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Terrestrial mollusc succession and stratigraphy of a Holocene calcareous tufa deposit from the Fyledalen valley, southern Sweden

B. Gedda*

(Department of Quaternary Sciences, Lund University, SE-22362 Lund, Sweden)

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Abstract: A Holocene calcareous tufa deposit in the Fyledalen Valley in southern Sweden was investigated with respect to molluscs, pollen, plant macrofossils and Coleoptera remains. The investigation recovered four mollusc species that today are severely threatened and included in the Swedish Red List of Endangered Species and/or the European Community's Natura 2000 programme. These include *Vertigo genesii* (Gredler), *Vertigo geyeri* Lindholm, *Cochlicopa nitens* (Gallenstein) and *Vertigo moulinsiana* (Dupuy). Tufa formation was initiated in the early Preboreal (after 11 500 cal. BP), when an open birch–pine forest dominated the area and stopped in the late Boreal (after 8800 cal. BP) when deciduous trees had become established. The presence of the molluscan species *Vallonia pulchella* (Müller), *Columella columella* (Martens), *Vertigo genesii, Pupilla muscorum* (L.) and *Euconulus alderi* (Gray), coupled with an almost complete lack of shade-demanding taxa, suggests an open marsh environment throughout the time of tufa deposition. The mollusc succession shows evidence of increasing temperature. *Columella columella*, commonly associated with open arctic-alpine habitats is present at the base of the profile in the early Preboreal, whilst *Vertigo genesii*, which commonly is associated with open arctic-alpine habitats or calcareous springs, persists until the mid-Boreal (~8800 cal. BP). The tufa deposition ends when the regional groundwater levels rise, approximately 8800 cal. BP, more thermophilous molluscs, such as *Vertigo moulinsiana* and *V. angustior* Jeffreys and the aquatic *Bithynia tentaculata* (L.), *Radix peregra* (Müller) and *Planorbis planorbis* (L.) colonize the site. Stratigraphic correlations, as well as faunal and floral comparisons, are made with nearby sites.

Key words: Tufa, mollusca, biostratigraphy, pollen, succession, climate, conservation, landscape change, Sweden, Skåne, Holocene.

Introduction

Calcareous tufa deposits occur in most climatic regions throughout the world. There are several sites in Europe with tufa deposits attributed to the Lateglacial and Holocene (Pedley, 1990; Goudie, *et al.*, 1993; Ford and Pedley, 1996). These deposits have been shown to be excellent archives of well-preserved mollusc shells and other types of animal and plant remains. A number of studies on tufa deposits were carried out at the beginning of the twentieth century in Sweden (eg, Hulth, 1898; Kurck, 1904, 1922; Sernander, 1915, 1916; Thunmark, 1926). While these studies, in their day, were of great scientific value, important as they were in the understanding of past climatic variations, they unfortunately lack detailed chronologies and are based on stratigraphic resolutions too low to be of much use in modern investigations.

The history of land snails in Swedish is equally poorly known. Little has been done in this area since the early twentieth century and, at that time, high stratigraphic resolution was rarely considered important (eg, Kurck, 1904, 1922; Odhner, 1909, 1910; Munthe, 1910; Sernander, 1915). A few recent attempts to reconstruct Holocene immigration history of land snails have been made. Waldén (1986) made a comprehensive review of older literature combined with re-examination of the associated collections. Later, Meyrick (1999) and Gedda (2001) combined these results with new investigations with higher stratigraphic resolution.

A study of a calcareous tufa deposit at the nearby site Pipers Mosse in Fyledalen, southernmost Sweden (Gedda *et al.*, 1999), investigated climatic and local environmental change during the early part of the Holocene. The rich record of terrestrial molluscs showed distinct changes in the openness of

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*Author for correspondence at: Klarinettgränden 7b, SE-44368 Lund, Sweden (e-mail: bjorngedda@otorn.org)

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the landscape, and shifts in humidity. The present investigation was carried out about 6 km from Pipers Mosse, in the same river valley. The main objective of the present investigation is to test, by applying the same methods, if the previous results are repeatable. The study includes analyses of lithology, pollen, plant macrofossils, molluscs, insect remains and AMS-dating.

Site description

Valleröds Mosse is situated on the southwestern side of the bottom of the Fyledalen valley in south-central Skåne, southern Sweden (55°34″5′N, 13°49″2′E, Figure 1). The valley is oriented NW–SE, following the tectonic fault complex known as the Tornquist Zone (Ziegler, 1982). The bedrock of the catchment consists predominantly of Cretaceous and Tertiary limestone, sandstone, shale and crystalline rocks (Daniel, 1986). A small river, Fyleån, drains southeast through the bottom of the 30–40 m deep valley. The site is today an open wetland bordering the river and is highly influenced by grazing cattle. Within this wetland is one of the largest tufa deposits in the Fyledalen valley situated (Kurck, 1922), measuring more than 250 m along the valley and approximately 175 m across. The tufa is overlain by about 40 cm of marsh peat. The marsh was formerly fed by an extensive surface drainage network (Kurck, 1922), which supplied the calcium carbonate necessary for tufa formation. The area was artificially drained in the late nineteenth century so that today, all that remains is a small stream bordered by sedge marsh, fed by the Magle Ådra spring.

