

# Oribatid mites in a changing world

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Front drawing: *Suctobelbella longicuspis* by Arguitxu de la Riva-Caballero

To Adriana and Matteo

**Supervisors:**

**Main supervisor:** Torstein Solhøy

**Co-supervisor:** Hilary H. Birks

**Co-supervisor:** Lita G. Jensen



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# *Oribatid Mites in a Changing World*

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De la Riva-Caballero, A. 2011. Oribatid Mites in a Changing World. PhD thesis, Bergen Museum and Faculty of Mathematics and Natural Sciences, University of Bergen, Norway

## **Abstract**

The main scope of this thesis is to illustrate the validity of oribatid mites as tools for palaeoecological reconstructions. Palaeoecology studies the responses of past organisms to past environmental changes. This can be accomplished through the use of biological proxies, which are indicators of past conditions. The search for additional means of distinguishing climate change has only recently led to the use of other commonly found biological proxies such as tiny oribatid mites known as moss-mites. Oribatid mites are among the most numerous biological remains in anoxic sediments, yet until now oribatids have not been widely used due to the uncertainties about their present distribution and the lack of expertise to identify them to species level. This thesis contains four papers which provide evidence about how oribatid mites, when they are properly identified to species level and their background distribution is adequately known, can give useful additional and supporting information for reconstructing past habitat and environmental conditions.

Paper I studied oribatid preferences and ecology in different habitats, mainly forested, in western Norway. One hundred and ninety two species were found of which 64 were

new records for Norway. The species *Chamobates borealis*, *Oppiella nova*, *Moritzoppia neerlandica*, and *Rhinoppia subpectinata* characterised the oribatid communities of *Betula*, mixed, and *Picea* forest subsets. Deciduous forest oribatid communities were characterised by *Achipteria coleoptrata*, *Acrotritia ardua*, *Ceratozetes gracilis*, and *Oribatella calcarata*. *Hemileius initialis*, *Nanhermannia dorsalis*, *C. borealis*, *Tectocepheus velatus*, and *Atropacarus striculus* characterised wet habitats. In water-logged habitats, *Limnozetes ciliatus*, *Mucronothrus nasalis*, and *Trimalaconothrus glaber* dominated. *Carabodes labyrinthicus*, *C. marginatus*, *Melanozetes mollicomus*, and *T. velatus* characterised the oribatid community of the lichen and moss subset. The tree-line ecotone was dominated by the euryceous species *H. initialis*, *T. velatus*, and *Oribatula tibialis*. This study represents a thorough survey of oribatid communities in western Norway, and the insights it gives are an important tool for habitat reconstructions, as they provide the background knowledge about modern oribatid fauna needed to identify the type of past plant community and past environments represented in Quaternary sediments.

Paper II studied the oribatid communities at the tree-line in western Norway and compared them with the

oribatid fossil assemblages found in Lake Trettetjørn. The modern oribatid assemblage provided a guide to the reliability of the fossil assemblages to reconstruct ecological and environmental changes and, in addition, to find the most favourable coring point within the small lake. Results showed that the core retrieved from the middle of Lake Trettetjørn basin represented the oribatid fauna from the catchment area. Aquatic oribatids were the best group represented in the lake sediments, followed by oribatids from the habitats adjacent to the lake. This constitutes good evidence that oribatids are excellent indicators of local habitats. Comparison of the oribatid fauna found in the lake traps with the oribatid assemblages from paper III illustrated the importance of identifying the mites to species level, as this increased the ecological indicator value and, therefore, the reliability of the palaeoreconstructions.

In Paper III, sub-fossil oribatid mites, pollen, plant macrofossils, and diatoms from a lake sediment core from western Norway were studied. This multi-proxy study attempted to reconstruct tree-line fluctuations and their impact on Lake Trettetjørn's environment. Evidence from pollen, plant macrofossils, and oribatids complemented and corroborated each other in the reconstruction of the vegetational development. A semi-open grassland developed into forest.

Mires began to replace forested areas on the landscape as a more oceanic climate began to prevail. All proxies indicated increasingly intensive human land-use as the Upsete settlement grew to accommodate the construction of the Bergen-Oslo railway.

In Paper IV, oribatid mites and pollen were used to reconstruct the local habitat at an archaeological excavation. The study aimed to identify the start of cereal cultivation at Kvitevoll farm, on Halsnøy island, western Norway. The high number of oribatid remains identified to species level and the close match to pollen stratigraphy led to a detailed palaeoenvironmental reconstruction. Oribatids and pollen indicated the development of a moist forest followed by vegetation openings and mire expansion over the site. At the top of the sequence, the presence of oribatids such as *Tectocephus velatus* and the increase in members of the family Oppiidae indicated a higher degree of disturbance, probably from grazing. Pollen of *Cerealia* indicated the start of cultivation around the same time.



## Acknowledgments

It is difficult to thank all the people who have helped me with this thesis. I am certain I will forget mentioning some, but please do not be offended. I am grateful to all of you.

Torstein Solhøy deserves a special thanks, not only because he has been my supervisor, but also because he was the one who introduced me to oribatid mites and gave me the chance to fall in love with them during that first summer of 2001. He is an extraordinary person in many ways. He knows when he is really needed, and then he is there.

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Luis S. Subías has been an invaluable help. He was able to pass on his love for oribatid mites, especially for oppiids, and I suddenly discovered that I was completely fascinated by those golden little creatures. He has shared knowledge about not only mites but also life in our coffee breaks and meetings whenever I visited Madrid, and he patiently listened to my thesis or everyday life problems and tried to help me out. In other words, he became not only a guide in the oribatid world but also a friend. Thank you Luis!!

At Bergen Museum I would especially like to thank Ingrid Herø, who is now retired. She has been the most effective and helpful woman in administration that I have ever met. Moreover, she was always in a good mood and smiling regardless of the “strange” situations I came to explain in my funny Norwegian.

The last year and a half I have been living in Milan. I do not have working colleagues there, but I have a wonderful mother-in-law, mamma Vale, who has made my everyday work a pleasure. She has not only invited me into her house, but also cooked for me! She has been my coffee break “colleague” and has listened patiently to all of my achievements and complaints. In addition, she has always helped at home not only with cooking and cleaning but also, and most importantly, by playing with Adriana. Thank you very much Vale!

Thank you to Hanneke, Usman, Danyal, and Ishaq, unconditional friends despite the distance. They are our Norwegian family, and they always made our weekends something to look forward to, always supported me, and have offered not only their house whenever I was in Bergen during this last year and a half, but also made me feel like one of their family.

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My family, mamá, papá, Pilar, Fernando, María, Isabel, and Txema, though not always close physically, are always close to me. Their support has been crucial through this process. They have always understood me and guided me. Thank you very much! You are probably the strangest but the best family in the world. I love you all.

And last but not least I am extremely grateful to my husband, Matteo, and my daughter, Adriana. Matteo is, without a doubt, my better half. He understands me and supports me unconditionally. Adriana is still too young to understand what mummy was doing but her laughs, her first words, her first steps, her hugs, and her kisses made this last year much easier. I do not think that I will ever have words to tell you how grateful I am and how much I love you both.

## List of papers

This thesis is based on four individual papers, which will be referred to by their Roman numbers in the synthesis.

**Paper I:** de la Riva-Caballero, A. Oribatid mite communities in western Norway. To be submitted to *Norwegian Journal of Entomology*

**Paper II:** de la Riva-Caballero, A., H. J. B. Birks, A. E. Bjune, H. H. Birks, and T. Solhøy. Oribatid mites assemblages across the tree-line in western Norway and their representation in lake sediments. *Journal of Paleolimnology* **44**: 361-374

**Paper III:** Larsen, J., A. E. Bjune, and A. de la Riva-Caballero. 2006 Holocene Environmental and Climate History of Trettetjørn, a Low-alpine Lake in Western Norway, Based on Subfossil Pollen, Diatoms, Oribatid Mites, and Plant Macrofossils. *Arctic, Antarctic and Alpine Research* **38**:571-583.

**Paper IV:** de la Riva-Caballero, A. and L. S. Halvorsen. Neolithic impact on local vegetation at Kvitevoll, Halsnøy Island, western Norway reconstructed from oribatid mites and pollen analysis. To be submitted to *Journal of Archaeological Science*.

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## **Declaration**

Papers II to IV are co-authored, and the nature of the contributions by the different authors are listed below.

### **Paper II**

de la Riva-Caballero, A., H. J. B. Birks, A. E. Bjune, H. H. Birks, and T. Solhøy.

Oribatid mites assemblages across the tree-line in western Norway and their representation in lake sediments. *Journal of Paleolimnology* **44**: 361-374

A. de la Riva-Caballero: Acari identification and analyses, numerical analyses, writing.

HJB. Birks: Numerical analyses, editing.

AE. Bjune: Experimental design, field sampling, editing.

HH. Birks: Project management, experimental design, field sampling, editing.

T. Solhøy: Acari identification, editing.

### **Paper III**

Larsen, J., A. E. Bjune, and A. de la Riva-Caballero. 2006 Holocene Environmental and Climate History of Trettetjørn, a Low-alpine Lake in Western Norway, Based on Subfossil Pollen, Diatoms, Oribatid Mites, and Plant Macrofossils. *Arctic, Antarctic and Alpine Research* **38**:571-583.

J. Larsen: Project management, field sampling, diatom analysis, writing

AE. Bjune: Field sampling, pollen and plant macrofossils analyses, writing.

A. de la Riva-Caballero: Oribatid mites analysis, writing.

### **Paper IV**

de la Riva-Caballero, A. and L. S. Halvorsen. Neolithic impact on local vegetation at Kvitevoll, Halsnøy Island, western Norway reconstructed from oribatid mites and pollen analysis. Submitted to *Journal of Archaeological Science*.

