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Notes on the larval taxonomy, ecology, and distribution of the Dutch *Chaoborus* species (Diptera, Chaoboridae)

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Abstract

In the Netherlands *Chaoborus flavicans, C. crystallinus, C. obscuripes,* and *C. pallidus* occur. A key based on larval characters to these Dutch species is given.

The validity of the identification characters of the larvae has been tested. It became evident that the place of the seta on the anterior face of the antenna base and the ratio of longest and shortest antennal blades are valuable as a support to other characters only. The shape of the dorsal process and of the anal papillae have identification value, but the labral appendices have not. The head capsule length of the four larval instars of *flavicans* and *crystallinus* has been given, but Dyar's rule does not hold.

The distribution in the Netherlands is discussed. All four species can be found in small, shallow waters but only *flavicans* can be found in large lakes which may either be shallow or stratified. The species all have great ecological plasticity to physico-chemical conditions.

Flavicans and *crystallinus* are very common, *obscuripes* is a little less common, and *pallidus* is only known from 3 places in our country.

Coexistence of 2 or 3 species is the rule rather than the exception.

1. Introduction

The Chaoborinae (Corethrinae) once considered to be a subfamily of the Culicidae are now on the authority of Dyar (1905), generally considered to be a separate family which is closely related to the Culicidae and Dixidae (Stone, 1956; Freeman, 1962; Cook, 1965; Peus, 1967) The family contains 8 genera of which *Chaoborus* Lichtenstein, 1800, of world-wide distribution, is best-known. Three subgenera are distinguished, viz., *Chaoborus* s.str., *Schadonophasma* Dyar & Shannon, 1924 and *Sayomyia* Coquillet, 1903. However, in due time a revision will be published by Saether (in print, b).

Chaoborus species have an aquatic larval and pupal stage, the adults live only a few days. Biologists have always taken an interest in the larvae, be-

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cause of their commonness, permanent presence in lakes and ponds, beautifully transparant body, remarkable behaviour, and their importance as fish-food.

Larvae and pupae were already described by the Dutch naturalist Slabber (1778), but the total number of Dutch publications is very small. De Meijere (1911 : 151), Redeke (1948 : 345) and Arnoud (1952) give some superficial information about the aquatic stages and the genus is sometimes mentioned in plankton lists (Otto, 1930: 8, 14; Leentvaar, 1955: 182; Higler, 1964: 349).

In Europe 5 species occur, viz., *C. flavicans* (Meigen, 1818), *C. crystallinus* (De Geer, 1776), *C. obscuripes* (van der Wulp, 1867), *C. pallidus* (Fabricius, 1792) and *C. nyblaei* (Zetterstedt, 1838). From the Netherlands *crystallinus, obscuripes* and *pallidus* are mentioned as adults by de Meijere (1939 : 144). *Flavicans* is very common in the surrounding countries (Peus, 1967 : 333) and was sampled by Mrs. C. N. van Utrecht-Cock (pers. comm.) and also by us from several places. *Nyblaei* has an arctic distribution (Hirvenoja, 1961; Saether, in print a, b) and is not to be expected from our country.

In this paper we give morphological and ecological data and a key to the larvae of the Dutch species. Furthermore it will contain some data about larval distribution in the Netherlands.

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I also received samples from Mrs. A. Sikorowa (Poland), G. Bonomi (Italy), U. Grimås (Sweden), H. V. Herbst (German Federal Republic), T. T. Macan (Great Britain), T. C. Northcote (Canada), N. N. Smirnov (U.S.S.R.), E. A. Thomas (Switzerland), and J. Zieba (Poland)

2. Identification

2.1. Introduction.

Features of the larvae and pupae of *Chaoborus* species were first described by Peus (1934). With his key it was possible to identify the European species *flavicans, crystallinus, obscuripes* and *pallidus*. The tables of Sládeček (1952), Prokešová (1959a) and Brindle (1962) are based on the work of Peus.

Hirvenoja (1961) gives characters of these four species and also of *C. alpinus* (described in 1938 by Peus) and of *C. nyblaei*.

C. flavicans and *C. borealis* Cook, 1956 (a synonym of *C. crystallinus* according to Saether, in print b) are also included in the key of Cook (1956), dealing with the nearctic Chaoboridae.

Meanwhile, Saether (1967) showed clearly that *alpinus* is synonymous to *flavicans*. He distinguished within the species *flavicans* three new forms, viz. f. *flavicans* s.str., f. *alpinus* and f. *infuscatus*.

Sikorowa (1967a) stressed the taxonomic importance of some larval characters for the European species not previously described.

A further discussion of these larval characters is presented in this paper. The results of this are pertinent to material from Great Britain, Belgium, the

Netherlands, German Federal Republic, Switzerland, Sweden, Italy, Poland, and the U.S.S.R. All measurements were carried out on larvae, preserved in 4% formalin and without treatment with KOH. The larvae are fourth instars, unless otherwise indicated.

An exact description of the four larval instars of *flavicans* is in preparation.

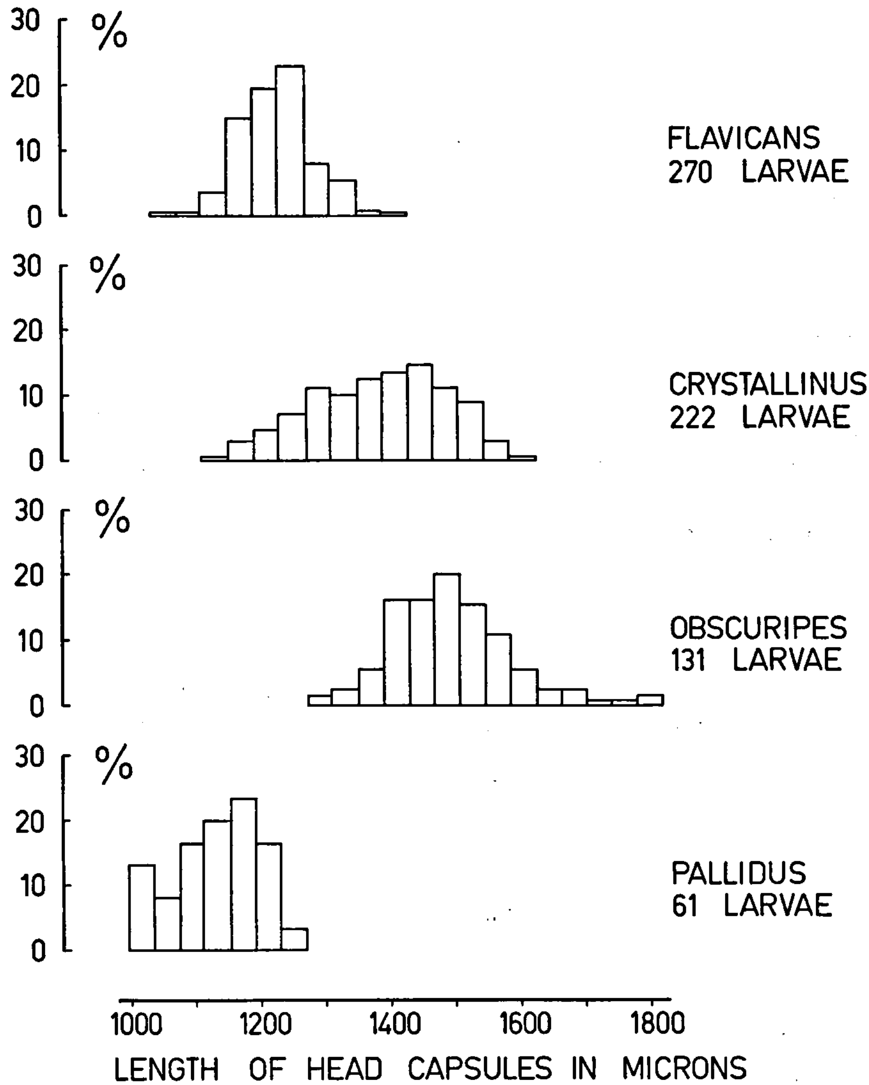

FIG. 1. Frequency distributions of the length of fourth instars of four *Chaoborus* species.

2.2. Morphology.
2.2.1. Head capsule.

Measurements of the length of the head capsule are given by Cook (1956), Prokešová (1959a: 145), Teraguchi & Northcote (1966: 166), and Saether (1967, table 1).