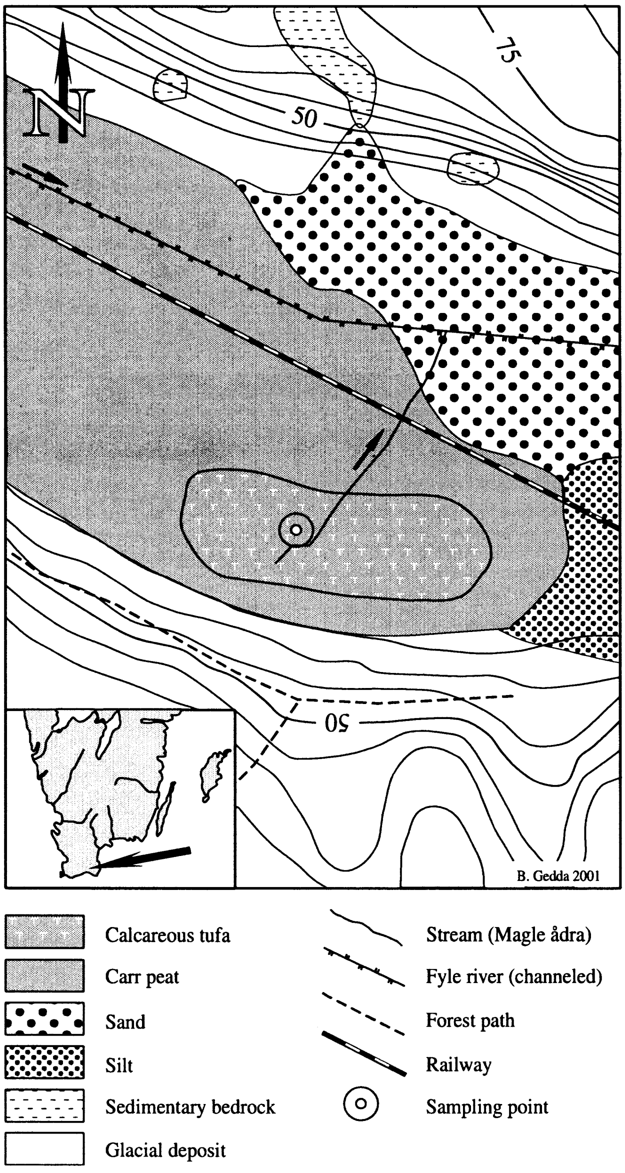

Figure 1 Map of the study area and the geological setting at Valleröds Mosse. Inset shows the position of the study area in Sweden

At the coring point, the sediments consisted of compacted basal grey clay of unknown thickness with occasional lenses of tufa, overlain by 3.35 m of grey to white tufa, in turn covered by 0.42 m of highly humified alder carr peat (Table 1). The tufa predominantly consists of plant casts with particle sizes varying from clay up to gravel through the profile. Casts of mosses dominate, although below 329 cm casts of vascular plants are common. The tufa, which has a relatively low organic content, is rich in mollusc shells and may be classified as a paludal tufa formation according to Pedley (1990).

Sedge communities (*Carex* spp.) presently dominate the field layer at the site and in the surrounding area are beech groves (*Fagus silvatica*), planted stands of spruce (*Picea abies*) and alder (*Alnus glutinosa*). The study area is situated within the temperate vegetation zone of broadleaved deciduous forests (Ahti *et al.*, 1968). The climate is today characterized 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).

Methods

Samples were collected using a 10 cm diameter Russian Corer (Jowsey, 1966). A minimum of three cores were taken at each level, with the exception of the lowermost 50 cm, which was represented by only two. The top 30 cm of the stratigraphy was not sampled since it does not contain mollusc shells and most likely has been reworked. The cores were taken close enough so that correlations between them could be made by ocular inspection, with the assistance of lithological boundaries and markers made at the time of sampling.

In the laboratory, the cores were subsampled for macrofossil analysis at 5 cm intervals, taking into account lithological boundaries. Samples for pollen analysis were taken from the same cores as those used for AMS dating. Samples for macrofossil analyses were washed through a set of 3 mm, 0.5 mm and 0.25 mm meshes. After drying, all shell, plant macrofossil and insect remains > 0.5 mm were sorted out. The mollusc shells and the remaining tufa were stored dry, whereas the plant and insect remains were preserved in tubes with slightly acidified water. Macroscopic remains were counted and sorted at selected levels using a stereo microscope. Complete shells and fragments were identified mainly using keys by Kerney and Cameron (1979) and Lozek (1964). Plant remains were identified using keys by Beijerinck (1976), Nilsson (1962) and Schoch *et al.* (1988), and the reference collection in the Department of Quaternary Geology, Lund University. Insect and other macroscopic remains were also sorted and identified. Pollen samples were treated according to standard preparation methods (Berglund and Ralska-Jasiewiczowa, 1986).

Two samples adjacent to the upper and lower boundaries of the tufa were selected for AMS ^{14}C dating. Carbonized wood remains were sorted out and submitted dry to the radiocarbon laboratory of Lund. Calibration of the radiocarbon dates to calendar years was performed using the OxCal program

Table 1 Lithostratigraphy of the sampled column at Valleröds Mosse

Level	Depth (cm)	Description
P	0–42	Alder peat, highly humified, grainy, almost black. Lower boundary: sharp (0.5 cm) but undulating, possible erosive contact
T7	42–104	Tufa, light grey, fine grained. Lower boundary: 1 cm
T6	104–155	Tufa, dark grey, fine-coarse grained, some organic content. Lower boundary: 1 cm
T5	155–164	Tufa, light yellowish, fine grained. Lower boundary: 1 cm
T4	164–185	Tufa, light yellowish, coarse grained. Lower boundary: 1 cm
T3	185–197	Tufa, light yellowish, fine grained. Lower boundary: 0.5 cm
T2	197–329	Tufa, light yellowish, coarse grained with 1–3 cm thick, fine-grained layers. Lower boundary: 1 cm
T1	329–377	Tufa, dark grey, fine- medium- and coarse-grained layers (323–326 fine, 326–331 medium, 331–336 fine, 336–242 medium, 342–352 fine, 352–360 coarse, 360–363 medium, 363–368 fine, 368–373 fine). Clearly more dense than above. Lower boundary: 1 cm
C	377–395+	Compact grey clay with a few lamina of tufa. There does not seem to be any tufa below 385 cm. The tufa is clearly denser than from T2 and above. Last sampling point: 390–395

The following conventions are used: fine, few grains larger than 3 mm; medium, few grains larger than 10 mm; coarse, abundant grains larger than 10 mm.

(Bronk Ramsey *et al.*, 1995) on the INTCAL98 calibration curve (Stuiver *et al.*, 1998).

Results

Molluscs

The mollusc shells were well preserved throughout the tufa deposit and a total of 30 mollusc taxa (Figure 2) could be identified. In accordance with common practice, the counts refer to whole shells or apical fragments; however, occasional non-apical fragments were also included if they did not have any associated apex. The counts therefore represent minimum numbers of each species from each horizon. Information concerning the present distribution and biology of the taxa was derived from Kerney and Cameron (1979), Lozek (1964) and von Proschwitz (1993a,b). The ecological classification presented here is based on the system published by Lozek (1964), which subdivides taxa into five major groups and numerous subgroups. Of these, only the five major groups: Shade, Open, Catholic (indifferent), Marsh and Aquatic have been considered in producing the mollusc diagram (Figure 2). Major changes are traced in the molluscan succession, which are defined as three separate faunal zones.

