SUBFOSSIL SHELL MARGINS AND TAIL SPINES OF Daphnia
IN FINNISH LAKE SEDIMENTS – IS Daphnia UNDERREPRESENTED
IN CLADOCERA ANALYSIS?

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Abstract
One of the shortcomings of the analysis of subfossil Cladocera (water flea) remains is that preservation of remains is selective. Of Daphnia spp. which are very common in zooplankton assemblages of lakes, usually only postabdominal claws and ephippia are found. In the present paper I describe Daphnia shell margins and some tail spines from the Holocene sediments of a lake in southern Finland where the margins were much more abundant than the postabdominal claws, indicating that postabdominal claws may be underrepresented. Daphnia claws, shell margins and tail spines were found also in surface samples of 17 Finnish lakes and thus the abundance of tail spines could be compared with that of postabdominal claws. The results showed that in most cases the tail spines are more abundant than postabdominal claws and may give a closer estimate of the true abundance of Daphnia. However, in some lakes claws were clearly more frequent than tail spines. Apparently, there are differences in preservation of different types of Daphnia remains between lakes, possibly connected with water chemistry. Overall, the results indicate that probably Daphnia remains are always underrepresented in lake sediments.

Key words: subfossil Daphnia remains, tail spines, shell margins, lake sediments, Finland

INTRODUCTION
In analysis of subfossil Cladocera (water flees) chitinous exoskeletal body parts of these animals are counted from lake sediments and used to reconstruct e.g. past ecological and limnological conditions (reviewed by e.g. Frey 1986, Korhola & Rautio 2001). One of the shortcomings of the analysis is that preservation of remains is selective and not all body parts of all species do preserve. For example, remains of Daphnia, a very common genus in zooplanktonic assemblages of lakes, do not preserve well, and in sediments, only postabdominal claws and ephippia (modified shells protecting the resting eggs) are usually found.

However, some finds of subfossil remains of Daphnia other than ephippia or postabdominal claws have been reported. Frey (1991) described well-preserved headshields from Greenland, the remains being ca. 10,000 years old. Manca et al. (1999) and Manca & Comoli (2004) found well-preserved Daphnia headshields in sediments of a Himalayan mountain lake. Szeroczyńska & Zawisza (2005) encountered headshields of Daphnia pulex group and shell fragments in the early Holocene sediments of a lake in Finnish Lapland and shells of Daphnia longispina group from recent sediments in a lake in northeastern Poland. They also found tail spines of Daphnia in the early Holocene sediments of the latter lake (Szeroczyńska & Zawisza 2005). These finds indicate that occasionally also body parts other than ephippia and postabdominal claws are preserved.

In the present paper I report finds of outer margins of Daphnia shells and tail spines in the Holocene sediments of a lake in southern Finland. I also present preliminary results of finding similar remains in surface samples from 17 lakes in Finland. These enable a comparison between the preservation of tail spines and postabdominal claws. How underrepresented is Daphnia in analyses of subfossil cladoceran remains?

METHODS
All analyses were performed from lake gyttja. The Arapisto samples were taken from a long core collected by a Livingstone corer, whereas the surface sediment samples were taken with a Limnos sampler. In laboratory samples were heated in 10% KOH (potassium hydroxide) for 20–30 min, sieved through a 44 µm mesh and mounted in glycerine jelly stained with safranine. The remains were counted under a light microscope with a × 200 magnification. More than 500 cladoceran remains were counted from each of the 17 surface sediment samples listed in Table 1, including the Daphnia remains. The significance of differences between the abundance of tail spines and postabdominal claws was tested using $\chi^2$ test and Fisher’s exact test. All the 17 lakes were included in the statistical tests. A contingency table contained 34 cells, each lake had a cell for the number of tail spines, and the number of postabdominal claws. The degree of freedom was 16.
RESULTS AND DISCUSSION

During cladoceran analysis of the sediments of Lake Arapisto, southern Finland (Nevalainen 2004, Sarmaja-Korjonen & Seppä, subm.), it was noticed that among other remains there were abundant thread-like structures (Fig. 1) but their origin remained unknown. Later, similar thread-like structures were found in the surface sediment samples of Lake Mustalampi (see below), but this time they were attached to well-preserved tail spines of Daphnia (Fig. 2), well-preserved probably because of the recent age of the surface samples. There were also small spinules, typical to Daphnia, still attached to the margins (cf. Szeroczyńska & Zawisza 2005, Fig. 1F).