Our measurements of the head capsules of four species show that there is a large overlap between the species (fig. 1) but their means are significantly different ($p < 0.001$) (table I). It must be stressed, however, that the form of the frequency distribution graphs can change when material from more places is included. The head capsule length of our *flavicans* specimens fluctuated mainly between 1.1 and 1.3 mm. Roth (pers. comm.) found a range of 1.3—1.4 mm in his North American specimens.

Table I. Mean length of the head capsules of the fourth instars of four *Chaoborus* species

species	number of animals	mean length of headcapsule in μ	standard deviation
flavicans	270	1207	61
crystallinus	222	1371	102
obscuripes	131	1488	88
pallidus	61	1128	66

Prokešová (1959a: 145), McDonald (1956: 43), Teraguchi & Northcote (1966: 166), and Malueg (1966: 74) showed that the length of the head capsule could be used to distinguish between the four larval instars. However, the American authors demonstrated that the interbladder distance of the larvae does not permit an instar distinction. In fig. 2 we have given frequency distributions for the four larval instars of *flavicans* and *crystallinus*. A maximum of 5% of the specimens from the "Pond" of the Limnological Institute at Nieuwersluis, the Netherlands, belongs to the species *flavicans* and *pallidus* (Parma, 1969). The third and fourth instar larvae in this graph are from *crystallinus*, the younger ones are not identified. In table II the means are given. We had at our disposal 20 third instars only of *obscuripes*. The mean length was 905 μ and the variation was 740—1015 μ.

Table II. Mean length in μ of the head capsules of the fourth instars of *crystallinus* and *flavicans*.

	flavicans		*crystallinus*	
instar	Vechten	Baarn	"Pond"	several localities
1	227	227	258	—
2	419	425	480	456
3	744	738	824	809
4	1152	1196	1202	1334

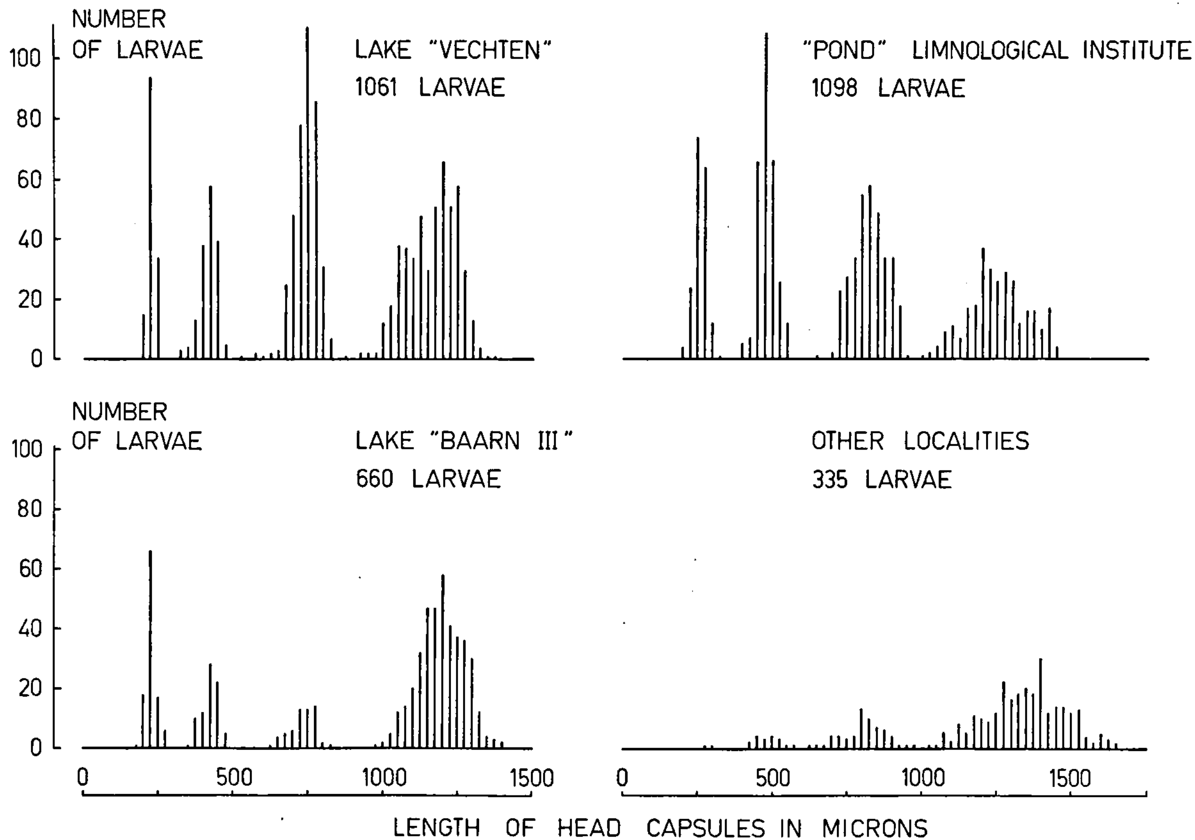

Fig. 2. Frequency distributions for the four instars of *C. flavicans* and *C. crystallinus* in several localities.

Dyar (1890) showed that the head capsules of succeeding caterpillar instars increase in width with a constant index. In several species examined different growth ratios occur. This empirical law applies according to MacDonald (1956: 43) with respect to length also to two *Chaoborus* species from Lake Victoria. The growth index was 1.68. From table III we can conclude that Dyar's rule does not hold for *flavicans* and *crystallinus*. Malueg (1966, fig. 14) gives frequency histograms of the head capsules of *C. punctipennis* (Say, 1823), from Tub Lake, Wisconsin. We determined the growth index from his graphs. Also for this species Dyar's rule does not apply. There is a relative decrease in growth during the larval development.

Table III. Growth ratios of the length of the head capsules of three *Chaoborus* species.

species	locality	growth index from instar		
		1 to 2	2 to 3	3 to 4
flavicans	Vechten	1.85	1.78	1.55
	Baarn	1.87	1.74	1.62
crystallinus	"Pond" Nieuwersluis	1.86	1.72	1.46
	several localities	—	1.77	1.65
punctipennis	Tub Lake (Malueg, 1966)	1.94	1.89	1.70

2.2.2. Antennae and postantennal filaments.

The length of the antenna base, longest antennal setae, and postantennal filaments cannot be used as specific characters (table IV).

Table IV. Length in μ of antenna base, longest antennal setae, and post-antennal filaments in three *Chaoborus* species. n = number of animals; s.d. = standard deviation.

character	*flavicans*			*crystallinus*			*obscuripes*		
	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.
antenna base	151	503	29	74	575	45	132	630	43
longest ant. setae	148	491	24	72	556	39	132	612	31
postant. filaments	78	538	32	77	583	30	116	680	35

For the European species Sikorowa (1967a: 1711) drew attention to the fact that one of the 5 antennal setae is clearly shorter than the others. The ratio longest/shortest antennal setae is in the species *crystallinus*, *flavicans*, *obscuripes* and *pallidus* c. 2.0, c. 1.5, c. 1.3, and c. 1.1, respectively. Table V gives the means and standard deviations of this ratio for three species. In 5 specimens of *pallidus* the ratio was 1.1. The means correspond with those of Sikorowa, but the variation makes their value for identification arbitrary. This is also illustrated by the data of Saether (1967, table 1). We calculated the ratio for *flavicans* from his figures and found a variation of 1.7 to 1.9.

Cook (1956, fig. 17) showed that the place of the seta on the anterior face of the antennal base can vary in different species. In *flavicans* this seta is on $^3/_4$ to $^2/_3$ of the proximal end (see also Saether 1967: 574). In table V data for the four species are given for this distance as a percentage of the total length. In 5 individuals of *pallidus* this value ranged from 43 to 50 and consequently corresponded with that of *obscuripes*. There is also an overlap between *flavicans* and *crystallinus* at one the hand and *obscuripes* (and *pallidus*) on the other.

Table V. The ratio of long/short antennal setae and the place of the small seta on the anterior face of the antenna base of three *Chaoborus* species.

species	ratio long/short antennal setae			distance of seta on anterior face of the antenna base from proximal end as percentage of total length		
	n	mean	s.d.	n	mean	s.d.
flavicans	159	1.63	0.09	161	67.1	4.2
crystallinus	70	1.98	0.13	73	67.5	4.1
obscuripes	139	1.38	0.09	137	53.0	4.3

The ratio between longest and shortest antennal setae and the place of the short seta on the anterior face of the antenna can be a good support to a correct identification.