A. de la Riva-Caballero: Field sampling, oribatid mite analysis, numerical analysis, writing.

LS. Halvorsen: Field sampling, pollen analysis, writing



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De la Riva-Caballero, A. 2011. Oribatid Mites in a Changing World. PhD thesis, Bergen Museum and Faculty of Mathematics and Natural Sciences, University of Bergen, Norway

## **Introduction**

### *Archives and Proxies*

Palaeoecology is the study of responses of past organisms to past environments. This includes the study of past climatic changes which are reflected in the change of abundance and occurrence of different biological proxy indicators through time. Palaeoecological reconstructions enable the comparison of past and present ecosystems, which can reveal possible causes and mechanisms of biological change over time (Birks and Birks 1980, Berglund 1986, Willis and Birks 2006, Douglas 2007, Gamble 2007).

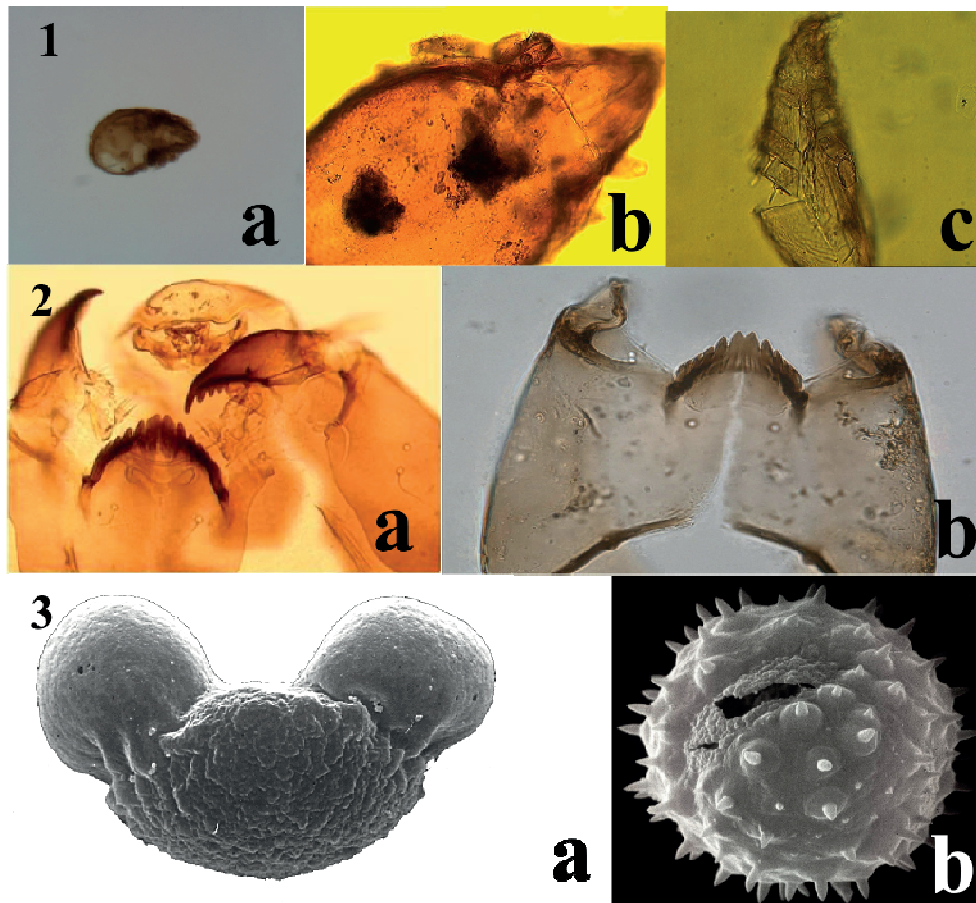
A biological proxy is a biological indicator of past environmental conditions (Smol *et al.* 2001, Douglas 2007). Among a wide variety of biological proxies, the most widely used are pollen, plant macrofossils, chironomids (non-biting midges) (Fig 1), and diatoms (Douglas 2007). The search for additional means of distinguishing climate change has only recently lead to the use of other also commonly found biological proxies such as the tiny oribatid mites known as moss-mites (Solhøy and Solhøy 2000, Erickson and Platt 2007). Remains of animals and plants are deposited and preserved in sediments of lakes, mires

and other anoxic locations, which become archives of past environments. One can reconstruct the development of the environment in and around the lake or mire using continuous sequences of the sediments and the biological proxies contained in them. The use of only one proxy in a palaeoenvironmental reconstruction will always be less satisfactory than reconstructions in which several proxies are combined, as the strengths and weaknesses of the individual proxies are then counterbalanced (Birks and Wright 2000, Birks and Birks 2006).

In palaeoecology one can reconstruct the organism assemblages as presence or absence data, populations as numbers of individuals of the taxa, and communities as a combination of the assemblages and the individual abundances. This thesis concentrates on the reconstruction of communities, which allows one to draw inferences about the environment and habitat of past ecosystems (Birks and Birks 1980). Each species in a community has an optimum and a niche within its range of environmental tolerance. There is also a community niche, which is the range of environmental factors common to all the species that comprise the community. Identifying a complete past community of oribatid mites is almost impossible because life assemblages are modified by taphonomic processes.

These are the processes the deceased mites go through from the moment they die until they are finally deposited into the sediments. They include transportation from the source to the lake or mire, predation, preservation, and possible redeposition (Birks and Birks 1980, Erickson 1988, Erickson and Platt 2007). There are three main approaches used to reconstruct past habitats: (1) modern analogue, which compares modern communities with the fossil assemblage; (2) numerical

analysis of fossil data to identify possible gradients that reflect environmental change; and (3) analysis of the abiotic component of the sediment (Birks and Birks 1980, Birks 2003). In this study, the first and second approaches are used. These approaches assume that little or no change in the ecological requirements of the species found in Holocene sediments has occurred since the deposition of the fossil assemblage.



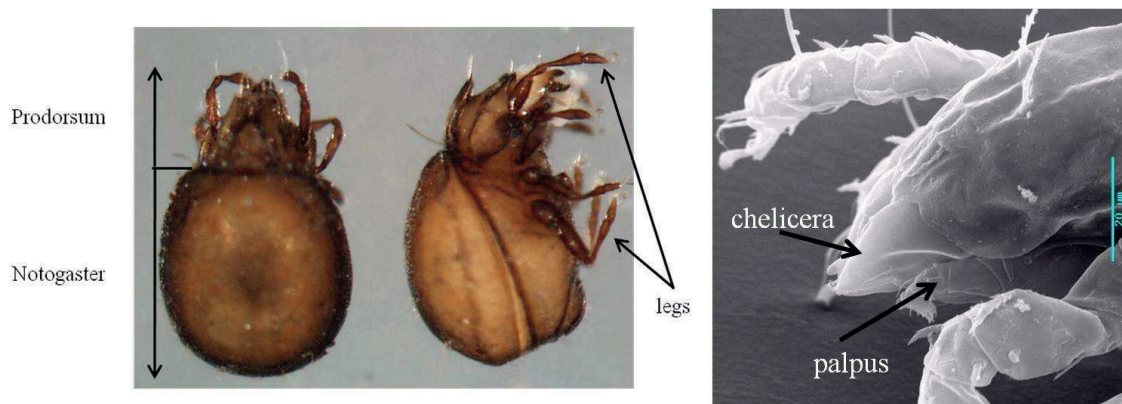
**Figure 1.** Some examples of biological proxies. **1.** Oribatid mites. a. *Tectocephus velatus*. b. *Dometorina plantivaga*. c. *Cosmochthonius lanatus* (Picture 1 A. De la Riva-Caballero, pictures 2 and 3. J. Arroyo). **2.** Chironomids a. *Chaetocladius cf. piger* b. *Limnophyes* sp. (pictures G. Velle) **3.** Pollen a. *Pinus*. b. *Valeriana sambucifolia*. (pictures J. Berge).



### ***What are oribatid mites?***

The word oribatid comes from the Greek words *oreos* – mountain and *batein* – travel (*i.e.* those that travel around in the mountains). They are also known as moss or box mites. Oribatids are among the most abundant inhabitants of the soil system (Travé *et al.* 1996, Walter and Proctor 1999). There are *ca.* 11000 known species, and their local diversity can be high, for example with up to 150 species may coexist in a small area of temperate forest floor (Hansen and Coleman 1998, Solhøy and Solhøy 2000, Norton 2007, Schatz and Behan-Pelletier 2008, Norton and Behan-Pelletier 2009).

Oribatid mites are tiny, flightless arthropods belonging to the subphylum Chelicerata with sizes ranging from 0.13 to 1.2 mm (Walter and Proctor 1999, Norton and Behan-Pelletier 2009). As chelicerates they have two pairs of chelicerae and palpi in the oral region, a body divided in two parts, prodorsum and notogaster (Fig. 2), and three pairs of legs in the larval stages and four in the nymphal and adult stages (Fig. 3). Except for some primitive families, oribatids have a hard, darkly pigmented (chitin) exoskeleton as adults but are usually soft-bodied as immatures (Norton and Behan-Pelletier 2009).



**Figure 2.** Mite morphology: prodorsum, notogaster, and legs are indicated on a picture of *Xenillus tegeocranus* (left picture, by Stefan Hewig – *X. tegeocranus* average length 720-1100µm, Weigmann 2006), chelicerae and palpi are indicated on a SEM picture of an *Hydrozetes* sp. juvenile (right picture, by Anna Seniczak); blue line on the right indicates the measure scale for *Hydrozetes* sp. (20µm).

Among oribatids, there are both sexual and asexual species. Generally, ancestral groups have asexual reproduction through thelytoky (production of females, from females, keeping the diploid condition), while most derivative groups tend to show sexual reproduction instead (Travé *et al.* 1996, Walter and Proctor 1999, Norton and Behan-Pelletier 2009). These minute creatures have a life cycle that

usually takes one or two years in temperate to boreal regions (Norton and Behan-Pelletier 2009), but it can take up to seven years in extreme habitats (Søvik *et al.* 2003). Their full developmental sequence is typical of Chelicerata, with egg, pre-larva (immovable), larva, three nymphal stages (proto-nymph, deuto-nymph and trito-nymph) and the adult, which is the reproductive stage. They do not have

parental care, but they carefully choose where to lay their eggs (Norton 1990).

