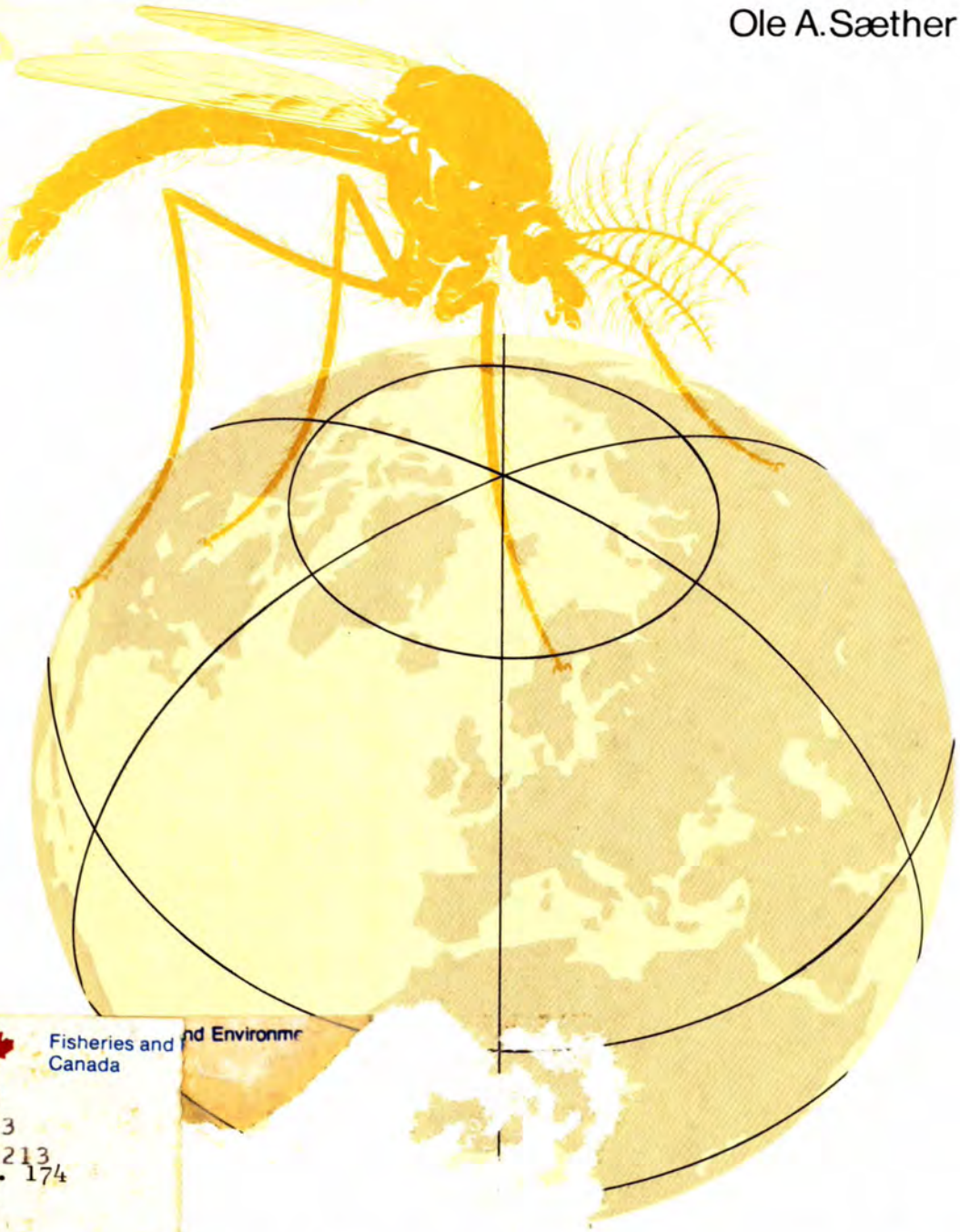
BULLETIN 174

NEARCTIC and PALAEARCTIC CHAOBORUS

(Diptera: Chaoboridae)

Ole A. Sæther



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By Ole A. Sæther

Fisheries Research Board of Canada
Freshwater Institute
Winnipeg, Manitoba

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Contents

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ABSTRACT

New descriptions, redescriptions, supplementary descriptions, taxonomical comments, and new distribution records are given for the 14 known Nearctic and Palaearctic species of *Chaoborus*. One new subgenus, *Peusomyia*, is erected for the species *Chaoborus pallidus* (Fabr.). Two new species are described: *Chaoborus* (*Schadanophasma*) *brunskilli* and *Chaoborus* (*Schadanophasma*) *cooki*. Two other species, *Chaoborus* (*Schadanophasma*) *nyblaei* (Zett.) and *Chaoborus* (*Schadanophasma*) *trivittatus* (Loew), are redefined. One new synonym is given: *Chaoborus* (*Chaoborus*) *crystallinus* (De Geer) (syn. *Chaoborus borealis* Cook). *Chaoborus* (*Chaoborus*) *americanus* (Joh.) is divided into two forms, *C. americanus* f. *typica* f.nov. and *C. americanus* f. *sonjai* f.nov. The phylogeny of the genera of the Chaoboridae and of the species of *Chaoborus* is discussed. Thirty-six phylogenetic trends have been deduced from characters found in the adults, 10 from characters found in the pupae, and 22 from characters in the larvae. Many of these trends are found as parallelisms within different genera and even subgenera. The evolutionary level, indicated by the "Evolution Index" of Illies, is calculated for the species of *Chaoborus*. An adjusted evolution index giving each trend equal value regardless of number of steps also is calculated. The interrelationships of the Chaoboridae in general, and of the species of *Chaoborus*, are elaborated by means of the trends and represented in a synapomorphic diagram. The tribe Chaoborini seems an apomorphic sister group of the more plesiomorphic tribe Cryophilini. These two tribes together probably are the sister group of the tribe Mochlonyxini and all three tribes together constitute the subfamily Chaoborinae.

INTRODUCTION

The taxonomy of *Chaoborus*, as compared with other genera of Diptera, is relatively well known. The revision of Nearctic species by Cook (1956) (adults and immatures) and the treatment of Palaearctic species, adults by Martini (1929) and immatures by Peus (1934), Prokešová (1959), Hirvenoja (1961), Sikorowa (1966), Sæther (1967), Parma (1969), and others makes further revision at first seem not of a great priority. However, many problems still remain unsolved. The variation reported for several species especially in the larval stage (see for instance Smith, 1960b) leads one to suspect that more than one species is involved in some cases. As questioned by Peus (1967, p. 330): "Sind die mehr oder weniger deutlich auftredenden Verschiedenkeiten ökotypische oder artliche Charaktere?"

At least in some cases a large variation indeed exists as shown by Sæther (1967) who synonymized the two species *Chaoborus flavicans* (Meig.) and *Chaoborus alpinus* Peus. The large variation found for instance within such species as *Chaoborus crystallinus* and *Chaoborus americanus* does not seem to justify a division of either of these species. On the other hand the largest variation of all known species has been reported from *Chaoborus* (*Schadanophasma*) *nyblaei* (Zett.) (Smith, 1960b; Cook 1956; Hirvenoja, 1961). The present paper shows that the subgenus *Schadanophasma* is not monotypic, but consists of at least four separate, closely related species.

A close comparison between Nearctic and Palaearctic specimens has not previously been attempted and there is considerable doubt as to which species are truly Holarctic. The placement of *Chaoborus pallidus* (Fabr.) in the subgenus *Sayomyia* (Edwards, 1930a, p. 533, 1930b, p. 165, 1932, p. 27) may not be justified. The revision by Cook (1956) for the Nearctic species makes a modern taxonomic treatment of the European adult *Chaoborus* desirable.

A morphological and ecological treatment as well as a key to Palaearctic and Nearctic species is given by Sæther (in press) and will therefore not be included in this paper.

Holotypes, allotypes, and, if sufficient material is available, some paratypes will be deposited in the Canadian National Collection (CNC) in Ottawa. Any remaining paratypes will be retained at the collection of the Freshwater Institute in Winnipeg.

METHODOLOGY AND ABBREVIATIONS

The specimens used for measurements were mounted on slides after treatment with the method mentioned in Sæther (1969, in press).

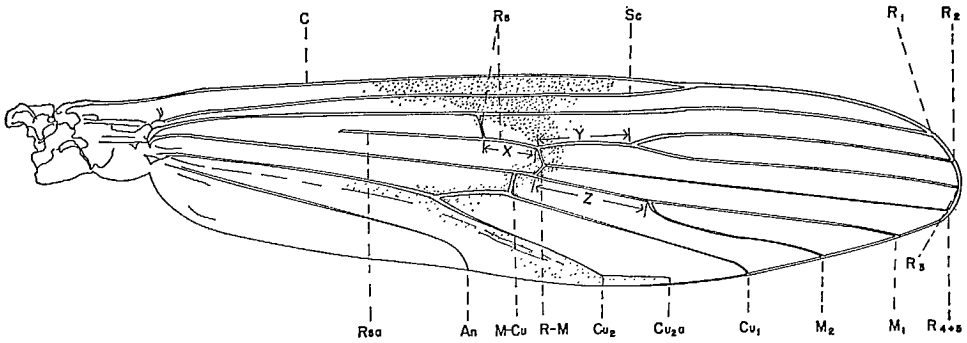

FIG. 1. *Chaoborus* (*Peusomyia*) *pallidus* (Fabr.) Male wing.

The following symbols will be used for the imaginal descriptions:

$$\text{BR(bristle ratio)} = \frac{\text{longest bristle of ta}_1}{\text{width of ta}_1 \text{ about } \frac{1}{3} \text{ from apex}}$$

Cu_2a = appendix vein of Cu_2 (see Fig. 1)

$$\text{HR(hypopygium ratio)} = \frac{\text{length of basistyle}}{\text{length of dististyle}}$$

$$\text{HV(hypopygium value)} = \frac{\text{length of male}^1}{\text{length of dististyle} \times 10}$$

$$\text{HW/CL} = \frac{\text{head width}}{\text{clypeus length}}$$

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

$$\text{HW/WBE} = \frac{\text{head width}}{\text{width between eyes at narrowest point}}$$

$$\text{LR(leg ratio)} = \frac{\text{ta}_1}{\text{ti}}$$

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

Rsa = appendix vein of Rs (see Fig. 1)

$$\text{WL/HW} = \frac{\text{wing length}}{\text{head width}}$$

$$\text{WL/Pf} = \frac{\text{wing length}}{\text{length of profemur}}$$

$$\text{WL/WW} = \frac{\text{wing length}}{\text{wing width}}$$

X = Vein Rs between R-M and Rsa (see Fig. 1)
Y = Vein Rs between R-M and fork of R_2 and R_3 (see Fig. 1)
Z = Vein M between R-M and fork of M_1 and M_2 (see Fig. 1)

The number in parentheses after the measurements gives the number of specimens measured (*n*). All measurements are in microns except where otherwise stated.

[1]The length is measured as the length of the thorax from the apex of the pronotum to the posterior end of the metathorax plus the length of the abdomen from the anteriomedian margin of the first tergite to the apex of the basistyle.

TAXONOMY OF *CHAOBORUS* SPECIES

Chaoborus Lichtenstein 1800

(*Corethra* Meigen 1803)

Generic descriptions are given by Martini (1929), Edwards (1932), Cook (1956), and Sæther (in press). The genus *Chaoborus* was divided into three subgenera, *Chaoborus s. str.*, *Schadanophasma*, Dyar & Shannon, and *Sayomyia* (Coquillett), by Dyar and Shannon (1924). A few corrections and additions to the subgeneric characters given by Dyar and Shannon (1924), Edwards (1930a, 1932), and Cook (1956) are presented in this paper.

Cook (1956, p. 28) mentions that females of *Chaoborus trivittatus* (as *Chaoborus nyblaei*) lack a comblike setal row on the caudal face of the third mesothoracic tarsus. This comb is, however, present at least in some females of *C. trivittatus* and its presence is in all likelihood a generic character. Cook (1956, p. 28, 30) also mentions the absence of a seta on the anterior face of the larval antenna in *C. crystallinus* (as *Chaoborus borealis* Cook) and in *C. trivittatus* (as *C. nyblaei* (Zett.)). In fact, this bristle is apparently present in all species of *Chaoborus*. Similarly all species, except *C. pallidus* (Fabr.), have three pairs of setae on the anterior face of the larval labrum. The basal and median pairs are obvious; the apical pair usually is very inconspicuous and often hidden among the apical scales and setae. The number, shape, and general placement of the setae of the seventh abdominal segment of the pupae are apparently not useful as specific characters. This is in contradiction to the findings of Cook (1956) (see Sæther, 1967, p. 579, 581).

Subgenus *Sayomyia* (Coquillett)

MALE

Ommatid-free upper part of eye small, less than the diameter of 2 ommatids in length (Fig. 2A). Other subgeneric characters as given by Cook (1956, p. 31–32).

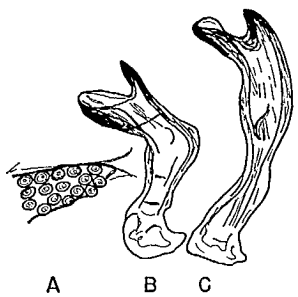

FIG. 2. *Chaoborus* (*Sayomyia*) *punctipennis* (Say). Male. (A) Upper part of eye; (B) and (C) Penis valve.

FEMALE

Tergite IX and segment X of female both bilobed (Cook, 1956, fig. 15B).

PUPA

Width:length of abdominal segment VII less than 1.4. Median rib of anal paddle reduced, not reaching the distal margin of paddle membrane, not curved at apex, with a plumose and a simple seta medially (Fig. 3Q, R).

LARVA.

Larval tentorium thin, weakly sclerotized (Fig. 3N). Other characters as mentioned by Cook (1956, p. 32).

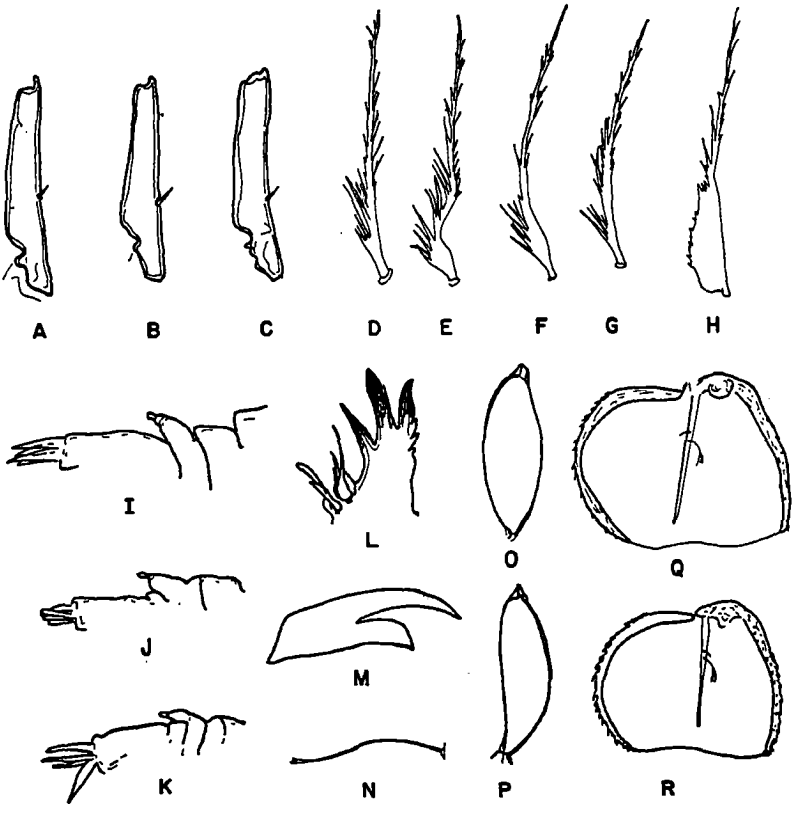

FIG. 3. Larvae and pupae of the subgenus *Sayomyia*. (A–C) Antenna: (A) *Chaoborus punctipennis* (Say); (B) *Chaoborus astictopus* Dyar & Shannon; (C) *Chaoborus albatus* Johns; (D–H) Prelabral appendage: (D) and (E) *C. punctipennis*; (F) and (G) *C. astictopus*; (H) *C. albatus*; (I–K) Dorsal process and anal tubules: (I) *C. punctipennis*; (J) *C. astictopus* (from Lake Chabot, California); (K) *C. albatus*; (L) Mandible of *C. punctipennis*; (M) Anal hook of *C. punctipennis*; (N) Tentorium of *C. punctipennis*; (O–P) Thoracic organ: (O) *C. punctipennis*; (P) *C. albatus*; (Q–R) Anal paddle: (Q) *C. punctipennis*; (R) *C. albatus*.

Chaoborus (*Sayomyia*) *punctipennis* (Say)

Corethra punctipennis Say, 1823: 16.
Corethra appendiculata Herrick, 1884: 10.
Sayomyia punctipennis (Say), Felt 1904: 361.
Chaoborus (*Sayomyia*) *punctipennis* (Say), Dyar & Shannon 1924: 213.

This species is well described by Cook (1956, p. 32–35). A few additions and corrections, however, can be made.

MALE (n = 2)

Wing — Y/X = 2.11–2.97; Y/Z = 1.31–1.45; Y/R_3 = 0.77–0.87; Z/M_1 = 0.56–0.61; R_3/M = 0.94–1.04. Rsa 175–227 long, distinct. Penis valve Fig. 2B, C.

Other characters as mentioned by Cook (1956, p. 32–35).

FEMALE (n = 5)

Wing — Y/X = 2.15–3.22 mean 2.86; Y/Z = 1.40–1.65 mean 1.53; Y/R_3 = 0.69–0.78 mean 0.72; Z/M_1 = 0.42–0.52 mean 0.44; R_3/M_1 = 0.92–1.00 mean 0.95. Rsa 170–318 mean 244 long, distinct.

Other characters as mentioned by Cook (1956, p. 32–35).

PUPA (n = 8)

Thoracic organ Fig. 3O. Width:length of abdominal segment VII 1.22–1.33 mean 1.28.

Other characters as mentioned by Cook (1956, p. 32–35), Sæther (1967, p. 581), and Roth (1968 p. 276–277). As mentioned by Sæther (1967, p. 581), the differences between pupae of *C. punctipennis* and of *Chaoborus astictopus* given by Cook (1956, p. 18) do not hold when the variation is known. *Chaoborus punctipennis* at least may have pupae with both types of serrations on the inner rib (Fig. 3Q).

LARVA (n = 10, except when otherwise stated)

Longer antennal blades 1.42–1.62 mean 1.48 times as long as shorter blades; seta on anterior face of antenna 20–38 mean 27 long, 3.0–3.8 mean 3.3 wide, situated 0.35–0.46 mean 0.42 from base (Fig. 3A). Tentorium Fig. 3N. Prelabral appendage Fig. 3D, E. Three pairs of setae on anterior face of labrum, median pair 83–142 mean 107 long, 3.4–5.0 mean 4.1 wide; 10–15 setae in each labral fan, 7–9 setae in each sublabral fan. Mandible Fig. 3L. Two pairs of anal tubules[2] unequal in length, longer pair 246–391 mean 282 (8) long, shorter pair 216–385 mean 269 (8) long, width of tubules 31–48 mean 38 (8) (Fig. 3I). Anal hook Fig. 3M.

Other characters as given by Cook (1956, p. 34).

The difference in size of the seta on the anterior face of the antenna, used by Cook (1956, p. 18) for separating *C. astictopus* from *C. punctipennis*, does not always hold up as a distinguishing character (Stahl, 1959, p. 66). However, when the mean of a large number of specimens is used and the width as well as the length is taken into consideration this character may still separate the two species. The size of the median pair of setae on the anterior face of the labrum may also separate the two species. The examined larvae of *C. punctipennis* and *C. astictopus* could be separated

[2]The term "anal tubules" is used here instead of the more commonly used anal papillae. The term anal papillae has, for instance in the Chironomidae, been used for three different structures. To avoid confusion the term anal tubules is introduced for the analogous structure of the Chaoboridae.

on the basis of the shape of the anal tubules. However, the anal tubules of some specimens of *C. astictopus* may be indistinguishable from those of *C. punctipennis* (Cook, 1956, fig. 18J).

SPECIMENS EXAMINED

1 male, 1 female, 2 pupal exuviae, Frains Lake, Michigan, J. C. Roth; 58 larvae, Douglas Lake, Michigan, J. C. Roth; 7 larvae, Mountain Lake, Virginia, J. C. Roth; 2 larvae, Yellowwood Lake, Indiana?, J. B. Stahl; 8 larvae, Kenosee Lake, Sask., A. L. Hamilton; 1 male, 4 females, 1 pupa, 5 pupal exuviae, Heming Lake, Man., A. P. Wiens; 10 larvae, Lake 122, 48 larvae, Lake 227, 1 larva, Lake 230, 1 larva, Lake 239, 84 larvae, Lake 240, 44 larvae, Lake 261, 42 larvae, Lake 302, 62 larvae, Lake 304, 16 larvae, Lake 305, 104 larvae, Lake Mad Dog, Fisheries Research Board of Canada Experimental Lakes Area, Kenora, Ont., A. L. Hamilton, G. P. McRae, and J. Johnson.

REMARKS

Chaoborus punctipennis is very similar to *C. astictopus* in all stages and it may well be that *C. astictopus* is merely a subspecies or even a form (cf. Sæther, 1967, p. 581). However, only the larvae of *C. astictopus* have been examined in this investigation; all adults of *C. punctipennis* examined have had spots around the setae on the scutum and the abdomen, and the male genitalia have all been close to those shown by Cook (1956, fig. 16A, B). As no intermediate adults have been observed, *C. astictopus* should, for the moment, remain a valid species.

Chaoborus (*Sayomyia*) *astictopus* Dyar & Shannon

Chaoborus (*Sayomyia*) *astictopus* Dyar & Shannon 1924: 214.
Chaoborus lacustris Freeborn, 1926: 161.

No adults or pupae were examined.

FOURTH INSTAR LARVA (n = 10, except when otherwise stated)

Longer antennal blades 1.36–1.60 mean 1.43 times as long as shorter blade; seta on anterior face of antenna 30–39 mean 33 long, 4.0–4.8 mean 4.1 wide, situated 0.35–0.41 mean 0.38 (12) from base (Fig. 3B). Prelabral appendage Fig. 3F, G. Three pairs of setae on anterior face of labrum, median pair 123–145 mean 131 (11) long, 7.7–9.5 mean 8.6 (11) wide; 10–13 (9) setae in each labral fan, 7–10 setae in each sublabral fan. Pairs of anal tubules unequal in length; longer pair 142–185 mean 163 long, 31–40 mean 35 wide; shorter pair 80–169 mean 128 long, 25–37 mean 32 wide; tubules rounded apically, only slightly tapering (Fig. 3J).

