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Southwards migration of freshwater invertebrates from northern Norway

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Remains of larvae of caddis flies (Insecta, Trichoptera) and non-biting midges (Insecta, Chironomidae) were recorded in core samples dated at 12 000-11 000 and about 20 000 B.P., respectively, from lakes on Andøya, Norway (69°15'N). All caddis remains belonged to *Apatania zonella* (Zetterstedt). 4 Orthocladinae species, *Pseudodiamesa* sp., *Metriocnemus obscuripes* (Holmgren), Sp. A and Sp. B (*Ortocladius* sp.?) were found.

Fragments of a crustacean, *Lepidurus arcticus* Krøyer, were present in sediments dated to ca 12 800 B.P.

Ice-free areas and lotic/lentic (running/standing water) habitats have been present on Andøya at least from ca 22 000 B.P. Of insects, chironomids must have been one of the earliest colonizers of freshwater habitats, and we suggest that *A. zonella* was the first arctic/alpine caddis species to colonize Norway after the last ice age.

The existence of an ice-free coastal refugium, from at least 22 000 B.P. on Andøya, strongly suggest an early southwards migration of arctic/alpine aquatic and terrestrial invertebrates from this area through Norway and Sweden, in addition to immigration from the south and east during and after the deglaciation.

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Introduction

At the peak of the last glaciation (ca 20 000 to 18 000 B.P.), almost the entire Scandinavian peninsula was covered by ice. The main deglaciation occurred approximately 14 000 to 9 000 years B.P. However, some areas along the coast of Norway were deglaciated earlier. On the island of Andøya (69°15'N), where this study was carried out, deglaciation started about 22 000 B.P. (Alm 1993). Thus, in a geological perspective the fauna of Norway is young.

The climate in front of the inland ice placed severe demands on aquatic animal life, for example, because of low water temperature, as it does near glaciers today. Vik (1971) put forward some general theories about an early aquatic insect fauna in front of glaciers in Norway, but few fossil data were available. Our study of sediment samples from two lakes on Andøya gives some clues on this matter. The objective of this paper is to present some evidence that an early southern migration of invertebrates into Scandinavia could occur from its northernmost areas, and not only from south and east which has been a common opinion.

Sediment columns extending back to 18 000-22 000 B.P. are available from several lakes on Andøya. They offer unique possibilities for studying the macro- and microfossils of Late Weichselian lacustrine and terrestrial environments. So far, most studies have been centred on pollen, spores and other microfossils (K.-D. Vorren 1978, T. Vorren et al. 1988, Alm 1990). A few macrofossils, e.g. mammal and avian bones, have also been recorded (Fjellberg 1978, K.-D. Vorren 1978).

Alm & Birks (1991) carried out a study of phanerogam diaspores in the Nedre Æråsvatn sequence. The samples investigated also contained insect remains, in particular head capsules of midges (Diptera, Chironomidae), which were studied by Alm & Willassen (1993). The present paper focuses on the remains of caddis larvae (Insecta, Trichoptera) in samples from Nedre Æråsvatn, but notes on the crustacean *Lepidurus arcticus* Krøyer are also given. However, we also comment on finds of larvae of non-biting midges (Diptera, Chironomidae) from Øvre Æråsvatn.

The use of caddis remains as indicators of past environments has been explored in North America and Europe for the last 30 years. In Scandinavia, Lemdahl (1991) reported fossil caddis remains from southern Sweden, and Birks et al. (1993) from western Norway. Because the insect larvae and the crustacean considered here do not fly, their remains represent local assemblages, even though lotic depositional sites may include specimens transported from upstream areas.

Study area

Andøya is the northernmost of the Lofoten - Vesterålen islands in northern Norway (**Figure 1**). This study concerns samples from two lakes, Nedre and Øvre Æråsvatn. They are situated near the northern tip of the island, at 69°15'N. Nedre Æråsvatn (35 m a.s.l.) is a small (about 450 x 600 m) shallow lake, with a present-day maximum depth of only 2.5 m. Øvre Æråsvatn is slightly larger, with present-day depths up to 6 m (**Figure 2**).