Oribatids are mostly particle-feeding detritivores (*i.e.* obtain nutrients from decomposing organic matter) and mycophages (*i.e.* feed on members of the fungus kingdom) that live in soil and litter (Luxton 1972, Walter and Proctor 1999, Norton 2007). They play an active role in ecosystems, for example in the decomposition of organic matter, nutrient cycling, and soil formation. In addition, they are good indicators of moisture and pH in both terrestrial and aquatic ecosystems (Behan-Pelletier 1999).

Oribatid mite community composition changes with vegetation composition. The composition of the mite community is controlled partly by food availability, soil type, and moisture (Walter and Proctor 1999, Solhøy and Solhøy 2000). Certain oribatids have rather narrow niches and are obligatory or facultative inhabitants of substrates like trees, rocks, lichens, and mosses

(Norton 1990), which makes them ideal palaeo-indicators of such habitats.

Moss mites are generally not considered to be phoretic organisms; they do not use other organisms for transportation mean. Both Berthet (1964) and Hammer (1965) state that oribatids do not show long dispersal, in part because of their flightless condition and gregarious nature. However, several investigators have shown that dispersal over more than the few meters that oribatids can cover in their lifespans is possible through some kind of phoresy on insects (Norton 1980, Coulson 2009), mammals (Miko and Stanko 1991), and even on birds (Lebedeva and Krivolutsky 2003, Lebedeva and Lebedev 2008). However, none of these studies discusses whether this is common within oribatid mites. To date, only one family (Mesoplophora) has been shown to have body modifications that enable attachment to other organisms (Norton 1980).



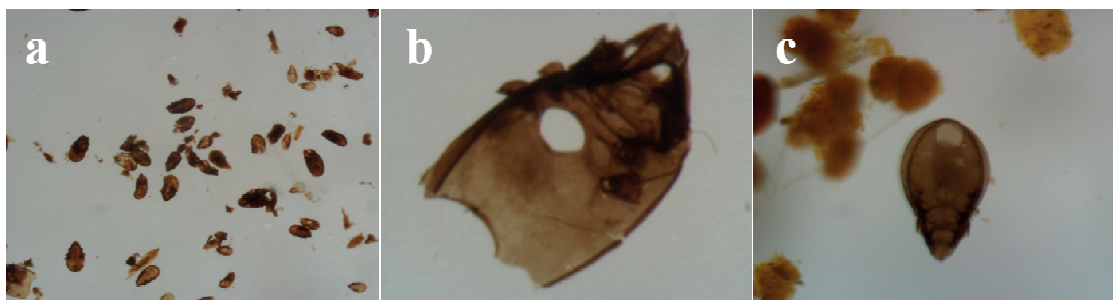
**Figure 3.** Adult (left) and larva (right) of *Hydrozetes* sp. (pictures by Anna Seniczak). Blue lines on the right of both pictures indicate a scale of 200 $\mu$ m for the adult (left) and 80 $\mu$ m for the larva (right).

### *Oribatids in palaeoecology*

**Brief history** - Oribatid mites are known from the early Ordovician (Bernini *et al.* 2001) and the Devonian (Norton *et al.* 1988), with some other evolved genera dating back to the Jurassic (Krivolutsky and Drouk 1986) (Fig. 4).

According to Hammer (1965) and Hammer and Wallwork (1979), most extant species had already arisen sometime between the Eocene –

Oligocene and the Pleistocene. Labandeira *et al.* (1997) gives an overview of pre-Pleistocene records. Krivolutsky and Drouk (1986) state that the major trends in the evolution of oribatids were established before the Jurassic, and they suggest that oribatid mites have very low morphogenetic rates. I, therefore, assume that oribatid fossils from the Holocene do not differ in their morphology and behaviour from those of today.



**Figure 5.** Oribatid subfossils. **a.** general view of the washed out oribatid fragments from a sample **b.** *Liacarus keretinus* (average measure for *L. coracinus* 650-1100 $\mu$ m (Weigmann 2006)). **c.** *Oribatula tibialis* (average measure 410-530 $\mu$ m (Weigmann 2006)) (pictures A. de la Riva-Caballero).

Their flightless condition, hard chitinous exoskeleton (well preserved in anoxic sediments) and narrow niches make oribatid mites very suitable indicators of local past habitats (Erickson 1988, Drouk 1997, Solhøy and Solhøy 2000, Solhøy 2001, Erickson and Platt 2007). However, the use of fossil oribatid mites as palaeo-indicators is a relatively new discipline (Erickson 1988, Solhøy and Solhøy 2000, Solhøy 2001, Erickson and Platt 2007, Elias 2010). Nordenskiöld (1901) was the first author who identified fossil oribatid mites in his work. After him, many others in the first half of the 20<sup>th</sup> century mentioned fossil oribatid mites and listed them in their works, but they

did not interpret them ecologically. One of the main problems they faced was that the sediments/layers were not radiocarbon dated, as the technique was not developed until the 1950s by Libby (Gosse 2007). During the second half of the 20<sup>th</sup> century, the use of fossil oribatids started to expand. In Europe, Knülle (1957a), Karppinen *et al.* (1979), and Golosova *et al.* (1985) presented records of fossil oribatids from northern Europe, Greenland, and northern Siberia. Schelvis (1989) was the first researcher to use fossil oribatid mites as indicators of past ecosystems, interpreting the fossil oribatid assemblages found in archaeological sediments from an ecological point of

view and even implementing a semi-quantitative method (Schelvis 1989, Schelvis and van Geel 1989, Schelvis 1990a, Schelvis 1990b, Schelvis 1992, Schelvis 1997a, Schelvis 1997b). The most recent works published using fossil oribatid mites from lake sediments are from Solhøy and Solhøy (2000), Hodgson and Convey (2005), Larsen *et al.* (2006), and Heggen *et al.* (2010). The work from Solhøy and Solhøy (2000) is outstanding because of the high resolution of the sediment core, abundant radiocarbon dates, identification to species level of all the adults found, and good documentation of the species' present-day distributions and habitat requirements (Solhøy 2001). Recently, oribatids have been used in palaeolimnology and in archaeology, for example by Schatz *et al.* (2002), Arroyo *et al.* (2007), Chepstow-Lusty *et al.* (2007), and Wild *et al.* (2007). In North America, Erickson (Erickson 1988, Erickson 1997, Erickson *et al.* 2003, Erickson and Solod 2008) was the first researcher to use fossil oribatids retrieved from lake sediments to infer climatic/habitat changes.

**Sampling sites and identification-** The use of oribatid mites as indicators of past habitats relies on their good preservation in anoxic sediments (Fig. 5). Thus, sediments from lakes and mires and other waterlogged environments are usually optimal. Figure 6 illustrates the process of oribatid deposition in a lake. The oribatids most commonly found in lake sediments are aquatic and wetland species living on aquatic plants and other vegetation on the lake shore. However, terrestrial oribatids that reached the lake mainly through surface

water run-off and streams or by falling from the nearby vegetation can also be found. Taphonomic processes filter the species and number of oribatids that are finally incorporated into the sediments.

Million Years Ago	Eras	Major Divisions	Important Events
0.01...	Quaternary	Holocene	
1.64		Pleistocene	ICE AGES
5.2	Tertiary	Pliocene	
23.3		Miocene	
35.4		Oligocene	Mesostigmatans in amber
56.5		Eocene	Fossil ticks
65		Palaeocene	End of dinosaurs
145.6	Mesozoic	Cretaceous	
208		Jurassic	Evolved fossil oribatid genera – Krivolutsky and Drouk 1986
245		Triassic	Mass extinction
290	Upper Palaeozoic	Permian	
362.5		Carboniferous	
408.5		Devonian	Fossil endeostigmatans and oribatids – Norton <i>et al.</i> 1988, Norton <i>et al.</i> 1989
438.1	Lower Palaeozoic	Silurian	
505		Ordovician	Fossil oribatid mites from Sweden – Bernini <i>et al.</i> 2001
545		Cambrian	First potential cheilicerate
2500	Precambrian	Proterozoic	
3500		Archaean	

**Figure 4.** Acarocentric point of view of the history of life. Modified after Walter and Proctor 1999. Only references related to oribatid mites are indicated.

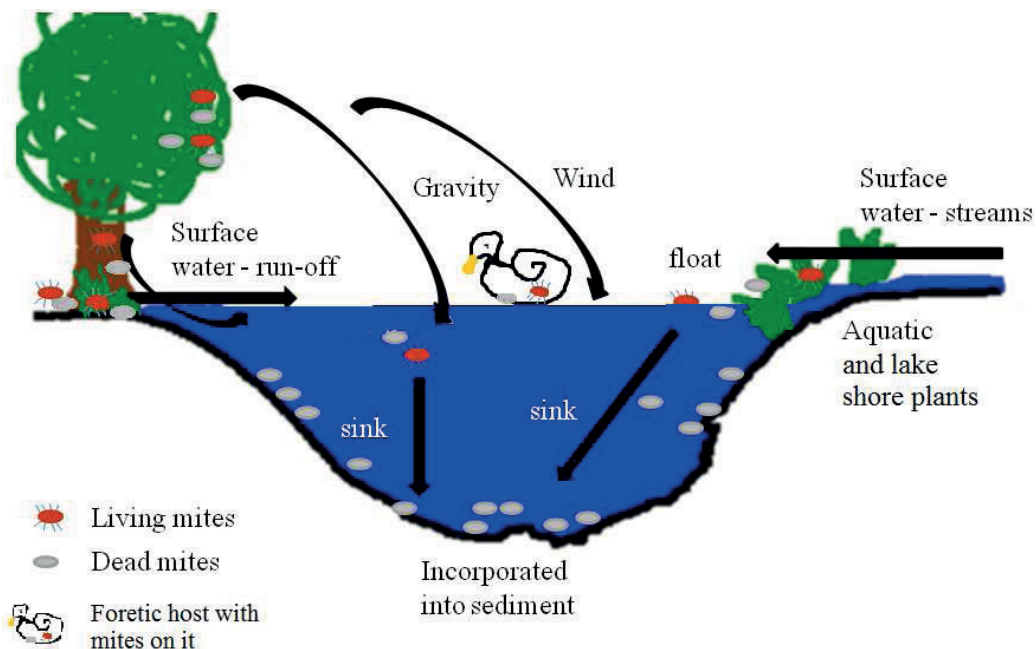
Identification to species level and a good knowledge of their present-day ecology is of extreme importance for obtaining a reliable reconstruction of the past environment. This knowledge allows oribatid species to be grouped according to their present-day ecology. As with plant macrofossils (Birks 2001), oribatids are usually used to reconstruct local habitat changes as their occurrence and distribution are highly dependent on local substrate



type. In addition, oribatid remains are normally not transported far from their area of origin (Fig. 6) as, in contrast to pollen, they are not wind transported.