Other characters as given by Cook (1956, p. 37).

THIRD INSTAR LARVA (n = 4, except when otherwise stated)

Total length 3.7–4.2 mm (2).

Head — Head capsule length 0.53–0.56 mm. Antenna 231–259 long; longer antennal blades 250–262, shorter blades 194–222, longer blades 1.18–1.30 times as long as shorter one; seta on anterior face of antenna 0.27–0.35 from base. Postantennal filaments 261–271 long. Prelabral appendages 13–17 (3) times as long as wide. Median pair of labrum setae 62–66 (3) long; 8–9 (2) setae in each labral fan, 5–6 (2) setae in each sublabral fan. Mandibular fan with 9–10 (3) setae.

Abdomen — Anal fan with 16 (3) rays.

SECOND INSTAR LARVAE (n = 4, except when otherwise stated)

Total length 2.1–2.8 mm.

Head — Head capsule length 0.28–0.33 mm. Antenna 120–129 long; longer antennal blades 151–169, shorter blades 123–136 (3), longer blades 1.11–1.30 (3) times as long as shorter one; seta on anterior face of antenna 0.40–0.43 from base. Postantennal filaments 111–126 long. Median pair of labrum setae 28 (1) long. Mandibular fan with 6–8 (3) setae.

Abdomen — Anal fan with 13–15 rays.

SPECIMEN EXAMINED

69 larvae, Lake Chabot, Alameda Co., California, R. A. Main.

REMARKS

This species may be merely a subspecies or form of *C. punctipennis* (see p. 6).

Chaoborus (*Sayomyia*) *albatus* Johnson

Chaoborus albatus Johnson, 1921: 11.
Chaoborus (*Sayomyia*) *albatus* Joh., Dyar & Shannon 1924: 214.

Only a few larvae and pupae have been examined. The imago is described by Cook (1956, p. 38–39), the pupa by Roth (1968), and the larva by Cook (1956, p. 39), Sæther (1967, p. 578), and Roth (1967, p. 66). The descriptions of Cook (1956, p. 39) and Sæther (1967, p. 578) were based on single specimens.

PUPA ($n = 6$)

Thoracic organ Fig. 3P.

Width:length of abdominal segment VII 1.16–1.21 mean 1.19. Anal paddle Fig. 3R. Other characters as described by Roth (1968).

FOURTH INSTAR LARVA ($n = 7$, except when otherwise stated)

Total length 7.0–9.4 mean 8.4 mm.

Head — Head capsule length 0.89–1.12 mean 1.03 mm. Antenna (Fig. 3C) 429–493 mean 461 long; longer antennal blades 424–478 mean 447 long, shorter blades 233–323 mean 278, longer blades 1.40–1.90 mean 1.62 times as long as shorter one; seta on anterior face of antenna 0.24–0.47 mean 0.35 from base. Postantennal filaments 426–472 mean 452 long. Prelabral appendage (Fig. 3H) 5.7–10.0 mean 7.1 times as long as wide. Median pair of labrum setae 45–77 mean 68 long; 8–11 (5) setae in each labral fan, 5–8 (5) setae in each sublabral fan. Mandibular fan with 9–10 (5) setae.

Abdomen (Fig. 3K) — Anal fan with 16–22 mean 18.7 rays.

THIRD INSTAR LARVA ($n = 1$)

Total length 6.4 mm.

Head — Head capsule 0.64 mm. Antenna 276 long; longer antennal blades 282, shorter blades 209, longer blades 1.35 times as long as shorter one; seta on anterior face of antennal 0.53 from base. Postantennal filaments 270 long. Prelabral appendage 8.5 times as long as wide. Median pair of labrum setae 46 long; 9 setae in each labral fan, 5 setae in each sublabral fan. Mandibular fan with 8 setae.

Abdomen — Anal fan with 14 rays.

SPECIMENS EXAMINED

6 pupae, 6 larvae, Munro Lake, Michigan, J. C. Roth; 4 larvae, Lake 303, Fisheries Research Board of Canada Experimental Lakes Area, Kenora, Ont., A. L. Hamilton and G. P. McRae.

REMARKS

The presence of Rsa was thought to be a subgeneric character of *Sayomyia* (Edwards, 1932, p. 26). According to Cook (1956, fig. 13F), *Chaoborus albatus*,

however, does not have such an appendix vein. This species differs also from the above-mentioned two species in several other characteristics such as the lack of a lobe on the basistyle, the simple penis valve, and the relatively broad prelabral appendage of the larvae.

Other Species

The Nearctic species *Chaoborus* (*Sayomyia*) *annulatus* Cook and *Chaoborus* (*Sayomyia*) *maculipes* Stone have not been examined. *Chaoborus annulatus* (Cook, 1956, p. 39–41, 1960, p. 25–26) has a lobe on the basistyle and obviously belongs to the subgenus *Sayomyia*. *Chaoborus maculipes*, however, is said by Stone (1965, p. 231–232) to lack subapical lobes or enlarged setae on the basistyle. It may therefore belong to the subgenus *Peusomyia* or possibly to another undescribed subgenus. The immatures of both these species, however, are needed in order to decide their subgeneric position.

Subgenus ***Peusomyia*** subgen.n.

MALE

Wing with indistinct brown patches, legs with brown rings.

Ommatid-free upper part of eye small, slightly pointed (Fig. 4E). 0–1 parascutellar setae. Scutellar setae generally in 3 irregular rows.

Wing with a basally directed appendix vein at base of Rs (Rsa in Fig. 1). Cu_2 with a distal appendix vein extending forward from near its tip (Cu_2a in Fig. 1); extreme tip of Cu_2 often faint; vein An rarely surpasses the level of M-Cu.

Pulvilli about half as long as the claws.

Basistyle without a lobe and without paired, stout setae on inner face; dististyle with an apical clawlike protuberance (Martini, 1929, fig. 80). Penis valve without apical or preapical claw, and with head rounded at apex, L-shaped (Fig. 4A–D).

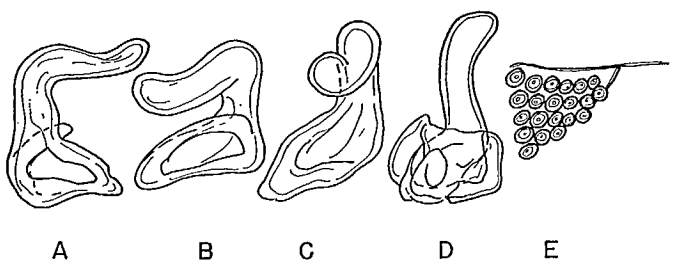

FIG. 4. *Chaoborus* (*Peusomyia*) *pallidus* (Fabr.). Male. (A–D) Penis valve in different positions (only A in good position); (E) Upper part of eye.

FEMALE

A comblike setal row is present along caudal margin of mesothoracic legs as in other subgenera. Tergite IX almost entirely covering segment X. Neither tergite IX nor segment X bilobed (Fig. 5).

PUPA

Thoracic organ usually swollen in the middle; apical papilla at least 2.5 times as long as width of basal constriction of papilla (Peus, 1934, fig. 10d; Fig. 6G).

Median rib of anal paddle not curved apically, reaching the distal margin of paddle membrane, with a plumose and a simple seta medially (Fig. 6H).

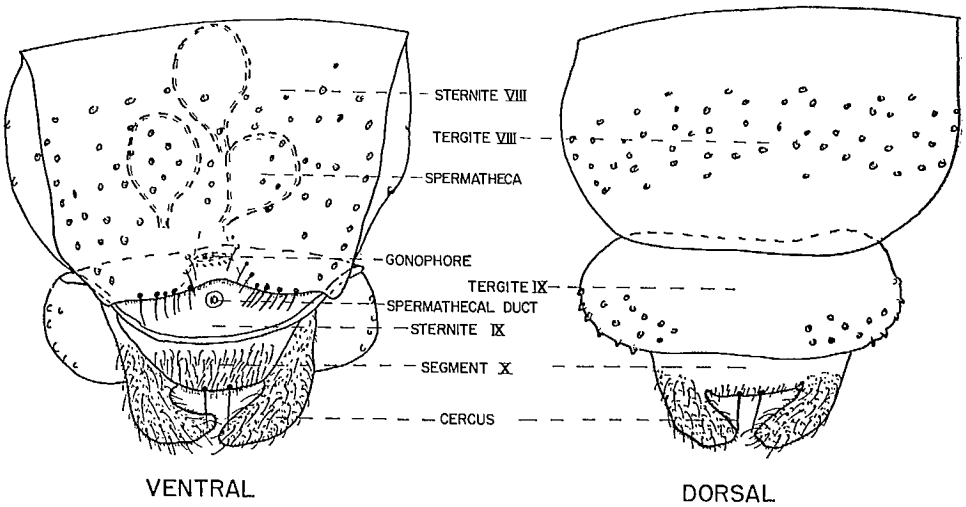

FIG. 5. *Chaoborus* (*Peusomyia*) *pallidus* (Fabr.). Female genitalia.

LARVA

Antenna without curve at base (Fig. 6A). Prelabral appendage with posterior spines, at least 7 times longer than wide (Fig. 6B). Postantennal filaments with strong curvature at base (Fig. 6C). Anterior face of labrum with two subequal pairs of setae. Larval tentorium relatively strongly sclerotized (Fig. 6F).

Dorsal process of segment IX absent (Sæther, in press, fig. 13K). Anal hook slender (Fig. 6E).

Type species: *Chaoborus* (*Peusomyia*) *pallidus* (Fabricius). The subgenus is monotypic.

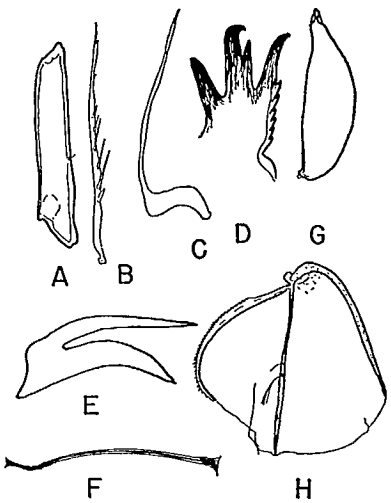

FIG. 6. *Chaoborus* (*Peusomyia*) *pallidus* (Fabr.). Larva and pupa. (A) Antenna; (B) Prelabral appendage; (C) Postantennal filament; (D) Mandible; (E) Anal hook; (F) Tentorium; (G) Thoracic organ; (H) Anal lobe.

SYSTEMATICS

Edwards (1930, p. 533) placed *C. pallidus* in the subgenus *Sayomyia*. The imagines resemble the species of *Sayomyia* in having reduced pulvilli and marked legs and

wings. However, there are usually only 2 rows of scutellar setae in *Sayomyia* and 3 rows in *C. pallidus*; the shorter scales at the wing margin (as measured at An) are half as long as the longer one in *C. pallidus*, although in all other species of *Chaoborus* they are proportionately shorter; the pulvilli are about half as long as the claws in *C. pallidus*, more vestigial in *Sayomyia*; the basistyle of *C. pallidus* has neither lobe nor paired, stout setae on inner surface; the dististyle has an apical protuberance unique among *Chaoborus*, and the penis valve is lacking a preapical or apical spine or claw, has a rounded head, and does not closely resemble the penis valve of any other species.

The pupae of *C. pallidus* also show some resemblance to pupae of *Sayomyia*. The median rib of the anal paddle lacks an apical bend, but does bear a plumose and a simple seta medially. However, the median rib reaches the posterior margin of the anal paddle and is not reduced as in *Sayomyia*.

Furthermore *C.* (*Chaoborus*) *americanus* Joh. has a plumose and a simple seta medially. The papilla of the thoracic organ seems to be unique. However, some forms of *C. crystallinus* (De Geer) may have papillae approaching the shape found in *C. pallidus*.

The larva of *C. pallidus* shows little relationship to the larvae of *Sayomyia*. The only thing it has in common with *Sayomyia* and not with the other subgenera is the general shape of the prelabral appendage. However, the prelabral appendages of *Sayomyia* have distinct anterior and less distinct posterior serrations, whereas the larva of *C. pallidus* has only posterior spinelike serrations. The shape of the antenna as well as the presence of only 2 pairs of subequal setae on the anterior face of labrum is unique. The relatively strongly sclerotized tentoria resemble those present in *Schadanophasma* and are much stronger than in *Sayomyia*. The mandible is of the same shape as in *Chaoborus s. str.* and *Schadanophasma*. The curve of the upper edge of the head starts posterior to the middle. In *Sayomyia* this curve is almost straight; in *C. americanus* (Joh.) and *Chaoborus obscuripes* (v.d. Wulp) it is more rounded as in *C. pallidus*. *Chaoborus americanus*, *C. obscuripes*, *Chaoborus cooki* sp.n., *C. nyblaei* (Zett.), and *C. pallidus* all have a much reduced to absent dorsal process of abdominal segment IX.

This new subgenus seems to be a sister group of *Schadanophasma* plus *Chaoborus s. str.*, i.e., in evolutionary terms it is more closely related to these genera than to *Sayomyia*. The similarities with *Sayomyia* consist of plesiomorphic (= archaic, original) characters and none of the common features seem to be true synapomorphic (apomorph = derived, i.e., either highly differentiated or reduced) trends in the sense that they do not appear in other subgenera as a parallel development (see p. 42, 52). It therefore seems justified to erect a new subgenus if subgenera at all shall be maintained. The subgeneric name *Peusomyia* is proposed in honour of Professor Dr F. Peus, Freie Universität, Berlin.

Chaoborus (*Peusomyia*) *pallidus* (Fabr.)

Tipula pallida Fabricius, 1794: 245.
Chaoborus pallidus (Fabr.), Edwards 1920: 264.
Corethra pallidus (Fabr.), Akehurst 1922: 352.
Chaoborus (*Sayomyia*) *pallidus* (Fabr.), Edwards 1930a: 533.

MALE (n = 7, except when otherwise stated)

Length 5.8–6.5 mean 6.1 mm (Martini (1929, p. 58) mentions 5 mm). Coloration of various parts as mentioned by Martini (1929, p. 58).

Antenna — Scapus $\frac{\text{length}}{\text{width}}$: $\frac{13–20}{213–239}$. Pedicel $\frac{\text{length}}{\text{width}}$: $\frac{53–93}{226–266}$. Longest bristle of flagellum 588–901 (6), of last segment about 265. Flagellar segments (1, 2–3[3], 4–10[3], 11, 12, 13) $\frac{\text{length}}{\text{width}}$: $\frac{227–439}{53–67}$, $\frac{126–219}{53–73}$, $\frac{79–146}{53–80}$, $\frac{120–173}{53–73}$, $\frac{259–306}{47–60}$, $\frac{173–226}{20–27}$ (4). P/U = 1.22–1.50 mean 1.36 (4).

Head — Head width 0.74–0.81 mean 0.78 mm. Width between eyes 0.36–0.40 mean 0.38 mm. Clypeus length 239–279 mean 265. Prementum length 279–319 mean 298. HW/WBE = 1.85–2.22 mean 2.08; HW/CL = 2.64–3.22 mean 2.90; HW/PL = 2.22–2.77 mean 2.54. Vertex with 47–91 setae. Clypeus with 36–72 setae. Palp lengths: 80–120 mean 101; 180–253 mean 202 (6); 133–146 mean 143 (6); 320 (1).

Thorax — 28–32 pronotal setae; 2–5 postpronotals. 2–5 proepisternals; 2–3 preepisternals; 7–9 anepisternals; 7–9 upper mesepimerals; 0–1 parascutellars, present in 4 out of 9 specimens. 36–44 scutellar setae in 3 irregular rows.

Wing (Fig. 1) — Length 2.97–3.26 mean 3.09 mm; width 0.76–0.85 mean 0.81 mm; WL/WW = 3.60–4.13 mean 3.82; WL/HW = 3.80–4.41 mean 3.83; WL/Pf = 1.87 (1). Lanceolate scales of wing margin of two alternating lengths 216–236 and 110–120 (measured at apex of An); scales slightly longer at wing base. Vein An terminates 48–212 mean 146 short of M-Cu. Y/X = 1.43–2.92 mean 2.23; Y/Z = 0.67–0.91 mean 0.84; Y/R_3 = 0.22–0.35; Z/M_1 = 0.39–0.48; R_3/M_1 = 1.23–1.44. Rsa 495–660 long. Squama with 21–46 mean 31 setae.

Haltere — Capitulum with 1 (3) anterior and 3 (5) posterior setae.

Legs — Claw of hind leg 49–69 (6) long. Pulvilli faint, 26–29 (5) long on hind leg.

Lengths (ranges) and proportions (ranges and means) of legs of males and females (most legs were broken off but present in the vials; therefore males and females are not separated. n of different segments is 6–10):

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BR
p_1	1663–1902	1636–2062	838– 971	459–585	305–439	226–279	146–206	0.47–0.59, 0.49	5.66– 7.85, 6.40
p_2	1370–1603	1164–1397	539– 665	279–386	233–279	166–200	146–193	0.39–0.51, 0.46	5.33– 6.85, 5.86
p_3	2195–2554	1889–2128	745–1170	552–652	266–426	226–266	186–200	0.50–0.60, 0.54	8.37–10.00, 9.15

Genitalia — Tergite IX with long setae (11–18 mean 13) on each lobe. Basistyle without lobe or stout apical setae. Dististyle with an apical, clawlike protuberance (Martini, 1929, fig. 80). Penis valve (Fig. 4A–D) without apical or preapical spine, with head rounded, L-shaped. Length of valve 90–109 mean 99; head length 37–53 mean 45 (6); head width 16 (6). Basistyle 386–466 mean 429 long; dististyle 346–392 mean 371 long. HR = 0.76–1.00 mean 0.87; HV = 1.53–1.81 mean 1.65.

[3]Ranges given as ranges of individual segments.

FEMALE (n = 5, except when otherwise stated)

Length 5.1–5.5 mean 5.3 mm. Coloration of various parts as in male.

Antenna — Scapus $\frac{\text{length}}{\text{width}}$: $\frac{7–13}{106–146}$. Pedicel $\frac{\text{length}}{\text{width}}$: $\frac{67–93}{106–113}$. Longest bristle of flagellum about 420 (1); of last segment 32–42 (3). Flagellar segments (1, 2–10, 11, 12) $\frac{\text{length}}{\text{width}}$: $\frac{186–200}{53–67}$, $\frac{93–133}{27–53}$, $\frac{120–140}{27–33}$, $\frac{146–173}{33–40}$. Last segment lost in all specimens examined.

Head — Head width 0.70–0.80 mean 0.76 mm. Width between eyes 0.30–0.42 mean 0.36 mm. Clypeus length 319–372 mean 346. Prementum length 280–319 mean 303. HW/WBE = 1.83–2.55 mean 2.16; HW/CL = 2.11–2.30 mean 2.26; HW/PL = 2.30–2.86 mean 2.51. Vertex with 42–93 setae. Clypeus with 49–101 setae. Palp lengths: 113–126 mean 121; 186–200 mean 196 (4); 120–173 mean 148 (4); last segment lost in all specimens examined.

Thorax — 35–47 pronotal setae; 3–6 postpronotals. 4–5 proepisternals; 3–10 preepisternals; 7–9 anepisternals; 10–17 upper mesepisternals; no parascutellars. 42–59 scutellar setae in 3 irregular rows.

Wing — Length 3.33–5.48 mean 3.39 mm (4); width 0.72–1.08 mean 0.98 mm. WL/WW = 3.09–4.85 mean 4.47; WL/HW = 4.18–4.81 mean 4.47. Lanceolate scales of wing margin 294–302 and 154–164 long. Vein An terminates 185 short of M-Cu to 13 beyond M-Cu mean 58 short of M-Cu (4). Y/X = 1.16–1.73 mean 1.48 (4); Y/Z = 0.77–1.12 mean 0.91 (4); Y/R_3 = 0.18–0.28 (4); Z/M_1 = 0.28–0.34 (4). Squama with 25–37 mean 31 (4) setae.

Haltere — Capitulum with 2–4 anterior and 2 posterior setae.

Legs — (see p. 11).

Genitalia (Fig. 5) — Tergite IX and segment X both undivided. Spermathecae (Fig. 5) heavily sclerotized and darkly pigmented; diameter 66–76.

PUPA (n = 2)

Total length 6.0–6.3 mm. Cephalothorax only about one-fifth of total length. Colourless and transparent. Thoracic organ (Fig. 6G) 0.71–0.76 mm long, 0.20–0.24 mm wide; length:lateral width 3.2–3.6, about 60 reticulations in longitudinal direction and about 15 in lateral transverse direction.

Abdominal segment VII 0.95–1.00 mm wide, width:length of segment VII 1.12–1.15. Anal paddle (Fig. 6H) with inner rib closely toothed for apical three-fourths: outer rib with very fine distal serrations. Median rib not curved at apex, but reaching margin of paddle membrane, bearing a plumose and a simple seta medially.

Other characteristics as mentioned by Peus (1934, p. 654–657).

LARVA

The larva has been described in sufficient detail by Peus (1934), Prokešová (1959), Sikorowa (1966), Parma (1969), and Sæther (in press). Some details are illustrated in Fig. 6.

SPECIMENS EXAMINED

Male with associated pupal exuvia, 11 males, 14 females, 1 pupal exuvia, 7 larvae, Riihimäki, Finland, T. and M. Hirvenoja; 37 larvae, Breda, Netherlands, G. Postema; 26 larvae, Parku Kortowskim, Poland, A. Sikorowa.

Subgenus *Schadanophasma* Dyar & Shannon

MALE

Wing with several spots, leg segments at most with one apical and one basal spot. Large species.

Ommatid-free upper part of eye pointed, elongate, at least as long as the diameter of 3 ommatids (Fig. 9). Parascutellar setae absent. Scutellar setae in 3–4 irregular rows.

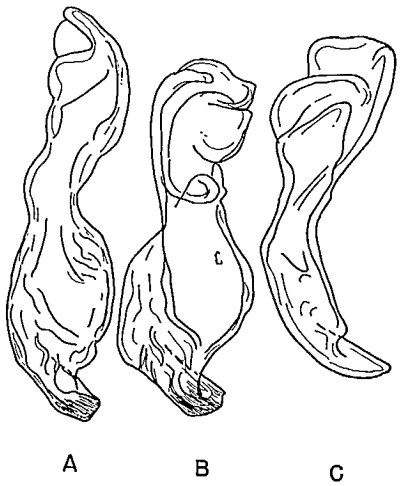

FIG. 7. *Chaoborus* (*Schadanophasma*) spp. Male. Penis valve. (A) *C. nyblaei* (Zett.) from Baffin Island; (B) *C. nyblaei* (Zett.) from Finland; (C) *C. brunskilli* sp.n.