Zone MVa1 (365–320 cm)

The earliest finds of mollusc shells occurred at a depth of 390 cm in the stratigraphy, which is about 15 cm below the clay/tufa boundary (Table 1). *Vertigo genesii*, a species that today has a pronounced arctic-alpine distribution, is common in all but the lowermost levels within this zone. In fact, it is likely that *Vertigo* sp. in the lowermost levels represents *V. genesii*. In Sweden, this species is mostly restricted to the Scandinavian mountain range (von Proschwitz and Bennike, 1998), with the exception of a few relict-like communities in more southern, calcareous fens (Kerney and Cameron, 1979; von Proschwitz and Bennike, 1998). *Columella columella* is present in this zone. This species has an even more pronounced arctic-alpine distribution than *Vertigo genesii*, typically being found at high altitudes in marshy grassland, wet subalpine forests on calcareous soils and calcareous fens (von Proschwitz and Bennike, 1998). *Carychium minimum* (Müller) is strongly hygrophilous and is today common in all types of marshes, except for the most oligotrophic (von Proschwitz, 1998). The presence of *Vallonia pulchella* is an indication of damp open habitats, whilst *Pupilla muscorum* is associated with dry short-tufted grasslands and screes. The specimens of *Pupilla muscorum* found in this zone, and in the following, vary in size, with a tendency to increase in both length and width higher up in the stratigraphy.

Zone MVa2 (320–80 cm)

At the base of this zone *Columella columella* disappears and *Pupilla muscorum* decreases in frequency and subsequently disappears. *Nesovitrea* cf. *petronella* (Pfeiffer), *Aegopinella nitidula* (Draparnaud), *Bradybaena fruticum* (Müller), and *Carychium tridentatum* (Risso) are relatively shade-tolerant species, which occur sporadically throughout this zone. There is a slight decrease in the number of *Vallonia pulchella* between 252 and 145 cm. *Pupilla muscorum* f. *pratensis* (Clessin), appearing at the top of the zone, is a large toothless, form of *P. muscorum* (von Proschwitz, 1998) that, unlike *Pupilla muscorum* f. *typica*, *Pupilla muscorum* f. *pratensis*, prefers open fens and wet meadows. *Cochlicopa lubricella* (Porro) appears sporadically, normally being found on dry islets and adjacent drier biotopes (von Proschwitz, 1998).

Cochlicopa nitens is normally associated with warm climatic conditions (Lozek, 1958; Preece, 1992), commonly in association with relatively thermophile species such as *Vertigo moulinsiana*, *Vertigo angustior* and *Vallonia enniensis* (Gredler). However, Preece (1992) reports early Lateglacial and Holocene (12 300–9000 ^{14}C BP) finds of *Cochlicopa nitens* from several British sites in association with arctic-alpine species (eg, *Vertigo genesii*). It also occurs during the Lateglacial at Ringen, Germany, where it precedes the appearance of *Columella columella* (Meyrick, 1999).

Zone MVa3 (80–35 cm)

A major change in the mollusc fauna occurs at 80 cm, as the abundance of aquatic molluscs (eg, *Bithynia tentaculata*) and marsh species (eg, *Pupilla muscorum*, *Vertigo geyeri*, *V. antivertigo*) increase significantly. Populations of *Nesovitrea hammonis*, *Vallonia pulchella*, *Euconulus alderi* and *Succineal Oxyloma* spp. are stable throughout this zone, whilst *Vertigo genesii* disappears. *Vertigo geyeri*, a species that prefers wet parts of open calcareous marshes, gradually increases. This species is only rarely seen in less nutrient-rich marshes and not at all in shaded woodland marshes. Norris and Pickrell (1972) state that it requires habitats with luxuriant growth of narrow-leaved plants, ie, grass, sedge or rush, that must be free of *Sphagnum* mosses. *Vertigo geyeri* is rarely found above the tree limit in Sweden (von Proschwitz, 1998). A few shells of *Pupilla muscorum* were found in the topmost samples that were

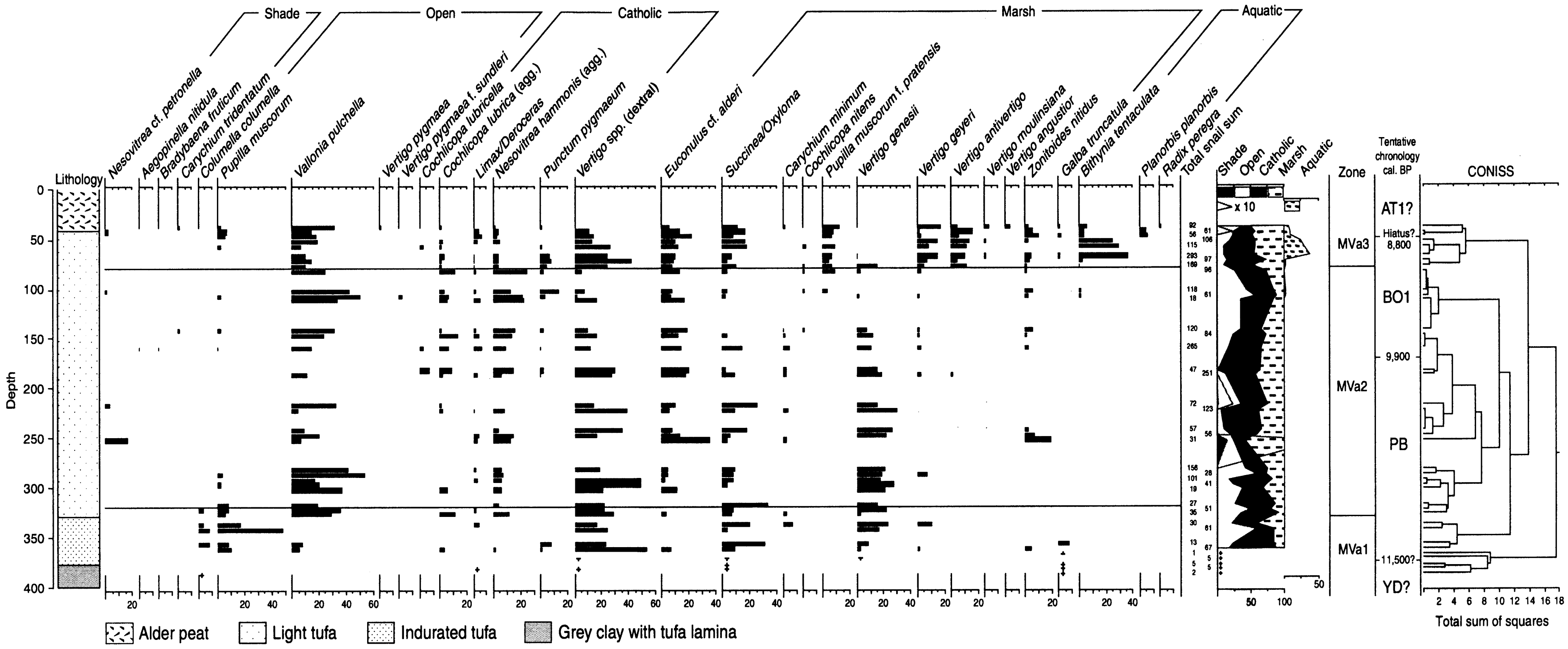

Figure 2 Mollusc percentage diagram. The percentages of the terrestrial molluscs are based on the minimum number of terrestrial gastropods while the percentages of aquatic molluscs are based on the total minimum number of molluscs. The classification of species follows Lozek (1964), modified by Swedish studies (eg, von Proschwitz, 1993a,b, 1998, 2000; and von Proschwitz, personal communication)

identified as f. *typica*. The presence of these corresponds with a decline in *Bithynia tentaculata*.

