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Invertebrates of Norwegian caves I. Gastropoda, Oligochaeta, Araneae, Acari, Amphipoda, Collembola, Coleoptera, Lepidoptera and Diptera

EIVIND ØSTBYE, STEIN-ERIK LAURITZEN, ARNE FJELLBERG, ERLING HAUGE, HANS PETTER LEINAAS, PREBEN OTTESEN AND TORSTEIN SOLHØY

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The invertebrate fauna of 14 Norwegian limestone caves, 6 in the southern and 8 in the northern part of the country, has been studied with regard to species composition and regional distribution. The species are discussed with respect to their ecological classification as type of cave dwellers, viz. trogloxenes, troglophiles and troglobites. The Norwegian limestone caves can roughly be divided into two main types of ecosystems: 1. Open systems, connected directly to the surface, with rivers or brooks entering through discrete openings. 2. Infiltration systems, which are fed by ground water or seepage water from overlying material. In this study little attention has been paid to the fauna of open system caves, as most of the animals found here are brought in with the running water. More attention has been paid to caves of the second category, infiltration systems, as they have more complex and stable ecosystems. A total of 70 species belonging to 9 orders has been recorded. Of these only 19 species are characterized as troglophiles, while all the other species must be regarded as trogloxenes, several of them habitual trogloxenes, but most of them accidental ones.

Eivind Østbye & Preben Ottesen, Dept. of Biology, Div. of Zoology, University of Oslo, Postbox 1050-Blindern, N-0316 Oslo 3, Norway.
Hans Petter Leinaas, Dept. of Biology, Div. of Marine Zoology, University of Oslo, Postbox 1064 Blindern, N-0316 Oslo 3, Norway.
Stein-Erik Lauritzen, Dept. of Geology, Sect. B, University of Bergen, Allégt. 41, N-5000 Bergen, Norway.
Erling Hauge & Torstein Solhøy, Zoological Museum, University of Bergen, N-5000 Bergen, Norway.
Arne Fjellberg, Tromsø museum, University of Tromsø, N-9000 Tromsø, Norway.

INTRODUCTION

Little is known of the invertebrate fauna of Norwegian caves. Except for a few casual observations (Natvig 1923, Horn 1947, Drakes 1966, Hjorthen 1968), most of the hitherto recorded species originate from two caves in northern Norway (Hippa et al. 1984 a, b, 1985 a, b, 1986). The invertebrate fauna of the other Fennoscandian countries is also poorly investigated. Some information exists from Sweden, all from caves in the southern part of the country (Gislén & Brinck 1950, Tell et al. 1967, Engh 1980, Hippa et al., op.cit.). In Finland only a few species have been listed from a small cave in the south of the country (Krogerus 1926). Caves are not rare in Norway; more than 800 are registered altogether, most of them in the northern part of Norway (Schrøder & Bergan 1983). The majority are karst or limestone caves, with tectonic and lava caves as a minority.

The Norwegian Karst Research Project was launched in 1977; its main goal is to investigate the genesis and development of karst processes on the land surface as well as the subsurface, together with the biological components in the hypogean (under-ground) ecosystems. This encompasses subprojects on the cave ecosystems with their floral and faunal components as well as biostratigraphic excavations of the hypogean sediments to obtain information on the quaternary history of plants and animals in Norway.

The aim of the present study is to improve our knowledge of the species composition and regional distribution of the invertebrate component of the Norwegian speleofauna (cave fauna), and to provide some information on abundance and distribution within the caves. The species are discussed with respect to their ecological classification as types of cave dwellers, viz. trogloxenes, troglophiles and troglobites, following the Schiner-Racovitza system (Schiner 1854, Racovitza 1907).

Three main categories can be recognized (cited after Jefferson 1983):

I «TROGLOXENES: animals which do not spend the whole of their lives underground; many of these roost there or use the caves seasonally, mostly in winter for hibernation but in some cases for aestivation during the summer. Trogloxenes generally feed outside the cave.

II TROGLOPHILES: species which can live permanently underground and establish properly reproducing populations there, but which also occur on the surface.

III TROGLOBITES: obligate cave-dwellers; these are the animals which often (but not always) show the characteristic cave-modifications of loss of pigment and reduction of the eyes.

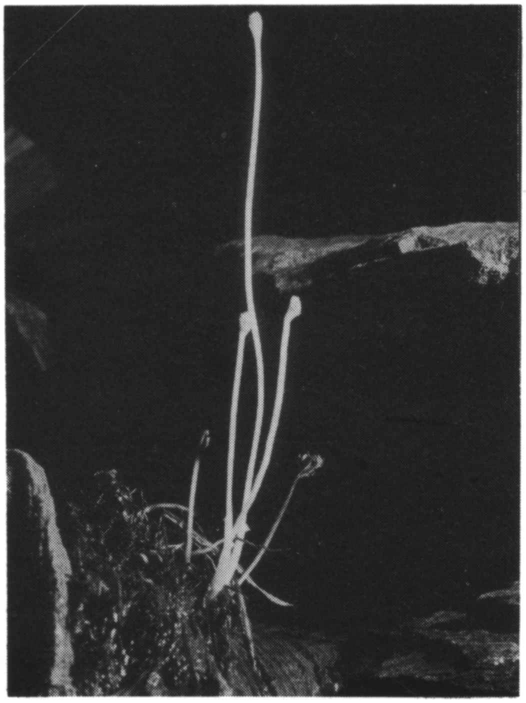


Fig. 2. Etiolated seed in a cave in Mo i Rana. Seeds and plant debris that is washed into the zone of total darkness may still sprout without developing chlorophyll, within the limits of energy that is brought in with the seed. Photo: S.E.L.

There have been numerous criticisms of the Schiner-Racovitza system and many proposals for its modification but it has stood the test of time and is widely used. As set out above the scheme does not cover animals which enter the cave purely by accident — most commonly stream animals carried underground in swallets. These are sometimes treated as a separate category —«accidentals» — but since they come within the definition of trogloxenes they can be accommodated there by subdividing this category into «accidental» and «habitual» trogloxenes.»

In this study we have only used the sam-

Fig. 1. Accidental cave fauna. Caddis flies washed into stream sinks and hatched underground. The imago caddis flies are probably starved to death on the barren marble walls of the main sump in Fosshølet Cave, North Norway. Photo: S.E.L.

pling methods as a first unspecific attempt to record as much information as possible concerning the composition of the cave fauna. Interpretation of population structure and density falls outside the scope of this work.

CAVE ECOSYSTEMS

The Norwegian limestone caves can roughly be divided into two main types of ecosystems:

I OPEN SYSTEMS, connected directly to the surface, with rivers or brooks entering through discrete openings.
II INFILTRATION SYSTEMS, which are fed by ground water or seepage water from overlying material.

In caves of the first type all faunal components belonging to the limnic ecoystems above — lakes, ponds, rivers or brooks — can be found, brought in with the running water. Water-borne debris also provides much of the energy flux through such open systems (Figs. 1 & 2). The surface or surface-related forms may survive for a period but rarely reproduce underground, even if they are able to run through some stages of their life cycle there. Most of these waterdrifting forms must be classified as accidental trogloxenes, only a few might be classified as habitual trogloxenes. At this stage in our survey, little attention has been paid to the fauna of this category of cave ecocystems, except for a cave in the southern part of Norway with a stable population of a cavernicolous crustacean, *Gammarus lacustris.*

In caves of the second category, infiltration systems, several examples of more complex and stable ecosystems are found. No faunal inhabitant of the Norwegian cave ecosystems hitherto investigated can be classified as a true troglobite, possibly because of the northern latitude and glacial history (the age of caves) of Norway. Only a few troglophiles and some more trogloxenes, both habitual and accidental, have been recorded. In our survey we have mainly concentrated the biological sampling to the caves of the infiltration system type.