Wing (Cook, 1956, fig. 13G) with a basally directed appendix vein at base of Rs (Rsa). Cu_2 without a distal appendix vein. Ratio Y/X of male wing 1.4–2.8. Wing veins (aside from marginal scales) obviously scaled.

Pulvilli well developed, more than half as long as claws.

Basistyle without lobes or setae. Penis valve with an apical spine or claw (Fig. 7, 8).

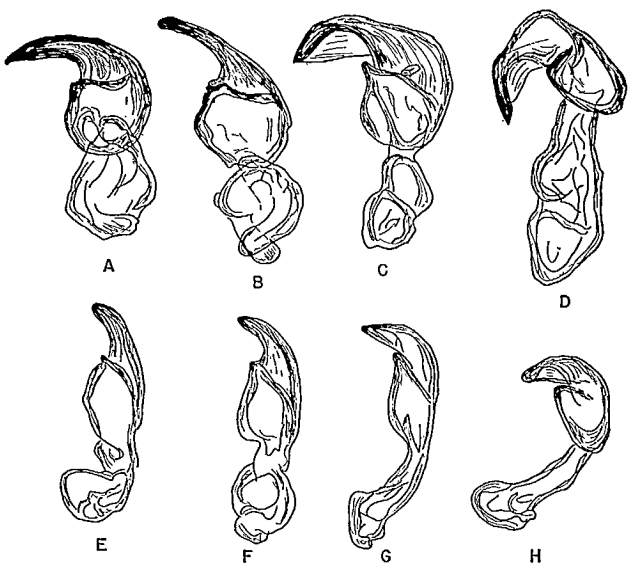

FIG. 8. *Chaoborus* (*Schadanophasma*) spp. Male. Penis valve. (A–D) *C. cooki* sp.n.: (A) From Whitehorse, Y.T.; (B) From Great Whale River, Que.; (C) From Gillam, Man.; (D) From Yellowknife, N.W.T.; (E–H) *C. trivittatus* (Loew): (E) From Kalso, B.C.; (F–H) From Terrace, B.C.

FEMALE

A comblike setal row is present on caudal face of third mesothoracic tarsus at least in some females although it is mentioned to be absent by Cook (1956, p. 28).

Tergite IX and segment X both undivided. Tergite IX leaves the apical half of segment X uncovered from a dorsal view (Cook, 1956, fig. 15A). Spermathecae ovoid, with a short straight neck (Cook, 1956, fig. 14J).

PUPA

Width:length of abdominal segment VII usually more than 1.45 and always greater than 1.3. Median rib of anal paddle slightly thinner than lateral ribs, with a single plumose seta medially and a minute seta at the curved apex. Membrane of anal lobe usually distinctly marked with brown on basal parts or at least with heavy shagreenation. Outer rib without teeth or serrations, but with a sparse shagreenation.

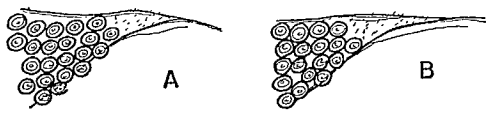

FIG. 9. *Chaoborus* (*Schadanophasma*) spp. Male. Upper part of eye. (A) *C. brunskilli* sp.n.; (B) *C. cooki* sp.n.

LARVA

Fourth instar larvae at least 9.5 mm long, usually more than 15 mm long; head capsule at least 1.44 mm long.

Seta on anterior face of antenna very inconspicuous, placed 0.80–0.95 from base (Fig. 11H–J). Larval tentorium relatively strongly sclerotized (Fig. 11L).

Dorsal process of segment IX absent or well developed, but one-segmented (Fig. 11Q–R).

Other characteristics as in *Chaoborus s. str.*

Type species: *Chaoborus* (*Schadanophasma*) *nyblaei* (Zett.).

Chaoborus (*Schadanophasma*) *nyblaei* (Zett.)

Erioptera nyblaei Zetterstedt, 1838: 830.
Chaoborus pallidus Edwards (nec Fabricius), 1920: 265, pro parte.
Chaoborus nyblaei (Zett.) Edwards, 1930a: 533.
Chaoborus nyblaei Edwards (nec Zett.), 1932: 26, pro parte.
Chaoborus nyblaei Cook (nec Zett.), 1956: 28, pro parte.
Chaoborus nyblaei (Zett.), Hirvenoja 1961: 78.

From a comparison between the specimens examined here and the specimens included in Cook (1956, p. 31) it can be seen that Cook probably included specimens of *C. nyblaei* (from Baffin Island), of *C. cooki* sp.n. (from Man., NWT., Y.T., Ont., and Que.), and of *C. trivittatus* (Loew) (from B.C., California, Massachusetts, New York, N.S., and Oregon) in *C. nyblaei.*

The only useful previous description of *C. nyblaei* is that of Hirvenoja (1961).

MALE (n = 1, except when otherwise stated)

Length 8.0 mm. General body coloration and coloration of various parts as in other members of the subgenus (Cook, 1956, p. 29–30).

Antenna — Scapus $\frac{\text{length}}{\text{width}}: \frac{43}{313}$. Pedicel $\frac{\text{length}}{\text{width}}: \frac{159}{307}$. Longest bristle of flagellum 1.53 mm, of last segment 0.26 mm. Flagellar segments (1, 2–11, 12, 13) $\frac{\text{length}}{\text{width}}: \frac{227}{74}, \frac{117\text{–}159}{74\text{–}80}, \frac{288}{61}, \frac{245}{25}$. P/U = 1.18.

Head — Head width 0.93 mm. Width between eyes 0.38 mm. Clypeus length 393. Prementum length 405. HW/WBE = 2.45; HW/CL = 2.38; HW/PL = 2.30. Vertex with 119 setae. Clypeus with 125 setae. Palp lengths: 141, 251, 233, 503.

Thorax — 39 pronotal setae; 6 postpronotals. 9 (?) proepisternals; 4 preepisternals; 14 anepisternals; 13 upper mesepisternals; no parascutellars. 85 scutellar setae in 3–4 irregular rows.

Wing — Wing markings as in other members of the subgenus (Cook, 1956, p. 29–30). Wing length 4.33 mm; width 1.06 mm. WL/WW = 4.06; WL/HW = 4.64; WL/Pf = 1.99. Lanceolate scales of wing margin of two alternating lengths, 172 and 80 (measured at apex of An). Vein An terminates 98 beyond M-Cu. Y/X = 1.46; Y/Z = 1.49; Y/R_3 = 0.80; Z/M_1 = 0.51; R_3/M_1 = 0.96. Rsa about 210 long, distinct. Squama with 44 setae.

Haltere — Capitulum with 3 anterior and 3 posterior setae.

Legs — Claw of hind leg 65 long. Pulvilli of hind leg 60 long.

Lengths and proportions of legs:

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BR
p_1	2171	2245	1079	687	552	356	233	0.48	4.29
p_2	1963	1877	1006	601	491	294	196	0.54	6.33
p_3	2490	2355	1448	785	546	313	215	0.61	8.75

Genitalia — Tergite IX with 11 setae on each lobe. Penis valve (Fig. 7A, B) luteous, with a short apical, darker spine and a large head. Valve length 186–210 (2); head length 76–100 (2), head width 51–70 (2); spine length 32–46 (2), spine width 16–23 (2). Basistyle length 638–883 (2); dististyle length 503–626 (2). (The higher measurements are from a male hypopygium from Finland.) HR = 0.71–0.79 (2); HV = 1.59.

FEMALE (n = 1, prepared from a female pupa)

Antenna — Scapus $\frac{\text{length}}{\text{width}}:\frac{16}{180}$. Pedicel $\frac{\text{length}}{\text{width}}:\frac{101}{154}$. Flagellar segments (1, 2–7, 8–11, 12, 13) $\frac{\text{length}}{\text{width}}:\frac{143}{74}, \frac{85–117}{37–53}, \frac{122–154}{32–37}, \frac{180}{32}, \frac{228}{32}$. P/U = 0.79.

Head — Head width 106 mm. Width between eyes 0.48 mm. Clypeus length 486. HW/WBE = 2.22; HW/CL = 2.19. Clypeus with 116 setae.

Genitalia — Spermathecae 74 in diameter.

Other characters not distinguishable.

PUPA (n = 12, except when otherwise stated)

Total length 8.3–11.4 mean 9.8 mm. Exuvia yellowish brown, general coloration darker than in *Chaoborus brunskilli* sp.n., but spots of setae, anterior and posterior lines of segments, genital sac, and basal parts of paddle membrane, although darker than the rest of the exuvia, lighter than in *C. brunskilli*. Anterior and posterior lines of segments slightly darker than in *C. cookі* sp.n.

Thoracic organ (Fig. 10D) 1.46–1.80 mean 1.63 mm (11) long; 0.29–0.48 mean 0.39 mm wide; length:lateral width 3.47–5.20 mean 4.23 (11); 108–152 reticulations in the longitudinal direction and 20–27 at the widest point in the transverse direction.

Abdominal segment VII 1.82–2.46 mean 2.22 mm wide; width:length of segment VII 1.70–1.82 mean 1.77 (Hirvenoja (1961, p. 81) mentions 1.7–1.9). Genital sac 1.22–1.30 mm (2) long. Median and outer rib of anal lobe (Fig. 10A) distinctly darker than inner rib. Median rib with a plumose seta medially and a simple seta apically.

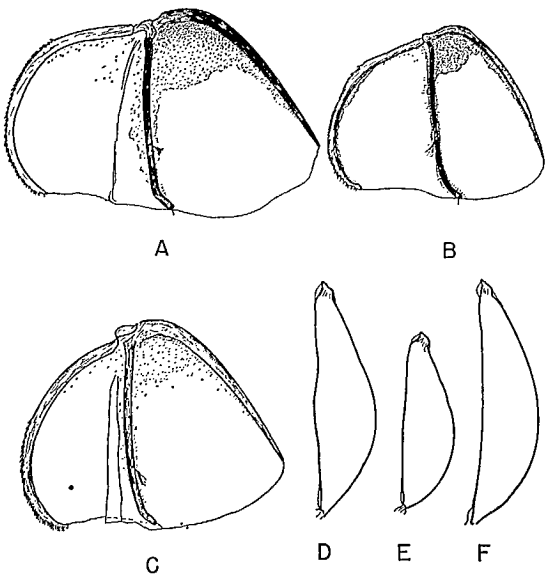

FIG. 10. *Chaoborus* (*Schadanophasma*) spp. Pupa. (A–C) Anal paddle: (A) *C. nyblaei* (Zett.); (B) *C. brunskilli* sp.n.; (C) *C. cooki* sp.n.; (D–F) Thoracic organ: (D) *C. nyblaei* (Zett.); (E) *C. brunskilli* sp.n.; (F) *C. cooki* sp.n.

LARVA (n = 10, except when otherwise stated)

Total length 16.0–20.1 mean 17.5 mm (Hirvenoja (1961) mentions 18–22 mm).

Head — Head capsule (Fig. 11B) length 2.17–2.50 mean 2.35 mm. Antenna (Fig. 11I) 0.96–1.25 mean 1.09 mm long; longer antennal blades 589–748 mean 681 long, shorter blade 362–515 mean 455 long, longer antennal blades 1.32–1.71 mean 1.50 times as long as shorter one, longer antennal blades 0.47–0.73 mean 0.63 times as long as antenna; seta on anterior face minute, 0.87–0.91 mean 0.89 from base. Postantennal filaments 0.83–1.0 mean 0.91 mm long. Prelabral appendage (Fig. 11G) 2.2–5.4 mean 3.7 times longer than wide. Labrum with 3 pairs of seta on anterior face, apical pair inconspicuous, median pair 110–190 mean 171 (6) long; 15–18 (8) setae in each labral fan; 9–12 (9) setae in each sublabral fan. Mandible (Fig. 11K) as in other species of the subgenus; mandibular fan with 11–14 mean 11.9 (11) setae.

Abdomen — Abdominal segment IX without a dorsal process (Fig. 11O). However, there is a slight indication of a hump, more so than in *C. cooki* sp.n. Anal fan with 34–38 mean 36.9 (11) rays. Anal tubules (Fig. 11N) irregularly tapering.

SPECIMENS EXAMINED

Male, Lake Harbor, Baffin Island, W. J. Brown; male hypopygium, female pupa, 14 exuviae, 32 larvae, pond and puddle, Nuorgam-Utsjoki, Finland, M. Varama.

REMARKS

The subgenus *Schadanophasma* consists of four closely related species. Although the larvae of *C. nyblaei* and *C. cooki* sp.n. are practically inseparable from each other,

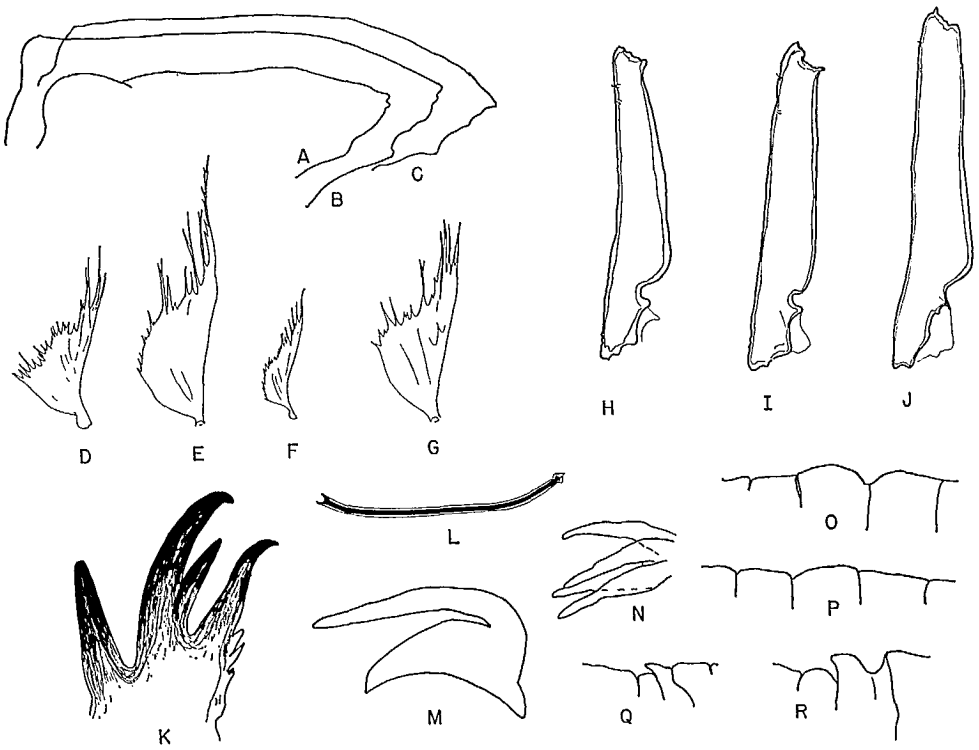

FIG. 11. *Chaoborus* (*Schadanophasma*) spp. Larva. (A–C) Outline of head: (A) *C. brunskilli* sp.n.; (B) *C. nyblaei* (Zett.); (C) *C. cooki* sp.n.; (D–G) Prelabral appendage: (D) *C. cooki* sp.n.; (E) *C. brunskilli* sp.n., fourth instar; (F) Same, third instar; (G) *C. nyblaei* (Zett.); (H–J) Antenna: (H) *C. brunskilli* sp.n.; (I) *C. nyblaei* (Zett.); (J) *C. cooki* sp.n.; (K) *C. nyblaei* (Zett.) mandible; (L) *C. nyblaei* (Zett.) tentorium; (M) *C. nyblaei* (Zett.) anal hook; (N) *C. nyblaei* (Zett.) anal tubules; (O–R) Abdominal segment IX: (O) *C. nyblaei* (Zett.); (P) *C. cooki* sp.n.; (Q) *C. brunskilli* sp.n. from East Henry Pond, Jasper, Alta.; (R) Same from Lake 241, Fisheries Research Board of Canada Experimental Lakes Area, Kenora, Ont.

they are, however, clearly distinct from the larvae of *C. trivittatus* (Loew) and *C. brunskilli* sp.n. Larvae of *C. nyblaei* and *C. cooki* have no dorsal process on ninth abdominal segment, 11–16 setae in the mandibular fan, prelabral appendages that nearly always are less than 4 times as long as wide, and 34–38 rays in anal fan. Larvae of *C. trivittatus* and *C. brunskilli* have a well-developed, conical, dorsal process on ninth abdominal segment, 15–20 and 23–32 setae, respectively, in the mandibular fan, prelabral appendages that are nearly always more than 4.5 times as long as wide, and 24–33 rays in the anal fan. The penis valves of *C. nyblaei* and *C. brunskilli* on the other hand are essentially of the same type (although apparently clearly different from each other) and clearly distinct from the type in common to *C. trivittatus* and *C. cooki*. These combinations of larval and imaginal characters can only be explained by the presence of four species. This conclusion is further supported by the trends of

the other measurements. The male of *C. cooki*, for instance, has a Y/X ratio of 2.2–2.8; all the other species taken together show a variation of 1.5–2.1. The width:length ratio of eighth abdominal segment of the pupa is 1.4 in *C. trivittatus*, 1.5 in *C. brunskilli*, 1.6 in *C. cooki*, and 1.7–1.9 in *C. nyblaei*. Other measurements, for instance the HV-values, also separate the four species although some of these differences are probably not statistically significant on this material, which may not contain a large enough sample of some stages in some of the species.

Some of the counts, measurements, and ratios of the species of *Chaoborus* may overlap. However, although the variation, for instance of number of setae in the larval mandibular fan, may be large, the overwhelming majority are to be found within rather narrow limits. Parma (1969) mentions that there are 8–13 setae in the larval mandibular fan of *C. crystallinus* (De Geer); however, 88% of his specimens had 10–11 setae. If this and similar comparisons are applied on the species of *Schadanophasma* the differences between larvae of *C. brunskilli* sp.n. from Ont. and from Alta. may perhaps indicate that the specimens from Alta. belong to a fifth species. At least it seems very unlikely that a variation of 11–32 setae, the total variation within *Schadanophasma*, may be accounted for by the presence of only one or two species.

There may still be some doubt whether the single male from Baffin Island is *C. nyblaei* or a fifth species, as only a hypopygium of *C. nyblaei* from Finland was available for comparison.

Chaoborus (Schadanophasma) cooki sp.n.

? *Chaoborus trivittatus* Dyar & Shannon (nec Loew), 1924; 212, pro parte.
Chaoborus nyblaei Cook (nec Zett.), 1956: 28, pro parte.

The male is characterized by the penis valve, which has a nearly globular head and a long apical spine lying mostly perpendicular to the long axis of the valve. The ratio Y/X is higher than in other members of the subgenus, 2.2–2.8 in the male 3.4–4.3 in the female.

The pupa has a width: length ratio of segment VII of about 1.6. The median rib of the anal paddle is very slightly to distinctly darker than the lateral ribs.

The larva has 13–16 setae in the mandibular fan, the longer antennal blades are 1.26–1.74 times as long as the shorter one and 0.45–0.61 times as long as the antenna. There is no dorsal process on segment IX.

MALE (n = 7, except when otherwise stated)

Length 6.0–7.4 mean 6.7 mm (6). General body coloration yellowish to dark brown.

Antenna — Scapus $\frac{\text{length}}{\text{width}} : \frac{13\text{–}33}{173\text{–}279}$. Pedicel $\frac{\text{length}}{\text{width}} : \frac{80\text{–}113}{253\text{–}306}$. Longest bristle of flagellum 429–514, of last segment 80–90 (4) long. Flagellar segments (1, 2–11, 12, 13) $\frac{\text{length}}{\text{width}} : \frac{246\text{–}306}{53\text{–}73}, \frac{93\text{–}160}{40\text{–}87}, \frac{319\text{–}399}{53\text{–}67}, \frac{200\text{–}279}{20\text{–}33}$. P/U = 1.23–1.67 mean 1 46.

Head — Head capsule coloration as in *C. brunskilli* sp.n. Head width 0.93–1.06 mean 0.98 mm. Width between eyes 0.36–0.52 mean 0.44 mm. Clypeus length 333–452 mean 387. Prementum length

372–426 mean 400. HW/WBE = 2.08–2.59 mean 2.26; HW/CL = 2.03–2.80 mean 2.55; HW/PL = 2.19–2.61 mean 2.44. Vertex with 162–237 mean 198 (6) bristles. Clypeus with 95–125 mean 114 bristles. Palp lengths: 133–160, 213–253, 213–253, 419–532 (5).

Thorax — Coloration as in *C. brunskilli*. 42–58 mean 48 (6) pronotal setae; 4–5 postpronotals. 6–10 (6) proepisternals; 4–7 preepisternals; 12–17 mean 15.2 (5) anepisternals; 9–18 mean 12 upper mesepimerals; no parascutellars. 61–98 (6) scutellar setae in 3–4 irregular rows.

Wing — Wing markings as mentioned by Cook (1956, p. 29, fig. 13G) for *C. "nyblaei."* Wing length 3.95–4.39 mean 4.19 mm; width 0.97–1.14 mean 1.02 mm. WL/WW = 3.73–4.85 mean 4.13; WL/HW = 4.07–4.72 mean 4.30; WL/Pf = 1.72–1.98 mean 1.88 (6). Lanceolate scales of wing margin of two alternating lengths 175–212 (6) and 69–90 (6) (measured at apex of An). Vein An terminates 0–160 (6) short of M-Cu. Y/X = 2.17–2.77 mean 2.41 (6); Y/Z = 1.26–1.48 mean 1.36 (6); Y/R = 0.81–0.98 mean 0.89 (6); Z/M_1 = 0.51–0.74 mean 0.65 (6); R_3/M_1 = 0.94–1.05 mean 0.99 (6). Rsa 160–279 mean 230 (6) long, distinct. Squama with 38–47 (5) setae.

Haltere — Capitulum nearly spherical, white to pale grey, with 2–5 (6) anterior and 2–3 (5) posterior setae.

Legs — Coloration as mentioned by Cook (1956, p. 30) for *C. "nyblaei"* and about as in *C. brunskilli* sp.n. Claw of hind leg 64–74 (5) long. Pulvilli of hind leg 40–53 (5) long.