Five shells of *Vertigo moulinsiana* were recovered from this zone. Today *V. moulinsiana* is recorded only at one locality in Sweden, namely Lake Yddingesjön, S. Skåne (Lohmander, 1959; Gärdenfors *et al.*, 1988). It climbs on reed plants such as *Typha*, *Glyceria*, *Iris* and *Phragmites*, in wet fens and lake margins, where it feeds on fungi (Steusloff, 1937).

Vertigo angustior, which was recorded in the topmost sample, is also a relatively thermophilous species. Within its modern distribution area, it is found in two specific habitats (von Proschwitz, 2000): (1) rich, rather dry semi-open to open, screes or dry calcareous slopes; and (2) calcareous marshes and fens. The first habitat type is common in coastal areas, while the second is found both along the coast and at inland sites (von Proschwitz, 2000). A new occurrence is also *Vertigo antivertigo* (Draparnaud), which is a wetland species found in eutrophic alder marshes, wood marshes and at lake and river margins (Kerney and Cameron, 1979; von Proschwitz, 1993a). It occurs today in the central and southern parts of the Scandinavian Peninsula, with large gaps in areas with oligotrophic waters (von Proschwitz, 1993b). The aquatic component of the molluscan fauna increases considerably in the top 50 cm of this zone, with the appearance of *Bithynia tentaculata*, *Planorbis planorbis* and *Radix peregra*. *Bithynia tentaculata* is found in places with abundant vegetation and calm flowing water (Boycott, 1936; Fretter and Graham, 1978). It is a somewhat calciphile species which thrives in conditions of increasing eutrophication (von Proschwitz, 1997). *Planorbis planorbis* is more of a southern species, reaching the summer isotherm of 14°C (66°N) in Sweden (Økland, 1990). It requires aquatic vegetation and prefers slow-flowing, shallow water (Økland, 1990). *Radix peregra* lives in oligo- and mesotrophic shallow water and cannot survive if its habitat dries out (Hubendick, 1949).

Pollen

The pollen abundances vary considerably between samples. This is probably due to water-level changes after deposition, leading to periods of oxidation of the organic material. Such processes would also explain why many pollen grains were so severely corroded that they could not be identified, as is frequently the case in tufa deposits (Kerney, *et al.*, 1980; Preece and Day, 1994). This phenomenon implies that pollen assemblages are biased towards taxa that have resistant pollen walls and/or have easily recognizable grains even when badly preserved. In the pollen diagram from Valleröds Mosse, unidentifiable grains often represent $>10\%$.

The pollen stratigraphy can be subdivided into five pollen zones. This subdivision follows the results of the cluster analysis at a total sum of squares of 0.70, except that level 290 cm was not retained as a separate zone. However, level 155 cm was chosen as a separate zone, even though it is defined by CONISS at a lower total sum of squares (0.20). This final zonation appeared to be most useful as a basis for interpretation of the pollen data.

LPAZ – PVa1 (320–400 cm)

The lowermost zone is characterized by a dominance of *Pinus*, with percentages ranging between 75% and 85% and low values of *Betula* (3–8%). *Salix* occurs in all samples, although at low abundance, whilst NAP is represented by low values of Poaceae percentage, Tubuliflorae percentage and 2–15 Cyperaceae percentage. Spores of *Dryopteris*-t. reaches an abundance of almost 30% in the second sample.

LPAZ – PVa2 (190–320 cm)

The base of this zone, which coincides with a change in lithology, is defined by the first occurrence of *Corylus*, a slight decrease in *Pinus* to values less than 70% and a related increase in *Betula* percentages. The zone is similar to LPAZ PVa1, except that it is characterized by high values of *Equisetum* in two levels, and that *Corylus, Alnus, Quercus* and *Ulmus* pollen are present for the first time, albeit at very low frequencies.

LPAZ – PVa3 (155 cm)

The base of this zone is defined by the disappearance of *Equisetum* spores, a decrease in *Betula* percentages and an increase in *Corylus*, representing the start of a regular occurrence with percentages higher than 1%. In this zone *Pinus* declines to lower values (50–60%), whereas *Corylus* becomes more common (*c*. 15%), except for the upper sample. The number of *Dryopteris*-t. spores decrease, whereas Poaceae (probably *Phragmites*) becomes abundant.

LPAZ – PVa4 (40 cm)

PVa5 corresponds to a single level (40 cm) characterized by the highest percentages of *Alnus*, *Quercus*, *Ulmus*, *Tilia* and *Corylus* recorded in the profile.

Plant macrofossils

The only abundant plant macrofossils occurring in the sequence are *Eupatorium cannabinum* and *Cladium mariscus* (Figure 4). Fruits of *E. cannabinum* are resistant to severe oxidation and are common in tufa deposits (eg, Preece and Day, 1994). The highest values of Tubuliflorae (155 cm) may be related to the occurrence of *Eupatorium*. Today, it is a common plant on wet, nutrient-rich soils. The occurrence of *Cladium mariscus* between 110 and 50 cm is related to high pollen percentages of Poaceae (PVa4).

Insects

A few exoskeletal parts of Coleoptera were recovered from the tufa deposits (Figure 4). A total of eight taxa were identified. On the basis of the few recorded species, it is not possible to identify any changes in the beetle fauna.

The larvae of the melyrid beetle, *Dolichosoma lineare* (Rossi), live in rotting wood of *Acer* and *Pinus* (Palm, 1959). This beetle is widely distributed today in Fennoscandia, but is absent in the Scandinavian mountain range. The weevil *Otiorhynchus nodosus* (Müller) is today restricted mainly to alpine/subalpine environments in central and northern Europe, particularly on heaths with *Empetrum* and *Dryas*. It is also a characteristic species of subalpine birch forests (Böcher, 1988; Palm, 1996) and was common and widespread in southern Sweden during the entire Lateglacial period (Lemdahl, 1997). However, there are also a few modern records of *O. nodosus* from southern Sweden (Palm, 1996). The leaf beetles *Plateumaris discolor* (Herbst) and *P. sericea* (L.) are found on reed vegetation such as *Carex*, *Acorus*, *Eriophorum* and *Calla* throughout Fennoscandia (Hansen and Henriksen, 1927).