These finds indicated that the unknown structures found in Lake Arapisto were, in fact, margins of Daphnia shells. Margins were found in sediments deposited during the entire Holocene (ca. 11,500 years) and indicated that in certain conditions the margins of Daphnia shells can be preserved as well as postabdominal claws. However, many margins were fragmented and it was impossible to estimate the number of individuals they represented. When the Lake Arapisto samples were re-examined, also some crumpled tail spines could be identified (Fig. 3), each representing an individual. Occasionally also some preserved marginal spinules were visible on the margins. The margins and the tail spine in Figs. 1 and 3 are ca. 8200 cal yr old (Sarmaja-Korjonen & Seppä subm.). The postabdominal claws found in Lake Arapisto belonged to Daphnia longispina group.

Based on the frequency of postabdominal claws found during cladoceran analyses (Nevalainen 2004, Sarmaja-Korjonen & Seppä, subm.) Daphnia was never very common in Lake Arapisto, even though the maximum depth of the lake is presently ca. 7 m and it could be expected to have had abundant zooplankton. The proportion of Daphnia of all species varied from sporadic finds to ca. 10% and only once, ca. 5000 cal BP, it rose to ca. 20% (Nevalainen 2004). Daphnia spp. are common in modern lakes, especially if the nutrient level is high. Their occurrence can be limited by very acidic waters and heavy fish predation.

Räsänen & Sarmaja-Korjonen (in prep.) studied surface sediment samples from 21 lakes in southern Finland with cladoceran analysis and at that time could identify only postabdominal claws and ephippia of Daphnia. The TP (Total Phosphorus) of the lakes varied between 6 and 170 µg l⁻¹ and the maximum depth between 1.6 and 22.8 m. In spite of the
fact that most of the lakes were meso/eutrophic and deeper than 5 m, proportions of remains of *Daphnia* were exceptionally low (ca. 0–3% of all taxa) in all lakes but one (Hor-

majärvi, max. depth 20 m, TP 13 µg l⁻¹) where the proportion of remains of *Daphnia* was almost 50%. The results suggested that most probably the remains, mainly postabdominal claws of *Daphnia* were underrepresented in lake sediments (cf. Korhola 1999).

Now, as tail spines could be identified, the underrepresentation could be investigated by comparing the quantities of *Daphnia* claws and spines found in surface sediment samples from 17 lakes in southern Finland (Table 1). As every *Daphnia* individual has one tail spine and two postabdominal claws the numbers of claws in Table 1 below refer to pairs of claws. All postabdominal claws belonged to *Daphnia longispina* group. Shell margins were not included in the comparison because, if not attached to spines, they cannot be used to reliably estimate the number of individuals.

The results indicate that in 10 lakes out of 17, the tail spines were more abundant than the postabdominal claws. In some lakes the difference was considerable, e.g. in Lake Kär-

vaslampli 86 tail spines were found whereas no postabdominal claws and only one ephippium. In case tail spines were not identified *Daphnia* would have been considered rare in the lake. In Lakes Mustalampi and Suonalanen tail spines were also much more common than the pairs of postabdominal claws, 61 vs 20 and 56 vs 4, respectively. Tail spines were also significantly (p<0.001) more abundant in lake sediment than pairs of claws when taking into account all lakes.