MATERIALS AND METHODS

During The Karst Research Project a very large number of caves has been inspected, mostly in connection with investigations of the processes leading to karst formations and for conservation assessment. Biological observations and samples have been taken when possible, mostly in the form of hand-picking and occasional pitfall-trapping. Two caves, however, have been subjected to a more ex-

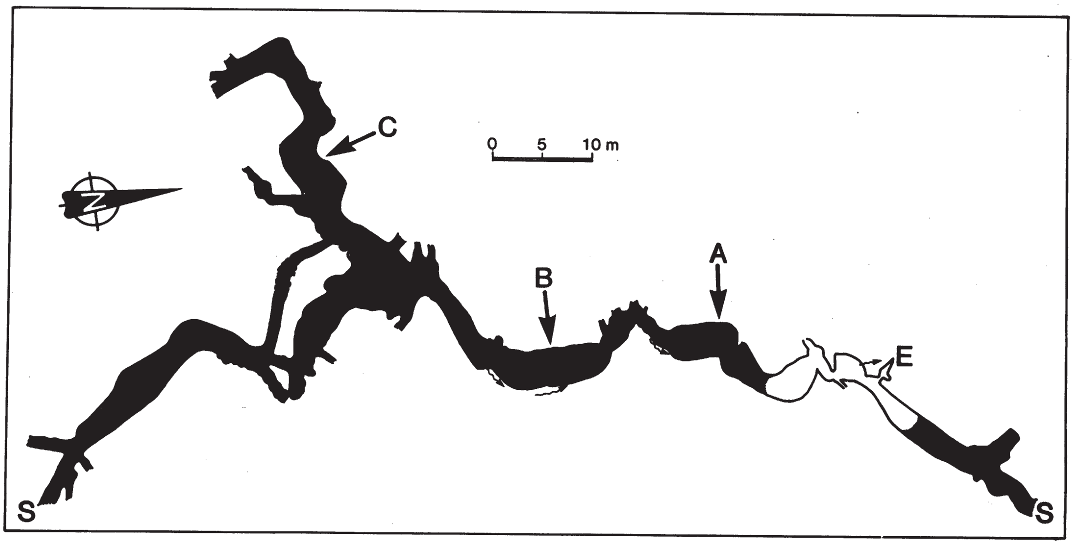


Fig. 3. The Bevergrotta Cave at Lauar (No 1 in Fig. 4). E: entrance. S: syphons. Light area: Twilight zone. Shaded areas: deep cave environment of complete darkness. Large arrows indicate approximate positions of pitfall traps A, B, and C. Undulated arrows indicate directions of streams. Survey from Lauritzen (1983).

tensive study of their ecosystems; the Bevergrotta Cave in South Norway and the Sirijordgrotta Cave in North Norway. In these two caves pitfall-trapping was carried out in addition to hand-picking. The pitfall-traps used were small plastic cups, 9,5 cm high with an upper diameter of 6,5 cm. As killing and conserving agent the traps were filled 1/3 with 4% formaldehyde. The traps were carefully dug into the soil to the upper brim, trying not to disturb the surrounding micro-habitat. Usually 5 traps were placed in a row, one meter apart from each other when possible, but the ground and soil conditions often made it necessary to place the traps in an irregular pattern. The minimum trapping period was 5 days. In the Bevergrotta Cave the traps were emptied each spring and autumn over a two year period. As a rule one trap line was placed in the threshold zone near the entrance, one or more in the dark zone in the middle part of the cave and one as deep inside the cave as possible. The threshold zone is here defined as the zone where the daylight from the entrance is visible (Fig. 3). Soil samples (diameter 10 cm) for extraction of soil living animals were taken at the pitfall-trapping locations, usually 5 samples at each site. Tullgren funnels were used for the extraction.

In the Bevergrotta Cave large soil samples (1 m^2) were dug out and sifted for lumbricids. This was only done where excrements from these animals were observed on the soil surface.

The material has been determined by the following persons: A. Fjellberg (Collembola, Coleoptera), W. Hackman (Helsinki, Finland) (Diptera), E. Hauge (Aranea), H.P. Leinaas (Collembola), R. Mehl (Oslo) (Lepidoptera), K.A. Økland (Oslo) (Amphipoda), P. Ottesen (Coleoptera), T. Solhøy (Gastropoda, Acari) and C. Støp-Bowitz (Oslo) (Oligochaeta).

The material is deposited partly in the Zoological Museum in Bergen and Tromsø and the University of Oslo.

HABITAT DESCRIPTION OF THE CAVES STUDIED

The records of invertebrates are based on investigations in 14 different caves, 6 in South Norway and 8 in North Norway. Fig. 4 shows the location of these caves in Norway: the numbers refer to the entries in Table 1 where the morphology and habitat properties of the individual caves are listed. In the remaining Tables (3—11) the individual caves are abbreviated as in Table 1.

South Norwegian Caves

Bevergrotta (No 1 in Fig. 4, and abbreviated as BEV in Tables 1—11) is situated in the Lauar area, in the foothills of the Skrim mountain range, in Kongsberg municipality. The elevation at the entrance is approximately 350 m. The bedrock is upper Silurian limestone faulted downwards into a Permian intrusive body, yielding progressively metamorphosed marbles (Rohr-Torp 1973), of which the Tretaspis and Stricklandia Series karstify well (Lauritzen 1983).

The vegetation above the cave is a mixed forest dominated by pine *(Pinus sylvestris)* and birch *(Betula pubescens* and *B. pendula)*. Until now only about 200 m of the cave system have been investigated and mapped (Fig. 3). The entrance is a narrow opening approximately 50 cm high, at the bottom of a 5 m deep shaft. The cave conducted large discharges in the past, but a progressive downcutting of the nearby river, which earlier drained through the system, has reduced the input through the cave to a low, constant, infiltration-fed discharge with little tempera-

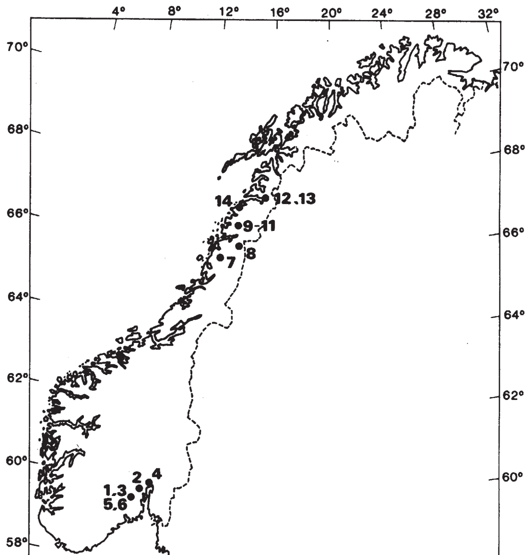


Fig. 4. Key maps to the caves investigated. Numbers refer to the entries in Table 1.

Table 1. Morphology and habitat characteristics of the caves investigated.

Cave	Municipality	Ref. in Fig. 4&6 and tables 3-11	Altitude m	Total length, m	Depth m	Average cross sect. m^2	Cave habitat type	Min:Age ka	References
Bevergrotta	Kongsberg	1 BEV	350	190	5	2	Diffuse input with stream	60	1
Svarttjern 1	N.Eiker	2 SVA	220	150	10	2	Discrete input with stream	2.5	1,2
Svarttjern 2	"	3 SVA	205	100	2	0.5	Discrete input with stream	-	1
Båntjern	Oslo	4 BÅN	230	50	5	0.5	Discrete input with stream	-	1
Gammarusgrotta	Kongsberg	5 GAM	370	50	2	5	Flooded resurgence cave	-	1
Finneguriggruven	"	6 FIN	290	30	5	2	Fossil cave, no stream	-	1
Sirijordgrotta	Vefsn	7 SIR	200	1400	90	5	Discrete and diffuse input, large cave, with active stream	7.5	3,4
Revhølet	Hemnes	8 REV	560	2400	70	2	Fossil, no stream in this part	160	1,2
Pikhågvassgrotta	Rana	9 PIK	549	100	16	2	Discrete input with stream	-	5
Kalkrastgrotta	"	10 KAL	350	600	50	1.5	Fossil cave, no stream	-	1
Fosshølet	"	11 FOS	450	490	30	9	Discrete input with stream	-	6
Svarthamarhola	Fauske	12 SVA	250	1730	160	3000	Fossil, ice cave	120	1,7
Okshola	"	13 OKS	170	11000	300	10	Fossil and active, discrete input streams	350	1,8
Nonshauggrotta	Gildeskål	14 NON	300	1200	30	2	Fossil network, no stream	10	1,9

Legend: Ka = Kiloannum (1000 years). Total length is cumulative passage length of the cave. Depth is greatest vertical difference within the cave. Passage cross-section, estimated (m^2).

