

Mass occurrence and sporadic distribution of *Corynocera ambigua* Zetterstedt (Diptera, Chironomidae) in Danish lakes. Neo- and palaeolimnological records

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Abstract

The chironomid *Corynocera ambigua* (Tanytarsini) is commonly reported as a cold-stenothermal species living in shallow lakes in arctic and subarctic regions. In palaeoecological studies of temperate lakes, larval remains of *C. ambigua* are usually found in late-glacial sediments from the Allerød and Younger Dryas periods, and often in association with subfossil *Chara* oospores. During a surface sampling program of chironomid head-capsules in 41 Danish temperate lakes, *C. ambigua* was found to comprise 25% of the chironomid assemblages in two lakes, and was sporadically found in 8 other lakes (0.5–10%). A 70 cm palaeo-stratigraphy from the shallow (max depth 1.2 m) and eutrophic (total phosphorus = 150 µg P l⁻¹) Lake Stigsholm showed that *C. ambigua* has been abundant in the last 4–5 centuries. At a sediment level of 25 cm (~ year 1925, ²¹⁰Pb dating), *C. ambigua* began to decrease in frequency while *Chironomus plumosus*, *Procladius* sp., *Cladotanytarsus* gr. *manicus* and *Tanytarsus* spp. increased, suggesting an increased nutrient loading and an approach to eutrophic conditions. In 1995 *C. ambigua* was still very abundant in Lake Stigsholm but in early March 1997 no living larvae were found. An extremely heavy growth of *Elodea*, *Enteromorpha* and filamentous algae in the summers of 1995 and 1996, with following degradation in the fall, might have influenced the invertebrate population dynamics. No significant distinguishing characteristics were found for the lakes supporting *C. ambigua*. Its occurrence in warm (~20°C) Danish lakes brings into question the perception of the species as being cold-stenothermal.

Introduction

In 1943, Frode Søgaaard Andersen described the Tanytarsini species *Dryadotanytarsus edentulus* Andersen based on fossil larval remains in late-glacial deposits from a pond near Næstved, Denmark (Andersen, 1938, 1943). The larval remains were found in the Older and Younger Dryas layers, hence the name. In 1955, Deevey found another fossil species, *D. duffi* Deevey, from New Zealand sediments, and in 1958 Livingstone et al. reported findings of fossil *Dryadotanytarsus* throughout a sediment core from Eight Lake in Alaska and proposed that the species might still be living in the lake. In 1959, Hirvenoja (1960) observed a mass

occurrence of *Corynocera ambigua* Zetterstedt in Lake Sompiojärvi, Finnish Lapland. One year later, Hirvenoja (1961) described the larvae of *C. ambigua* as being identical to *D. edentulus*.

Notes on the present occurrence of *C. ambigua* in Fennoscandia are given by Lindeberg (1970) and Fjellberg (1972), in Northern Europe by Reiss & Gerstmeier (1984) and in Canada by Moore (1978), Walker (1990) and Walker & MacDonald (1995).

Corynocera ambigua has always fascinated palaeo-ecologists (Stahl, 1969; Walker & Mathewes, 1988), partly because it is easy to identify from subfossil remains, but also because it diverges from all other chironomids in several characteristics:

1. *Corynocera ambigua* cannot fly. The brachypterous adults swarm by using the reduced wings to make rapid whirling movements on the surface of the lake water. They hatch and mate when water temperature reaches 7–8 °C.
2. The species is often observed in mass occurrences.
3. The very unusual structure of the larval mentum suggests a highly specialized feeding strategy.
4. In palaeoecological studies of temperate lakes, *C. ambigua* remains are usually only found in late-glacial sediments and often in association with subfossil *Chara* oospores.
5. In recent studies *C. ambigua* is commonly reported as a cold-stenothermal species living in shallow lakes in arctic and subarctic regions under oligo- to mesotrophic conditions.

In this study, we were surprised to find large living populations of *Corynocera ambigua* in the eutrophic and temperate Lake Stigsholm in Denmark. In 1995 *C. ambigua* was still highly abundant in Lake Stigsholm but in early March 1997 no living larvae were found. A sediment core was used to reconstruct the development of the chironomid communities in Lake Stigsholm. Chironomid assemblage data from a surface sediment data set, covering a wide range of Danish lakes, was used to assess the environmental characteristics of *Corynocera*-lakes.

Methods

Core study of Lake Stigsholm

Lake Stigsholm is a small (21 ha) shallow lake, with a mean depth of 0.8 m. The lake is eutrophic with a summer mean (May–September) total phosphorus range from 100–150 µg P l⁻¹ and a lakewater chlorophyll *a* concentration ranging from 23–71 µg chl *a* l⁻¹ (1988–1992). The turbidity of the water varies considerably among years, with the Secchi depth reaching the bottom between 27–73% of the time in summer period (Søndergaard et al., 1996).

The core used for chironomid analysis was taken in May 1993 from the deepest part of Lake Stigsholm (1.2 m) using a HON-Kajak sediment corer (Renberg, 1991) in the uppermost 20 cm and a Russian corer (Jowsey, 1966) for the sediments below (20–70 cm). The sediment cores were cut into 1 cm slices and were correlated by loss-on-ignition profiles (Dean, 1974).