Lengths (ranges) and proportions (ranges and means) of leg segments (n = 3–6; for BR, n = 1–2):

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BR
p_1	2195–2221	2035–2620	1104–1303	705–798	519–625	346–399	200–233	0.47–0.52, 0.49	3.81–4.50, 4.16
p_2	1829–2075	1623–2181	798– 984	479–599	412–466	253–306	180–239	0.32–0.52, 0.46	6.00–6.89, 6.45
p_3	2314–2953	2128–2647	1370–1583	758–811	519–572	319–359	186–226	0.34–0.70, 0.56	7.63

Genitalia — Tergite IX with 7–11 mean 8.6 (5) setae on each lobe. Penis valve (Fig. 8A–D) light to dark brown, variable in shape, head usually nearly globular, apical spine long, mostly perpendicular to the long axis of the valve. Length of valve 180–201, mean 192 (6); head length 48–56 mean 52, width 35–58 mean 47; spine length 58–80 mean 67, width 21–27. Basistyle length 599–758 mean 688; dististyle length 532–625 mean 577. HR = 0.74–0.90 mean 0.84; HV = 0.98–1.31 mean 1.13.

FEMALE (n = 4, except when otherwise stated)

Length 5.6–8.5 mean 7.0 mm. Coloration of different parts as in male or somewhat paler.

Antenna — Scapus $\frac{\text{length}}{\text{width}}$: $\frac{20–33}{133–186}$. Pedicel $\frac{\text{length}}{\text{width}}$: $\frac{40–80}{120–173}$. Longest bristle of flagellum about 250 (1), of last segment 160–173 (2). Flagellar segments (1, 2–11, 12, 13) $\frac{\text{length}}{\text{width}}$: $\frac{153–213}{53–93}$, $\frac{87–146}{27–73}$, $\frac{173–286}{27–40}$, $\frac{193–253}{27}$ (3). P/U = 0.87–1.13 (3).

Head — Head width 1.04–1.17 mm. Width between eyes 0.40–0.51 mm. Clypeus length 412–479. Prementum length 372–492. HW/WBE = 2.29–2.69 mean 2.49; HW/CL = 2.44–2.73 mean 2.55; HW/PL = 2.38–2.97 mean 2.75. Vertex with 211–236 (3) setae. Clypeus with 124–134 (3) setae. Palp lengths: 146–166, 220–279, 253–206, 479–652.

Thorax — 31 (1) pronotal setae; 4–6 (3) postpronotals. 8 (2) proepisternals; 7–11 preepisternals; 11–14 anepisternals; 16–21 (3) upper mesepimerals; no parascutellars. 48–86 (4) scutellar setae.

Wing — Wing length 4.12–5.09 mean 4.67 mm; width 1.26–1.64 mean 1.43 mm. WL/WW = 3.02–3.55 mean 3.28; WL/HW = 3.88–4.36 mean 4.23; WL/Pf = 1.90–2.06 mean 1.95. Lanceolate scales of wing margin of two alternating lengths 244–276 and 117–122 (measured at apex of An). Vein An terminates 0–23 beyond M-Cu. Y/X = 3.35–4.32 mean 3.80; Y/Z = 1.33–1.57; Y/R_3 = 0.73–0.87; Z/M_1 = 0.50–0.58; R_3/M_1 = 0.87–0.93 mean 0.93. Rsa 173–306 mean 236 long. Squama with 48–52 (3) setae.

Haltere — Capitulum with 5–6 (2) anterior and 4 (1) posterior setae.

Legs — Claw of hind leg 72 (2) long. Pulvilli of hind leg 48–53 (2) long.

Lengths (ranges) and proportions (ranges and means) of leg segments (n = 2–4):

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR
p_1	2151–2660	2261–2993	1091–1370	658–838	505–559	333–412	213–279	0.46–0.48, 0.42
p_2	1490–2447	1516–2394	865–1117	439–665	372–479	253–319	200–239	0.47–0.52, 0.50
p_3	2261–3285	2367–2926	1370–1835	771–984	505–625	319–379	213–266	0.57–0.72, 0.63

Genitalia — Genitalia as in *C. "nyblaei"* (Cook, 1956, fig. 15A). Spermathecae 64–80 in diameter.

PUPA (n = 4)

Total length 9.3–10.4 mm. Exuvia yellowish to greyish brown, general coloration darker than in *C. brunskilli* sp.n., but bristle spots, anterior and posterior lines of segments, genital sac, basal parts of paddle membrane, and median rib of anal paddle, although darker than the rest of the exuvia, lighter than in *C. brunskilli*. Thoracic organ (Fig. 10F) 1.48–1.62 mm long, 0.39–0.45 mm wide; length:lateral width 3.60–4.65; 112–137 reticulations in the longitudinal direction and 19–26 at the widest point in the transverse direction.

Abdominal segment VII 1.77–1.97 mm wide; width:length of segment VII 1.55–1.59. Genital sac 1.30–1.35 mm long. Median rib of anal paddle (Fig. 10C) the same shade as to slightly darker than lateral ribs.

LARVA (n = 2, except when otherwise stated)

Total length 20.0 mm (1). Larvae nearly colourless, but slightly infuscated dorsally.

Head — Head capsule (Fig. 11C) length 2.37–2.40 mm. The largest specimens treated by Cook (1956, p. 30) as *C. nyblaei*, however, probably belong to *C. cooki* sp.n. and the head capsule may be as long as 2.78 mm. The same applies to the other length measurements given by Cook. The larger ones probably belong to *C. cooki*, the smaller ones probably to *C. trivittatus* (Loew). Antenna (Fig. 11J) 1.05–1.20 mm (3) long; longer antennal blades 540–644 (3), shorter blades 368–429 (3), longer blades 1.26–1.74 (3) times as long as shorter one, longer antennal blades 0.45–0.61 (3) times as long as antenna; seta on anterior face minute, 0.90–0.91 from base. Postantennal filaments 846–932 long. Prelabral appendages (Fig. 11D) 2.4–3.8 times longer than wide. Labrum with 3 pairs of setae on anterior face; apical pair inconspicuous, median pair 172–184 long; 14–17 setae in each labral fan; 9–11 setae in each sublabral fan. Mandible as in other species of the subgenus; mandibular fan with 13–16 setae.

Abdomen — Abdominal segment IX (Fig. 11P) without dorsal process. Anal fan with 34 (1) rays. Anal tubules irregularly tapering.

TYPE MATERIAL

Holotype, male with associated exuvia, Yellowknife, N.W.T., 17.VII.1949, R. R. Hall (CNC No. 10959). Allotype, female, Great Whale River, Que., 29.VIII.1949, J. R. Vockeroth. Paratypes, 1 male, 3 pupal exuviae, Yellowknife, N.W.T., 6.VII.1949, R. R. Hall; 1 male, same data as allotype; 1 male, Whitehorse, Y.T., 19.VII.1950, R. H. Robertson; 2 males, Gillam, Man., 19 and 30.VI.1950, J. F. McAlpine; 2 females, Churchill, Man., 23 and 28.VII.1948, R. W. Fisher and W. R. Richards; 2 larval head capsules, Fort Churchill, Man., 24.VI.1950, B. C. Smith; 1 male, 1 female, Chisholm, Ont., 13 and 19.VI.1959, J. R. Vockeroth.

REMARKS

The immature stages of *C. cooki* and *C. nyblaei* probably cannot always be separated from each other with certainty. In *C. nyblaei* both median and outer rib of the pupal anal paddle are darker than the inner rib; in *C. cooki*, at most, the median rib is darker. The width:length of abdominal segment VII of the pupa is less than 1.6 in *C. cooki*, 1.7–1.9 in *C. nyblaei*. The dorsal process of the larval abdomen seems more reduced in *C. cooki* than in *C. nyblaei* and there seems to be normally fewer mandibular setae in *C. cooki*. However, these small differences in the immatures may not hold up when more material has been examined.

Chaoborus (*Schadanophasma*) *brunskilli* sp.n.

The male is characterized by the slender penis valve with its smooth and slender head and its short apical claw. The ratio Y/X is relatively low (about 1.7).

The pupa has a width:length ratio of abdominal segment VII of 1.45–1.50, and the median rib of the anal paddle usually is darker than the lateral ribs.

The larva has 23–32 setae in the mandibular fan, the longer antennal blades are 1.8–2.3 times as long as the shorter one and 0.70–0.79 times as long as the antenna, and the dorsum of segment IX has a distinct conical process.

MALE (n = 1)

Length 7.3 mm. General body coloration dark yellowish brown.

Antenna — Scapus $\frac{\text{length}}{\text{width}}$: $\frac{31}{307}$. Pedicel $\frac{\text{length}}{\text{width}}$: $\frac{98}{282}$. Longest bristle of flagellum 1.23 mm, of last segment 0.29 mm. Flagellar segments (1, 2–11, 12, 13) $\frac{\text{length}}{\text{width}}$: $\frac{245}{86}$, $\frac{110\text{–}123}{74\text{–}86}$, $\frac{294}{61}$, $\frac{245}{25}$. P/U=1.20.

Head — Head capsule pale in colour, darkened over vertex; pedicel fuscous; flagellar segments with dark basal ring that is pale basal of whorl, dark at whorl, somewhat paler distal of whorl; lateral margins of clypeus, maxillary stipes, palpi, and sclerotized portion of labellae infuscated.

Head width 1.02 mm. Width between eyes 0.40 mm. Clypeus length 412. Prementum length 359. HW/WBE = 2.55; HW/CL = 2.46; HW/PL = 3.20. Vertex with 137 setae. Clypeus with about 155 setae. Palp lengths: 123, 239, 233, 454.

Thorax — Ground colour luteous with dark fuscous vittae. 34 pronotal setae; 4–6 postpronotals. 11 proepisternals; 6–7 preepisternals; 12 anepisternals; 13–15 upper mesepimerals; no parascutellars. 70 scutellar setae in 3–4 irregular rows.

Wing — Regularly marked with dark grey cloudy spots mainly on the scales and setae and less distinctly on the wing membrane. Spots placed as in other species of the subgenus *Schadanophasma* (Cook, 1956, fig. 136) except there is an additional conspicuous spot at apex of R_1. Wing length 3.95 mm; width 0.96 mm. WL/WW = 4.13; WL/HW = 3.88; WL/Pf = 1.84. Lanceolate scales of wing margin of two alternating lengths 172 and 80 (measured at apex of An). Vein An terminates 49 beyond M-Cu. Y/X = 1.71; Y/Z = 1.42; Y/R_3 = 0.86; Z/M_1 = 0.56; R_3/M_1 = 0.95. Rsa about 200 long, distinct. One annular organ on Rs at R-M with a small microchaeta in it. Basal vein with about 10 setae and about 25 annular organs. Squama with 40 setae.

Haltere — Capitulum nearly spherical, white, with 3 anterior and 4 posterior bristles.

Legs — Legs pale brownish in ground colour; femora with dark ring apically; tibiae with dark brown rings apically and lighter brown rings basally; metatarsi dark apically and basally; ta_2–ta_5 slightly darker at apex. Claw of hind leg 65 long. Pulvilli of hind leg 40 long.

Lengths and proportions of legs:

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BR
p_1	2147	2220	1098	650	491	301	184	0.49	–
p_2	1730	1644	889	497	380	245	184	0.54	8.08
p_3	2392	2233	1239	699	491	282	184	0.55	7.33

Genitalia — Tergite IX with 12 setae on each lobe. Penis valve (Fig. 7C) luteous, with a short apical spine, and a smooth, slender head without ridges. Valve length 164; head length 84, head width 36; spine length 40, spine width 15. Basistyle length 613; dististyle length 552. Longest bristles on basistyle about 740. HR = 0.90; HV = 1.32.

PUPA (n = 1)

Total length 9.3 mm. Exuvia pale greyish brown, but with dark brown posterior and anterior lines of abdominal segments, all bristles in distinct brown spots, genital sac dark, basal part of anal

paddle membrane with distinct brown markings. Overall impression lighter than *C. nyblaei* and *C. cooki*. Thoracic organ (Fig. 10E) 1.24 mm long, 0.36 mm wide; length:lateral width 3.50; 97 reticulations in the transverse direction.

Abdominal segment VII 1.50 mm wide; width:length of segment VII 1.46. Genital sac 1.09 mm long. Median rib of anal paddle (Fig. 10B) slightly darker than lateral ribs, plumose seta 0.54 from base.

FOURTH INSTAR LARVA (n = 11, except when otherwise stated)

Total length 9.5–15.9 mean 13.5 mm (smaller larvae from East Henry Pond, Alta., larger larvae from Lake 241, Fisheries Research Board of Canada Experimental Lakes Area, Kenora, Ont.). Newly collected larvae slightly infuscated dorsally in larvae from Lake 241, rather dark from East Henry Pond. The larvae become more transparent after living for some time in rearing vials.

Head — Head capsule (Fig. 11A) length 1.46–2.03 mean 1.84 mm (12). Antenna (Fig. 11H) 0.74–1.02 mean 0.90 mm long; longer antennal blades 564–736 mean 661 long, shorter blade 245–380 mean 319 long, longer blades 1.77–2.30 mean 2.07 times as long as shorter one, longer blades 0.70–0.79 mean 0.74 times as long as antenna; seta on anterior face of antenna minute 0.82–0.94 mean 0.88 from base. Postantennal filaments 675–834 mean 775 (12) long. Prelabral appendage (Fig. 11E) 3.8–6.5 mean 4.8 times longer than wide, similar to that of *C. trivittatus*, irregular long-serrate on anterior face. Labrum with 3 pairs of setae on anterior face, apical pair inconspicuous, median pair 141–245 mean 179 (9) long; labral fans with 13–18 mean 16.7 (9) setae each; sublabral fans with 11–16 mean 13.9 (9) setae each. Mandible with 23–32 mean 27.3 setae in mandibular fan (23–29 (7) in specimens from Lake 241, 27–32 (3) in specimens from East Henry Pond).

Abdomen — Abdominal segment IX (Fig. 11Q, R) with a stout conical process on dorsum, slightly more pointed in specimens from East Henry Pond. Anal fan with 26–28 mean 27 (12) rays. Anal tubules irregularly tapering.

THIRD INSTAR LARVA (n = 12, except when otherwise stated)

Total length 6.8–11.5 mean 8.5 mm (13) (all larvae from Lake 241, Fisheries Research Board of Canada Experimental Lakes Area, Kenora, Ont.).

Head — Head capsule length 1.08–1.24 mean 1.16 mm. Antenna 0.46–0.53 mean 0.50 mm long; longer antennal blades 429–466 mean 442 long, shorter blades 184–227 mean 201 long, longer blades 2.00–2.40 mean 2.19 times as long as shorter one; seta on anterior face of antenna 0.68–0.81 mean 0.77 from base. Postantennal filaments 442–503 mean 476 (13) long. Prelabral appendages (Fig. 11F) 4.2–8.0 mean 6.5 times longer than wide. Median pair of labral setae 74–117 mean 91 long; 8–11 (10) setae in each labral fan; 5–7 (10) setae in each sublabral fan. Mandibular fan with 16–20 mean 18.1 (11) setae.

Abdomen — Anal fan with 20–24 (13) rays.

SECOND INSTAR LARVA

Total length 3.6–6.9 mean 5.2 mm (11) (smaller larvae from East Henry Pond, Alta., larger from Lake 230, Fisheries Research Board of Canada Experimental Lakes Area, Kenora, Ont.).

Head — Head capsule length 0.55–0.67 mean 0.60 mm (10). Antenna 0.22–0.29 mean 0.25 mm (12) long; longer antennal blades 244–323 mean 277 (12) long, shorter blade 117–180 mean 135 (9) long, longer blades 1.79–2.32 mean 2.07 (8) times as long as shorter one; seta on anterior face of antenna 0.43–0.67 mean 0.60 (11) from base. Postantennal filaments 150–265 mean 219 (11) long. Median pair of labral setae in each labral fan; 1–3 (9) setae in each sublabral fan. Mandibular fan with 9–14 mean 11.2 (11) setae.

Abdomen — Anal fan with 18–21 mean 19.1 (12) rays.

FIRST INSTAR LARVA (n = 1)

Total length 3.1 mm (larva from East Henry Pond, Alta.).

Head — Head capsule length 0.35 mm. Antenna 0.10 mm long; longer antennal blades 224; seta on anterior face of antenna 0.32 (?) from base. Mandibular fan with 9 setae.

Abdomen — Anal fan with 15 hair roots.

TYPE MATERIAL

Holotype, male with associated exuvia, meromictic lake, Lake 241, Fisheries Research Board of Canada Experimental Lakes Area, Kenora, Ont., leg 13.VI, emerged 14.VI.1968, G. Brunskill (CNC No. 10958). Paratypes, 22 larvae same data as holotype; 4 larvae, Lake 81, 15 larvae, Lake 230, 6 larvae, Lake 241, Fisheries Research Board of Canada Experimental Lakes Area, Kenora, Ont., 7–14.V.1969, A. L. Hamilton and J. Johnson; 8 larvae, East Henry Pond, Jasper National Park, Alta., 12.IX.1968, R. S. Anderson.

REMARKS

The larvae from East Henry Pond, Alta., are smaller than those from Kenora and the processes of segment IX are slightly more pointed. In other characters, however, they seem identical, and it has been presumed that they belong to the same species. If these larvae also belong to *C. brunskilli* sp.n., the ecology of this new species seems to be peculiar, the Kenora lakes being more or less brown-water lakes and East Henry Pond a clear, well-oxygenated, alpine pond.

It is not impossible that some of the specimens examined by Cook (1956, p. 31) as *C. nyblaei* (Zett.), and especially those from Banff, Alta., belong to this new species. However, only part of his material has been examined and none of the specimens examined belong to *C. brunskilli* sp.n.

Chaoborus (*Schadanophasma*) *trivittatus* (Loew) s.meo

Corethra trivittata Loew, 1862: 186.
?*Corethra punctipennis* Giles (nec Say), 1902: 502.
Sayomyia trivittata (Loew), Felt 1904: 361.
?*Sayomyia knabi* Dyar, 1905: 16.
Chaoborus (*Schadanophasma*) *trivattus* Dyar & Shannon (nec Loew), 1924: 212, pro parte.
Chaoborus nyblaei Edwards (nec Zett.), 1932: 26, pro parte.
Chaoborus nyblaei Cook (nec Zett.), 1956: 28, pro parte.

3 larvae and 1 pupa were present in my material, none of them reared. The characters given for the larvae are therefore partly based on Felt (1904) and an evaluation of the description by Cook (1956, p. 30–31) of *C. nyblaei* (Zett.).

The imago of *C. trivittatus* is characterized by the penis valve, which has an apical claw with a basal transverse ridge that lies mainly parallel to the long axis of the valve, and by the ratio Y/X, which is 1.6–2.1 in the male, 2.0–2.9 in the female.

MALE (n = 7, except when otherwise stated)

Length 5.7–7.4 mean 6.8 mm. General body coloration and coloration of various parts as stated by Cook (1956, p. 29–30, as *C. nyblaei*).

Antenna — Scapus $\frac{\text{length}}{\text{width}}$: $\frac{20\text{–}40}{226\text{–}266}$. Pedicel $\frac{\text{length}}{\text{width}}$: $\frac{80\text{–}146}{279\text{–}306}$. Longest bristle of flagellum 0.80–1.20 mm (6), of last segment 0.17–0.21 mm (5). Flagellar segments (1, 2–11, 12, 13) $\frac{\text{length}}{\text{width}}$: $\frac{146\text{–}306}{53\text{–}87}$, $\frac{93\text{–}173}{40\text{–}93}$ $\frac{306\text{–}372}{40\text{–}67}$, $\frac{226\text{–}326}{20\text{–}33}$. P/U = 1.04–1.47 mean 1.27.

Head — Head width 0.86–1.00 mean 0.93 mm (6). Width between eyes 0.34–0.45 mean 0.39 mm (6). Clypeus length 333–439 mean 388. Prementum length 306–412 mean 358. HW/WBE = 2.03–2.82

mean 2.40 (6); HW/CL = 2.15–2.76 mean 2.39 (6); HW/PL = 2.29–3.00 mean 2.61 (6). Vertex with 83–134 mean 111 (6) setae. Clypeus with 94–127 mean 110 setae. Palp lengths: 126–160, 200–266, 186–266, 359–579.

Thorax — 24–34 mean 26.8 (6) pronotal setae; 6–7 (5) postpronotals. 4–14 mean 8.2 proepisternals; 4–6 (6) preepisternals; 9–18 mean 12 (6) anepisternals; 11–19 mean 13.8 (6) upper mesepimerals; no parascutellars. 47–75 (6) scutellar setae, mostly in 3 irregular rows.

Wing — Wing markings as mentioned by Cook (1956, p. 29, fig. 136, as *C. nyblaei*). Wing length 3.54–4.81 mean 4.31 mm, width 0.77–1.12 mean 1.01 mm. WL/WW = 4.11–4.59 mean 4.26; WL/HW = 3.86–5.19 mean 4.59 (6); WL/Pf = 1.86–2.53 mean 2.05 (5). Lanceolate scales of wing margin of two alternating lengths 164–186 (6) and 64–90 (6) (measured at apex of An). Vein An terminates 16 short of M-Cu to 42 beyond M-Cu mean 17 (6) beyond M-Cu. Y/X = 1.63–2.08 mean 1.82; Y/Z = 1.27–1.53 mean 1.36; Y/R_3 = 0.60–0.97 mean 0.81; Z/M_1 = 0.46–0.72 mean 0.69; R_3/M_1 = 0.95–1.04, mean 1.00. Rsa 80–180 mean 125 (6) long, distinct. Squama with 20–42 (4) setae.

Haltere — Capitulum with 4–5 (4) anterior and 1–2 (4) posterior setae.

Legs — Claw of hind leg 48–62 (5) long. Pulvilli of hind leg 25–48 (5) long.

Lengths (ranges) and proportions (ranges and means) of leg segments (n = 4–7; for Br n = 1–2):

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BR
p_1	1397–2487	1715–2447	865–1277	466–785	333–585	239–319	173–200	0.42–0.54, 0.49	6.67
p_2	1397–2234	1250–2168	612–1104	386–652	293–492	239–286	146–193	0.48–0.53, 0.50	5.38
p_3	1796–2713	1742–2500	1091–1609	612–865	386–545	226–319	166–200	0.46–0.65, 0.60	5.00–7.78, 6.39

Genitalia — Tergite IX with 9–12 mean 10.2 (6) setae on each lobe. Penis valve (Fig. 8E–H) light to dark brown, variable in shape, head not globular, with an apical transverse ridge, apical claw about as long as head of valve and lying mostly parallel to the long axis of the valve. Valve length 117–148 mean 132; head length 37–58 mean 48, head width 21–48 mean 33; spine length 37–69 mean 58, spine width 16–21 mean 19 (6). Basistyle length 479–612 mean 551; dististyle length 326–505 mean 455. HR = 0.60–0.95 mean 0.83; HV = 1.36–1.73 mean 1.50.