Both lakes have yielded extensive Late Weichselian sediment columns. The bottom sediments in Nedre Æråsvatn were deposited about 20 000 B.P., but were disturbed and compressed by a brief glacial advance about 18 500 B.P. (T. Vorren et al. 1988, Alm 1990). Neighbouring Endletvatn was deglaciated about 18 000 B.P. (K.-D. Vorren 1978, Alm 1990).

Øvre Æråsvatn, in a somewhat more protected position, has not been directly affected by glacial activity since at least 22 000 B.P. (Alm 1990). Here, undisturbed lacustrine strata testify to the existence of a small, unglaciated lowland area and at least one freshwater basin about 22 000 B.P. (Alm 1990).

The sediments deposited in Nedre Æråsvatn at ca 20 000 to 15 500 B.P. contain numerous tissue fragments of marine algae (T. Vorren et al. 1988, Alm 1990, Alm & Birks 1991), indicating a glaciomarine origin for this part of the sequence. Isolation from the sea took place about 15 500 B.P. Subsequent lacustrine strata comprise various freshwater algae (e.g. *Pediastrum boryanum* (Turp.) Meneghini) and variable numbers of chironomid remains (Alm & Willassen 1993).

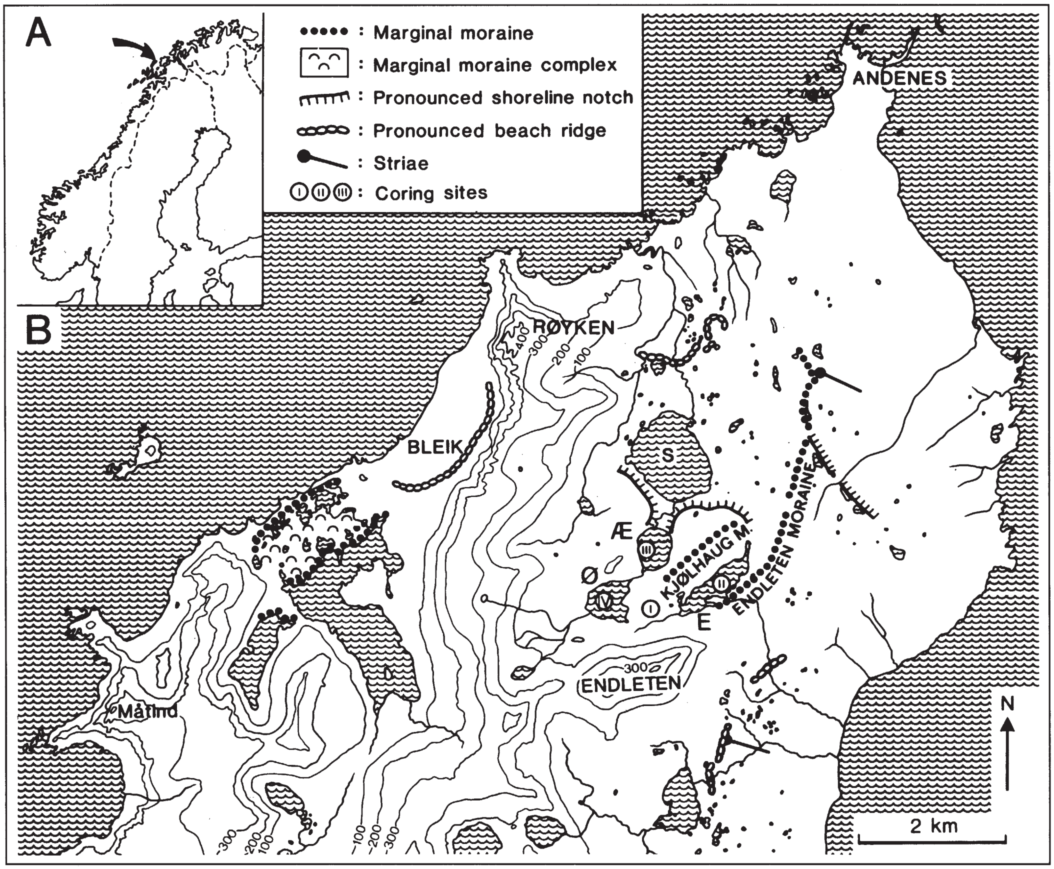

Fig. 1
A. Key map. B. Map of northern Andøya showing the position of Nedre Æråsvatn (Æ), Øvre Æråsvatn (Ø), Endletvatn (E) and Storevatn (S).

