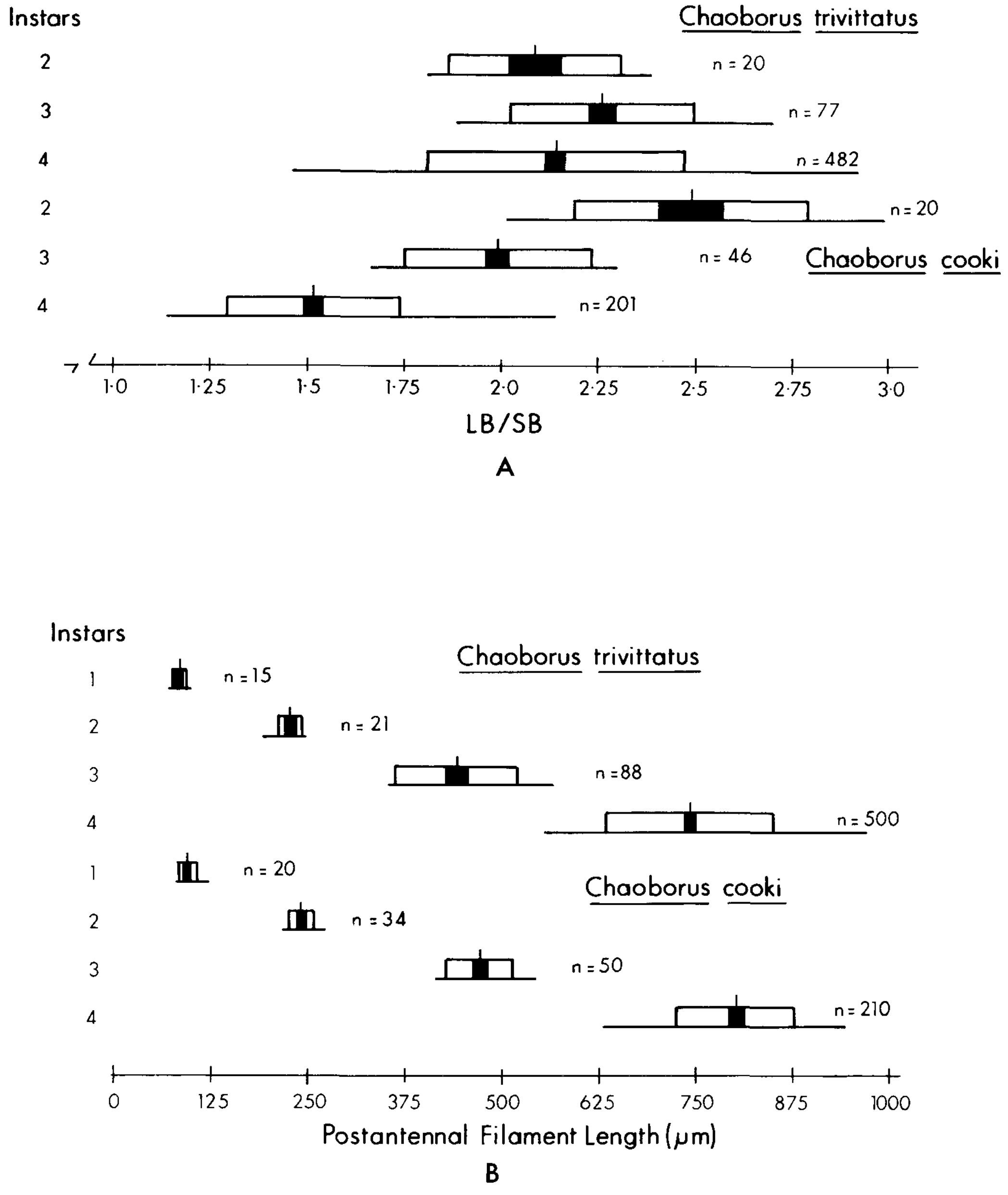

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Figure 23. Variation of characters of larval instars of *Chaoborus trivittatus* and *Chaoborus cooki*. A. LB/SB. B. Postantennal filament length.

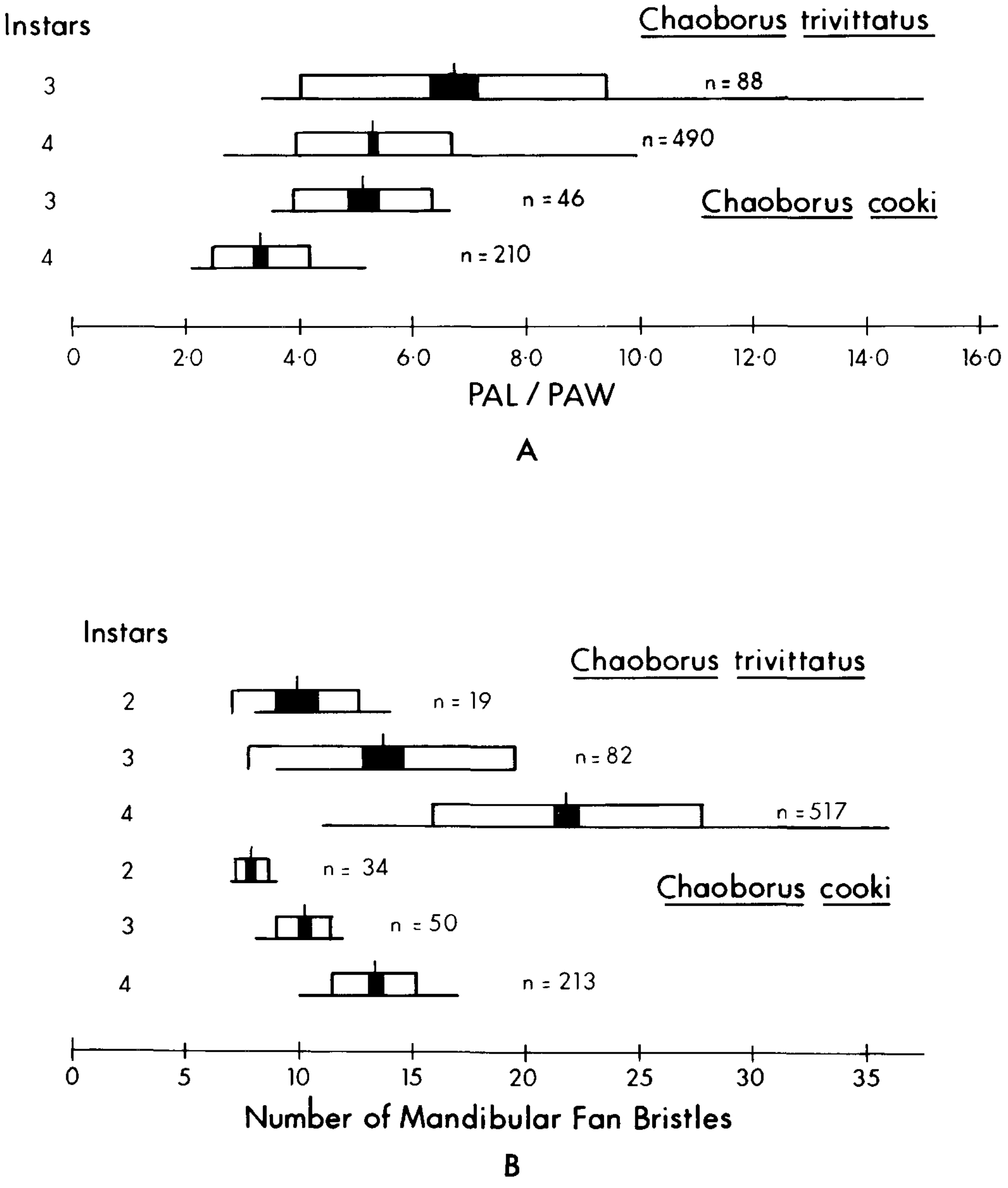

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Figure 24. Variation of characters of larval instars of *Chaoborus trivittatus* and *Chaoborus cooki*. A. PAL/PAW. B. Number of mandibular fan bristles.