References: 1) Lauritzen, S.E. unpubl. mapping and stalagmite dating (1975-87), 2) Lauritzen & Gascoyne (1980), 3) Faulkner (1980), 4) Lauritzen & StPierre (1982), 5) Lauritzen (1977a,b), 6) Jenkins (1959), 7) Heap (1970), 8) Heap (1969), Holbye (1974), 9) Holbye & Trones, unpubl. map.

ture variation; only from 3° to 6°C during the year. Abundant gravel and sand fills obstruct the possible leads in the cave. The gravel is largely cemented into an iron oxide hardpan, and the upstream parts of the cave contain a silty mud cap, representing a backflood deposit (Fig. 5). Sediment sequences, fining upwards like these, are very common in Norwegian caves (Lauritzen unpublished). The cave is at least of pre-Weichselian age, as a stalactite base gave an Uranium-series date of approximately 60.000 years.

The locations of the pitfall traplines and soil samples are given in Fig. 3. One trapline was set in the threshold zone, 15—20 m from the entrance. Only a very faint light prevails in this part of the cave, due to the shading effect of the shaft leading down to the entrance. In the dark zone, one trapline was set halfway in, at approximately 40 m from the entrance, and one approximately 80 m from the entrance.

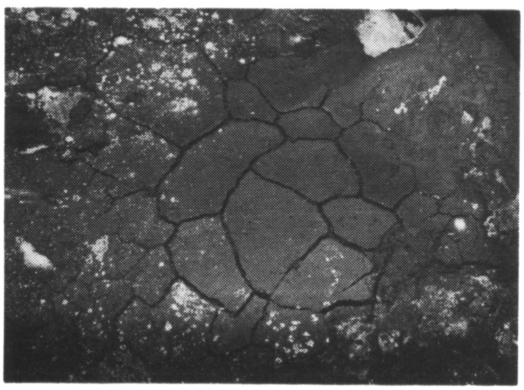


Fig. 5. Organic «Cap Mud» with drying cracks, calcareous precipitates and fungal colonies. Bevergrotta Cave, South Norway. Photo: S.E.L.

As the cave was discovered as late as 1976, the influence of man has, until the present date, been moderate, although some disturbances have been noted in the last few years, mostly caused by tourists but also by scientists.

Svarttjernsgrottene 1 & 2. (No 2 & 3 in Fig. 4 and 6A, abbreviated SVA in Tables 1—11). Both cave No 1 and 2 are of the open system type and are developed along shorter underground courses of the Svartbekken stream at Krokstadelva, Nedre Eiker municipality. The local vegetation is predominantly spruce *(Picea abies),* alder *(Alnus incana)* and hazel *(Corylus avellana).* Cave No 1 is a largely dry and fossil trunk passage, partly filled in with breakdown blocks and silty/clayey sediments. In addition, the cave possesses several high-level, dry annexes. The relatively large entrance of cave No 1 provides a 4—5 m deep twilight zone. Svartbekken, which occupies the floor of the trunk passage, is apparently underfit for this large cave. Cave No 2 consists of partly waterfilled passages up to about 1 m in diameter, upstream of a small spring. The entrance is a squeeze through scree blocks, and the twilight zone is rather short (1—2 m). Upstream, the tubular passages end in several syphons. There is an underground hydrological con-

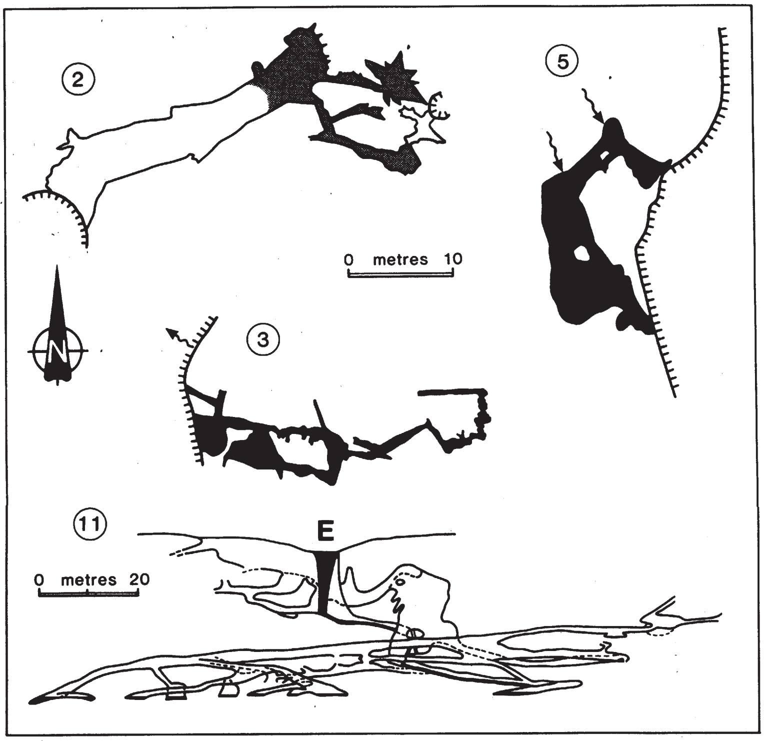


Fig. 6A. Plan of the smaller caves of this study. Hacked lines = escarpments. This figure shows 2 = Svarttjern 1 (cf. Table 1), 3 = Svarttjern 2, 5 = Gammarusgrotta, 11 = Fosshølet, the entrance E is coloured black. In Svarttjern 1 (2 in the fig.), white and shaded areas exemplify twilight and deep cave zones, respectively.

nection between the two caves (the same stream invades both of them), as proved by water tracing techniques (Lauritzen 1983).

Pitfall traps were placed in the dry, upper galleries of cave No 1, and in moist side annexes of cave No 2. In the latter, the side annexes were filled with wet, organic silt, probably of backflooding origin. Arachnids and larger insects were hand-picked from dry annexes in both caves. Both cave systems are situated only 2—5 m below the present day-surface.

The upper cave (No 1) has been known for almost 100 years (Vibe 1895, p 275), whilst the lower cave (No 2) was first discovered and dug into in 1975.

Båntjernsgrottene (No 4 in Fig. 4, abbreviated as BÅN in Tables 1—11) consists of two caves which are the inlet and outlet of the approximately 50 m underground course of a small brook which runs into Båntjern in Oslo municipality. Both caves consist of squeezing-size passages, which are further obstructed by slab breakdown, garbage and silty, organic, back-flooding mud. Carnivore (fox) droppings are abundant in the explorable sections of both caves. The caves are of the open system type with an active stream which floods the system periodically, but they also function as effective sediment traps for waterborne organic mud and forest debris. Both caves are less than 4 m below the surface at all points. The surface vegetation is an open pine and hazel forest with grass. The human impact on these two rather inhospitable caves is mainly from garbage which has been thrown down the sinkhole of the surface stream (Fig. 7). Specimens were mainly hand-picked, and a few pit-fall traps were placed in a silted chamber in the upstream cave and left for a week.

Gammarusgrotta (No 5 in Fig. 4 and 6A and abbreviated as GAM in Tables 1—11). This is the resurgence cave of the Sandåa stream, hydrologically connected to upper and lower Sandågrotta. The cave is part of the Lauar karst at Skrimfjell. Gammarusgrotta is almost full of water; only in dry periods may one explore it into an extensive underground «lake» which is fed by several syphons about 1—2 m below the water table (Fig. 8).

The floor of the cave is covered with gravel and sand; finer sediments are occasionally seen on high-level ledges and in small annexes. In spring and after heavy rainstorms, the

Fig. 7. Upper entrance to the Båntjerngrotta Cave, Oslo. Such stream sinks take organic debris, sediments and garbage into the deep cave environment. Photo: S.E.L.

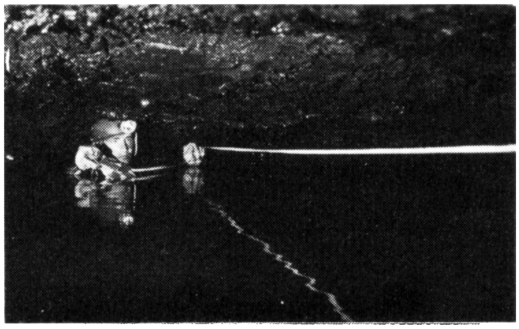


Fig. 8. Surveying the underground «lakes» in the Gammarusgrotta Cave, Skrimfjell. The cave is explorable when the water level is low. A population of *Gammarus lacustris* exists in this underground water habitat. Photo: S.E.L.