In general, knowledge about the broad-scale geographical distribution of oribatid mites is imperfect (Drouk 1997, Behan-Pelletier 1999, Weigmann 2006). This limits detailed reconstruction of past climate using only fossil oribatid assemblages. Oribatid distribution patterns do not correspond with biogeographic boundaries and are not limited by known climatic factors, and oribatid's species composition's within-zone variability is as high as its among-zone variability (Drouk 1997). These factors limit the use of oribatid mites to qualitative studies. Nonetheless, Schelvis (1989, 1990b) and Erickson and Platt (2007) have demonstrated the application of oribatid mites in semi-quantitative methods (Schelvis 1990a,

Erickson and Solod 2008). Oribatid mite analysis requires patience and good knowledge of not only mite identification from fragments but also the ecology of the species found (Schelvis 1997a, Solhøy 2001, Erickson and Platt 2007). It is far more informative to find a set of species indicating the same type of vegetation than to find many individuals of the same species (Schelvis 1997a). In some instances there are very few remains of mites found in the sediments or too many representatives of generalist species, restricting the interpretation of the past environment and vegetation (Wild *et al.* 2007). It is, therefore, optimal to combine the study of fossil mites with other proxies that will aid in obtaining a comprehensive understanding of the palaeo-environment (Birks and Birks 2006).



**Figure 6.** Processes leading to the deposition of terrestrial and aquatic oribatid mites in lake sediments.

## **Aims of this thesis**

My work deals with extant and past oribatid communities. The study of extant oribatid communities improves the knowledge on the ecology and biology of oribatid mites, which is of extreme importance in order to infer habitat changes through oribatid mites. The main scope of the entire thesis is to demonstrate the usefulness of oribatid mites as tools for inferences about past habitats in paleoecology and archaeology and to address questions related to the use of oribatid mites as proxies in palaeoecology and archaeology. This has resulted in 4 papers that address different research questions:

**Paper I** - Are there distinct oribatid mite communities characteristic of different vegetation types in western Norway? Can we detect characteristic oribatid communities in the tree-line ecotone? The oribatid communities associated with mixed (coniferous and deciduous), birch, pine, and deciduous forests, lichens and mosses, wet habitats, and the tree-line ecotone are characterized. This type of study is invaluable for palaeoecological reconstructions, as it helps in identifying the type of plant community and environment the fossil oribatid assemblages might reflect.

**Paper II** - Which oribatid ecological groups are best represented in lake sediments? Which is the best coring point within Lake Trettetjørn basin? In this paper I study the representation of oribatid communities at the tree-line ecotone in western Norway and compare it with the

oribatid fossil assemblages found in the Holocene sediments of Lake Trettetjørn, a small lake situated at the present tree-line. The modern oribatid fauna from different vegetation zones along an elevational gradient across the tree-line was characterised as a basis for comparison with the fossil oribatid assemblages found in sediments from a lake at tree-line within the altitudinal gradient. The ecological information acquired, in addition to that from Paper I, will also be of use in future investigations. The modern assemblages provide a guide to the reliability of the fossil assemblages to reconstruct ecological and environmental changes and, in addition, to finding the most favourable point to take a sediment core within the small lake.

**Paper III** - Does the mite fauna in lake sediments of Trettetjørn reflect Holocene environmental changes? What does the addition of oribatid mites to a multiproxy study add to the overall environmental interpretations? In this paper I use oribatid mites as proxies to reconstruct the Holocene environmental history of Trettetjørn, the low-alpine (800 m a.s.l.) small lake in Paper II. This is a multi-proxy study combining mites with pollen, plant macrofossils, and diatoms analyses in an attempt to reconstruct the fluctuations in tree-line and their impact on the lake environment.

**Paper IV** - Can oribatid mites be used to detect Neolithic or later impact on the surroundings of the settlement? In this study I use oribatid mites in an archaeological context. Mite data are combined with pollen data to reconstruct the environment surrounding a human settlement from

the Norwegian Bronze Age. The study also aimed to identify the start of cereal cultivation at Kvitevoll farm, on Halsnøy Island, western Norway.

## Study Areas

The climate in Norway is determined by its northerly location in Europe on the east side of the Atlantic Ocean and the marked relief of the country (Moen 1999). The world climate is divided in 5 major regions based on precipitation and temperature, and Norway falls into 3 of them: the arctic and alpine climate, found in the mountains and the areas far north; the cool temperate climate, found in most of the land below the tree-line; and the warm temperate climate, found in the lowlands in southern and western Norway (Moen 1999).

The study areas of this thesis are mainly situated in western Norway, in the counties of Hordaland and Sogn og Fjordane (papers I, II, III, IV). Thus, I focus on the climate of western Norway. According to Moen (1999), coastal regions of western Norway have an oceanic climate influenced by the sea and characterised by relatively low summer (12°C in average) and high winter (>0°C) temperatures and high precipitation and atmospheric humidity (eKlima 2009). Both precipitation and temperature vary widely not only geographically but also annually. In general, coastal districts receive most of the precipitation during autumn and early winter, while inland precipitation is higher during summer (Moen 1999).

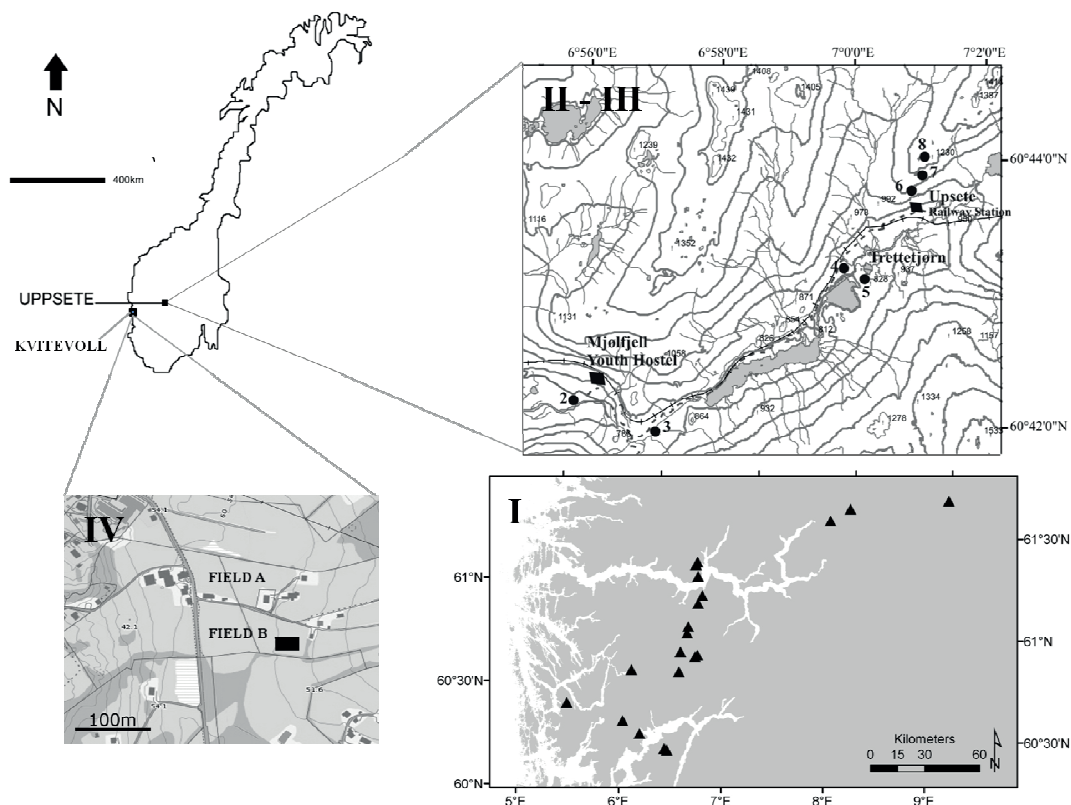
The geology in Norway is complex, but Moen (1999) divides it into two main categories: basement rock and Caledonian mountain chain. The

basement rocks date from the Precambrian and are basically unaffected by later events. They are mainly gneiss, granite, and quartzite and are found in northern and southern Norway. The Caledonian orogeny developed during the Silurian and Devonian periods. The resulting mountain chain stretches southwest to northeast in Scandinavia, and in Norway from Rogaland to Finnmark. In addition to the bedrock, the superficial deposits are also important for the vegetation cover that will eventually develop. These deposits vary greatly over Norway. In western Norway there are mainly three types: till, deposited by glaciers; mass-movement deposits, which are rocks, stones, and earth that have slid down a slope and accumulated at its foot; and exposed bedrock with a thin cover of superficial deposits (Moen 1999). The third type dominates the study area of this thesis. The type of soil that develops on top of the superficial deposits depends on climate and bedrock. In western Norway, which has an oceanic climate, podsollic soils are typical in forests producing acid litter. Peaty soils are also common in areas with high ground water and where the production of plant material exceeds its decomposition.

Elevation above sea level of the study area varies in each of the studies comprising this thesis. Thus, in paper I there are different transects which vary in elevation from 300 to over 1000 m a.s.l. Lake Trettetjønn is situated at 810 m a.s.l. (paper II and III), but the study area in paper II ranges from 663 m a.s.l. to 1120 m a.s.l. Kvitevoll farm (paper IV) is situated at 55 m a.s.l. Figure 7 shows the position of the study sites.