Surface samples from Danish lakes

Surface samples from the deepest part of 41 Danish lakes were screened for chironomid head capsules. The samples were taken with a Kajak tube-corer and the uppermost 0–1 cm was sampled. Three samples were taken from each lake, pooled and stored in plastic bags. Environmental monitoring data (summer mean) for total phosphorus, total nitrogen, chlorophyll *a*, pH, alkalinity, and Secchi depth, were available from the Nationwide Lake Monitoring Program for all 41 lakes. Sediment organic content (loss-on-ignition at 550°C from dried sediments) were measured for only 24 lakes in the data set and were analyzed separately.

Laboratory procedures

Sediment samples for chironomid analysis were treated following the procedures of Hofmann (1986) with deflocculation in hot 10% KOH, acid treatment and sieving on a 112 µm screen. Chironomid head capsules were sorted under a stereo microscope at 50× magnification, dehydrated in 99% ethanol, and mounted in Euparal®. The head capsules were identified according mainly to Hofmann (1971a), Wiederholm (1983) and Møller Pillot (1984a, 1984b).

Results

Core study

Radionuclide profiles of the sediment core from Lake Stigsholm showed a well defined ¹³⁷Cs peak at 15 cm which was used to recalculate the constant-rate-of-supply (CRS) model ²¹⁰Pb dates (Appleby & Oldfield, 1978; Oldfield & Appleby, 1984). Accumulation rates at this site appear to have increased from a 19th century value of ~0.020 g DW cm⁻² y⁻¹ (~0.14 cm y⁻¹) to a mean value for the period 1940–70 of ~0.035 g DW cm⁻² y⁻¹, with a further substantial increase during the past decade.

The chironomid stratigraphy in Lake Stigsholm shows a uniform sequence with little change in the frequencies of the less abundant taxa (Figure 1). From the oldest layers studied (70 cm) to the 25 cm level *Corynocera ambigua* and *Tanytarsus* spp. comprise more than 55 and 10% of the chironomid fauna, respectively. From 25–10 cm *C. ambigua* decreases and *Tanytarsus* spp. increases. This change suggests a switch in dominance between these two taxa. Increases