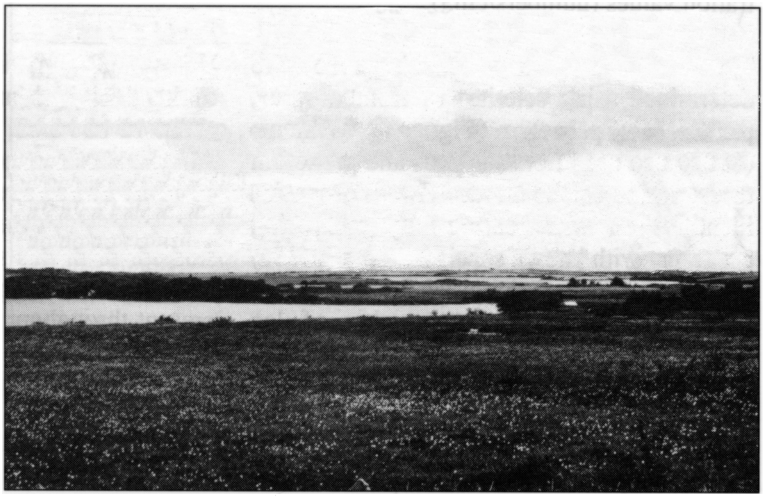

Fig. 2
View east from the top of the Æråsen hill, showing Nedre Æråsvatn (foreground), Endletvatn (background), and Øvre Æråsvatn (to right).

Material and methods

At Nedre Æråsvatn, cores were taken through the frozen lake in April 1982 using a Geonor piston corer and 110 mm PVC tubes. Sediment depths of up to 10.6 m were recorded, including more than 6 m of clay, silt and gyttja deposited about 20 000 to 10 000 B.P. A detailed litho-, chrono- and biostratigraphical account has been given by T. Vorren et al. (1988), supplemented by Alm (1990), Alm & Birks (1991) and Alm & Willassen (1993).

Fossil samples were taken from the cores described by T. Vorren et al. (1988) and Alm (1990), in the form of 1 to 5 cm thick half-core slices. Their volumes were measured by displacement in water. Samples were treated with 10 % KOH for 24-48 hrs, and sieved through 2.0 and 0.25 mm sieves. Residues were studied under a binocular microscope, and the fossils were picked out.

Our fossil data are based on 45 samples from Nedre Æråsvatn, covering the 20 000 to 11 000 B.P. interval, supplemented by nine Øvre Æråsvatn samples (ca 22 000 to 19 000 B.P.). To compensate for the very variable sample sizes, the results from Nedre Æråsvatn (**Figure 3**) are presented in terms of concentration values (numbers/cm3).

The genus and species of caddis larvae were determined using sclerites of frontoclypeus, parietals and pronotum (**Figure 4**). Williams (1989) also used frontoclypeus and pronotum to determine caddis larvae. The final species identification was achieved by comparing pronotum with known species. Solem (1985a) gave the characteristics used for identifying Nordic **Apatania** spp. A number of leg remains were also present, but were not used in the identification work.

The chironomids (non-biting midges) were identified by remains of head capsules. Loose caudal segments and mandibles of the crustacean *Lepidurus arcticus* were compared with drawings made by Sars (1896). This identification is based on the fact that *L. arcticus* is today the only *Lepidurus* sp. now occurring in Fennoscandia.

Results

Only three macrofossil samples from Nedre Æråsvatn yielded remains of Trichoptera. They are situated in the uppermost part of the section at about 12 000 to 11 000 B.P., in layers deposited during the Allerød amelioration (**Figure 3**). Only one species, *A. zonella*, was present. In Øvre Æråsvatn, remains of chironomid head capsules were found in two samples near the base of the sequence, dating from 19 000 to 22 000 years B.P., and *Pseudodiamesa* sp. (4 specimens), *Metriocnemus obscuripes* (7 specimens), Sp. A (1 specimen) and Sp. B (*Ortocladius* (?), 1 specimen) were identified.

Remains of the crustacean *L. arcticus* were recorded in several samples from Nedre Æråsvatn. Loose caudal segments were found in 7 samples from about 12 800 B.P. to about 11 400 B.P.