The study sites are situated in the boreonemoral, southern boreal, middle boreal, northern boreal, and low alpine zones (Moen 1999). Coastal areas and areas along the fjords are in the boreonemoral and southern boreal zones, which are characterised by coniferous and broad-leaved woodlands. Ombrotrophic bogs and dry grasslands are common along the coast and inland along the fjords (Fremstad 1997). Scots pine (*Pinus sylvestris*) is common on

swallow soils and dry areas, while Norway spruce (*Picea abies*) grows in richer soils. Downy birch (*Betula pubescens*) is a constant element of the woodlands in this part of the country. Usually, the woodland field layer is dominated by members of the Ericaceae, such as *Calluna*, *Empetrum*, and *Vaccinium*. At higher altitudes, the field layer is often dominated by bilberry (*Vaccinium myrtillus*) (Fremstad 1997).



**Figure 7.** Map of the study areas. Numbers I- II-III-IV on the upper left corner correspond to the different papers. Triangle marks on map I correspond to the sampling sites in paper I from Hardanger northwards to Sognefjord. Scale of map II-III is about 1:100000, see paper II.

Mires are a consistent component of the landscape in western Norway. They are frequently ombrotrophic bogs with dwarf shrubs such as *Calluna*. The tree layer is not common in bogs unless they have dried out. The ground layer is usually dominated by a carpet of *Sphagnum* species (Fremstad 1997). In areas where

the groundwater level is periodically high, swamp woodlands might be found. There are several swamp types in western Norway. Species-poor swamp woodland and grey alder – willow woodland are common in the lowlands (Fremstad 1997, Moen 1999). Soligenous mires, often dominated by Cyperaceae, and lake-margin fens



dominated by Cyperaceae and *Equisetum*, are also common.

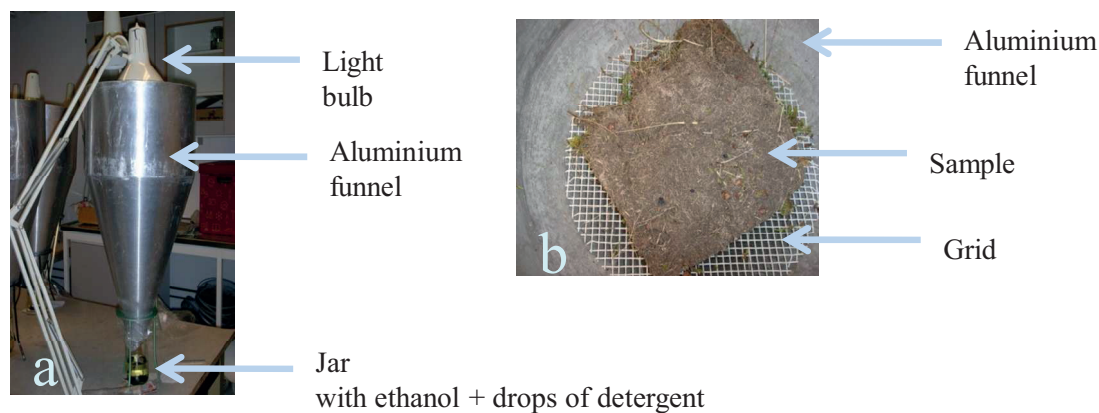
## Methods

### *Field sampling*

Different sampling methods were selected to match the purpose and scope of the different projects.

**Paper I** – This project studied the composition of oribatid mite

communities in different habitats in western Norway. Soil samples of 25 x 25 x 5 cm were collected from different vegetation types in the selected habitats. After collection, the samples were extracted using Berlese-Tullgren funnels (Fig. 8) until they were completely dry (ca. one week) and the extracted material was stored in 70% ethanol until sorted and identified.



**Figure 8.** a. Berlese-Tullgren funnel as used at the Department of Biology, UiB. b. Inverted sample placed inside the Berlese-Tullgren funnel, viewed from above.

**Paper II** – In order to study the plant and animal debris that is deposited on the ground and potentially transported into a lake, terrestrial traps were set out in the vegetation types along the elevation gradient. A terrestrial trap consisted of a plastic AstroTurf® doormat, 50x80 cm, which was laid out in the field for a season, winter (September – June) or summer (June - September), and then collected and replaced to collect another season. The sampling was done during four seasons (two years). In addition, to evaluate which oribatid ecological groups were best represented in the modern lake sediments, three traps were set in the lake (Trettetjørn), one at the

inlet, one in the middle, and one near the outlet. These traps were large plastic containers weighted down with a large rock and attached to a float to mark their exact location (Birks and Bjune 2010).

**Paper III** – The sampling followed the standard methodology of palaeoecological studies (Douglas 2007). During winter 2001 a sediment core from the deepest part of the lake (Trettetjørn) was retrieved, using a 110-mm modified piston corer (Nesje 1992).

**Paper IV** – The sampling followed the standard methodology in archaeology and in the study of Quaternary insects in general (Elias 1994, Elias 2010), in which the size of

the samples analysed tends to be much larger than in palaeolimnology. Samples at different depth intervals (every 3 cm) in the archeological trench were taken and sealed in labelled plastic bags. In addition, a peat block was retrieved from a trench dug in the mire beside the archaeological excavation. The block was wrapped in heavy-gauge aluminium foil in order to preserve it as well as possible until it was sub-sampled in the laboratory.

### ***Laboratory methods***

**Preparation of samples** – Depending on the nature of the project and where the samples were taken, different techniques were needed to prepare the samples so that they could be examined under the stereo microscope to extract the oribatid specimens. Therefore, I describe briefly what was done in each study. Mites were identified following mainly, Gilyarov (1975), Subías and Arillo (2001), and Weigmann (2006). In addition, special papers and reference collections were used in some cases. Specialist were consulted when needed. Nomenclature was, afterwards, standardized to Subías (2004, 2010).

**Paper I** – After collection, the samples were transported to the Department of Biology at UiB. Mites were extracted from the soil samples using modified Berlese-Tullgren funnels into 70% ethanol with a few drops of detergent (as illustrated in figure 8). After extraction, which usually took one week, the sample was inspected for mites under a stereo microscope. Soil samples might contain more than a thousand individuals of oribatid mites, resulting in tedious and time consuming lab work. Thus, I used

a subsampling method which allows for extrapolation. The methodology was developed by Southwood (1978) and modified by Johannessen (2002) and is described in detail in paper I.

Some oribatid species can be identified to species under a stereo microscope, but most need to be examined under a compound light microscope, following treatment in concentrated lactic acid that renders the chitinous cuticle of most oribatids clear. Dorsal and ventral characteristics of oribatid mites are important to identify them to species. Therefore, they are mounted on non-permanent cavity slides in some drops of concentrated lactic acid which allows them to be turned so that the desired character can be observed at the correct angle.

**Paper II** – The samples discussed in this paper were collected in doormats or submerged boxes. The doormats were washed using a shower head and the water was passed through a sieve of 125 µm mesh. The residues were stored in water with a little phenol to prevent fungal growth. The rest of the laboratory procedure was similar to many palaeo-studies. Mites were picked out under a stereo microscope and identified to species under the stereo microscope and compound microscope. Because these samples were not palaeo-samples, most oribatids still retained their hard chitinous cuticles. These specimens were treated with concentrated lactic acid to make their cuticles clear.

**Paper III and IV** – These two papers provide practical examples of how oribatids can be used in palaeo-reconstructions. In paper III, a sediment core (350 cm long) was retrieved from

Trettetjørn under a water depth of 6.8 m, using a 110-mm modified piston corer (Nesje 1992). Samples for plant macrofossil analysis were taken from 26 levels. The residues of those samples were used for mite analysis.

In paper IV, samples were cut every three cm from the peat-block (83.6 cm long and 16 cm wide) retrieved from a trench excavated in the mire next to the archaeological excavation.

Displacement of water in a measuring cylinder was used to estimate the volume of each sediment sample. In both papers, a sample was usually ca. 30 cm<sup>3</sup>. It is also possible to measure the weight instead of the volume in order to estimate the total number of oribatid mites found, but I find it less time consuming to measure the volume.

Palaeo-samples are usually disaggregated in dilute sodium pyrophosphate or, if necessary, in 10% KOH (Birks 2001, Solhøy 2001, Elias 2010) and rinsed through two sieves, 125 µm and 250 µm mesh size, in order to divide the sample into two fractions. This facilitates finding the mites when examining the samples under the stereo microscope. Some authors who work in palaeo-studies use flotation techniques to separate the mites from the palaeo-samples (see Erickson and Platt 2007 for examples). However, afterwards the residues should also be inspected for mites under the stereo microscope. Therefore, I found it less time consuming to pick out the mites from the complete sieved samples under the stereo microscope.

Detailed identification of mite species is done by placing the specimens in some drops of

concentrated lactic acid in cavity slides and examining them under a compound light microscope. The identified mites were counted and the numbers normalised to a constant volume (100 cm<sup>3</sup>) as concentrations.

### ***Data analysis***

Depending on the research questions addresses different analytical methods were used.

**Paper I** – TWINSPAN (Two-way Indicator Species Analysis, Hill 1979) and DISCRIM (simple discriminant analysis, ter Braak 1986) were used to explore the large and noisy data-set and uncover patterns in oribatid distribution. Canonical Correspondance Analysis (CCA) was used to organise the data in relation to the environmental variables. Forward selection and Monte Carlo permutation test were also performed to detect those variables that significantly explain, in a statistical sense, the variance in the data. Variation partitioning was used to assess the relative importance of the spatial variables and habitat conditions in influencing the oribatid communities. The program CANOCO 4.5 for Windows (ter Braak and Šmilauer 2002) was used to perform CCA and Variation partitioning.

**Paper II** – Diagrams were made using TILIA and TGView (Grimm 1993, 2004). CANOCO 4.5 for Windows (ter Braak and Šmilauer 2002) was used to perform Principal Components Analysis (PCA) to summarise the patterns within the modern assemblages, to explore the relationship to the different habitats along the transect, and to compare the modern oribatid fauna along the altitudinal gradient to the fossil oribatid

assemblages in the Trettetjørn sediments. A simple percentage approach was used to assess how well is the oribatid fauna of the area represented in the Trettetjørn sediments.