FEMALE (n = 5, except when otherwise stated)

Length 5.2–7.2, mean 6.3 mm. Coloration of various parts as in male or somewhat paler.

Antenna — Scapus $\frac{\text{length}}{\text{width}}$: $\frac{13–20}{153–173}$. Pedicel $\frac{\text{length}}{\text{width}}$: $\frac{40–106}{126–140}$. Longest bristle of flagellum 599 (1), of last segment 213–253 (3). Flagellar segments (1, 2–11, 12, 13) $\frac{\text{length}}{\text{width}}$: $\frac{146–200}{53–80}$, $\frac{93–160}{33–67}$ (4–5), $\frac{160–200}{27–40}$ (4), $\frac{193–266}{27–33}$ (4). P/U = 0.65–0.87 mean 0.80 (4).

Head — Head width 0.92–1.14 mean 0.98 mm. Width between eyes 0.35–0.43 mean 0.38 mm. Clypeus length 372–486 mean 426. Prementum length 399–466 mean 438. HW/WBE = 2.46–2.69 mean 2.58; HW/CL = 2.08–2.57 mean 2.32; HW/PL = 2.19–2.46 mean 2.29 (4). Vertex with 90–139 (4) setae. Clypeus with 94–138 setae. Palp lengths: 146–186 (4), 239–306 (4), 226–279 (4), 532–698 (3).

Thorax — 20–28 pronotal setae; 4–5 postpronotals. 6–16 mean 11.2 proepisternals; 4–6 preepisternals; 13–29 mean 20 (4) anepisternals; 13–15 upper mesepimerals; no parascutellars. 66–108 scutellar setae.

Wing — Wing length 4.64–5.36 mean 4.97 mm; width 1.34–1.67 mean 1.51 mm. WL/WW = 3.12–3.51 mean 3.30; WL/HW = 4.53–5.30 mean 5.06; WL/Pf = 2.01–2.22 mean 2.07. Lanceolate scales of wing margin of two alternating lengths 217–239 and 95–127 (measured at apex of An). Vein An terminates 253–319 beyond M-Cu. Y/X = 1.71–2.92 mean 2.22; Y/Z = 1.27–1.61 mean 1.45; Y/R_3 = 0.71–0.84 mean 0.77; Z/M_1 = 0.48–0.57 mean 0.52; R_3/M_1 = 0.92–1.02 mean 0.98. Rsa 53–260 mean 113 long. Squama with 25–54 setae.

Haltere — Capitulum with 3–6 (3) anterior and 1 (3) posterior setae.

Legs — Claw of hind leg 53–69 (4) long. Pulvilli of hind leg 32–40 (4) long.

Lengths (ranges) and proportions (ranges and means) of leg segments:

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR
p_1	2221–2554	2341–2899	1131–1436	705–851	479–638	279–386	146–213	0.46–0.50, 0.48
p_2	1955–2394	1862–2301	918–1264	559–738	399–532	279–359	173–213	0.49–0.55, 0.52
p_3	2700–2860	2421–2846	1330–1802	692–904	452–612	279–359	186–226	0.55–0.64, 0.60

Genitalia — Genitalia as shown by Cook (1956, fig. 15A, as *C. nyblaei*). Spermathecae 80–90 in diameter.

PUPA ($n = 1$)

Total length 9.1 mm. Exuvia paler than in *C. brunskilli* sp.n., brown anterior and posterior lines of segments, bristles in indistinct brown spots, basal part of anal paddle membrane without distinct brown markings, but with heavy shagreenation. Thoracic organ about 1.13 mm long (crumpled and bent in this imperfect specimen), about 0.47 mm wide; length:lateral width about 2.4; about 65 reticulations in the longitudinal direction and about 22 at the widest point in the transverse direction.

Abdominal segment VII 1.53 mm wide; width:length of segment VII 1.37. Median rib of anal paddle slightly darker than lateral ribs; plumose seta 0.57 from base.

According to Cook (1956, fig. 18G) the width:length of segment VII seems to be about 1.5 at least in some pupae of *C. trivittatus*.

LARVA ($n = 3$, except when otherwise stated)

Total length 12.6–13.1 mm (2). Cook (1956, p. 30–31) probably described some head capsules of *C. cooki* sp.n. together with larvae of *C. trivittatus* under the name of *C. nyblaei* (see p. 20). He gives the total length range of the larvae as 15.0–19.0 mm, i.e., the total length range of *C. trivittatus* probably is at least 12.6–19.0 mm.

Head — Head capsule length 1.44–1.94 mm. Antenna 0.72–0.90 mm long; longer antennal blades 505–599, shorter blade 253–306, longer blades 1.95–2.00 times as long as shorter one, longer blades 0.70–0.76 times as long as antenna; seta on anterior face of antenna minute, 0.90–0.91 from base. As all the shorter measurements in Cook (1956, p. 30–31) presumably belong to *C. trivittatus*, the shorter measurements of the blades may sometimes be only 1.89 times as long as the shorter blade and the range at least 1.89–2.00. Postantennal filaments 625–758. Prelabral appendage (Felt, 1904, fig. 100) 4.7–6.1 times longer than wide, similar to that of *C. brunskilli* sp.n. (Fig. 11E), irregular long-serrate on anterior face. Labrum with 3 pairs of setae on anterior face, apical pair inconspicuous, median pair 146–159 long; labral fans with 10–12 setae each; sublabral fans with 8–9 setae each. Mandible (Felt, 1904, fig. 99) with 15–18 setae in mandibular fan. Cook (1956, p. 30–31) gives a range of 13–20 setae in the mandibular fan. The range found in *C. cooki* sp.n. is 13–16 setae and the specimens with 20 setae in the mandibular fan thus probably belong to *C. trivittatus* giving a range of 15–20 setae in the mandibular fan.

Abdomen — Abdominal segment IX with a stout conical process on dorsum as in *C. brunskilli* sp.n. (Fig. 11Q, R). Anal fan with 26 (2) rays. Cook (1956, p. 30–31) mentions 24–33 rays. Anal tubules irregularly tapering.

The larvae of *C. brunskilli* sp.n. and *C. trivittatus* differ from each other only in the number of setae in the mandibular fan (23–32 in *C. brunskilli*, 15–20 in *C. trivittatus*) and in that the longer antennal blades seem usually to be more than 2.0 times as long as the shorter blade in *C. brunskilli*, apparently less than 2.0 times as long as the shorter blade in *C. trivittatus*.

SPECIMENS EXAMINED

4 males, 3 females, Terrace, B.C., G. E. Shewell; 7 males, Kalso, B.C.; 1 male, Lac Phillipe, Que., J. R. Vockeroth; 2 females, 1500 feet, Old Chelsea, Que., J. R. Vockeroth; 1 male, well, N.S.; 1 pupa, 3 larvae, Stanford, California, E. F. Cook.

REMARKS

At least 3 species seem to have been included in Cook's *C. nyblaei*, one of them being *C. trivittatus*. Cook's description seems to be mainly based on *C. trivittatus*.

His figures of the penis valve and of the larval prelabral appendage undoubtedly belong to *C. trivittatus*. The pupae seem to belong exclusively to *C. trivittatus*. In the imagines the smaller measurements given by Cook probably are measurements taken from specimens of *C. trivittatus*; the higher measurements probably from specimens of *C. cooki* sp.n. or *C. nyblaei* (Zett.). According to the description of the larva of *C. trivittatus* by Felt (1904, p. 361), Cook probably had head capsules but no larval abdomen of *C. cooki* when his examination was carried out since the abdominal characters given fit *C. trivittatus* but not *C. cooki*.

The species described here are regarded as *C. trivittatus* (Loew) even if the types have not been examined. According to Cook's description of *C . nyblaei* (1956, p. 31) at least all American larvae examined by him seem to belong to *C. trivittatus*; the Canadian larvae probably belong to *C. cooki* sp.n. The specimens described by Felt (1904, p. 361–363) from New York in all likelihood belong to the species here described as *C. trivittatus*. The other species of *Schadanophasma* seem to be more northern species. As *C. trivittatus* was first described from Maine it is likely that it is synonymic with the species described here.

Subgenus *Chaoborus s. str.*

MALE

Wing and legs unmarked.

Ommatid-free upper part of eye small, shorter than or about as long as the diameter of 2 ommatids (Fig. 12H, 15). Parascutellar setae usually present (except in *C. obscuripes*). Scutellar setae mostly in 2 irregular rows.

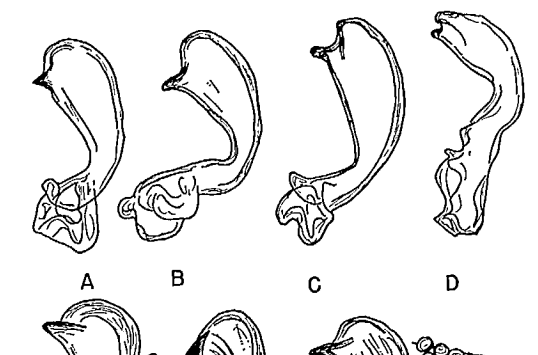

FIG. 12. *Chaoborus* (*Chaoborus*) *americanus* (Joh.). Male. (A–G) Penis valve: (A) From Ledges State Park, Iowa; (B–D) From Arboretum pond, Madison, Wisconsin; (E) From Great Whale River, Que.; (F) From Ramsey Co., Minnesota; (G) From Seddons Corner, Man. ((D) is forma *sonjai* f.n.; (E–G) forma *typica*; (C) an intermediate form); (H) Upper part of eye.

Wing (Sæther, in press, fig. 4A) with the appendix vein Rsa usually short, indistinct, or absent, occasionally distinct and reaching up to 200 in length. Cu_2a vein not present. Ratio Y/X of male wing 0.6–1.2, usually 0.7–0.9.

Pulvilli at least half as long as claws.

Basistyle without lobes or setae. Spine of penis valve preapical or, in *C. flavicans* (Sæther, in press, fig. 11B, C), nearly apical. Head of penis valve usually well developed, broad (Fig. 12A–G, 14, 16).

FEMALE

From a dorsal view tergite IX usually covers segment X, segment X slightly bilobed, tergite IX not bilobed (Cook, 1956, fig. 10).

PUPA

Width:length of abdominal segment VII less than 1.45.

Median rib of anal paddle stoutly developed and complete reaching the distal margin of paddle membrane, curved apically, with a single medial plumose seta or with both a plumose and a simple seta medially. Membrane of anal paddle without distinct brown markings. Outer rib usually with teeth or fine serrations (except in *C. flavicans*).

LARVA

Fourth instar larvae less than 16 mm long; head capsule at most 1.8 mm.

Seta on anterior face of antenna less than 0.8 from base. Larval tentorium very thin, weakly sclerotized (Fig. 18A).

Dorsal process of segment IX always present, although sometimes weak. Anal hook as in Fig. 18B.

Chaoborus (*Chaoborus*) *americanus* (Joh.)

Corethra plumicornis var. *americana* Johannsen, 1903: 398.
Sayomyia americana (Joh.), Felt 1904: 368.
Sayomyia hudsoni Felt, 1904: 371.
Chaoborus (*Chaoborus*) *crystallina* Dyar & Shannon (nec De Geer), 1924: 210, pro parte.
Chaoborus americanus (Joh.) Matheson 1925: 159.

The species is well described in Cook (1956). Nevertheless, a few additions should be made for comparison with related species and a few corrections have to be made to the description of the immatures.

MALE (n = 9)

Wing — Y/X = 0.60–0.89 mean 0.73; Y/Z = 0.93–1.04 mean 0.97; Y/R_3 = 0.42–0.58 mean 0.51; Z/M_1 = 0.59–0.77 mean 0.63; R_3/M_1 = 1.09–1.30 mean 1.22. Rsa 0–106, present in 3 of 9 specimens.

Genitalia — The penis valve is variable. There are at least two distinct morphological forms[4]: *C. americanus* forma *typica* f.n. (Fig. 12E–G) and *C. americanus* forma *sonjai* f.n. (Fig. 12D). Intermediate forms (Fig. 12C) also occur.

Other characters as mentioned by Cook (1956, p. 4–12, 20–21).

FEMALE (n = 1)

Wing — Y/X = 0.82; Y/Z = 1.01; Y/R_3 = 0.31; Z/M_1 = 0.37; R_3/M_1 = 1.18. Rsa 48 long.

Other characters as mentioned by Cook (1956, p. 4–12, 21–22).

PUPA (n = 5)

Width:length of abdominal segment VII 1.09–1.23 mean 1.19.

[4]According to the International Code of Zoological Nomenclature (1961, articles 1, 10b, 15, 45c, e) names given to infrasubspecific forms are excluded from the code. However, according to the preface (p. V) of the Code, the failure to deal with such forms "arises from no failure to recognize the necessity of such names. It exists because the practice of zoologists in regard to them is not sufficiently uniform to permit the formulation of rules covering them at this time."

The median rib of the anal paddle has a plumose seta and a simple seta situated medially (Fig. 13J). The simple seta was overlooked by Cook (1956, p. 18, 22). This seta is on the margin of the rib and not in the middle of it as in other species. If the bristle is not lying in a good position it is very difficult to observe, and if it is broken the bristle mark cannot be distinguished. The possibilities that this simple seta may sometimes be absent cannot be excluded.

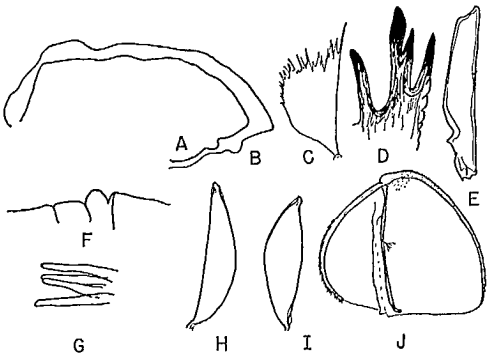

FIG. 13. *Chaoborus* (*Chaoborus*) *americanus* (Joh.). Larva and pupa. (A–B) Outline of head: (A) Forma *sonjai* f.n.; (B) Forma *typica*; (C) Prelabral appendage; (D) Mandible; (E) Antenna; (F) Dorsal abdominal process; (G) Anal tubules; (H–I) Thoracic organ: (H) Forma *typica*; (I) Forma *sonjai* f.n.; (J) Anal lobe.

There seems to be a slight difference between the pupal horns of *C. americanus* f. *typica* and those of *C. americanus* f. *sonjai*. In forma *typica* the greatest width of the thoracic organ is usually at the middle (Fig. 13H); in forma *sonjai* the greater width seems to be slightly distal to the middle (Fig. 11I). This difference may not hold up when a larger number of specimens is examined, judging from the large variation within other species.

Other pupal characters as mentioned by Cook (1956, p. 14–15, 22).

LARVA (Fig. 13A–G) (n = 30)

The ratio of the longer to the shorter antennal blades is variable in this species, ranging from 1.27 to 2.00. However, it seems possible to separate the larvae into two groups, one group having this ratio about 1.3–1.6 and the other having a ratio of 1.7–2.0. Larvae of the first group have been reared to the typical form; some of the larvae of the second group occur in the same locality as *C. americanus* f. *sonjai*, and may therefore belong to this form. This is the only character that seems to differ in these two larval forms; larvae of *C. obscuripes* from Norway show an equally wide variation in this ratio. A few intermediates have also been found. The minute seta on the anterior face of the antenna (Fig. 13E) was overlooked by Cook (1956, p. 18, 22). This seta is 0.50–0.59 from the base. The labrum bears 3 pairs of setae on its anterior face, the median pair reaches 46–63 in forma *typica*, 62–77 in forma *sonjai*. Labral fans with 15–20 setae each; sublabral fans with 11–15 setae each.

Other characters as mentioned by Cook (1956, p. 12–14, 22).

SPECIMENS EXAMINED

9 males, 37 females, 12 pupae, 9 pupal exuviae, 49 larvae, pond, arboretum, University of Wisconsin, Madison Wis., S. Teraguchi; 3 larvae, Lake 81, 1 larva, Lake 132, 4 larvae, Lake 230, Fisheries Research Board of Canada Experimental Lake Area, Kenora, Ont., A. L. Hamilton, G. Brunskill, and J. Johnson; 2 males, 5 females, 1 pupa, 5 pupal exuviae, 5 larvae, gravel pit, Seddons Corner, Man., J. F. Flannagan and G. P. McRae; 22 larvae, Fort Churchill, Man., J. R. Vockeroth; 13 larvae, Goose River, Churchill, Man., J. R. Vockeroth; 2 larvae, dugout, Stoughton, Sask., A. L. Hamilton; 6 larvae, Bear Lake, Alta., R. S. Anderson; 7 larvae, Rolling Hills, Alta., J. R. Vockeroth; 6 pupae, 25 larvae, Beardmore, Ont., J. R. Vockeroth; 1 female, Aylmer, Que., G. S. Walley; 2 males, 1 female, Great Whale River, Que., J. R. Vockeroth; 2 males, 7 females, Ramsey Co., Minnesota, D. G. Dennig and R. Daggy; 1 female, Cushing, Minnesota, Pratt and Peterson; 2 females, Wyoming, Minnesota, D. G. Dennig; 1 male, 1 female, Ledges State Park, Iowa, J. Laffoon; 1 male, 1 female, Brighton, Utah, J. S. McCloy; 8 larvae, Bryants Bog, J. C. Roth and Main.

REMARKS

The possibility cannot be excluded that forma *sonjai* may constitute a valid species separate from that of *C. americanus*. However, as intermediate forms exist, larvae of forma *sonjai* have not been reared, and as the variation within related species is equally large, the erection of a new species cannot at the moment be justified. Most likely *sonjai* is merely an ecotype or a morphological form as is known to occur for instance in *C. flavicans* (Sæther, 1967).

Chaoborus americanus shows similarities with *C. pallidus* in such characters as the shape of the penis valve head, the placement of hairs on the median rib of the pupal anal paddle, the outline of the head of the larva, and the reduced protuberance of abdominal segment IX of the larva. However, *C. obscuripes* is probably the closest related species and the larvae of these two species can be separated only with difficulty. In *C. americanus* the apices of the subordinate and posterior teeth of mandible extend to approximately the same level; in *C. obscuripes* the apex of the subordinate tooth does not attain the level of the apex of the most posterior tooth.

Chaoborus (*Chaoborus*) *obscuripes* (v.d. Wulp)

Corethra obscuripes v.d. Wulp, 1859: 160.
Corethra plumicornis Wesenberg-Lund (nec Fabr.) 1914: 81 pro parte.
Chaoborus obscuripes (v.d. Wulp), Martini 1929: 57.
Chaoborus (*Chaoborus*) *obscuripes* (v.d. Wulp), Edwards 1932: 26.

The male of this species is characterized by the lack of parascutellar setae, by the short median flagellar segments, by the large head and the long preapical spine or claw of the penis valve, by the low Y/X ratio (0.6–0.8), the low Y/Z ratio (0.9–1.2), and the high R_3/M_1 ratio (1.2–1.3).

The pupal thoracic organ is usually widest at the middle, the ribs of the anal paddle are about equally wide, and the outer rib has fine distal serrations.

The larvae have a reduced process on abdominal segment IX, broad prelabral appendages, 13–21 setae in the mandibular fan, and anal tubules nearly equal in width for their full length.

MALE (n = 6, except when otherwise stated)

Length 7.1–7.7 mm (5). Coloration of various parts as stated by Martini (1929, p. 57).

Antenna — Scapus $\frac{\text{length}}{\text{width}}$: $\frac{27\text{–}40}{279\text{–}333}$. Pedicel $\frac{\text{length}}{\text{width}}$: $\frac{73\text{–}153}{279\text{–}333}$. Longest bristle of flagellum 1.00–1.40 mm, of last segment 0.13–0.17 mm. Flagellar segments (1, 2–7, 8–11, 12, 13) $\frac{\text{length}}{\text{width}}$: $\frac{186\text{–}333}{93\text{–}106}$, $\frac{80\text{–}160}{80\text{–}106}$, $\frac{133\text{–}200}{73\text{–}100}$, $\frac{339\text{–}412}{73\text{–}93}$, $\frac{226\text{–}279}{27\text{–}40}$. P/U = 1.38–1.55 mean 1.48.

Head — Head width 1.01–1.13 mean 1.09 mm. Width between eyes 0.60–0.72 mean 0.67 mm. Clypeus length 366–412 mean 396. Prementum length 319–353 mean 337. HW/WBE = 1.54–1.70 mean 1.64; HW/CL = 2.62–2.80 mean 2.75; HW/PL = 3.02–3.44 mean 3.21. Vertex with 125–170 mean 145 setae.

Clypeus with 68–156 mean 117 setae. Palp lengths: 120–146, 213–239, 160–213, 213–319 (5).

Thorax — 43–60 mean 50 pronotal setae; 3–11 mean 8.7 postpronotals. 6–15 proepisternals; 3–7 preepisternals; 23–29 anepisternals; 6–11 upper mesepimerals; no parascutellars. 63–96 scutellar setae in 2–3 irregular rows.

Wing — Length 4.11–4.39 mean 4.28 mm; width 0.94–1.08, mean 1.01 mm. WL/WW = 3.94–4.48 mean 4.24; WL/HW = 3.73–4.09 mean 3.93; WL/Pf = 1.91–2.30 mean 2.14 (5). Lanceolate scales of wing margin of two alternating lengths 412–439 and 133–186 (measured at apex of An). Vein An terminates 239–386 mean 342 short of M-Cu. Y/X = 0.61–0.84 mean 0.72; Y/Z = 0.87–1.21 mean 1.03; Y/R_3 = 0.33–0.48 mean 0.41; Z/M_1 = 0.38–0.55 mean 0.47; R_3/M_1 = 1.17–1.34 mean 1.24. Rsa 0–80 long, present in 4 of 6 specimens. Squama with 24–58 mean 40 (4) setae.

Haltere — Capitulum with 4–6 anterior and 1–3 posterior setae.

Legs — Claw of hind leg 58–80 long. Pulvilli of hind leg 35–56 long.

