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Abstract

Although deposition of freshwater calcium carbonates, tufa, has occurred in large areas with carbonate soil or bedrock in Sweden, no tufa formation has been observed in Sweden. To better understand the factors controlling tufa formation in southern Sweden, bio- and lithostratigraphical studies were carried out on (paludal) calcareous tufa deposits in the province of Skåne. The biostratigraphical methods include mollusc, pollen, plant macrofossil and insect analysis. These were supplemented by lithological and chemical analyses. An additional aim of the study was to provide new information on the postglacial immigration of terrestrial molluscs into Sweden. The chronology was based on pollen stratigraphical correlation and radiocarbon dating.

Tufa formation was found to have occurred at several sites during the early Preboreal and Boreal [11,500-7,800 calibrated years BP (cal. BP)]. A tufa deposit was also recorded at one site dating to the Subboreal period (5,600-5,400 cal. BP). These periods were characterised by low lake levels in southern Sweden, suggesting that tufa deposition was favoured by drier conditions. The results thus indicate that Holocene tufa deposition in Skåne is likely to be controlled climate.

Terrestrial molluscs proved to be potentially valuable as environmental indicators and were important in the palaeoenvironmental reconstructions. During the early Preboreal to early Boreal (11,500-7,800 cal. BP) the carrs remained open to semi-open. In the late Boreal (around 7,800 cal. BP) they became well shaded.

A number of species were recorded that are rare in the region today. These include *Vertigo genesii*, *Vertigo geyeri*, *Cochlicopa nitens* and *Vertigo moulinsiana*, which are all on the national Red List of endangered species and included in the European Community's habitat and species directory. Whereas *Cochlicopa nitens* and *Vertigo moulinsiana* seem to have been rare in Skåne during the early Holocene, which is also the case today, *Vertigo genesii* and *Vertigo geyeri* appear to have been common in the early Holocene. It was shown that the historical record is necessary to understand the full extent of the species biological requirements.

An attempt to use carbon and oxygen stable isotope analysis of tufa and land molluscs to reconstruct palaeoclimatic conditions suggests that the method is worth testing in a full-scale investigation.

Methodological and other questions related to the analysis of tufa deposits and malacology are also addressed.

Key words:

Calcareous tufa, mollusc, Early Holocene, climate, environment, southern Sweden, Skåne.

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Environmental and climatic aspects of the early to mid Holocene calcareous tufa and land mollusc fauna in southern Sweden

by

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"*Humans smile with so little provocation*"

Spock

This thesis is based on four separate papers and a summary and extension. The papers are listed below as App I-IV. In the text they are referred to using their respective Roman numbers. Paper I is reprinted with the permission of GFF, whereas papers II and IV are submitted to Journal of Biogeography and III is submitted to The Holocene.

App. I: Gedda, B., Lemdahl, G. and Gaillard, M.-J. 1999: Lateglacial and Early Holocene environments inferred from a tufa deposit at Fyledalen, S. Sweden. *GFF, 121,* 33-42.

App. II: Gedda, B. and von Proschwitz, T. Recent and fossil distribution of Vertigo moulinsiana (Dupuy) (Gastropoda: Vertiginidae) in Scandinavia. Manuscript submitted to *Journal of Biogeography.*

App. III: Gedda, B. Terrestrial mollusc succession and stratigraphy of a Holocene calcareous tufa from the Fyledalen valley, southern Sweden. Manuscript submitted to *The Holocene.*

App. IV: Gedda, B. Palaeoenvironment and molluscan succession of early and middle Holocene calcareous tufas at Saxtorp, western Skåne, Sweden. Manuscript submitted to *Journal of Biogeography.*

Introduction

Historical background and previous research on calcareous tufa

Terrestrial calcareous deposits, tufa, also termed travertine, are generally found in semi arid and temperate regions in places where calcium carbonates are available for dissolution. These deposits have long been recognised as valuable natural resources. Marcus Vitruvius Pollio described its forms and uses in what is called the first handbook in architecture (Vitruvius Pollio c. 25 BC), *de Architectura* (On Architecture). Later, Plinius the Elder referred to tufa in *Naturalis Historiae* (Plinius 77)(c.f. Pentecost 1993). At this time tufa was mainly used as a lightweight building material in colonnades and valves [e.g. Colloseum in Rome, St Peters Cathedral in the Vatican and the vaults in Lunds Cathedral (Brunius 1950; 1954)], as well as chimneys and ovens (Halle 1915). Later, at least during the 19th and 20th century, it also became valuable as fertiliser. The economic value of calcareous tufa deposits today is limited in northern Europe, since carbonates may be found in larger deposits in other forms such as limestone. However, their varied geology and often rich fossil content provide important archives of terrestrial Quaternary floras and faunas.

In the literature there is some confusion as to the definition of the term tufa, or travertine, which is another common term emanating from the Italian word *travertino* (Emig 1917), a corruption of the Latin term *Lapis tiburtinus* - the stone of Tibur (now the city of Tivoli). Both terms cover, in a wide sense, all kinds of non-marine calcareous deposits. These range from huge landform building deposits like in Pamukkale, Turkey or Yellowstone, USA, to small friable porous spring deposits found in calcareous carrs (Fig 1 and 2).

A number of alternative definitions of tufa have been suggested during the 20th century, much depending on what types of studies that have been conducted. One example is a biological classification based on the incorporated organisms, primarily algae, moss or vascular plant species (Sernander 1915, 1916; Irion and Müller 1968; Pentecost and Lord 1988). Pavelek (1935) used a classification in Plitvice where he note that different organisms colonise the tufa depending on the flow conditions. The classification is thus also relevant for the depositional mechanics and flow conditions. A special type is chironomid tufa (Stirn 1964) which is rich in burrows of chironomides.

There have also been a number of morphological classifications which have often aimed at reflecting the physical deposition conditions. Pentecost (1993) used a classification which subdivides the deposits into 'Gentle slope' (c. <10º) which forms paludal deposits, 'Steep slope' (c. >10º) which forms cascades, barrages, stream crusts, lake crusts and cements rudites and 'Clastics'. Chafetz and Folk (1984) recognised the morphological deposit types 'waterfalls or cascade', 'lake-fill', 'steeply sloping mounds', 'fans or cones', 'terraced mounds' and 'fissure ridges'. They also noted that bacterially deposited calcium carbonate forms a large percentage of the tufa in many deposits.

Botanical and morphological classifications can often overlap as in the present thesis where floral information can give further information to the overall morphological classification. An example is the classification of Pentecost and Lord (1988) who noted that what structure is formed depends on the flow regime, which also affects the vegetation.

Since the present thesis only includes unconsolidated friable freshwater deposits, it is appropriate to use the morphological definition of Pedley (1990). Tufa is thus classified as a porous freshwater or spongy freshwater carbonate deposit, generally rich in macro- and microphytic growth, precipitated in cold or slightly thermal springs.

In Europe, the Mid Holocene tufa decline attracted a great deal of attention towards the end of the 20th century. Early on it was recognised that, although large deposits of tufa could be found, many of these are now inactive (e.g. Ford 1989; Goudie et al. 1993). The reason for this decline has been debated, and climate change has often been seen as the main cause (e.g. Griffiths and Pedley 1995). All authors do, however, not agree (e.g. Reid 1896; Willing 1985; Goudie et al. 1993; Meyrick 1999), suggesting that changes in local depositional conditions, mainly through human activity like clearance of forest and agriculture, are often more likely causes. Baker and Simms (1998) claim that there is a significant
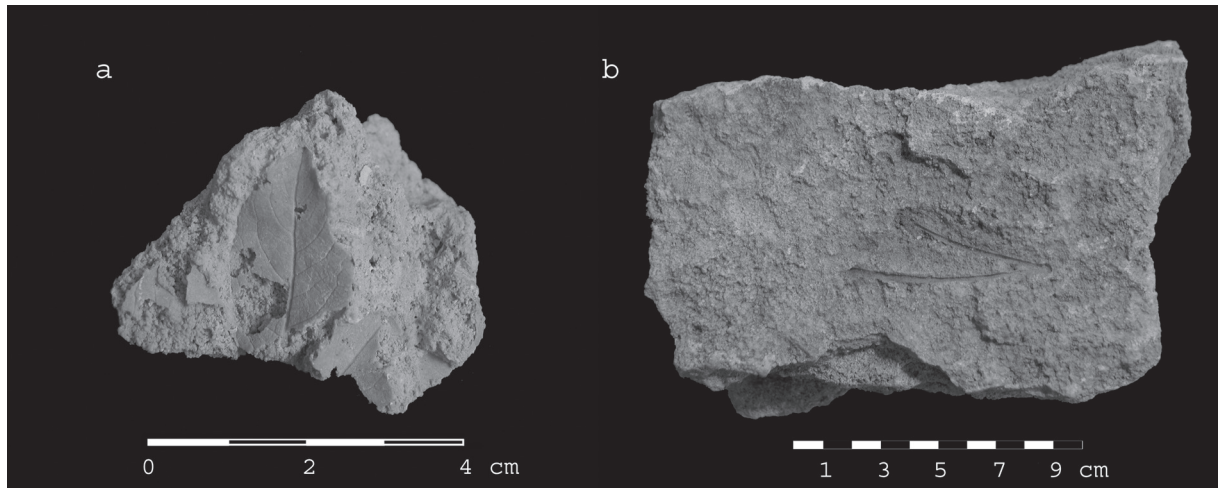
Fig 1. Two impressions of plant remains of unknown age from Benestads Backar, one of Sweden's larger tufa deposits: a) Salix *leaf, b)* Pinus *needles. Both scale bars have 9 mm increments.*

underreporting of contemporary tufa deposition and that the cessation, where such has occurred, can not be solely be attributed to climatic variations.

Sweden

In Sweden, research on calcareous tufa deposits has for a long time been virtually non-existent. To find Swedish literature on the subject, one has to look back to the late 19th and early 20th centuries, at which time a large number of Swedish calcareous tufas were investigated. The investigations, which were primarily conducted in southern Sweden, concerned consolidated as well as unconsolidated deposits and were focused mainly on stratigraphy and thorough description of fossil content. The results from these studies were to some extent suitable for reconstruction of past vegetational, faunal and climatic changes.

According to contemporary common practise, their stratigraphic resolution in relation to the described fossils was generally low but despite the lack of reliable chronologies, these investigations still provide valuable information.

Among the first people to do research on calcareous tufas in Sweden were A. G. Nathorst (e.g. 1886, 1895) and J. M. Hulth (e.g. 1895, 1898) who in the tufa found evidence for a prehistoric arctic flora with species such as *Dryas octopetala*, *Betula nana* and *Salix herbacea*. R. Sernander (1915; 1916) and S. Thunmark (1926) both worked on the genesis and description of calcareous tufa and found that deposition to a large extent may be controlled by photosynthesis of Cyanobacteria and plants. Sernanders thorough inventories of Swedish tufa deposits have also been important for the present thesis in that they have assisted in locating suitable sites. However, the
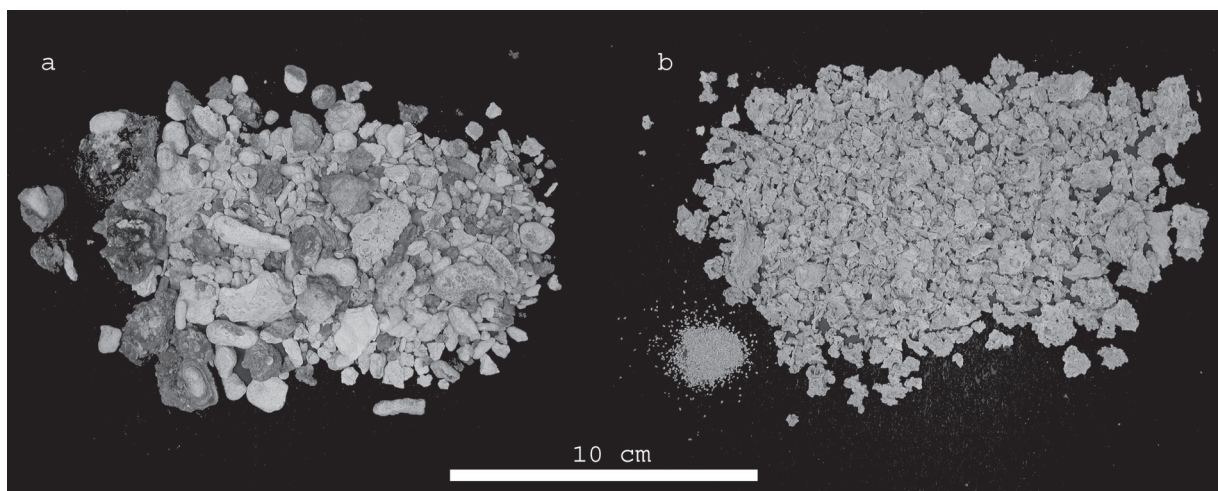

Fig 2. Two examples of the sandy-gravelly type of tufa discussed in this thesis: a) Iron stained rounded tufa pebbles, which dominate much of the tufa at the Kivik locality. This example is from 65-70 cm below surface. b) Casts of mosses dominate most of the deposit in the Valleröds Mosse locality. This example is from 140-145 cm below surface.

most important of the early 20th century publications are the ones by C. Kurck (c.f. Kurck 1901; Kurck 1904; Kurck 1922a; Kurck 1922b). Kurck mainly worked in Skåne, S. Sweden with the malacological content of unconsolidated tufas. He mainly described their faunal and floral contents, focusing on terrestrial malacology. Many of Kurck's sites have been visited during the course of the present investigations. All sites, except the previously unknown tufa deposit at Saxtorp (App IV), are mentioned in his papers. Also worth mentioning is J. C. Moberg who published a paper of a study at Sularpsbäcken (Moberg 1908), close to Lund, where he found fossil shells of the snail family Helicideae. In addition, O. Gertz showed the excellent quality of the imprints, which commonly can be found on tufa surfaces, when he was able to discern a number of different gallgrowths on leaf-imprints (Gertz 1914).

Around the mid 20's, the Swedish interest in tufa research ceased and very little has been done in that field of science since.

The aim of this thesis has been to resume the exploration of tufa and to elucidate some of the main questions concerning the South Swedish tufa deposits and their local environments. My main objectives have been to answer the following questions: 1) Why is no, or very little, tufa currently being deposited in Sweden? 2) When did the deposition start and end and can this timing be connected to periods of environmental changes and/or the alleged European mid Holocene tufa decline, which currently is being discussed (c.f. Goudie et al. 1993; Pentecost 1995; Baker and Simms 1998)?

In the course of my studies, a number of different methods were employed. Of these, terrestrial malacology, studies on terrestrial snail shells, became increasingly important, as land snails were by far the most common fossil found in the tufas studied. Palynology and plant macrofossil studies were also used. However, poor preservation of organic material caused problems concerning identifications and interpretations of the results. Pollen and plant macrofossil analysis was important important for the establishing of a chronology, as dating tufa may be dificult. The bad state of preservation may cause problems obtaining material apropriate for radiocarbon dating, such as seeds and fruits of terrestrial plants. Insect (Coleoptera) analysis has also proved to be useful as the state of preservation was generally good, although the number of retrieved parts was small. An attempt to use stable oxygen and carbon isotope analysis on the tufa and on selected snail shells provided interesting data concerning local and regional environmental changes.

Depositional processes

Chemical

The precipitation of calcareous tufa is highly dependent on climate, especially temperature and precipitation (aridity).

Calcium carbonate precipitation follows the general formula:

$$Ca^{2+} + 2HCO_3^- \rightarrow CaCO_3 + H_2O + CO_2 \quad (1)$$

However, as found by Goudie et al.(1993) $CaCO_3$ does not precipitate immediately but is preceded by loss of CO_2 according to:

$$2H^+ + 2HCO_3^- \rightarrow H_2CO_3 + H_2O + CO_2 \quad (2)$$

Consequently, the solution gets more and more supersaturated by $CaCO_3$ until crystallisation nuclei are formed and precipitation takes place:

$$Ca_2^+ + CO_3^{2-} \rightarrow CaCO_3 \quad (3)$$

Reaction 2 is replaced by reaction 1 when nucleation occurs (Dandrun et al. 1982).

Usually, carbonate precipitation does not occur until the solution is strongly supersaturated. Herman and Lorah (1987) measured a supersaturation of more than 15 times before precipitation took place. Supersaturation is caused by loss of CO_2 from the water which might have a number of different causes: e.g. evaporation –

assisted by turbulence, mixing of water with different temperature or $CaCO_3$ concentration and biological activity like photosynthesis (Viles and Goudie 1990). Generally, calcareous tufa originating from athermic springwater predominantly consists of calcite (Pentecost 1993). Although Pedley (1987) reported traces of aragonite in cold spring tufa from Caerwys, Great Britain, this is normally only associated with thermal deposits.

Biological

As mentioned earlier, the chemical reactions are facilitated and/or caused by biological activity that lowers the CO_2 concentration of the water and acts as a bonding surface for calcareous and minerogenic particles. For example, many species of the cyanobacteria genus *Nostoc*, in addition to being a photosynthesist, are equipped with a sticky polysaccharide sheet used for capturing small particles, including carbonate crystals (Thunmark 1926; Pentecost 1992). Also a number of algae and moss species grow on or in the tufa. For example the moss *Eucladium verticillatum* grows in dense pillows where the older parts are actively incrusted with tufa, acting as a protective casing (Pentecost 1992). Such moss incrustations can be the main component of an unconsolidated tufa. Evertebrate faunas are commonly rich in tufa environments and may participate in forming the deposits. Among the most specialised are two species of the *Pericoma*-fly, the larvae of which live in a protective crust of tufa, which is actively directed to precipitate on certain sites on the body (Satchell 1949).

History of Quaternary terrestrial malacology in Sweden

A large part of this thesis concerns malacology. This was from the beginning just one of the biostratigraphical methods tested, but turned out to be the most important tool for palaeoenvironmental reconstruction in my studies. There are several reasons for this:

- Finds of well-preserved shells are common whereas the oxidising nature of the tufa environment rapidly destroys most organic fossils, such as pollen and plant macrofossils.

- Apart from reflecting regional climate changes, with appearance/disappearance and abundance of key taxa associated to for example northern/southern communities, molluscs also reflect very local environmental conditions such as dry/wet and open/shaded and local vegetation.

- Molluscs are commonly identifiable to species level.

The majority of Swedish Quaternary molluscan studies were carried out in the late 19th and early 20th century. During this period, terrestrial molluscs were interesting as geological source material. Studies were carried out mostly in the southernmost part of Sweden but single studies including mollusc analysis were also carried out in, for example, Östergötland (Odhner 1909; 1910a), Västergötland (Hulth 1898; Odhner 1910b), Närke (Kjellmark 1897), Jämtland, (Kjellmark 1904) and the island of Gotland (Munthe 1910). Apart from the works of Odhner (1910a; b) which contain detailed studies of the malacology of a few mid Swedish tufa deposits, most of these investigations were mainly concerned with the vegetation history. The malacological history in those papers was usually only presented as short species lists or just notes of particularly interesting finds. The most prominent works in early Swedish malacology were carried out in the province of Skåne by Kurck (Kurck 1901; 1904; 1922a; b; 1931; 1933).