2.2.3. Prelabral appendage.

Peus (1934: 642) used the form of the prelabral appendage (= "Messerhaare") to distinguish *obscuripes* from *flavicans* and *crystallinus*. From fig. 3 can be concluded that there is some variation of this character within one *crystallinus* population. Similar variation was also found in *flavicans* and *obscuripes* populations. In *obscuripes* even intermediates to the *flavicans/crystallinus* type have been seen. Sikorowa (1967a: 1710) found that in her specimens of *obscuripes* the typical form of the appendage only appeared prior to pupation. But we observed two totally different knifeblades in the same animal (figs. 3P, Q). The difference in form between *flavicans/crystallinus* and *obscuripes* is also expressed by the length and the width, and the ratio between these values (table VI). Saether (1967, table 1) gave as the lower limit for the length/width ratio of *flavicans* 3.3, and Roth (1967: 64) gave for the same species a ratio of 5 to 7.

Worth mentioning is the result of Smith (1960b: 398) who found that the ratio differs in males and females of *C. borealis*.

Table VI. Length and width in μ, and the ratio length/width of the "Messerhaare" in three *Chaoborus* species. n = number of animals, s.d. = standard deviation.

	flavicans			*crystallinus*			*obscuripes*		
character	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.
length	78	271	21	72	248	17	117	226	33
width	81	57	7	73	54	6	117	77	8
ratio	81	4.7	0.5	69	4.7	0.6	132	3.1	0.5

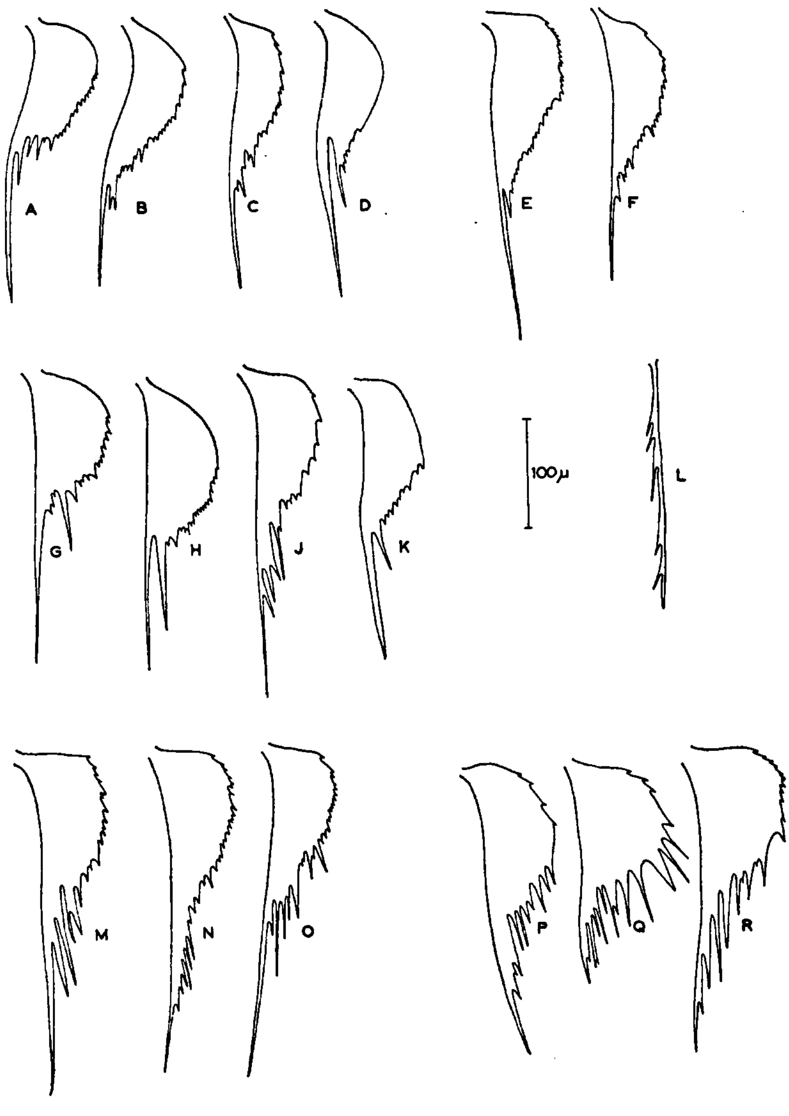

FIG. 3. Prelabral appendages from four *Chaoborus* species. A-D, *crystallinus* from Breda, Netherlands; E-F, *crystallinus* from Schiermonnikoog, Netherlands; G-K, *crystallinus* from Borok, U.S.S.R.; L, *pallidus* from Wanneperveen, Netherlands; M-O, *flavicans* from Bunnik, Netherlands; P-R, *obscuripes* from Duszniki-Zdroj, Poland.

2.2.4. Labrum.

Eckstein (1936: 487) described very carefully the variation in form of the labrum and labral appendices, namely labral and sublabral setae ("Labral- und Sublabralfedern"), the bifurcate setae ("Gabeldornen") and bristled scales ("Borstenschuppen"). He suggested that these appendices were of taxonomic value.

Saether (1967, fig. 1) used the form of the bifurcate setae for the separation of his formae within *C. flavicans*.

To test these possibilities suggested by Eckstein we submitted the labral appendices of the four species to further investigation.

The three pairs of setae at the anterior face of the labrum of *flavicans* (see Saether 1967: 574) occur also in *obscuripes* and *crystallinus*. *Pallidus* has only two pairs of inconspicuous hairs.

The form of the labral setae is represented in fig. 4. Except in size no dif-

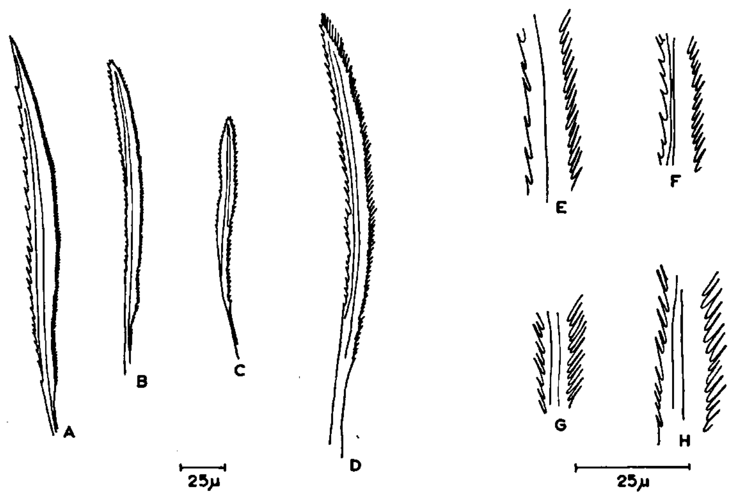

FIG. 4. Labral setae from four *Chaoborus* species. A, *obscuripes* from Duszniki-Zdroj, Poland; B, *flavicans* from Bunnik, Netherlands; C, *pallidus* from Breda, Netherlands; D, *crystallinus* from Loenen aan de Vecht, Netherlands; E-H, details from A-D.

ference could be found. They resemble Eckstein's figure 6c and also figure 1 j in Saether (1967). Setae like figures 6b and 6d in Eckstein have also been observed, but in this case it was where the narrow part of the vane was pushed under the keel. The setae of *pallidus* represented in Eckstein's fig. 6 a have not been found in our material. The number of labral and sublabral setae in *flavicans*, *crystallinus* and *obscuripes* is given in Table VII. Eckstein (1936: 492) gives 15 labral and 14 sublabral setae for his material from Plön. According to Saether (1967, fig. 1) the maximum variation in *flavicans* is 12 to 19 and 8 to 15, respectively. Cook (1956: 25) found 12 to 15 labral setae in *flavicans*.