The rove beetle *Lathrobium brunnipes* (Fabr.) is common on moist ground, particularly among leaf-litter or moss (Palm, 1963). *Quedius fuliginosus* (Grav.) and *Q. curtipennis* (Bernh.) are two closely related species that are found in similar habitats such as densely vegetated swamps, along borders of water and on floating *Sphagnum*-carpets (Palm, 1963), where they are predators on other arthropods. All three of the rove beetles are common in most parts of Fennoscandia.

The dytiscid beetle *Rhantus grapii* (Gyllh.) is found in permanent, stagnant water bodies with dense vegetation, often in floating *Sphagnum*-carpets at lake margins (Nilsson and

Holmen, 1995). It is distributed in southern Fennoscandia, with scattered occurrences along the entire Baltic coast. The ground beetle *Agonum fuliginosum* (Panz.) is a hygrophilous carnivorous species mainly found on shady ground in habitats such as alder swamps, but also along the border of eutrophic lakes and rivers (Lindroth, 1986). It is a common and widespread species in Fennoscandia today. Scirtid beetles of the genus *Cyphon* are found in pools and ponds, where several species select oligotrophic habitats with *Sphagnum* vegetation (Nyholm, 1972).

Radiocarbon dates

The radiocarbon dates are summarized in Table 2.

Discussion

Chronology and deposition rate

The two radiocarbon dates obtained from the sequence (9775 cal. BP at 360–365 cm and 9825 cal. BP at 70–75 cm) are statistically indistinguishable. The reason for this is, at this point, unresolved but it seems clear that at least one of the samples have a problematic date. This is evident when comparing the changes in the pollen and mollusc diagrams, which clearly show an expected succession, similar to those seen in early Holocene tufas from other, nearby sites (ie, Meyrick, 1999; Gedda *et al.*, 1999; Gedda, 2001) and must have taken much more than 50 years to develop. The results, however, suggest that the deposit dates to the first part of T. Nilsson's Early Preboreal zone (PB1, Nilsson, 1964), which agrees with previous investigations.

Since the two ^{14}C-dates cannot be used for the basis of a chronology, the timescale largely had to be based on the pollen stratigraphical evidence. The pollen record suggests that the tufa was deposited in the early Holocene, during the period of establishment and expansion of *Corylus*, but prior to the expansion of *Alnus*. Thus, the lower part of the sequence, below 200 cm, has the pollen-stratigraphical characteristics of T. Nilsson's Preboreal zone (PB).

Unfortunately, the pollen data cannot help with the dating of the basal clay sediment. However, the occurrence of the land snail *Columella columella*, which today inhabits high alpine localities, may indicate that the sequence starts at the very beginning of the Holocene, ie, around 11 500 cal. BP. The pollen-stratigraphical changes, with an increase of Corylus and a decrease in Betula at 155 cm, can be correlated with the Preboreal/Early Boreal transition, dated to about 9900 cal. BP in Skåne (Gaillard *et al.*, 1996; M.-J. Gaillard, personal communication). The pollen stratigraphy from Valleröds Mosse and Pipers Mosse (Gedda *et al.*, 1999) are similar both in terms of the immigration of trees and the local herbaceous vegetation. In both cases the period before the expansion of hazel is characterized by high values of *Dryopteris*-type and *Equisetum* spores, whereas the latter are absent or rare during the time of the hazel expansion.

There is a rapid change in the pollen composition between the uppermost two pollen samples. The frequencies of *Tilia* and *Alnus* reach relatively high values (5% and 10%, respectively) within a few centimetres, while *Pinus* decreases to less than half of its former value. The values of *Ulmus* and *Tilia* suggest that the uppermost sample belongs to T. Nilsson's Early Atlantic zone (AT1) rather than the Late Boreal (BO2) and thus indicates a hiatus in sediment accumulation, alternatively a drastically decreased sedimentation rate, at the transition between the upper tufa and the *Alnus* peat. The upper part of the tufa deposit may, however, be dated to the BO1/BO2 transition (youngest age), ie, to about 8000 uncal. BP (8800 cal. BP) according to the revised Holocene chronology of Skåne (Gaillard *et al.*, 1996; M.-J. Gaillard, personal communication).

Deposition rates of 0.12 cm/yr have been recorded for British tufa (Kerney *et al.*, 1980), approximately the rate that is calculated for Valleröds Mosse, ie, with 0.12 cm/yr (325 cm of tufa). When compared with Pipers Mosse (Gedda *et al.*, 1999), with a mean tufa accumulation rate of *c.* 0.08 cm/yr (150 cm of tufa), the estimated mean deposition rate at Valleröds Mosse is significantly higher, based on maximum and minimum ages for the lower and upper parts of the tufa deposition, respectively, ie, 11 500 and 8800 cal. BP.

Local environment and vegetation history

In the earliest, Preboreal, part of the section, pollen data (Figure 3) suggest that the local vegetation consisted of a semi-open pine and birch woodland with *Salix* shrubs. The tufa casts of plants show imprints of a moss-dominated field layer vegetation with a significant reed/grass-like component. No identifiable plant macrofossils were found.

The mollusc fauna includes species typical of an open calcareous marsh, such as *Vertigo genesii*, *Vertigo geyeri*, *Columella columella*, *Galba truncatula* and *Zonitoides nitidus*. Also, the insect record provides vegetation evidence, for example by the presence of the melyrid beetle *Dolicosoma lineare*. Its presence may be an indication that pine grew close to the site, since this beetle is known to mainly live in the rotting wood of *Pinus*. The leaf beetle *Plateumaris serica/discolour* suggests a marsh environment with reed vegetation.

At 329 cm, around early to mid-Preboreal, there are changes in the colour and structure of the tufa (Table 1). The tufa becomes lighter and imprints of vascular plants are scarce, which may be inferred as a development from a moss-reed/grass field layer to a moss-dominated vegetation. At about 270 cm, the temporary disappearance of *Pupilla muscorum*, together with a marked decline in *Vallonia pulchella*, may have been caused by a slight increase in shade. However, the continued presence of *Vertigo genesii* makes it more plausible that other, at present unknown, environmental changes were responsible.