Snails were early appreciated as palaeoenvironmental indicators (e.g. Kurck 1904; 1922a; Munthe 1910; Odhner 1910a). The appearance and disappearance of molluscs with narrow ecological ranges was used both for dating and for reconstructing past environmental changes such as moisture and air temperature. *Vertigo moulinsiana* (e.g. Odhner 1910a) and *Columella*

columella are examples of species that were regarded as signs of warm and cold periods respectively. Other examples are the *Vertigo genesii*, which indicates open environments and *Galba truncatula*, which was regarded as a good moisture indicator (e.g. Kurck 1922a; 1922b; Munthe et al. 1925). These studies are, however, hampered by low, or lack of, stratigraphical resolution. According to tradition, the malacological finds were usually merely presented as lists of species. When there was an associated stratigraphy, it usually corresponded to lithological units without regard to differences in depositional time between units and possible environmental changes within units.
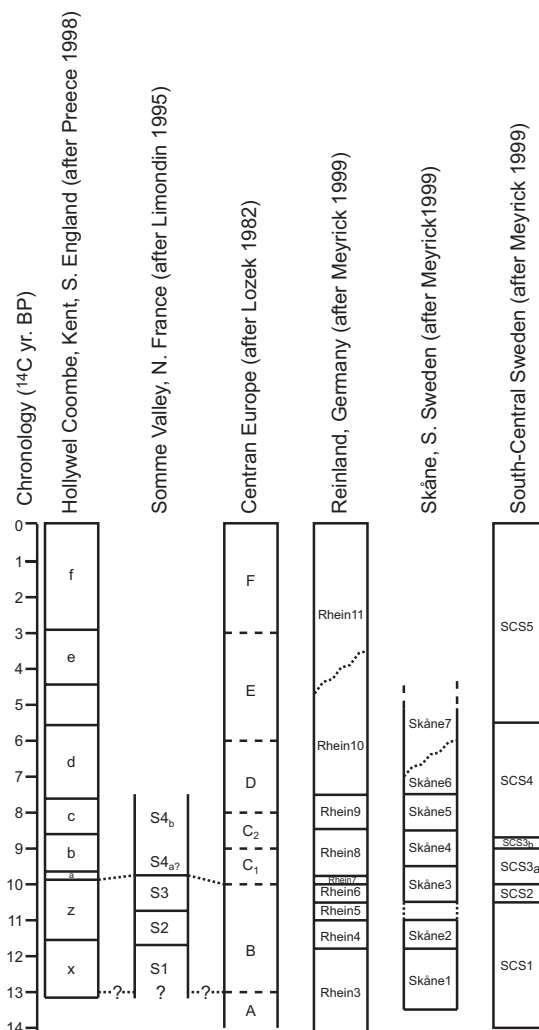

Fig 3. Postglacial regional mollusc zones for northern and western central Europe. After (Meyrick 1999). Note that the zones for Sweden are provisional.

In the 1920:s, as palynology became a widely acknowledged method for palaeoenvironmental reconstructions, the interest in Holocene terrestrial molluscs declined to such extent that it took about 70 years before any major new investigation on this subject was published in Sweden (Gedda et al. 1999; Meyrick 1999). The notable exception is a paper on the molluscs on the island of Ven (Nilsson 1948), which unfortunately lacks any stratigraphical information.

In other parts of Europe, work on molluscs has continued up to the present (e.g. Lozek 1964; 1967; Kennard 1945; Evans 1973; Preece 1992). A great deal is known about molluscan postglacial dispersal in Europe and molluscan zonations (Fig 3) have been presented for various regions [e.g. south-eastern England (Kerney 1977; 1980; Preece and Day 1994), central Europe (Lozek 1982), France (Limoundin 1995) and Germany (Meyrick 1999)]. Meyrick (1999) also suggested a zonation for southern Sweden (Fig 3) which, because of limited previous knowledge of the region, should be seen as provisional (Meyrick 1999 p. 248).

Largely, the regional mollusc zones of Europe (Kent [southern England], Somme Valley [northern France], Central Europe, Rheinland [Germany]) display similar postglacial environmental development. Early pioneer communities (Kent z; Somme Valley S1; Central Europe A, Rheinland 2, 3, 4) indicate open land with *Pu-pilla muscorum, Vallonia species and Vertigo genesii* as common faunal elements. After the initial colonisation there is a period of diversifying of the faunas (Kent z, a; Somme Valley S2, S3; Central Europe B, Rheinland 5). In this period *Columella columella* is a common faunal element. Among the first shade demanding taxa to appear are *Carychium tridentatum* and *Aegopinella* (Kent b; Somme Valley S4a, Rheinland 7, 8) and *Bradybaena* and *Euomphalia* (Central Europe C_1). In the Somme Valley (S4a-b) and Central Europe (C_2) there is around this time an increased importance of more thermophilous taxa. In England (d) that increase is postponed a few hundred years. The last stages of all records display a shift towards open land faunas (Kent e, Somme Valley S5; Central Europe 5, Rheinland 11), evidently a sign of the increasing importance of man as an environmental factor.

The Swedish records seem to follow the trends of continental Europe and southern England, although some hundred years postponed. Skåne 1, 2 and 3 are charactarised by open land taxa. In Skåne 4 are catholic taxa beccoming important. *Carychium tridentatum* does not enter until Skåne 5. In South-Central Sweden (Östergötland) the fauna is open in SCS1 and 2. In SCS3 some shade develops and in SCSb the relatively thermophilous species *Vertigo moulinsiana* appear. *Carychium tridentatum* appear in SCS4.

Study areas

The studied sites were selected after consulting older literature on tufa studies (e.g. Nathorst 1886; Kurck 1901, 1904, 1922a; Moberg 1908; Odhner 1909; 1910a; Sernander 1915, 1916) as well as geological maps. About 50 sites were reconnoitred during the course of this thesis and the most promising were chosen for palaeoecological studies. These sites are mainly located in south-eastern – south-western Skåne, but sites in central and south-central Sweden were also surveyed. The most promising sites were selected for further studies and are described in detail in the chapter '*Results - summary of papers and unpublished research*' and *Appendixes I, III and IV*. To investigate possible differences in timing of tufa deposits, species immigration and environment, sites were selected along an east-west transect through southern Skåne (Fig 4).

The following three areas were investigated: The Fyledalen Valley, Saxtorp and Kivik. Because of chronological problems, results from three sites, Slagstorpshult and Örup from the Fyledalen area Kivik, were not considered suitable for publication, but they are included here and treated separately since they contain valuable information concerning the distribution and composition of Holocene mollusc species and faunas.

The study areas are situated within the temperate vegetation zone of broad-leaved deciduous forests (Ahti et al. 1968). The climate today is characterised by mean July temperatures around 17°C, mean January temperatures around -1°C and an annual precipitation of between 700 and 800 mm (Raab and Wedin 1995).

The Fyledalen valley

The Fyledalen valley is situated in south-central Skåne, southern Sweden. The valley is orientated NW-SE, following the tectonic fault complex known as the Thornquist zone (Ziegler 1982). It is a 30-40 m deep canyon drained by the Fyleån river towards SE. Cretaceous-Tertiary limestone, sandstone, a predominance of shale, and crystalline rocks, form the bedrock in the catchment area (Daniel 1986). Two sites were studied in the area:

Pipers Mosse (55°31'4 N, 14°53'6 E, Fig 4), situated on the western slope of the Fyledalen valley, is today a small alder carr fen. The site is interpreted as corresponding to the site 'Källmyr å Högestads ägor' (Kurck 1922a pp.2-6) and shows the following stratigraphy: About 50 cm of carr peat, 150 cm of calcareous tufa, 50 cm of silt and silty carr peat and sandy till to an unknown depth. The organic content is unusually high for a tufa deposit in this region. The site was artificially drained around 1880 but is still not completely dry. The surroundings are domi-
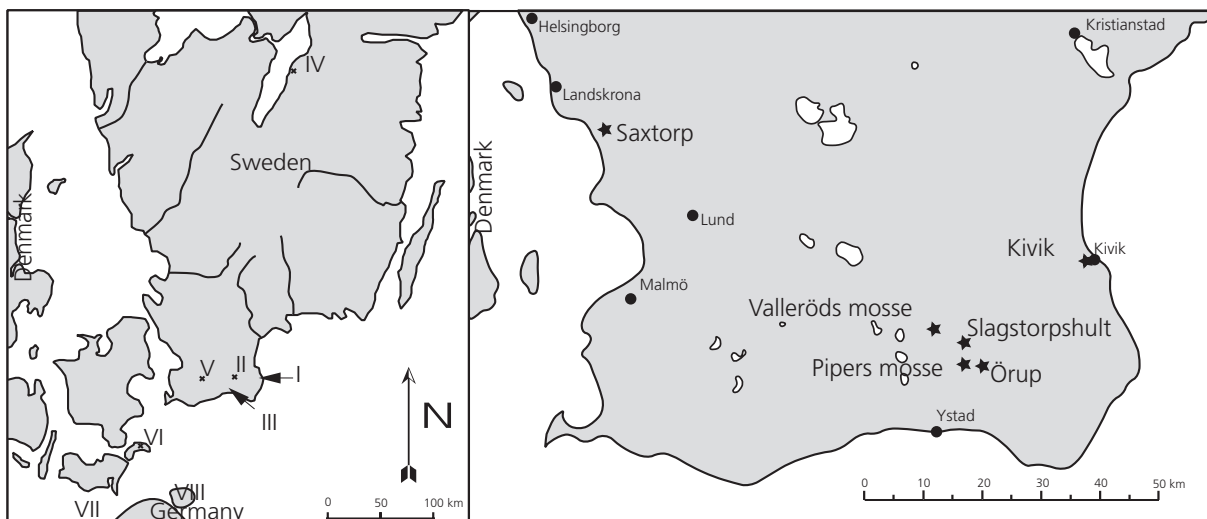
Fig 4. Map of southern and central Skåne showing the location of sites mentioned in this thesis: Pipers Mosse (App I), Valleröds Mosse (App III), Saxtorp (App IV), Slagstorpshult (unpublished), Örup (unpublished) and Kivik (unpublished). Roman numerals refer to significant sites mentioned in this thesis where others have performed research on land snails and calcareous tufa: I. Sigridslund (Meyrick 1999), II. Högestad (Meyrick 1999), III Stora Bäddinge (Meyrick, unpublished), IV. Vitlerbacken (Meyrick 1999), V. Toppeladugård (Holst 1906), VI. Møn (Noe-Nygaard and Heiberg 2001), VII Meclenburg Bay (von Proschwitz and Bennike 1998, Jensen 1997) and VIII Rügen (Plate 1950).

nated by pastures and planted forest. The present vegetation at the site consists of an alder grove (*Alnus glutinosa*), but stands of spruce (*Picea abies*) and beech (*Fagus silvatica*) are also found within the catchment.

Valleröds Mosse (55°34"5'N, 13°49"2'E, Fig 4) is situated on the SW side of the Fyledalen valley bottom. The stratigraphy was the following: About 45 cm of carr peat, 300 cm of calcareous tufa and clay to an unknown depth. (Kurck 1922a) probably refers to this site as 'Källmosse å Eriksdals ägor' (pp. 25-31) with a size of 250x175 m. Today the site is an open wetland bordering the river and is highly influenced by grazing cattle. The site was artificially drained around 1880 so that today, all that remains is a small stream boarded by sedge carr, fed by the Magle Ådra spring. Some of the tufa has been excavated, primarily in the south-eastern part, and used as fertiliser. Sedge communities (Carex spp.) and grass presently dominate the field layer at the site. In the surroundings beech groves (*Fagus silvatica*), planted stands of spruce (*Picea abies*), and alder (*Alnus glutinosa*) are present.

Slagstorpshult (55°34'35 N, 14°51'19 E, Fig. 4) is located at the bottom of a tributary valley on the north-eastern slope of the Fyledalen valley, between the sites Pipers Mosse (App I) and Valleröds Mosse (App III). It probably corresponds to Slagstorpshult (Kurck 1922a p. 17-25). The deposit was heavily quarried already in 1890 and not much of the original 0.25 hectars remains. The site consisted of about 150 cm of calcareous tufa with almost no visual organic content. The surrounding vegetation consists of a beech groove (*Fagus silvatica*) with a field layer consisting of various herbs.

Örup (55°32'11 N, 14°57'11 E, Fig 4), on the northern side of a tributary valley to the Fyledalen valley, is situated in a beech-grove about 8 km from Slagstorpshult and Pipers Mosse. It probably corresponds to 'Örup' in (Kurck 1922a pp. 31-46). The deposit consisted of 155 cm of tufa with heavy iron staining and, at intervals, up to 10 cm large concretions. The surrounding vegetation consists of a dense beech-groove with a field layer consisting of various herbs.

Saxtorp

The Saxtorp site (55°50'40''N, 12°58'15''E; Fig. 4) in western Skåne, is situated in a trough on the west-facing slope of the Saxå river valley, about 130 m from the river. The soil surface at the site today reaches about 7 m above sea level. The bedrock of the catchment area consists predominantly of Tertiary (Danien) limestone (Fredén 1994). The area is close, about 3.5 km, to Öresund and has during the Atlantic and early Boreal time, about 7,500-5,500 cal. BP, been subjected to a number of marine transgressions and regressions. The studied site was probably only affected by the highest transgression which occurred in the late Atlantic period, about 6,000 cal. BP, although the sea must have been close during the previous two transgressions. The tufa was discovered when sediment samples for biostratigraphical analysis were taken in connection with an archaeological rescue excavation of a Stone Age - Bronze Age settlement (Lindahl Jensen and Nilsson 2000). The complete deposit consisted of, from the bottom, boulder clay of unknown thickness, 40 cm of tufa, 20 cm of marine transgressive clay, 15 cm of tufa and 180 cm of wood carr peat with anthropogenic remains. Only the two tufa layers, the clay and the lowermost 20 cm of the peat contained molluscs and were included in my study. The site has, until recently, been a carr but is now completely drained and cultivated (Lindahl Jensen and Nilsson 2000). Pastures and beech-groves now dominate the area. At the time of sampling, the site was a ploughed field but at the time of printing the new West Coast Railway has been constructed on top of it.

Kivik

The Kivik site (55°41' N, 14°12'20 E, Fig 4) is situated on the northern slope of a ravine through which the stream Hjärtabäck drains in an easterly direction towards the town of Kivik, on the eastern coast of Skåne. A number of tufa deposits are found in the valley and this particular deposit is probably equivalent to 'Mellby' (Kurck 1904 p. 294). The surrounding area is today a region of high diversity in a number of floral and fauna groups, including herbs and molluscs. The region consists of a mosaic of woodland, pastures and plantations. The woodland is a mixed broad-leaved forest with *Tilia*, *Quercus*, *Fraxinus*, *Ulmus* and *Acer*.

Methods

The methods used varied slightly between the different studies. A general outline of the methodology is given here. Further information is available in the methods section for each site in App I, III and IV.

Field work

In the field, samples were collected using Russian corers (Jowsey 1966) with 5-10 cm diameters at Pipers Mosse and Valleröds Mosse and with a 10x10x100 cm metal box at Saxtorp, Slagstorpshult, Örup and Kivik. At Saxtorp, the lowermost unit was sampled using a spade in an open section. Care was taken to avoid contamination from younger layers. Preliminary description of lithostratigraphies, and correlation between cores, was made directly in the field before wrapping the retrieved sequences in plastic film for transport back to the department.

Laboratory methods

In the laboratory, cores were re-described and subsampled for further analyses. The subsamples were then stored either wet in a cold room (+8°C), or dried, until further treatment was performed.

Loss on ignition

To aid lithological descriptions, estimates of organic and calcium carbonate ($CaCO_3$) content were derived through loss on ignition (Bengtsson and Enell 1986) on the sediments from Pipers Mosse (App I), Slagstorpshult and Örup. The method was later abandoned because it did not seem to provide enough significant information. Samples of about 5 cm^3 of sediment were dried at 105°C for 24 hours, and then heated to 550°C and 900°C for four hour respectively. Sample weights (M_{Dry}, M_{550} and M_{900}) were measured after cooling in a dessicator. Organic content (A) was deduced, on the assumption that all organic content is burned at 550°C, from:

$$A\% = 100 * (M_{Dry} - M_{550}) / M_{Dry} \qquad (1)$$

$CaCO_3$ content (B) was deduced, on the assumption that all $CaCO_3$ is split into CaO and CO_2 at 900°C, from:

$$B\% = 100 * 2.27 * (M_{550} - M_{900}) / M_{Dry} \qquad (2)$$

where 2.27 is derived from the specific mass relationship of $CaCO_3$ / CO_2 = 100 / 44 = 2.27.

The residual equals the minerogenic content (C) according to:

$$C\% = 100 - A\% - B\% \qquad (3)$$

Pollen and spore analyses

5 cm^3 subsamples were taken from the centre of each macrofossil sample for pollen and spore analysis. In the case of Saxtorp 50 cm^3 samples were used because of the very low pollen content. Attempts were made to extract pollen and spores from all sites. However, due to the fact that pollen grains and spores are often badly preserved in calcareous tufas (Preece and Day 1994), the analyses of only three sites were successful [*i.e.* Pipers Mosse (App I), Valleröds Mosse (App III) and Saxtorp (App IV)]. The preparation followed standard methods according to Berglund and Ralska-Jasiewiczowa (1986) including treatment with HCl, HF and acetolysis. Note that
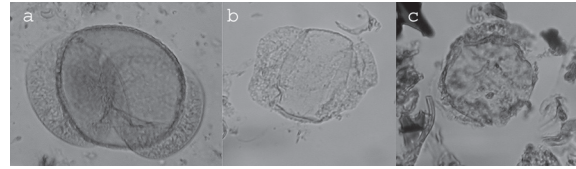

Fig 5. Examples of pollen preservation. 5a show a typically preserved Pinus *pollen grain from a lake or bog. 5b and 5c show* Pinus *pollen grains with two kinds of degradation that commonly occur in tufa deposits. The grain in 5b is dissolved until only a thin film is left. This is common when sediments are exposed to air (Moore et al. 1991 p. 180). 5c is compressed into itself and its features are distorted.*

since the majority of the samples consisted of carbonate deposits with low pollen concentration, large volumes of sediment (up to 50 ml, as compared to lake sediments where <5 ml usually is enough) had to be dissolved to extract sufficient numbers. Hence follows that very large quantities of HCl had to be used to dissolve the carbonates. Microscopic slides were prepared from the residues. In the study of Pipers Mosse (App I) *Lycopodium* tablets were added to each sample in an attempt to estimate pollen influx (Stockmarr 1971). This was not done for the other sites, because of the lack of reliable and detailed chro-

nologies. Due to poorly preserved pollen (Fig 5) and low concentrations, pollen analysis was very time consuming. It commonly took two days to achieve a sum of 300 identified tree pollen grains, which was the limit set that would ensure a statistical representation of tree pollen taxa. This may be compared with the identification of pollen from mires and lakes where 2-4000 grains usually can be counted during an equivalent period of time. Herb pollen were noted when encountered since they often provide important environmental information, but because of the state of preservation the analyses focused on the identification of tree taxa, which are the basis for the south Swedish pollen chronology. A general limit was also set at two complete slides although occasionally up to 4 slides had to be counted. Routine analysis was performed at a magnification of 400x, while a magnification of 1000x and oil immersion was used for critical analysis of difficult grains. For identification, the key of Moore et al. (1991) was used, as well as the reference collection at the Department of Quaternary Geology, Lund University.

Macrofossil remains

Samples for macrofossil analysis were dispersed in water and wet-sieved through 3.0, 0.5 and 0.25 mm meshes. In the studies of Valleröds Mosse, and the sites of Kivik, Örup and Slagstorpshult, samples were initially dried to aid dispersion and to prevent possible degradation by microbial growth and dissolution in storage. After sieving the macrofossil remains were sorted and identified under a stereo dissecting microscope at magnifications of 6-50x. In the study of Pipers Mosse (App I), macrofossil remains were sorted out in wet condition under a stereomicroscope. In the other studies (App III, IV and Unpublished), the residuals were first dried and sorting was performed in a dry state to eliminate dissolution damage on mollusc shells and vertebrate remains during storage. Shells and bones were then stored dry, while plant macrofossils and insect remains were stored in distilled water, made slightly acid to minimise growth of micro-organisms.