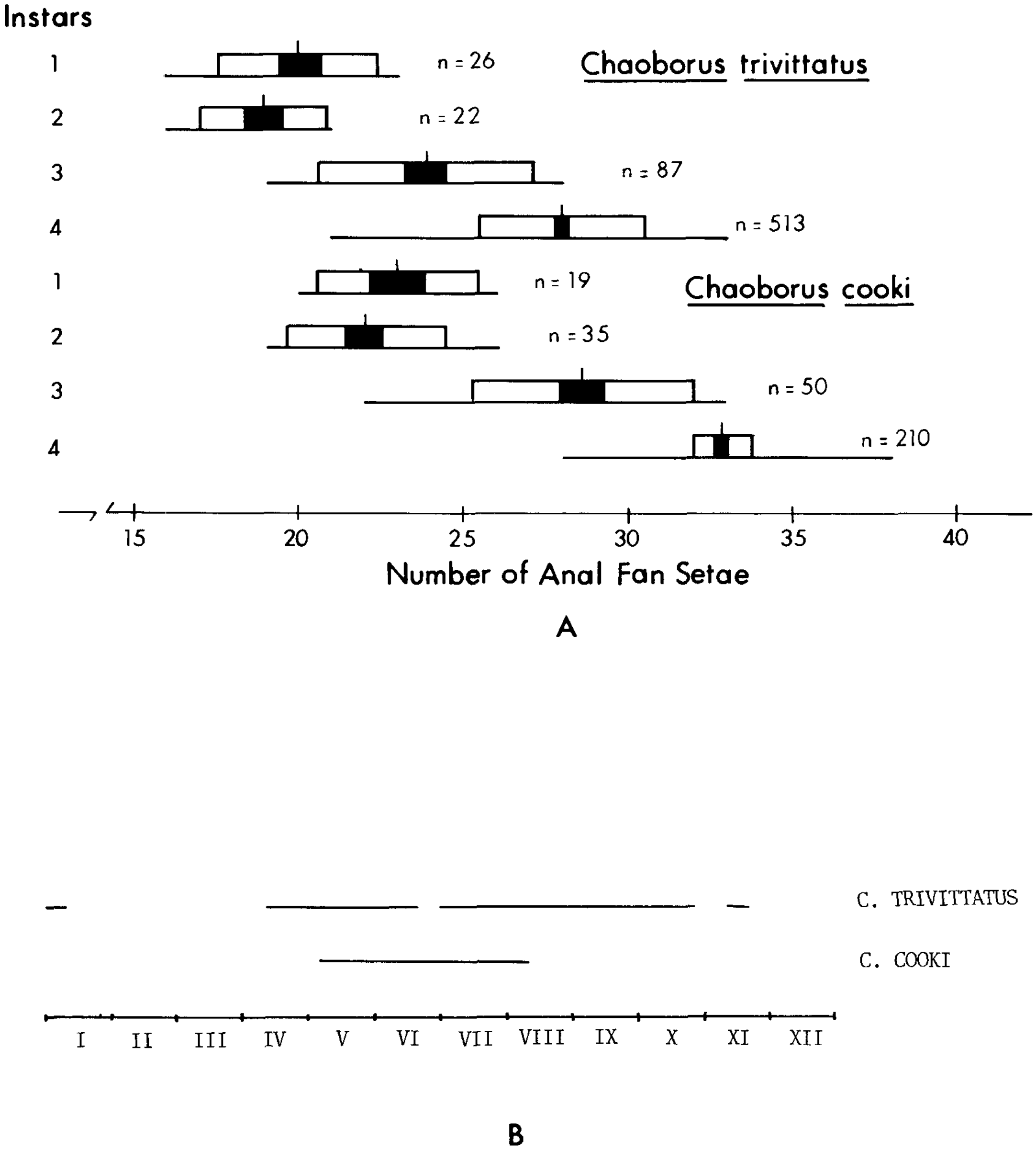

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Figure 25. Variation of characters of larval instars of *Chaoborus trivittatus* and *Chaoborus cooki*. A. Number of anal fan setae. B. Temporal distribution of fourth instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki*.

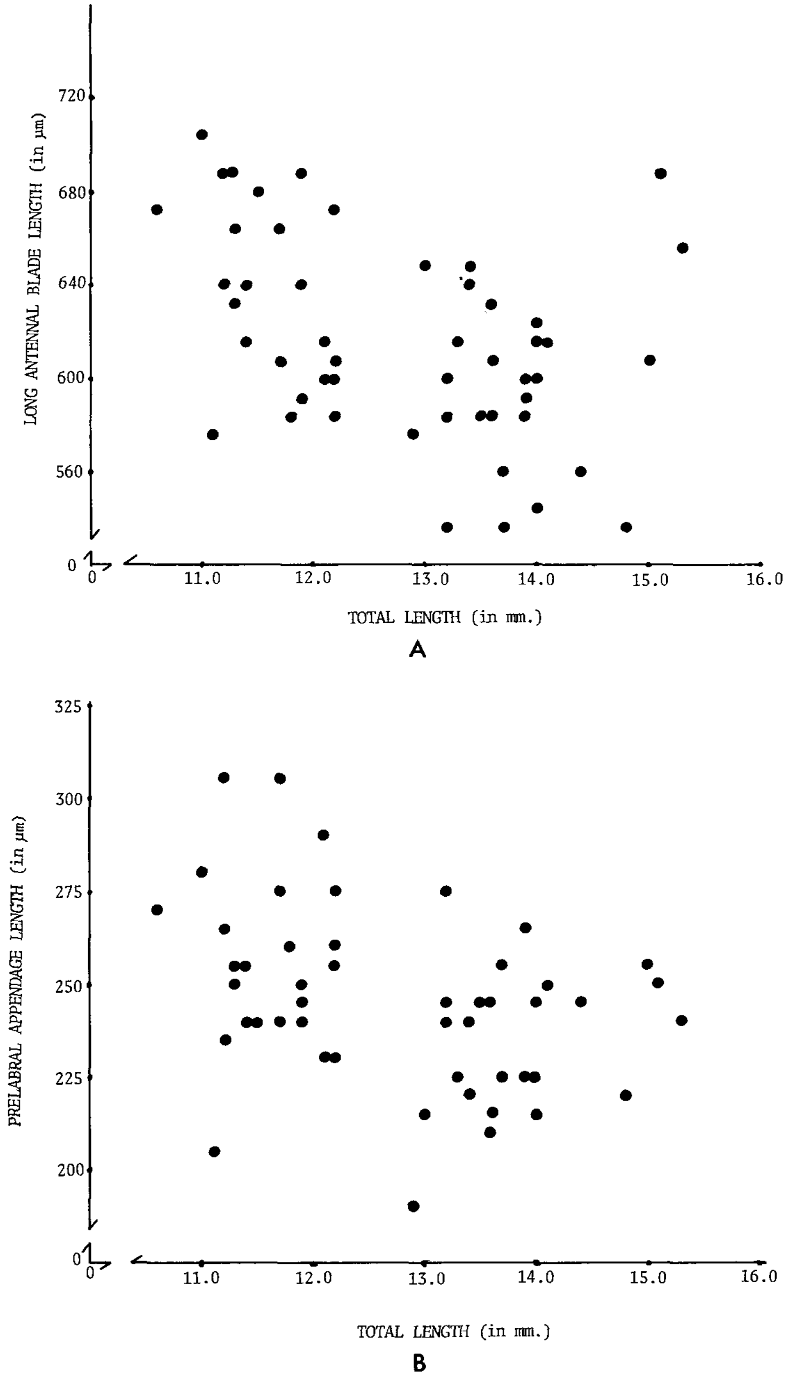

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Figure 26. Age-related variation of male fourth instar larvae of *Chaoborus cooki*. A. Relationship between total length and long antennal blade length. B. Relationship between total length and prelabral appendage length.