**Paper III** – TILIA and TGView (Grimm 1993, 2004) were used to make the stratigraphic diagrams. CANOCO 4.5 for Windows (ter Braak and Šmilauer 2002) was used to perform a Detrended Correspondence Analysis (DCA) to summarise the main trends in the mite data through the core.

**Paper IV** – TILIA and TGView (Grimm 1993, 2004) were used to make the stratigraphic diagrams. CANOCO 4.5 for Windows (ter Braak and Šmilauer 2002) was used to perform a PCA to summarise the main trends in the oribatid data in that part of the sequence where they were found.

## Outline of main results in the four papers

### *Background fauna characterisation*

#### **Paper I - Oribatid mite communities in western Norway**

Distinct oribatid mite communities are characteristic of different vegetation types in western Norway. The TWINSpan (Hill 1979) and DISCRIM (ter Braak 1986) analysis (Fig. 9 and Paper I), and also the CCA, conveniently divided the whole dataset into subsets according to the main habitat. This facilitated the characterisation of the oribatid communities found in each of the modern habitat types included in the study.

This work comprises the most exhaustive study of oribatid mites in Norway since Karppinen's work in 1971. A total of 64 new oribatid records for Norway were documented. Numbers of single species vary between several thousand to a few hundred individuals, and total sample numbers are always several thousand individuals.

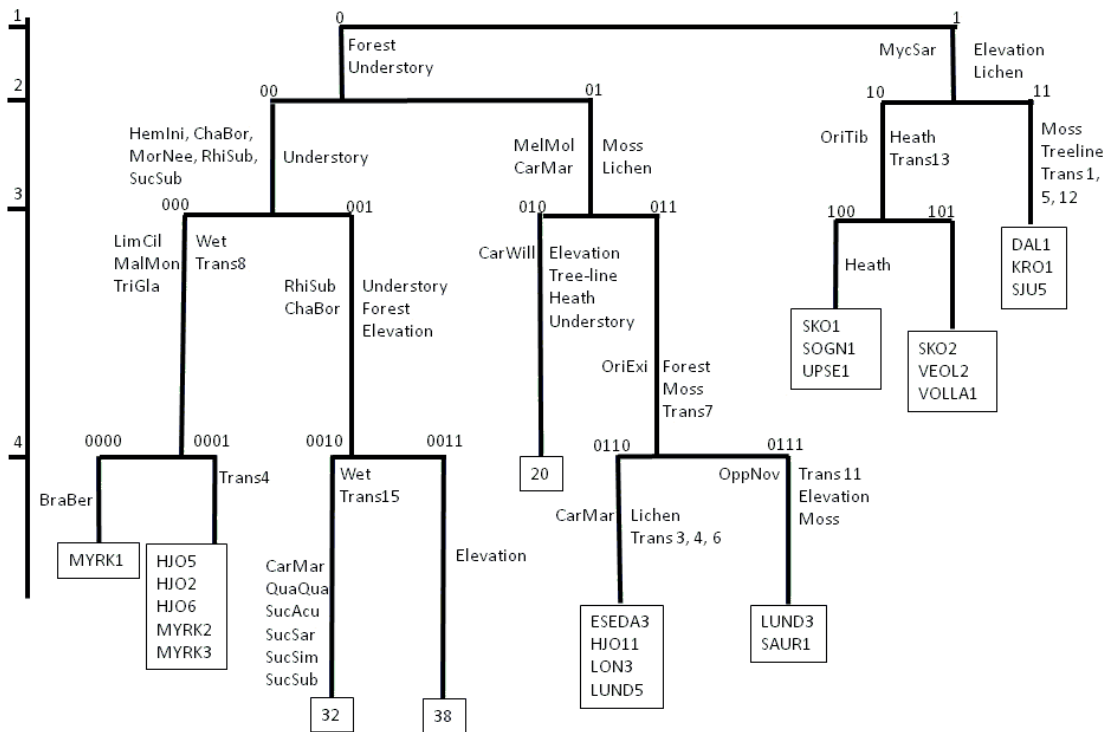
*Chamobates borealis*, *Oppiella nova*, *Moritzoppia neerlandica*, and *Rhinoppia subpectinata* characterised the oribatid communities from *Betula*, mixed, and *Picea* forest. *Achipteria coleptrata*, *Acrotritria ardua*, *Ceratozetes gracilis*, and *Oribatella calcarata* were the most common species in deciduous forest.

*Hemileius initialis*, *Nanhermannia coronata*, *C. borealis*, *Tectocepheus velatus*, and *Atropacarus striculus* were the most common species in wet habitats. *Limnozetes ciliatus*, *Mucronothrus nasalis*, and *Trimalaconothrus glaber* appeared only in waterlogged habitats, which confirms their status as true aquatic species. The lichen and moss habitat was characterised by *Carabodes labyrinthicus*, *C. marginatus*, *Melanozetes mollicomus*, and *T. velatus*. The forest species *Parachipteria punctata* (Schatz 1983, Weigmann 2006) was rather common in this habitat, which can be explained by the frequent presence of moss in the samples from this habitat type.

Can we detect characteristic oribatid communities in the tree-line ecotone? The reconstruction of the tree-line is a recurrent topic in palaeoecology (Bjune 2005, Larsen *et al.* 2006, Birks and Bjune 2010). The characterisation of the fauna inhabiting

this ecotone may help in identifying this ecotone in Holocene sediments, and this study of the oribatid communities in this ecotone in western Norway addresses this need. Generalist species such as *T. velatus*, *H. initialis*, and *Oribatula tibialis* dominated this habitat. However, forest species such as *Camisia biurus* (Schatz 1983, Gjelstrup and Solhøy 1994), and lichen associated species such as *Carabodes marginatus* (Seyd and Seaward 1984) were also found at the tree-line ecotone, which exemplifies the boundary character of this habitat.

Several authors have underlined the importance of a good knowledge of the modern ecology of the oribatid fauna when using them in palaeo-studies (Schelvis 1990a, Solhøy 2001, Erickson and Platt 2007,). Therefore, studies like this one, in which oribatid communities from different habitats are characterised, are extremely useful in palaeoecology. In particular, the study provides thorough knowledge of the oribatid species and the communities that occur in western Norway today.



**Figure 9.** TWINSpan-DISCRIM diagram. The line on the left indicate the level of division. Indicator environmental variables are on the right of the class. Indicator species are on the left. The abbreviations at the end of each nodule correspond to the samples as indicated in table ESM1 from paper I.



***Oribatid mite representation in lake sediments and best coring point***

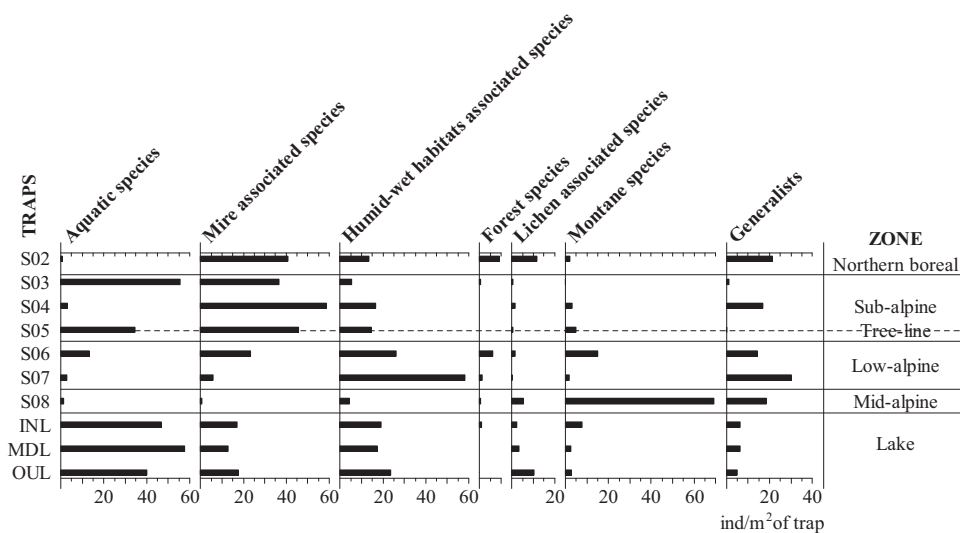
**Paper II - Oribatid mite assemblages across the tree-line in western Norway and their representation in lake sediments**

The best represented oribatid ecological group in the lake traps were aquatic, followed by oribatids from the habitats adjacent to the lake (Fig. 10). Similar results have been obtained in other studies using lake sediments (Solhøy and Solhøy 2000, Larsen *et al.* 2006, Heggen *et al.* 2010), providing good evidence that oribatids are excellent proxies of local habitats.

In a multidisciplinary approach the same sampling point might not be optimal for all the proxies analysed. In palaeolimnology, cores are usually retrieved from the deepest part of the basin in order to obtain the least

disturbed and the longest, most complete sequence (Birks and Birks 1980, Berglund 1986, Glew and Last 2001). However, it seems that for oribatid mite analysis this is not always the optimal location (Erickson 1988, Solhøy and Solhøy 2000). The results of this paper show that within Lake Trettetjørn basin a core retrieved from the middle of the basin adequately reflects the oribatid fauna of the catchment area.

The comparison of the Holocene oribatid assemblages from paper III and the oribatid fauna found in the lake traps from paper II showed the importance of identifying the oribatid individuals to species level. This increases the ecological indicator value and consequently the reliability of any palaeo-reconstruction done using oribatid mites.



**Figure 10.** Diagram showing the different ecological groups found along the altitudinal gradient and in the Trettetjørn traps. The horizontal axis represents the calculated number of oribatid individuals found per m<sup>2</sup> of doormat trap over the collection period of 2 years. From left to right: aquatic species, mire associated species, moist-habitats associated species, forest species, lichen associated species, montane species and generalists. The vertical axis represents the different traps along the altitudinal gradients (S02 to S08) and in Trettetjørn (INL – inlet, MDL – middle, OUL – outlet). The dashed line through S05 indicates that this trap site is situated at the tree-line.