Mollusc shells were handled with a fine slightly damp paintbrush or a pair of fine forceps. To ensure that the minimum number of individuals was recorded only snail apices and bivalve hinges (Fig 6) were sampled. Occasional identifiable non-apical fragments of snails were also counted [e.g. the mouth parts (Fig 7) of certain *Vertigo*

species], if they did not have any possible associated apex. To estimate the minimum number of bivalve shells (*i.e. Pisidium*), each valve was counted separately. The result was then rounded up to nearest even number and divided in half. Shells were classified into ecological group (Table 1), based on the system published by Lozek (1964). Taxa were divided into five major groups
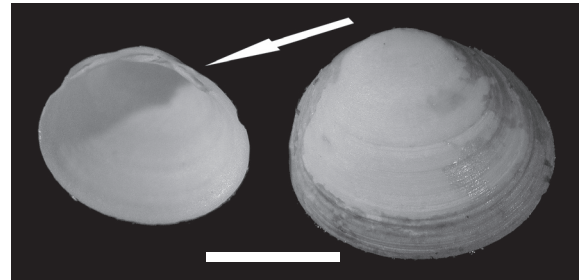

Fig 6. Pisidium *is a group of limnic bivalves. Species determination on subfossil specimens is difficult and are much based of the characters of the hinge teeth (indicated by the arrow). Length of scale bar is 1 mm.*

and numerous subgroups, but only the five major groups are included in the graphs. These groups are: 'woodland', 'open', 'catholic', 'marsh', and 'water'. It is obvious that certain species will not simply fall into one group but fall in between groups, or into two groups. For example this is the case with *Vertigo genesii*, which is a strong open-land indicator but also a stenotopic marsh species (Colville 1998; Preece and Day 1994). For this reason one has to take care before interpreting ecological implications of the diagrams. Non-malacologist readers might be interested to
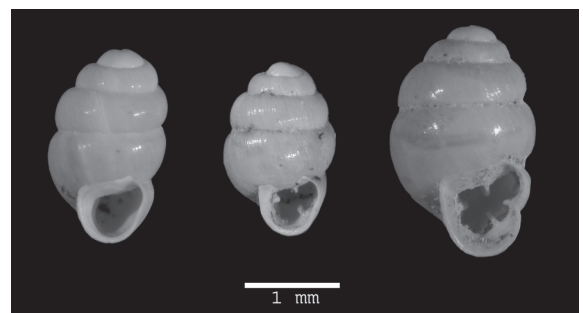
Fig 7. A selection of Vertigo-*species. Note the differences in the denticulation. a)* Vertigo genesii, *b)* Vertigo geyeri, *c)* Vertigo moulinsiana.

know that the term 'catholic' means indifferent. This does not necessarily mean that the species can be found in *any* environment, but rather that for the criteria generally discussed here (*i.e.* degree of shade and moisture) it might not be particularly selective. In the case of species groups (e.g. *Euconulus* sp., *Vertigo* sp. or *Limax/Deroceras*),

there are two ways in which these may be classified as catholic. This may be either because one or more of the included species are catholic or because the included species have so different biological demands that little can be said of the environment from the presence of the group. The shells were identified using keys (Cameron and Redfern 1976; Evans 1973; Kerney and Cameron 1979; Lozek 1964) and the reference collections

at the Department of Quaternary Geology, Lund University and the Natural History Museum in Gothenburg. The nomenclature follows for land molluscs, Kerney and Cameron (1979) and for aquatic molluscs Glöer and Meier-Brook (1998).

Plant macrofossils were handled with fine forceps. Material for dating was, when possible, collected from the same levels as samples for pollen analysis. To increase the amount of fossils suit-

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Table 1. Ecological categories assigned to the species encountered during this investigation.

Shade-demanding

Aegopinella pura (ALDER)	*Aegopinella nitidula* (DRAPARNAUD)
Acanthinula aculeata (MÜLLER)	*Bradybaena fruticum* (MÜLLER)
Carychium tridentatum (RISSO)	*Clausilia bidentata* (STRÖM)
Cochlodina lamminata (MONTAGU)	*Columella edentula* (DRAPARNAUD)
Discus ruderatus (FÉRUSSAC)	*Discus rotundatus* (MÜLLER)
Ena obscura (MÜLLER)	*Nesovitrea petronella* (PFEIFFER)
Perforatella incarnata (MÜLLER)	*Vertigo alpestris* ALDER
Vertigo modesta (SAY)	*Vertigo ronnebyensis* (WESTERLUND)
Vertigo pusilla MÜLLER	*Vitrea contracta* (WESTERLUND)
Vitrea crystallina (MÜLLER)	

Open-ground

Columella columella (MARTENS)	*Pupilla muscorum* (LINNEAUS)
Vallonia pulchella (MÜLLER)	*Vertigo pygmaea* (DRAPARNAUD)

Catholic

Arianta arbustorum (LINNEAUS)	*Balea perversa* (LINNEAUS)
Cepaea hortensis (MÜLLER)	*Cochlicopa lubrica* (MÜLLER)
Cochlicopa lubricella (PORRO)	*Euconolus fulvus* (MÜLLER)
Helicigona lapicida (LINNEAUS)	*Limax/Deroceras*
Nesovitrea hammonis (STRÖM)	*Oxychilus alliarius* (MILLER)
Punctum pygmaeum (DRAPARNAUD)	*Trichia hispida* (LINNEAUS)
Vallonia costata (MÜLLER)	*Vertigo substriata* (JEFFREYS)
Vitrina pellucida (MÜLLER)	

Marsh

Carychium minimum MÜLLER	*Cochlicopa nitens* (GALLENSTEIN)
Euconulus alderi (GRAY)	*Pupilla muscorum* f. *pratensis* (CLESSIN)
Succinea putris (LINNEAUS)	*Succinea/Oxyloma*
Vertigo angustior JEFFREYS	*Vertigo antivertigo* (DRAPARNAUD)
Vertigo genesii (GREDLER)	*Vertigo geyeri* LINDHOLM
Vertigo lilljeborgi (WESTERLUND)	*Vertigo moulinsiana* (DUPUY)
Zonitoides nitidus (MÜLLER)	**Amphibic:** *Galba truncatula* (MÜLLER)

Aquatic

Anisus leucostoma (MILLET)	*Anisus spirorbis* (LINNEAUS)
Bithynia tentaculata (LINNEAUS)	*Gyraulus acronicus* (FÉRUSSAC)
Physa fontanalis (LINNEAUS)	*Pisidium casertanum* (POLI)
Pisidium personatum MALM	*Planorbis planorbis* (LINNEAUS)
Radix peregra (MÜLLER)	**Marine:** cf. *Cardium*

able for dating, tufa from selected levels were dissolved in hydrochloric acid (HCl). Tufa from all layers was not dissolved since it was considered important to save sediment for future analyses such as stable isotope analysis (R. Preece pers. comm.). The fossils were identified using the keys of Beijerinck (1976) Nilsson (1962) and Schoch et al. (1988) and the reference collections at the Department of Quaternary Geology, Lund University. See also *14C dating*.

Insect and *vertebrate remains* were sent to experts for identification and interpretation. For Pipers Mosse a climatic reconstruction was performed using the MCR method described in, for example Atkinson et al. (1987) Coope and Lemdahl (1996) and Walking and Coope (1996).

Microscopic tufa analysis

Microscopic analysis of tufa was routinely performed on all sites in connection with the macrofossil analysis. This was done to see if the casts of plants, which commonly make up the bulk of this kind of tufa, could help with the interpretation of local vegetation. The aim was to get an overview of the casts and no quantitative records were made. Especially in the case of Valleröds Mosse this proved to be a valuable method.

Stable isotope analysis

Carbon and oxygen isotope analyses were performed on the calcareous tufa and on mollusc shells of the species *Vallonia pulchella* from Valleröds Mosse (App III). *Vallonia pulchella* was selected because it was present throughout the stratigraphy in sufficient numbers and it can be assumed that it has lived in the carr throughout its life cycle. The preparation followed the principles described by Buchardt (1977). Tufa particles and mollusc shells were collected under a stereo dissecting microscope to minimise contamination of alien material such as old carbonate and organic remains. 0.6-0.7 g of dried sediment samples and mollusc shells were crushed and sieved through a 250 μm mesh to increase reaction speed. Preheated 99% phosphoric acid (HPO_4) was added to the sample under vacuum at a constant temperature of 50°C. After cryogenic purification, carbon dioxide was trapped and analysed on a Finnigan-MAT 250 mass spectrometer at the stable isotope laboratory, University of Copenhagen, Denmark. Results are

presented as per mille deviation from the international V-PDB standard (Craig 1957) such that

$$\delta(^{13}C, {}^{18}O) = (R_{sample} / R_{standard} - 1)10^3 \text{ ‰} \quad (4)$$

where R is defined as the ratios $^{18}O/^{16}O$ and $^{12}C/^{13}C$ respectively.

Chronology

Accelerator mass spectronomy (AMS ^{14}C) dating was performed on plant macro remains from six sites in Skåne (App. I, II, IV and unpublished: Slagstorpshult, Örup, Kivik). Seeds or fruits of terrestrial plants, such as *Betula* seeds and *Carex* nuts were selected for dating. Charcoal remains were used as an alternative material. After identification the samples were dried in glass vials in a dessicator before sent to the AMS laboratory. Calibration to calendar years was made with OxCal (Bronk Ramsey et al. 1995) on the INTCAL98 calibration curve (Stuiver et al. 1998).

The AMS dates were, when possible, backed up by a relative pollen chronology. Pollen-stratigraphies were correlated the ^{14}C-dated pollen diagram from Ageröds mosse (Nilsson 1964), except for the Saxtorp site. In that case, the diagram from nearby Barsebäcks mosse (Digerfeldt 1972) was used for correlation. Moreover, the pollen records presented in this thesis were compared with each other for correlation.

All dates are here expressed in calibrated years before 1950 (cal. BP). The chronozone boundaries are according to the latest revision of the chronology of pollenstratigraphy in southern Sweden (Gaillard et al. 1996). The ages of the chronozone boundaries prior to the Younger Dryas/Preboreal transition are given in GRIP ice varve years (GRIP yr. BP). Unless otherwise stated, uncalibrated dates taken from literature (and Paper I) were calibrated with the same procedure, for ease of comparison.

The following chronozones are used in this thesis: AL (Alleröd, 13,900-12,650 GRIP yr. BP), YD (Younger Dryas, 12,650-11,500 GRIP yr. BP), PB (Preboreal, 11,500-9,900 cal. BP), BO1 (early Boreal, 9,900-8,800 cal. BP), BO2 (late Boreal, 8,800-7,800 cal. BP), AT (Atlanticum 7,800-5,700 cal. BP) and SB (Subboreal 5,700 - c. 2,600 cal. BP) (Björck et al. 1998; Gaillard et al. 1996; Mangerud et al. 1974; Skog and Regnell 1995).

Results - summary of papers and unpublished research

Paper I

Gedda, B., Lemdahl, G. and Gaillard, M.-J. (1999) Lateglacial and early Holocene environments inferred from a tufa deposit at Fyledalen, S. Sweden. GFF, 121 (1): 33-42.

This paper presents a reconstruction of Lateglacial and early Holocene climatic and environmental changes at the tufa site Pipers Mosse in the Fyledalen valley, south-eastern Skåne (Fig 4). Being the first study of calcareous tufa in southern Sweden carried out with modern methods, this could be regarded as a pilot study. A number of biostratigraphical methods were employed, including analysis of pollen, macroscopic plant remains, molluscs and insects, together with AMS-dating of selected material, and lithological studies. The results have much guided me concerning research strategy and objectives in the proceeding investigations. The study showed that the oxidising environment of calcareous tufas causes problems with analysis performed on non-calcareous organic remains, rendering strong corrosion or destruction of much of the material. Both absolute dating using AMS analysis and relative dating by pollen stratigraphical correlation suffered from the resulting low availability of suitable and recognisable material. Because palaeoecological interpretations are severely hampered by unsatisfactory preservation, it was concluded that subsequent investigations should involve a multiproxy approach to provide sufficient data on past climates and environments.

The entire formation was deposited during the Younger Dryas-Preboreal-Boreal chronozones, about 12,000-8,000 cal. BP (10,200-7,500 ^{14}C BP), whereas tufa deposition was restricted to the period 11,000-8,800 cal. BP (9,500 to 8,000 uncal. BP), *i.e.* mid Preboreal to late Boreal. This period is characterised by exceptionally low lake levels and high summer temperatures in southern Sweden (Digerfeldt 1988; Gaillard and Digerfeldt 1991; Gaillard and Lemdahl 1994; Harrison and Digerfeldt 1993), suggesting that optimal conditions for tufa formation in this region coincided with relatively warm and dry climate conditions, a low groundwater table and high evaporation rates. During periods with colder conditions and/or higher groundwater table, tufa deposition was replaced by peat deposition. The tufa was formed in a gently sloping paludal environment, according to the classification of Pedley (1990), and casts of bryophytes and vascular plants are present in the major part of the deposit. From the stratigraphy, it was evident that tufa deposition was preceded by carr peat formation. The end of the tufa deposition coincides with the regional rise of the groundwater table experienced during the Boreal period (c.f Digerfeldt 1988).

The pollen and plant macrofossil records of the earliest part of the deposit indicate an open landscape dominated by herbs, willows and dwarf birch during the Younger Dryas [before 11,500 cal. BP (10,000 ^{14}C BP)]. The local carr environment was probably dominated by *Selaginella selaginoides* and *Carex* species growing in a moss ground vegetation. A find of the dung beetle *Aphodius lapponum* suggests that the carr vegetation may have attracted grazing animals, possibly reindeer. MCR analyses on Coleoptera remains show that the temperatures at this time was about 9°C for the warmest month and about -10°C for the coldest. This agrees well with what is currently known about Younger Dryas temperatures in southern Sweden (e.g. Hammarlund and Lemdahl 1994; Lemdahl 1991).

It has been shown that a rapid climatic amelioration took place around 11,500 cal. BP with air temperatures for the warmest month increasing with about 10°C, to a level about 2°C above the present (e.g. Berglund et al. 1994; Gaillard and Lemdahl 1994; Hammarlund and Lemdahl 1994; Lemdahl 1991). Tree birch is presumed to have immigrated to the Fylealen area around this time (11,500 cal. BP) e.g. Berglund et al. 1994; Nilsson 1964) and formed open woodland. As tufa deposition started around 11,000 cal. BP (9,500 ^{14}C BP), pine was also established locally. At this time *Equisetum* dominated the local carr vegetation. Around 10,000 cal. BP (9,000 ^{14}C BP) the local mire vegetation changed abruptly as horsetail vegetation was replaced by ferns and *Eupatorium cannabinum*.

After 9,500 cal. BP (8,500 ^{14}C BP), broad-leaved deciduous tree species including alder, oak,

lime and elm began to immigrate into the area. Around 8,800 cal. BP (8,000 ^{14}C BP) when tufa deposition ended, the forest stood at the site with alder, elm, oak and lime.

The mollusc record is characterised by low recoveries, especially in the lower part of the record. Many species appear sporadically and care had to be taken in interpreting the diagram. Zone PIM1, about 11,000 cal. BP (9,500 ^{14}C BP) to 9,500 cal. BP (8,500 ^{14}C BP), is dominated by *Vallonia pulchella*, a species with two ecological optima: Screes in dry broad-leaved forests and moist sites like calcareous marshes and grassland. Most likely it is the latter type that is present here. Present are also carr species including *Euconulus alderi* with scattered appearances of *Zonitoides nitidus*, *Oxyloma pfeifferi* and *Vertigo geyeri*. The catholic species *Nesovitrea hammonis* and *Cochlicopa lubrica* are also present. From zone PIM2, about 9,500 cal. BP (8,500 ^{14}C BP) to about 8,500 cal. BP (7,700 ^{14}C BP), the record is more diverse with up to 17 species. All species from zone PIM1 are still present with the addition of the marsh species *Galba truncatula*, *Carychium minimum* as well as some species preferring drier habitats including *Pupilla muscorum*[1] and *Cochlicopa lubricella*.

[1]At the time of publication, the distinction between *P. muscorum* f. *typica* with preferences for relatively dry environments and *P. muscorum* f. *pratensis*, which prefers relatively wet environments, was not made. Later the material has been re-evaluated and the material, solely containing juveniles, is considered to consist of f. *typica* only.

The main conclusions of this paper are:
- Tufa was deposited between 11,000 to 8,800 cal. BP, coinciding with a period of exceptionally low groundwater tables and high summer temperatures.
- It was postulated that environmental factors such as humidity and air temperature control the deposition of southern Scandinavia tufa.
- Tufa formation seemed not to be directly related to changes in the local environment, except possibly changes in the microclimate.
- The site remained a marsh throughout the studied period, with a succession of different marsh plant communities.
- Palaeobotanical data indicate that the vegetation surrounding the site underwent a development from a lateglacial dwarf shrub thundra, to an open birch/pine woodland around 11,500 cal. BP, followed by hazel/birch woodland at 10,000 cal. BP and a deciduous broad-leaved forest with alder, oak, lime and elm around 9,500 cal. BP.
- The mollusc record, which proved to be a valuable complement to pollen and plant macrofossil data when interpreting the local environment, reflects a fairly open environment until 9,500 cal. BP, after which a more shaded environment is indicated.
- Coleopteran analysis was recognised as a valuable method worth pursuing. However, due to very low abundances of remains, sampling volumes must be very large.

Paper II

Gedda, B. and von Proschwitz, T. Recent and fossil distribution of *Vertigo moulinsiana* (Dupuy) (Gastropoda: Vertiginidae) in Scandinavia. Manuscript submitted to *Journal of Biogeography*

Vertigo moulinsiana is today mainly an Atlantic-Mediterranean- and Central European species, with scattered occurrences from the West-African Mediterranean coast to southernmost Sweden and Denmark, and from the British Isles to Transcaucasia. The species is now severely threatened and is included in the 'Red List' of threatened species in most countries where it occurs. This paper presents a revision of *Vertigo moulinsiana*'s fossil and recent distribution in Scandinavia and draws conclusions concerning the main controlling factors of the distribution of the species. The study summarises what is currently known about its biology and total distribution, as well as its Scandinavian historical record. One of the aims of the study has been to revise all samples of *V. moulinsiana* in Swedish collections as well as all literature concerning its fossil record. Notice is also drawn to problems concerning sampling and research on water margin and hillside deposits such as calcareous tufas.

The main expansion of *V. moulinsiana* appears to have occurred during the late Boreal (8,800-7,800 cal. BP) chronozone, at a time when there was a general rise in humidity and precipitation rates, as reflected in the geological record by a general rise of lake levels (Digerfeldt 1972). In the early 20th century it was believed that a rise in mean annual temperature occurred around the Boreal/Atlantic transition (7.800 cal. BP). The

northward expansion was thus attributed to the temperature increase and through comparison with present day European isotherms, a lowest annual mean temperature of at least 8-9°C was estimated for its survival (Odhner 1910a). This in turn was used as evidence that the Boreal/Atlantic temperature increase equalled at least 2-3°C above present (Fig 8). It has, however, later been argued that temperatures in this region had been at this level since the Younger Dryas/Preboreal transition at 11.500 cal. BP (e.g. Berglund et al. 1994; Gaillard and Lemdahl 1994; Hammarlund and Lemdahl 1994; Lemdahl 1991). It thus seems likely that other factors than temperature were more important at that time and we propose that moisture/humidity might have been the main controlling agent of *V. moulinsiana*'s northern distribution limit.

The timing of the species' decline is more difficult to determine since much fewer specimens are found from later periods, possibly due to the fact that few tufa deposits seem to be younger than 7,800 cal. BP in southern Sweden. The youngest dated fossil specimen of *V. moulinsiana* was found at Mästermyr, Gotland and probably dates to 5,000-5,500 cal. BP. At this time, groundwater levels were rising after a relatively low period at ~6,500 cal. BP. It is thus not possible to confidently estimate time when the decline began. It is, however, likely that the lowered mean July temperature, from 18.5 °C to 16.5 °C, around 2,600 cal. BP on Gotland (Mörner and Wallin 1977; Mörner et al. 1980) had negative effects especially on the northern distribution, if the species was still present at that time. *Vertigo moulinsiana* still exists at one locality in Sweden (lake Yddingesjön in Skåne) and at about 30 sites in Denmark (Bondesen 1966) but with the lack of historical records before modern time, it is difficult to argue that climate was the sole reason for its decline. There is reason to believe that the main threat to the species today is draining of wetlands and other human disturbances (Drake 1999).

A note is made to the fact that the recorded distribution in time and space of *V. moulinsiana* closely matches that of the European pond turtle *Emys orbicularis*. Since *E. orbicularis* requires a July mean temperature of at least 18ÚC to reproduce (Aaris-Sørensen 1988), it is likely to have been at least this warm during the late Boreal and Atlantic, the periods from which remains have been found (Persson 1992).

A further note is made to the fact that the lack of knowledge, especially of the immigration of *Vertigo moulinsiana* to Sweden, might relate to methodological problems. Since fossil terrestrial molluscs are almost solely found in terrestrial calcareous deposits, calcareous tufa, care must be taken when sampling. Usually, the deepest/thickest part of a deposit is sampled since this is expected to represent the longest timeperiod and is likely to provide the highest resolution. It is, however, unlikely that the oldest as well as the youngest parts of a hillside deposit, such as calcareous tufa, are represented at that spot. For example, a one-meter lake level raise at a bank with a 5° slope moves the shoreline 22 meters. For a snail like *Vertigo moulinsiana*, which commonly live in narrow water margin habitats, this would mean that its entire habitat, and consequently the historical record, would be moved away from the sampling point. Similar effects can be assumed with tufa deposits, which are commonly dependent of the groundwater level.