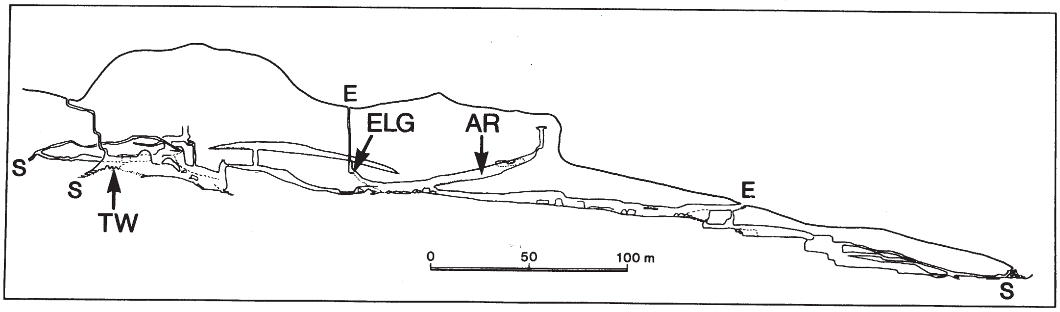
cave is totally filled with water; occasionally a fountain emerges through the entrance, proving that the main conduits do experience periods of very high flood discharges.

North Norwegian Caves

Sirijordgrotta (No 7 in Fig. 4, abbreviated as SIR in Tables 1—11) is a relatively large and complex cave system situated in Eiterådalen in Vefsn municipality. 1400 m of passages comprise a multilevel complex with an active stream in the bottom level canyon. This is shown in the longitudinal section in Fig. 9. The system is 90 m deep and the upstream end of the cave extends about 50 m below the surface. A few vertical shafts penetrate to the surface. At least two storeys of high-level, fossil galleries are known, ending in sediment blockages.

The sediments in the cave range from well-rounded boulders to gravel and sands. The sediment sequences are commonly covered with a «Cap Mud» (Bull 1977) of silt and clay sized laminates. One of the vertical shafts,

Fig. 9. The Sirijordgrotta Cave, Vefsn, North Norway. Longitudinal section, showing the multilevel galleries. E: entrance. ELG: Elgsjakta. AR: Arctic Passage. TW: Twin Ducks Passages. Survey after Faulkner (1980).



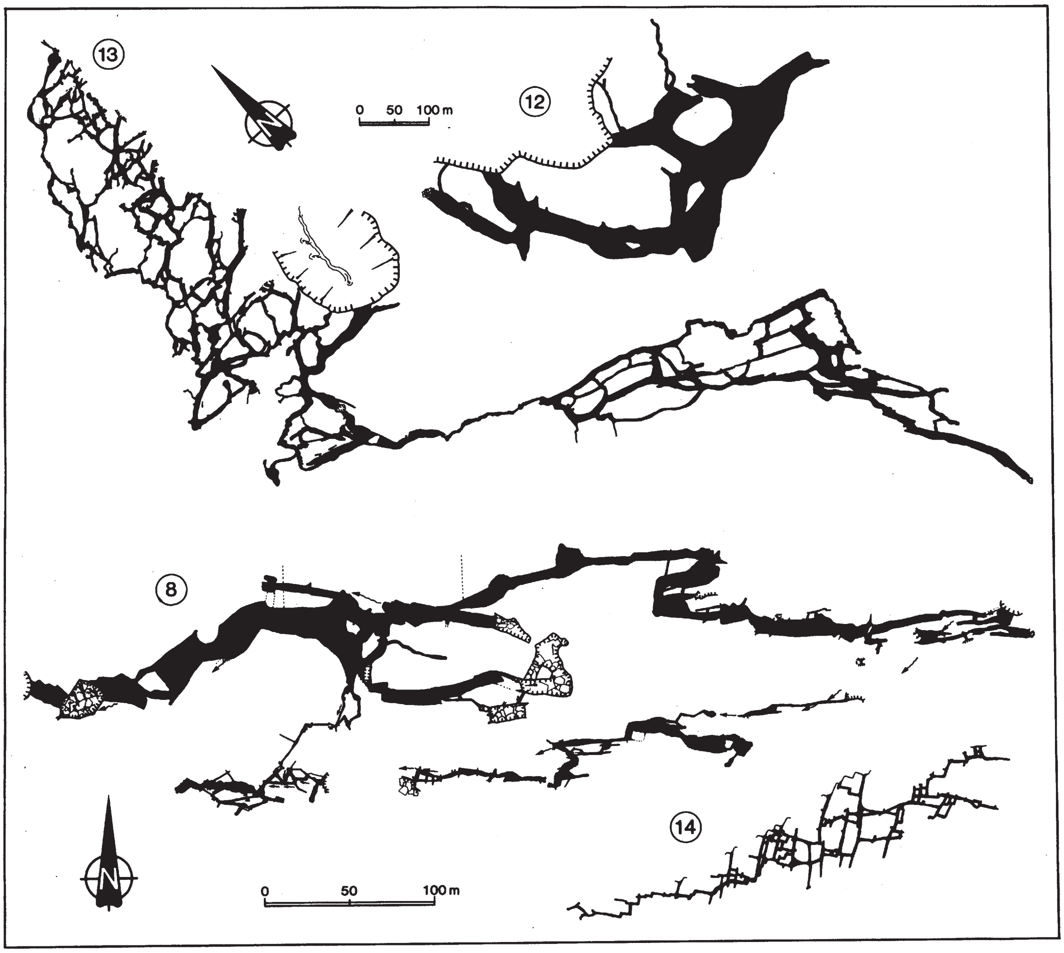


Fig. 6B. Plan of the larger caves of this study. Hacked lines = escarpments. This figure shows 8 = Revhølet (cf. Table 1), 12 = Svarthamarhola, 13 = Okshola and 14 = Nonshauggrotta.

«Elgsjakta», injects organic remains directly from the surface into the middle part of the system.

The morphology and size of the high level galleries, as well as the prolific sediment deposits, strongly suggest that the system is very old. A deposit of injected diamictic sediment (till) in one of the passages suggests that it at least predates the last glacial age.

Another sediment sequence was postdated by a stalagmite date of 7.500 years (Lauritzen & StPierre 1982).

The surface is covered with spruce and birch forest. Recent bulk timbering of the area may cause increased soil erosion and an increased organic input to the cave.

Pitfall traps were placed at 3 sites in the cave; one set at the bottom of the 40 m «Elgsjakta», another set in the «Arctic Passage», and a third set in «Twin Ducks Passage» at the very upstream reaches of the cave (Fig. 9).

The cave was first found in 1979 (Faulkner 1980, StPierre & StPierre 1980), and except for recent stratigraphic excavations, the cave bears few signs of human impact.

Revhølet (No 8 in Fig. 4 and 6B, abbreviated as REV in Tables 1—11) is a part of the Grønndalen cave system (Lauritzen 1977a). It is situated in a valley side near Okstindane in Hemnes municipality. The Grønndalen cave system, which includes a total of 2.500 m of passages, consists of a main, active river cave which conveys the Jordåga river along an underground course of 500 m. Connected to this river passage are several high level abandoned and fossil sections. Revhølet is one of these, and is the morphologically oldest part of the cave system. Other abandoned passages have been in existence for more than 140.000 years, as proved by Uranium Series dating of speleothems (Lauritzen & Gascoyne 1980).

The caves are situated just above the treeline at 560 m. The dominant vegetation above the cave is heather, grass and willow. Revhølet consists of a horizontal network of dry, crawling and walking size passages, partly filled by fluvial sand and slab breakdown. A few passages which lead towards the surface are blocked with talus debris from the surface escarpment. Carnivore (fox) droppings, as well as bear skeletons indicate that the cave has acted as a habitat for such animals in periods. This may account for some organic input.

Pikhågvassgrotta (No 9 in Fig. 4, abbreviated as PIK in Tables 1—11) is situated in the alpine zone at 540 m, close to the Svartisen glacier in Rana municipality. It is part of the Glomdalen-Pikhågan karst area in Svartisen. The cave is a short streamway passage, with a few upper level tubes (Lauritzen 1977b). The surface is bare karst, with a very scanty cover of moss, lichen and grass. The cave penetrates less than 10 m from the surface and shows no signs of human impact.