Lepidurus occurs in low concentrations (**Figure 3**). Maximum numbers occurred during the initial (main) Bølling amelioration, about 12 800 B.P., and in the late Bølling to Allerød strata deposited around 12 100 to 11 400 B.P. The apparent absence around 12 300 B.P. may reflect the small size of the sample studied. With this single exception, the even representation suggests that the species was present throughout the 12 800 to 11 000 B.P. interval.

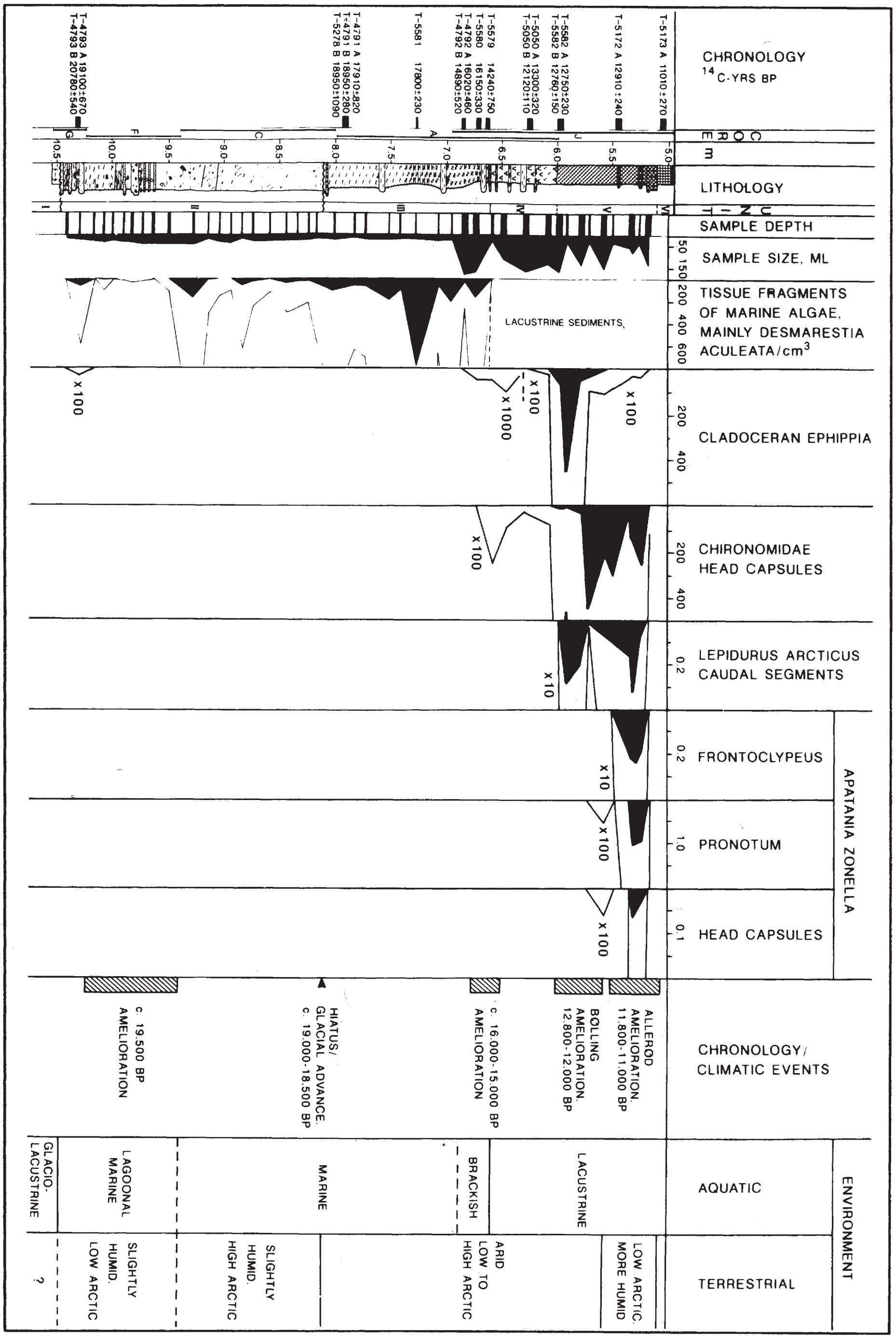

Fig. 3
Concentration diagram (numbers/cm³) showing distribution of some macrofossils in the Nedre Æråsvatn sequence (black). Supplementary curves x10 unless otherwise stated.