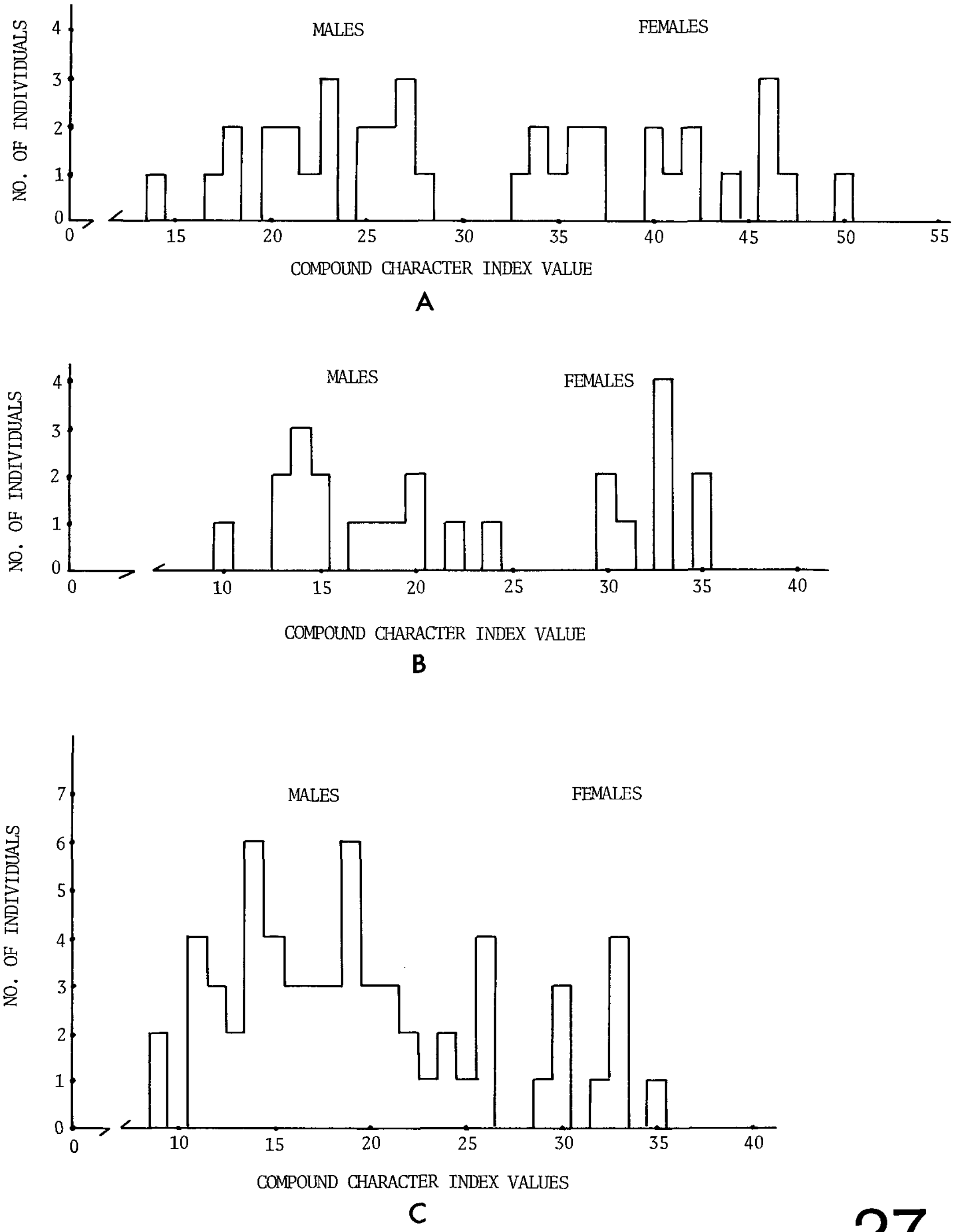

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Figure 27. Results of compound character index used to sex fourth instar larvae. A. Of *Chaoborus trivittatus* from 2.4 km west of Edmonton, Alberta. B. Of *Chaoborus cooki* from 32 km west of Edson, Alberta. C. Of *Chaoborus cooki* from 1.6 km south of Jasper, Alberta.

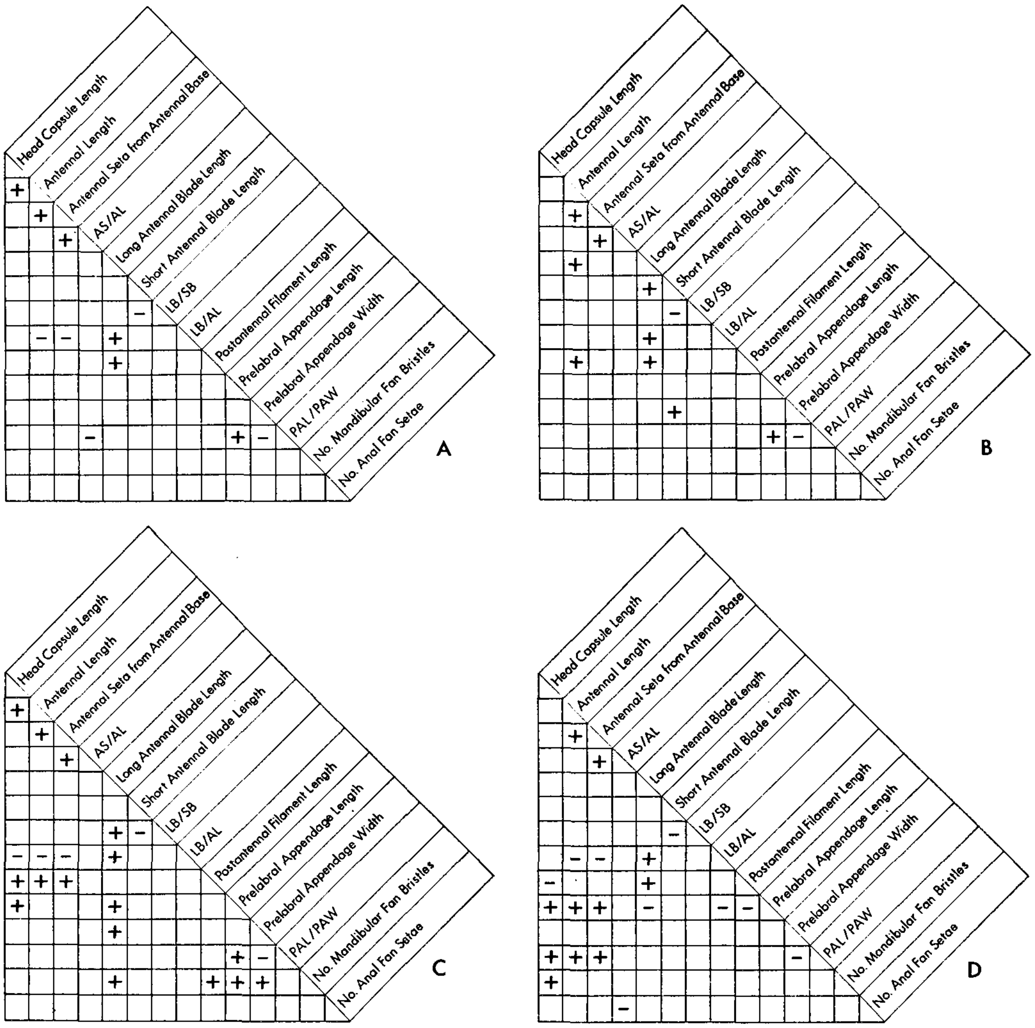

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Figure 28. Correlation of characters of fourth instar larvae. A. Male *Chaoborus trivittatus* B. Female *Chaoborus trivittatus*. C. Male *Chaoborus cooki*. D. Female *Chaoborus cooki*. Open spaces represent lack of significant correlation; + and - signify positively and negatively significant correlations, respectively.