Kalkrastgrotta (No 10 in Fig. 4, abbreviated as KAL in Tables 1—11) is also part of the Glomdal-Pikhågan karst. It is situated only a few meters beneath the surface of a barren limestone pavement with little or no present vegetation. The cave consists of a network of fossil tubular passages of crawling size (Lauritzen 1983). Scanty sediment deposits consist of boulders and sand. No human impact is apparent in the cave at present.

Fosshølet (No 11 in Fig. 4 and 6A, abbreviated as FOS in Tables 1—11) is a large streamsink cave in the Glomdal-Pikhågan area. Beneath a 15 m waterfall, the cave continues for another 450 m to a large syphon at 30 m depth (Jenkins 1959). The cave is largely a series of clean-washed tubular passages in marble. Sediments are only abundant in the syphons and in chokes at the upstream end of the cave. The sediments are largely well-rounded boulders, fluvial gravel and sand. Very little organic debris was seen in the cave (Fig. 1). The cave and the area itself are rather difficult of access, and no human impact has yet been detected in this cave. The surface vegetation is similar to that over Pikhågsvassgrotta.

Svarthamarhola (No 12 in Fig. 4 and 6B, abbreviated as SVA in Tables 1—11) has the largest volume of any natural chamber in Scandinavia, and is also one of the lowest altitude ice caves in Europe. It is situated in Fauske municipality at an elevation of 250 m. The largest chamber measures 300 x 100 x 40 m (Heap 1970) and contains a considerable mass of perennial ice, due to the Balch-ventilation effect between the two entrances (Wigley & Brown 1976). Side passages are choked with extensive silt and clay plugs, and most of the floor is covered with large fallen blocks. There is little if any organic debris in the cave, and little human impact, in spite of the fact that it is used frequently for introductory trips by local cavers. The surface vegetation is a spruce and birch forest.

Okshola (No 13 in Fig. 4 and 6B, abbreviated as OKS in Tables 1—11). This is the longest cave system in Norway by 11 + km total length (Heap 1969, Holbye 1974) and consists of a multientrance, multilevel network system with a major streamway canyon, about 30 m deep, with several tributary streams. The passages vary from large breakdown chambers to walking passages. All grades of sediments are seen in this cave: breakdown slabs, boulders, gravel, sand, silt and clay. Some passages may have sediment fills of a very uniform size, such as several large, sand-floored chambers. Downstream, the river passage ends in a series of large syphons, covered with organic mud. Upstream, the passages end in surface talus or till deposits. The surface is covered with spruce, birch and alder forest. Pitfall traps were placed at the downstream, silty syphons. Human impact in the cave is becoming rather obtrusive; litter, footpaths and vandalized speleothems are abundant in places.

Nonshauggrotta (No 14 in Fig. 4 and 6B, abbreviated as NON in Tables 1—11) is situated near the top of a steep cliff face in Gildeskål municipality. It comprises a network of totally fossil passages which end on one side as hanging entrances in the cliff escarpment, and on the other side of the system in sediment chokes (Fig. 6B). The sediments are mainly fine sand and silt, covering most of the floor of the cave. Abundant carnivore (fox) droppings as well as an impressive ac-

Fig. 10. Animal remains on silty sand. Nonshauggrotta Cave, Gildeskål. Photo: S.E.L.

cumulation of bone fragments demonstrate the importance of organic input from scavengers into horizontal cave ecosystems (Fig. 10). The vegetation above the cave consists only of a few scattered birches, willow and grass. Invertebrates were mainly collected in pitfall traps in the deeper reaches of the cave.

Table 2. The number of species and specimens of invertebrates recorded from Norwegian caves.

Taxa	Number of species	Number of specimens
class Gastropoda		
order Stylommatophora	6	18
class Clitellata		
order Oligochaeta	2	5
class Arachnida		
order Araneae	4	12
order Acari	(2-3)	4
class Crustacea		
order Amphipoda	1	25
class Insecta		
order Collembola	18	82
order Coleoptera	29	177
order Lepidoptera	2	6
order Diptera	8	23
Total	70 + (2-3)	352

RESULTS AND DISCUSSION

We have so far recorded 70 (+ 2—3) species belonging to 9 orders in the material collected (Table 2). The number of specimens collected is not high. In our investigation only 352 specimens were determined to species level.

Generally the number of individuals in cave invertebrate populations is rather low. The caves are rich in fissures, microcrevices and other hiding places suitable for small animals. All this makes it difficult to spot the animals on the ground, walls and roof, when searching for them with only light beams from head and hand lamps during hand-picking. There are several problems involved in the interpretation of samples collected by pitfall-trapping (e.g. Adis 1979). Experiments on two species of cave beetles showed e.g. that traps with a larger diameter yielded a better catch than traps with a smaller one (Kustor et Novak 1980). The same study further showed that glass traps were preferred in comparison with plastic traps. Significantly higher numbers were caught if the traps were baited with meat.

The fauna of the different parts of a cave, in a transect from wall to wall of a cave passage, has been investigated by long-term pitfall trapping (Novak et al. 1981). More animals were trapped at the sides than in the middle of the passage, depending on the microhabitat. Areas rich in fissures and loose substrate gave the richest catches. This clearly shows the importance of placing several traps at random to assure representative sampling. The detritus association of the cave fauna (the fauna of the cave bottom) is presumably better trapped with pitfall traps than the parietal association (i.e. the fauna on the walls and roofs), which has been found to be an important component of the cave fauna (see e.g. Jefferson 1983). Hand-picking was the only method used for sampling the parietal association. Extraction of soil samples was incorporated as a supplement to pitfall trapping in order to record the detritus association.

Gastropoda

Six species were recorded, all of which were found in South Norway, but only two in North Norway (Table 3). The Bevergrotta Cave had the most diverse fauna of gastropods, with five species. Although in the Bevergrotta Cave 6 of 9 specimens were found in the inner dark parts of the cave, most of the Norwegian specimens were found in the threshold zone. The species recorded must be classified as accidental trogloxenes, belonging to the threshold fauna. This is in accordance with records of these species in other parts of Europe. *Limax cinereoniger* is listed as an accidental trogloxene in Belgium (Boettger 1939) and is further only reported from Yugoslavia (Wolf 1934—38). *Clausilia bidentata, Oxychilus alliarius* and *Cepaea hortensis* have been found in England, and are there classified as trogloxenes (Hazelton 1975, 1977).

The cave distribution of the six species is in accordance with their epigean distribution in Norway (Økland 1925, Kerney & Cameron 1979, Andersen 1982).

Oligochaeta

Lumbricidae

Only two species of lumbricids were found, both in low numbers (Table 4). In the Bevergrotta Cave two specimens of *Allolobophora caliginosa* were found moving on the soil surface in small cracks in the soil in the dark inner part of the cave. Intensive digging and sifting of soil in mud banks with large amounts of earthworm excrements yielded no further specimens. Obviously these excrements have been piled up during many years. In these environments no other factors than flooding and human trampling can wipe out the signs of animals left on the soil surface. In this particular cave flooding no longer occurs.

Table 3. Number of individuals of Gastropoda species from Norwegian caves. For abbreviation of cave names, see cave descriptions. Symbols: ○ - trogloxene, ◑- troglophile and ● troglobite.

Species	Caves				Total
	South Norway		North Norway		
	Bev	Fin	Kal	Oks	
Endodontidae:					
○ *Discus ruderatus* (Férussac)	4	-	-	-	4
Zonitidae:					
○ *Oxychilus alliarius* (Miller)	1	-	-	-	1
Limacidae:					
○ *Limax cinereoniger* Wolf	1	-	1	-	2
Clausiliidae:					
○ *Clausilia bidentata* (Ström)	1	-	-	-	1
Helicidae:					
○ *Arianta arbustorum* (L.)	2	-	-	7	9
○ *Cepaea hortensis* (Müller) (morph: Yoooo)	-	1	-	-	1
Number of species	5	1	1	1	6
Number of individuals	9	1	1	7	18

Table 4. Number of individuals of Lumbricidae species from Norwegian caves. For symbols see table 3.