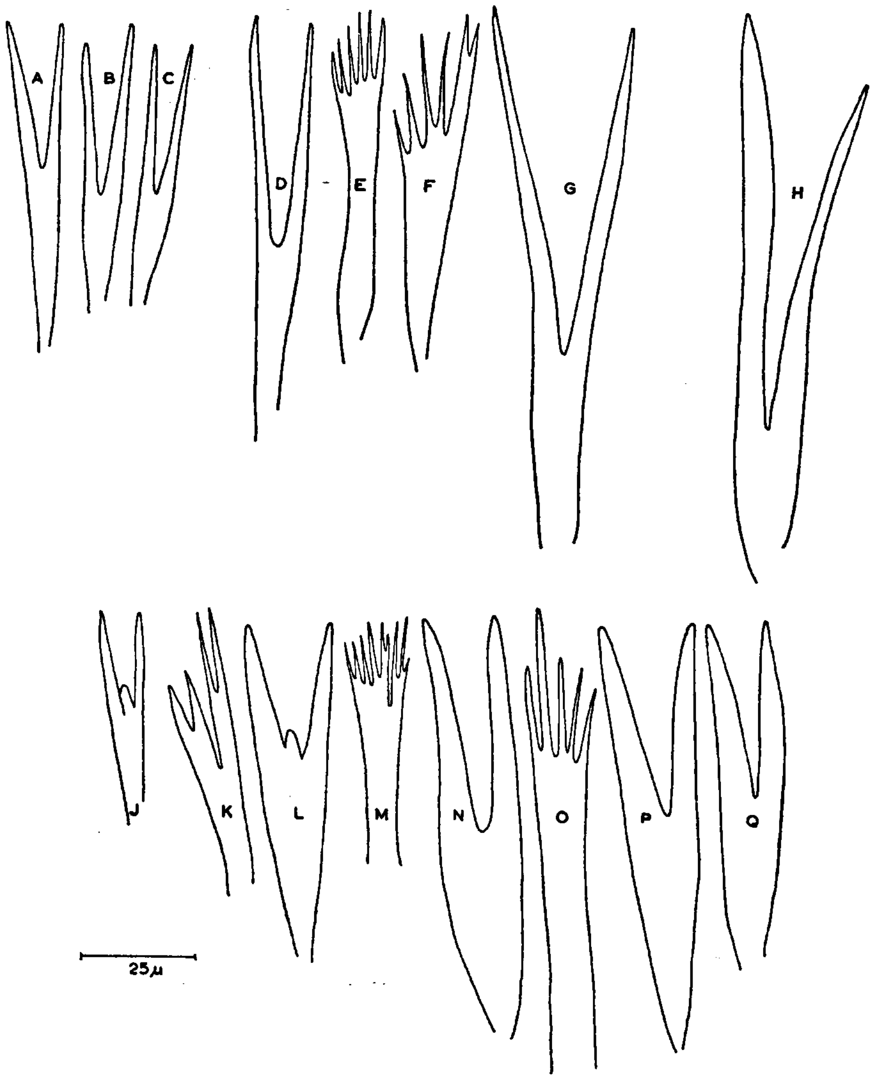

FIG. 5. Bifurcate setae from four *Chaoborus* species. A, *flavicans* from Amsterdam, Netherlands; B, *flavicans* from Mälaren, Sweden; C, *flavicans* from Bunnik, Netherlands; D, *crystallinus* from Schiermonnikoog, Netherlands; E-G, *crystallinus* from Loenen aan de Vecht, Netherlands; H, *pallidus* from Breda, Netherlands; J, *obscuripes* (3rd instar) from Herbeumont, Belgium; K-L, *obscuripes* from Epe, Netherlands; M-N, *obscuripes* from Borok, U.S.S.R.; O-P, *obscuripes* from Oisterwijk, Netherlands; Q, *obscuripes* from Duszniki-Zdroj, Poland.

Table VII. Number of labral and sublabral setae in three *Chaoborus* species. n = number of animals. s.d. = standard deviation.

character	*flavicans*			*crystallinus*			*obscuripes*		
	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.
labral setae	34	14.7	1.7	11	13.1	1.2	31	13.6	1.3
sublabral setae	26	12.0	1.5	8	11.3	1.0	30	13.7	1.8

The form of the bifurcate setae can vary greatly (fig. 5). In *obscuripes* they are of a thick-set nature and the branch can be shorter than the stem. At the base of the bifurcation sometimes a blunt tooth is present. Saether (1967: 84) mentioned that his *C. flavicans* f. *alpinus* and f. *infuscatus* were recognizable by a "small tooth at the base of the bifurcation". In *crystallinus* and *pallidus* the branches could be longer than the stem. Between *crystallinus* and *flavicans* intermediates have been found.

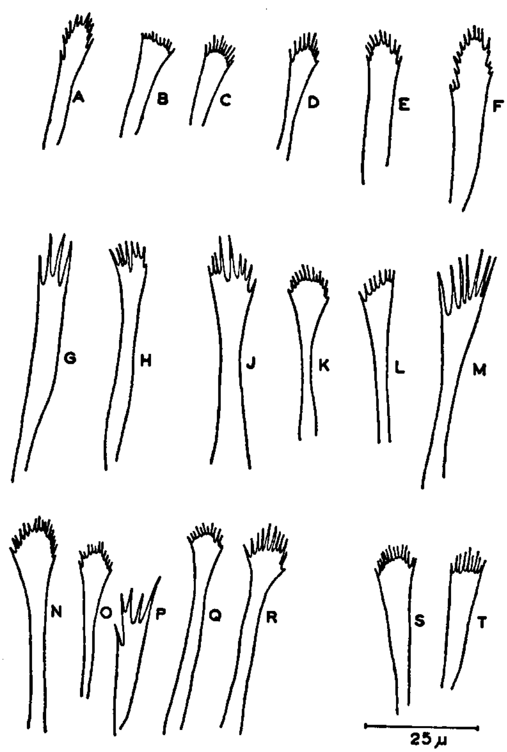

FIG. 6. Bristled scales from four *Chaoborus* species. A-C, *flavicans* from Bunnik, Netherlands; D, *flavicans* from Mälaren, Sweden; E-F, *flavicans* from Amsterdam, Netherlands; G-H, *crystallinus* from Schiermonnikoog, Netherlands; J-M, *crystallinus* from Loenen aan de Vecht, Netherlands; N, *obscuripes* from Borok, U.S.S.R.; O, *obscuripes* from Oisterwijk, Netherlands; P, *obscuripes* (3rd instar) from Oisterwijk, Netherlands; Q, *obscuripes* from Duszniki-Zdroj, Poland; R, *obscuripes* from Nunspeet, Netherlands; S-T, *pallidus* from Breda, Netherlands.

Notable in *crystallinus* and *obscuripes* is the presence of polyfurcate setae (figs. 5 E, F, K, M, O). They are mostly larger than the bristled scales. In *crystallinus* especially we found smaller setae forming intergradations to bristled scales (fig. 6). It is possible that upon further examination a complete series from bifurcate setae to bristled scales may be found, especially as Hirvenoja found a "bifurcate" seta with three fully developed branches in his *flavicans* specimens.

In our figure 6 several forms of bristled scales are represented. All types from Eckstein (1936, fig. 5) can be found within every species.

The general conclusion must be that there are indeed some differences in form of the labral appendices between the several species. In the bifurcate setae especially there seem to be forms characteristic of each species, but the variation in one population is so large that the taxonomic importance, supposed by Eckstein can not yet be confirmed.

2.2.5. Mandibles.

Peus (1934: 645) gives the number of bristles in the mandibular fan in the different species. *Crystallinus* has 10 bristles, sometimes 9; *pallidus* 13 and a few times 14; *obscuripes* 14 to 15 and *flavicans* 15. From Sikorowa (1967c: 88) it can be concluded that the variation in *flavicans* is 9 to 16. Hirvenoja (1961: 80) found in *crystallinus* and *obscuripes* variations of 10 to 13 and 13 to 16, respectively. Sikorowa (1967a: 1709) gave for *C. obscuripes* "aus den USA" 25 mandibular setae, with even an upper limit of 30. *Obscuripes*, however, does not occur in the USA and possibly we are dealing here with *C. americanus* (Johannsen, 1903) (see Cook, 1956: 22). Smith (1960b: 398) noted a difference in number of bristles between males and females of *C. borealis*.

In table VIII the number of bristles per mandible are given. The sex has not been determined. In *flavicans* numbers of 11 and 12 are in the majority, in *crystallinus* 10 and 11. In *obscuripes* 15 occurs frequently but also 14 and 16 can be found in reasonable numbers.