Fig 8. Present annual (top) and July (bottom) isotherms for southern Scandinavia. The areas investigated in this study are marked as: S= Saxtorp, F= Fyledalen (Pipers Mosse, Valleröds Mosse, Slagstorpshult and Örup), K= Kivik.

The main conclusions of this paper are:

- Although the current distribution and ecological requirements of *Vertigo moulinsiana* are well known, the present knowledge of its climatic requirements, and thus the cause of its decline in northern Europe, is based on old data and therefore not always correct.

- It is unlikely that temperature changes are the sole cause of timing of immigration or decline of the species .

- Defining the ecological and climatological requirements of a species, particularly in the case of a rare species, requires firm knowledge of its history.

- Good knowledge of the species history is also necessary if one discusses natural distribution, for example in association with conservation aspects.

- Similarities in distribution in time and space between *V. moulinsiana* and the European pond turtles, *Emys orbicularis*, suggests that the two species might be delimited by similar factors.

- Sampling of hillside deposits needs to take into account the possibility that a species habitat is likely to 'climb' up- or downslope, in response to environmental changes, for example changes in hydrology. A small change in groundwater level may move the habitat of a certain species, or even the entire deposit, away from the sampling point.

Paper III

Gedda, B. Terrestrial mollusc succession and stratigraphy of a Holocene calcareous tufa from the Fyledalen valley, southern Sweden. Manuscript submitted to *The Holocene*

This paper presents a reconstruction of vegetational and climatic changes around a calcareous tufa deposit at Valleröds Mosse, southeastern Skåne (Fig 4). It is situated in the Fyledalen valley, about 6 km from Pipers Mosse (App I). The objective was to test the hypothesis put forward in the Pipers Mosse investigation, that calcareous tufa deposition in the area took place during a time-period that experienced exceptionally low water levels. The mollusc record presented is one of the first dated land mollusc records from Sweden and reflects a development from an open ground community with species currently holding arctic alpine-northern distributions, to a community characterised by species with a more temperate affinity and southern distribution.

Tufa deposition was found to have occurred from about 11,500 to 8,800 cal. BP, although the start and the end of the tufa formation could not be securely dated. This was a time which experienced low groundwater levels, including the lowest of the entire Holocene during the period ~10,000-9,000 cal. BP (Digerfeldt 1988; Gaillard and Digerfeldt 1991). It appears that the more continental character of climate during the Preboreal and early Boreal time, with relatively high summer temperatures and low humidity, favoured tufa formation. Later as climatic continentality decreased, and precipitation and/or rate of discharge as well as humidity increased, tufa deposition ceased. The study thus supports the hypothesis put forward in Paper I that climate played an important role in the cessation of tufa deposition.

Tufa deposition occurred during a time when this region experienced a change in vegetation from open birch-pine forest to a fairly closed forest dominated by broad-leaved deciduous trees such as oak, elm and lime. The mollusc record, however, suggests that an open carr persisted locally throughout the entire depositional period. Based mainly on information from the mollusc record, but also supported by pollen data, it s shown that the dampness of the carr varied in a way similar to that of the regional lake levels as described by Digerfeldt (1988). Together, these records reflect a relatively moist period in the earliest Preboreal followed by a long slightly drier period with the lowest groundwater tables recorded during the Holocene. Later the regional groundwater table rose, the carr got increasingly moister and tufa deposition ended. An open water surface was present nearby during the last stages of tufa deposition. Local vegetation changed from open wet carr vegetation with a large portion of graminoid plants in the early phase of Preboreal to a calcareous carr with a moss dominated field layer in the later stages of Preboreal. The presence of *Vertigo moulinsiana* and the increase of *Poaceae* in the pollen diagram, suggest that around 8,800 cal. BP sedge-reed vegetation developed. Later, as tufa deposition ceased, a wood carr developed, as is indicated by the overlying carr peat.

In the recount of the faunal development, emphasis is put on the rare species *Columella columella*, and four Red Listed land snail species, including *Vertigo genesii, Vertigo geyeri, Cochlicopa*

nitens and *Vertigo moulinsiana*. These are today rare and severely threatened in many European countries (Gärdenfors 2000; Gärdenfors et al. 1988; von Proschwitz 1998c). Their Holocene fossil records as well as their recent distribution are summarised and notes are made about their ecological and climatic requirements.

In addition to molluscs, plant macrofossils and insects were collected and analysed. Because of the low recovery rate, however, these remains revealed limited information although they supported the general environmental interpretations.

The main conclusions of this paper are:

- Tufa formation was initiated during the early Preboreal (about 11,500 cal. BP) when an open birch-pine forest dominated the region. When the deposition ceased during the late Boreal (after 8,800 cal. BP), the surrounding vegetation consisted of a broad-leaved deciduous forest, with species such as oak, elm, and lime.

- The mollusc record suggests an open marsh environment throughout the time of tufa deposition although the last stages reflect a transition towards a more shaded environment.

- Tufa formation coincided with a time of low groundwater levels. The end of the deposition coincides with a rise in regional groundwater level.

- The first snails recorded are *Columella columella* and *Galba truncatula* in the early Preboreal.

- *Vertigo genesii* shows a continuous presence and is the dominant species throughout Preboreal and mid early Boreal. A possible cause to its disappearance may be rise in water temperature or increased shading.

- The find of *Cochlicopa nitens* was unexpected in association with high frequencies of *Vertigo genesii* since these two species today generally inhabit completely different geographical regions. *C. nitens* today is a southern species which generally is assumed to be thermophilous, while *V. genesii* has a mainly arctic/alpine distribution with a few scattered occurrences in connection with cold springs in mid to south Sweden and Great Britain.

- *Vertigo geyeri* is present throughout the deposit, except for the lowermost levels with very low recoveries (five levels with no more than five mollusc specimens in total). Numbers are, however, very low until the early/late Boreal transition (~9,000 cal. BP) when the environment became more damp. The richer record of this species coincides with the disappearance of *Vertigo genesii*.

- Around the early/late Boreal transition (~8,800 cal. BP), five specimens of the rare snail *Vertigo moulinsiana* (see App II) were found. With these included, the total number of recovered fossil specimens from Sweden of this species is now 90.

Paper IV

Gedda, B. The palaeoenvironment and molluscan succession of an early Holocene calcareous tufa at Saxtorp, western Skåne, Sweden. Manuscript submitted to *Journal of Biogeography*.

This paper presents a reconstruction of local environments and climate from analysis of a Holocene terrestrial tufa deposit in Saxtorp, close to the west coast of Skåne (Fig 4). The described deposit was situated 3.5 km from the coast, in a trough in the northern slope of the Saxå river valley. It is divided into four lithological units: lower tufa, marine clay, upper tufa and carr peat. Since the tufa deposit was found in connection with an archaeological excavation, also some aspects of human impact are taken in consideration.

During the highest Holocene transgression about 5,900 to 5,700 cal. BP, the Saxå valley constituted a sea bay and the site was reached by marine waters. The transgression is likely to have eroded the upper part of the lower tufa formation. The tufa was subsequently covered by clay originating from outwash of the boulder clay covering most of the surrounding bedrock and underlying post glacial sediments in the area.

Initially, dating of the sequence was problematic because ^{14}C dating unexpectedly gave ages inconsistent with previous knowledge. New dates were, however, obtained and dates from the lower tufa indicated lateglacial or early Preboreal age. The archaeological material in the overlying carr peat, as well as the well-dated upper marker horizon of the transgressive marine clay, provided ages for the upper tufa and the carr peat. The ages of the post transgressive sediments were found to be: upper tufa 5,600 - 5,400 cal. BP; the first part of the carr peat 5,400 - 5,100 cal. BP (early Neolithic remains); the second part of the carr peat 2,900 - 2,300 cal. BP (Bronze Age remains). The obtained ages are supported by the pollen record and archaeological context.

The radiocarbon dates suggested that the lower tufa was deposited in the earliest Holocene or

Younger Dryas. The unit displays pollen-stratigraphical characteristics of T. Nilsson's Preboreal zone: *Betula* and *Pinus* became established but *Corylus* had not yet expanded above 1%. The pollen sample also bears signs of an open heath environment with records of *Helianthemum*, *Calluna*, Poaceae, Cyperaceae and *Lycopodium*, which might be expected from a coastal site. The mollusc record reflects an open environment with a high number of vertiginides like *Vertigo genesii*, *V. lilljeborgi* and *Columella columella*. The local carr environment was completely open, vegetated only by mosses, *Carex,* herbs and grasses. There was probably no, or little, open water, the majority of the water-mass being transported as seepage. From the results reviewed above, it seems most probable that the lower tufa was deposited soon after the Younger Dryas/Preboreal transition, around 11,500 cal. BP.

When the clay was unit deposited, the site was inundated under about 50 cm of seawater.

Deciduous forest dominated the region as the upper tufa was deposited (Berglund 1986). Alder, oak, elm, lime and hazel were the main tree taxa at this time. The local carr environment was very different from that existing earlier. The mollusc diagram clearly reflects a shaded environment. The shade is likely to have been provided by hazel and alder while the field layer largely consisted of ferns, *Carex* and herbs. Along with carr peat development, the state of the plant macrofossil preservation improves and vegetation dominated by alder and including hazel, lime, beech and oak is indicated. The sporadic finds of oak macrofossils suggest that oak was locally present. At the previously mentioned hiatus, the carr becomes wetter, as exhibited by the mollusc record. The record also indicates a slight opening of the canopy with a decrease in shade demanding taxa. The vegetation records, plant macrofossil and pollen, on the other hand shows no marked change.

One find of a beech-nut (*Fagus silvatica*) was made in the upper tufa at 184 cm. This find pre-dates the suggested immigration of beech into the area with 1,500 to 2,000 years (Björkman 1996) and is thus likely to be a contamination that was introduced during sampling.
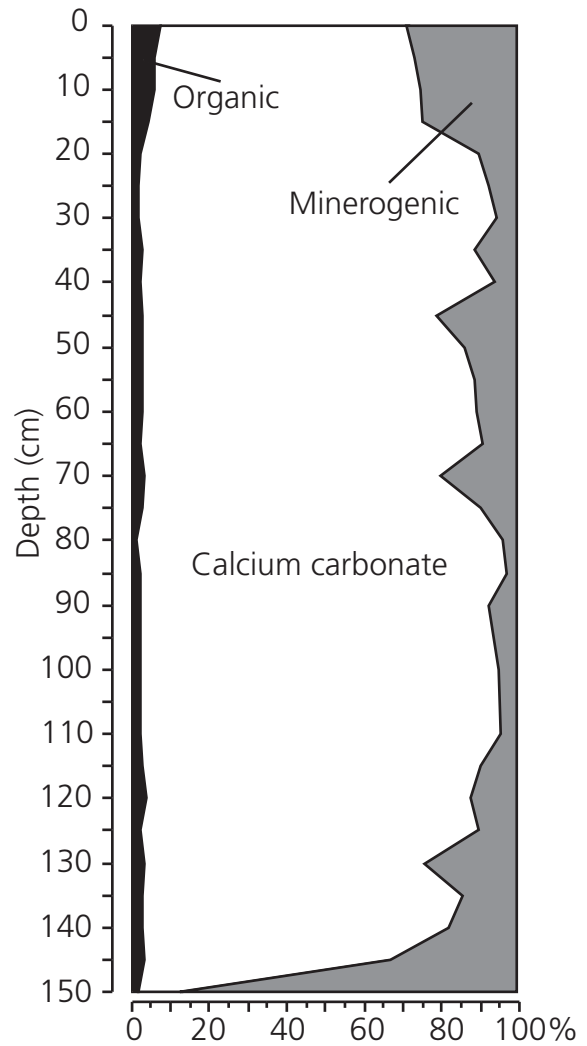

Fig 9. Results of the loss-on-ignition performed on the sediments from Slagstorpshult. Note the almost complete lack of organic material.

The mollusc record at Saxtorp displays two distinctly different faunal communities: An early Holocene species-poor community developed in an exposed slush environment and a mid-Holocene species-rich community developed under a shading canopy.

The lower tufa deposit is characterised by a mollusc community almost completely composed of open land species. Some of the species are mainly arctic alpine in their current distribution (*Columella columella*, *Vertigo genesii* and *Vertigo modesta*). At two levels, *Vertigo ronnebyensis* were surprisingly found in low numbers. In Sweden, early Holocene finds of this species has only been

Table 2. Radiocarbon dates from Slagstorpshult.

Lab nr.	Depth (cm)	14C BP	Cal. BP (68,2% conf.)
LuA-4581	15-20	530 ± 90	650 (1.00) 500
LuA-4582	95-100	350 ± 110	510 (1.00) 300

made twice before, in 'coastal Skåne' (Waldén 1986) and Högestad, south-central Skåne (Meyrick 1999). With regard to its current distribution, the species is believed to have immi-

Table 3. Lithostratigraphy of Slagstorpshult

Depth (cm)	Description
0-19	Tufa with topsoil contamination, grey
19-104	Tufa sand
104-147	Tufa clay
147-150	Green-gray minerogenic clay

grated from the north following the Holocene expansion of *Picea* forest. The previous finds in Skåne and Poland, however, suggest that these populations are reminiscences of an earlier, Preboreal, expansion from the south (Waldén 1986). The low pH of its preferred habitats, around 5.7, (von Proschwitz 1990, 1993a) might be one of the reasons that it is so infrequently found since, at this pH, shells are rarely preserved. It is thus an assumption that the finds were washed in from oligotrophic surroundings, with lower pH than in the calcareous carr.

The upper tufa and carr peat deposit exhibits a vastly changed fauna compared to that of the lower tufa. The fauna now reflects an enclosed deciduous forest-carr with a high percentage of more shade demanding taxa such as *Vitrea contracta*, *Aegopinella pura* and *Carychium tridentatum*. Also the number of taxa encountered has increased from 18 to 39 (including aquatics).

At the time of the second tufa deposition, Skåne experienced the last stages of a second period of low groundwater tables, which points to a continental climate with low precipitation rates. The less humid climate is reflected in the snail fauna by the presence of *Discus ruderatus,* which at present has a north-eastern distribution in Scandinavia, being rare on the west coast. The presence of open water is clear from the almost continuous presence of *Pisidium* sp. The sedimentary change from tufa to wood carr peat might be a sign of increasing humidity. This can, however, not be seen in the mollusc record until the hiatus in the carr peat, when there is a marked increase of carr species such as *Carychium minimum, Zonitoides nitidus* and *Galba truncatula* as well as *Pisidium* sp. At the same time the above mentioned dry-favoured taxa disappear or decrease.

Three mollusc species found during this investigation are Red Listed in the year 2000 list of Swedish species. These are *Vertigo ronnebyensis* (NT)*, Vertigo genesii* (NT) and *Cochlicopa nitens* (EN) (Gärdenfors 2000).

All units above the clay contained small amounts of insect remains. They mainly exhibit a preference for marshy habitats. Although no aquatic species were found, the insect assemblage indicates that open water was present close by as all recorded species live at the edges of stagnant water or are hygrophilic in general.

Considering the presence of a Neolithic and Bronze Age settlement, it is interesting to note that a change in the mollusc community, reflecting an opening of the canopy, is indicated. This seems to have occurred at some time between the periods of Early Neolithic and the Bronze Age and might well have been caused by local clearance.

The main conclusions of this paper are:
- Both tufa units were deposited during times with very low groundwater levels. Deposition of the upper tufa ended as groundwater level increased.
- The two tufa deposits display radically different environments and floral and faunal compositions. The lower tufa was deposited in an open heath environment with a mollusc fauna almost completely lacking shade-demanding species. The upper tufa was deposited in a shaded environment, surrounded by a closed deciduous, mixed broad-leaved forest.
- Local clearance is suggested to have occurred between the Early Neolithic and the Bronze Age.
- A find of *Vertigo ronnebyensis* supports the hypothesis that this species had an earlier expansion from the south.
- Three Red Listed mollusc species were encountered: *Vertigo ronnebyensis, Vertigo genesii* and *Cochlicopa nitens.*

Slagstorpshult

Site description

This site is located at the bottom of a tributary valley on the north-eastern slope of the Fyledalen valley in southern Skåne (55°34'35 N, 14°51'19 E, Fig. 4), between the sites Pipers Mosse (App I) and VallERöds Mosse (App III). The results from this site was never published because of conflicting AMS dates (Table 2). The site consists of a small, now dry, calcareous tufa deposit with 1.5
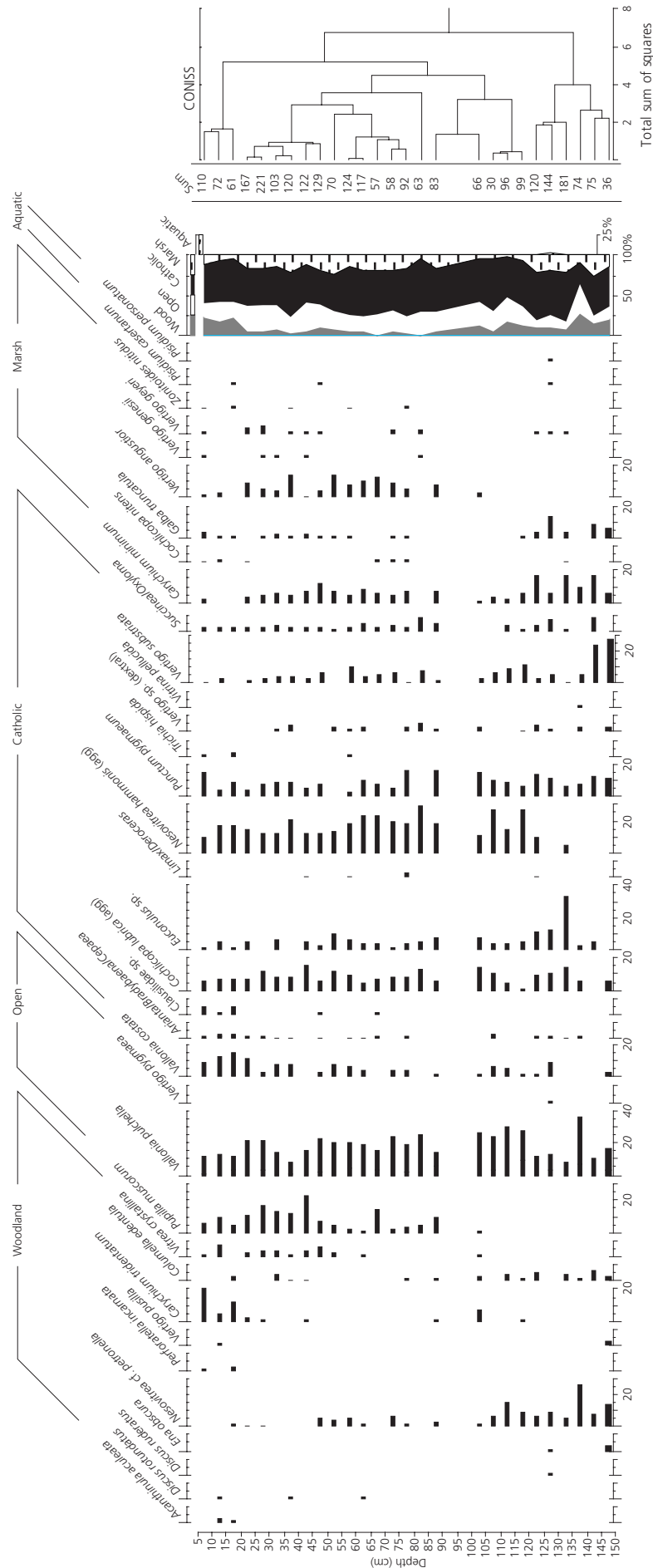
Fig 10. Percentage diagram of molluscs found at Slagstorpshult. In the malacological environment classification, aquatic molluscs are excluded from the terrestrial mollusc sum. The aquatic percentage is calculated on the total mollusc sum, including aquatics. Percentages are based on the estimated minimum number of gastropod individuals, normally equal to the numbers of apices [for bivalves (i.e. Pisidium), 0.5 times the number of half-shells was used]. Cluster analysis was performed as a support for identifying the assemblage zones (CONISS, as implemented by the program TILIA.GRAPH, Grim 1990).

m gravely sandy tufa, overlying a till layer of unknown thickness (Table 3). Loss on ignition was performed at 5 cm intervals to complement lithological description (Fig 9). No tufa is presently formed at the site. Cretaceous-Tertiary limestone, sandstone, a predominance of shale, and crystalline rocks, form the bedrock in the catchment area (Daniel 1986). The study area is situated in the temperate vegetation zone of broad-leaved deciduous forests (Ahti et al. 1968) but today the area is dominated by pastures and planted woodlands. The present local vegetation consists of a beech forest (*Fagus silvatica*) vegetation. (See also App I and III)

Mollusc analysis

35 mollusc taxa, 33 gastropod and 2 bivalve taxa were identified (Fig 10). Some juvenile *Nesovitrea* could not be determined to species level. These are referred to as *N. hammonis* agg, including *N. hammonis* and *N. petronella*. The dextral *Vertigo* sp. group most likely includes apexes of *V. geyeri* and *V. genesii*. Three malacological zones (SLM 1-3), were identified and are described and interpreted as follows:

SLM1 (150-105 cm): This zone is characterised by the absence of *Pupilla muscorum*, *Vitrea crystallina* and *Vertigo angustior*. SLM 1a (145-120 cm) is a significant group of samples as defined by the cluster analysis. *Nesovitrea hammonis* and *Euconolus* sp. appear in this zone and are present throughout the rest of the sequence. *Vallonia costata* is absent from three layers and *Ena obscura* is only present in two. *Ena obscura* have a relatively southern distribution reaching southern to middle Sweden. It is a fastidious woodland species preferring calcareous soil (Kerney and Cameron 1979; von Proschwitz 1993b). Also *Vertigo pusilla* is a woodland species reaching the Arctic Circle in Norway, Finland and western Sweden. *Nesovitrea petronella* and *Discus ruderatus*, represented by a single specimen, are found in this zone. These have at present a relatively continental/north-eastern distribution in Sweden,

being very rare at the west coast. *Punctum pygmaeum* is a catholic species that, except for one level, is present throughout the deposit. *Carychium minimum* and *Vertigo substriata* are both carr species although the latter prefer shaded areas (von Proschwitz 1993a; von Proschwitz 1998b). *Vallonia pulchella* thrives in open to semi open habitats although it has a second ecological optimum in screes in broad-leaved woodland (von Proschwitz 1993b).