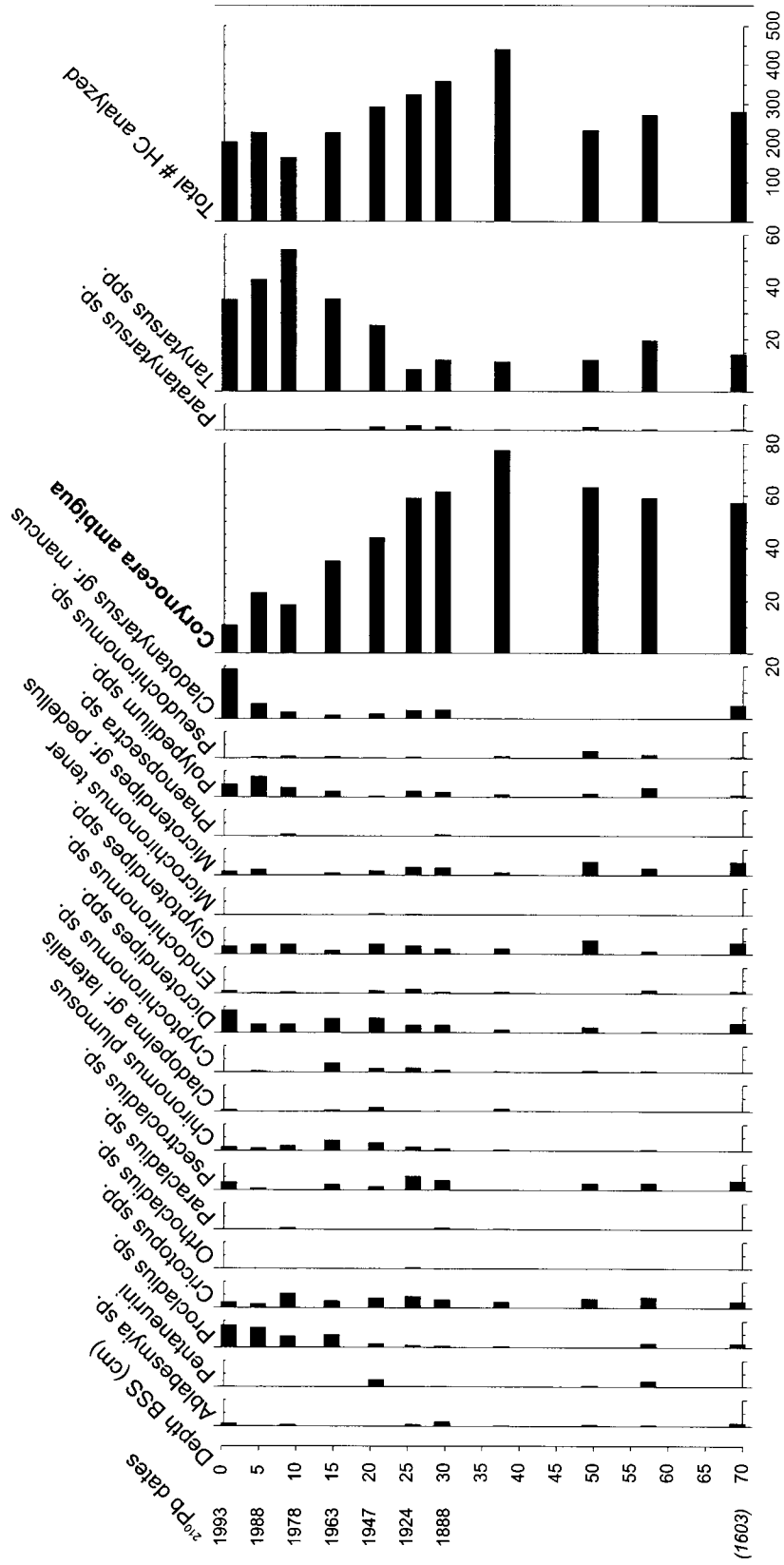


Figure 1. Chironomid head capsule stratigraphy (percentages) from the shallow Lake Stigsholm, Denmark. Depth scale is cm below sediment surface (BSS), HC is the total number of head capsules examined. Ages older than 1888 are extrapolated from the radionuclide chronology.

in the frequency of *Procladius* sp. and *Cladotanytarsus* gr. *mancus* through the last 20 years is indicated in the top-most part of the core.

Surface samples

A total of 5,810 head capsules (mean 140 lake⁻¹) were examined from the surface sediment samples. *Corynocera ambigua* was found in 25% of the 41 Danish lakes and showed no distinct geographical pattern (Figure 2). In the shallow part of Lake Nors, 30 specimens made

up 23% of the total number of head capsules, but in 4 of the lakes only one specimen was found (0.5–1.1% of total).

The 41 lakes were grouped by group average clustering of euclidean distances using available environmental data (Clarke & Warwick, 1994). Three groups were outlined and two (outlier) lakes were held separate, due to very large areas and volumes (Figure 3). The lake groupings are visualized as gradients in a principal components analysis (PCA) ordination and summary data for the lake groups are listed in Table 1.

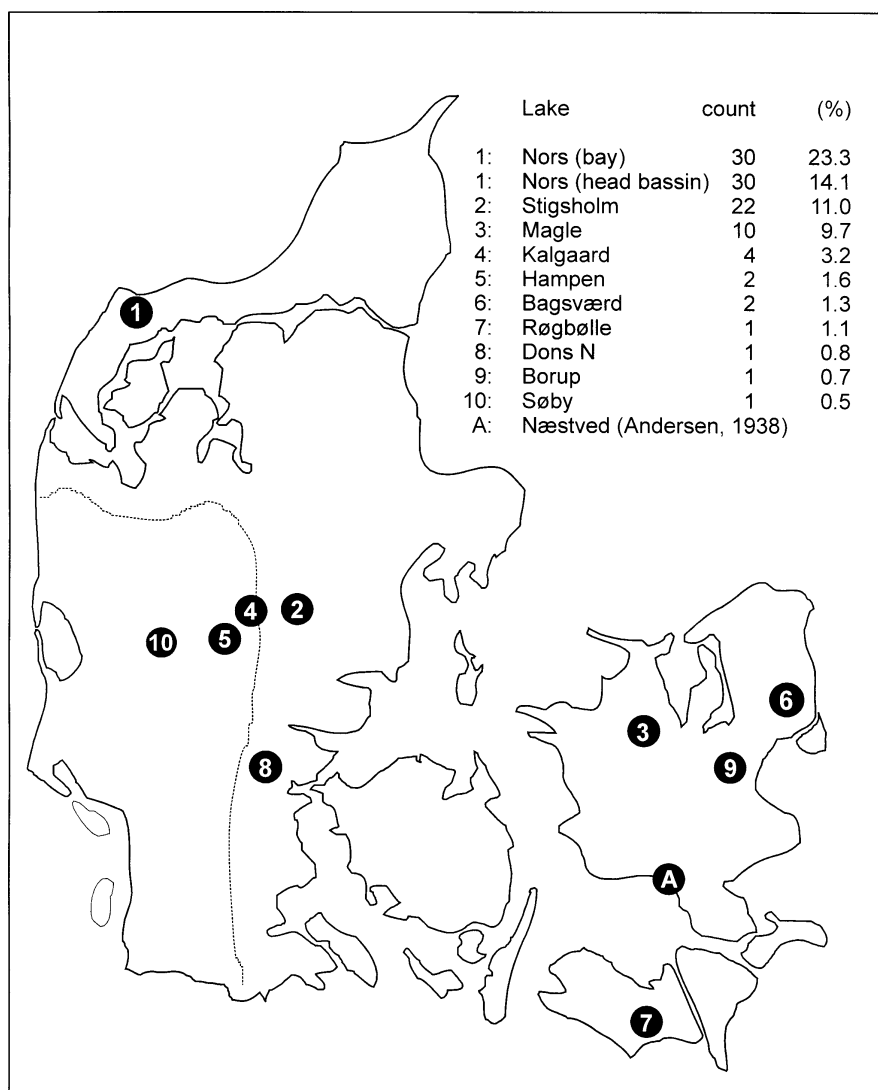


Figure 2. Map of Denmark showing the location of the 10 lakes supporting *Corynocera ambigua* head capsules in the surface sediments. Total number of specimens and their percentage contribution to the chironomid assemblages are listed. Numbers corresponds to Table 1 and Figure 3. Site A is the coring site of Andersen (1938). The dotted line marks the main stationary line of the Weichselian (last) glaciation.