Lengths (ranges) and proportions (ranges and means) of leg segments (n = 4–6):

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BR
p_1	1902–2221	1929–2141	851– 998	492–592	426–492	239–306	146–200	0.44–0.47, 0.45	–
p_2	1636–1889	1716–1968	712– 831	386–505	339–399	213–246	160–186	0.39–0.47, 0.43	7.22–9.56, 8.31
p_3	2155–2354	2075–2421	1131–1264	652–732	466–532	253–306	160–213	0.48–0.55, 0.53	7.92–11.55, 9.11

Genitalia — Tergite IX with 8–10 setae on each lobe. Penis valve (Fig. 14) with a long preapical spine and a large, almost globular head. Valve length 154–217 mean 174; head length 106–127 mean 114, head width 80–101 mean 91; spine length 95–143 mean 119, spine width 21–29 mean 24. Basistyle length 678–745 mean 705; dististyle length 505–545 mean 528. HR = 0.73–0.79 mean 0.76; HV = 1.35–1.52 mean 1.40 (5).

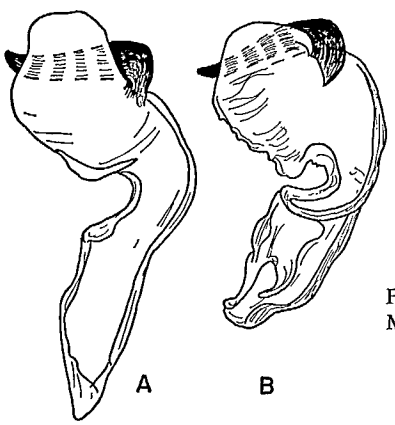

FIG. 14. *Chaoborus* (*Chaoborus*) *obscuripes* (v.d. Wulp). Male. Penis valve. (A) Obersee, Germany; (B) Spejldam, Hilleröd, Denmark.

FEMALE (not examined)

PUPA (n = 15, except when otherwise stated)

Total length 7.8–9.3 mean 7.8 mm (16). Thoracic organ 1.01–1.18 mean 1.10 mm long; lateral width 0.23–0.35 mean 0.28 mm; length:lateral width 3.35–4.61 mean 3.92; 73–106 mean 89 reticulations in the longitudinal direction and 14–25 mean 18 reticulations in lateral, transverse direction.

Abdominal segment VII 1.06–1.30 mean 1.16 mm wide; width:length of segment VII 1.21–1.33 mean 1.26.

Other characteristics as given by Peus (1934, p. 655–657) and Sæther (in press).

LARVA

The larva has been described in sufficient detail by Peus (1934), Prokešová (1959), Sikorowa (1966), Parma (1969), and Sæther (in press).

SPECIMENS EXAMINED

6 males, Abisko, Sweden, J. R. Vockeroth; 1 male hypopygium, Spejldam, Hilleröd, Denmark, K. Berg; 23 larvae, Overbugmyra, Andøya, Norway, A. Klemetsen; 4 larvae, Cabinpond A, Vassfaret, Norway, K. Elgmork; 24 larvae, Vütasaari, Findland, A. Luthers; 43 pupae, 40 larvae, Säräisniemi, Y. Wuorentaus, Finland; 13 larvae, ditch at Borok, Yaroslavl District, USSR, N. N. Smirnov; 10 larvae, Tacko Lake, Poland, A. Sikorowa; 10 larvae, pond, Experimental Fisheries Farm, Golysz, Katowice, Poland, J. Zięba; 7 larvae, bog south of Duszniki-Zdroj, Poland, S. Parma; 11 pupae, 18 larvae, Obersee, Germany, V. Herbst; 18 larvae, Heiven at Oisterwijk, Netherlands, C. Davids.

REMARKS

Chaoborus obscuripes differs in some ways from the other members of this subgenus. The adults lack the parascutellar setae found in the other species, the antenna has very short median segments, and the penis valve spine is much more well developed than in any other *Chaoborus*. However, the immature stages show clearly that it belongs to this subgenus, the closest relative apparently being *C. americanus*.

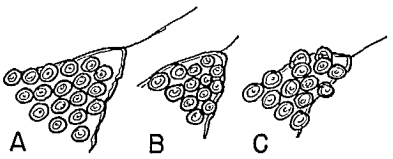

FIG. 15. *Chaoborus* (*Chaoborus*) spp. Male. Upper part of eye. (A) *C. obscuripes* (v.d. Wulp); (B) *C. crystallinus* (De Geer); (C) *C. flavicans* (Meig.).

Peus (1934, p. 658–659) regards *C. obscuripes* as a more or less stenotopic species restricted primarily to humic waters. However, it has been found in all kinds of localities with the exception of the most saprobic localities (Parma, 1969). In the high mountain areas and in the northern parts of Fennoscandia it apparently is the most common species.

Chaoborus (*Chaoborus*) *crystallinus* (De Geer)

Tipula crystallina De Geer, 1776: 386.
Tipula pilicornis Fabricius, 1787: 325.
?*Tipula hafniensis* Gmelin, 1788: 2826.
Tipula plumicornis Fabricius, 1794: 246.
?*Chaoborus antisepticus* Lichtenstein, 1800: 174.
Corethra lateralis Meigen, 1804: 8.
Corethra fusca Staeger, 1839: 556.
?*Corethra pilipes* Gimmerthal, 1845: 297.
?*Proboscistoma pellucens* Saccardo, Album varia lett. Vicenza, 1864: 21. Cited by Edwards 1932: 25.
Corethra culiciformis Theobald (nec De Geer), 1901: 296.
Corethra plumicornis Wesenberg-Lund (nec Fabr.) 1914: 8, pro parte.
Chaoborus crystallinus (De Geer), Akehurst 1922: 341.
Chaoborus borealis Cook, 1956: 25, syn.n.
nec *Chaoborus crystallina*, Dyar & Shannon, 1924: 210, pro parte.

MALE (n = 17, except when otherwise stated)

Length 5.3–7.0 mean 6.4 mm (Cook (1956, p. 26) mentions 4.5–6.0 mm). Coloration of various parts as mentioned by Martini (1929, p. 55–56) and Cook (1956, p. 26–27).

Antenna — Scapus $\frac{\text{length}}{\text{width}}$: $\frac{13\text{–}37}{213\text{–}307}$ (12). Pedicel $\frac{\text{length}}{\text{width}}$: $\frac{53\text{–}141}{220\text{–}268}$ (13). Longest bristle of flagellum 0.66–1.17 mm (13), of last segment 0.16–0.22 mm (7). Flagellar segments (1, 2–8, 9, 10, 11, 12, 13) $\frac{\text{length}}{\text{width}}$: $\frac{193\text{–}270}{53\text{–}86}$ (12), $\frac{87\text{–}120}{53\text{–}86}$ (12), $\frac{106\text{–}129}{53\text{–}80}$ (12), $\frac{116\text{–}135}{53\text{–}80}$ (12), $\frac{147}{40\text{–}80}$ (12), $\frac{226\text{–}356}{40\text{–}55}$ (12), $\frac{160\text{–}239}{20\text{–}31}$ (9). P/U = 1.18–1.80 mean 1.56 (9) (Cook (1956, p. 26) mentions 1.06–1.21 for *C. "borealis"*).

Head — Head width 0.79–0.94 mean 0.85 mm (16). Width between eyes 0.39–0.50 mean 0.42 mm. Clypeus length 253–325 mean 293. Prementum length 239–333 mean 287. HW/WBE = 1.86–2.13 mean 1.97 (15); HW/CL = 2.75–3.47 mean 2.92–(16) (Cook (1956, p. 26) mentions 3.36–3.58 in *C. "borealis"*); HW/PL = 2.69–3.67 mean 3.04 (16).

Vertex with 83–148 mean 100 (16) setae. Clypeus with 72–150 mean 106 (16) setae. Palp lengths: 67–123 mean 99 (16); 172–233 mean 189 (14); 93–190 mean 154 (14); 253–331 mean 303 (12).

Thorax — 24–42 pronotal setae; 2–7 (7–10 in *C. "borealis"*) postpronotals. 3–9 (16) proepisternals; 3–11 preepisternals; 8–16 (15) anepisternals; 5–14 (16) upper mesepimerals; 1–2 (16) parascutellars. 35–68 scutellar setae in 2 irregular rows.

Wing — Length 2.97–3.78 mean 3.23 mm (16); width 0.59–0.90 mean 0.75 mm (16). WL/WW = 4.08–5.11 mean 4.39 (16); WL/HW = 3.60–4.03 mean 3.81 (15); WL/Pf = 1.70–2.10 mean 1.89 (10). Lanceolate scales of wing margin of two alternating lengths 143–175 and 56–74 (measured at apex of An). Vein An terminates 93–293 mean 191 (16) short of M-Cu. Y/X = 0.65–1.18 mean 0.87 (16); Y/Z = 1.02–1.41 mean 1.18 (16); Y/R_3 = 0.37–0.63 (16); Z/M_1 = 0.33–0.70 mean 0.51 (16); R_3/M_1 = 1.01–1.30 mean 1.15 (16). Rsa present in 9 of 16 specimens, 27–180 mean 71 long. Squama with 19–58 mean 26 (15) setae.

Haltere — Capitulum with 2–5 (10) anterior and 1–4 (16) posterior setae.

Legs — Claw of hind leg 43–70 (8) long. Pulvilli of hind leg 28–56 (8) long.

Lengths (ranges) and proportions (ranges and means) of legs (n = 9–10; for BR, n = 6–8):

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BR
p_1	1490–1949	1556–2072	599– 969	432–588	366–454	220–282	147–208	0.39–0.53, 0.47	3.46–7.20, 4.60
p_2	1264–1924	1277–1557	599– 803	346–490	279–368	180–233	133–172	0.47–0.52, 0.49	6.00–10.83, 8.11
p_3	1623–2096	1556–2182	818–1287	466–711	372–490	200–282	159–196	0.53–0.59, 0.57	5.71–8.62, 7.44

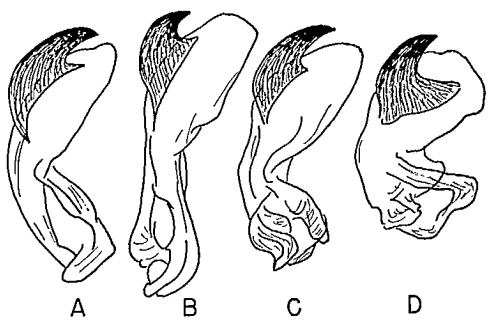

FIG. 16. *Chaoborus* (*Chaoborus*) *crystallinus* (De Geer). Male. Penis valve. (A) From Norman Wells, N.W.T.; (B) From Schiermonnikoog, Netherlands; (C) From Riihimäki, Finland; (D) From "Vijverhof," Netherlands.

Genitalia — Tergite IX with long setae (8–14 mean 10 (11)) on each lobe. Penis valve (Fig. 16) with a relatively short preapical spine. Valve length 85–159 mean 114 (14); head length 58–98 mean 71, head width 27–52 mean 44; spine length 40–58 mean 51, spine width (measured perpendicular to the strongest curvature at inner face) 11–18. Basistyle length 459–576 mean 498; dististyle length 337–466 mean 398. HR = 0.71–0.95 mean 0.79; HV = 1.32–1.76 mean 1.49.

FEMALE (n = 11, except when otherwise stated)

Length 4.6–6.6 mean 5.2 mm (10). Coloration as in male.

Antenna — Scapus $\frac{\text{length}}{\text{width}}$: $\frac{13\text{–}27}{93\text{–}146}$. Pedicel $\frac{\text{length}}{\text{width}}$: $\frac{40\text{–}93}{106\text{–}126}$. Longest bristle of flagellum 350–403 (4), of last segment 133–170 (3). Flagellar segments (1, 2–11, 12, 13) $\frac{\text{length}}{\text{width}}$: $\frac{106\text{–}146}{40\text{–}67}$, $\frac{53\text{–}80}{20\text{–}53}$, $\frac{106\text{–}153}{20\text{–}27}$, $\frac{126\text{–}186}{20\text{–}33}$. P/U = 0.65–0.92 mean 0.83 (7).

Head — Head width 0.72–0.89 mean 0.82 mm (8) (Cook (1956, p. 27) mentions 0.92–0.97 mm for *C.* "*borealis*"). Width between eyes 0.36–0.43 mean 0.40 mm (9) (0.45–0.48 mm for *C.* "*borealis*"). Clypeus length 266–306 mean 291. Prementum length 253–293 mean 270 (270–300 for *C.* "*borealis*"). HW/WBE = 1.91–2.12 mean 2.03 (7); HW/CL = 2.44–3.31 mean 2.84 (8) (3.42–3.47 for *C.* "*borealis*"); HW/PL = 2.73–3.30 mean 2.94 (8) (3.09–3.57 for *C.* "*borealis*"). Vertex with 74–114 setae. Clypeus with 79–100 setae. Palp lengths: 93–113, 146–193 (8), 146–180 (8), 319–333 (4).

Thorax — 19–33 (10) (24–44 in *C.* "*borealis*") pronotal setae; 4–5 (5–10 in *C.* "*borealis*") postpronotals. 4–9 proepisternals; 4–10 (9) (10–15 in *C.* "*borealis*") preepisternals; 9–11 (9) (14–17 in *C.* "*borealis*") anepisternals; 9–14 (10) (13–19 in *C.* "*borealis*") upper mesepimerals; 1–2 parascutellars. 42–49 (9) scutellar setae in 2 irregular rows.

Wing (Sæther, in press, fig. 4A) — Length 3.36–3.74 mm; width 0.97–1.10 mm (1.07–1.14 mm in *C.* "*borealis*"). WL/WW = 3.20–3.64 mean 3.44; WL/HW = 4.12–5.78 mean 4.66 (10) (3.77–4.08 in *C.* "*borealis*"); WL/Pf = 2.19–2.29 (6). Lanceolate scales of wing margin 249–292 and 95–111 long. Vein An terminates 93 short of M-Cu to 27 beyond M-Cu mean 39 short of M-Cu. Y/X = 0.67–1.05 mean 0.91 (10); Y/Z = 1.13–1.42 mean 1.22 (10); Y/R_3 = 0.32–0.47 mean 0.41; Z/M_1 = 0.29–0.42 mean 0.36 (10); R_3/M_1 = 0.98–1.13 mean 1.07 (10). Rsa 0–159 long, present in 7 out of 11 specimens. Squama with 28–46 mean 38 (10), setae.

Haltere — Capitulum with 3–6 (10) anterior and 1–2 (8) posterior setae.

Legs — Claw of hind leg 22–27 (8) long. Pulvilli 16–20 (8) long.

Lengths (ranges) and proportions (ranges and means) of legs (n = 4–9; for BR, n = 1–3):

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR	BR
p_1	1530–1663	1782–1889	778–811	452–519	372–412	220–259	146–173	0.42–0.46, 0.44	3.07–3.88, 3.44
p_2	1264–1476	1330–1536	625–678	386–426	279–333	186–220	146–180	0.43–0.49, 0.46	3.38
p_3	1556–1982	1756–2128	971–1117	532–638	372–452	233–266	160–193	0.52–0.60, 0.55	3.33–4.13, 3.73

Genitalia — Tergite IX covers segment X completely in a dorsal view, segment X slightly bilobed. Spermathecae 74–93 (8) in diameter.

PUPA (n = 14)

Total length 7.0–9.3 mean 8.4 mm. Thoracic organ (Fig. 17) variable, 0.82–1.48 mean 1.25 mm long, lateral width 0.28–0.47 mean 0.35 mm; length:lateral width 2.49–4.09 mean 3.57; 65–135 mean 107 reticulations in the longitudinal direction and 20–33 mean 24 reticulations in the lateral transverse direction.

Abdominal segment VII 1.10–1.69 mean 1.40 mm wide; width:length of segment VII 1.20–1.44 mean 1.31. Other characters as given by Peus (1934, p. 655–657) and Sæther (in press).

LARVA

The larva has been described in sufficient detail by Peus (1934), Eckstein (1936, only the form from Escheburger Moortümpel), Cook (1956, p. 28, as *C. borealis*), Prokešová (1959), Smith (1960a, b, as *C. borealis*), Sikorowa (1966), Parma (1969), and Sæther (in press). The statement by Cook (1956, p. 28) about the absence of a seta on the anterior face of the antenna in *C. borealis* is incorrect.

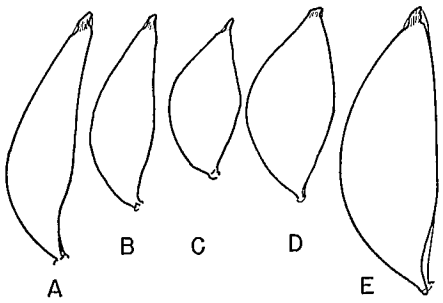

FIG. 17. *Chaoborus* (*Charoborus*) *crystallinus* (De Geer). Pupa. Thoracic organ. (A) From Schiermonnikoog, Netherlands; (B) From Riihimäki, Finland; (C) From Lükimaki, Finland; (D) From Churchill, Man.; (E) From Tvärminne, Finland.

SPECIMENS EXAMINED

Paratypes of *C. borealis* Cook: 1 male, Whitehorse, Y.T., L. C. Curtis; 1 male, Norman Wells, N.W.T., W. R. M. Mason; 1 male, Churchill, Man., W. R. M. Mason.

31 males, 63 females, 170 pupae, 119 pupal exuviae, 17 larvae, pond (= "Vijver") Nieuwersluis, Netherlands, S. Parma; 14 males, 5 pupae, 2 pupal exuviae, 11 larvae, pond on the island of Schiermonnikoog, Netherlands, S. Parma; 28 larvae, moat around castle Bovigny, Breda, Netherlands, G. Postema; 2 larvae, pond in the "Zoo," Amsterdam, Netherlands, A. C. Ellis-Adam; 12 larvae, drinking pool for cattle, Terhorne, Netherlands, H. Hoogveld; 94 males, 58 females, 2 pupae, 1 larva, pond, Riihimäki, Finland, M. Hirvenoja; 5 pupae, 78 larvae, Oulu, Finland, M. Hirvenoja; 7 pupae, Tvärminne, Finland, B. Lindeberg; 6 larvae, Lake Prestvatn, Tromsø, Norway, A. Klemetsen; 31 larvae, bog, south of Duszniki-Zdroj, S.W. Poland, S. Parma; 12 larvae, pond, Experimental Fisheries Farm at Golysz, prov. Katovice, J. Zięba; 1 pupa, 66 larvae, pond Kortowo Park, Olsztyn, Poland, A. Sikorowa; 71 larvae, a dying lake near Olsztyn, Poland, A. Sikorowa; 8 pupae, 5 pupal exuviae, 33 larvae, pond at outflow of Angara from Lake Baikal, USSR, N. N. Smirnov; 53 larvae, ditch at Borok, Yaroslavl District, USSR, N. N. Smirnov; 39 larvae, Fort Churchill, Man., B. C. Smith and M. Platek; 2 pupae, 9 larvae, Goose River, Churchill, Man., M. Platek; 1 larva, Lake 127, Fisheries Research Board of Canada Experimental Lakes Area, Kenora, Ont., G. Brunskill.

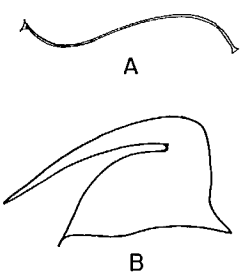

FIG. 18. *Chaoborus* (*Chaoborus*) *crystallinus* (De Geer). Larva. (A) Tentorium; (B) Anal hook.

REMARKS

Cook (1956, p. 25–26) gives the differences between *C. crystallinus* and his new species *C. borealis*. When the considerable variation is taken into account none of

these differences holds up for a separation into distinct species. Also, some European specimens have, for instance, a distinct Rsa appendix vein at base of Rs. Rsa may be distinct in one specimen and absent in another specimen from the same locality. The measurements and ratios given by Cook (1956, p. 25–26) for *C. borealis* constitute mostly extremes of variation in *C. crystallinus* if the two species are regarded as conspecific. However, it is customary to find the extremes in variation in the more arctic, subarctic, or alpine surroundings. The difference in general habitat mentioned by Cook is probably mostly a reflection of misidentifications and the lack of intensive investigations rather than an ecological difference. For instance a larva of *C. crystallinus* was found in the Kenora district of Ont., an area that cannot be considered subarctic. Also, in North America, *C. crystallinus* will be more exposed to competition as there are more species present here.

The fourth instar larva of *C. crystallinus* and the third instar of *C. brunskilli* sp.n. are similar. Differences, however, may be found in the more sclerotized larval tentorium, the more numerous mandibular setae, the longer antennal blades, and the longer postantennal filaments in *C. brunskilli*.

Chaoborus (Chaoborus) flavicans (Meigen)

Corethra flavicans Meigen 1830: 243.
Corethra albipes Johannsen, 1903: 398.
Sayomyia albipes (Joh.), Felt 1904: 363.
Sayomyia rotundifolia Felt, 1904: 366.
Chaoborus plumicornis Wesenberg-Lund (nec. Fabr), 1914: 8.
Chaoborus (Chaoborus) albipes (Joh.) Dyar & Shannon 1924: 211.
Chaoborus (Chaoborus) crystallina Dyar & Shannon (nec De Geer), 1924: 210, pro parte.
Chaoborus (Chaoborus) eluthera Dyar & Shannon, 1924: 211.
Chaoborus (Chaoborus) flavicans (Meig.), Dyar & Shannon, 1924: 211.

This species is well described by, among others, Martini (1929, p. 56), Peus (1934, 1938), Cook (1956, p. 23–25), Sæther (1967, in press), and Parma (1969).

A few details of the adult and of the pupa should be described for comparison with related species.

MALE (n = 3)

Wing — Y/X = 0.73–0.83; Y/Z = 1.03–1.09; Y/R_3 = 0.34–0.43; Z/M_1 = 0.39–0.45; R_3/M_1 = 1.15–1.18. Rsa 53–133 (absent in some other unmeasured specimens).

Other characters as mentioned by Cook (1956, p. 23–25).

FEMALE (n = 6, except when otherwise stated)

Wing — Y/Z = 0.52–1.07 mean 0.70 (5); Y/Z = 1.11–1.30; Y/R_3 = 0.22–0.43 mean 0.29; Z/M_1 = 0.21–0.36 mean 0.28; R_3/M_1 = 1.06–1.14. Rsa 0–101 long, present in 4 of 6 specimens.

Other characters as mentioned by Cook (1956, p. 23–25).

PUPA (n = 12)

Width:length of abdominal segment VII 1.20–1.31 mean 1.25. Other characteristics as mentioned by Peus (1934, p. 1938), Cook (1956, p. 25), and Sæther (1967, in press).

LARVA

The larva is well described by Peus (1934, 1938), Eckstein (1936, as *C. crystallinus* from Gr. Madenbröken See), Cook (1956), Prokešová (1959), Sæther (1967, in press), and Parma (1969).