### ***Palaeolimnological and archaeological reconstructions using oribatid mites***

The use of oribatid mites as indicators of past habitats, as stated above, is a rather recent approach. The fact that many aspects of oribatids' biology and ecology are unknown makes it difficult to implement quantitative techniques using oribatid fossil data. However, this is not a problem when reconstructing past habitats, as outstanding studies using oribatid mites have been published, including one from Kråkenes in western Norway (Solhøy and Solhøy 2000). This thesis is also comprised of two reconstructions of past habitats using oribatid mites as habitat indicators, paper III and paper IV.

### **Paper III: Holocene environmental and climate history of Trettetjørn, a low-alpine lake in western Norway, based on subfossil pollen, diatoms, oribatid mites, and plant macrofossils**

This study combined data on oribatids with pollen, plant macrofossil, and diatom data. The results obtained from the fossil oribatid analysis added reliability to this study, as they point to the same direction of environmental change as the other proxies involved in this project. In addition, the weaknesses and strengths of the different proxies are counterbalanced.

The Holocene oribatid mite sequence was divided into 6 phases, following the pollen zones (Figures 3 and 4 in paper III) with a time span between 8500 and 1000 cal. yr. BP. In the first or pioneer pollen zone (8575–8270 cal. yr. BP) no mites were

recovered. After deglaciation most probable few oribatids populated the landscape, and therefore few or no oribatid is likely to be incorporated into the sediments. The unstable landscape might also have an stronger physical effect on the fossil mites during deposition, *i.e.* in the processes of being washed from the catchment.

Aquatic oribatid species became abundant in the second zone with the development of aquatic and shore vegetation after 8578 cal yr BP. This might also indicate a wetter climate, with a higher number of oribatids being washed into the basin. The oribatid assemblage was a combination of open habitat and woodland species such as *Liebstadia similis* and *Dometorina plantivaga* (Grandjean 1950, Travè 1963, Solhøy 1976, Solhøy 1979, Maraun and Scheu 2000) during the second zone (8270–7760 cal. yr. BP).

The macrofossil record indicated that woodland of birch and pine became closed around Trettetjørn during the third phase (7760–5200 cal. yr. BP) associated with the occurrence of the oribatid species *Ophidiothricus tectus* and *D. plantivaga* that are typical woodland species (Weigmann 2006).

During the fourth phase (5200–4175 cal. yr. BP), there was a retreat of the forest probably due to a cooling of the climate. No oribatid species associated with woodland were found. This corresponded to the increase in oribatids indicating more open habitats such as *Hypochthonius rufulus*. This species is also associated with wet to soaked habitats (Solhøy 1979). According to the pollen record it seems that mires developed locally during this phase, but judging from the oribatid

record, mire formation had already started in the previous phase, in which the oribatid species *Trimalaconothrus* spp., *Malacothonrus* sp., *Moritzoppia neerlandica*, associated with wet habitats (Solhøy 1979, Weigmann 2006), increased.

Trees around Trettetjørn disappeared in the fifth phase (4175–1555 cal. yr. BP). Forest oribatids were still absent from the sediments, and there was a slight increase of oribatids characteristic of mires and grassland such as *Nanhermannia dorsalis* (as *N. coronata* in the paper) and *Banksinoma lanceolata* (Karppinen 1955, Tarras-Wahlberg 1961, Solhøy 1976, Solhøy 1979). During this phase, members of the family Camisiidae, an oribatid taxon often associated with heath (Solhøy 1979), were also found. This increase of terrestrial oribatids might be a result of increased water transport to the lake by increased precipitation. This might also have resulted in the increase in fern spores as soil was washed in from the catchment.

During the last phase (1555 cal. yr. BP–AD 2000) there were few oribatid remains. The pollen record indicated a more intense use of the landscape through grazing and summer farming, which would result in an artificial lowering of the local tree-line. There was an increase in microscopic charcoal, which is further evidence for human impact in the area. Aquatic plants disappeared and also aquatic mites, only oribatids associated with mires and few others indicating heath were found. There were several remains of oribatids from the Oppiidae family. According to Behan-Pelletier (1999) and Iturrondobeitia *et al.* (2005) the

number of oribatid species decreases with human disturbances. However, members of the Oppiidae family seem not to suffer as much as other oribatid taxa and are still present after habitat disturbance. Therefore, even if the remains found at Trettetjørn were not identified to species level, they could be an indication of a higher disturbance level in the area by sheep and goat grazing around the lake.

#### **Paper IV: Neolithic impact on local vegetation at Kvitvoll, Halsnøy Island, western Norway reconstructed from oribatid mites and pollen analysis**

This work is the first study in Norway in which oribatids are used as indicators of past environments in an archaeological context. A peat sequence was analysed and the preservation of oribatid remains was exceptional. Therefore, it was possible to identify the oribatids to species level. This, in addition to the high abundance of oribatid remains, increased the reliability and robustness of the palaeoenvironmental reconstruction.

The time span ranges from the late Mesolithic to the Late Neolithic; 7725 <sup>14</sup>C yr BP (6300 cal. yr. BP) at the bottom to 3130 <sup>14</sup>C yr BP (1300 cal. yr. BP) at the top of the sequence. Zonation of the sequence followed major changes in the mite abundances (Fig. 11) and pollen followed the same zonation.

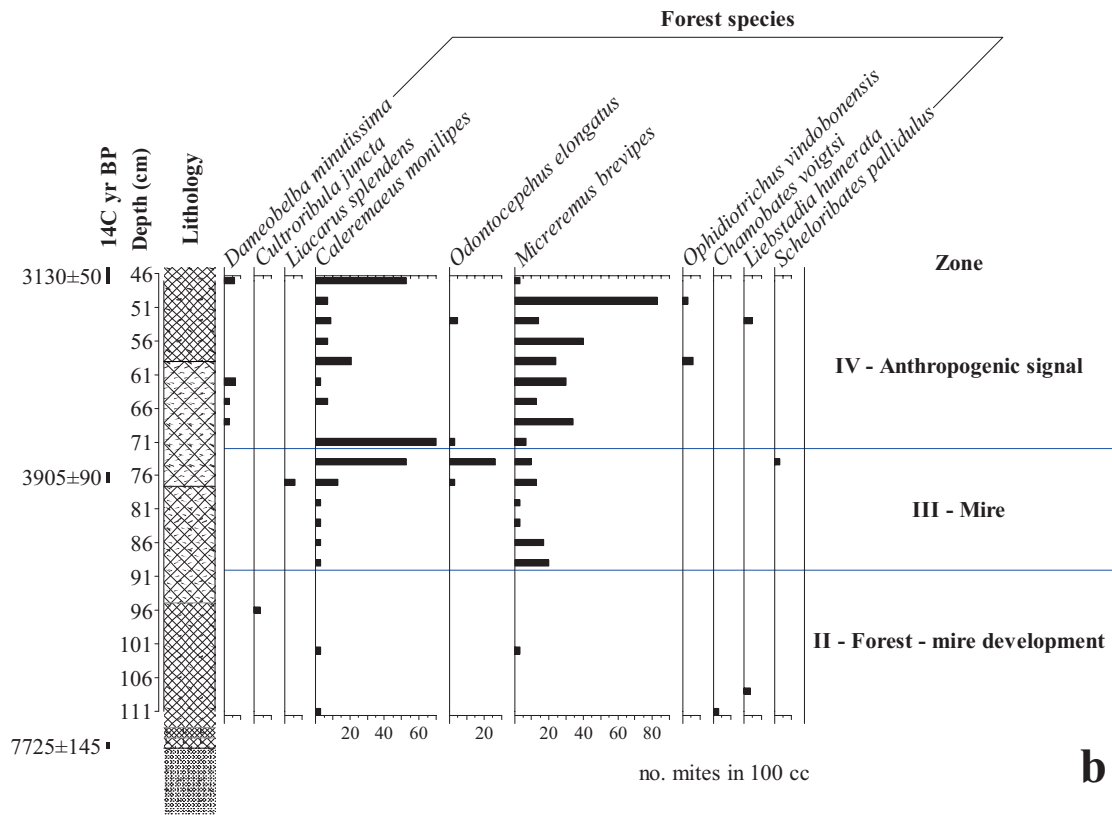
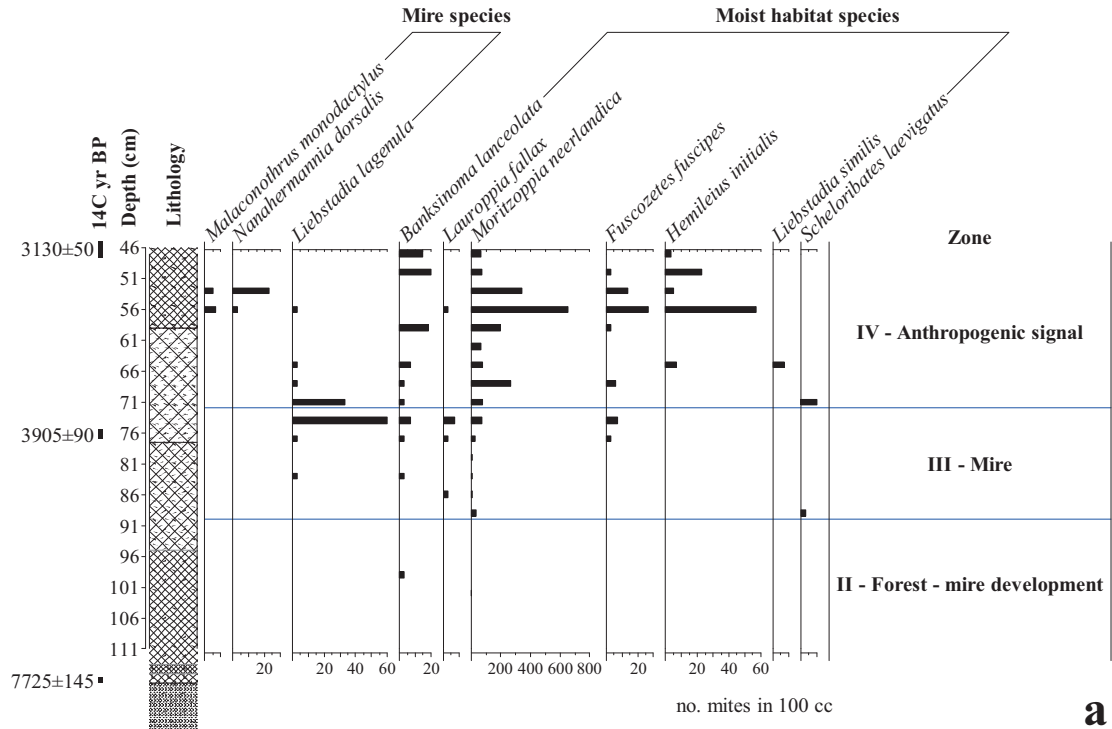
The bottom of the sequence was devoid of oribatid remains and pollen was scarce. It seemed that at this stage there was running water through the site, which was an open landscape dominated by shrubs and wet areas.