SLM1b (120-105 cm) is similar to SLM1a but separated on the basis of the cluster analysis. *Nesovitrea hammonis* increases and *Carychium minimum* decreases.

SLM2. (105-20 cm): This is a very homogeneous zone with its lower boundary defined by the presence of *Vitrea crystallina*, *Pupilla muscorum* and *Vertigo angustior*. *Vitrea crystallina* is a mesotrophic woodland species that today primarily has a

Table 5. Lithostratigraphy of Örup.

Depth (cm)	Lithology
0-15	Grey calcareous topsoil
15-41	Yellowish-brown, fine-grained tufa
41-50	Hard concretion
50-58	Grey-white sandy tufa
58-63	Grey-white clayey tufa sand
63-81	Iron oxide stained sandy gravelly tufa
81-90	Iron oxide stained sandy tufa
90-106	Iron oxide stained and white gravelly tufa with up to 2 cm tufa concretions
106-120	White calcareous gravel with a black discolouration at 110-111cm*
120-140	Grey-white, slightly iron oxide stained calcareous gravel with a dark brown iron oxide stain at 126-127 cm
140-156	Grey-white clayey tufa with several 1-2 mm thin black lamina. The lowermost lamina (at 154-156 cm) were brown.
156-157	Iron oxide stained layer
157-163	Iron oxide stained coarse gravel
163-?	Grey coarse sand

*An attempt to analyse the pollen content on this layer was unsuccessful.

Table 4. Radiocarbon dates from Örup.

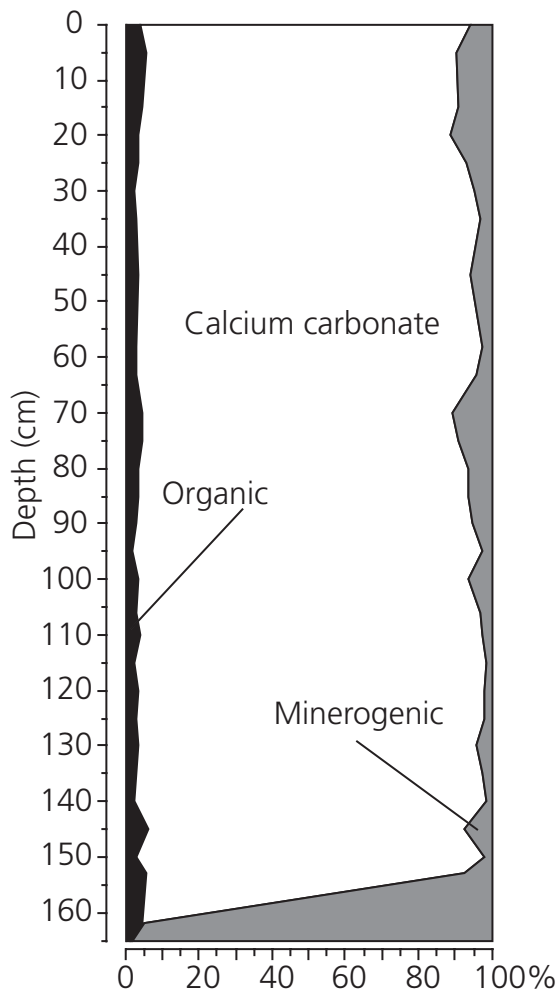| Lab nr.	Depth (cm)	¹⁴C BP
LuA-4580	25-30	>Modern; 114±2.0 pM
LuA-4579	90-105	>Modern; 127±2.0 pM
LuA-4578	135-140	>Modern; 114±1.3 pM
LuA-4577	140-150	>Modern; 118±1.8 pM

Fig 11. Results of the loss-on-ignition performed on the sediments from Örup. Note the almost complete lack of organic material.

congener to the more northern *Discus ruderatus* (Meyrick 1999). Present are also the rare and shade intolerant *Vertigo genesii* as well as *Vertigo geyeri*. Both species are classified as NT (near threatened) in the Swedish Red List of endangered species (Gärdenfors 2000).

SLM3 (20-5 cm): This zone is classified by the cluster analyses as a significant group. *Carychium tridentatum* is a congener to *C. minimum*, indicating somewhat drier and more shaded environments (Evans 1973). Also *Perforatella incarnata, Vertigo pusilla* and *Acanthinula aculeata* are found in this zone. In Europe, *Perforatella incarnata* has a pronounced continental modern distribution while in Sweden it is south-western (Kerney and Cameron 1979; von Proschwitz 1998a). *Acanthinula aculeata* is a woodland species, not generally a member of the carr fauna but prefer the drier fringes.

Plant macrofossils

A small number of plant macrofossils was encountered, most of them in the uppermost 15 cm. *Rubus* was present in the uppermost sample (0-5 cm) and *Sorbus* sp. in the top three samples (0-15 cm). Pine was present in three levels above 50 cm. *Eupatorium cannabinum* is usually common in tufa deposits but is here only found at 70-75 cm. A small piece of a *Betula* leaf was found at 125-130 cm.

Conclusions from this investigation

The mollusc community in Slagstorpshult (Fig 10) reflects a damp environment throughout the sequence. There seems to have been a moderate amount of shading with open and shaded patches, as indicated by the presence of both the fastidious open land species *Vertigo genesii* (Colville 1998; Preece and Day 1994) and fastidious woodland species such as *Ena obscura, Columella edentula, Perforatella incarnata* and *Acanthinula aculeata* (Kerney and Cameron 1979). The tufa seems to have developed later than at corresponding sites on the opposite side of Fyledalen since the mollusc community contains a number of species such as *Vertigo angustior, Cochlicopa nitens, Perforatella incarnata, Trichia hispida* and *Acanthinula aculeata* that appears in the upper part of the deposits at Pipers Mosse and Valleröds Mosse.

south-western distribution in Sweden which is likely to depend on precipitation (von Proschwitz pers. comm.). *Vertigo angustior* is an inhabitant of wet marshy open grasslands. In Sweden it is mainly found in coastal areas south of Stockholm, but also in calcareous inland areas. The species has two ecological optima. Screes in dry broad-leaved forests is the most common inland habitat, while open calcareous marshes and wet meadows are most common in coastal areas (von Proschwitz 2000). Other marsh species such as *Galba truncatula* and *Zonitoides nitidus* as well as the somewhat hygrophilous *Vitrea crystallina* are also present. Most species found in SLM1 are generally also found in the samples of SLM2, although *Nesovitrea petronella* usually shows lower numbers. There are also rare finds of a number of other species like *Trichia hispida*, which today reaches mid-Sweden, and *Discus rotundatus*, which in Europe and Great Britain is seen as a southern

Environmental and climatic aspects of the early to mid Holocene
calcareous tufa and land mollusc fauna in southern Sweden
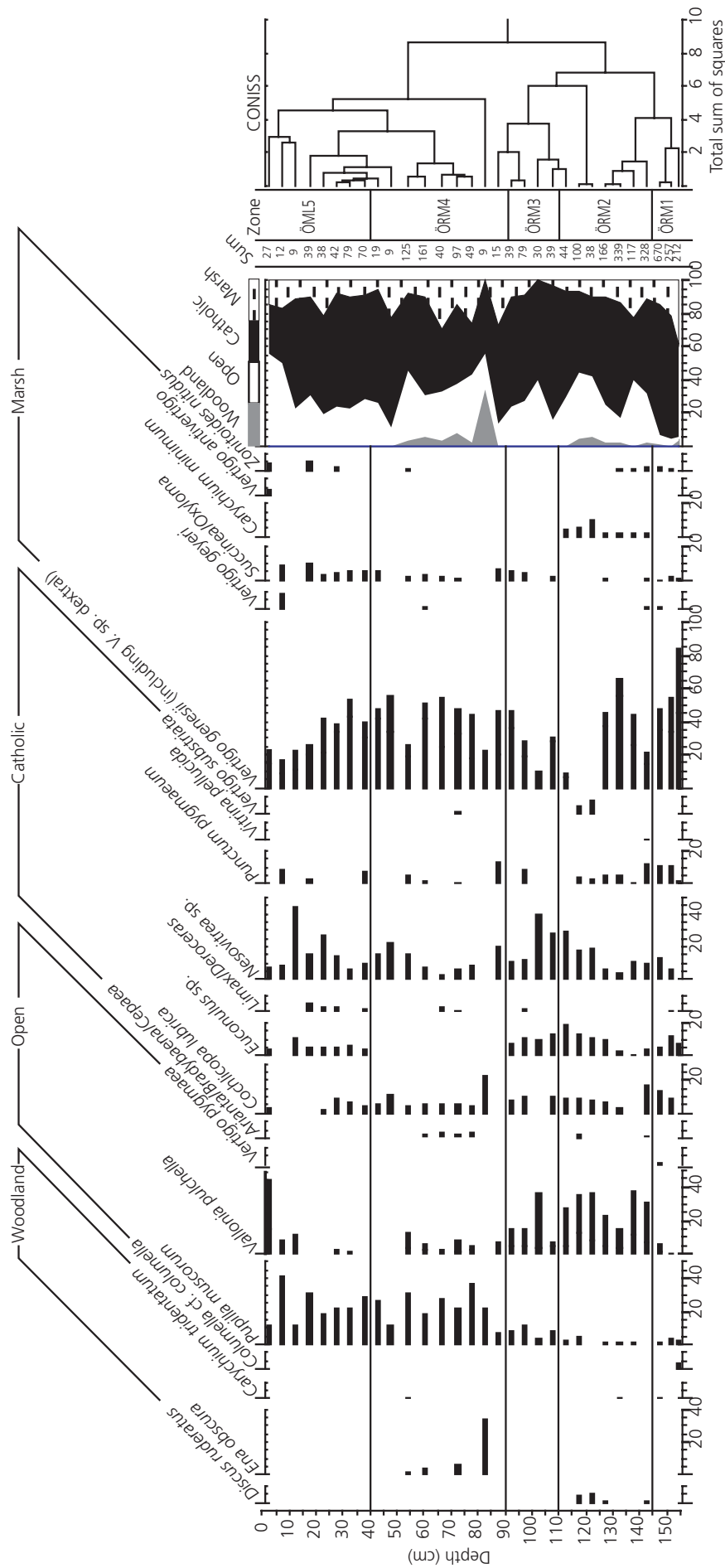

Fig 12. *Percentage diagram of molluscs found at Örup. Percentages are based on the estimated minimum number of gastropod individuals, normally equal to the numbers of apices [for the bivalves (i.e. Pisidium), 0.5 times the number of half-shells]. Cluster analysis (CONISS, as implemented by the program TILIA.GRAPH, Grim 1990) was performed to support the identification of assemblage zones.*

Örup

Site description

Örup (55°32'11 N, 14°57'11 E, Fig 4), on the northern side of a tributary valley of Fyledalen, is situated in a beech grove about 8 km from Slagstorpshult, in the temperate vegetation zone of broad-leaved deciduous forests (Ahti et al. 1968). The investigation was never published because of conflicting dates (Table 4). The deposits comprise 1.63 m of clayey – sandy tufa which at many levels is heavily iron stained, sometimes to the extent that iron concretions have formed (Table 5). It is underlain by sand and overlain by brown earth topsoil. Loss on ignition was performed to facilitate sediment description (Fig 11). Note the almost complete lack of organic and minerogenic constituents during the time of tufa deposition. No tufa is presently formed at the site. Cretaceous-Tertiary limestone, sandstone, a predominance of shale, and crystalline rocks, form the bedrock in the catchment area (Daniel 1986). (See also App I and III)

Mollusc analysis

24 gastropod taxa were identified (Fig 12). *Nesovitrea hammonis* and *N. petronella* suffered from iron-staining, making differentiation difficult. Consequently, these were combined into one taxa; *Nesovitrea hammonis/petronella*. Since few specimens of *Vertigo geyeri* were identified, dextral *Vertigo sp.* is grouped with *Vertigo genesii*. Other *Vertigo* species found (*V. substriata*, *V. pygmaea* and *V. antivertigo*) are easily differentiated from these, even as juveniles. A single fragment of an unidentified fragment of a large shell (*Arianta/Bradybaena/Cepaea* at 115-120 cm) was grouped with *Cepaea hortensis*. Five mollusc assemblage zones (ÖRM 1-5) were identified and are described as follows:

ÖRM1 (155-145 cm): The basal zone consists of three samples, limited upwards by the definition of ÖTU2. A number of open land carr species are present in the unit, including *Vallonia pulchella*, *Vertigo pygmaea*, *V. genesii* and *V. geyeri*. *Carychium tridentatum* is a hygrophilous species found in both open and closed environments.

Zonitoides nitidus is a marsh species preferring very wet places such as flood banks. The species' *Cochlicopa lubrica*, *Euconulus* sp., *Nesovitrea hammonis*, *Vertigo* sp. (dextral), *Punctum pygmaeum* and *Succinea/Oxyloma* have been classified as catholic. *Pupilla muscorum* is classified as open land with a drier affinity (f. *typica*) although it can not be completely ruled out that some of the specimens might be f. *pratensis*, which is associated with carr environments. *Vertigo genesii* and *V. geyeri* are classified as NT (near threatened) in the Swedish Red List of endangered species (Gärdenfors 2000).

ÖRM2 (145-110 cm): This zone is delimited from ÖRM1 and ÖRM3 by the presence of *Carychium minimum* and *Discus ruderatus*. *Carychium minimum* is a species characteristic of carrs or very moist woods. *Discus ruderatus* is a species typically found in oligo- and mesotrophic coniferous and mixed forests. It has a modern north-western continen-
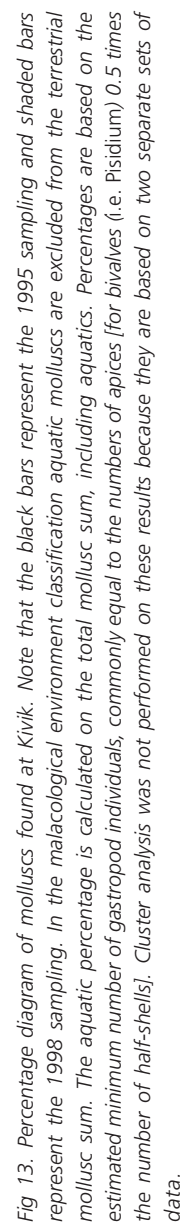
Table 6. Lithostratigraphy of Kivik

Depth (cm)	Description
0-100	Sandy to clayey tufa with up to 10-cm rounded casts of branches.

tal distribution with its southern limit in the northern part of Skåne, corresponding to that of *Picea* (von Proschwitz 1993b). *Vertigo genesii* (and *Vertigo* sp.) are absent from two samples, coinciding with a slight increase in the numbers of *D. ruderatus*. This might be an indication that the carr was less open at this time. A single specimen of *Vitrina pellucida* was found in this zone, a catholic species found in a wide variety of moderately moist places. *Zonitoides nitidus* is still present in the lowermost samples. The species is a marsh species preferring very wet places such as flood banks.

ÖRM3 (110-90 cm): This zone is delimited downwards by the first sample without *Carychium minimum* and upwards by the last sample before the occurrence of *Ena obscura*. The fauna in this zone resembles those found in the over-

Table 7. Radiocarbon dates from Kivik. Both dates were performed on plant macrofossils found in the 1998 samples.

Lab nr.	Depth (cm)	δ^{13}C	^{14}C BP	Cal. BP (68,2% conf.)
Ua-14604	20-25	-25.4	5,100 ± 80	5930 (1.00) 5740
Ua-14605	95-100	-25,7	3,160 ± 80	3470 (1.00) 3260

Fig 13. Percentage diagram of molluscs found at Kivik. Note that the black bars represent the 1995 sampling and shaded bars represent the 1998 sampling. In the malacological environment classification aquatic molluscs are excluded from the terrestrial mollusc sum. The aquatic percentage is calculated on the total mollusc sum, including aquatics. Percentages are based on the estimated minimum number of gastropod individuals, commonly equal to the numbers of apices [for bivalves (i.e. Pisidium) 0.5 times the number of half-shells]. Cluster analysis was not performed on these results because they are based on two separate sets of data.

and under lying zones, although with a slightly lower number of taxa as well as the absence of the species just mentioned. Compared to ÖRM2 is also *Discus ruderatus* absent, *Pupilla muscorum* has increased and *Vallonia pulchella* has started to decrease.

ÖTU4 (90-40 cm): This zone is characterised by the lack of *Euconulus* sp. and the presence of *Ena obscura. Ena obscura* today is a rare fastidious woodland species preferring calcareous soils (Kerney and Cameron 1979; von Proschwitz 1993b). In Scandinavia the species is fairly southern. *Vallonia pulchella* decreases.

ÖTU5 (40-0 cm): This zone is delimited by the reappearance of *Euconulus* sp. *Vertigo antivertigo* is found in the uppermost sample. This is a marsh species, often found on dead sedge leaves and under flood debris.

Conclusions from this investigation

The mollusc record from Örup reflects an open environment, primarily indicated by the almost continuous presence of *Vertigo genesii*. When compared to the nearby sites Valleröds Mosse and Pipers Mosse as well as Högestad (Meyrick 1999) it seems likely that the tufa was deposited during the Preboreal and at least throughout the early Boreal (11,500 - 8,800 cal. BP). The presence of the relatively southern woodland species *Ena obscura* in samples with a high number of the open land species *Vertigo genesii* is unexpected and might be a sign that the stratigraphy is disturbed. As with the Slagstorpshult record, no absolute or relative dates were achieved and it is therefore not possible to assess the credibility of the sequence.

Kivik

Site description

The site is situated on the eastern coast of Skåne, about 1.5 km WSW of the harbour of Kivik, along a small stream formerly called Hjärtabäck (55°41' N, 14°12'20 E, Fig 4). The results from this site were never published because no correlation could be made between the two cores and because of conflicting radiocarbon dates. It also proved impossible to produce a pollen diagram to support the obtained dates or assign the validity of the chronology.