During the early BO1 (between 220 and 150 cm), the increase in *Corylus* pollen, probably reflects its local presence at this time. At 180 cm, *Eupatorium cannabinum* appears in the plant macrofossil record at the same time as *Equisetum* disappears (Figures 3 and 4). At the nearby site of Pipers Mosse, the first occurrence of *E. cannabinum* fruits, at about 10 200 cal. BP (9000 uncal. BP), corresponds with a general change in the local vegetation. *Eupatorium cannabinum* is a typical species of open birch or alder woods on wet, nutrient-rich calcareous soils. The local succession *Equisetum/Dryopteris*-type (spores) → *Eupatorium* (fruits) → *Cladium mariscus* (seeds) → Poaceae (pollen), may reflect a gradual change

Table 2 Radiocarbon dates expressed in uncalibrated ^{14}C yr BP and calibrated (95.4% confidence) yr BP

Depth (cm)	Lab. code	Uncal. date (^{14}C yr BP)	Cal. date (yr BP)	Material
70–75	LuA-4731	8780±110	9825±325	Charcoal – unidentified wood fragments
360–365	LuA-4730	8710±110	9775±325	Charcoal – unidentified wood fragments

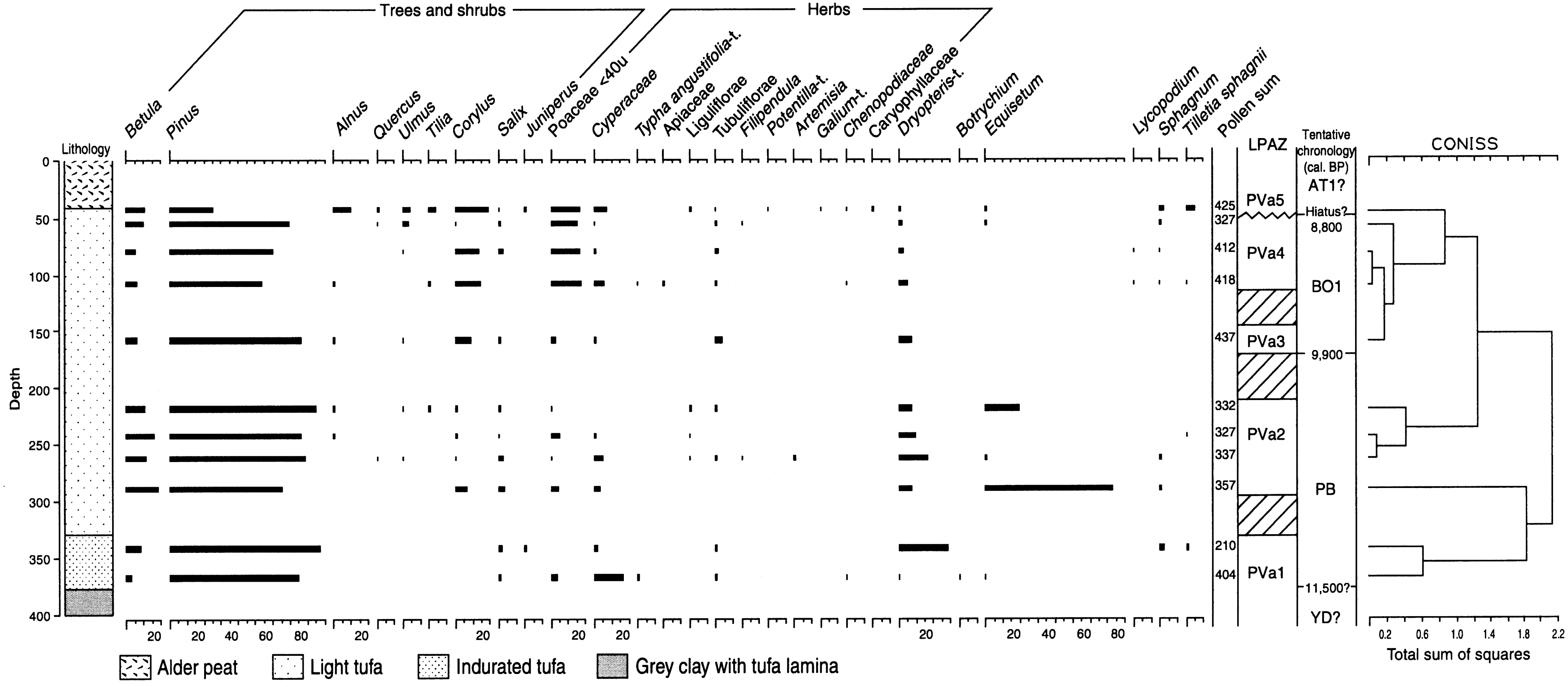

Figure 3 Pollen and spore percentage diagram. At least 300 tree-pollen grains were counted in all but two cases, 52 cm (no. 273) and 341 cm (no. 201)

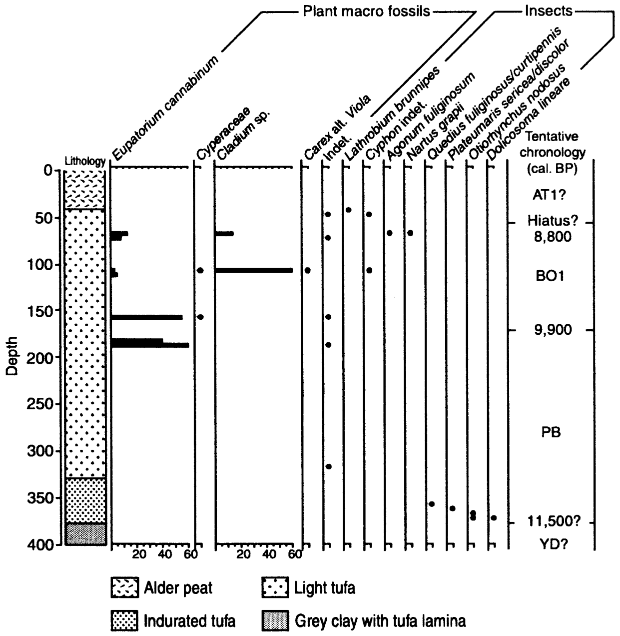

Figure 4 Plant macrofossil and Coleoptera diagram. The solid bars show absolute numbers of identified remains. All Coleopteran records were single individuals

towards higher groundwater level, that peaks in the upper part of the sequence (end of BO1 and AT). During most of the early BO1, the mollusc community shows that the site remained open.

During the deposition of the uppermost part of the sequence (late BO1/AT), the site was probably influenced by the river Fyleån. The aquatic mollusc *Bithynia tentaculata* appears in all the top eight samples, accompanied by *Vertigo moulinsiana*, which mostly lives on reed and sedges growing in water (Gärdenfors *et al.*, 1988). Changes in ground vegetation can also be inferred from the mollusc record, since *Vertigo antivertigo* and *Vertigo geyeri* are both associated with narrow-leaved plants such as sedges and rushes (Kerney and Cameron, 1979; von Proschwitz, 1993a). Several marsh species first appear and/or expand rapidly, *Vertigo geyeri, Zonitoides nitidus, Vertigo antivertigo, Galba truncatula, Pupilla muscorum* f. *pratensis* and *Vertigo moulinsiana.* This component of the terrestrial snail community becomes more important during this period. Higher water levels at this time are also indicated at Pipers Mosse by the appearance of *Pisidium* spp. (Gedda *et al.*, 1999).