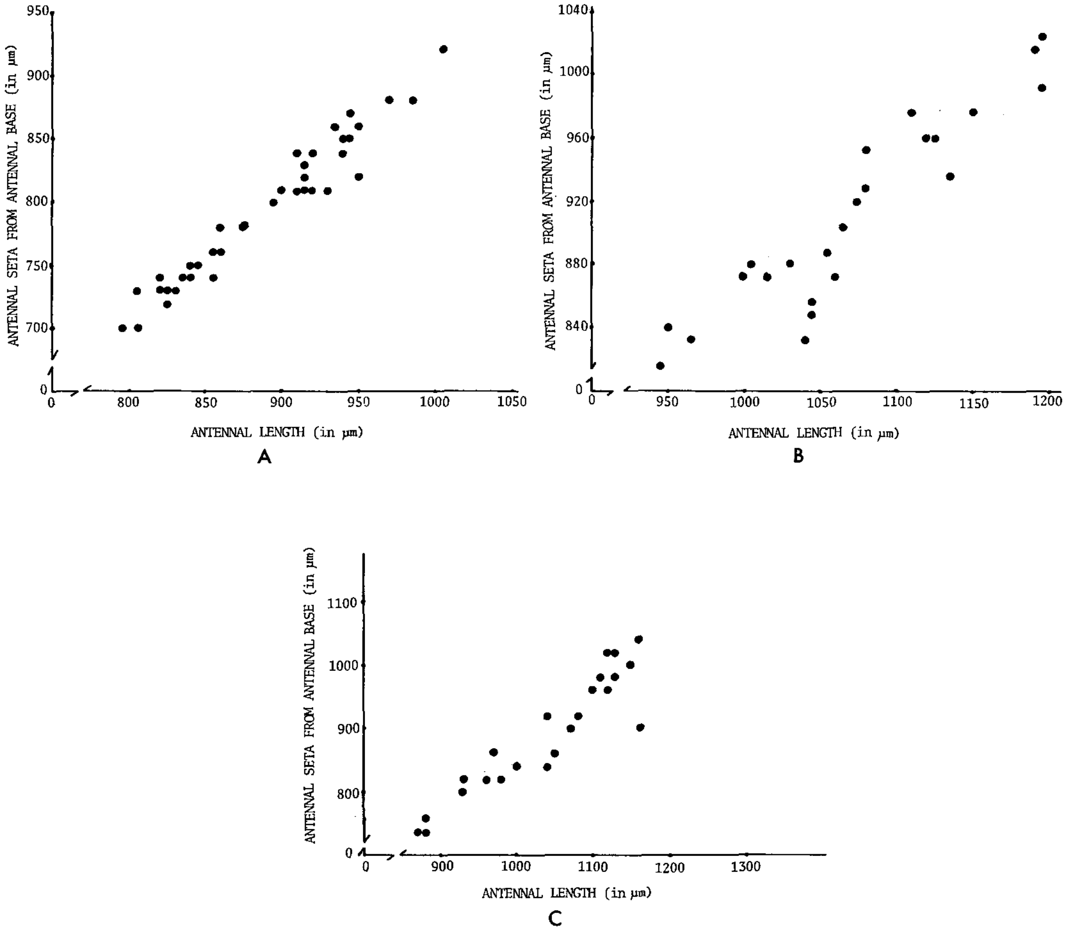

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Figure 29. Relationship between antennal length and distance of antennal seta from base of antenna of fourth instar larvae. A. *Chaoborus trivittatus*. B. *Chaoborus cooki*. C. *Chaoborus nyblaei*.

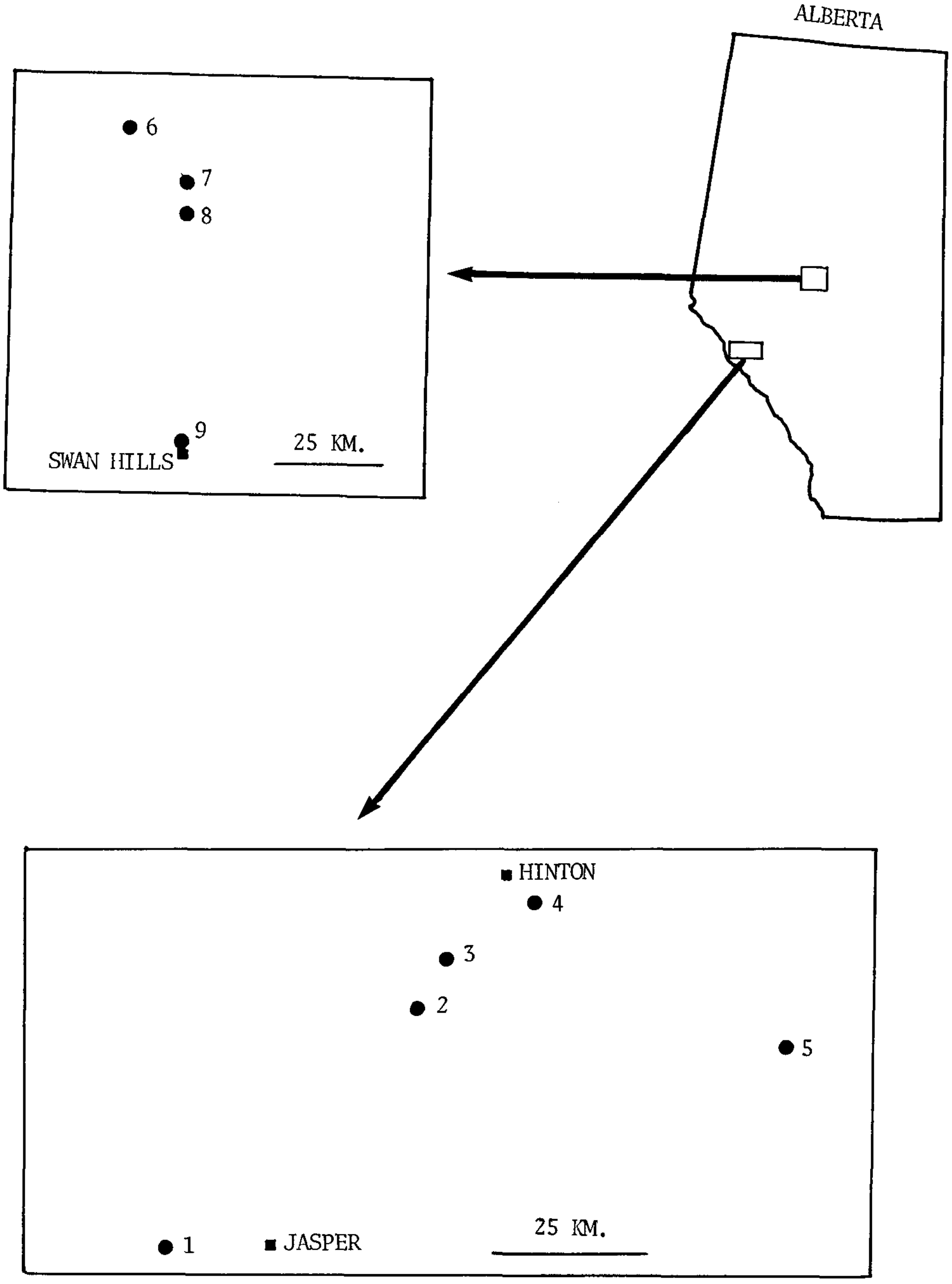

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Figure 30. Localities of samples used to study geographical variation of characters of fourth instar larvae of *Chaoborus trivittatus* in Alberta. Samples from: 1. 16 km west of Jasper; 2. 45 km east of Jasper; 3. Pond nr. Kinky Lake; 4. 4.8 km south of Hinton; 5. 2.4 km south of Robb; 6. 69 km east of High Prairie; 7. 61 km north of Swan Hills; 8. 53 km north of Swan Hills; 9. 1.6 km north of Swan Hills.

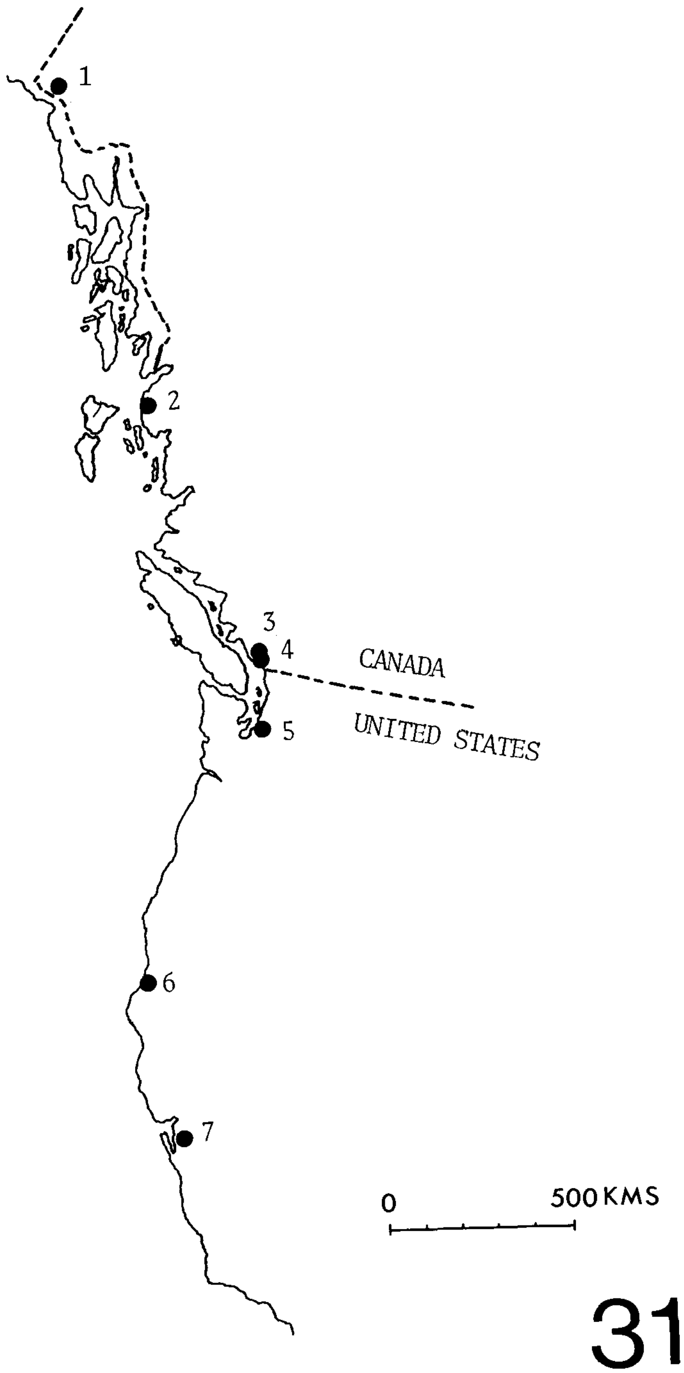

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Figure 31. Localities of samples used to study geographical variation of characters of fourth instar larvae of *Chaoborus trivittatus* from the west coast of North America. Samples from: 1. Klutlan Glacier moraine, Yukon Territory; 2. Prince Rupert, British Columbia; 3. Gwendoline Lake, British Columbia; 4. Eunice Lake, British Columbia; 5. Hall Lake, Washington; 6. Mad River, California; 7. Stanford and Jewel Lake, California.

