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Holocene mammals (Insectivora, Rodentia, Chiroptera) of Dollsteinhola Cave, Western Norway

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The Dollsteinhola cave comprises a sequence of Holocene deposits dating from the late Atlanticum to the first half of the Subboreal period. Climate-sensitive species were found in layers V (*Sciurus vulgaris*) and layers II-III, IV, IV-V (*Apodemus flavicollis*). Two humerus of *Barbastella barbastellus* were also recognised. The faunal assemblage were grouped in three climatic complexes: species which lived both in cold and warm climates; species connected with warmer phases of the climate and species typical for a cold climate.

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INTRODUCTION

Small mammals such as rodents and insectivores are rarely described from fossil and subfossil sediments from Norway, and every finding is important to improve our knowledge of the natural history of Norwegian micromammals. Norwegian records are mainly from Holocene and only a few papers describe remains of small mammals from Weischelian (Larsen et al. 1987; Lauritzen et al. 1996). Lie (1989) described Holocene fauna from the Dollsteinhola cave. This cave is located on the island of Sandsøy, Sunnmøre, Western Norway (Figure 1) and was excavated in 1954 by the archaeologist Erik Hinsch. Chronology of the material based on radiological C14-datings determined that this material originated from the end of Atlanticum and to the first half of Subboreal time e.g. from 6600 to 3600 years B.P. (Table 1). The material studied here comes mostly from material described as Rodentia and Insectivora by Lie (1989). Two species described as *Plecotus auritus* and *Rattus sp.* were renamed here.

The purpose of this study was to provide a more detailed description of the small mammal remains originally described by Lie (1989) and to reconstruct the environment around the cave during the relevant time period.

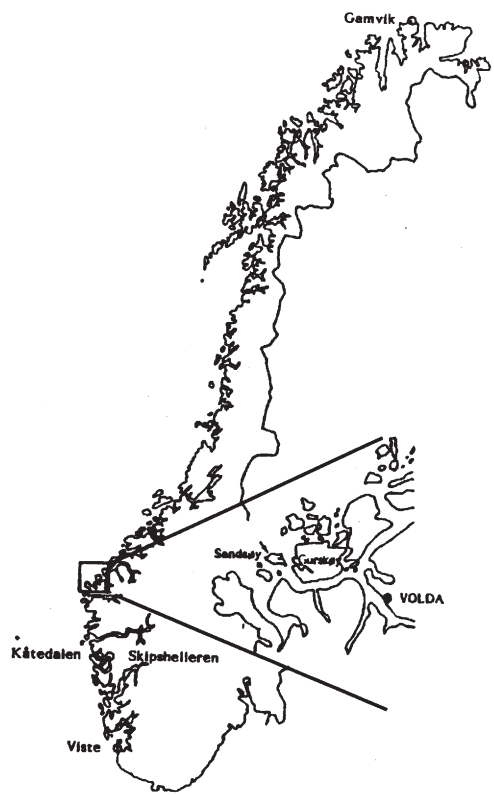

Figure 1
Map of Norway. The southern part of Sunnmøre with Sandsøy is enlarged. (After Lie, 1989).

Table 1. Datings of bones from Dollsteinhola. The calibrated age (in calendar years) is given following a method developed by Stuiver and Pearson (1986). Table after Lie (1989).

Laboratory's no.	Material	Layer	Age BC	Age BP	Radiocarb. Age, uncal.
T-6172	bone	II	1920-1680	3869-3629	3466±104
T-6173	bone	III	2485-2209	4434-4158	3886±85
T-6174	bone	IV	4656-4362	6605-6311	5633±94
T-6175	shell	III	2457-2242	4406-4191	3771±75

Table 2. Dimension of M_1 of the Holocene material of *L. lemmus*, *C. glareolus*, *A. terrestris* and *M. agrestis* from Dollsteinhola compared with Recent material.

Species	N	Period	Length of M_1		Width of the anterior loop	
			Min - Max	SD	Min - Max	SD
L. lemmus	51	Holocene	2.64-3.60	0.202	0.88-1.20	0.080
	16	Recent	2.72-3.36	0.222	0.88-1.12	0.066
C. glareolus	9	Holocene	2.24-2.32	0.040	0.80-0.88	0.050
	0	Recent	2.08-2-50	0.154	0.76-0.88	0.028
A. terrestris	9	Holocene	3.84-4-56	0.240	1.44-1.80	0.100
	7	Recent	3.60-4.56	0.333	1.44-1.76	0.136
M. agrestis	297	Holocene	2.56-3.28	0.118	0.72-1.28	0.066
	16	Recent	2.56-3.12	0.154	0.80-1.04	0.064

Table 3. Dimension of M_1 of the Holocene material of *A. flavicollis* from Dollsteinhola compared with Recent material. Measurements of Recent *A. sylvaticus* is added. X= data from literature (Nadachowski 1982).