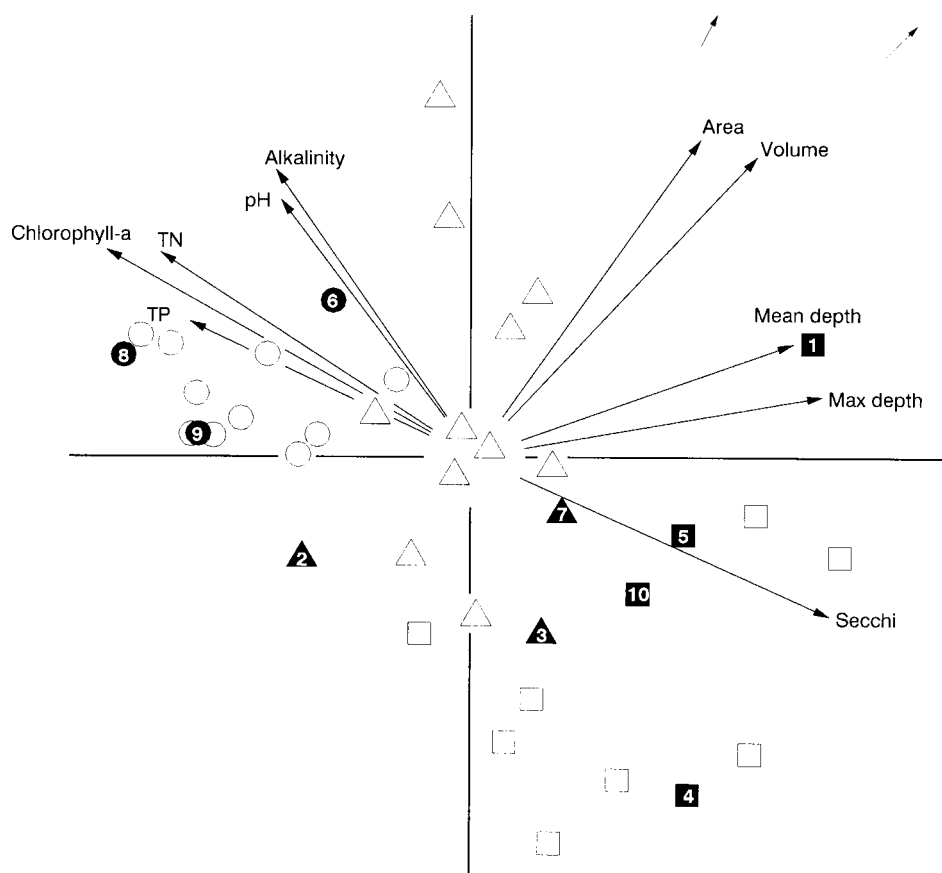


Figure 3. Principal components analysis (PCA) of environmental factors for the 41 lakes in the surface data set. Squares, triangles and circles denotes lake group I, II and III, respectively. Filled markers denotes presence of *Corynocera ambigua* head capsules in the surface sediments and the numbers corresponds to Table 1 and Figure 2. Two sites are outliers and not shown.

Group I (squares in Figure 3) comprises the deep lakes, relatively low in alkalinity, phosphorus, nitrogen and chlorophyll *a* and with high Secchi depth. Group III (circles) defines the opposite end of the gradient, which are shallow alkaline lakes, rich in nutrients and chlorophyll *a*, and with low Secchi depth. Group II (triangles) is moderate in all variables and falls in between the two other groups. The three lake groups were significantly different ($p < 0.01$, ANOVA) in all (ln-transformed) variables, except for lake area and lake volume.

Corynocera ambigua was present in lakes representing all three lake groups and along all environmental gradients (filled markers in Figure 3). There were no significant differences in any variables when testing *Corynocera*-lakes to non-*Corynocera* lakes (*t*-test), and the percentage contribution of *C. ambigua* was not correlated to any of the variables ($p > 0.05$, Pearson

correlation). Sediment organic content data were available from four *Corynocera*-lakes and ranged from 50.8–76.6% of dry weight. The organic content for twenty non-*Corynocera* lakes ranged from 37.0–84.6%. There was no significant difference between the two groups ($p < 0.17$, Mann-Whitney U-test).

A number of available fossil and recent records of *Corynocera* are summarized in Table 2. In 20 palaeolimnological studies, *C. ambigua* were reported as common in late-glacial and early Holocene sediments. Nine studies of younger (Holocene and historical) sediments suggests that *C. ambigua* might still be present in some of the study lakes. Among the recent records, the species were commonly found in arctic and subarctic regions, however several unpublished records of temperate occurrences exist (personal communications, Table 2). Five reports of *Corynocera* sp. from New Zealand are included in Table 2, but probably refer

Table 1. Summary data for the 41 lakes with surface samples. The lakes are grouped according to group average clustering of euclidean distances and PCA of 10 variables. Numbers are mean values for the groups. Numbers in brackets are range for the groups. All variables are summer mean (May-September). OL1 and OL2 (outliers) are extreme in some variables. *Corynocera*-lakes corresponds to numbers in Figure 2 and Figure 3