C. Kurck reported (Kurck 1904) from a number of tufa deposits in the area which all had a highly diversified fauna. Even at that time the number of undisturbed deposits had radically decreased compared with 1880 when Kurck first noticed them and the sediments still were mostly undisturbed. Between 1880 and 1904 extensive quarrying was carried out to obtain calcium carbonate to be used as fertiliser, possibly brought about by the 1889 description of the geological maps of the area (De Geer 1889). The present work was an attempt to localise Kurck's localities and to reinvestigate one of the sites with a higher stratigraphical resolution. The site chosen approximately corresponds to *Mellby profile b* (Kurck 1904 p. 299-304). The area was up to the beginning of the 20th century a region with high diversity in a number of floral and faunal groups, including herbs and molluscs. South of Kivik, a remnant of the coastal forest comprising lime, oak, ash, elm and maple which used to cover the raised beaches towards Stenshuvud still existed although much of it had been cut down to prepare for agriculture (Kurck 1904). This forest as well as many other habitats have since been destroyed or severely diminished to prepare for agriculture and settlements.

This site was sampled on two different occasions. During a survey in 1995, the top 50 cm was sampled. After sorting and identification of the mollusc fauna, it was decided that the site should be resampled in its full length, which was done in 1998 about one meter upstream from the original sampling point. The lithology comprises 1.0 m of very fine grained (mostly sand to clay fraction) tufa with large (<10 cm) casts, probably of branches (Table 6, Fig 2a). The tufa overlays a clayey till, of which there are some traces in the lowermost samples.

Dates

As seen in Table 7, the dates (approximately 5,800 cal. BP at 20 cm and 3,400 cal. BP at 95 cm) are in reversed order and might thus indicate a disturbed sequence. The ages are however interesting since they suggest that the deposit is much younger than the tufas previously studied. The deposition might have occurred during the Subboreal-Subatlantic (after 5,700 cal. BP). The tufas described in App I, III and the lower deposit in App IV, are all Boreal (>7,800 cal. BP) in age at the youngest, except for the upper tufa in Saxtorp (App IV) which has an age of about 5,700 - 5,500 cal. BP (early Subboreal).

Molluscs

With 48 mollusc species; 45 land gastropods, 2 aquatic gastropods and one bivalve (aquatic), the site contains the highest diversity of any of the sites surveyed (Fig 13). The number of recovered molluscs varied greatly between samples. At eight levels the numbers were even lower than 48, the total number of taxa.

There are some features of the diagram that are worth special attention:

- *Columella columella* is today a high-arctic/alpine open land species. In Skåne it seems to be characteristic of early Preboreal or older sediments, *i.e.* before 11,000 cal. BP. It is found in two of the lower levels, which might be expected. Its presence together with or after a high number of woodland taxa like *Cochlodina laminata*, *Aegopinella nitidula*, *Aegopinella pura*, *Vitrea contracta* and *Acanthinula aculeata* is unexpected and a reason for doubting the integrity of the sequence.

- *Vertigo genesii* is sensitive to shade and according to Colville (1998) and Preece and Day (1994), indicative of sites that never were shaded. It does not seem probable that the species should be present after a long period of shading. Although *V. genesii* is very rare today, it appears to have been a very common snail during the early Holocene (c.f. App. III and IV). *Vertigo genesii* is classified as NT (near threatened) in the Swedish Red List over endangered species (Gärdenfors 2000).

Conclusions from this investigation

Due to the fact that no chronology was obtained it is impossible to say anything about the age of the deposit with certainty. It also seems likely that the deposit is reworked, possibly during the late 19th century. Key species are found in faunal assemblages that seem unlikely to be original. An example of such assemblage is the presence of the open land species *Vertigo genesii* in association with the shade demanding species *Ena obscura*. In addition, the slightly chaotic appearance of the diagram may indicate a disturbance. The potential of the site is nevertheless high and a new re-sampling should be conducted.

Stable isotope analysis

Background

Previous to this study, no stable isotope measurements had been conducted on Swedish calcareous tufas. In other parts of Europe [e.g. England (Andrews et al. 1994), Germany, (Arp et al. 2001), Spain (Andrews et al. 2000), Poland (Pazdur et al. 1988)], a number of investigations have been carried out, and during the 1980s and 1990s it was concluded that the method may yield valuable information concerning a variety of environmental parameters, such as palaeoclimate, water isotopic composition, soil composition changes, etc (Andrews et al. 2000; Andrews et al. 1997; Pazdur et al. 1988). Stable isotopes of oxygen in calcareous tufa has proved to be in equilibrium with meteoric water, and evaporative and residence time effects have a minor influence on ^{18}O fractioning in this type of deposits (Andrews et al. 2000; Andrews et al. 1997; Friedman 1970; Hays and Grossman 1991). Furthermore, Usdowski et al. (1979) showed that the oxygen isotope composition is independent of whether the tufa is of biogenic or inorganic origin (*i.e.* whether or not plants or animals have contributed to the depositional process). This is important since both processes may occur at the same time in different parts of a stream environment.

Most European studies have been undertaken on riverine or lake tufas where microbial influences and possible atmospheric exchange as well as water transportation effects such as turbulence might affect the results. In this study the paludal (Pedley 1990) tufa of Valleröds Mosse has been selected. Paludal tufas have the advantage relative to lake and river tufas in that they are spring deposits, which means that the carbonate-saturated water has a short flow distance from the spring to the deposition point. The short flow distance minimises the above mentioned effects.

In a temperate climate, the oxygen isotopic compositions of terrestrial mollusc shells has been shown to be directly related to the mean δ^{18}O of the meteoric water of the snails growing season (Lécolle 1985). For areas with no or negligible winter non-growth period, the δ^{18}O of terrestrial molluscs reflects the annual mean δ^{18}O of the precipitation. For the south-Swedish region the composition is likely to record the mean spring-summer-autumn composition.

The mollusc chosen for isotopic analysis is the terrestrial snail *Vallonia pulchella* which occurs throughout the studied sequence. *V. pulchella* has two, ecological optima: Screes in dry broad-leaved forests and moist sites like calcareous marshes and grassland (von Proschwitz 1999). At Valleröds Mosse the environment was that of a calcareous carr and thus the specimens are likely to be of the carr form which means that their shells were

formed in equilibrium with ambient groundwater.

It has been shown that carbon isotope components in tufas record the dominant carbon source, in this case the surrounding terrestrial environment (Andrews et al. 1997). The carbon in the body fluids and shell of land snails originates from a variety of sources, including metabolic CO_2 from food and respiration, CO_2 from ingested carbonate and atmospheric CO_2 (Goodfriend and Hood 1983; Leone et al. 2000). However Goodfriend and Magaritz (1987) found correlation with rainfall, humidity and altitude.

Note - For chronological, environmental, climatological, zoological and vegetational data obtained from the site, see App III. This also applies to the geological setting and interpretation and description of the lithology.

Results (Fig 14)

- The records of $\delta^{18}O_{tufa}$ and $\delta^{18}O_{mollusc}$ exhibit broadly consistent trends.

- The offset between $\delta^{18}O_{tufa}$ and $\delta^{18}O_{mollusc}$ indicate that tufa and molluscs have somewhat different oxygen sources. The reason for the difference might be that that tufa is mainly precipitated during the spring (Pazdur et al. 1988) when groundwater originates to a large extent from snow-melt with a relatively low $\delta^{18}O$. Molluscs on the other hand build their shells throughout the warm season (Lécolle 1985) during which the available groundwater is enriched in ^{18}O.

- The distinct decrease in $\delta^{13}C_{tufa}$ in the lower part of the record probably reflects establishment of terrestrial vegetation and a related increase in soil respiration supplying ^{13}C depleted carbon dioxide to the local groundwater (Andrews et al.
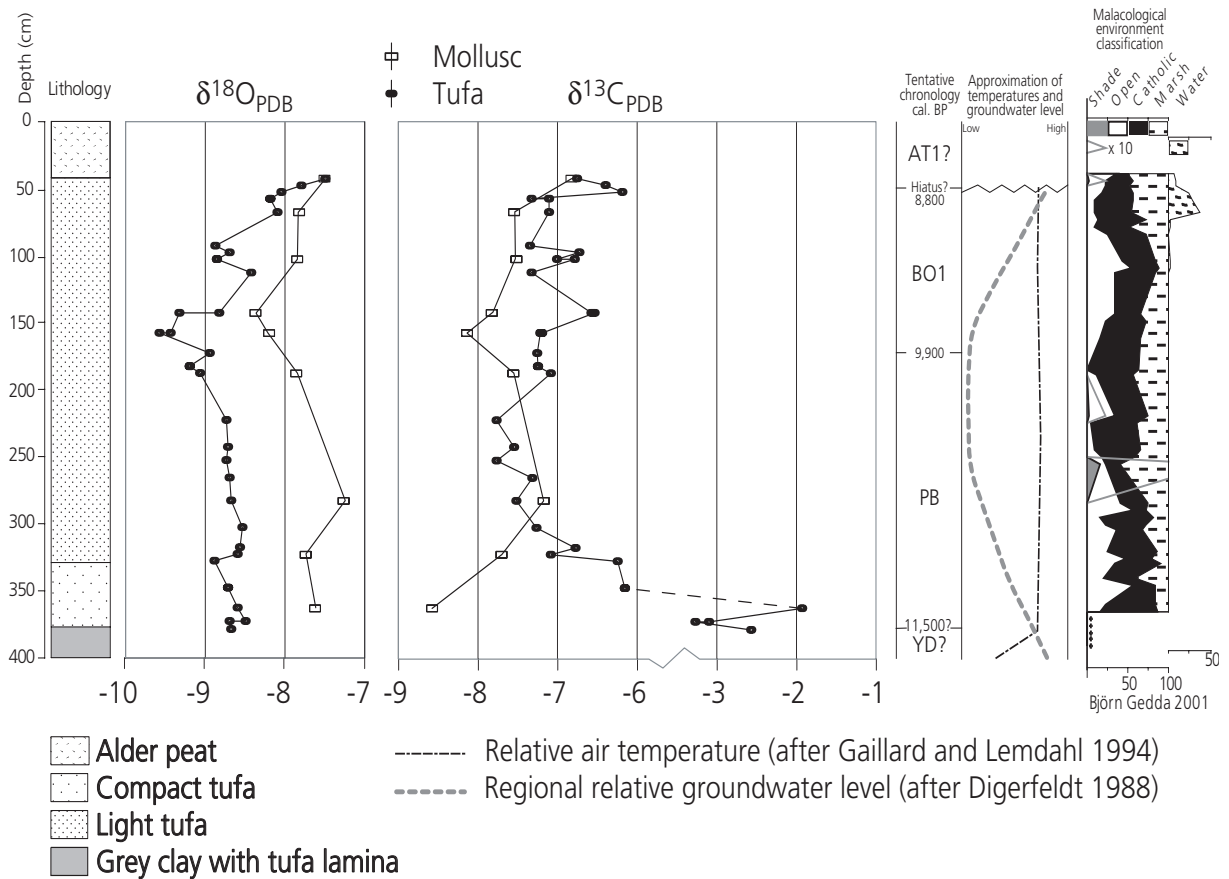
Fig 14. Isotopic profiles for calcareous tufa (left) and terrestrial molluscs (right, Vallonia pulchella) from Valleröds Mosse. Because of lack of material, there are less data points for molluscs than for tufa. Note that the tufa $\delta^{13}C$ record is truncated at c. 305 cm. Capital letters refer to significant changes explained in the text. General trends: A. Terrestrial vegetation is established locally. B. Increased groundwater temperature (annual air temperature). C-D: Stronger influence of surface (river) water. The lowermost part of the malacological environmental interpretation is not plotted because of an insufficient number of individuals. The ithology, chronology, regional groundwater levels, regional temperature estimates and malacological environmental interpretations are explained in App III.

1997; Hammarlund et al. 1997). This change might be coupled to the Younger Dryas/Preboreal transition, at which time there was a significant change in terrestrial vegetation and soil stabilisation occurred (e.g. Berglund et al. 1994)

- Towards the Preboreal/Boreal transition there is a decrease in $\delta^{18}O_{tufa}$ which might reflect an increase in groundwater temperature. This rise in groundwater temperature could be caused by an increase in mean annual temperature.

- The Boreal increase in $\delta^{18}O_{tufa}$ likely reflects increased influence of surface water with a higher $\delta^{18}O$ than corresponding groundwater. The enrichment in ^{18}O coincides with regional rise in groundwater level (c.f. Digerfeldt 1988). This also induces larger variability since surface water has a larger $\delta^{18}O$-variation.

- Local disequilibrium effects as well as short term variability in water chemistry and tempera-ture might be expected to cause small excursions in $\delta^{18}O_{tufa}$. This is probably what is recorded in the upper, Boreal, part of the $\delta^{18}O_{tufa}$ record where there is a larger variability between samples. In the lower, Preboreal, part of the record, the water is mainly originating from the groundwater which has a more stable $\delta^{18}O$ due to homogenisation of seasonal variations.

- The decreased offset between $\delta^{18}O_{tufa}$ and $\delta^{18}O_{mollusc}$ during the Boreal indicates a change in depositional environment, probably related to increased influence of river water. The $\delta^{18}O_{mollusc}$ is not affected to the same extent, probably because of the snails' mobility which allows the it to move up and out of the river water. Another reason might be that parts of the shell are built during summer and autumn. As the groundwater already is enriched in ^{18}O at this time, the effect of river water is reduced.

Discussion

In the following chapters, the environmental, vegetational and malacological development s around early Holocene calcareous tufa deposits, are discussed in a wider sense to form a synthesis of the published (App. I-IV) and unpublished material.

Chronology

Throughout the investigation of calcareous tufas, AMS-dating on terrestrial plant remains (*i.e.* seeds) has proved problematic. As a result of oxidising conditions during deposition, organic content of tufa is generally low, which makes it difficult to extract sufficient material for dating. Apart from the large statistical errors introduced when carbon mass approaches the minimum amount required for analysis, low organic content also makes samples more prone to contamination by older or younger material and errors induced by the preparation method (Wohlfarth et al. 1993). For these reasons, the AMS dates reported in this thesis are generally difficult to interpret. Possible sources of error include preparation procedures, possible contamination by older or younger material and reservoir effects. However, since exclu-

sively terrestrial material has been used for dating, reservoireffects may be disregarded (Wohlfarth et. al. 1993).

Pollen analysis was used as a chronological tool to verify ^{14}C chronologies. In spite of the relatively low resolution of the pollen records, correlation to well-dated diagrams from bogs (Berglund and Ralska-Jasiewiczowa 1986; Nilsson 1964) was remarkably successful.

In the future, it may be possible to establish local chronologies based on malacological evidence. Although the precision of such a chronology would be low, it could be used to support AMS dates in situations when pollen analysis fails. Well-dated faunal changes are used for relative dating in other parts of Europe (e.g. Evans 1973; Meyrick 1999). In Sweden, more research is still needed before terrestrial snails may be used as chronological evidence. There are, however, some species and events that have the potential to form a basis for a Swedish/South Swedish malacochronology. One example is the disappearances of taxa with a presently more northern distribution such as *Columella columella*, whose disappearance in Skåne appears to be dated to the ear-
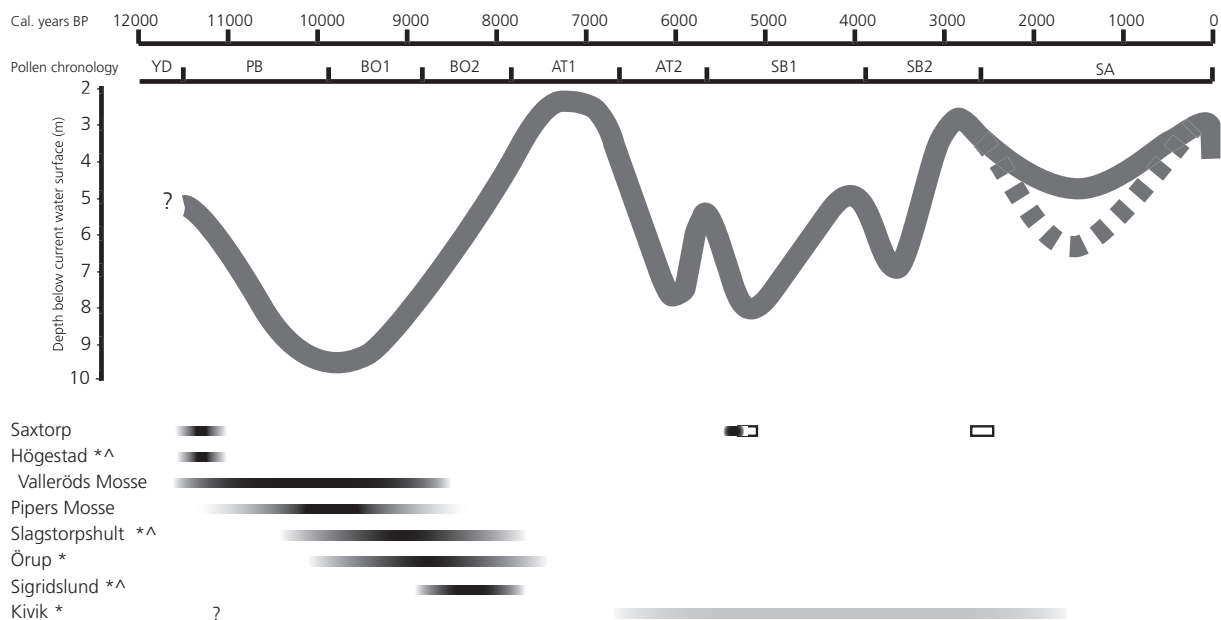

Fig 15. Estimated chronologies for recently investigated mollusc and tufa deposits in southern Skåne in relation to South Swedish lake level changes. The thick curve represents a reconstruction of South Swedish lake levels during the Holocene (after Digerfeldt 1988). The curve has been calibrated to calendar years. The part of the curve spanning the last 3,000 years has been modified after suggestions made by G. Digerfeldt. The dotted line represents the original curve. * The chronology is based on molluscs alone. ^ After Meyrick (1999) (note that I have reinterpreted the mollusc compositions and shifted Högestad from Younger Dryas to early Preboreal and Sigridslund from Preboreal to late Boreal). Hollow squares represent terrestrial malacological records from other sediments than tufa (i.e. wood carr peat).

liest part of the Holocene. Other examples include the appearance of taxa such as *Vertigo antivertigo* and *Carychium tridentatum* and the transition from a fauna characterised by *Discus ruderatus*, which has a northern/continental distribution to a fauna characterised by *D. rotundatus*, which has a southern/oceanic distribution (von Proschwitz 1999). This transition has been identified at a number of sites across Europe (Meyrick 1999). At present there are, however, not enough well dated sequences to enable the construction of a South Swedish mollusc-based chronology.

Despite these problems of dating, this work provides important and new data on the age of formation of tufa in Skåne. The early part of the Holocene (11,500 to 8,000 cal. BP) in Skåne, is represented by three sequences with absolute chronologies, two in the south-central and one on the western coast (App I, III and IV). Mid and late Holocene (after 8,000 cal. BP) is represented by one dated sequence (App IV) that only covers the periods 5,600-5,100 cal. BP and 2,900-2,300 cal. BP. North of Skåne one dated sequence exists – Vitlerbäcken (about 9,800-5,500 cal. BP) by the lake Vettern (Meyrick 1999).

At Valleröds Mosse the unpublished oxygen isotope curve (See *Stable isotope analysis*) may be taken as indication of tufa deposition during the Younger Dryas. A drastic decrease in $\delta^{13}C_{tufa}$ about 25 cm from the base of the tufa deposit could indicate a stabilisation of the soil (Hammarlund and Lemdahl 1994) that might correspond to the Younger Dryas/Preboreal transition. Further research is needed to see if such an interpretation is supported by other data.

There are indications that tufa deposition occurred on the east-coast of Skåne as late as during the Subboreal. The record from Kivik has two associated ^{14}C dates, but these are in reversed order; approximately 5,800 cal. BP at 20 cm and 3,400 cal. BP at 95 cm. It is clear that the dates can not be regarded as conclusive but the mollusc record, as well as other mollusc records from this region (*i.e.* Kurck 1904), includes species with a modern southern distribution. Examples are *Cochlodina lamminata*, *Balea perversa* and *Helicigona lapicida*, none of which has been present in the records from Fyledalen or Saxtorp. However, a Subboreal age is compromised by the presence of *Columella columella*, which occurred during the early Preboreal at Fyledalen and Saxtorp. It should, however, be stressed that the Swedish mollusc chronology is not known well enough to be used as a dating tool.