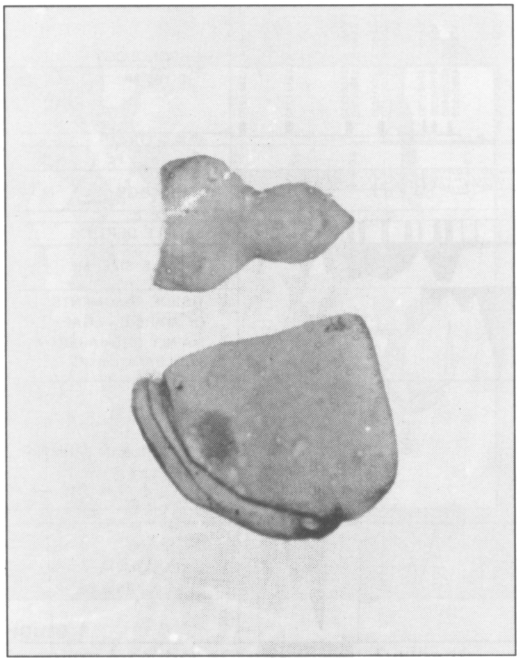

Fig. 4
Frontoclypeus and pronotum of Apatania zonella *from sediments on Andøya.*

Discussion

In recent years, remains of caddis larvae have proved a promising palaeoecological tool (Williams 1987, 1988), even if only a single species was found. In the present study only *A. zonella* was found.

In view of the current knowledge of the habitat requirements of caddis (and chironomid) larvae it is pertinent to ask what species assemblage could be expected to manage to live in a habitat as that on Andøya 22 000 to 12 000 years B.P. and thus be early immigrants in other areas of Norway? The abundance of glacial meltwater produces low water temperatures in front of a glacier, influencing the aquatic vegetation and the composition of the aquatic insect fauna.

Climate has both direct and indirect effects on insects. Air temperatures and winds directly affect the ability of adults to move about, mate and oviposit. Development of the aquatic larval and pupal stages is influenced directly by water temperatures and indirectly through the effects of air temperature and precipitation on terrestrial and aquatic vegetation and soils, and in turn affects the water chemistry and supply of food for aquatic insects (Williams 1989).

A. zonella is a cold-stenothermous species living in running and standing waters in mountainous areas of Scandinavia. It is the only caddis fly recorded on Spitsbergen, as far north as 80°N (Solem et al. 1977). Thus, the aquatic habitat(s) on Andøya around 11 000-12 000 B.P. and earlier may have been quite similar to the sites inhabited by *A. zonella* today. It is also the only species that may be abundant in high mountainous areas in Norway (Solem 1985b). This agrees with the assumption made for Coleoptera by Coope (1977), that morphological stability implies physiological stability and therefore similarity in ecological requirements.

A. zonella feeds by grazing algae and other organisms (periphyton), that grow or live on stones. It is a high arctic/alpine and northern Holarctic species with a flexible (one, two or more? year) life cycle, mostly reproduces by parthenogenesis (Gislason 1981, Solem 1985a), and has many features needed for living and surviving in extreme habitats.

The pre-22 000 B.P. glacial record and lacustrine history of Andøya is basically unknown. Chironomid remains from about 22 000 and 16 000 B.P., and Fjellberg`s (1978) finds from 17 000-18 000 B.P., show that insect communities have existed on Andøya during the Late Weichselian. Even if the fossil record is sparse and fragmentary, the cold-stenothermal *A. zonella* may have been present on Andøya throughout the Late Weichselian, but in low numbers.

Sedimentation in Øvre Æråsvatn started about 22 000 B.P. and Alm (1993) suggested a slightly humid climate during this early deglaciation phase, with modest precipitation supporting small streams. The records of chironomid larvae in layers in Øvre Æråsvatn, dating back to 19 000-22 000 B.P., show that habitats for freshwater invertebrates that can endure low water temperatures, e.g. chironomids and *A. zonella*, were present during this early phase. Like *A. zonella*, the chironomids *Pseudodiamesa* and *Metriocnemus obscuripes* inhabit both running and standing water, and therefore the type of aquatic habitat that was present 19 000-22 000 B.P. cannot be stated.