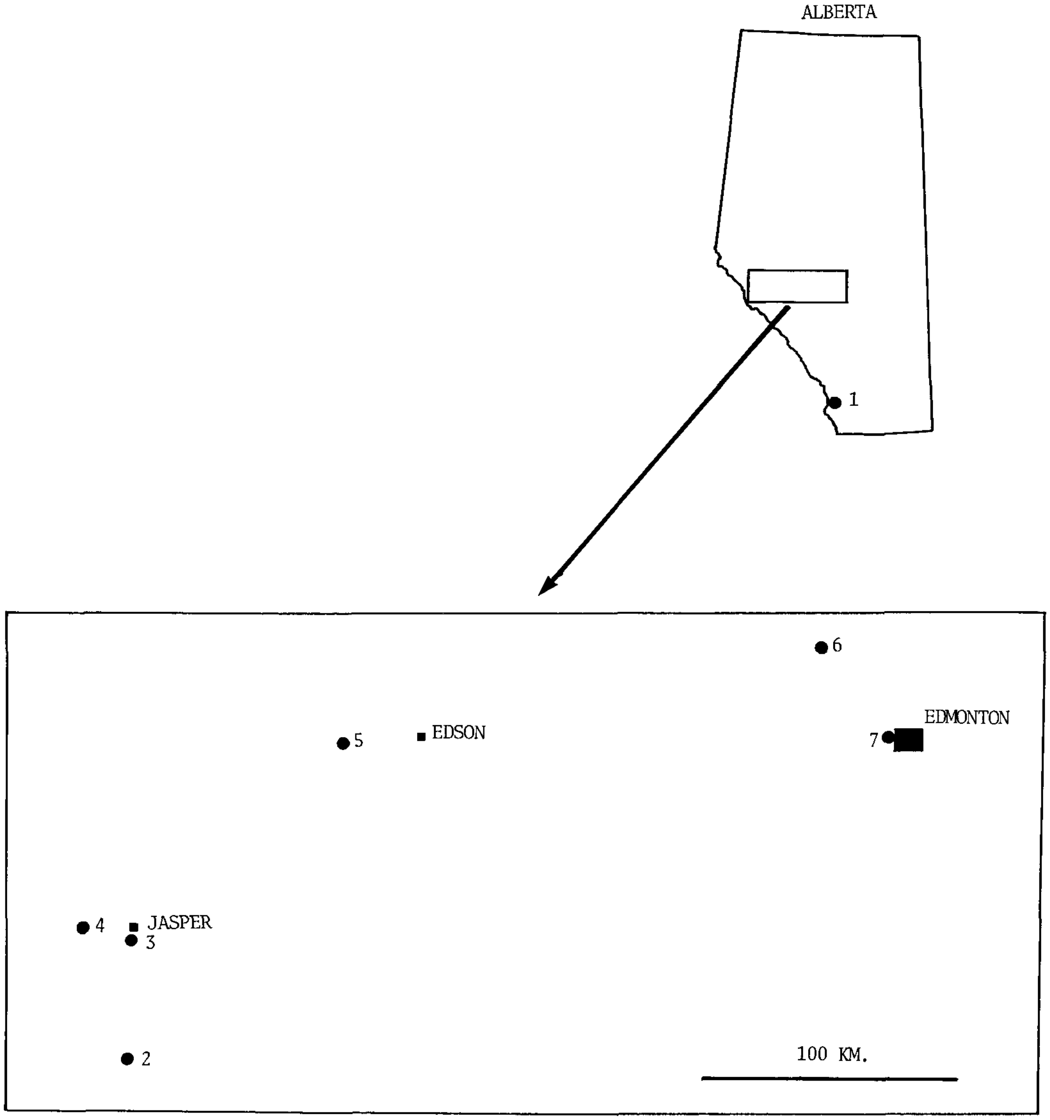

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Figure 32. Localities of samples used to study geographical variation of characters of fourth instar larvae of *Chaoborus cooki* in Alberta. Samples from: 1. 69 km north of Coleman; 2. 53 km south of Jasper; 3. 1.6 km south of Jasper; 4. 6.4 and 23.3 km west of Jasper; 5. 32 km west of Edson; 6. 1.4 km west of George Lake; 7. 2.4 km west of Edmonton.

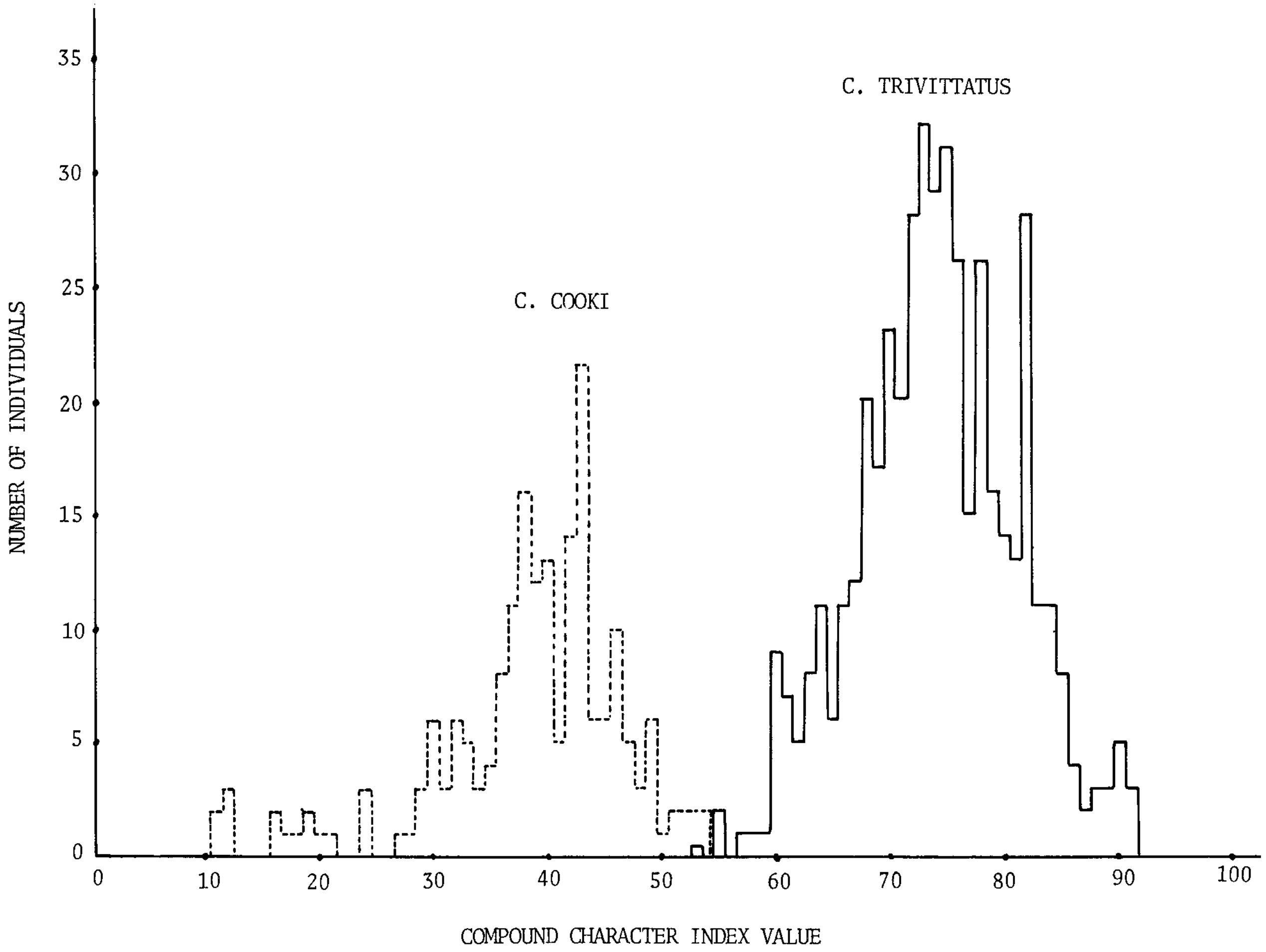

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Figure 33. Results of compound character index used to recognize fourth instar larvae of *Chaoborus trivittatus* and *Chaoborus cooki*.