Tufa formation and climate

There is today a debate on whether or not climate is a controlling factor for tufa deposition, especially in connection with the alleged mid Holocene tufa decline. Since the early Holocene, tufa deposition across Europe and Asia has decreased drastically (Goudie et al. 1993; Pentecost 1995). In the paper concerning Pipers Mosse (App. I), the hypothesis was presented that south Swedish tufa deposition was dependent on climatic conditions, especially precipitation and
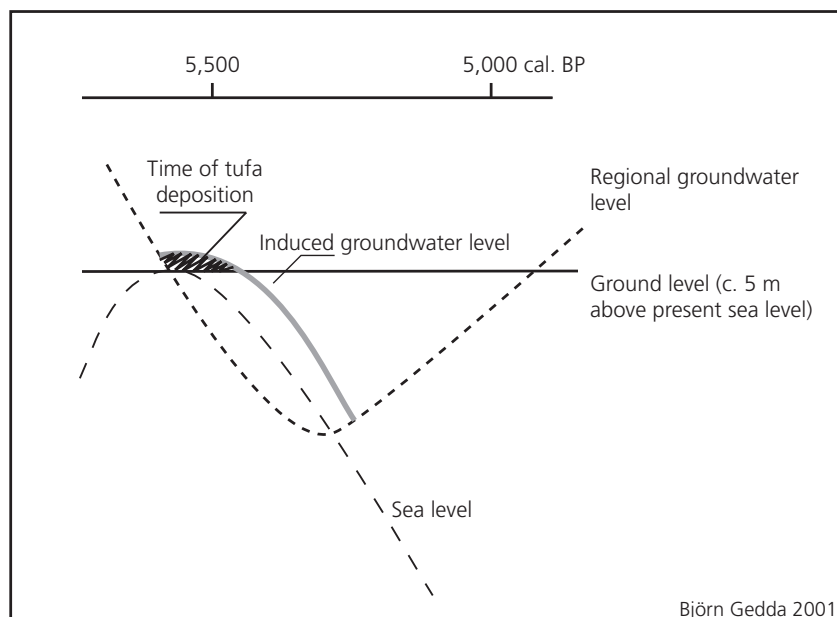
Fig 16. Giving that favourable condition are present (i.e. an arid and warm climate), a high sea-level causing a rise in the near shore groundwater level might have initiated tufa deposition. This cartoon explains how a rise in sea level may initiate tufa deposition by inducing an increase in the local groundwater level during a period of regionally low groundwater levels. Sea level according to M. Regnell in prep. and regional groundwater level according to Digerfeldt (1988).

temperature. This hypothesis was later tested in the papers about Valleröds Mosse (App III) and Saxtorp (App IV).

Formation of tufa in the Fyledalen area of Skåne is likely to have started in the early Preboreal (some time after 11,500 cal. BP). Climatic conditions at this time have been interpreted as warm, with July mean temperature about 2-3°C above present values (Coope et al. 1998; Gaillard and Lemdahl 1994), and dry (Digerfeldt 1988). The oldest parts of the records from both Valleröds Mosse and Högestad (Meyrick 1999) exhibit mollusc faunas that in England or France would be considered to belong to the Younger Dryas (e.g. Kerney 1980; Limondin 1995; Preece 1998). It is, however, unlikely that carbonate precipitation could take place in Skåne at this time when mean July temperatures were about 9°C (Coope et al. 1998) and the ground was frozen with permafrost.

It is interesting to note that the mollusc record from Slagstorpshult, on the south-facing slope of Fyledalen, matches those of Valleröds Mosse and Pipers Mosse, which are north facing, but with earlier appearances of species such as *Vertigo substriata, V. angustior* and *Carychium minimum* that appear near the top of the tufas in the latter records. It might thus be speculated that tufa deposition at Slagstorpshult started later and continued longer, possibly until the end of the Boreal (7,800 cal. BP) than the tufa at the north facing sites. The difference might however also be the effect of differences in local environment or climate, induced for example by differences in solar insolation.

The inland tufa deposition around Fyledalen continued at least until the mid Boreal (around 9,000 cal. BP). This is indicated by the pollen diagrams from Valleröds Mosse and Pipers Mosse; in the latter with a shift from a hazel woodland with alder oak and elm to a mixed deciduous woodland between the last tufa samples and the first wood carr samples (c.f. Berglund 1986). The presence of *Vertigo angustior* and Clausiliidae sp. in the mid part of the record from Slagstorpshult, in contrast to Valleröds Mosse where these species only appear in the uppermost samples, suggests that deposition might have continued for a longer time on the south-facing slope. It seems likely that the tufa deposition on the west coast of Skåne was coincident with that of south-central Skåne. The pollen record for the lower tufa deposit from Saxtorp shows good correspondence

those of Valleröds Mosse and Pipers Mosse and there is a ^{14}C date which places the deposition around the lateglacial/Holocene transition. As noted above, it seems unlikely that carbonate precipitation could take place during the harsh Younger Dryas climatic conditions in southern Skåne, and consequently the earliest tufa deposition is likely to have occurred in the early Preboreal.

Tufa deposition occurred as late as the earliest Subboreal (about 56500 cal. BP) on the west coast, as indicated by the deposit from Saxtorp. This is probably the best dated tufa in Sweden as it is supported by sea-level data, archaeological data and a pollen record. The time of deposition coincides with a second period of the Holocene that experienced regionally lowered lake levels (Digerfeldt 1988) which might explain tufa deposition at this time (Fig 15).

It could be argued that the high sea-level stand during the time when the second tufa was formed at Saxtorp (Christensen 1995; Regnell pers. comm.) should have affected the deposition. Rising sea-level might have caused a rise in the near shore groundwater level, despite the regionally low groundwater levels. If climatic conditions were favourable for tufa formation (*i.e.* an arid and warm climate) but groundwater levels were low, a rise of the groundwater level in response to a rise in base level (*i.e.* a sea level rise) might have initiated tufa deposition (Fig 16). The subsequent ceassation of tufa formation may then be explained by a) a lowering of the groundwater level beneath the sediment surface as a result of a fall in base level (*i.e.* a sea level fall) or b) a change to climatic conditions that no longer favoured tufa deposition.

No observations of modern tufa deposition are known from Skåne. During reconnaissance for fossil tufa deposits during the cause of this the-
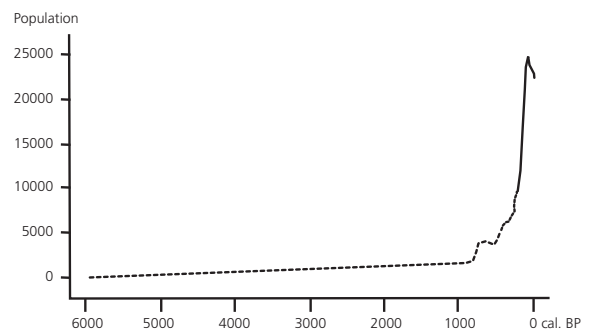
Fig 17. Population development in the Ystad area (about 30x30 km²) from 6,000 to 2,000 cal. BP (from Berglund et al. 1991).

sis, *precipitation* of calcium carbonate, tufa, has been observed in adjacent streams. This carbonate has, however, not accumulated and it is likely that although some precipitation occurs during the spring and summer, this tufa is eroded/dissolved during the autumn and winter, preventing build-up.

It seems clear that the deposition of south Swedish tufa is dependent on the climatic regime. All investigated sequences with an associated chronology were deposited during times with regional lows in the groundwater table (Fig 15) (Digerfeldt 1988) which suggests low humidity/precipitation (=high evaporation rate). Temperatures were, at least during the formation of the Preboreal-Boreal deposits, relatively high (Gaillard and Lemdahl 1994; Lemdahl 1997) (=high evaporation rate and low solubility of $CaCO_3$). It might also be speculated that higher temperatures could favour tufa deposition by promoting the growth of plants (e.g. Goudie et al. 1993). The overall respiratory processes (*i.e.* photosynthesis) by plants in the water body would thus increase. Since photosynthesis consumes CO_2, increased photosynthetic activity may be expected to increase the rate at which CO_2 is depleted from the water environment, which in turn might increase the possibility of carbonate deposition.

Faunal assemblages may provide information regarding temperature and other climatic aspects. MCR analysis (Mutual Climatic Range) (Atkinson et al. 1987) is a method that compares present day assemblages and their correspondence to present day climate and their geographical ranges, to past assemblages (Coope et al. 1998). Thereby, a quantitative estimation of palaeotemperatures can be generated. The method has successfully been used on insects where selected species with well-known global range and climate requirements are selected as key species. Another method is to apply transfer functions indiscriminately to the entire fauna, (Guiot et al. 1993). The method produces estimates of palaeotemperatures buy calculating the similarity between the fossil and modern assemblages. The two methods also differ in that transfer functions includes the abundances of the species whereas MCR only depend on their presence/absence (Guiot et. al. 1993).

Coleoptera is one of the best known groups used for palaeotemperature estimation and it has been used for reconstruction of palaeotemperatures of the lateglacial and the Holocene

(e.g. Coope and Lemdahl 1995; Coope et al. 1998; Lemdahl 1991). Although insect remains are generally well preserved in tufas, concentrations are generally low. In this study, only the sediments from one site, Pipers Mosse, yielded enough species for an MCR analysis to be performed. In the case of molluscs, the low number of species (only about 50 have been recognised in Preboreal South Swedish deposits), suggests that transfer functions might be the most appropriate method. Molluscs are often numerous and well preserved and the present ranges are well known, at least in northern Europe. Pollen and plant macrofossils are generally less well-preserved in tufa, and also very low in abundance. In the records analysed here, the groups have not contributed to the climatic interpretations.

A test of the possibility to use stable isotope records ($\delta^{18}O$ and $\delta^{13}C$) from tufa and terrestrial molluscs to reconstruct palaeotemperatures indicated that the method is promising although it only produces relative temperature estimates (see *Stable isotope analysis*).

A number of scientists have suggested that the Holocene tufa decline might be related to anthropogenic effects (e.g. Goudie et al. 1993; Meyrick 1999; Willing 1985). Changes in land use in the mid and late Holocene such as intensified deforestation and agriculture is suggested to have caused a number of changes in the natural environment, including lowering of the groundwater tables, increased weathering, trampling by livestock etc (Goudie et al. 1993). On the basis of the tufa deposits considered here, whether newly investigated or from literature, it appears that anthropogenic effects are unlikely to be the primary factor controlling changes in tufa deposition during the Holocene. Apart from the correlation that can be made to the rise and fall of groundwater tables, there are a number of other arguments against such explanations:

The human population in Sweden during the early to Mid Holocene was small (Fig 17, from Berglund et al. 1991). It is unlikely that this population could affect all tufa deposits in such a way that deposition ceased.

Organised agriculture is generally considered to have become established around 5,000 cal. BP, after the 'elm decline (Berglund 1991; Iversen 1973). At this time the influence was limited. Pollen records from Denmark (Iversen 1973) and Skåne (Berglund 1991) show local occurrences of grazing and small scale cultivation. Trampling

by cattle might have had an effect on formation since it is likely that cattle was taken out into wetland for grazing (see above). The cattle density is, however, likely to have been low in the Neolithic compared to the numbers of wild large grazers like elk and deer, also which would have favoured wetlands.

It is unlikely that drainage could explain the cessation of tufa deposition in Skåne. Draining of wetlands with the intention of creating arable land was not a method practised at a larger scale in Sweden until the middle of the 19th century. Before this, wetlands were considered an asset, giving high quality food for live-stock (Möller 1984).

It has been argued that deforestation might have had a negative effect on tufa deposition (Baker and Simms 1998; Goudie et al. 1993). This does not, however, seem to have been the case in Skåne. On the contrary, malacological records from most of the sites reviewed here suggest an increase in forest species towards the end of deposition.

Local environments

As mentioned earlier, organic remains such as pollen and plant macrofossils are scarcely preserved in tufas to such extent that palaeoenvironmental reconstructions can be made solely from that kind of information. Consequently, little is known about prehistoric environments in and immediately around the calcareous carrs in which a large portion of the South Swedish calcareous tufa was formed. One of the aims of this thesis has been to test whether malacology can be used to improve our knowledge of the history of these diverse biotopes.

The degree of openness is one of the parameters that best can be interpreted from a molluscan record. From the records presented in this thesis it is apparent that calcareous carrs initially were open. This is indicated by the presence of strongly heliophilious species such as *Vertigo genesii*. Some shade demanding species are often sporadically present but these can in most cases be interpreted as inwashed species from surrounding areas. One example might be the finds of *Vertigo ronnebyensis* in the early Saxtorp deposit (App IV). Sporadic occurrences of shade demanding species may also be explained by patchy vegetation, where shade might have been provided by, for example shrubs, dense herb vegetation or scattered trees that might have found stable

grounds in drier parts of the carr. Considering the casts of plants which are often the main constituent of tufa, it appears that the field layer in Valleröd Mosse (App III) a few hundred years into the Preboreal changed from a moss and graminoid vegetation to one almost solely composed of mosses. *Equisetum* and Polypodiaceae (*Dryopteris* type) seem to have been important parts of the field vegetation at this time, especially in Fyledalen where an *Equisetum* peak can be seen in the pollen diagrams around 10,000 cal. BP. The presence of *Helianthemum* in the pollen record from the early tufa from Saxtorp indicates an open, dry surrounding environment, which is in good agreement with the mollusc record. The genera have a relatively southern distribution, reaching Stockholm on the east-coast. The phytophagus insect record, *Plateumaris braccata*, *Notaris bimaculatus* and *Limnobarium t-album* from Pipers Mosse indicates reed and sedge in the carr environment towards the end of the Preboreal.

At some time in the early Boreal, or possibly in the beginning of the late Boreal transition (8.800 cal. BP), the carrs seem to have become more shaded. The pollen records from Fyledalen indicate the presence of deciduous broad-leaved tree species around 10,000 cal. BP, but it is not until about 9,000 cal. BP that they become dominant in the pollen spectra. In the malacological record, increased shading is mainly indicated by an increase in the absolute number of species but also by the disappearances of heliophilous key species, such as *Vertigo genesii* from Valleröds Mosse. However, a portion of the open land fauna generally prevailed thereby suggesting a patchy environment. The earliest finds of *Eupatorium cannabinum* in the Fyledalen deposits, around 10.000 cal. BP, appaear to be synchronous. This possibly indicates the species immigration to the area. This plant is typical on nutrient rich calcareous soils and it is commonly found in tufa deposits because its seed capsules are resistant to severe oxidation (Preece and Day 1994).

The Subboreal (5,700-5,500 cal. BP) mollusc record from Saxtorp is highly influenced by shade, and from the pollen and plant macrofossil record it is evident that broad-leaved deciduous tree species dominated the vegetation. The mollusc records from a number of south-eastern tufa deposits (*i.e.* sites in Kurck 1904, the Stora Beddinge site, R. Meyrick unpublished and the

Kivik site) also seem to indicate denser woodland dominated by broad-leaved trees.

The effect of human impact on land snails and the possibility to trace it through the analysis of mollusc records, archaeomalacology, has often been discussed in literature (e.g. Evans 1973; Evans 1978; Rousseau et al. 1992; Thomas 1985). As many snails are strongly anthropophobe (e.g. von Proschwitz 1993b) it is likely this is feasible, especially through local extinction after, for example, slash-and-burn or clearance. Little research on the subject of archaeomalacology has, however, been performed in Sweden. To this date, Saxtorp (App IV) is the only Swedish study where human impact has been recognised through terrestrial malacological records.

Faunal history

One of the main objectives with this thesis is to increase the knowledge of the faunal history of land snails in southern Sweden. Generally, little is known about the immigration patterns of the organisms that today inhabit this region. Exceptions are vascular plants and insects, two groups that have been successfully used as palaeoclimatic and palaeoenvironmental indicators (e.g. Berglund 1986; Lemdahl 1997) and larger vertebrates, which are relatively well known (Liljegren and Lagerås 1993). The history of Swedish terrestrial snails is poorly known, and most of our present knowledge can be derived from Waldén (1986) and Meyrick (1999). Waldén made a comprehensive review of the Swedish literature as well as a number of revisions of associated collections. He also revised parts of A. Nilssons mostly unpublished material, which contains a number of rare finds particularly from the western part of Skåne. Besides adding new sites, Meyrick proposed regional molluscs zones for Skåne and Östergötland.

Alleröd (13,900-12,650 GRIP yr. BP)

The only Swedish record from this period is described from Toppeladugård in southern Skåne (Fig 4) and includes (in the original nomenclature) "*Pupa* (*Sphyradium*) *edentula* var. *turritella*, *Pupa* (*Sphyradium*) *columella*, *Pupa muscorum* and *Pupa parcedentata* var. *genesii*" (Holst 1906) . According to Waldén (1986), these correspond to *Columella edentula*, *Pupilla muscorum* and *Vertigo genesii*. It should be noted, however, that in 1906, *Vertigo geyeri* and *V. genesii* had not been

split into separate species and there was some confusion concerning *Columella columella* and *C. edentula*. Both *Vertigo geyeri* and *V. genesii* have been found in the oldest layers of Valleröds Mosse, although V. *genesii* is far more common and is found in other early records as well [e.g. Saxtorp and Högestad (Meyrick 1999)]. Of the *Columella* species, only *C. columella* has been found in early layers at other sites than Toppeladugård. Holst (1906) also makes a note of a "lateglacial find of *Succinea elegans*". The age estimation of Toppeladugård is strengthened by a later investigation of a nearby ("a few hundred metres") section with similar lithological sequence (Liedberg Jönsson 1988). The layer containing molluscs described by Holst (1906) is likely to correspond to "Layer 2, Peaty sand" in the study of Liedberg Jönsson (1988) which was estimated to have an age of around 13,700 cal. BP ("11,800-?11,600 BP").

From the Danish island of Møn (Fig 4) is reported that "…land snails such as *Pupilla muscorum* and Limacidae [*Deroceras* is noted in Table 1] occur in abundance" in coarse detritus gyttja (Noe-Nygaard and Heiberg 2001), dated to early Alleröd, 13,970 cal. BP (11,940 ^{14}C BP). The complete section covers Bølling to early Preboreal. Terrestrial molluscs (unnamed) were also mentioned from the Older Dryas (dated to 14,120-14,020 cal BP). No terrestrial molluscs were recorded in the Younger Dryas or Preboreal sediments from Møn.

Younger Dryas (12,650-11,500 GRIP yr. BP)

There are no indisputable Younger Dryas records from Sweden although a few records possibly extend back to this period [*i.e.* Högestad (Meyrick 1999), Valleröds Mosse (AppIII) and Saxtorp (App IV)]. A sandy layer with *Columella columella* and *Vertigo genesii* has been reported from a core retrieved in Mecklenburg Bay (some 200 km to the south-east) during the Younger Dryas (von Proschwitz and Bennike 1998, Jensen 1997). The layer is part of a lithological unit that has been radiocarbon dated to the Younger Dryas, around 12.500 cal. BP (10,500 ^{14}C BP). Mean July temperature is estimated to have been similar, about 9ºC in the entire southern Baltic region, including Skåne at this time. It is likely that, if the climatic conditions allowed *P. muscorum* to survive in Mecklenburg, it should also have been present in Southern Skåne.

Meyrick (1999) reasons that the earliest layers at Högestad are of Younger Dryas age based on faunal comparisons with Northern english and french lateglacial faunas. This fauna includes *Pupilla muscorum, Columella columella, Vertigo genesii, Succinea/Oxyloma, Deroceras/Limax, Euconulus fulvus* (agg.), *Punctum pygmaeum, Vertigo ronnebyensis* and possibly *Nesovitrea hammonis* (agg). The earliest layers from Valleröds Mosse (App III) would, if the above mentioned assumptions are correct, also be of Younger Dryas age and would add *Galba truncatula* to the species present at the end of the Younger Dryas[1]. However, since it is unlikely that any major tufa deposition occurred in this part of Skåne during the Younger Dryas (see *Tufa formation and climate*), the molluscs encountered in the earliest parts of the tufa in Valleröds Mosse and Högestad are more likely to represent early Preboreal faunas. In Valleröd Mosse, a gravely clay that is found below the tufa, possibly was deposited during the Younger Dryas. A small number of snails was recovered from this clay, including *Columella columella, Limax/Deroceras, Succinea/Oxyloma, Galba truncatula* and *Vertigo* sp. (presumably either *V. genesii* or *V. geyeri*).