In Nedre Æråsvatn, Alm & Willassen (1993) found no indications of a true lentic chironomid fauna before 15 500 B.P., but larvae of the chironomid *Metriocnemus obscuripes* were found in samples from around 16 000 to 15 800 B.P. The fossil record (**Figure 3**) indicates that chironomids, cladocerans and eubranchiopods established a lentic community before *A. zonella* appeared.

According to Banarescu (1991, p. 851), *A. zonella* belongs to the "Northern ice cap marginal species", where he also places *L. arcticus*, with the following definition of such species: "cold-adapted species, originally from the extreme north of the continent (or from entire Eurasia), pushed southward during the Ice Age into Central Europe, where they entered the glacial mixed fauna, but were restricted to the northern belt inhabited by this fauna."

This may be true for *A. zonella* also, but it may equally well have survived in Asia where the group most probably originated (Malicky 1988). Our opinion is that *A. zonella* and other arctic/alpine freshwater invertebrates colonized ice-free areas in northern Scandinavia from the east and migrated south from these ice-free areas after the last deglaciation. The migration route thus has both an eastern and a northern component. Some northern invertebrates probably met their southern distribution limit for climatical reasons. Lillehammer (1974) and Lillehammer et al. (1980) showed how the number of Plecoptera increases towards the east of North Norway, and partly linked this with an immigration from east. In the case of Plecoptera, historical immigration was considered one of the main factors for explaining the geographical distribution today. In Norway, one northern species of freshwater snail (Gastropoda), *Valvata sibirica* Middeldorff, is restricted to the southeastern part of Finnmark (cf. J. Økland 1990). It has obviously originally immigrated from the east. Lack of continuous waterways prevented its further distribution southwards (J. Økland 1990). However the plecopteran species in question, like the gastropod *Valvata sibirica*, immigrated from the east to southeastern Finnmark. But, after the deglaciation *A. zonella* may have migrated to southeastern Finnmark from the west (Andøya) as well as from the east.

Today, the genus *Apatania* is widely distributed in the Northern Hemisphere, and is one of the few caddis genera that has a circumpolar distribution. The present distribution of *A. zonella* is Russia, Finland, the Baltic countries, north Sweden, Norway (common in montane areas), Spitsbergen, Iceland, Greenland and northern North America. There is no record of *A. zonella* in south Sweden, Denmark, Germany, Great Britain (one record in Britain has proved not to be *A. zonella*, J. O'Connor pers. comm.) or Ireland. Nor is there any fossil data on *A. zonella* from these areas.

Kverndal & Sollid (1993) state that nunataks plausibly existed in northern Troms, north of

Andøya, during the Late Weichselian maximum. Our data (and those of others) show that ice-free areas existed on Andøya during the Late Weichselian maximum and that some hardy arctic/alpine species survived there. Thus, the records of insect and crustacean remains on Andøya strongly indicate that some freshwater (and terrestrial) invertebrates survived the Late Weichselian maximum on Andøya and were able to colonize central and southern Norway and Sweden from the north during the deglaciation period, and not only from the south and east, as has been generally held in response to the "tabula rasa" thinking which arose around 1850. During the subsequent deglaciation, *A. zonella* probably closely followed the ice front from the north.

The Allerød record of *A. zonella* in Nedre Æråsvatn coincides with a marked climatic shift about 12 000 B.P. In terrestrial habitats, this change is characterized by fewer grasses (as recorded by pollen and seeds) and a strong increase of *Oxyria* pollen (T. Vorren et al. 1988, Alm 1990, Alm & Birks 1991). T. Vorren et al. (1988) interpreted this as a shift towards a more humid climate, leading to increased precipitation and surface runoff. The *Apatania* record may support this, indicating an increased availability of freshwater habitats.