Species	Caves South Norway Bev	North Norway Sir	Total
O *Allolobophora caliginosa* (Savigny)	2	-	2
O *Lumbricus rubellus* Hoffmeister	-	3	3
Number of species	1	1	2
Number of individuals	2	3	5

Three specimens of *Lumbricus rubellus* were recorded in the Sirijordgrotta Cave, and all of them were found on the soil surface in the threshold zone beneath the great pitfall Elk Shaft. The soil here consists mainly of minute bone fragments mixed with smaller portions of fragmented plant material and inorganic soil components. Both species have been recorded from caves in southern Sweden (Gislén & Brinck 1950, Hippa et al. 1984 b), Belgium (Leruth 1939), Germany (Lengersdorf 1932—33, Michaelsen 1933, Wolf 1934—38, Griepenburg 1935, Mühlman 1942) and England (Hazelton 1975). *L. rubellus* has also been reported from Yugoslavia (Cernosvitov 1935). Only in Belgium is *A. caliginosa* classified as a troglophile in the threshold zone, otherwise both species are regarded as trogloxenes, which must be the correct classification for Norway too. The distribution of the species in the Norwegian caves is within the limits of their epigean distribution (Støp-Bowitz 1969, Terhivuo 1982).

Araneae

Four species were found, two in South Norway and two in North Norway (Table 5). In addition there were two unidentified juvenile linyphiid specimens. Most specimens were found in the threshold zone, both in the outer and in the inner. In the Bevergrotta Cave, one specimen of *Meta* sp. and one juvenile linyphiid were trapped in the dark zone in the inner part of the cave. *Metellina merianae* and *Meta menardi* (Fig. 11) have been regarded as typical species for the threshold zone in caves in South Sweden (Gislén & Brinck 1950, Hippa et al. 1984) as well as in most other European countries and in Algeria and USA (Wolf 1934—38, Strouhal & Vornatscher 1975, Dixon 1974, Hazelton 1975, 1977). *M. menardi* was also reported to be a cave inhabitant in Japan (Yaginuma 1976). Elsewhere in Norway it is distributed in the southern areas north to Oslo and Sogn, where it exclusively inhabits cellars, outhouses and similar habitats. Both species must be classified as troglophiles in Norwegian caves. *Porrhomma convexum* is also regarded as a threshold troglophilous species. It has been recorded from South Sweden (Gislén & Brinck 1950, Hippa et al. 1984 a), from Germany (Dobat 1975), where it is characterized as between a troglophile and troglobite, and from England (Dixon 1974, Hazelton 1975, 1977). In Norway there are a few scattered records north to the Svartisen area (Nordland). *Saaristoa abnormis* is elsewhere in Norway known in the southern areas north to Hordaland and Southern Oppland. In Europe it is regarded to be a troglophilous species, being reported from caves in Belgium, Germany, France and Italy (Wolf 1934—38) and from one cave in Great Britain (Jefferson 1983). The following species have previously been recorded from North Norwegian caves: *Nesticus cellulaneus* (Clerck), *M. merianae, M. menardi, Leptorhoptrum robustum* (Westring), *P. convexum* and *Leptyphantes pallidus*

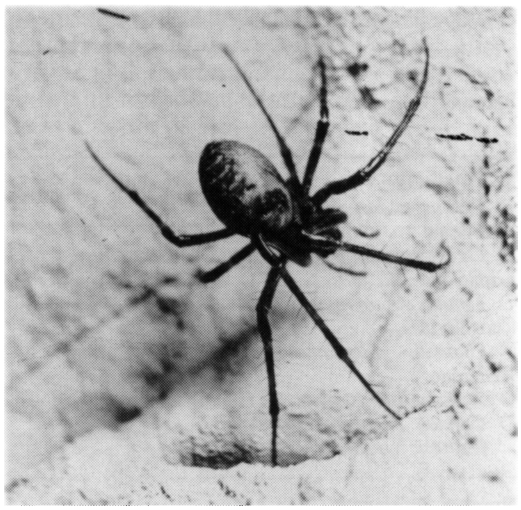


Fig. 11. *Meta menardi* in natural habitat, upper level of Svarttjernsgrotta Cave No 2. Photo: S.E.L.

Table 5. Number of individuals of Araneae species from Norwegian caves. For symbols see table 3.

	Caves							
		South Norway				North Norway		Total
Species	Bev	Gam	Fin	Sva	Bån	Sir	Pik	
Metidae:								
◑ *Metellina merianae* (Scopoli)	-	1	3	2	1	-	-	7
◑ *Meta menardi* (Latreille)	-	-	-	1	-	-	-	1
Meta sp.	1	-	-	-	-	-	-	1
Linyphiidae:								
◑ *Porrhomma convexum* (Westring)	-	-	-	-	-	-	1	1
○ *Saaristoa abnormis* (Blackwall)	-	-	-	-	-	1	-	1
Linyphiidae spp.	1	-	-	-	-	-	-	1
Number of species	1	1	1	2	1	1	1	4
Number of individuals	2	1	3	3	1	1	1	12

(O.P. Cambridge) (see Hippa et al. 1984 a). Together with our present records a total of 7 spider species is thus known from Norwegian caves.

Acari

Mites were found in very low numbers, even in the soil extractions. Only two specimens of Prostigmata and one of Mesostigmata (Gamasidae) were found in the Bevergrotta Cave. In the north Norwegian Okshola Cave one specimen of Prostigmata was found. As the specimens could not yet be determined to species level and the number of specimens found was very low, no further comments seem appropriate except for the statement that mites do not seem to be an important component of the fauna of Norwegian caves, contrary to caves further south in Europe.

Amphipoda

Cave amphipods are rather common in southern European countries, but this is not the case in Norway. Only in one cave, the Gammarusgrotta, has an amphipod species been recorded. Relatively numerous populations (>1000 individuals observed) of the species *Gammarus lacustris* (G.O. Sars) live in a few smaller lakes in the cave (Fig. 8). It is paler in colour and has reduced eyes compared with specimens from the nearest lake population, 1,5 km downstream of the cave. Investigations of the brook between the cave and the lake yielded no specimens except for some individuals in the cave resurgence. Several high waterfalls make it impossible for the amphipods to migrate upstream from the lake into the cave. No lake is situated upstream of the cave, the brook being fed by some small bogs, containing no population of amphipods. *G. lacustris* has not previously been recorded from European caves. The Norwegian *G. lacustris* population must be characterized as troglophilic, since it reproduces within the cave.

Collembola

A total of 18 species of Collembola was collected by pitfall trapping and soil sampling in this study (Table 6). Of these species, 9 were found in the Bevergrotta Cave in South Norway and 10 from the Sirijordgrotta Cave in North Norway. The records of the species are in accordance with their epigean distribution in Norway.

In the Bevergrotta Cave 17 months of pitfall trapping yielded only 3 specimens of Collembola (Table 7). The extraction of soil samples gave a much better result, with 45 specimens found in 10 samples. Most animals were found in the outer threshold zone, mainly because of a high number of *Tullbergia sylvatica*. The number of species, however, was higher in the inner, darker part of the cave. The scanty material from pitfall trapping gave no indication of the seasonal activity of the species. This method must be regarded as unsuitable for trapping soil dwelling Collembola, to which all but one *(Entomobrya nivalis)* of the species from the Bevergrotta Cave belong.

Table 6. Number of individuals of Collembola species from Norwegian caves. For symbols see table 3.

Species	Caves South Norway Bev	North Norway Sir	North Norway Fos	Tot.
Neanuridae:				
○ *Neanura muscorum* (Templeton)	1	-	-	1
Onychiuridae:				
◑ *Onychiurus schoetti* (Lie-Pettersen)	10	1	-	11
○ *O. ursi* Fjellberg	-	3	-	3
○ *O. absoloni* (Börner)	1	-	-	1
○ *Tullbergia arctica* Wahlgren	2	-	-	2
○ *T. tenuisensillata* (Rusek)	-	4	-	4
◑ *T. sylvatica* Rusek	21	-	-	21
Isotomidae:				
○ *Folsomia fimetaria* (L.)	-	2	-	2
○ *Agrenia bidenticulata* (Tullberg)	-	-	1	1
○ *Isotoma olivacea* Tullberg	-	1	-	1
○ *I. hiemalis* Schött	-	1	-	1
○ *I. viridis* Bourlet	-	3	-	3
○ *I. notabilis* Schäffer	2	-	-	2
Entomobryidae:				
◑ *Lepidocyrtis lignorum* (Fabricius)	-	15	-	15
○ *Entomobrya nivalis* (Linné)	1	-	-	1
Neelidae:				
○ *Neelus minimus* (Willem)	4	-	-	4
Sminthuridae:				
○ *Arrhopalites* sp.	7	1	-	8
○ *Bourlettiella* sp.	-	1	-	1
Number of species	9	10	1	18
Number of individuals	49	32	1	82

In the Sirijordgrotta Cave, on the other hand, surface-dwelling Collembola constituted 50% of the species collected (Table 8). Because of their size and activity, these species are much more easily trapped in pitfall-traps than the deeper-dwelling soil species. Consequently the pitfalls appeared more successful in this northern cave, one week of trapping giving 20 specimens. The soil extraction, however, resulted in a scanty material from the Sirijordgrotta Cave. Most of the species from the Sirijordgrotta Cave were found in the threshold zone. In the inner, darker parts of the cave system only 3 species were recorded. However, one of these species, *Lepidocyrtus lignorum,* appeared to be fairly common in the inner zone.