SPECIMENS EXAMINED

2 males, 3 females, Lake 120, 13 larvae, Lake 122, 1 male, 4 females, 6 pupae, 504 larvae, Lake 132, 41 larvae, Lake 227, 6 pupal exuviae, Lake 230, 71 larvae, Lake 240, 14 larvae, Lake 261, 64 larvae, Lake 302, 11 larvae, Lake 303, Fisheries Research Board of Canada Experimental Lakes Area Kenora, Ont., A. L. Hamilton, G. Brunskill, G. P. McRae, and J. Johnson; 1 larva, Mildred Lake, Jasper National Park, Alta., R. S. Anderson; 1 hypopygium, Myers Lake, Indiana, J. B. Stahl; 5 larvae, a dying lake near Olsztyn, Poland, A. Sikorowa; 3 larvae, Lake Mutek, near Olsztyn, Poland, A. Sikorowa; 5 pupae, pond (= "Vijver"), Netherlands, S. Parma; 1 larva, Lake Prestvatn, Tromsø, Norway, A. Klemetsen. In addition, the material examined by Sæther (1967).

REMARKS

This is the only species known to occur outside the littoral zone of European lakes deeper than 5 m (Stahl, 1966). As mentioned by Stahl (1966) and Parma (1969) the records of *C. crystallinus* from deeper lakes are in all likelihood all misidentifications of *C. flavicans*. A previously overlooked misidentification is that of Eckstein (1936). Eckstein described two forms of *C. crystallinus*, one from Gr. Madebröken See and one from Escheburger Moortümpel. The form from Gr. Madebröken See is clearly *C. flavicans* as can be seen from the drawing of the penis valve given by Eckstein (1936, fig. 9a).

Chaoborus flavicans in several particulars resembles the members of the subgenus *Schadanophasma*. The ratio of HW/PL is less than 2.6 as in most specimens of *Schadanophasma* and lower than in the other species of *Chaoborus s. str.* The claw or spine of the penis valve is apical as in *Schadanophasma* rather than preapical as in the other species of *Chaoborus s. str.* The median rib of the pupal anal paddle is more slender and sometimes darker than the lateral ribs in *C. flavicans*; it is very slightly thinner and often darker than the lateral ribs in *Schadanophasma*. The fourth instar larva of *C. flavicans* and the undescribed third instar larva of *C. trivittatus* may only be separable by means of the subordinate mandibular tooth that in *C. flavicans* is unique in that it is placed almost exactly between the second and third teeth.

PHYLOGENY OF THE GENERA OF CHAOBORIDAE AND OF THE SPECIES OF *CHAOBORUS*

To be able to recognize the phylogenetic relationships (monophyletic groups) Hennig (1950, 1957) developed a theoretical synapomorphic diagram. This account of the phylogeny has been used by Illies (1965) for Plecoptera, by Brundin (1966) for chironomids especially of the subfamily Podonominae, and by Schlee (1968) for the *Corynoneura* group of the chironomid subfamily Orthocladiinae. The conclusions reached by Illies and Brundin have a far-reaching importance and if correct prove the

previous existence of a land bridge from Australia and New Zealand to South America via the Antarctic. The most complete coverage of the phylogeny of a small group of insects, however, is probably that of Schlee (1968). Schlee introduced the "Evolution Index" of Illies to the synapomorphic diagram. In this not only are the probable relationships between sister groups indicated, but also the probable height of evolution a species may have attained. He also stressed the importance of the several steps into which the different trends may be divided, especially in groups consisting of closely related species as for instance in the genus *Chaoborus*. This means that a trend does not only have to be found in its apomorphic or plesiomorphic character, but also that "relatively apomorphic" and "relatively plesiomorphic" characters must be taken into account. The following presentation is mainly after Schlee (1968). An equally detailed presentation, however, has not been found necessary.

Evolution Index

The evolution index was first used by Illies (1960) for the families of the Plecoptera and was also used by Schlee (1968) for the *Corynoneura* group of the chironomid subfamily Orthocladiinae. The calculation consists of assigning the different recognizable steps of each trend different numbers starting with 1 for the plesiomorph (= original, archaic) and proceeding to the highest number (2 if only two steps) for the apomorph (= derived, i.e., highly differentiated or reduced). The arithmetic mean of the step values of all trends gives the evolution index. The lowest possible evolution index equals 1; the highest belongs to the most evolved from. However, when the evolution index is given in this form the trends with the most steps get the highest values and are accordingly regarded as more important than the others. They may be more important in some cases but not always. In order to give all trends equal importance a second index is given together with the evolution index (Table 1). This second index, here called the "adjusted evolution index," gives all trends and steps equal value regardless of the number of steps, i.e., instead of using the scale 1–5 when there are five steps each number is adjusted to the scale 1–2.

The adjusted evolution index has been used to give the height of evolution for the genera of the Chaoboridae and the species of *Chaoborus* along the ordinate in Fig. 19. The genera and the species (Table 1) are arranged in order of height of evolution, i.e., how far they have evolved from a theoretical archetype. This will, however, not give direct evidence of the descent, i.e., not give the relationships between sister groups or species.

Trends

The trends are divided into steps. "Step 1" means a plesiomorphic form, "Step 2" a higher, more apomorphic form or, if only two steps, the most apomorphic form. These steps are also used in calculation of the evolution index (Table 1).

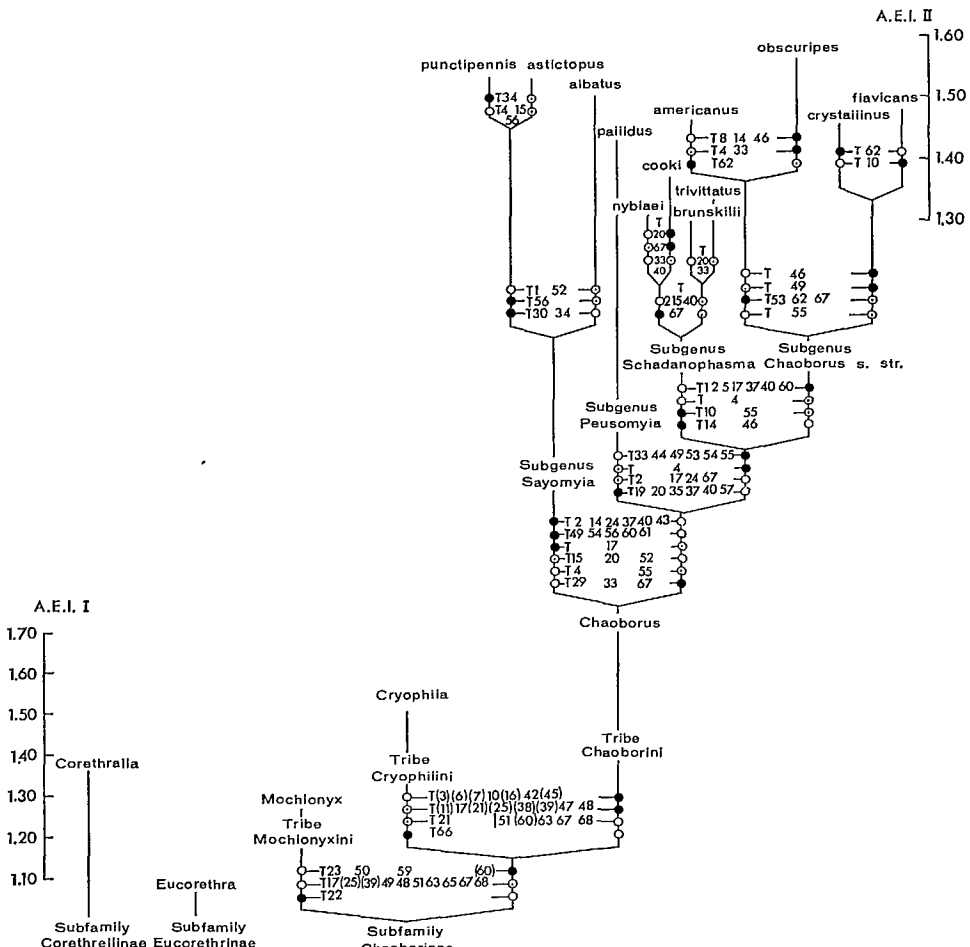

FIG. 19. Synapomorphic diagram (Hennig, 1950, 1957) giving the phylogeny of the Chaoboridae. The level of the specific names represents the height of the evolution for that particular species. The numbers marked with T represent the different trends given on p. 42–50. The solid circles give the more apomorphic character of the two alternatives, the open circles the plesiomorphic character. The open circles with a dot in the center give a relatively apomorphic or a relatively plesiomorphic character.

TABLE 1. The evolutionary level of chaoborid genera and the species of *Chaoborus* as indicated by the evolution index and the adjusted evolution index (see p. 37).

T[a]	*Eucorethra*	*Mochlonyx*	*Corethrella*	*Cryophila*	*Chaoborus*	Max. no. steps	*C. nyblaei*	*C. brunskilli*	*C. trivittatus*	*C. cooki*	*C. pallidus*	*C. americanus*	*C. crystallinus*	*C. flavicans*	*C. albatus*	*C. astictopus*	*C. punctipennis*	*C. obscuripes*	Max. no. steps
1							1.2	1.2	1.2	1.2	1.2	2	2	2	1.8	1	1	2	2
2	1	1.4	2	1.2	1.2	2	1	1.2	1.2	1.5	2	1.5	1.5	1.5	2	2	2	1.4	2
3	1	1.2	1	1.2[b]	2	2													
4							1.5	1.5	1.5	1.8	2	2	2	2	1	1.2	1.1	3	3
5	1	2	1	2[b]	2	2	1	1	1	1	2	2	2	2	2	2	2	2	2
6	1	1	1	1[b]	2	2													
7	1	1	2	1[b]	2	2													
8							1	1	1	1	1	1	1	1	1	1	1	2	2
9	2	1	1	1[b]	1.5	2													
10	1	1	1	1[b]	2	2													
11	1	2	1	2[b]	3	3													
12	1	2	1	2[b]	1	2													
13	1	1	2	1[b]	1	2													
14							2	2	2	2	1.5	1	1	1	2	2	2	2	2
15							1	1.1	1.1	1	1.5	1.1	1.1	1.2	1.9	2	1.8	1.1	2
16	1	1	1	1[b]	2	2													
17	1	1	1	1.5	2	2	1	1	1	1	2	2	2	2	2	2	2	2	2
18	1	1	2	1	1	2													
19							1	1	1	1	2	1.5	1.5	1.8	1.1?	1.1?	1.1	1.8	2
20							1	1.1	1.5	2	2	1	1.1	1	2?	2?	2	1	2
21	1	1.5	2	1.5[b]	3	3													
22	1	2	1	1.5	1	2													
23	1	1	1.9	2	2	2													
24							1	1	1	1	1.5	1	1	1	2	2	2	1	2
25	2	3	1	2[b]	4	4													

(Continued)

TABLE 1. The evolutionary level of chaoborid genera and the species of *Chaoborus* as indicated by the evolution index and the adjusted evolution index (see p. 37). — (*Concluded*)

T[a]	*Eucorethra*	*Mochlonyx*	*Corethrella*	*Cryophila*	*Chaoborus*	Max. no. steps	*C. nyblaei*	*C. brunskilli*	*C. trivittatus*	*C. cooki*	*C. pallidus*	*C. americanus*	*C. crystallinus*	*C. flavicans*	*C. albatus*	*C. astictopus*	*C. punctipennis*	*C. obscuripes*	Max. no. steps
26	1	1	2	1.5[b]	2	2													
27	1	2	2	2	2	2													
28	1	1	2	1	1	2													
29	1	1	1.5	1.5[b]	2.5	3	2	2	2	2	2	2	2	2	1	1	1	2	2
30							1	1	1	1	1	1	1	1	1	2	2	1	2
31	1	1	2	1	1	2													
32	2	1	1	1	1.2	2													
33							3.1	3.1	3.5	3.5	2	3	3.5	3.5	1	1	1	4	4
34							1	1	1	1	1	1	1	1	1	1.5	2	1	2
35							1	1	1	1	2	1	1	1	1	1	1	1	2
36	1	1	2	1	1	2													
37							1	1	1	1	2	2	2	2	2	2	2	2	2
38	1	2	1	2	3	3													
39	2	2	1	2.5[b]	3	3													
40							1	1.5	1.5	1.2	2	1.9	1.7	1.8	1.9	1.8	1.8	1.8	2
41	2	2	1	2	2	2													
42	1	1	1	1[b]	2	2													
43							1	1	1	1	1	1	1	1	2	2	2	1	2
44							2	2	2	2	1	2	2	2	1	1	1	2	2
45	1	2	1	2.5[b]	3	3													
46							2	2	2	2	1	1	2	2	1	1	1	2	2
47	1	2	1	2	3	3													
48	1	2	1.5	2	3	3													
49							2	2	2	2	1	1.5	2	1.8	2	2	2	1.5	2
50	1	3	4	3	4	4													

51	1	3	1	3	4	4												
52							1	1	1	1	1	1	1	1	3	2	2	1	3
53							4	3	3	4	1	4	3	3	1	1	1	4	4
54	1	1	1	1	1.8	2	2	2	2	2	1	2	2	2	2	2	2	2	2
55							3	3	3	3	1.8	1.9	2	2.2	1	1.1	1.2	1.8	3
56							1	1	1	1	1.1	1.1	1.1	1.2	1.5	2	1.8	1.1	2
57							1	1	1	1	2	1	1	1	1	1	1	1	2
58	1	1	2	1	1	2													
59	1	1	1	2	2	2													
60	1	1	1	1.5[b]	2	2	1	1	1	1	1	2	2	2	2	2	2	2	2
61							1	1	1	1	1	1	1	1	2	2	2	1	2
62							1	1	1	1	1	2	1	1	1	1	1	1.2	2
63	1	1.5	2.5	2	3	3													
64	1	1	2	1	1	2													
65	1	2	1	3	4	4													
66	1	1	1	2	1	2													
67	1	1	1	2	3	3	2.8	2	2	3	3	2.5	2	2	1	1	1	2.5	3
68	1	1	4	2	3	4													
EI[a]	1.12	1.40	1.50	1.64	2.14	2.47	1.49	1.46	1.48	1.55	1.52	1.63	1.61	1.66	1.54	1.55	1.56	1.76	2.25
AEI[a]	1.09	1.27	1.37	1.41	1.70	2.00	1.31	1.32	1.33	1.36	1.44	1.47	1.47	1.48	1.51	1.53	1.54	1.56	2.00

[a]T = trend; EI = evolution index; AEI = adjusted evolution index.

[b]These steps numbers are only estimated as the available description of *Cryophila lapponica* does not allow for a confident placement.

The direction of the evolution in the most apomorphic genus, *Chaoborus*, is indicated by the form present in the more plesiomorphic genera, *Cryophila* and *Mochlonyx*, since these can be regarded as being closer to the common theoretical plesiomorphic archetype. In some cases it is very difficult to decide whether a character is plesiomorphic or apomorphic within *Chaoborus*. This, however, may be of little importance as long as the majority of trends are correct. The supposed relationships will usually be supported even if the apomorphic characters are supposed to be the more plesiomorphic. A more serious problem is to decide which characters in this phylogenetic diagram may be the result of parallelism and which are clear monophyletic trends. If for instance the development of a curvature of the base of the larval antennae is *not* regarded as due to parallel development within the subgenera *Chaoborus s. str.* and *Schadanophasma* on the one hand and *Sayomyia* on the other, then the subgenus *Peusomyia* must be the sister group not only of *Schadanophasma* and *Chaoborus s. str.* as regarded here, but of all the remaining three subgenera. This could even be the case. Other features can more readily be regarded as exposed to parallel development. The reduction of the larval tentorium has evolved further in *Chaoborus s. str.* and in *Sayomyia* than in the other subgenera. However, these two subgenera are very unlikely to be a sister group of the two remaining genera as the subgenus closest related to *Chaoborus s. str.* by means of other characters is obviously *Schadanophasma* and not *Sayomyia.*

The intraspecific variation within *Chaoborus* seems to be very large. In numerous length measurements the variation may be more than 100%. As a result of this variability, some ecotypes have incorrectly been given specific rank. For example, two formerly recognized species, *C. alpinus* and *C. borealis*, are now believed to be only ecotypes of *C. flavicans* and *C. crystallinus*, respectively. Geographical variation seems to be important in the variation of shape and form of the Chaoboridae; the seasonal variation probably expresses itself more only in the relative length variations. This importance of geographical variation is contrary to that found, for instance, in chironomids where the seasonal variation usually seems to be more important. The variance within *Chaoborus* makes it more difficult to place a character of a species in a particular "Step." In some characters the variation may be, for instance, from Step 1 to Step 2 in a three-step trend. In such a case, the value of 1.5 has been given in the calculation of the evolution index and the species is regarded as relatively more plesiomorphic than a species that shows little variance and belongs in Step 2.

Trends of general phylogenetic interest, which consequently are often represented in different groups by parallelism, are marked with an asterisk. The trends and steps here used only for the genus *Chaoborus* are marked with two asterisks.

IMAGO

**T1 (Trend 1)

Coloration of wings and legs

Step 1 — Wings with several distinct spots. Legs with several brown rings.
Step 2 — Neither wings nor legs spotted.

*T2

Body size

Step 1 — *Eucorethra* is the largest of the Chaoboridae, the adults obtaining a length of 9.0–10.0 mm and the larvae 14.0–16.0 mm.

Step 2 — The smallest Chaoboridae belongs to *Corethrella* measuring only 1.3–2.5 mm as adults and maximum 2.9 mm as larvae. Within *Chaoborus* the subgenus *Schadanophasma* has the largest specimens, *Sayomyia* the smallest.

HEAD

*T3

Position of eyes

Step 1 — Eyes mostly lateral (Cook, 1956, fig. 24A).

Step 2 — Eyes ventrolateral (Cook, 1956, fig. 2B).

**T4

Diminution of the ratio HW/WBE

Step 1 — HW/WBE = 2.5–4.2.

Step 2 — HW/WBE = 1.8–2.3.

Step 3 — HW/WBE = 1.5–1.8.

*T5

Dorsal elongation of eyes

Step 1 — Eyes C-shaped (Cook, 1956, fig. 24A, 29A).

Step 2 — Eyes kidney-shaped, ommatid-free upper part of eye elongated (Fig. 9).

***Step 3* — Ommatid-free upper part of eye reduced (Fig. 2A, 4E, 12H, 15).

T6

Step 1 — Coronal suture distinct.

Step 2 — Coronal suture not present.

*T7

Step 1 — Posterior tentorial pits not separated from maxillary cardines.

Step 2 — Posterior tentorial pits separated from maxillary cardines by solid band of sclerotization.

**T8

Step 1 — Median flagellar segments almost twice as long as wide.

Step 2 — Median flagellar segments almost as wide as long.

T9

Step 1 — Clypeus small, not much larger than prementum (Cook, 1956, fig. 19A, 29A).

Step 2 — Clypeus elongated, about twice as long as prementum (Cook, 1956, fig. 24A).

T10

Step 1 — Prementum small (Cook, 1956, fig. 19A, 24A, 29A).

Step 2 — Prementum elongated (Cook, 1956, fig. 1C; Sæther, in press, fig. 2C).

THORAX

T11

Position of anterior and posterior pronotal lobes

Step 1 — These lobes connected.

Step 2 — Two lateral sclerites of posterior pronotum separated.

Step 3 — Anterior prothoracic lobes of females separated by anterior expansion of mesothoracic tergum.

***T12**

Step 1 — Setae present on katepisternum 3 (Cook, 1956, fig. 20A).

Step 2 — No setae on katepisternum 3 (Cook, 1956, fig. 4A, 25A, 30A; Sæther, in press, fig. 3).

***T13**

Proepisternum, preepisternum, anepisternum, and scutellum

Step 1 — Setae present on these sternites. Scutellum with more than one row of strong setae (Cook, 1956, fig. 4A, 20A, 25A; Sæther, in press, fig. 3).

Step 2 — These sternites without setae. Strong setae of scutellum in one row (Cook, 1956, fig. 30A).

****T14**

Step 1 — Parascutellar setae present (Cook, 1956, fig. 4A; Sæther, in press, fig. 3).

Step 2 — Parascutellar setae absent.

*, ****T15**

Step 1 — More than 30 anterior pronotal plus mesepimeral setae.

Step 2 — Less than 30 anterior pronotal plus mesepimeral setae.

T16

Step 1 — Metanotal processes absent.

Step 2 — Metanotal processes present (Cook, 1956, fig. 4A; Sæther, in press, fig. 3).

WINGS

***T17**

Scales on veins of wings

Step 1 — Scales obvious, not bristlelike.

Step 2 — Scales reduced in width, but their nature still clear.

***Step 3* — Scales bristlelike, scale structure only visible by electron microscope.

T18

Step 1 — Vein R_1 ends near end of R_2.

Step 2 — Vein R_1 terminates just beyond distal end of Sc (Cook, 1956, fig. 30C).

****T19**

Vein part Y of Rs

Step 1 — Ratio Y/R_3 higher than 0.6.

Step 2 — Ratio Y/R_3 smaller than 0.6.

**T20

Vein part X of Rs

Step 1 — Ratio Y/X less than 1.2 if T19 has taken place, less than 2.1 if T19 has not taken place.
Step 2 — Ratio Y/X higher than 1.2 with T19, higher than 2.1 without T19.

HALTERES

*T21

Step 1 — Numerous setae on pedicel and capitulum (Cook, 1956, fig. 25B).
Step 2 — Numerous setae only on capitulum (Cook, 1956, fig. 30B).
Step 3 — Less than 10 setae on capitulum (Cook, 1956, fig. 9A; Sæther, in press, fig. 3).

LEGS

T22

Step 1 — ta_1 not reduced (Cook, 1956, fig. 7A).
Step 2 — ta_1 about one fourth of ta_2 (Cook, 1956, fig. 20B).

*T23

Step 1 — Tarsal claws complex, with sexual differences (Cook, 1956, fig. 20D).
Step 2 — Tarsal claws simple, without sexual differences (Cook, 1956, fig. 7C, 30D, E).

*.**T24

Step 1 — Pulvilli more than half as long as claws.
Step 2 — Pulvilli less than half as long as claws.

ABDOMEN

*T25

Length of abdominal segment VIII

Step 1 — Segment VIII equal in length to VII.
Step 2 — Segment VIII a little more than half as long as VII.
Step 3 — Segment VIII half as long as segment VII.
Step 4 — Segment VIII about one fourth as long as segment VII.

*T26

Step 1 — Abdominal spiracles distinct, well developed.
Step 2 — Abdominal spiracles minute, inconspicuous.

GENITALIA

*T27

Step 1 — Hypopygium not rotated.
Step 2 — Hypopygium rotated 180°.