Species	N	Period	Length of M_1		Width of M_1	
			Min - Max	SD	Min - Max	SD
A. flavicollis	6	Holocene	1.84-2.08	0.097	1.04-1.12	0-033
	X	Recent	1.62-2.05		1.01-1.27	
A. sylvaticus	15	Recent	1.60-1.76	0.052	0.88-1.04	0.043

MATERIAL AND METHODS

Mainly teeth, mandibles and rostrum fragments were selected from the collections stored in the Museum of Zoology, University of Bergen, Norway. Microtidae were identified based on the enamel pattern of M_1. Measurements of M_1 length and anterior loop width were compared with measurements of Recent specimens (Figure 2, Table 2). In *Apodemus*, M_1 length and width were compared with Recent specimens (Table 3). All measurements were taken with a caliper with accuracy of 0.01 mm viewed through an eye-binocular.

Of the more than 1 000 bone remains extracted, further analysis was possible on 294 M_1, 7 M_2, 305 mandibles, 9 skull fragments and 2 humerus. Distribution in records were as following; layer I: 39 M_1, 2 M_2, 39 mand., 2 parts of rostrum; layer II: 55 M_1, 51 mand.; layer II-III: 4 M_1, 2 M_2, 11 mand., 2 humerus; layer III: 22 M_1, 3 M_2, 13 mand., 1 part of rostrum , layer III-IV: 1 M_1, layer IV: 106 M_1, 50 mand.; layer IV-V: 16 M_1, 91 mand.; layer V: 48 M_1, 48 mand., 5 fragments of skull; layer VI: 3 M_1, 1 mand., 1 fragment of skull; layer VII: 1 mand.

RESULTS

The following species were found in Dollsteinhola. Measurements of specimens are given in Table 2 and 3.

***Sorex araneus* L., 1758**

Subfossil material: layer III: 1 fragment of right mand.; layer IV-V: 1 fragment of left mand., 1 fragment of right mand.

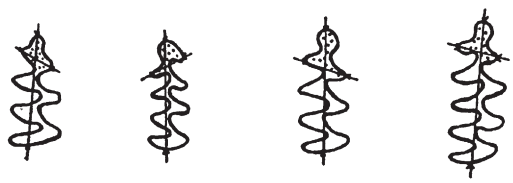

Figure 2
Measurement methods for vole molars. 1- M_1 of *Lemmus lemmus*, 2- M_1 of *Clethrionomys glareolus*, 3- M_1 of *Arvicola terrestris*, 4- M_1 of *Microtus agrestis*. Areas with dots indicate anterior loops.

General remarks: *S. araneus* is similar in dimension and dental features to *S. isodon*. In *S. isodon*, foramen mentale is located below P_4 and M_1, while in *S. araneus* it is below M_1. Upper incisors of *S. araneus* have large medial tines while in *S. isodon* they are very small (Dannelid 1991). *S. araneus* is common all over Norway and inhabits forests, brushy spots in meadows, and old parks. It was found previously in Dollsteinhola in layer V (Lie 1989).

***Neomys fodiens* (Pennant, 1771)**

Subfossil material: layer II: 1 fragment of left mand.; layer III: 1 fragment of skull; layer IV: 1 fragment of left mand..

General remarks: *N. fodiens* is common all over Norway. This species is strictly associated with water .

***Barbastella barbastellus* (Schreber, 1774)**

Subfossil material: layer II-III: 2 humerus. These were previously described as *Plecotus auritus* in Lie (1989).

General remarks: This is currently a very rare species, with only four recent records. This species is now known in three counties: Akershus (Collett 1911-12; Barth 1963), Buskerud (Hafslund 1949; Barth 1963) and Oslo (Wollebæk 1927; Barth 1963). *B. barbastellus* is a rather eurytopic species, but can also occur in forested areas and mountains.

***Sciurus vulgaris* L., 1758**

Subfossil material: layer V: 1 fragment of right mand.. This specimen was previously described as *Rattus sp.* (Lie 1989).

General remarks: A major amount of remains of this species were found in the Dollsteinhola in layers III, IV, V and VI (Lie 1989). This material was not available for this study. *S. vulgaris* is distributed all over Norway and is a typical forest-dwelling animal found in both coniferous and deciduous forests.

***Lemmus lemmus* (L., 1758)**

Subfossil material: layer I: 1 M_1, 2 M_2, 1 fragment of left mand., 2 fragments of right mand.; layer II: 4 M_1, 2 fragments of left mand., 6 fragments of right mand.; layer II-III: 1 M_1, 2 M_2, 2 fragments of right mand.; layer III: 13 M_1, 3 M_2, 4 fragments of left mand., 3 fragments of right mand.; layer IV: 10 M_1, 8 fragments of left mand., 6 fragments of right mand.; layer IV-V: 8

M_1, 5 fragments of left mand., 5 fragments of right mand.; layer V: 2 M_1, 1 fragments of right mand., 2 fragments of skull.
Recent material: 15 specimens (Hordaland county, Norway)
General remarks: This species inhabits tundra and the northern forest-tundra zones, as well as some deforested places in taiga. No significant differences ($p>0.05$) was found between measurements of *L. lemmus* from the Dollsteinhola and Recent specimens (Table 2).