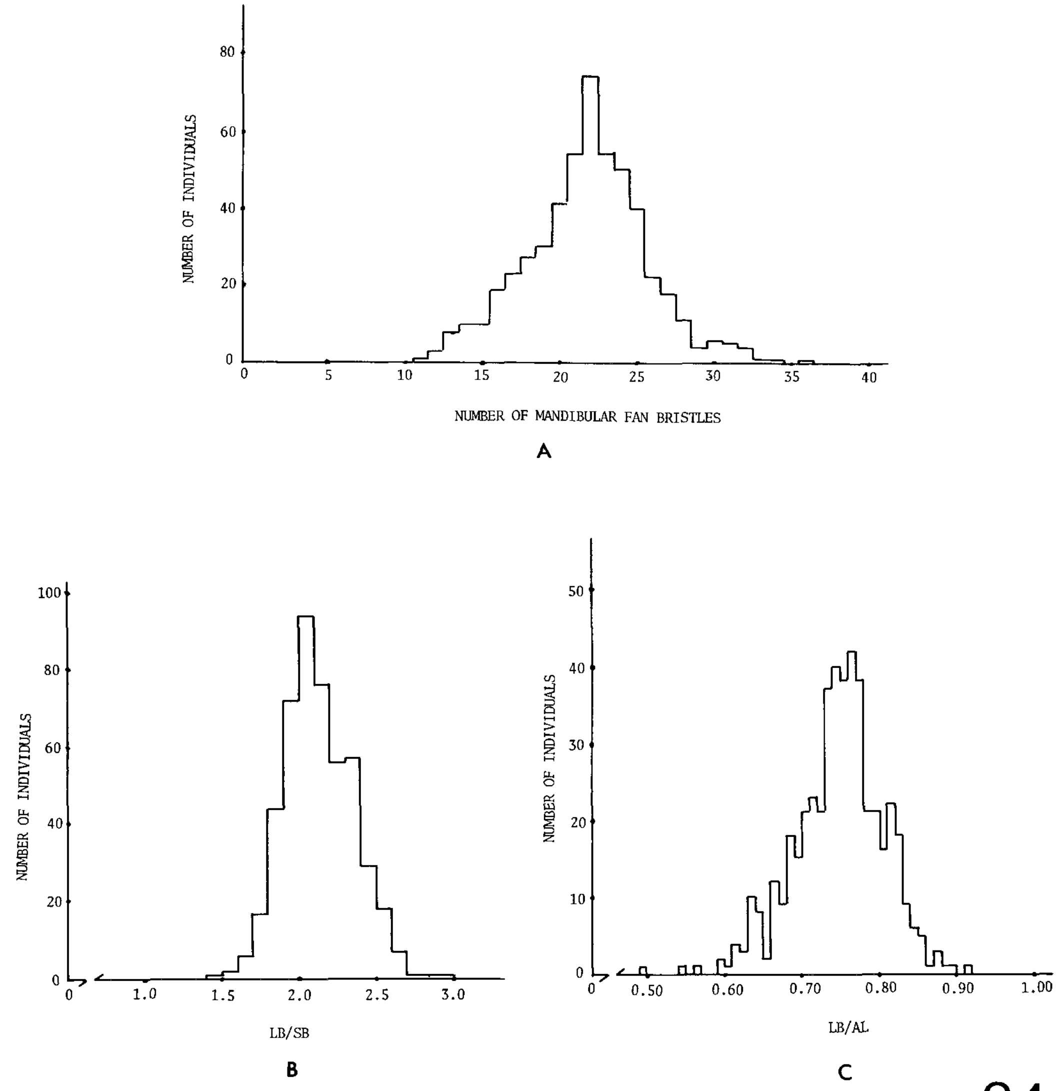

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Figure 34. Variation of characters of fourth instar larvae of *Chaoborus trivittatus*. A. Number of mandibular fan bristles. B. LB/SB. C. LB/AL.

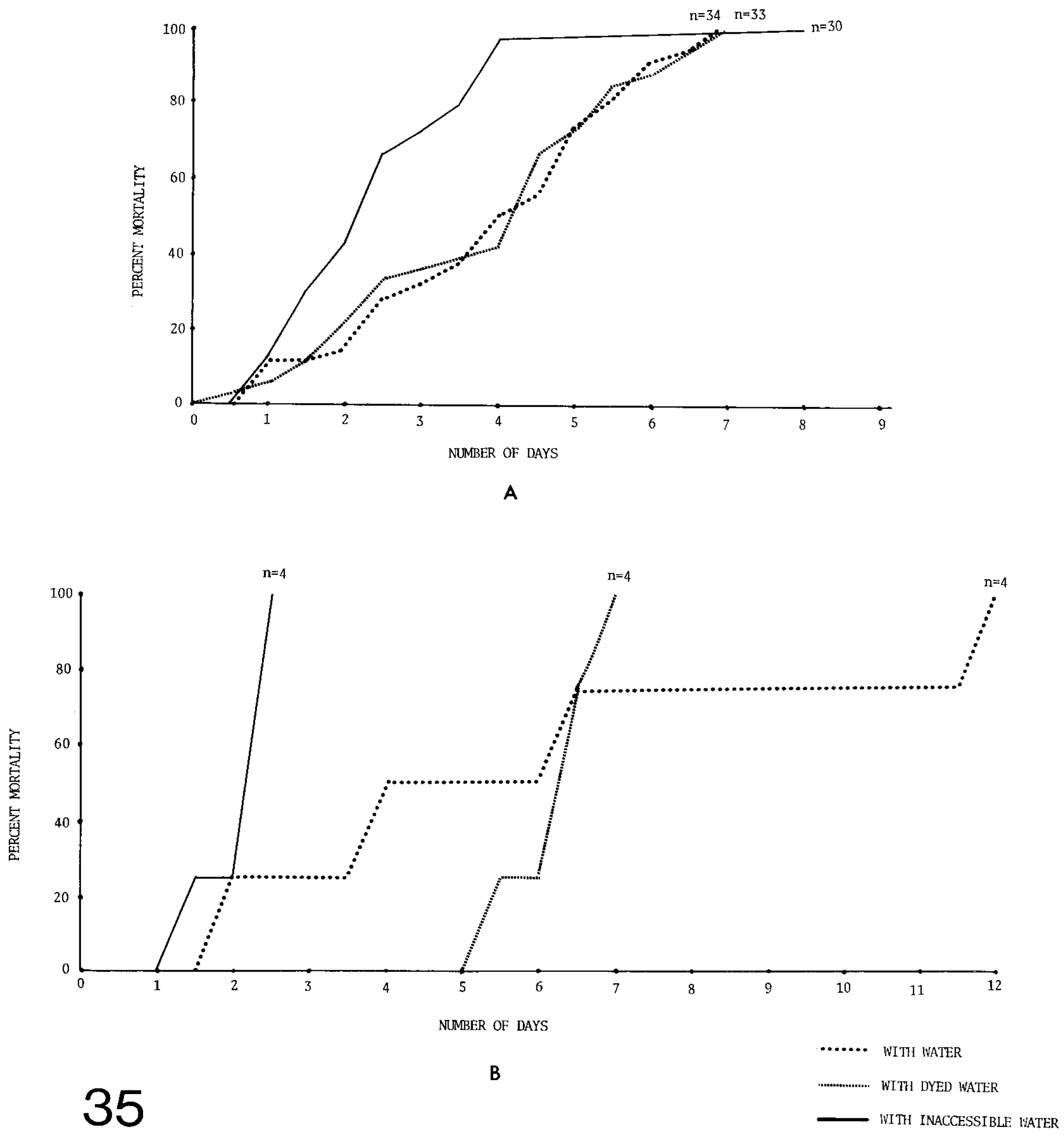

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Figure 35. Mortality of adult *Chaoborus trivittatus*. A. Males. B. Females.