Table VIII. Number of setae per mandibular fan in three *Chaoborus* species.

species	number of animals	mean number of mandibular setae	standard deviation
flavicans	106	11.9	1.0
crystallinus	412	10.2	0.6
obscuripes	168	15.0	1.3

Frequently the number of bristles in the two mandibular fans of one individual are different. In *crystallinus* of "Meyendel" (Netherlands) several combinations have been found (table IX). In 25 individuals of *obscuripes* from Pod Zielencem (Poland) 13 (52%) had an unequal number of bristles in the two fans. Smith (1960a) gives for *C. americanus, C. borealis* and *C. nyblaei*, 7%, 4% and 76% respectively of the larvae with unequal number of bristles.

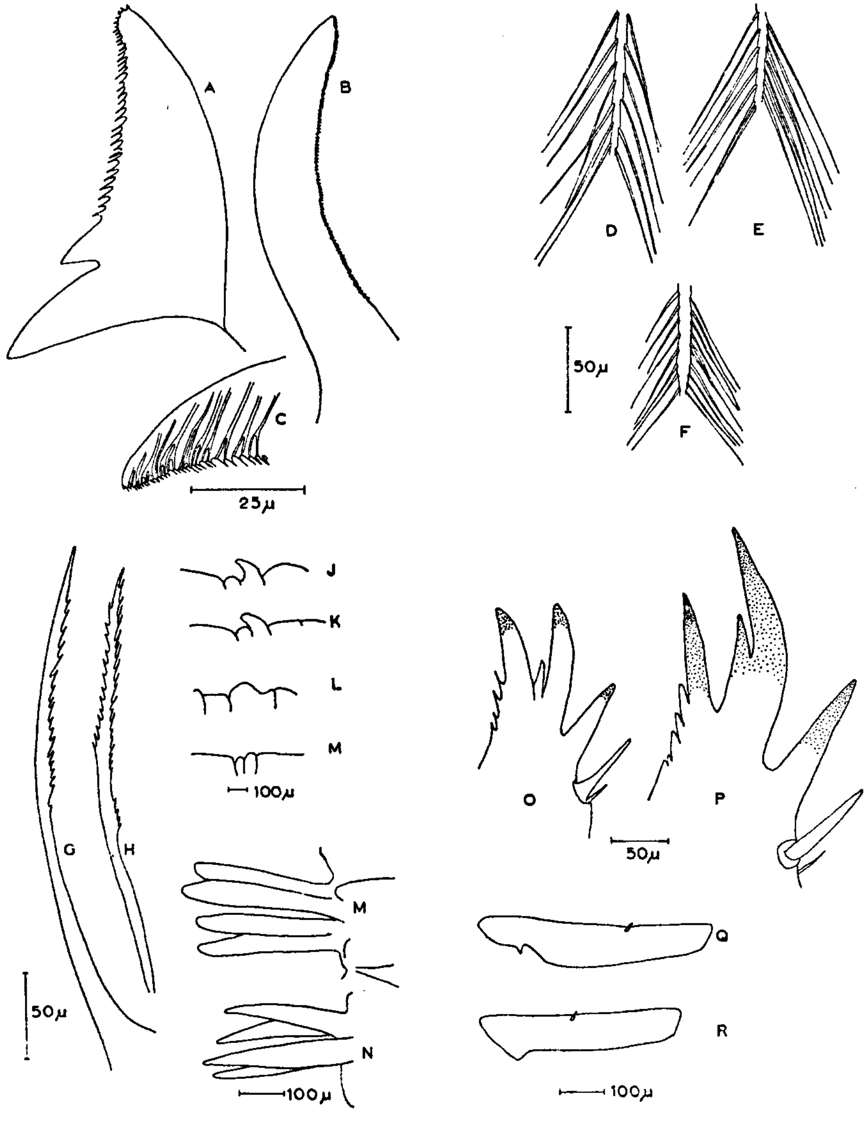

FIG. 7. Some morphological details of four *Chaoborus* species. A-C, scales of anal apparatus from *flavicans* (Bunnik, Netherlands); D-E, details of lower and upper setae above the anal gills in *flavicans* (Bunnik, Netherlands); F, detail of seta from anal fan in *flavicans* (Bunnik, Netherlands); G, pectinate seta from mandibular fan from *crystallinus* (Schiermonnikoog, Netherlands); H, most anterior seta from mandibular fan of *obscuripes* (Oisterwijk, Netherlands); J-M, dorsal process from *crystallinus, flavicans, obscuripes* and *pallidus* resp.; M, anal papillae from *obscuripes*; N, anal papillae from *flavicans, crystallinus*; O, mandible from *flavicans*; P, mandible from *crystallinus* and *obscuripes*; Q, antennal base from *crystallinus*; R, antennal base from *pallidus*.

Cook (1956) noticed in several American species the presence of some pectinate setae at the anterior side of the fan. They also exist in our species. The most anterior setae is often a two-sided pectinate (figs. 7 G, H). This dentation possibly has a function during the food uptake.

Table IX. Number of setae in the mandibular fan of one individual. *C. crystallinus* from "Meyendel" (Netherlands).

combination	number of animals	percentage
8 + 10	2	1.6
9 + 10	8	6.4
9 + 11	1	0.8
10 + 10	47	37.6
10 + 11	31	24.8
11 + 11	32	25.6
12 + 12	4	3.2

2.2.6. Maxille.

The occurrence of "four short but relatively broad bristles" at the base of the maxillary palpus was mentioned by Saether (1967: 574). Except in *flavicans* these hairs can also be found in the three other species.

According to Saether (1967: 574) the length of the peg on the maxillary palpus varies in *flavicans* from 85—115 μ, while the variation in the length of the peg on the stipes is 35—60 μ. In table X the lengths of both pegs are given for *flavicans, crystallinus* and *obscuripes.*

Table X. Length in μ of the peg on the maxillary palpus and stipes in three *Chaoborus* species. n = number of animals. s.d. = standard deviation.

	flavicans			*crystallinus*			*obscuripes*		
the peg on	n	mean	s.d.	n	mean	s.d.	n	mean	s.d.
maxillary palpus	79	91	7	60	94	8	92	113	8
stipes	77	53	7	64	55	7	55	54	6

2.2.7. Tracheal bladders.

Several authors (von Frankenberg, 1915: 515; Bardenfleth & Ege, 1916: 27; Northcote, 1964: 89) pointed out that the anterior tracheal bladders are longer than the posterior pair. In our population of *flavicans, crystallinus* and *obscuripes* this phenomenon also occurs. The ratio between anterior and posterior bladders varies strongly, presumable owing to transformation during preservation, but the ratio is always larger than 1.

2.2.8. Abdomen.

On the ninth abdominal segment a slight protuberance can be present, known as the "dorsal process" (Eckstein, 1936; Cook, 1956). In *flavicans* and *crystallinus* this process is conical (fin-shaped in lateral view), in *obscuripes* it is no more than a small tubercle and in *pallidus* it is practically absent (figs. 7 J-M). In the third instars of *flavicans* and *crystallinus* a clear fin is already visible. Identification of *crystallinus* and *obscuripes* in this stage is therefore possible (see Prokešová, 1959a: 148).

The anal papillae of *obscuripes* are nearly always rounded, in the other species pointed (figs. 7 M, N). The ventral pair is slightly longer than the dorsal pair, as already known for *C. ceratopogones* (Theobald, 1903) (Ingram & Macfie, 1917: 154).

Above the anal papillae is a cluster of two pairs of pectinate setae. The lower two are 1.2 to 1.4 times longer than the upper ones. There is also a difference in form (figs. 7 D, E). In the lower setae the distance between the setulae is larger than in the other two.

Felt (1904: 362) paid attention to the so-called anal apparatus of *Chaoborus*. Akehurst (1922: 349) and von Frankenberg (1915: 513) also discussed this retractile organ. Stadmann-Averfeldt (1923: 144) described the structure extensively of *Mochlonyx* Loew, 1844. Peus (1934: 652) went further into the function. Cook (1956: 76) gave some figures of the different kinds of blades in *C. americanus*. Our figures 7 A-C are details of the apparatus in *flavicans*. The longest processes have a rib-like structure on the surface.