Table 7. Collembola trapped in pitfalls and extracted from soil samples from the Bevergrotta Cave, 24.06.77-01.11.78. Three trap-lines, each of 5 traps: A: threshold zone — 15 metres from the entrance, B: halfway in — 40 metres from the entrance, C: inner part — 70 metres from the entrance. Soil samples taken 01.11.78 at localities A and C.

Species	Trapping period 24.06.77-01.11.78 A	B	C	Soil samples 01.11.78 A	C	Tot.
Neanura muscorum	-	-	-	-	1	1
Onychiurus schoetti	1	-	-	5	4	10
O. absoloni	-	-	-	1	-	1
Tullbergia arctica	-	-	-	-	2	2
T. sylvatica	-	-	-	17	4	21
Isotoma notabilis	-	-	1	-	1	2
Entomobrya nivalis	-	-	-	-	1	1
Neelus minimus	-	-	-	2	2	4
Arrhopalites sp.	-	-	2	4	1	7
Number of species	1	0	2	5	8	9
Number of individuals	1	0	2	26	16	45

Several of the collembolan species of this study are known from other European cave studies, and each species may differ in its association with cave systems from area to area.

A. Surface-dwelling species

Most of the active species of the soil surface were found in very low numbers, and may represent more or less accidental visitors to the caves. One exception is *Lepidocyrtus lignorum* which has probably established a population in the Sirijordgrotta Cave system.

Neanarura muscorum has been recorded from Germany, where it is characterized as trogloxene (Dobat 1975), and also from England (Dixon 1974, Hazelton 1975). *Agrenia bidenticulata* has previously been recorded from caves in England (Dixon 1974), Germany and Czechoslovakia (Wolf 1934—38). This species and *Isotoma olivacea* are common hygrophilous species in Norway, and their occurrence in caves is probably accidental. Earlier references to *I. olivacea* in Euro-

Table 8. Collembola trapped in pitfalls (I) and extracted from soil samples (II) from the Sirijordgrotta Cave, 28.06.—03.07.86. A: Elk shaft; upper plateau, threshold zone, 40 metres from the «pit-fall» entrance. B: Elk passage, layer with bone fragments, inner threshold zone, 10 metres from A. C: Arctic passage, silt bank, 80 metres from A. D: Twin ducks passage, silt bank, 160 m into the cave close to the inlet stream. 5 pitfall traps used in localities A, C and D, for a period of 5 days.

Species	Locality							Tot.
	A		B	C		D		
	I	II	II	I	II	I	II	
Onychiurus schoetti	-	-	1	-	-	-	-	1
O. ursi	-	2	1	-	-	-	-	3
Tullbergia tenuisensillata	-	4	-	-	-	-	-	4
Folsomia fimetaria	-	-	1	-	-	1	-	2
Isotoma olivacea	-	1	-	-	-	-	-	1
I. hiemalis	1	-	-	-	-	-	-	1
I. viridis	3	-	-	-	-	-	-	3
Lepidocyrtus lignorum	1	-	1	12	-	1	-	15
Arrhopalites sp.	-	1	-	-	-	-	-	1
Bourlettiella sp.	-	-	-	1	-	-	-	1
Number of species	3	4	4	2	0	2	0	10
Number of individuals	5	8	4	13	0	2	0	32
Number of species	7		4	2		2		
Number of individuals	13		4	13		2		

pean caves (Mühlmann 1942, Dixon 1974, Hazelton 1955 et seq., 1965 et seq.), probably concern the species *I. tigrina* (Nicolet) which has been confused with the boreal species *olivacea* (Fjellberg 1979). *I. tigrina* is not on the record from Norwegian caves. *I. hiemalis* has been found in Czechoslovakian caves (Wolf 1934—38). *I. viridis* has been recorded as trogloxene in Mid-Germany (Mühlmann 1942), and further recorded in Austria (Strouhal & Vornatscher 1975), Czechoslovakia and Hungary (Wolf 1934—38) and England (Dixon 1974, Hazelton 1975). *L. lignorum* has been found in England (Hazelton 1955 et seq., 1965 et seq.).

B. Soil-dwelling species

The sluggish true soil species have a low dispersal capacity. In contrast to the active surface dwelling Collembola, they are not able to migrate many metres into the cave during their life time, unless they are transported by water or can move down from the top-soil through cracks or crevices in the roof of the cave. The last possibility cannot be totally ruled out even in the innermost part of the Bevergrotta Cave (site C). Material from a single series of soil samples is insufficient to state unambiguously whether some of the species permanently inhabit the cave. However, the high number of *T. sylvatica* found in the different parts of the Bevergrotta Cave suggests the existence of a cave population. *T. sylvatica* is a common inhabitant of forest soils in Norway (Hågvar 1982), and the cave population may thus be in regular contact with populations outside the cave. It has not been reported as troglophilic from any other European cave. Perhaps more interesting, and worth further investigation is the alpine and arctic species *Tullbergia arctica,* which has not previously been reported from forest areas. The present material of only two specimens, however, is too scanty for any speculation about a cave population.

In addition to *T. sylvatica, Onychiurus schoetti* also turned out to be fairly common in the Bevergrotta Cave. This species occurs in British caves, where it is suggested to be troglobitic (Dixon 1974, Hazelton 1975, 1977). It is also reported from Polish caves (Stach 1947). Its distribution in Norway is not well-known, but — like the related species *ursi* — it has been collected among plant roots and gravel along lakes and rivers both in South and North Norway (Fjellberg in press). This association with water probably facilitates spreading into caves, and thus they may both turn out to be trogloxenes in many Norwegian caves. However, in the Bevergrotta Cave, there is no possibility that the species can be washed into the cave from any creek or river outside. Altogether, it seems reasonable to regard *O. schoetti* as troglophilic in this cave. More information about its distribution in the Skrim area is needed to discuss whether the population may be in contact with conspecific populations outside the cave.

Folsomia fimetaria has been found in Belgium, Germany, Italy, Spain and USA (Wolf 1934—38), and in England (Dixon 1974, Hazelton 1975, 1977). The species is characterized as troglophilic in Belgium (Leruth 1939). It is common in decaying organic debris in Norway, and the association in the caves is hardly more than trogloxene.

The other soil-dwelling species reported from this study (*Onychiurus absoloni, T. tenuisensillata, Isotoma notabilis, Neelus minimus* and *Arrhopalites sp.*) should according to our present knowledge only be characterized as trogloxenes.

Coleoptera

A total of 29 species was recorded, most of them, 17, in the Sirijordgrotta Cave (Table 9).

In the Sirijordgrotta Cave all species were caught in the threshold zone. All species in the Bevergrotta Cave, however, were caught in the dark inner part of the cave.

Nebria gyllenhali has previously been recorded from British caves (Dixon 1974). *Calathus micropterus* and *Pterostichus melanarius* have been found in South Sweden (Hippa et al. 1985 b). *P. oblongopunctatus* has been reported from South-West Germany, where it is regarded as trogloxene (Dobat 1975).

The *Choleva* species have been reported from South Sweden (Hippa et al. 1985 b), and *C. fagniezi* also from France (Wolf 1934—38). *C. septentrionis* has formed a separate subspecies in a cave in Germany (Freude et al. 1971). The summer and winter catches of *C. septentrionis* in the present study were approximately equal, and one larva was even trapped in the winter period. *C. fagniezi* and *Calathus micropterus* were only caught in the summer.