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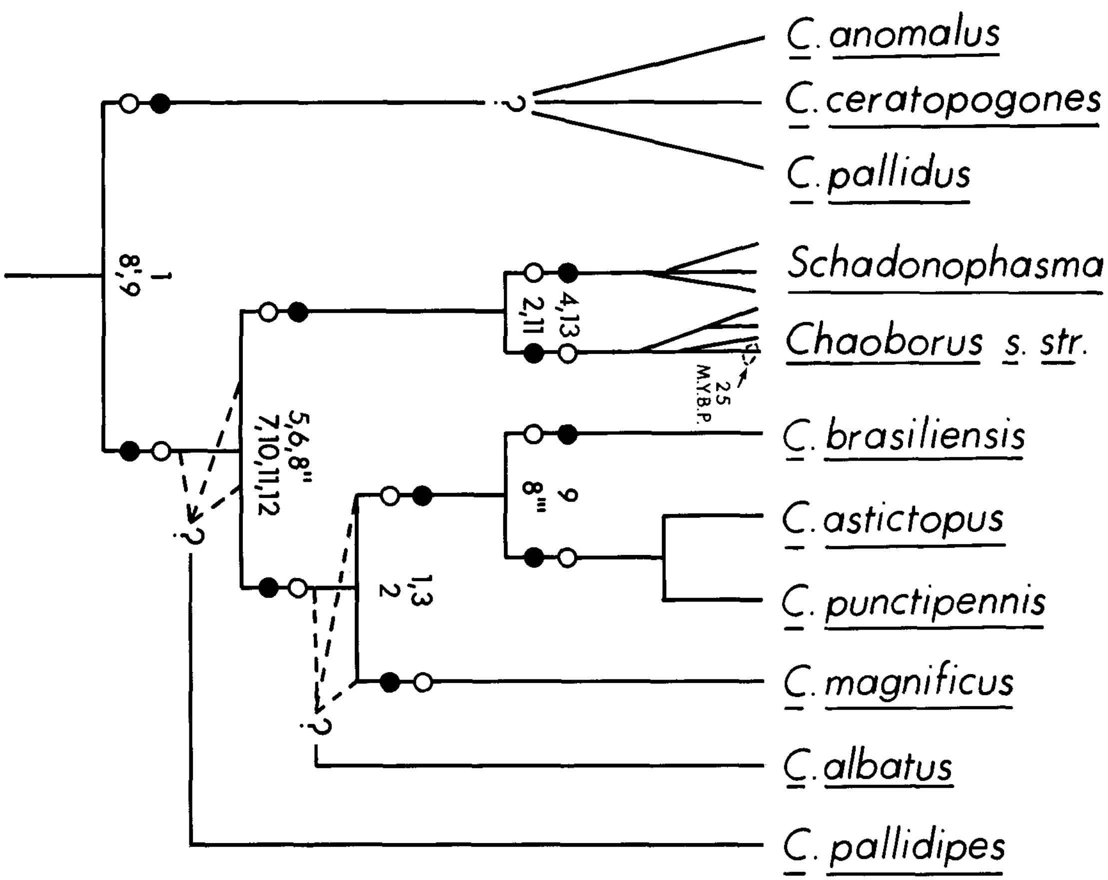

Figure 36. Phylogeny of species of *Chaoborus*. Black circles signify apomorphic states, open circles plesiomorphic states. M.Y.B.P. indicates million years before present.

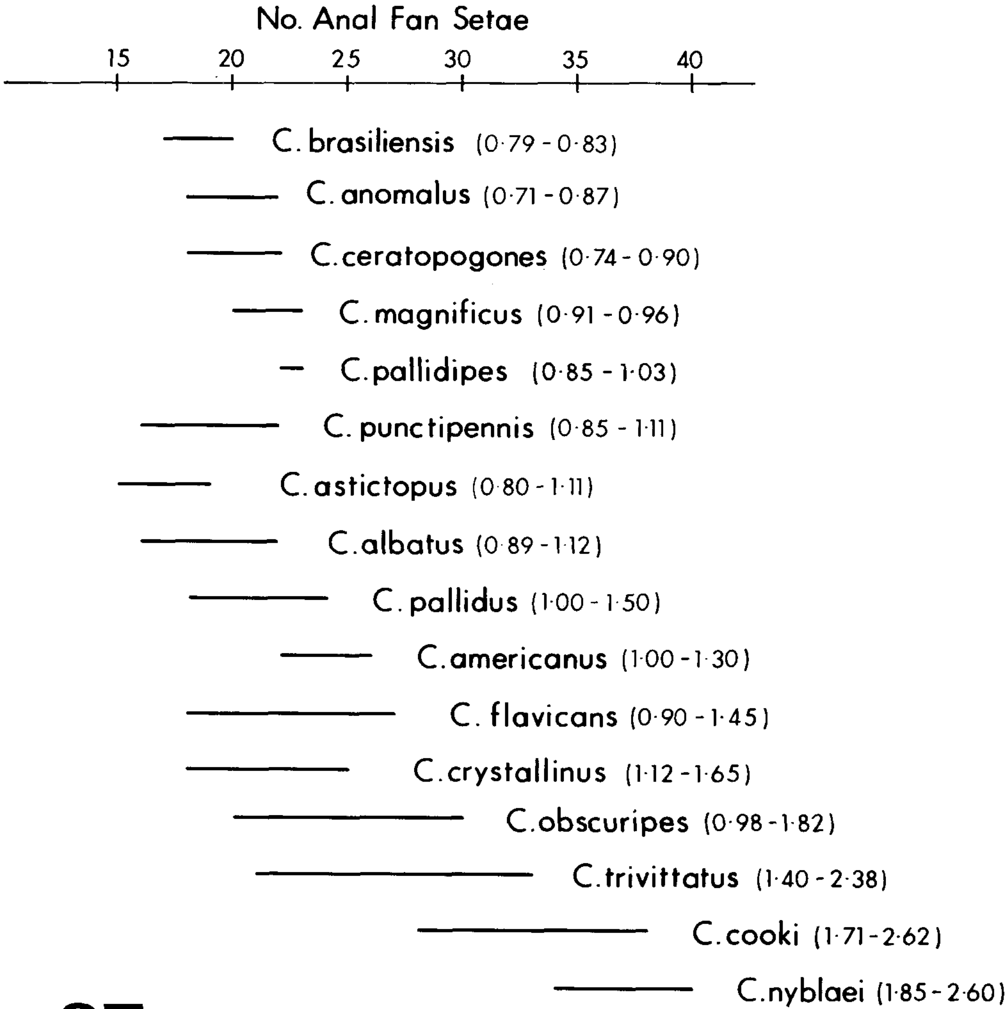

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Figure 37. Relationship between number of anal fan setae and head capsule length (given in parentheses as mm) of fourth instar larvae of *Chaoborus* species.

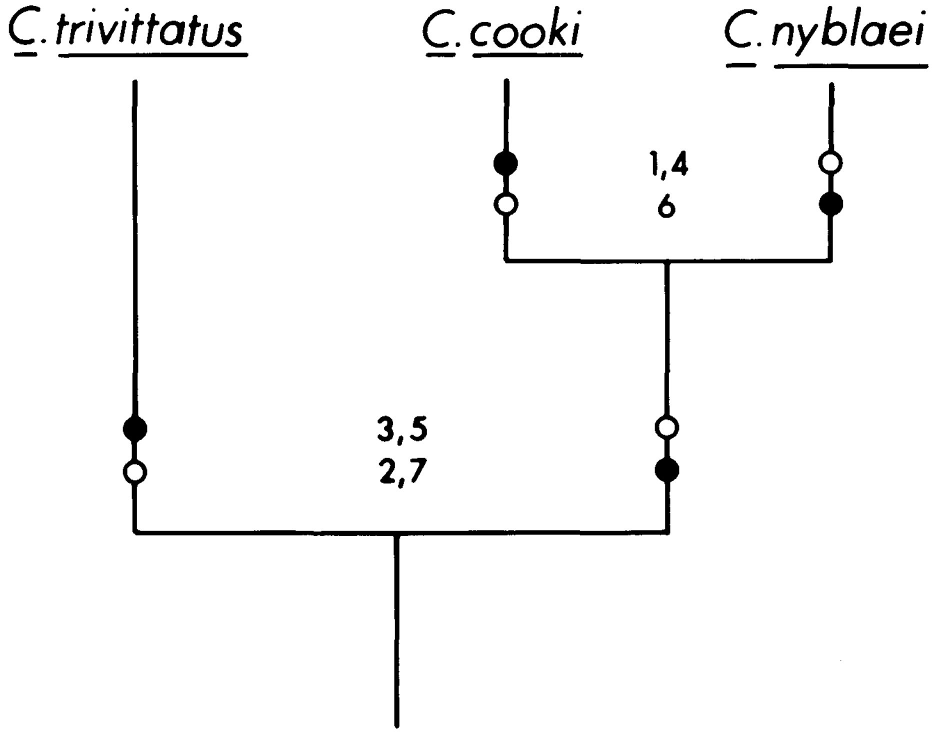

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Figure 38. Phylogeny of species of *Schadonophasma*. Black circles signify apomorphic states, open circles plesiomorphic states.