	GROUP I	GROUP II	GROUP III	OL1	OL2
Number of lakes	12	14	13	1	1
Total phosphorus (mg P l ⁻¹)	0.028 (0.009–0.085)	0.123 (0.027–0.496)	0.394 (0.077–1.003)	0.077 –	0.150 –
Total nitrogen (mg N l ⁻¹)	0.559 (0.271–1.055)	1.526 (0.856–3.464)	2.714 (0.650–3.730)	2.948 –	0.650 –
Chlorophyll (µg Chl a l ⁻¹)	8.6 (3.6–24.5)	47.5 (9.5–143.8)	150.1 (8.0–326.4)	31.6 –	8.0 –
pH	6.4 (4.5–8.2)	8.5 (7.9–9.1)	8.7 (8.0–9.6)	8.5 –	8.1 –
Alkalinity (meq l ⁻¹)	0.308 (–0.177–1.519)	1.861 (0.484–2.726)	2.871 (1.623–3.974)	3.203 –	2.370 –
Secchi depth (m)	3.7 (1.2–7.7)	1.5 (0.5–2.5)	0.6 (0.3–1.0)	1.4 –	3.5 –
Mean depth (m)	3.7 (0.8–10.4)	3.1 (0.8–6.5)	1.5 (0.9–3.1)	8.2 –	12.3 –
Maximum depth (m)	9.6 (1.8–20.5)	6.9 (1.2–14.7)	2.9 (1.2–6.6)	13.5 –	22.0 –
Area (km ²)	0.70 (0.05–3.48)	0.97 (0.15–3.34)	0.42 (0.05–1.22)	12.5 –	17.3 –
Volume (10 ⁶ m ³)	2.65 (0.08–12.67)	2.60 (0.21–9.80)	0.66 (0.10–2.33)	100.64 –	218.10 –
<i>Corynocera</i> -lakes	1, 4, 5, 10	2, 3, 7	6, 8, 9	–	–

to a different species *Corynocera duffi*). Furthermore, although Walker & Mathewes (1987, 1988) and Walker & MacDonald (1995) report '*Corynocera* nr. *ambigua*' from British Columbia (Canada) and northern Canada, comparison of mouthparts suggest that their material belong to one or more undescribed *Corynocera* spp., and not to *C. ambigua* (Walker, pers. commun.).

Discussion

Temperature relations

The high northern distribution and late-glacial occurrences of *C. ambigua* (Table 2) have supported a widespread general assumption that the species is cold-stenothermous, with a preference for oligotrophic lakes (Fjellberg, 1972; Pinder & Reiss, 1983, 1986; Walker & Mathewes, 1988). This conflicts with our record of large populations in the warm, temperate and eutrophic Lake Stigsholm. The temperature in the full water column of the shallow (1.2 m) Lake Stigsholm is between 18–25°C for longer periods each summer (Lindegaard & Brodersen in prep.). This is far above what is generally considered as habitat for cold-

stenothermous and glacial relict species. However, Brundin already in 1949 reported the larvae as being eurythermous and only the pupae as cold-stenothermous. In Nehmitzsee, Mothes (1968) proposed that *C. ambigua* survived the high summer temperatures as eggs in the lake sediments and had a growth period from September to late November. In Lake Stigsholm we have found third instar larvae in mid August, and no change in individual biomass from November to February (unpublished data). Thus, only swarming behavior of adults in the very early spring, when water and air temperatures are below 8°C, can be considered as a true adaptation to cold climate. The existence of the species in temperate waters seems feasible when other environmental requirements are met.

Habitat and lake type

It was not possible to show any significant pattern in the distribution of *C. ambigua* head capsules in surface samples from 41 Danish lakes. The results of the PCA showed that the species was present along all gradients of measured environmental variables. In studies of 20 Alaskan lakes, no clear pattern was found either (Kling et al., 1992), but in 20 arctic and subarctic Canadian

Table 2. Fossil and recent records of *Corynocera ambigua* in Europe, North America and New Zealand¹. Chronozones are according to Mangerud et al. (1974). Core levels are in meters below sediment surface (BSS). (M) records of Mass occurrence and (C) relation to Charophytes