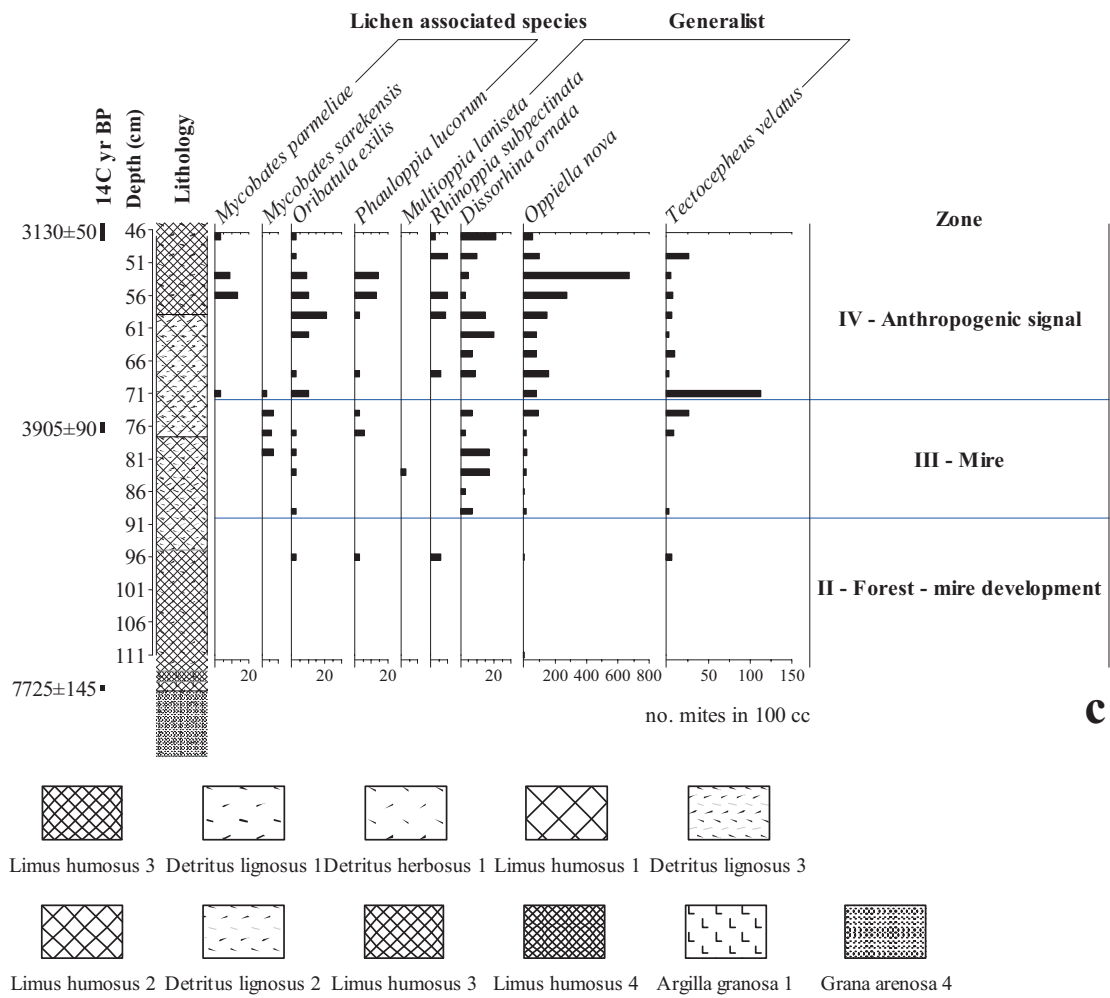


This was followed by a rapid increase in trees such as *Betula* and *Salix*, and an increase in *Sphagnum* moss, indicating the onset of mire succession (Fig.4 in Paper IV).

Fossil oribatids do reflect changes in the surroundings of the settlement. The oribatid sequence showed the steadily opening of the woodland around the site (Zone II Fig. 11). The oribatid assemblage was dominated by forest species such as *Caleremaeus monilipes* and *Micreremus brevipes*, *Cultroribula juncta* (Schatz 1989, Subías and Arillo 2001, T. Solhøy pers. comm.), throughout the peat sequence (Fig. 11), but steadily species associated with more open habitats appeared, indicating the opening of the woodland (Fig. 11a). Mire became a more dominant element of the landscape. The oribatid fossil assemblage reflected the typical forest-mire oribatid community (Zone III, Fig. 11a,b), as suggested by the presence of the oribatids *Fuscozetes fuscipes*, *Moritzoppia neerlandica*, and *Liebstadia lagenula* all considered peat soil dwellers (Knülle 1957b, Weigmann and Miko 2002, Schatz 2004, Weigmann 2006, Schatz and Fischer 2007, Schatz 2008) and forest species such as *Liacarus splendens* and *Scheloribates pallidulus* (Subías and Arillo 2001, Weigmann 2006). Towards the end of the sequence the mire got

drier. Oribatid species tolerating drier conditions such as *Malacoconothrus monodactylus* and *Nanhermannia dorsalis* (Knülle 1957b, Popp 1962, Markkula 1986) replaced *Liebstadia lagenula*, which prefers wetter conditions. Mites species typical of more open and moist biotopes such as *Scheloribates laevigatus*, *Liebstadia similis*, *Lauropia fallax*, *Moritzoppia neerlandica*, and *Banksinoma lanceolata* (Knülle 1957b, Wunderle *et al.* 1990, Subías and Arillo 2001, Weigmann 2006) indicated the further opening of the woodland (Zone IV, Fig.11a). However, the mite signal still showed an important presence of trees in the area (Fig. 11b). Species such as *Damaeobelba minutissima*, *Odontocepheus elongatus*, and *Ophidiothricus vindobonensis* indicated the presence of well-established (deciduous) forest (Pérez-Íñigo 1997, Weigmann 2006, Schatz and Fischer 2007). Oribatids cannot directly indicate human disturbances, but the increase in members of the family Oppiidae, considered common in disturbed areas (Behan-Pelletier 1999, Clapperton *et al.* 2002, Iturrondobeitia *et al.* 2005), as well as the generalist species *Tectocepheus velatus*, during zone IV, indicated higher disturbances in the area, although not necessarily anthropogenic.





**Figure 11. a.** Mite concentrations from the Kvitevoll peat sequence showing mire species, moist-habitat associated species, and lichen associated species. **b.** Mite concentrations from Kvitevoll showing forest species. **c.** Mite concentrations from Kvitevoll peat sequence showing lichen associated species and generalists. The data are shown on a depth basis with the three radiocarbon dates ( $7725 \pm 145$ ,  $3905 \pm 90$ ,  $3130 \pm 50$ ) on the left-hand side on all diagrams. Lithology symbols follow of all diagrams follow top legend.

## Conclusions, problems, and further work

The primary aim of this thesis is to investigate and evaluate the usefulness of oribatid mites as past habitat indicators and to characterise some present day oribatid communities relevant for palaeoecological reconstructions. The results indicate that fossil oribatid mites are valuable and useful indicators of past habitats. Despite the results shown in this and

other works, there is still a long way to go before the usefulness of oribatids in palaeoecological studies is fully developed. Among the main reasons are the lack of knowledge about oribatids' biology and ecology, about the taphonomical processes controlling which species are incorporated into the sediments, and about oribatid mite's taxonomy. The four papers comprised in this thesis contribute to overcome these problems. Paper I does not provide new aspects of their biology, but it characterises the oribatid communities found in common

vegetation types in western Norway. This knowledge is of vital importance when using oribatids as proxies in palaeoecological studies, especially in western Norway. Further meticulously planned studies of community structure, habitat choice of oribatid mites, and changes due to anthropogenic disturbances will be of invaluable use in palaeoecology; they are definitely needed.

The abundance of oribatid remains found, especially in lake sediments, also constitutes an interesting problem. There are many aspects of oribatid taphonomy that are still not known, yet they affect which species are incorporated and preserved in the sediments. It could be hypothesised that better preserved and higher numbers of mites might be retrieved from sediment cores taken closer to the lakeshore. However, paper II shows that this is not always necessarily true. The problem is less acute when analysing mire-peat sediments, but in this case, species associated with mires will dominate the sequence. Paper IV shows that peat sequences may result in robust habitat reconstructions, and oribatids can indicate the changes in the surrounding local environment.

There is no doubt that reliability and robustness of any palaeo-reconstruction using oribatid mites increases with increasing taxonomic resolution. This is because within the same genus there might be species living in completely different habitats. Paper III shows that even if the mite remains are identified at a low level of detail, this taxonomic resolution is also

able to reflect habitat changes in the lake catchment.

Scientific knowledge is not built quickly. It may take years, decades, even centuries before a new concept or paradigm is accepted. Much work is still needed in the palaeo-acarological world, but it is, after all, only a century since oribatids were first discovered as fossils. Thus far, their use in palaeoecological contexts has demonstrated that they can provide unique palaeoenvironmental interpretations. These generally cannot stand alone, but need to be seen in a multi-proxy context where they enhance habitat and environmental reconstructions made from the other proxies.

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