The number of setae in the anal fan can vary in the different species. Peus (1934: 650) mentions the following extremes and means: *flavicans* 24—26 (24.5), *crystallinus* 21—24 (22.4), *obscuripes* 24—26 (25.5), and *pallidus* 19—23 (21.4). In our material the variation is larger, undoubtly owing to the greater number of animals (table XI). A larva with 26 or more setae belongs in all probability to the species *obscuripes*.

According to Saether (1967, table 1) the variation in *flavicans* is 21 to 26, while we calculated from his data a mean of 23.5 (373 individuals). This is in good agreement with our figures. Hirvenoja (1961: 80) found in *obscuripes* as many as 30 setae. Smith (1960a) found in the larger specimens of *americanus* and *nyblaei* the greatest number of bristles in the anal fan.

Table XI. Number of rays in anal fan of four *Chaoborus* species.

species	number of animals	mean	standard deviation	range actually observed
flavicans	567	23.7	1.1	19—27
crystallinus	682	22.8	1.0	18—25
obscuripes	273	26.5	0.9	24—29
pallidus	102	21.7	0.9	20—24

3. Key to the Dutch *Chaoborus* larvae

The key is based on the papers of Peus (1934), Hirvenoja (1961), Saether (1967), and Sikorowa (1967a), and on our own data from section 2.

1a. Prelabral appendages at least 7 times longer than wide, posteriorly serrate (fig. 3 L). Antennae without curve at the base (fig. 7 R). Thorax bulb-shaped from above. Dorsal process absent (fig. 7 M) . . . . *C. pallidus*

b. Prelabral appendages at most 7 times longer than wide, anteriorly serrate (figs. 3 A-K, M-R. Thorax oval from above. Dorsal process present 2
2a. Mandibles with three major teeth, a subordinate tooth is situated exactly between 2 and 3. Pigmentation on the mandibles restricted to the tips of the three major teeth (fig. 7 O) . . . . *C. flavicans*
b. Median tooth of the mandible with large attached tooth (fig. 7 P). The dark pigmentation extending at least to half the length of the teeth 3
3a. The anterior edge of the prelabral appendage forms a clear S.-formed curve (figs. 3 A-K, M-O). Dorsal process a conical hook (fig. 7 K). Anal papillae pointed (fig. 7 N) . . . . *C. crystallinus*
b. The anterior edge of the prelabral appendage forms most of the times a convex, at any case not a distinct S-formed curve (figs. 3 P-R). Dorsal process knob-shaped (fig. 7 L). Anal papillae round (fig. 7 M) . . . . *C. obscuripes*

4. Ecology

4.1. Identification of the species.

From the litterature it is apparent that larvae of *C. crystallinus* (often called *Corethra plumicornis* Fabricius, 1776) are very common in various types of European waters. Stahl (1966: 101), however, doubted the validity of the identification of *crystallinus* from lakes deeper than 5 meters and suggested that they refered in reality to *flavicans*. He showed that records of *crystallinus* from Windermere (Humphries, 1936) and Längsee (Frey, 1955) were incorrect and that only *flavicans* was present, which agrees with the finding of Dunn (1961: 279).

Chaoborus larvae from the Ekoln basin of Lake Mälaren (Sweden) and Greifensee (Switzerland) are described as *crystallinus* (Åhren & Grimås, 1965: 52; Thomas, 1944: 168) but we identified them as *flavicans*.

Kajak (1964: 23; 1965: 25) and Tarwid et al. (1953: 119) published records of *crystallinus* from deep lakes in N. Poland. Sikorowa (1967b: 410) on the contrary found in the same area *crystallinus* in "fishponds, pools and other small bodies of water in woods and meadows, but not in lakes".

A recent record of *crystallinus* in deep lakes is from Peus (1967). Presumably his assertion is based on his misinterpretation of the data of Wesenberg-Lund (see Stahl, 1966: 101). Peus himself (1934: 662) found *crystallinus* only in shallow pools.

Because of these data and our own experience I agree with Stahl (1966: 108) that "this species is seen to be restricted almost entirely to ponds". Records of *crystallinus* from for instance Montiggler Seen (Huber, 1906), Lake Kara-Kel (Decksbach, 1922), lakes in Holstein and the Eiffelmaare (Thienemann, 1922), Hallwiler See (Brutschy, 1922), lakes in Finland (Valle, 1930), lakes in W. Poland (Rzoska, 1936), lakes around Zürich, Switzerland (Kuhn, 1950), Kärnter Seen (Findenegg, 1955), Holzmaar (Herbst, 1961), Lake Erken (Sandberg, 1969) must be misidentifications.

There seem to be some exceptions. Eckstein (1936) found *crystallinus* in shallow but also in deep waters, his material being identified with the key of Peus (1934). He says that in his sample "sich die Form aus der Tiefe gröszerer Seen von der aus kleineren Wasseransammlungen unterscheidet......" (p. 496). But from his figure 9a it can be concluded that the specimens from the 12 m deep Gr. Madenbröken See also belong to the species *flavicans*[1]).

Lellak (1953: 136) sampling in a 6 meter deep stratified lake of about ½ ha found both *crystallinus* and *flavicans* burrowed together although *flavicans* had a greater density.

The records of *crystallinus* both from deep lakes and shallow ponds must be regarded with caution. It appears that the environmental requirements of the four species are similar and they may even be found in the same pond. Clearly identification of only a few specimens is insufficient. Zieba (1963) found only *crystallinus* in fishponds of the Upper Wisla region. In material from this area we found, however, also *flavicans* and *obscuripes*. Parma (1969) initially identified only *crystallinus* in a Dutch pond, but a closer check revealed also the presence of *flavicans* and *pallidus*.

The general conclusions are that (a) all larval identifications of *crystallinus* (= *plumicornis*) before the publication of the key of Peus (1934) are unreliable and (b) after 1934 only those publications are reliable from which it is clear that a serious identification has been carried out.

4.2. Sampling method.

The correct statement of the occurrence of a species in a certain watermass depends upon an adequate sampling technique. Observations in shallow ponds mostly bear upon net samples. In very shallow spots some bottom material will also be whirled up. In deeper lakes usually a bottom grab will be used.

The effectiviness of the sampling method depends upon the larval stage, the species and the time of sampling. The burrowing behaviour during the day and the vertical migration during the night by fourth instars is known from stratified and unstratified lakes (Berg, 1937; Northcote, 1962; Scott & Goldspink (in preparation)). This larval stage can also be pelagic during its whole life (Malueg, 1966) or only during certain periods of the life cycle (Berg, 1937).

In shallow water a continuous free swimming way of life is possible. In net samples from the "Pond" of the Limnological Institute at Nieuwersluis, Netherlands, (Parma, 1969) *flavicans, crystallinus* and *pallidus* larvae occur throughout the whole year. In infiltration ponds in the dunes of "Meyendel" (Netherlands) we sampled free swimming *crystallinus, flavicans* and *obscuripes* larvae all the year. Prokešová (1959b: 63) found pelagic *flavicans* larvae in pools in a woody area. In addition burrowing behaviour has also been observed in similar environments. *Flavicans* from inundation pools were in the mudlayer during the day (Prokešová 1959b: 63). In large but shallow Dutch lakes (Loosdrecht, Tjeukemeer) we found *flavicans* larvae only in the benthos. Albertova (1957: 191) mentions *obscuripes* as a bottom dweller. Harnisch (1953: 108), Lellek (1953), and Prokešová (1959a: 148) sampled *cry-*

[1]) Mr. Ole A. Saether Cand. real. drew my attention to this fact.

Table XII. List of localities in the Netherlands and other European countries of four *Chaoborus* species.