Lake	Country	Chronozone	Core level (m BSS)	M, Mass occ. C, Charophytes	Reference
PALAEO RECORDS					
Lake Endletvatn	N. Norway	Late- mid Weichselian	9.05–8.95		Fjellberg (1978)
Gr. Segeberger See	Germany	Bølling	13.5–13.2		Hofmann (1978)
Lobsigensee	Switzerland	O. Dryas	2.2–1.3	C	Hofmann (1983b)
Næstved	Denmark	O. Dryas - Y. Dryas	1.62–0.75	C	Andersen (1938)
Jären	SW Norway	O. Dryas - Y. Dryas	–		Fjellberg (1972)
Lake Kruklin	Poland	Allerød	–		Frey (1964)
Loch na Muilne	British Isles	Allerød	–		Sadler & Jones (1997)
Loch Bharavat	British Isles	Allerød	–		Sadler & Jones (1997)
Torreberga	S. Sweden	Allerød - Y. Dryas	1.90–1.05	C	Berglund & Digerfeldt (1970)
Holzmaar	Germany	–	–		Hofmann (1993)
Loch Dhu	British Isles	Allerød - E. Pre-boreal	–		Sadler & Jones (1997)
Lake Poolsee	Germany	Allerød - Atlantic	13.7–10.5		Hofmann (1983a)
Schöhsees	Germany	Y. Dryas - E. Subatlantic	7.0–0.5 ²		Hofmann (1971b)
Tegeler Sees	Germany	Y. Dryas - Subatlantic	27.0–2.0		Schakau & Frank (1984)
Misty Lake	B.C. Canada	Late Glacial	8.0–7.0	C	Walker & Mathewes (1988) ⁸
Whitrig Bog	British Isles	Late Glacial	–		Brooks et al. (1997)
Loch Na Beinne Bige	British Isles	L. Glacial - E. Holocene	5.15–4.45		Sadler & Jones (1997)
Schalk. Maar	Germany	Pre-boreal	6.3		Hofmann (1993)
Lake Flarken	S. Sweden	Pre-boreal - E. Atlantic	5.2–3.8		Brodin (1986)
Gr. Segeberger See	Germany	Boreal	10.6–8.5		Hofmann (1978)
Hippa Lake	B.C. Canada	Holocene	3.5–0.0	M, C	Walker & Mathewes (1988) ⁸
Eight Lake	Alaska, USA	Holocene	2.0–0.0	M	Livingstone et al. (1958)
Mike Lake	B.C. Canada	–	–		Walker & Mathewes (1988) ⁸
Marion Lake	B.C. Canada	–	9.0–0.0	(C)	Walker & Mathewes (1987) ⁸
Växsjösjön	S. Sweden	Historical	2.5–1.7		Brodin (1982)
Lake Søbygaard	Denmark	Historical	1.0–0.55	C	Brodersen (in prep.)
Cathedral Lakes	B.C. Canada	–	3.5–0.0		Palmer (in prep.) ⁸
Whitrig Bog	British Isles	–	–		Livingstone et al. (1958)
Lake Stigsholm	Denmark	Historical	0.7–0.0	M, C	present study
Lake Grasmere	New Zealand ¹	5,500–1,200	3.2–0.5		Schakau (1990)
Lake Taylor	New Zealand ¹	3,000–present	1.85–0		Schakau (1986)
Pyramid Valley	New Zealand ³	–	–	M	Deevey (1955)
RECENT RECORDS					
Arctic Lakes	Alaska, USA				Kling et al. (1992)
Arctic/subarctic L.	Canada				Moore (1978)
Tundra lakes	Canada				Walker & MacDonald (1995)
Målsjön	Norway				Aagaard (1978)
Norwegian lakes	Norway			M, C	Fjellberg (1972)
Subarctic lakes	Sweden				L. Erikson (1997) ⁴
Subarctic lakes	N. Fennoscandia				Lindeberg (1970)
Lake Sompiojärvi	Finnish Lapland			M	Hirvenoja (1960)
Subarctic lakes	Finland			M	H. Olander ⁵
Temperate lakes	Finland				L. Paasivirta ⁶
Gr. Plöner Sees	Germany	(until 1922)			Thienemann (1954)
Mid-European lakes	–				Reiss & Gerstmeier (1984)
Lake Võrtsjärv	Estonia				K. Kangur ⁶
Lake Corrib	Ireland				Murray & Ashe (1983)
Temperate lakes	Denmark			(M), (C)	present study
Lake Gault	New Zealand ¹				Timms (1982)
Lake Letitia	New Zealand ⁷				Timms (1983)
Lakes, ponds	New Zealand			C	Boubee (1983)

¹*Corynocera* sp.; ²Sub-boreal peak at 3.0–0.7 meter; ³*Dryadotanytarsus duffi* Deevey; ⁴2nd Nordic Benthological Meeting, Silkeborg; ⁵pers. commun.; ⁶13th International Symposium on Chironomidae, Freiburg; ⁷Reported as 'unidentified Tanytarsini' (in Schakau, 1990); ⁸Reported as '*Corynocera* nr. *ambigua*' but belongs to an undescribed species (Walker, pers. commun.)

lakes, Moore (1978) found *C. ambigua* in the small, shallow, 'warm' and oligotrophic lakes. Similarly, having examined 20 lakes, Walker & MacDonald (1995) found the species to be most common in shallow tundra lakes of the Northwest Territories. In the study by Olander et al. (1997) in Finnish Lapland the species was present in the deepest (25 m) and the shallowest (1 m) as well as in warm (15°C) and cold (6°C) lakes, but not in lakes with sediment organic content above 65% (Olander, pers. commun.). Sediment organic content (as a single factor) did not have any influence in the Danish data set. The two lakes with mass-occurrences (Lake Nors and Lake Stigsholm) had a sediment organic content of 71.2 and 66.5%, respectively. Boubée (1983) reports *Corynocera* sp. in New Zealand to occur in clear water lakes (with charophytes) up to one meter deep with a distinct substrate consisting of a flocculant organic layer with a very high concentration of diatom algae and decaying reeds. This corresponds very close to Lake Stigsholm in Denmark, but not to the deep Lake Nors.

Relation to charophytes

The many observations on co-occurrence of *C. ambigua* and charophyte plants suggest a pattern (Table 2), although it should be noted that samples were not analyzed for plant macrofossils in all investigations. Palaeolimnological investigations in the shallow Danish Lake Søbygaard has shown a clear decline in both these two components at the same time (Brodersen, in prep.). In Lake Stigsholm there is also a significant decline in *Chara* and *Nitella* oospores at the 25 cm level (Odgaard et al., in prep.), where *C. ambigua* also starts to decline. Charophytes were present in several *Corynocera*-lakes in the surface data set: Lake Nors (14–23% *C. ambigua*) holds 7 species of charophytes, L. Søby (4 species), L. Magle (2 species), L. Røgbølle (2 species) and L. Kalgaard (1 species).