The record of *L. arcticus* in Nedre Æråsvatn coincides with the late-glacial Bølling through Allerød ameliorations (about 12 800 to 11 000 B.P.). Both freshwater algae and other microfossils (T. Vorren et al. 1988, Alm 1990) and chironomid remains (Alm & Willassen 1993) suggest increased lacustrine productivity during this phase (**Figure 3**). Today, *L. arcticus* is distributed in high mountainous areas in Norway, and is found at sea level on Bjørnøya and Spitsbergen. It is regarded as an arctic relict in Scandinavia (Sars 1896). However, *L. arcticus* is common in Late Weichselian sediments dated to 13 000-12 500 and 11 000-10 300 B.P. in southern Sweden and easternmost Finland. In Norrbotten, northern Sweden, Aronsson et al. (1993) recorded it in 100 000 year old sediments. It has also been recorded in sediments dating from 12 000 to 10 000 years B.P. in western Norway (K.A. Økland 1978). Fossil remains of *L. arcticus* are also found in the British Isles (Morrison 1959, Taylor & Coope 1985). Hence, these fossil records show that *L. arcticus* could colonize Norway and Scandinavia from the north, east and south, and thus we think the immigration pattern of *L. arcticus* differed from that of *A. zonella*.

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Sammendrag

Nordlig innvandring av ferskvannsinvertebrater i Norge, med kommentarer til skjoldkrepsen *Lepidurus arcticus*, fjærmygg og utbredelsen av vårfluen *Apatania zonella*.

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Rester av fjærmygg (4 Orthocladinaearter) er funnet i sedimentprøver som er 22 000 til 19 000 år gamle og kommer fra vann på Andøya, Troms (69°15'N). Det er også funnet fjærmygg i sedimenter ca 16,000 år gamle, og skjoldkreps (*Lepidurus arcticus*) og en vårflueart (*Apatania zonella*) i sedimenter 13 000 til 12 000 år gamle. Andre botaniske og zoologiske funn viser at nordlige deler av Andøya har vært isfri så langt tilbake som 22 000 år,

kanskje lenger, og at det har vært dyreliv der i alle fall tilbake til den tiden. Da ismassen som dekket Skandinavia hadde sin største utbredelse for 20 000 til 18 000 år siden var dette området totalt adskilt fra dyrelivet sør for isranden. Da isen smeltet, med hovedavsmelting mellom 14 000 og 9 000 år tilbake, kunne dyrepopulasjonene på Andøya, og som hadde overlevd maksimum isutbredelse, kolonisere sydligere deler av Norge og Sverige fra nord. *A. zonella* som i dag ikke har utbredelse sør for maksimum sydlig isrand, og som heller ikke oss bekjent er funnet i noe sydlig fossilt materiale, må ha kolonisert mellom og syd Skandinavia fra nord. Noe annerledes er situasjonen for fjærmygg og skjoldkreps. Fossilt materiale av skjoldkreps er funnet i sydlige Norge, sydlige Sverige og sydlige Finland. Den kan derfor ha fulgt isranden både fra nord, sør og øst til de områder den lever i dag. Dette er også et mønster som fjærmygg kan ha hatt.

References

Alm, T. 1990. Late Weichselian vegetation and terrestrial/lacustrine environments of Andøya, Northern Norway - a palaeoecological study. 263 pp. Thesis, University of Tromsø.

Alm, T. 1993. Øvre Æråsvatn - palyostratigraphy of a 22,000 to 10,000 B.P. lacustrine record of Andøya, northern Norway. Boreas 22: 171-188.

Alm, T. & Birks, H.H. 1991. Late Weichselian flora and vegetation of Andøya, Northern Norway - macrofossil (seed and fruit) evidence from Nedre Æråsvatn. Nordic Journal of Botany 11: 465-476.

Alm, T. & Willassen, E. 1993. Late Weichselian chironomidae (Diptera) stratigraphy of Nedre Æråsvatn, Andøya, Northern Norway. Hydrobiologia 264: 21-32.

Aronsson, M., Hedenäs, L., Lagerbäck, R., Lemdahl, G. & Robertsson A.-M. 1993. Flora och fauna i Norrbotten för 100 000 år sedan. Svensk Botanisk Tidsskrift 87: 241-253.

Banarescu, P. 1991. Distribution and dispersal of freshwater animals in North America and Eurasia. Pp. 519-1091. Aula-Verlag, Wiesbaden.

Birks, H.H., Lemdahl, G., Svendsen, J.I. & Landvik, J.Y. 1993. Palaeoecology of a late-Allerød peat layer at Godøy, Western Norway. Journal of Quaternary Science 8: 147-159.

Fjellberg, A. 1978. Fragments of a Middle Weichselian fauna on Andøya, north Norway. Boreas 7: 39.