Municipality in the Netherlands	Locality	Date (day, month, year)	Description	Number of animals	percentage of individuals per species: *flavicans*	*crystallinus*	*obscuripes*	*pallidus*
Lemsterland	Tjeukemeer	Whole year	Large shallow lake, 21 km², eutrophic.	10	100			
Lemsterland	Lemster Rijn	Summer '68	Canal with stagnant water.	2	100			
Heereveen	Terhorne	16-12-'68	Heather pool with Sphagnum.	18	6	94		
Heereveen	Katlijk	16-12-'68	Heather pool with Sphagnum.	6		100		
Schiermonnikoog	Oosterend	15- 5-'66	Shallow dunewater.	27		100		
Anlo	Schipborg	14-10-'65	Heather pool with peaty bottom.	6	67	33		
Rolde	Ekehaar	22- 4-'65	Peat pool.	1		100		
Rolde	Amerdiepje	13- 5-'65	Slow running rivulet, very shallow, eutrophic.	1	100			
Rolde	Grollo	21- 4-'65	Peat pool.	8		63	37	
Beilen	Knijpstra's veentje	26- 9-'62	Eutrophic pool in meadow.	12	42	58		
Wanneperveen	Venematen	26- 8-'68	Eutrophic peat pool (Leentvaar 1965).	1	100			
Wanneperveen	Dirkswijde	27- 7-'65	Eutrophic peat pool (Leentvaar 1965).	1				100
Ermelo	Waskolk	22- 8-'67	Oligotrophic "ven".	20			100	
Bunnik	"Vechten"	Whole year	Sandpit, 4.7 ha, max. depth 12 m.	>1000	100			
Baarn	Zandput	Whole year	Sandpit, 1.5 ha, max. depth 3 m.	>1000	100			
Loosdrecht	Loosdrechtse plassen	Whole year	Large shallow lake, 20 km², eutrophic.	25	100			
Loenen/Vecht	"Pond" Limnol. Inst.	Whole year	Saprobic pond (Parma 1969).	>1000	4	94		2
Kamerik	Spengelpolder	11-11-'64	Sandpit, about 2 ha, max. depth 15 m.	10	100			
Veenendaal	De Hel	30- 8-'66	Eutrophic "ven".	4	75	25		
Zeist	Krakeling	Oct. '67	Temporary pool in wood.	1			100	
Kortenhoef	't Hol	28- 4-'66	Eutrophic peat pool (Meyer & de Wit 1955).	2	100			
Amsterdam	Amsterdamse Bos	10- 9-'65	Ditch.	8	88		12	
Amsterdam	Zoo ("Artis")	22- 3-'68	Saprobic pond.	13		100		
Amsterdam	Botanical garden	8- 3-'65	Garden pond.	1		100		
Hilversum	Waterworks	[illegible]	[illegible]	[illegible]	[illegible]			

Broek in Waterland	Uitdam	2- 5-'68	Eutrophic pond.	1	100			
Texel	Moksloot in Bleeke Vallei	23-11-'67	Ditch in the dunes, eutrophic.	1		100		
Everdingen	Waai	Summer '64	"Wiel", 3.3 ha, max. depth 15 m.	10	100			
Wassenaar	Meyendel	Whole year	Dune valleys inundated with Rhinewater (Cosquino de Bussy 1961)	>100	1	98	1	
Rockanje	Breede Water	2- 4-'62	Pool in dunes (Leentvaar 1963).	5		100		
Rockanje	Goudvispoel	22- 9-'61	Duck-pond.	83		100		
Yerseke	"de Koeyer"	25- 6-'64	Watering place for cattle.	15	60	40		
Goes	Kloetinge	4- 4-'64	Eutrophic pond in meadow.	4		100		
Tholen	Thuis Vermijden	24- 2-'61	Watering place for cattle.	8		100		
Oisterwijk	Achterste Choorven	14- 9-'65	Oligotrophic "ven" (Van Dijk et al. 1960)	1			100	
Nederweert	Ospelse Peel	30-10-'66	Peat pools.	2			100	
Nederweert	Aan 't Elfde	30-10-'66	Peat pool.	1		100		
Oisterwijk	Heiven	14- 9-'65	Oligotrophic "ven".	47			100	
Breda	Bouvigne	29-10-'68	Castle-moat.	218	48	24		28
Bergen (L.)	Pikmeeuwen water	4- 8-'65 11- 4-'57	"Ven".	55	98	2		
Country	Locality	Date	Description					
Great Britain	Hodson's Tarn	28- 9-'65	Moorland fishpond (Macan 1965).	45	100			
Sweden	Mälaren, Ekoln basin	17- 5-'63	Stratified eutrophic lake (Åhren & Grimås 1965).	16	100			
Belgium	Herbeumont	15- 6-'66	Fishponds.	11	27		73	
German Federal Republic	Obersee	15- 5-'68	5.6 ha, 3½ m deep, originated in 1964 in brown coal area.	34			100	
Switzerland	Zugersee	13- 2-'67	Stratified eutrophic lake.	20	100			
Poland	Golysz	23- 4 and 13- 8-'63	"Third fry pond" (Zieba 1963).	10		80	20	
Poland	Golysz	26- 9-'62 aug. '63	"Third fry pond" (Zieba 1963).	19	42	58		
Poland	Duszniki-Zdroj	16- 9-'65	Peat moor (Hajduk 1965).	49			100	
U.S.S.R.	Borok	15- 9- and 8-10-'65	Ditch.	182	½	82	11½	
U.S.S.R.	Baikal area	16- 6-'66	Pond at outflow of river Angara from Baikal Lake.	43		100		

stallinus with a bottom grab. Duhr (1955: 389, 410) observed the burrowing behaviour of *crystallinus* and *pallidus*.

The causes of the burrowing behaviour of *Chaoborus* larvae are still unknown. In any case it is clear that during the development a change in behaviour can occur. But whether this depends upon a certain time in the larval development or is induced by external factors is not known. Observations in *crystallinus* larvae which never burrowed in their natural habitat suggest the latter explanation. Under experimental conditions only a few fourth instar larvae burrowed during the first few days. Gradually more larvae disappeared into the mudlayer. These animals had no migratory rhythm. Pupae of *crystallinus* also showed a burrowing behaviour during the experiments, but never in Nature. Obviously the conditions in the experimental tubes are inducing a burrowing behaviour of larvae and pupae.

For a better understanding of the biological meaning of the burrowing behaviour we need much more data from different species in several environments. Also knowledge about the variation in physical factors (0_2-content, temperature, light) and biological factors (food, predators) in these habitats are of importance.

Our data show clearly that for statements about occurrence of *Chaoborus* larvae in a certain watermass net *and* bottom samples are required.

4.3. Ecology

From section 4.1. it can be concluded that *C. crystallinus* occurs in small and shallow ponds. In the literature the following habitats are known: ponds in gardens, parks, woods and meadows, cemented ponds in botanical gardens, pools in heather and moorland, bogs, "vennen" (pools which owe their existence to aeolian erosion in a pleistocene sand region), loam pits, watering places for cattle, fish ponds, ditches, water-filled road ruts and bomb holes. The tolerance of this species to various environmental conditions can be seen from table XII.

C. flavicans has been found in the same places, but can also occur in water masses with a larger surface area. High densities can be reached in stratified eutrophic and dystrophic lakes. Bonomi (1962) found a maximum of 65,000 larvae per m^2 in Lago di Varese and Borutski (1939) as many as 94,000 per m^2 in Lake Beloie. Because the other *Chaoborus* species are restricted to shallow water masses, all unidentified records from the bottom of deep European lakes can be considered as *flavicans* (Lang, 1931; Worthington, 1931; Schweng, 1937; Wundsch, 1940; Albrecht, 1957; Mothes, 1967; and many others). In the Netherlands stratified lakes only exist as „Wielen", originating from old dike bursts, and as deep excavations. Both are excellent biotopes for *C. flavicans*. Extensive research has been done in the sandpit „Vechten", where densities of 10,000 larvae per m^2 occur (Parma, in preparation).

C. obscuripes and *C. pallidus*, like *crystallinus*, are restricted to shallow and small waters, but the number of observations is smaller. This is partly because they are less common and partly because identification has only been possible since 1934.

Our records of *obscuripes* illustrate its large ecological plasticity. The species is certainly very common in eutrophic environments (see also Albertova, 1957: 189; Prokešová, 1959a: 146; Hirvenoja, 1960: 42). Table XII contains indications of its abundance in oligotrophic waters but a certain scarcity in saprobic ones. Also Harnisch (1926: 89), Remm (1957: 159), and Brindle (1962: 181) mention peatmoors as a biotope of *obscuripes* larvae.

There are little data on *pallidus* but those there are agree with that of other authors who found this species in waters of all types. Like *crystallinus* and *flavicans*, the species is resistant to saprobic conditions (Kreutzer, 1945: 975; Sikorowa, 1964; Parma, 1969).