***Clethrionomys glareolus* (Schreber, 1780)**
Subfossil material: layer III: 1 M_1; layer IV-V: 3 M_1, 2 fragments of left mand., 5 fragments of right mand.
Recent material: 10 specimens (Hordaland county, Norway)
General remarks: *C. glareolus* inhabits both deciduous and coniferous forests. In Norway it occurs north of Salten in Nordland.

***Clethrionomys rufocanus* (Sundevall, 1846)**
Subfossil material: layer II: 1 M_1
Recent material: 6 specimens (Norway, Hordaland county), 5 specimens (Finnmark county, Norway).
General remarks: This is a typical inhabitant of taiga and tundra zones. In Norway this species is distributed from Rogaland and Telemark in south and north to coastal Finnmark.

***Arvicola terrestris* (L., 1758)**
Subfossil material: layer II: 1 fragment of left mand.; layer II-III: 1 fragment of right mand.; layer IV: 1 fragments of right mand.; layer IV-V: 4 fragments of left mand., 3 fragments of right mand.; layer V: 1 M_1, 2 fragments of left mand., 1 fragment of right mand., 2 fragment of skull; layer VII: 1 fragments of left mand.
Recent material: 1 specimen (Lilleroel, Denmark), 2 specimens (Telemark county, Norway), 1 specimen (Finmark county, Norway), 2 specimens (Halberstadt, Germany).
General remarks: *A. terrestris* is a eurytopic species which inhabits different environments in mountains and lowlands. This species is found all over Norway except on high mountains and some islands.

***Microtus agrestis* (L., 1761)**
Subfossil material: layer I: 38 M_1, 19 fragments of left mand., 15 fragments of right mand., 2 fragments of upper jaws; layer II: 50 M1, 21 fragments of left mand., 20 fragments of right mand.; layer II-III: 2 M_1, 4 fragments of left mand., 3 fragments of right mand.; layer III: 8 M_1, 3 fragments of left mand., 2 fragments of right mand.; layer III-IV: 1 M_1; layer IV: 93 M_1, 15 fragments of left mand., 18 fragments of right mand.; layer IV-V: 5 M_1, 22 fragments of left mand., 31 fragments of right mand.; layer V: 45 M_1, 18 fragments of left mand., 24 fragments of right mand., 3 fragments of skull; layer VI: 3 M_1, 1 fragments of right mand., 2 fragments of skull.
Recent material: 15 specimens (Hordaland county, Norway), 1 specimen (Finnmark county, Norway)
General remarks: There are large similarities between the enamel pattern of *M. agrestis* and *M. arvalis*. However, it is possible to distinguish between these species based on size. Nadachowski (1982, 1984) gave some information on the discrimination of these taxa based on measurements of the anteroconid of M_1. Measurements of described specimens agree with that of Recent *M. agrestis* from Norway (Table 2) and no significant differences between them were found ($p>0.05$). *M. agrestis* inhabits mainly forests, fields and meadows. It is common all over Norway.

***Apodemus flavicollis* (Melchior, 1834)**
Subfossil material: layer I: 2 fragments of right mand.; layer II-III: 1 M_1, 1 fragment of left mand., 1 fragment of right mand., 2 fragment of skull; layer IV: 3 M_1, 1 fragment of right mand.; layer IV-V: 3 fragments of right mand.
Recent material: *A. sylvaticus* - 15 specimens (Hordaland county, Norway). *A. flavicollis* - 1 specimen (Sogn og Fjordane county, Norway) and data from the literature (Nadachowski 1982).
General remarks: Within the family Muridae, the amount and distribution of cusps on the teeth play an important role in the identification procedure. In the present work the species determination was based on the morphological features and dimension of the M_1. Dimension of M_1 of *A. flavicollis* is bigger than in *A. sylvaticus* (Table 3). *A. flavicollis* inhabits deciduous and coniferous forests. In Norway it is distributed from the eastern part of Norway along the coastline north to Trondheim.

DISCUSSION

Based on rodents ecological preferences it is possible to describe environmental conditions which occurred in the Holocene period in Sunmøre. The thanatocoenosis described from Dollsteinhola cave represents subfossils which probably come from the neighbourhood of the cave and were accumulated in different ways. The owls inhabiting the cave probably played on important part in the accumulation of bones and teeth of micromammals. It is important to remember that the described micromammal fauna do not reflect exactly the fauna which occurred near the cave, but depends on the food preferences of predators.