Gislason, G. 1981. Distribution and habitat preferences of Icelandic Trichoptera. Pp. 99-109 in: Moretti (ed.) Proceedings of the 3rd International Symposium on Trichoptera. Series Entomologica. 20. Dr. W. Junk Publishers, The Hague

Kverndal, A.-I. & Sollid, J.L. 1993. Late Weichselian glaciation and deglaciation in northeastern Troms, northern Norway. Norsk geografisk Tidsskrift 47: 163-177.

Lemdahl, G. 1991. A rapid climatic change at the end of the Younger Dryas in south Sweden - palaeoclimatic and palaeoenvironmental reconstructions based on fossil insect assemblages. Palaeogeography, Palaeoclimatology, Palaeoecology 83: 313-331.

Lillehammer A. 1974. Norwegian stoneflies. II. Distribution and relationship to the environment. Norsk entomologisk Tidsskrift 21: 195-250.

Lillehammer, A., Borgstrøm, R. & Skulberg, O.M. 1980. Miljøpåvirkninger i norske vassdrag I. Økosystembeskrivelse. Fauna 33: 109-116.

Malicky, H. 1988. Spuren der Eiszeit in der Trichopterenfauna Europas (Insecta, Trichoptera). Rivista di idrobiologia 27: 247-297.

Morrison, M.E.S. 1959. *Lepidurus arcticus* in the Irish Late-Glacial. Nature 184: 739.

Nesje, A., Anda, E., Rye, N., Lien, R., Hole, P.A. & Blikra, L.H. 1987. The vertical extent of the Late Weichselian ice sheet in the Nordfjord - Møre area, western Norway. Norsk geologisk tidsskrift 57: 125-141.

Økland, J. 1990. Lakes and snails. Environment and Gastropoda in 1,500 Norwegian lakes, ponds and rivers. Universal Book Services/Dr. W. Backhuys, Oegstgeest, The Netherlands. 516 pp.

Økland, K.A. 1978. Storkreps i ferskvatn. Pp. 44-47 in: Lye, K.A. (ed.) Jærboka. Naturmiljøet. Vol. 2. Norsk Oikos A/S. 288 pp.

Sars, G.O. 1896. Fauna Norvegiæ. I. Phyllocardia og Phyllopoda. Aktie-Bogtrykkeriet, Christiania. 140 pp.

Solem, J.O. 1985a. Norwegian *Apatania* Kolenati (Trichoptera, Limnephilidae: identification of larvae and aspects of their biology in a high-altitude zone. Entomologica scandinavica 16: 161-174.

Solem, J.O. 1985b. Distribution and biology of caddisflies (Trichoptera) in Dovrefjell mountains, Central Norway. Fauna norvegica Ser. B, 32: 62-79.

Solem, J.O., Senstad, E., Bergvik, T. & Hegstad, A. 1977. New record of *Apatania zonella* from Svalbard. Norwegian Journal of Entomology 24: 85.

Taylor, B.J. & Coope, G.R. 1985. Arthropods in the Quartenary of East Anglia - Their role as indices of local palaeoenvironments and regional palaeoclimates. Modern Geology 9: 159-185.

Vik, R. 1971. Hvordan Norges dyreliv ble til. Pp. 12-31 in Frislid, R. & Semb-Johanson, A. (eds) Norges dyr, vol. 5. Cappelen, Oslo.

Vorren, K.-D. 1978. Late and Middle Weichselian stratigraphy of Andøya, north Norway. Boreas 7: 19-38.

Vorren, T., Vorren, K.-D., Alm, T., Gulliksen, S. & Løvlie, R. 1988. The last deglaciation (20,000 to 11,000 B.P.) on Andøya, northern Norway. Boreas 17: 41-77.

Williams, N.E. 1987. Caddisflies and Quaternary palaeoecology -what have we learned so far? Pp. 55-60 in Bournaud, M. & Tachet, H. (eds): Proceedings of the 5th International Symposium on Trichoptera. Dr. W. Junk Publishers, Dordrecht.

Williams, N.E. 1988. The use of caddisflies (Trichoptera) in palaeoecology. Palaeogeography, Palaeoclimatology, Palaeoecology 62: 493-500.

Williams, N.E. 1989. Factors affecting the interpretation of caddisfly assemblages from Quaternary sediments. Journal of Paleolimnology 1: 241-248.