The very specialized feeding apparatus comprises toothless mandibles and a tube-shaped mentum having three median teeth and only one pair of lateral teeth (lying dorsal to the median teeth) (Figure 4). This suggests a very unique feeding strategy (Livingstone et al., 1958; Walker & Mathewes, 1988). It is easy to speculate in relation to feeding on charophytes (e.g. Mothes, 1968), but the presence of the species in lakes without charophyte plants argues against a strictly characeous diet (Livingstone et al., 1958). The larvae are not found in/on the charophytes, but are building detrital tubes mainly on the bottom, like most other

Tanytarsini. The diet should thus be fragments of living or detrital charophyte tissues reaching the bottom. However, Fjellberg (1972) and Boubée (1983) found the gut contents of *C. ambigua* larvae to consist of diatom/algal detritus and mineral grains, suggesting that the microbenthic production is an important food source. This was also what we observed from (formalin preserved) larvae in Lake Stigsholm, where diatoms were present but did not dominate either the larval tubes or the gut content. An obligate relationship between *C. ambigua* and charophytes probably does not exist, but it is possible that charophytes can have a positive influence on the midge populations as a regulating element in autotrophic interactions. A high water transparency in lakes with dense charophyte beds (Forsberg, 1965; Blindow, 1992a) will enhance the production of benthic diatoms around the patches and thus increase the food availability for zoobenthos. Charophyte beds will also have a physical stabilizing effect on the sediments in wind-exposed shallow lakes. The less turbulent conditions and lower resuspension will have a positive influence on these bottom dwelling and tube building species. The reduction in number of lakes supporting the phosphorus sensitive charophyte plants (Kristensen & Hansen, 1994; Blindow, 1992b) might be partly responsible for the reduction in *C. ambigua* populations in Northern Europe.

Mass occurrences

The core study from Lake Stigsholm and the surface samples from Lake Nors showed that *C. ambigua* may account for 23–50% of the chironomid community. In samples of living larvae in Lake Stigsholm (October 16th 1995), we found up to 85,000 m⁻² in a single sample. The average over the year was 10,000 m⁻² (unpublished data). Mass occurrences of swarming adults were also observed by Hirvenoja (1960) and Fjellberg (1972). In palaeoecological studies the concentration of chironomid head capsules (HC) is often very high in samples containing *C. ambigua*. Livingstone et al. (1958) found 8,000 HC ml⁻¹, Deevey (1955) 1,700 HC ml⁻¹ and Walker & Mathewes (1988) found 690 HC ml⁻¹ in one sample of which '*C. nr. ambigua*' made up 72% of the total chironomid remains. The high sedimentation rate in the eutrophic Lake Stigsholm causes a low total HC concentration of 28 HC g sediment wet weight⁻¹ on average. In surface samples from Finnish Lapland, *C. ambigua* was found to comprise up to 60% of the chironomid community (Olander, pers. commun.)