At approximately 45–50 cm, a hiatus or drastically decreased accumulation rate is indicated by a change in the arboreal pollen assemblage. At the same time, tufa deposition stops and the calcareous marsh is replaced by an alder carr. *Bithynia tentaculata* is a relatively tolerant and adaptable species, although sensitive to oligotrophication of the aquatic environment, which is probably the reason for its decline in the upper three samples. The vegetational changes indicated by the pollen record (ie, a succession towards broadleaved deciduous woodland) are also reflected in the insect record. The beetle, *Lathrobium brunnipes*, is especially common in the leaf litter of moist deciduous woodland, whilst the rove beetle, *Agonum fuliginosum,* thrives in alder carrs.

Climate

The faunal assemblage of the earliest (early Preboreal) levels from Valleröds Mosse, particularly the occurrence of the snail *Columella columella*, seems to suggest that cold and open conditions prevailed at this time. However, this is not in agreement with MCR-reconstructions (Mutual Climatic Range) based on stenothermous Coleoptera from southernmost Sweden, which show that a rapid climatic amelioration took place around the YD/PB transition, when mean temperatures of the warmest month increased by 10°C, to conditions slightly warmer than at present (Lemdahl, 1991, 1997; Gaillard and Lemdahl, 1994). Furthermore, in the study of the tufa deposit at Pipers Mosse (Gedda *et al.*, 1999), it was concluded that tufa formation took place during the time of the lowest lake levels of the entire Holocene (eg, Digerfeldt, 1988; Gaillard and Digerfeldt, 1991), a period when relatively dry and warm conditions are supposed to have prevailed.

It is postulated here that what is actually reflected in the molluscan record is the temperature of the spring water, rather than the summer air temperature. It might be expected that a rapid shift in the climatic regime caused a lag between the warming of the atmosphere and the groundwater aquifers. The groundwater would thus remain at a low temperature, whereas the air temperatures and evaporation would be high enough to allow tufa deposition and the immigration of more thermophilous Coleoptera. Thus, the colder spring water caused a favourable microclimate for *Columella columella*, which could remain at the site for several hundred years despite the increasing air temperature.

The continued presence of *Vertigo genesii* suggests that there was no major change in the degree of shade and that spring-water temperatures remained relatively low. It is not until the end of BO1, when the regional groundwater tables had risen to the same levels as during the YD/PB transition (Digerfeldt, 1988), that evidence of increased temperatures can be seen in the mollusc record. At that time *Vertigo genesii* decline and more thermophilous species enter, such as *V. antivertigo, V. moulinsiana* and, in the uppermost sample, *V. angustior.*

Faunal history

A number of snails that today have a very limited distribution in Sweden were found during the present investigation. One of these is *Vertigo genesii*, commonly found in early Holocene sediments. It is rare in Sweden today and restricted to the Scandinavian mountains and a few calcareous fens in central and southern Sweden (von Proschwitz and Bennike, 1998). From other parts of Europe, there are only a few scattered records, from the Alps, the Carpathians and a few records from the British Isles (Colville, 1998). The species is classified as 'Near Threatened' (NT) on the Swedish Red List of Endangered Species (Gärdenfors, 2000). It is also listed in Natura 2000, the European Union's species and habitat list. The oldest Swedish finds are of Alleröd age (13 900–12 650 cal. BP), recovered from Toppeladugård in Skåne (Holst, 1906; Waldén, 1986). This identification must, however, be interpreted with care since, in the early twentieth century, *Vertigo geyeri* was commonly considered to be a subspecies of *Vertigo genesii* (von Proschwitz, 1998) and it is at this point unclear which species was considered. Three specimens of Younger Dryas age of *V. genesii* are also known from the southeastern Baltic Sea, east of Gedser (von Proschwitz and Bennike, 1998). The first indisputable record of *V. genesii* at Valleröds Mosse was from the second tufa sample from the bottom (370–375 cm), although the single specimen of *Vertigo* sp. (dextral) from 380–385 cm is also likely to be *V. genesii. Vertigo genesii* has a continuous and dominant presence throughout the Preboreal until the middle of the Early Boreal. Whether this species still inhabited the region later on is not clear, but there are some relict-like occurrences in southern Sweden and, according to Limondin and Rousseau (1991), it is known from the Atlantic period in Bourgonge, France.

The modern distribution of *Columella columella* is similar to that of *Vertigo genesii,* although it does not occur in the Swedish lowlands or in Great Britain (Kerney and Cameron, 1979), being mainly restricted to high-terrain habitats and cold springs. During the Younger Dryas it spread over most of northern and central Europe, including the British Isles (Lozek, 1967; Limondin, 1995; Preece, 1998). *Columella columella* was, together with *Galba truncatula*, one of the first two species to be recorded in Valleröds Mosse, already 10 cm below the tufa/clay boundary. It is probable that *C. columella* was already present during the Younger Dryas, since it was widely distributed by the early Preboreal (Waldén, 1986; Meyrick, 1999; Gedda, 2006).

The occurrence of *Cochlicopa nitens* is unexpected in association with a high number of *Vertigo genesii*, as *C. nitens* generally is assumed to be relatively thermophilous. However, finds of *C. nitens* have been reported from Lateglacial deposits in Britain (alongside *V. genesii*; Preece, 1992), from the Czech Republic (with *Columella columella*; Lozek, 1958) and from Germany (Meyrick, 1999). *Cochlicopa nitens* seems to have been quite common during the early Holocene of Skåne. Although rarely found in large numbers, it is found at a few sites in southern Sweden, including Gotland (Waldén, 1986), Östergötland (Meyrick, 1999) and Landskrona (Gedda, 2006). The species is today one of the rarest elements of the Swedish land mollusc fauna (von Proschwitz, 1999), although it has been removed from the latest Swedish Red List (Gärdenfors, 2000). Its present distribution is strongly fragmented, which in light of its historically wider distribution and exclusive ecological demands (ie, environments that in themselves are decreasing in number because of changes in land use), implies that anthropogenic effects are partly responsible for its decline.