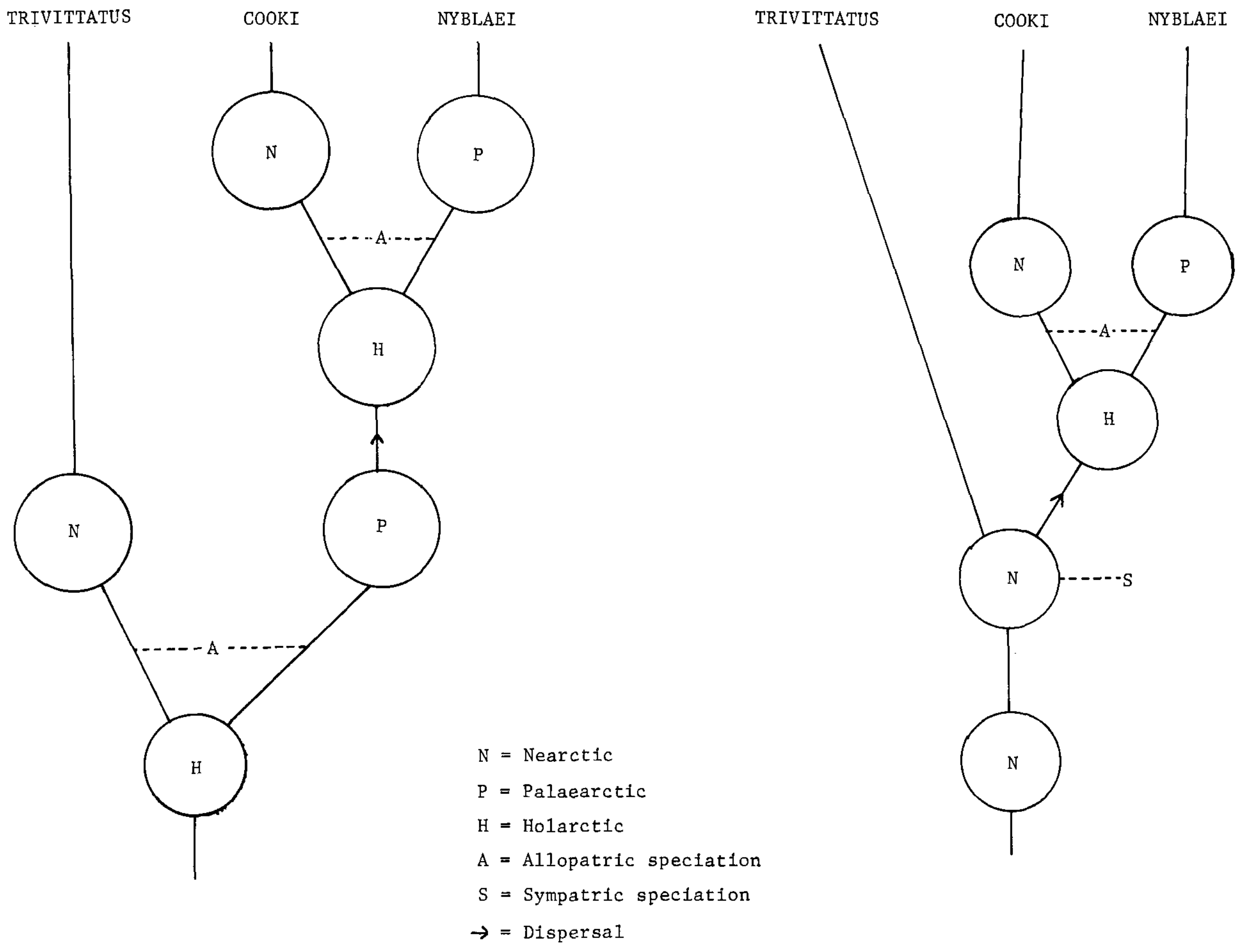

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Figure 39. Schematic representation of alternative zoogeographic hypotheses for *Schadonophasma* species.

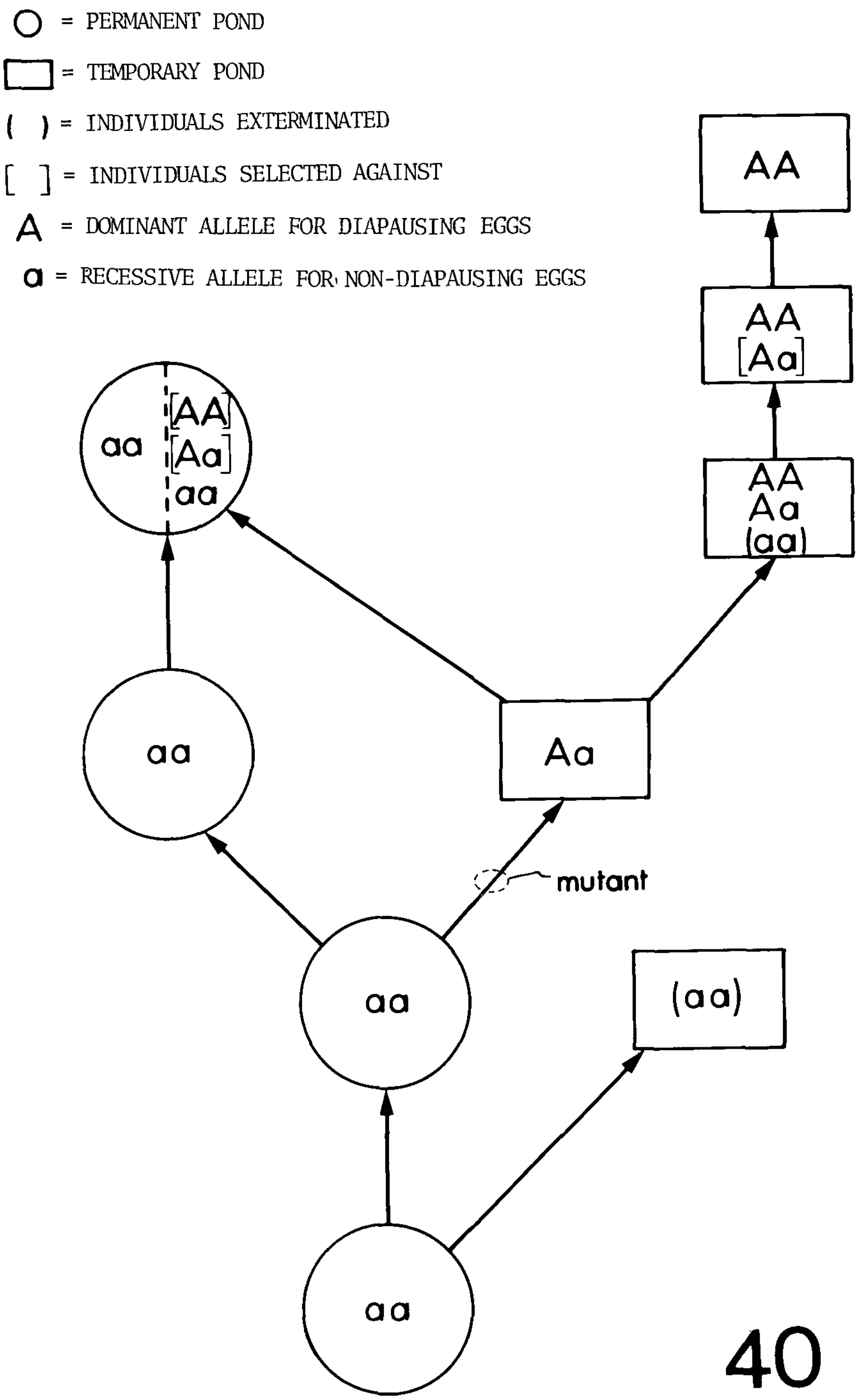

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Figure 40. Schematic representation of events of sympatric speciation of lineages giving rise to *Chaoborus trivittatus* and *Chaoborus cooki-nyblaei*.