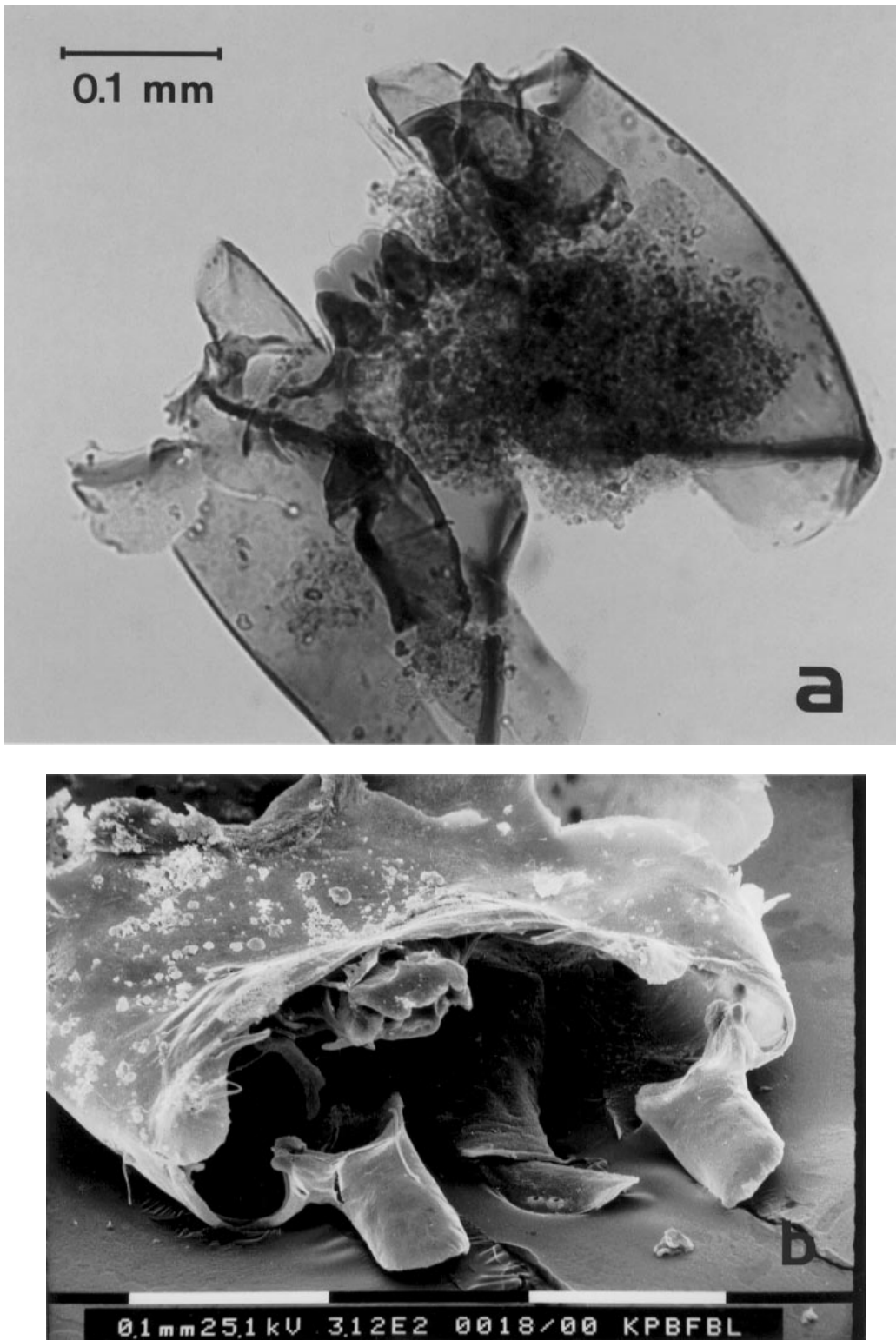


Figure 4. Light- and Scanning Electron Micrographs of *Corynocera ambigua* head capsules from Lake Stigsholm surface sediments (a) and from the 38 cm layer (b). Scale on LM and SEM photos are 0.1 mm.

It seems that once established, *C. ambigua* can develop huge populations. We suppose that one reason for this could be high breeding success due to tightly synchronous swarming in only two dimensions (i.e., the water surface). The probability of finding a mate is thus high and there is the certainty that eggs will be laid in water in which the life cycle was successfully completed. Since the adult midges do not fly, they might also be less sensitive to wind and weather conditions at this critical time of their life cycle.

Lake Stigsholm

The disappearance of *C. ambigua* from Lake Stigsholm is probably due to dramatic changes in biological structure in recent decades. The lake has fluctuated between a macrophyte-rich clear-water state and a macrophyte-poor turbid state. From 1995, coverage of the macrophyte *Elodea canadensis* Rich. and filamentous algae has increased to 50–70% with a subsequent increase in the number of coot (*Fulica atra* L.) and mute swan (*Cygnus olor* Gmel.) (Søndergaard et al., 1997). The heavy growth of *Elodea* may alter the conditions for the benthic invertebrate populations by (1) changing the sediment structure, (2) causing pronounced fluctuations in oxygen concentrations, (3) restraining the benthic microalgae production, (4) changing the available food source, and (5) causing severe oxygen depletion during decomposition. Physical disturbance of the lake sediment by waterfowl activity may occur, but is probably of minor importance. We believe that one or several of these factors, directly or indirectly, have interfered with the populations of *C. ambigua*, or have provided a competitive advantage to other taxa such as *Tanytarsus* spp.

Decline in numbers during the Holocene

It seems obvious to relate the *C. ambigua* decline often found in the early Holocene to the amelioration in climate. But the observations in temperate Denmark and the occurrences in the Atlantic periods (Table 2) mitigate against this hypothesis. In the late glacial *C. ambigua* thrived during periods of low temperature, in lakes with high water levels, silty and low organic sediments, abundant oxygen and probably extensive charophyte beds in the carbonate rich waters. With the rapid temperature increase following the Younger Dryas (Coope, 1986), a lowering in water levels (Berglund et al., 1996), extensive erosion, and redeposition of lake sediments (Digerfeldt, 1986) might have caused an increased

nutrient availability (Birks, 1980), an outward spread of aquatic macrophytes (Digerfeldt, 1986) and increased organic sedimentation (Birks, 1986). Thus, an overall change in lake type from 'Chara' - to 'Potamogeton-lakes' (Forsberg, 1965) might have contributed to reduction in *C. ambigua* populations in northern Europe, just as much as increased temperature.

Conclusion

We conclude that despite the generally northern, alpine and late-glacial distribution of *Corynocera ambigua*, temperature is not a limiting factor for its occurrence in temperate lowland lakes. *C. ambigua* was found in several types (25%) of the Danish lakes studied. Once established, a high specialization and high swarming success might explain the large populations and mass occurrences which is often observed for the species. Co-occurrence with charophyte plants is frequently observed both in neo- and palaeoecological investigations, but an obligate relationship is not likely and difficult to verify. A reduction in the number of shallow clear-water lakes with sediments stabilized by e.g. charophytes might have caused the patchy distribution of *C. ambigua* in Northern Europe. The decline following several hundred years of dominant *C. ambigua* in the temperate and shallow Lake Stigsholm coincides with a decline in charophyte oospores and recent heavy growth of the macrophyte *Elodea*. A low dispersal potential of the brachypterous adults can delay the recovery of populations. The ecological adaptations of *Corynocera ambigua* are complex and we believe that the species might be more widespread in shallow temperate standing-waters than previously assumed. Further studies of dispersion, feeding behavior, temperature and oxygen tolerances for this and related species, are needed.

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