T28

Step 1 — No long, strong seta at base of basistyle.
Step 2 — Long, strong seta set in spinelike cup present on inner surface at base of basistyle (Cook, 1956, fig. 31A).

T29

Reduction of stout setae on inner surface at apex of basistyle

Step 1 — Many such setae present (Cook, 1956, fig. 21A, 26B).

***Step 2* — Only two such setae present (Cook, 1956, fig. 16A, C, E).

***Step 3* — These setae lacking.

***, **T30**

Step 1 — Basistyle without preapical lobe.

Step 2 — Basistyle with preapical lobe (Cook, 1956, fig. 16A, E).

T31

Step 1 — Penis valves simple, separated.

Step 2 — Penis valves fused distally into single spinelike process (Cook, 1956, fig. 31A, C).

T32

Step 1 — Penis valve simple, pointed, without apical spines.

Step 2 — Penis valve with several small apical spines (Cook, 1956, fig. 26B).

****T33**

Step 1 — Penis valve simple, pointed, without distinct head or preapical or apical spine or claw.

Step 2 — Penis valve with well-developed broadened head, more or less rounded apically, but without preapical spine (Fig. 4A–D).

Step 3 — Penis valve with head and apical or preapical spine or claw (Fig. 7, 8, 12, 16).

Step 4 — Elongation of this claw or spine (Fig. 14).

****T34**

Step 1 — As Step 1 in T33.

Step 2 — Bifurcation of apex of valve (Fig. 2B–C).

(T33 and 34 are here interpreted as a development in different directions. T33 is a development of the point into an apical or preapical spine. T34 seems to be more of a bifurcation of the apex of the valve.)

****T35**

Step 1 — Dististyle simple.

Step 2 — Dististyle with apical clawlike protuberance (Martini, 1929, fig. 80).

***T36**

Step 1 — Three spermathecae (Fig. 5).

Step 2 — One spermatheca (Cook, 1956, fig. 31B).

PUPA

***, **T37**

Step 1 — Exuvia brownish with brown markings on membrane of anal paddle (Fig. 10A–C).

Step 2 — Exuviae colourless without markings.

***T38**

Reduction of aperture of thoracic organ

Step 1 — Aperture large (Cook, 1956, fig. 28F, 34C, D, E).

Step 2 — Aperture small, located at apex of main body of horn (Cook, 1956, fig. 23C).

Step 3 — Aperture small, located on small papilla on apex of horn (Fig. 3O–P, 6G, 10D–F, 13H–I, 17).

***T39**

Reduction of abdominal segment VIII

Step 1 — Segment VIII more than one fourth of VII (Cook, 1956, fig. 34A, B).
Step 2 — Segment VIII about one fourth of VII.
Step 3 — Segment VIII less than one fourth of VII.

***, **T40**

Reduction of ratio of width:length of abdominal segment VII

Step 1 — W/L about 1.7–1.9.
Step 2 — W/L about 1.1.

***T41**

Step 1 — Anal paddles not developed (Cook, 1956, fig. 34A, B).
Step 2 — Anal paddles developed (Fig. 3Q–R, 6H, 10A–C, 13J).

T42

Step 1 — No lateral ribs of anal paddle present (Cook, 1956, fig. 23C, 28D).
Step 2 — Lateral ribs of anal paddles well developed (Fig. 3Q–R, 6H, 10A–C, 13J).

****T43**

Step 1 — Median rib of anal paddle reaching margin of paddle membrane, straight at apex (Fig. 6H).
Step 2 — Median rib reduced (Fig. 3Q–R).

****T44**

Step 1 — As Step 1 in T43.
Step 2 — Median rib elongated, with an apical bend (Fig. 10A–C, 13J).

T45

Step 1 — Plumose seta of median rib of anal paddle near apex of rib (Cook, 1956, fig. 28D).
Step 2 — Plumose seta about one fourth of rib length from distal end (Cook, 1956, fig. 23C).
Step 3 — Plumose seta near middle of rib (Fig. 3Q–R, 6H, 10A–C, 13J).

***, **T46**

Step 1 — Simple seta of median rib close to plumose seta (Fig. 3Q–R, 6H, 13J).
Step 2 — Simple seta and plumose seta widely separated (simple seta at apex of rib) (Fig. 10A–C).

LARVA

***T47**

Step 1 — General coloration of larva dark.
Step 2 — Larva translucent.
Step 3 — Larva transparent.

T48

Elongation and lateral compression of head

Step 1 — Head wide. Anterior margin of labrum anterior to base of antennae (Cook, 1956, fig. 27A, B).
Step 2 — Development of a proboscislike structure that bears the antenna at apex (Montschadsky, 1936, fig. 43).
Step 3 — Head longer than wide.

***, **T49**

Step 1 — Curvature of upper edge of head starting before the middle (Sæther, in press, fig. 13D).
Step 2 — Slight curvature of upper edge of head starting distal to middle of head (Fig. 11A–C).

***T50**

Step 1 — Distance between antennae almost as large as width of head (Cook, 1956, fig. 27A, B).
Step 2 — Distance between antennae about half as long as width of head (Cook, 1956, fig. 22A, B).
Step 3 — Distance between antennae about one fifth of width of head (Montschadsky, 1936, fig. 43).
Step 4 — Antenna very closely approximated (Cook, 1956, fig. 11, 32A, B).

T51

Reduction of clypeus, enlargement of clypeal setae, and formation of prelabral appendages and postantennal filaments

Step 1 — Clypeus large, clypeal setae small (Cook, 1956, fig. 27A).
Step 2 — Clypeus large, clypeolabral setae enlarged (Cook, 1956, fig. 22A).
Step 3 — Clypeus slightly reduced, clypeolabral setae very long (Montschadsky, 1936, fig. 43).
Step 4 — Clypeus completely reduced, prelabral appendages and postantennal filaments developed.

****T52**

Step 1 — Prelabral appendage bristlelike, with posterior and slightly lateral spines (Fig. 6B).
Step 2 — Prelabral appendage flattened, narrow, spines changed to posterior and anterior serrations, appendages more than 10 times as long as wide (Fig. 3D–G).
Step 3 — Prelabral appendage posteriorly and anteriorly serrated, about 7 times as long as wide (Fig. 3H).

****T53**

Step 1 — As Step 1 in T52.
Step 2 — As Step 2 in T52, but only anterior serrated (not represented by any known species).[5]
Step 3 — Prelabral appendage only anteriorly serrated, 7 times as long as wide (Fig. 11E).
Step 4 — Prelabral appendage anterior serrated. About 3 times as long as wide (Fig. 11D, G, 13C).

(T52 and 53 are regarded as parallel developments with broadening of the prelabral appendages. However in one case a posterior serration has been developed, which in connection with other characters indicates the parallelism rather than the monophyletic character of the two trends.)

***, **T54**

Step 1 — No curvature at base of antenna (Fig. 6A).
Step 2 — Curvature present at base of antenna (Fig. 3A–C, 11H–J, 13E).

****T55**

Step 1 — Seta on anterior face of antenna 0.24–0.36 from base (Fig. 3C).
Step 2 — Seta 0.45–0.75 from base (Fig. 13E).
Step 3 — Seta 0.80–0.95 from base (Fig. 11H–J).

****T56**

Step 1 — Seta on anterior face of antenna minute.
Step 2 — Seta on anterior face of antenna 30–39 long (Fig. 3B).

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[5]This step is included here to make T52 and T53 comparable.

**T57

Step 1 — Three pairs of setae on anterior face of labrum.

Step 2 — Two pairs of setae on anterior face of labrum.

T58

Step 1 — Eyes of "normal" size (Cook, 1956, fig. 27A, B, 28A), or larger.

Step 2 — Eyes reduced to merely pigmented spots (Cook, 1956, fig. 32A, 33A).

T59

Step 1 — Eyes of "normal" size.

Step 2 — Compound eyes enlarged (Cook, 1956, fig. 11B; Montschadsky, 1936, fig. 43).

(T58 and 59 are developments of one character in two directions.)

*T60

Reduction of larval tentorium

Step 1 — Tentorium stout rods.

***Step 2* — Tentorium slender rods, distinctly sclerotized for their full length (Fig. 6F, 11L).

***Step 3* — Tentorium very thin rods without distinct sclerotization medially (Fig. 3N, 18A).

*T61

Step 1 — Subordinate tooth of mandible not spinelike (Fig. 11K).

Step 2 — Subordinate tooth of mandible spinelike (Fig. 3L).

**T62

Step 1 — Subordinate tooth of mandible placed at base of second tooth.

Step 2 — Apices of subordinate and posterior teeth of mandible extending to approximately same level (Fig. 13D).

*T63

Step 1 — Thorax more than twice as wide as first abdominal segment (Cook, 1956, fig. 28A).

Step 2 — Thorax about 1.5 times as wide as first abdominal segment, body relatively broad (Montschadsky, 1936, fig. 43).

Step 3 — Thorax less than 1.5 times as wide as first abdominal segment, body relatively slender.

*T64

Step 1 — Tracheal system fully developed, air sacs not developed (or reduced with development of air sacs).

Step 2 — Tracheal system reduced, but functioning. Air sacs not developed.

T65

Step 1 — Air sacs not developed, tracheal system fully developed.

Step 2 — Air sacs developed, tracheal system still fully developed.

Step 3 — Air sacs developed, tracheal system functioning, but reduced.

Step 4 — Air sacs fully developed. Tracheal system closed, nonfunctioning.

T66

Step 1 — Two abdominal air sacs.

Step 2 — Four abdominal air sacs (Montschadsky, 1936, fig. 43).

*T67

Step 1 — Siphon well developed (Cook, 1956, fig. 23A).

Step 2 — Siphon completely reduced, only a small circular sclerotization surrounds a pair of functional spiracles (Montschadsky, 1936, fig. 43).

***Step 3* — Spiracles nonfunctioning. Protuberance apparently two-segmented (Fig. 3I–K).

***Step 4* — Protuberance one-segmented, well developed (Fig. 11Q).

***Step 5* — Protuberance not present (Fig. 11P).

T68

Step 1 — Dense brush of plumose setae present on anal segment (Cook, 1956, fig. 28A).

Step 2 — Hair in anal brush single, but plumose, arranged in close double row (Montschadsky, 1936, fig. 43).

Step 3 — Hairs in anal fan single, feathered, almost in one line.

Step 4 — No dense brush of plumose setae present on anal segment (Cook, 1956, fig. 33A).

Sister Groups

Subfamily Corethrellinae — Subfamilies Eucorethrinae + Chaoborinae

[The mainly neotropical genus *Lutzomiops*, in North America represented only by *Lutzomiops kervillensis* Stone (Stone, 1965, p. 231), has not been dealt with here as the Nearctic species is known only from females.] *Corethrella* is in several synapomorphic characters distinct from the other chaoborids and therefore forms a monophyletic unity. The trends T13, 18, 28, 31, 36, 58, 64, and 68 in their most apomorphic form appear only in *Corethrella*; the trends T2, 7, 21, 27, and 50 are subject to parallelism and therefore may be appearing higher up on the "phylogenetic tree." Trend 23, the simplification of the tarsal claws, also appears at the division *Mochlonyx — Cryophila + Chaoborus*, but the simplification in *Corethrella* has taken a slightly different direction with no pulvilli and empodium and larger claws on the male prothoracic legs. The monophyletic unity of the subfamilies Eucorethrinae and Chaoborinae is secured by the trends T25 and T41.

Subfamily Eucorethrinae — Subfamily Chaoborinae

The monophyletic unity of Chaoborinae is indicated by 14 synapomorphic trends (Fig. 19), the monophyletic unity of Eucorethrinae by three synapomorphic trends of which the development of several spines on the penis valves is probably the most important one.

The genus *Eucorethra* is undoubtedly the most plesiomorphic genus among the Chaoborids.

Tribe Mochlonyxini — Tribes Cryophilini + Chaoborini

The monophyletic unity of the tribes Cryophilini and Chaoborini is indicated by at least 11 and possibly 14 trends. The three trends given in brackets in Fig. 19 may possibly take place at the following branching, i.e., between *Chaoborus* and *Cryophila*. The monophyletic unity of *Mochlonyx* is indicated by just one synapomorphic

trend, the reduction of ta_1, a trend that may not be important. However, if this trend is not taken into consideration the monophylogenetic unity of *Mochlonyx* is in some doubt. When the different stages of *Cryophila lapponica* have been redescribed this situation will likely be improved as several characters likely to be synapomorphic in *Mochlonyx* can not be shown as such until their development in *Cryophila* is known.

Tribe Cryophilini (*Cryophila lapponica*) — Tribe Chaoborini (*Chaoborus*)

The monophyletic unity of Chaoborini is indicated by at least nine, possibly 20, trends (see above); the monophyletic unity of Cryophilini is indicated by at least one important synapomorphic trend represented by the presence of four abdominal air sacs in the larvae of *Cryophila*. Other synapomorphic characters of *Cryophila* are likely to be found when the single species known has been redescribed.

SUBGENUS *Sayomyia* — SUBGENERA *Peusomyia* + *Schadanophasma* + *Chaoborus s. str.*

The monophyletic unity of the subgenus *Sayomyia* seems at first glance to be well established with 15 synapomorphic trends. However most of these trends are trends of a general character and parallel development takes place higher up among the other subgenera. The remaining trends are reduction of the median rib of the pupal anal paddle (T43), flattening and broadening of the prelabral appendages with retention of both a posterior and an anterior serration (T52), enlargement of the seta on the anterior face of the antenna (T56), and development of a spinelike subordinate tooth of the larval mandible (T61). These trends, possibly with the exception of the first and the third, are doubtful, and the monophyletic unity of the subgenus cannot be said to be 100% secured. The trends establishing the remaining subgenera as a monophyletic unit are reduction of the ratio HW/WBE (T4) (only relatively more plesiomorphic in *Sayomyia*), reduction of stout setae on the inner surface of the apex of the basistyle (T29) (probably not an important trend), development of a head and a spine or claw on the penis valve (T33) (a more or less parallel development takes place in *Sayomyia*), and reduction of the protuberance of the larval abdominal segment IX from an apparently two-segmented to one-segmented form (T67).

punctipennis + *astictopus* — *albatus*

The species of the subgenus *Sayomyia* are closely related and the trends are few. *Chaoborus punctipennis* and *C. astictopus* show synapomorphy in the development of a preapical lobe of the dististyle (T30), bifurcation of the penis valve (T34), and elongation of seta on the anterior face of the larval antenna (T56). The larva of *C. albatus*, however, has a more derived prelabral appendage.

punctipennis — *astictopus*

Perhaps *C. astictopus* is merely a subspecies of *C. punctipennis*. Accordingly there are only relatively apomorphic trends. The bifurcation of the penis valve (T34) is more constant and better developed in *C. punctipennis*; the HW/WBE ratio (T4),

number of anterior pronotal plus mesepimeral seta (T15), and the length of the seta on the anterior face of the larval antenna (T56) seem more derived in *C. astictopus*.

Subgenus *Peusomyia* — Subgenera *Schadanophasma* + *Chaoborus s. str.*

The monophyletic isolation of *C.* (*Peusomyia*) *pallidus* is indicated by 11 trends of which only two do not take place as parallel developments at another branching, namely the development of an apical clawlike protuberance of the dististyle (T35) and the reduction from three to two pairs of setae on the anterior face of the larval labrum (T57). The penis valves are regarded as being of the shape typical of step 2 of trend 33. However, they are quite distinct from the valves found in the other subgenera and the development of the penis valves could perhaps be regarded as going in three different directions, with those found in *C. punctipennis* (T34), in *C. pallidus* (a new trend), and in *C. obscuripes* (T33) as the most apomorphic representatives of these directions. The monophyletic unity of the subgenera *Schadanophasma* and *Chaoborus s. str.* is indicated by several trends of which the development of a preapical or apical spine or claw (T33), the elongation and curving of the median rib of the pupae (T44), and the widening of the prelabral appendages with the development of only anterior serration (T53) are the most important.

Subgenus *Schadanophasma* — Subgenus *Chaoborus s. str.*

Most of the trends given here are general trends likely to exhibit parallel development. As mentioned on p. 36, *C. flavicans* seems, in respect of the penis valve and the relatively long prementum, as well as in some immature characters, to be similar to *Schadanophasma*. At the moment, it seems difficult to decide whether *C. flavicans* (eventually also *C. crystallinus*) plus *Schadanophasma* is the sister group of the remaining species of *Chaoborus s. str.* or if *Schadanophasma* is the sister group of *Chaoborus s. str.* as regarded here. *Schadanophasma* is in many features the more plesiomorphic subgenus: it is larger (T1), has spotted wings and legs (T2), an elongated ommatid-free upper part of eye (T5), visible scales on the veins (T17), stronger coloured pupal evuvia (T37), wider pupal abdominal segments (T40), and a relatively strongly sclerotized larval tentorium (T60). Except for the coloration of the legs, these trends are represented here in their most plesiomorphic situation within *Chaoborus*. The apical placement of the seta on the anterior face of the antenna of the larva (T55), as well as the long prementum (T10), however, are in *Schadanophasma* more highly evolved than in other species of *Chaoborus*.

Chaoborus americanus may also constitute the sister group of the remaining species of *Chaoborus s. str.* plus *Schadanophasma*. Its penis valve is more similar to *C. pallidus* and seems more plesiomorphic than in the other species and the simple seta on the anal paddle is situated medially as in *Peusomyia* and *Sayomyia*. In respect of the placement of the subordinate tooth of the mandible (T62), however, *C. americanus* is more apomorphic than other species of *Chaoborus s. str.* or *Schadanophasma*.

nyblaei + *cooki* — *brunskilli* + *trivittatus*

The members of the subgenus *Schadanophasma* seem more closely related to each other than are the members of the other subgenera. *Chaoborus nyblaei* and *C. cooki* are larger (T2), have a larger number of thoracic bristles (T15), and have a broader abdominal segment VII of the pupa than the other two and are accordingly more plesiomorphic in these respects. The reduced larval siphon (T67) in *C. nyblaei* and *C. cooki*, however, is a synapomorphic character.

nyblaei — *cooki*

Chaoborus cooki shows some more derived features such as a higher Y/X ratio (T20), a more developed penis valve claw (T33), a less broad abdominal segment VII in the pupa (T40), and apparently an even more reduced protuberance of the larval abdomen (T67).

brunskilli — *trivittatus*

The penis valve head and claw (T33) are slightly better developed or more derived in *C. trivittatus*. The ratio Y/X (T20) probably is higher in *C. trivittatus*, but the intraspecific variation of *C. trivittatus* and the fact that only a single imago of *C. brunskilli* has been examined make this trend seem, at best, doubtful.

americanus + *obscuripes* — *crystallinus* + *flavicans*

The monophyletic unity of *C. americanus* and *C. obscuripes* is indicated only by the synapomorphic trends T53, 62, and 67 (prelabral appendage broad, subordinate tooth of mandible high up on second tooth, abdominal protuberance reduced). The upper edge of the head is less curved in *C. crystallinus* and *C. flavicans* (T49) and the seta at the anterior face of the antenna is placed higher up from the base (T55), both more derived trends than in the other two species.

americanus — *obscuripes*

Chaoborus obscuripes shows a number of more apomorphic characters, such as reduction in length of median flagellar segments (T8), absence of parascutellar setae (T14), an HW/WBE ratio of 1.5–1.7 as opposed to 1.9–2.1 in *C. americanus*, and the most well developed penis valve claw and head of all *Chaoborus* (T33). *Chaoborus americanus* differs from other members of *Chaoborus s. str.* by having the simple seta of the median rib of the pupal anal paddle close to the plumose seta and not at the apex (T46). This feature has here been regarded as plesiomorphic even if the simple seta is placed at apex in *Mochlonyx*. The position of this seta in *Peusomyia* and *Sayomyia* suggest that both the plumose and the simple seta of the median rib in the course of the evolution shifted to a more median position and that the simple seta later on shifted to an apical position. An examination of the undescribed pupae of *C. lapponica* may clarify this matter. *Chaoborus americanus* also has a penis valve that resembles that found in *Peusomyia*. The subordinate tooth of the mandible is, in *C.*

americanus, placed higher up on the median tooth than in any other species of *Chaoborus* (T62). The trends mentioned (T33, 46, and 62) should, if they can not be regarded as a result of parallel development, make *C. americanus* the sister group of the remaining species of *Chaoborus s. str.* plus *Schadanophasma*. Then, however, a higher number of other trends must have been the result of parallel development.

crystallinus — flavicans

The prementum is more elongated in *C. flavicans* than in other *Chaoborus s. str.* (T10), a more derived feature. However, the penis valve has an almost apical claw (T33) and the subordinate tooth of the mandible is almost exactly between the second and third teeth (T62). The last feature could perhaps be regarded as a separate trend if a placement of the subordinate tooth at the base of the second tooth is regarded as the most plesiomorphic condition.

Discussion on Phylogeny of the Chaoboridae

There seems to be very little doubt about the overall relationships and trends of evolution among the different genera. This has already been partly discussed by Montschadsky (1937) on the basis of the larvae. The separation of subfamilies seems to be clear with definite boundaries. The subfamily Corethrellinae, however, has little in common with the other subfamillies and might perhaps even deserve a full family status. The tribe Cryophilini seems to be closer to the Mochlonyxini than to the Chaoborini with respect to morphological characters; however, this is probably more a result of a low height of evolution rather than a closer phylogenetic relationship. There seems to be little doubt of the Mochlonyxini as a sister group of the Cryophilini plus the Chaoborini.

The real difficulties start with the tribe Chaoborini with the single genus *Chaoborus*. The intraspecific variation is considerable even within a single population and the morphological differences between species are often small. It seems justified to divide the genus into four subgenera, one of them, *Peusomyia*, new, but the justification of this is based more on the fact that all stages are morphologically separable into four groups than by any trenchant dissimilarities. The erection of the new subgenus is necessary if any other subgenera is to be retained. The position of this new subgenus in the synapomorphic diagram seems relatively well established (Fig. 19). The justification of a separation of *Chaoborus s. str.* and *Schadanophasma* into two subgenera is more doubtful. The synapomorphic diagram either may be as drawn here, in which case the subgenera can be maintained on a phylogenetic basis, or *C. americanus* may be the sister group of the remaining species of *Chaoborus s. str.* plus *Schadanophasma*, and *C. flavicans* plus *Schadanophasma* may be the sister group of the remaining *Chaoborus. s. str.* in which case there is no evolutionary justification of the subgenus *Schadanophasma*. A future study of *Cryophila lapponica*, of Chaoborids from the southern hemisphere, and of the immature stages of *C. annulatus* and *C. maculipes* will certainly change some of the details of the synapomorphic diagram presented here but will not likely lead to fundamentally different conclusions.

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