The rare snail *Vertigo moulinsiana*, classified as 'Endangered' (EN) because of extensive land use, has a modern distribution pattern that ranges from southern Europe and northwest Asia to a single site in southernmost Sweden (Gärdenfors *et al.*, 1988). It is a relatively thermophilous species, the northernmost localities probably being relict populations of warmer periods of the Holocene. Steusloff (1937) and Ant (1963) suggest that it is normally limited to areas with a mean annual temperature of at least 10°C. However, more important factors are likely to be precipitation and mean summer temperature (Gedda and von Proschwitz, unpublished data). This species seems to have entered Sweden at around the Early/Late Boreal transition (~ 8800 cal. BP) and, during its maximum distribution extent probably sometime during the Atlantic to sub-Boreal times, reached both Gotland and Östergötland (Odhner, 1909; Munthe, 1910; Waldén, 1986; Gedda and von Proschwitz, unpublished data). Unlike *V. geyeri* (see below) and *Vertigo genesii* it never seems to have been common in Scandinavia, with only a total of 90 individuals, from 19 Swedish and 3 Danish sites, known from fossil records in this area. *Vertigo moulinsiana* seems to have rapidly declined in Sweden as air temperatures decreased at the sub-Boreal/sub-Atlantic transition (Gedda and von Proschwitz, unpublished data; Mörner *et al.*, 1980).

Vertigo geyeri seems, like *Cochlicopa nitens*, to suffer from anthropogenic disturbances and is, like *Vertigo moulinsiana*, classified as 'Endangered' (EN) by extensive land use. Its modern range, although discontinuous, covers most of Europe, including the British Isles and northwest Russia, a distribution pattern that is more likely the result of habitat destruction than climatic reasons (von Proschwitz, 1998: 49). *Vertigo geyeri* is commonly found in early Holocene sediments and appears sporadically at Valleröds Mosse during the Preboreal, accounting for 10% of the total land mollusc fauna by the end of the Early Boreal. This is the only snail of the five mentioned threatened species (*Vertigo genesii*, *Columella columella*, *Cochlicopa nitens*, *Vertigo moulinsiana* and *Vertigo geyeri*) that can be found in the Fyledalen valley today.

Conclusions

In Gedda *et al.*, (1999) and Gedda (2001), it was hypothesized that tufa deposition in this part of Skåne took place when this region experienced exceptionally low lake levels. The tufa deposition at Valleröds Mosse appears to confirm this. It

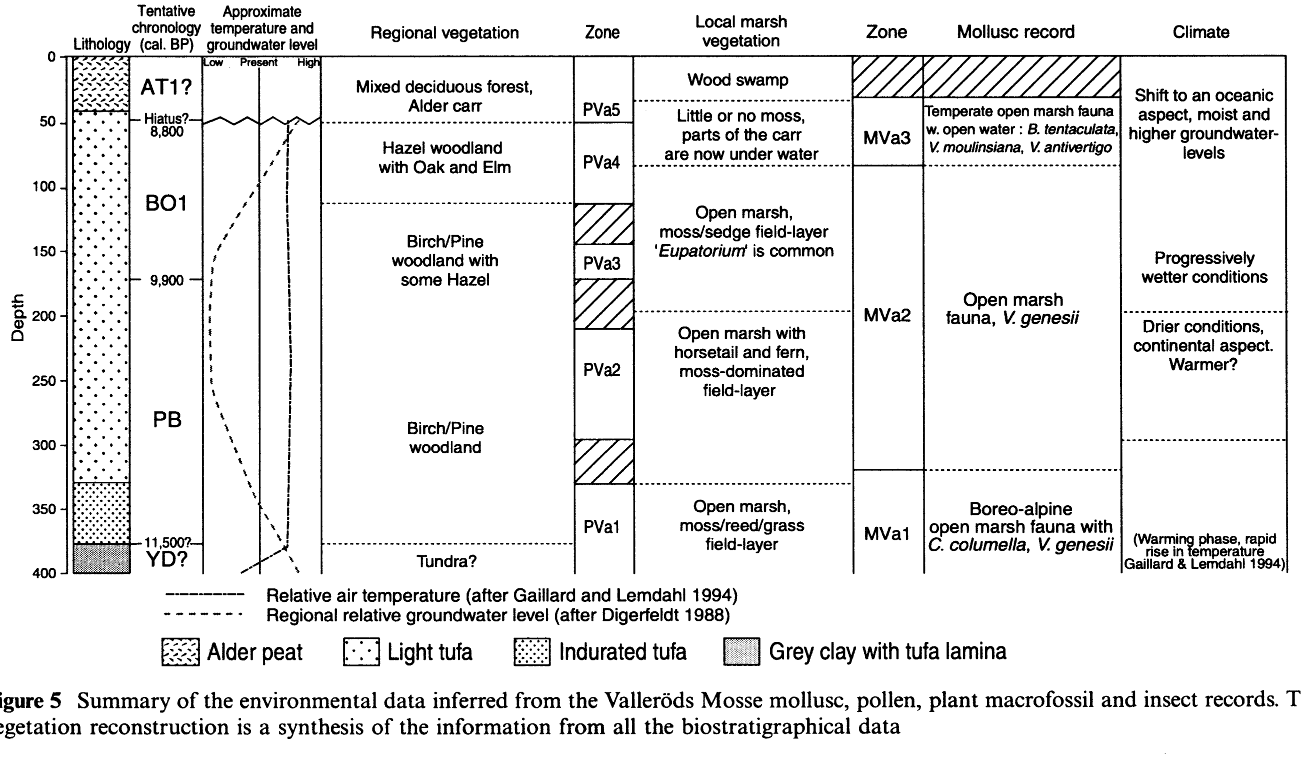

Figure 5 Summary of the environmental data inferred from the Valleröds Mosse mollusc, pollen, plant macrofossil and insect records. The vegetation reconstruction is a synthesis of the information from all the biostratigraphical data

appears that during the Preboreal and Early Boreal (BO1), an environment with a more continental character than present (dry, with relatively high summer temperatures) favoured tufa formation. Tufa deposition ceased most likely in response to a switch from a rather continental climatic regime to a more oceanic one, with an increase in precipitation and/or the rate of discharge.

The environment at Valleröds Mosse (Figure 5) developed from an open wet marsh with a dominance of grass-like vegetation in the early phase of the Preboreal, to a calcareous marsh with a moss-dominated field layer in the later stages of the Preboreal. During the Early Boreal the marsh gradually became drier until the Early/Late Boreal transition when precipitation increased and open water was present at the site. It is interesting to note that the faunal composition suggests an increased temperature during this latter stage.

Four species on the European Union's Natura 2000 list of endangered species have been found in the investigated deposit: *Vertigo genesii, Vertigo geyeri, Cochlicopa nitens* and *Vertigo moulinsiana*. Only one of these species, *Vertigo geyeri*, can presently be found in the study area. Of particular interest is the occurrence of *Vertigo moulinsiana*. This is today a threatened species, presumably mainly because of human interference. Its occurrence in the Holocene deposits at Valleröds Mosse is an important contribution to a better understanding of this rare snail's natural habitat requirements and distribution.

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