However, in some lakes the number of claws exceeded that of tail spines. In Lake Pieni Horilampi 75 claw pairs and 59 tail spines were encountered and in Lake Maaselänlampi 39 claw pairs and 11 tail spines. In Lake Anttilanjärvi 21 pairs of claws but no tail spines were found. In some lakes the numbers were equal or the difference very small. Only four single ephippia were found in the 17 lakes.

These results indicate that in many cases the tail spines (if preserved) may give a closer estimate of the real past abundance of *Daphnia*, whereas claws are very often underrepresented. During the laboratory treatment the sediment samples are usually heated in 10% KOH and sieved through a ca. 40 µm mesh, recommended by Frey (1986). This necessary treatment removes humic acids and smaller particles, thus enhancing concentration and facilitating identification of remains. It has been noted by Mirva Nykänen (pers. comm.) that small *Daphnia* claws (among other small remains) can be lost during sieving. This may be one of the reasons of the under-representation of the claws.

*Daphnia* ephippia were very rare in the sediments of the studied lakes. This might be expected because *Daphnia* reproduce asexually most of the open-water season and usually only in autumn sexual reproduction takes place, resulting in production of resting eggs, protected by ephippia. This re-

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**Fig. 1.** Preserved shell margins of *Daphnia* in sediments of Lake Arapisto, southern Finland. The sample represents an age of ca. 8200 cal yr BP. The scale bar is 100 µm.

**Fig. 2.** Shell margins of *Daphnia* still attached to a well-preserved tail spine in a surface sediment sample from Lake Suonalanen. The scale bar is 100 µm.

**Fig. 3.** Crumpled tail spine of *Daphnia*, attached to shell margins in sediments of Lake Arapisto, southern Finland. The sample represents an age of ca. 8200 cal yr BP. The scale bar is 100 µm.
sults in a small abundance of ephippia compared to the other remains (if preserved) of all Daphnia individuals present during the entire open-water season. The ephippia may be even more underrepresented in sediment cores collected from the deepest part of lake (as is the common practice) because they are buoyant and may be transported to the shore area before deposition.

The contrary results from all the lakes discussed in this paper indicate how selective the preservation of Daphnia remains actually is, varying between lakes and remain types. No indication of shells or headshields was encountered (or identified), except the shell margins. These, however, were well preserved in some lakes but decomposed in some other, the latter case indicated by the higher numbers of claws. It is also possible that the under-representation of claws may not be entirely due to penetration of the sieve, as they very often are larger than the mesh size. It is equally possible that in some lakes they just do not preserve.

The question why Daphnia remains preserve in some lakes, is still unsolved. Szeroczyńska & Zawisza (2005) suggested that good preservation of Daphnia shells and headshields might be connected to cold climate. However, for some reason, Daphnia shells and headshields did not preserve in Lake Arapisto, not even during the cold beginning of the Holocene. On the other hand, shell margins and some tail spines preserved for thousands of years.

It seems possible that the preservation of shell margins and tail spines is dependent on water chemistry, instead of climate, as many of the lakes discussed here are located in approximately similar climate conditions in southern and central Finland. If some special variable/variables of water chemistry contributed to the preservation, it cannot be investigated before specific water chemistry data are obtained and compared between the lakes.

It can be concluded that the preservation of Daphnia remains appears very selective between lakes. Shells and headshields preserve extremely rarely. Postabdominal claws probably preserve relatively well (as far as we know) but unfortunately can be lost during sieving. Shell margins and tail spines can be preserved in some lakes, at least in recent sediments. However, their presence in the sediments of Lake Arapisto representing the entire Holocene indicates that in some special conditions they can preserve for thousands of years. The high frequency of shell margins in Lake Arapisto suggested that the real abundance of Daphnia may have been considerably higher than that indicated by the frequency of postabdominal claws. If only margins are preserved, whereas spines decomposed as in many samples of Lake Arapisto, it is impossible to reliably enumerate the thread-like shell margins as individuals. Thus they remain only as indicators of the presence of Daphnia. Apparently, no matter what remains of Daphnia are counted, the abundance of this taxon appears underrepresented.

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