Based on radiocarbon datings, the material from the Dollsteinhola cave is from the end of Atlantic and the first half of Subboreal periods (Lie 1989). The finding of bones of domestic animals in almost all layers suggests that sediments layers have been mixed. However some suggestion about vegetation and climate is possible based on the micromammalian data and the material described earlier (Lie 1989).

The most numerous species is *M. agrestis* (ca. 80 %), an animal of forests, moist fields and meadows. This species is the most abundant in layers I, II, IV and V. The abundance of *M. agrestis* in Dollsteinhola does not mean that this species was dominant in the cave's surroundings, but that this species was most frequently hunted by owls.

The finding of *A. flavicollis* and *Sciurus vulgaris* indicates the presence of closed forest in the area studied. From the datings it is clear that both species were present in the Atlanticum period. During this time (8 000-5 000 years B.P.), summer temperature was 2.5-3.0 °C warmer than present (Nesje and Kvamme 1991). Lie (1989) suggested that the findings from layers IV and V belong to the middle of the Subboreal period and bird fauna of these layers reflect broad-leaved forest. However, according to his dating data, the layer IV (6 605-6 311 years B.P.) is of the Atlantic period. The mixture in the fauna of birds, both from deciduous and boreal forest, can be explained by the higher northern frontier of Nemoral Forest Zones, which was connected with increasing temperature (Lepiksaar, 1986). The occurrence of *C. glareolus* in layer III and *A. flavicollis* in layer II-III also reflect the presence of forest, which indicate the middle of the Subboreal period (Lie, 1989). Another interesting record is of *Barbastella barbastellus* which currently is regarded as rare in Norway. It prefers cold places with a temperature close to 0 °C during the hibernation period. This species hunts at the edges of forest, in tree alleys and parks (Pucek, 1981).

The Dollsteinhola fauna consist of several findings of *L. lemmus*. The recording of *L. lemmus* in Dollsteinhola may seem contradictory to the present alpine distribution of this species. However, this species has a high dispersion ability, especially during density peaks of the population cycle. Probably most of the *L. lemmus* specimens come from mass migration off the mountain area to the coast. It would be interesting for further studies to discover when this species arrived in Norway. This species was common during the coldest phases of the last glaciation in Europe and disappeared from Central Europe as the end of the Würm and beginning of the Holocene periods. Ekman (1922) proposed two immigration paths for this species to Scandinavia during the last glaciation: first from Denmark through southern Sweden; second from northern Russia to Finland. Remains of *L. lemmus* are known from north Kobbelgård in Denmark dating to the Middle Weischelian period (ca. 24 000 years B.P., Bennike et al. 1994). This can support Ekman's hypothesis that *L. lemmus* arrived in Norway from Denmark and spread along the coastline to Norway. Remains of this species were found in Skjonghelleren dating to the Ålesund interstadial (Larsen et al. 1987). The oldest known remains of *L. lemmus* from Norway are from Kjøpsvik, north Norway dating prior to 70 000 years B.P. (Lauritzen et al., 1996). Further investigation connected with the fauna from Kjøpsvik will be undertaken in the near future.

In summary, the fauna from the Dollsteinhola cave can be grouped in three climatic complexes:

1. Species which lived both in colder as well as warmer phases of climate during (*S. araneus, N. fodiens, B. barbastellus, A. terrestris, M. agrestis, C. glareolus* - the last species is a good indicator for the presence of forest).
2. Species which did not appear until a significant warming of the climate during the Holocene period, living in extensive forest areas (*S. vulgaris, A. flavicollis*) (Nadachowski 1982, Dagnan-Ginter 1992).
3. Species connected with a colder climate (*L. lemmus*)

All species except *B. barbastellus* found in the Dollsteinhola cave occur commonly today in Western Norway.

To get a better knowledge about the fauna history of mammals it is necessary to check localities older than the Holocene period and to focus more interest on studies of micromammals. Unfortunately, in both the above-mentioned pre-Holocene localities (Kjøpsvik and Skjonghelleren), sieves with a 1 mm diameter were used for washing sediments, which is too large for the teeth of most insectivores, bats and small rodents. Thus, this material is probably not representative for small mammals.

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SAMMENDRAG

Pattedyr fra Holocen i Dollsteinhola på Sunnmøre

Dollsteinhola inneholder Holocene sedimenteringer fra sen-Atlanticum til første halvdel av Subboreal periode. Varmekjære arter ble funnet i lag V (*Sciurus vulgaris*) og lagene II-III, IV og IV-V (*Apodemus flavicollis*). To humerus av *Barbastella barbastellus* ble også funnet. Faunaen ble inndelt i tre klimakomplekser; varmekjære arter, kuldekjære arter og arter som forekom både i varme og kalde klima.

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