It is often alleged that *Chaoborus* larvae are restricted to eutrophic and dystrophic conditions. The physico-chemical circumstances connected with the trophic situation do not seem to be essential. All species have a great ecological plasticity. Probably the amount of food, i.e., the zooplankton density, is of more importance. As well-known zooplankton organisms are abundant in eutrophic and dystrophic watermasses. For an explanation of the existence of *obscuripes* in oligotrophic waters or *flavicans* for instance in oligotrophic-oligohumic Swedish lakes (Brundin, 1949) more data about zooplankton densities and the relation between *Chaoborus* larvae and their prey are required.

These statements have a bearing upon the utility of *Chaoborus* as an indicator organism in palaeolimnology (Frey, 1964). This author says that „the phantom midge larva is typically associated with lakes exhibiting greatly reduced oxygen in deep water." (p. 72). In general this statement will be satisfactory for *C. flavicans* as far as Europe is concerned, but it is not a conditio sine qua non. *Flavicans* has been found by Goulden (1962) in post-glacial lake deposits of Esthwaite Water, which was essentially oligotrophic.

Several times *Chaoborus* larvae have been found in temporary pools (Peus, 1934; Remm, 1957). This has consequences for the life cycle of the larvae. Of importance in this respect is the observation of Gostkowski (1935) who found *Chaoborus* larvae in the bottom of drained fishponds. Also Zabolotskii (1964) found that larvae in a humid atmosphere can live for months, provided that the temperature is low.

5. Distribution in the Netherlands

Figures 8 — 11 show the location of the four species of *Chaoborus* larvae. The number of records is low. Also owing to our knowledge of the ecology it is clear that all four species are distributed over the whole country. There is for instance no connection with salinity. *C. flavicans* has been found in brackish water in the province of North Holland (about 500 mg Cl'/1). The tolerance of *Chaoborus* species to salinity is well-known. (Hirvenoja, 1960:

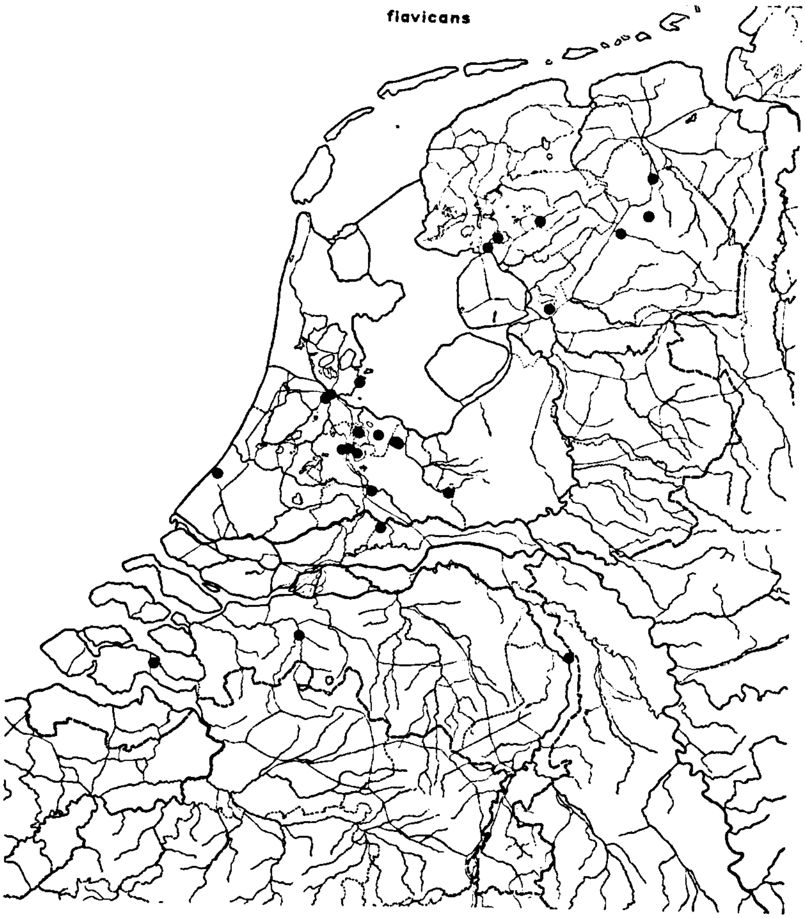

FIG. 8. Localities of *C. flavicans* in the Netherlands.

42; Schmitz, 1959: 198). Nellen (1967; pers. comm.) found *Chaoborus* larvae and pupae in salinities from 4.0—13.2‰.

Striking is the regular occurrence of two or three species in the same habitat. One species can dominate another for instance *crystallinus* in the „Pond" of the Limnological Institute or in the infiltration pools of the Meyendel dunes. But it is also possible that the species can occur in about equal percentages as in the castle moat of Bouvigne castle, Breda (see table XII).

Stahl (1966) summarized the data about coexistence of *Chaoborus* species. A combination of *pallidus* with one or more other species was unknown to him. We found this species with *flavicans* and *crystallinus*. Prokešová (1959a: 146) also mentions the occurrence of *pallidus* with other species. Even combinations of *flavicans, crystallinus, obscuripes* and *pallidus* are descdibed

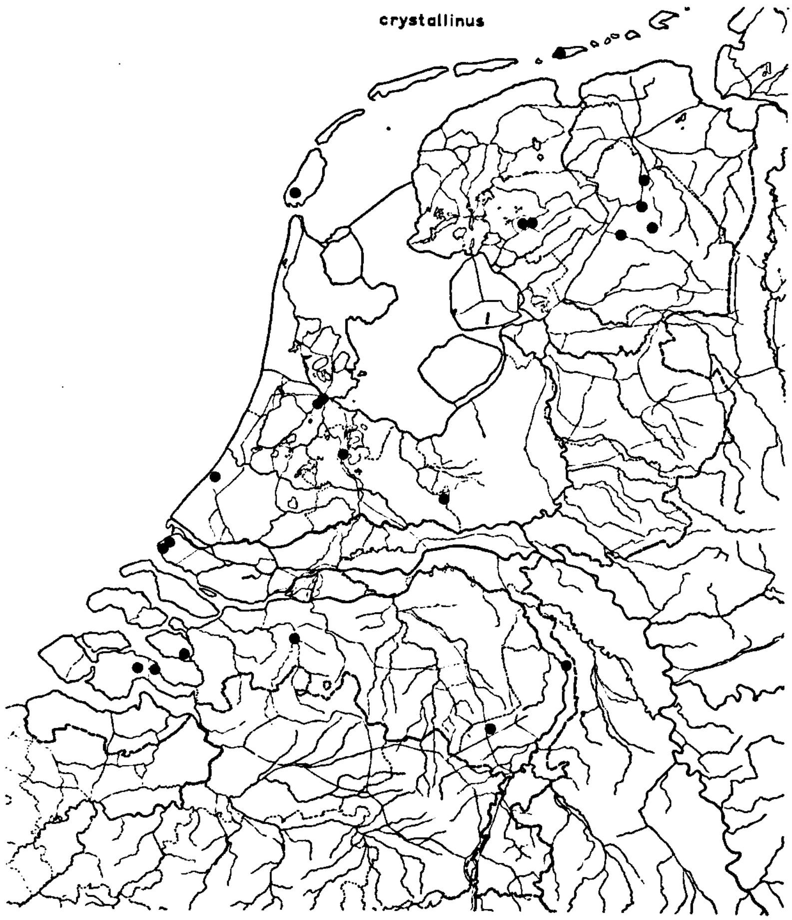

FIG. 9. Localities of *C. crystallinus* in the Netherlands.

(Hirvenoja, 1960: 35, and 1963; Sikorowa 1967b: 409). This confirms the supposition of Stahl (1966: 106) that „in Europe.. all sympatric species can coexist".

Stahl suggests that coexistence is possible because the species do no compete. The population should be below the level at which shortage of food occurs. Of importance is the opposite remark of Roth (1967: 68). He says that a water in which one special species has its optimal conditions can be injected regularly with other species which either lose the competition or maintain their position at a low density level. In this case different dispersive power of the adults can play a role. For example, both *crystallinus* and *obscuripes* were abundant in Hodson's Tarn (Macan, 1965; pers. comm.) prior to fish stocking in 1960. Following this all chaoborids disappeared from open water only returning when the fish experiment terminated. The dominant species

FIG. 10. Localities of *C. obscuripes* in the Netherlands.

was then *flavicans* and it is possible the dispersive power of this species was important in producing this situation.

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FIG. 11. Localities of *C. pallidus* in the Netherlands.

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