[1] Meyrick separates the zones Hog1 and Hog2 at the level where a number of new taxa, including *Cochlicopa lubrica, Vertigo substriata, Vallonia pulchella* and *Columella edentula*, appear. The level below is the first not to contain *Columella columella* and the first to contain *Nesovitrea hammonis*. When comparing with Valleröds Mosse it seems likely that the proposed YD/BP transition should be at least one sample 10 cm further down in the sequence than in the record of Meyrick and thus before the appearance of *N. hammonis*.

Preboreal (11,500-10,000 cal. BP)

Early Preboreal vegetation in Skåne has been described as open woodland (Berglund 1986; Gaillard 1984). The canopy, if continuous, was thin and although relatively much light would have reached the ground, shaded areas were common. The mollusc faunas of the calcareous carrs are dominated by open land and catholic taxa indicating that local conditions were rather open. Taxa becoming widespread in Skåne during the earliest part of the Preboreal include *Columella columella, Vertigo genesii, Nesovitrea hammonis, Vallonia pulchella* and *Pupilla muscorum*. *Columella*

columella continued to thrive in south-central Skåne for a few hundred years into the Preboreal and is then one of the first species to disappear from the region possibly as an effect of changing climate. *Vertigo genesii* is dominating in some of the records from this time. Examples of this are Valleröds Mosse and Högestad (Meyrick 1999). At some sites, however, like nearby Pipers Mosse and Slagstorpshult, as well as at Sigridslund (Meyrick 1999) it is rare or not present at all. The difference is likely to be caused by differences in local vegetation, although all records indicates similar fairly open environments. Alternatively these records are of different age.

The early part of the Saxtorp mollusc record is characterised by a large number of Vertiginides. Apart from *Nesovitrea hammonis* (agg) all above mentioned species are present with the addition of *Cochlicopa lubrica, Vertigo alpestris, V. modesta, V. substriata, V. lilljeborgi, Nesovitrea* cf. *petronella, Vallonia pulchella* and *Carychium minimum*. This single find suggests that there was a substantial difference between inland and coastal sites at this time.

Waldén (1986 p. 112) noted that *Pupilla muscorum* was represented throughout all "older layers" by the larger *P. muscorum* f. *pratensis* which is typical for wet conditions in contrast to *P. muscorum* f. *typica*, which is an important taxon in drier habitats (Kerney and Cameron 1979; von Proschwitz 1998b). This is not clear from the results reported here. The *pratensis* form is present in Valleröds Mosse but does not appear until the late Boreal when the carr gets moister, probably as an effect of the regional increase in precipitation (cf. App. III). The separation has, however, not been performed at the unpublished localities (Slagstorpshult, Örup and Kivik). Meyrick (*pers. com.*) did not find any *P. muscorum* f. *pratensis* in his Skåne sites.

Vertigo ronnebyensis is present during a short period of the Preboreal. At Saxtorp there are a few Preboreal finds and at Högestad it disappeared at the same time as *Columella columella*, probably in early Preboreal. Waldén (1986) refers to a possible Boreal find of *V. ronnebyensis* but notes that the age is unconfirmed. The species is eastern continental in northern Europe and believed to have immigrated to Sweden from the north, possibly following the immigration of the *Picea* forest (Waldén 1986). The fact that the species has some recent populations in Skåne (Waldén 1966) and one on Rügen (Plate 1950) implies

that the species survived at some places with exceptional environments up to today.

Boreal (9,900 - 7,800 cal. BP)

The mollusc history of the early Boreal period is fairly well covered in south-central Skåne as both Pipers Mosse and Valleröds Mosse and most likely Högestad (Meyrick 1999), Örup, Slagstorpshult and some sites described by Kurck (1922a) contain Boreal mollusc records. Neither the western nor eastern coast has any record that with certainty can be dated to this period. During the Boreal, the broad-leaved deciduous forest started to dominate the vegetation in Skåne (Berglund 1986; Lemdahl 1997). It seems that this type of vegetation also began to immigrate into the carrs, as reflected by an increasing portion of more shade demanding species in the mollusc diagrams. In the Fyledalen area *Carychium tridentatum*, *Vertigo antivertigo*, *Cochlicopa lubricella* and *Cochlicopa nitens* appear around the Preboreal/Boreal transition. Also *Aegopinella nitidula* and *Bradybaena fruticum* occurs around this time, but only as single finds in Valleröds Mosse. Around 9,500 cal. BP the number of species increases in both Pipers Mosse and Valleröds Mosse and the open woodland aspect of the fauna is accentuated. *Discus ruderatus*, *Vertigo moulinsiana*, *Vertigo substriata* and *Pupilla muscorum* f. *pratensis* appears at this time and *Vertigo angustior* and *Vertigo pygmaea* are recorded for the first time towards the end of the early Boreal. The records indicate that around this time *Vertigo genesii* becomes rare in Skåne. The southernmost modern Swedish localities with this species are at present in Östergötland and Västergötland (Kerney and Cameron 1979).

Atlanticum (7,800-5,700 cal. BP)

No South Swedish records can with certainty be considered to be of this age. It is therefore not possible to discuss this stage in the faunal development.

Subboreal (5,700-2,600 cal. BP)

Only the Saxtorp site on the west-coast of Skåne has a mollusc record that is reliably dated to this interval. The record, spanning the period ~5,600 to ~5,100 cal. BP, is species rich and dominated by woodland taxa including *Nesovitrea petronella*, *Vitrea contracta*, *Aegopinella nitidula*, *Aegopinella pura*, *Acanthinula aculeata* and *Carychium tridentatum*. Most species present during the Preboreal and Boreal in Fyledalen are also present

here. Most notable is the absence of *Vallonia pulchella* which is a dominant species in all the Fyledalen records. It is also notable that the carr was well shaded already at the time of tufa deposition and that no clear change can be seen in the mollusc record when the tufa deposition ceases.

When the obtained ^{14}C dates and the molluscan succession are considered it also seems likely that the record from Kivik extends over the Subboreal. This record displays a varied fauna that is consistent with a rich broad-leaved deciduous forest. Several of the species found at the sites reported in this thesis have only been recorded at Kivik. These include *Cochlodina lamminata*, *Clausilia bidentata*, *Helicigona lapicida*, *Trichia hispida*, *Ena obscura*, *Vitrina pellucida* and *Oxychilus alliarius*.

Subatlanticum (2,600 cal. BP - Present)

Only Saxtorp on the west-coast of Skåne has a mollusc record that is reliably dated to this interval (about 2,900 to 2,300 cal. BP). Note that this record probably extends back into the Subboreal. The fauna had not changed much since the early Subboreal. Most species that are present in Skåne today had already appeared at that time, and the vegetation structure was also similar. However, in the Subatlantic period, the effects of human impact on the landscape was increased in Skåne, as the practice of clearing forested areas for cultivation was intensified. The first signs of humans affecting the mollusc fauna may be detected in the uppermost part of the deposit as indicated by decrease of woodland taxa and increases in catholic and less shade demanding taxa.

It is possible that the by far most common fossil component of the tufas studied here, terrestrial molluscs, in the future may be used as climatic indicators, possibly in the same way as Coleoptera. In this thesis it has been shown that climatic interpretation based on presence or absence of single species' is unreliable. This can partly be explained by their dependence for local environmental factors such as shade, type of vegetation or moisture but also by the lack of knowledge of certain species actual climatic requirements. An example is the snail *Vertigo moulinsiana* that has its northern limit along the 10° mean year isotherm in mid Germany. This would be its low-temperature limit if it were not for a few sites around the southern Baltic Sea, close to the 8° mean year isotherm (App II). To prevent misinterpretations, it is necessary to better under-

stand what the limiting factors are. One way to minimise the risk of erroneous interpretations is to work with whole faunas. The modern regional dispersion of terrestrial molluscs in northern Europe is fairly well known and it should be feasible to combine this data with known contemporary climate data to establish the bases for MCR analyses, which is based on faunal assemblages rather than single species.

Despite these uncertainties, some climatic interpretations were made from the molluscan and other records.

The mollusc records of the oldest parts of the deposits from Fyledalen in south-central Skåne [*i.e.* Valleröds Mosse, Högestad (Meyrick 1999) and possibly Örup] as well as Saxtorp close to the western coast imply a climate similar to what today is expected in high mountain areas. This is not in accordance with Coleopteran data from this time, which reflect a rapid climatic amelioration with a mean annual temperature increase of about 10ºC, to a 2-3ºC above the present (Coope and Lemdahl 1995; Hammarlund et al. 1999; Lemdahl 1991). A hypothesis was proposed that it is the temperature of the spring water, rather than the summer temperature that is reflected in the mollusc record. It could be expected that a rapid shift in the climatic regime caused lag between the warming of the atmosphere and the groundwater aquifers. The groundwater would thus remain at a low temperature, whereas the evaporation and air temperature would be high enough to allow tufa deposition and the immigration of more thermophilous Coleoptera.

Nature conservation

One of the prime reasons for studying fossil snail assemblages is to provide a better understanding of the natural ranges and habitat requirements of modern snails. In dealing with nature conservation projects, one is usually restricted to information on the current distribution, biology and ecological restrictions of the concerned species. However, when dealing with prehistorical records it soon becomes apparent that that it is also important to have information on a species' past distribution.

Certain species belonging to the Scandinavian land gastropod fauna seem to have been common in the early Holocene but have now become rare or even regionally extinct (e.g. Gärdenfors 2000;

Kurck 1904; Kurck 1922a; Kurck 1931; Odhner 1909; Odhner 1910a; Waldén 1986; Waldén and Konigsson 1986). Of the about 125 terrestrial gastropod species present in Sweden today, 99 were assessed in 2000, of these 20 species were considered threatened and one extinct (Gärdenfors 2000). There might be several natural reasons for recessions, including natural causes such as changes in temperature, precipitation and vegetation but also destruction of habitats because of changes in land-use, including drainge of wetlands, intensified agriculture and forest management. If conservation actions are to be taken to preserve these species, an adequate knowledge of the cause of their disappearance is essential, and knowledge of their historical record is an important key to such knowledge.

One example is the biology of *Vertigo ronnebyensis*. It is believed to have colonised Sweden from the east and north-east, following the immigration of *Picea* (Waldén 1986; von Proschwitz 1993) and has a northern distribution with its southern limit, with the exception of a few 'relict like' (Waldén 1986) colonies further south, at the northern border of Skåne. The species is considered a woodland species with an optimum in old, dry, moss-rich coniferous to mixed forests where it often is found feeding on *Vaccinium* sp. (Pokryszko 1990; von Proschwitz 1990; von Proschwitz 1993a). However, three early Holocene finds have been made in Skåne: In 'coastal Skåne' (Waldén 1986), Högestad in south-central Skåne (Meyrick 1999) and Saxtorp (App IV) on Skånes western coast. The faunal composition is not known from 'coastal Skåne' but at both Högestad and Saxtorp, *V. ronnebyensis* are found in otherwise mainly open marsh faunas. Meyrick (1999: 265) argues that these finds indicate that the species full ecological range might not be known. Since calcareous carrs are eutrophic, it is likely that early Holocene specimens were either washed in from the surroundings or that shaded "oligotrophic islets", possibly vegetated by *Vaccinium* dwarf shrubs (c.f. Proschwitz 1990; 1993) was present in the carrs. It is clear that the early colonisation of *V. ronnebyensis* is less well known and it is quite possible that the immigration of the species into southern Sweden occurred from the south, rather than from the north, or both. The correlation to the distribution of *Picea* might well be a coincidence caused by similar habitat or temperature preferences.

Terrestrial mollusc records may also be used to reconstruct the vegetational history of a region, may it be natural or influenced by humans. An example is the record from Kivik, which is characterised by a high number of woodland species. Although the chronology is uncertain and the record might be disturbed, most of the samples seem to reflect a rich deciduous forest or grove. This is consistent with the type of forest C. Kurck described as present at the site in the late 19th century (Kurck 1904). Today, this forest is almost completely gone and information about the continuity of such a forest through time and its ecology is important, not the least from a nature conservation perspective.

In Europe, there is at present a debate among Quaternary scientists and nature conservationists as to the nature of early and mid Holocene woodlands. It is argued by some that the landscape was almost park-like, with large well-grazed corridors separating patches of full-grown woodland (e.g. Vera 2000). Others are of the opinion that woodland covered most of the landscape and opening mainly consisted of "forest hollows" (e.g. Berglund 1986). Many of the arguments are based on environmental reconstructions based on pollen records. However, recent models describing tree pollen dispersal in closed and semi open environments, show that little can be said about the degree of openness from pollen assemblages alone (Sugita et al. 1999). Assemblages of local fossils, such as snails, plant macrofossils and certain insects, as opposed to assemblages of regional fossils such as pollen, are likely to provide more reliable information about local environments, such as openness, moisture and vegetation.

Conclusions

- Tufa deposition in Skåne likely started soon after the Younger Dryas/Preboreal transition (about 11,500 cal. BP) and continued until the mid to late Boreal (8,500-7,800 cal. BP) when it seems to have ceased at most sites. On the western coast there was tufa deposition during the early Subboreal (about 5,600 cal. BP). There are indications of tufa deposition after the Boreal period on the eastern coast.

- Tufa deposition in Skåne is likely to have been controlled by climate. All dated sequences coincide with periods of regionally low lake levels. The main controlling factors are thus likely to be identical to those controlling regional lake levels, *i.e.* humidity, precipitation and temperature. The optimal conditions for tufa formation during the Holocene in southern Sweden has been shown to be drier and some degrees warmer than at present. Local environments of calcareous carrs, in which tufa studied in this study are formed, have undergone vegetational changes during the Holocene. During the Preboreal (11,500-9,900 cal. BP) an almost completely open environment is indicated. The calcareous carrs remained open to semi-open until the late Boreal when broad-leaved woodland started to enclose the carrs.

- In the very beginning of the Holocene, open land species such as *Columella columella* and *Vertigo genesii* immigrated into southern Sweden. At the end of the Preboreal a number of catholic species appear, including *Nesovitrea hammonis*, *Cochlicopa lubrica* and *Punctum pygmaeum*. *Vertigo genesii*, which often appears to have dominated the earlier faunas declined markedly towards the end of the Preboreal. In the mid Boreal, as the broad-leaved woodland enclosed the carrs, a more shade demanding fauna started to develop. The most prominent malacological change at this time occurred in the carr fauna with the appearance of new species with a modern relatively southern distribution, such as *Cochlicopa nitens*, *Vertigo moulinsiana*, and *Vertigo antivertigo*.

- At least one short Subboreal malacological record exists, covering the times around 5,600 and 2,600 cal. BP. It comes from the western coast and displays a highly diverse fauna reflecting closed wood carr environment. Also undated records from the eastern coast, possibly of Subboreal age, display a high variety of species and a shaded environment.

- A number of species that today are considered rare, seems to have been common during the early Holocene in Skåne, including *Vertigo genesii*, *Vertigo geyeri* and *Columella columella*. These species were commonly found in most Preboreal sites and the first two often dominates the records. *Vertigo genesii* and *Vertigo geyeri* as well as *Cochlicopa nitens* and *Vertigo moulinsiana*, also found during this investigation, are on the national Red List of endangered species and included in the European Community's habitat and species directory.

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Svensk sammanfattning

Denna avhandling är ett resultat av ett doktorandprojekt vid Kvartärgeologiska avdelningen, Lunds Universitet. Syftet med avhandlingen har varit att utröna huruvida bildningen av kalktuff i Sverige har varit beroende av klimatet samt under vilka tider och i vilken närmiljö tuffen bildats. I samband med undersökningen har ett stort antal landsnäckor påträffats och analyser baserade på dessa har blivit en viktig del av denna avhandling. Framförallt är det deras skånska historia och möjligheten att använda dessa för att tolka forntida miljöer och klimat som undersökts.

Kalktuff är ett material som bildas genom utfällning av kalk ur vatten, ungefär på samma sätt som stalaktiter, eller för den delen kalklager på diskbänken, bildas. Det finns en stor mängd olika definitioner på vad kalktuff är, från små porösa ansamlingar i källsprång till enorma landskapsbildande fasta former. Gemensamt för alla är att de är bildade i sötvatten och inte i saltvatten. De kalktuffer, som har avhandlats här, har varit av den porösa typen, bildade i kalkkärr. Övriga typer har inte berörts nämnvärt i denna avhandling.

För att bildning av kalktuff ska kunna ske i naturen måste berggrunden eller sedimenten ovanför vara kalkhaltiga så att maximal mängd kalciumkarbonat (kalk) kan lösas i grundvattnet. När sedan grundvattnet rinner fram i källsprång dunstar vatten och koldioxid varvid kalciumkarbonaten fälls ut i form av kalktuff.

Den här undersökningen har visat att kalktuff troligen började bildas kort efter den kraftiga uppvärmningen som skedde för ungefär 11.500 år sedan och fortsatte bildas till för ungefär 8.000 år sedan. Under denna period har man kunnat visa att grundvattennivåerna i Skåne var exceptionellt låga jämfört med idag vilket har tolkats som att klimatet var varmt och torrt. För ungefär 8.000 år sedan blev klimatet mindre torrt (grundvattennivåerna steg) och kalktuff-bildningen avstannade. Ungefär 5.600 år före nu sjönk grundvattennivåerna igen och för en kort period bildades åter kalktuff vid Skånes västkust och troligen också vid dess östkust. Idag bildas ingen kalktuff i Skåne. Sammanträffandena i tid mellan bildning av kalktuff och lågt vattenstånd tolkas som att ett relativt torrt och varmt klimat har varit nödvändig för bildningen.

Närmiljön runt lokalerna för 11.500 till 10.000 år sedan verkar ha bestått av nästan helt öppna kalkkärr vilket främst syns i sammansättningen av de snäckarter som påträffats. Enbart ett fåtal av arterna föredrar skugga samtidigt som en del arter kräver en öppen terräng för sin överlevnad. Ett exempel på de senare är den idag mycket sällsynta *otandade grynsnäckan* (*Vertigo genesii*) som på en del lokaler påträffats i stora mängder. Runt 10.000 år före nu blev närmiljön successivt mer sluten. Detta sammanföll med invandringen av ädellövskog, till skillnad från den tidigare tall-björk dominerade skogen, och märks främst av att flera snäckarter uppträder som har en vidare ekologisk tolerans. För 9.500 år sedan blev närmiljön än mer sluten och flera skuggkrävande arter invandrade. När kärren blev inneslutna av/i skogen blev den *otandade grynsnäckan* ovanlig emedan andelen skogsarter ökar. Flera av skogsarterna har idag en ganska sydlig utbredning i Sverige. Det främsta exemplet på detta är den *större grynsnäckan* (*Vertigo moulinsiana*) som idag endast påträffas vid Yddingesjön i sydvästra Skåne.

I och med att kalktuff slutade bildas för ungefär 8.000 år sedan försvann också förutsättningarna för att snäckskal skulle kunna bevaras och därför gjorts få fynd av landsnäckor som med säkerhet kan dateras till senare tid. Ett undantag är en sekvens från Skånes västkust som kan dateras till 5.600 före nu och en som kan dateras till 2.600 före nu. Dessa sekvenser representerar ganska korta tidsintervall, kanske några hundra år, men visar på en klart annorlunda miljö jämfört med tidigare. Kärren var vid den här tiden helt inneslutna i skog vilket ses av att de dels innehåller en stor mängd snäckor som föredrar skugga dels en stor mängd rester från bl.a. hassel och al.

Ett antal av de snäckarter som påträffats i den här undersökningen är idag betraktade som starkt hotade och är uppsatta på den svenska rödlistan över hotade arter samt på EUs Habitatdirektiv. Dessa är större agatsnäckan (*Cochlicopa nitens*), den otandade grynsnäckan (*Vertigo genesii*), kalkkärrsgrynsnäckan (*Vertigo geyeri*), större grynsnäckan (*Vertigo moulinsiana*) och skogsgrynsnäckan (*Vertigo ronnebyensis*).

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