The *Catops* species have been recorded from caves in several European countries, and most of them are regarded as troglophiles. *C. longulus* has been found in Austria (Strouhal & Vornatscher 1975), Belgium, Roumania, Germany, Czechoslovakia, Hungary (Wolf 1934—38) and England (Hazelton 1977), *C. tristis* in Austria (Strouhal & Vornatscher 1975), Belgium, Germany, France, Roumania, Czechoslovakia, Yugoslavia, Spain (Wolf 1934—38), South Sweden (Hippa et al. 1985 b) and Finland (Krogerus 1926), *C. nigrita* in Austria (Strouhal & Vornatscher 1975), Germany, Czechoslovakia and Yugoslavia (Wolf 1934—38), *C. nigricans* in South Sweden (Hippa et al. 1985 b), Finland (Krogerus 1926), Belgium, Germany (Wolf 1934—38) and England (Hazelton 1955 et seq., 1965 et seq.), and *C. picipes* in South Sweden (Hippa et al. 1985 b), South- West Germany (Dobat 1975), Belgium, Czechoslovakia, and Roumania (Wolf 1934—38). *Quedius xanthopus* has been reported from Belgium (Wolf 1934—38). *Q. mesomelinus* is characterized as troglophilic in South Sweden (Hippa et al. 1985 b), Austria (Strouhal & Vornatscher 1975), Belgium, France, Czechoslovakia (Wolf 1934—38) and England (Dixon 1974, Hazelton 1975). In south Sweden *Oxypoda spectabilis* and *Tachinus elongatus* (Hippa et al. 1985 b) have also been recorded.

In the north Norwegian caves Grønligrotta and Jordbrugrotta, Hippa et al. (1985 b) recorded the following species in addition to seven other species listed in Table 9: *Trechus rubens, Lesteva monticola, Olophrum consimile, Psephidonus longipes* and *Liogluta alpestris.* A total of 34 species of Coleoptera has thus been recorded in Norwegian caves.

Origin and biology of the beetle cave fauna

All the carabid species found in the present study prefer moist or rather moist habitats in their epigean environments, and their daily activity pattern is nocturnal (Lindroth 1985, 1986). They should thus be well preadapted to a life in caves, although they probably do not reproduce in this environment. All of them, except *N. gyllenhali,* have been recorded from the subterranean burrows of the vole *Arvicola terrestris* in southern Norway (Strand 1965). The similarity between the beetle fauna of vole burrows or mammal nests and caves is further indicated by the presence of *Choleva* spp., *Catops* spp. and *O.*

Table 9. Number of individuals of Coleoptera species from Norwegian caves. For symbols see table 3. a) pers. comm. O. Escola.

Species	Caves									Total
	South Norway			North Norway						
	Bev	Sva	Bån	Kal	Rev	Sva	Oks	Non	Sir	
Carabidae:										
○ *Cychrus caraboides* (L.)	-	-	-	-	-	1	-	-	1	2
○ *Nebria gyllenhali* Schönherr.	-	-	-	1	-	1	1	-	-	3
○ *Patrobus atrorufus* (Ström)	-	-	-	-	-	-	-	-	1	1
○ *Pterostichus melanarius* (Illiger)	1	-	-	-	-	-	-	-	-	1
○ *P. oblongopunctatus* (Fabricius)	-	-	-	-	-	-	-	-	1	1
○ *Calathus micropterus* (Duftschmid)	1	-	-	-	-	-	-	-	-	1
Leiodidae:										
○ *Agathidium seminulum* (L.)	-	-	-	-	-	-	-	-	1	1
Silphidae:										
◑ *Pteroloma forsstroemi* (Gyllenhal)	-	-	-	-	-	-	-	-	29	29
Catopidae:										
◑ *Choleva septentrionis* Jeannel	12	3	-	-	-	-	-	1	29	45
◑ *C. fagniezi* Jeannel	9	-	1	-	-	-	-	-	-	10
◑ *Catops longulus* Kellner	-	-	-	-	-	-	-	-	3	3
◑ *C. tristis* (Panzer)	-	-	-	-	-	-	-	-	21	21
◑ *C. nigrita* Erichson	-	-	-	-	-	-	-	-	28	28
◑ *C. nigricans* (Spence)	-	-	-	-	-	-	1a	-	-	1
◑ *C. picipes* (Fabricius)	-	-	1	-	-	-	-	-	-	1
Staphylinidae:										
○ *Quedius fulvicollis* (Stephens)	-	-	-	-	-	-	-	-	1	1
○ *Q. xanthopus* Erichson	-	-	1	-	-	-	-	-	-	1
◑ *Q. mesomelinus* (Marsham)	-	-	1	-	-	-	-	-	-	1
◑ *Olophrum fuscum* (Gravenhorst)	-	-	-	-	-	-	-	-	7	7
○ *Arpedium quadrum* (Gravenhorst)	-	-	-	1	-	-	-	1	-	2
◑ *Lesteva pubescens* Mannerheim	-	-	-	-	-	-	-	-	1	1
○ *Olisthaerus megacephalus* (Zetterstedt)	-	-	-	-	-	-	-	-	1	1
○ *Tachinus pallipes* Gravenhorst	-	-	-	-	-	-	-	-	2	2
○ *T. elongatus* Gyllenhal	-	-	-	-	-	-	-	-	7	7
○ *Atheta diversa* (Sharp)	-	-	-	-	-	-	-	-	1	1
○ *Oxypoda spectabilis* Märkel	-	-	1	-	-	-	-	-	-	1
○ *O. soror* Thomson	-	1	-	-	-	-	-	-	-	1
Cryptophagidae:										
○ *Cryptophagus setulosus* Sturm	-	-	-	-	-	-	-	-	1	1
Curculionidae:										
○ *Otiorhynchus* sp.	-	-	-	1	1	-	-	-	-	2
Number of species	4	2	5	3	1	2	2	2	17	29
Number of individuals	23	4	5	3	1	2	2	2	135	177

spectabilis, which frequently inhabit mammal-made subterranean habitats (Hansen 1968, Palm 1972). The cave/burrow faunal element of beetles typically consists of carrion and dung feeders depending on vertebrates that frequently fall into the cave (Figs. 10 and 12). Most of the staphylinid beetles of the present study share these feeding habits. Further, several of the staphylinid beetles prefer shady habitats along rivers and creeks. They are apparently able to follow the cold and humid riverside environment into the caves. Additional indications of the importance of scavenging Coleoptera is the high concentrations of remains (elytra, faecal pellets) in the close vicinity of vertebrate skeletons (Fig. 12).

The large numbers of the boreomontane

carrion beetle *Pteroloma forsstroemi* in the Sirijordgrotta Cave are interesting. It has previously been found in the nearby Grønligrotta Cave (Hippa et al. 1985 b), but not in any other caves in Europe. Its preferred epigean habitat is shady, moss-grown edges of creeks and lakes in coniferous forest, but also among stones and leaves on lake shores (Holdhaus & Lindroth 1939). Another interesting species is *C. longulus*. Although it is found in both southern, middle and northern parts of Norway, very few specimens from only a few localities are known (Refseth 1980). It may previously have escaped notice, as Freude et al. (1971) write that it is very frequently found in caves throughout Middle Europe.

Three species show no obvious connection to cave environments: *Agathidium seminulum* lives below the bark of fungus infested birch, while *Olisthaerus megacephalus* lives below moist, old bark of coniferous trees, occasionally birch (Palm 1951). *Cryptophagus setulosus* is curiously enough found in another type of «caves», i.e. the nests of bumble bees (Bruce 1936).

The majority of the Coleoptera species recorded in the Norwegian caves are trogloxenes, many of them accidental, but several habitual ones, belonging to the threshold fauna. Only the *Choleva* and *Catops* species, together with *Q. mesomelinus* and *Lesteva pubescens,* may be regarded as troglophiles.

Fig. 12. Remnants of a lemming on a sand bank in Fosshølet Cave, Rana. Most of the dark material among the bones is faecal material from scavenging beetles. Photo: S.E.L.

Lepidoptera

Only two species of Lepidoptera have been recorded (Table 10). *Scoliopteryx libatrix* has been found hibernating in three caves in South Norway, the Svarttjernsgrotta, Gammarusgrotta and Finnegurigruven Caves (Fig. 13). *Triphosa dubitata* has been found hibernating in the Svarttjernsgrotta Cave.

Both species are characterized as habitual trogloxenes belonging to the threshold fauna in most other European countries, *S. libatrix* further in USA and *T. dubitata* in Algeria (Wolf 1934—38, Leruth 1939, Dixon 1975, Hazelton 1975). In South Sweden they have both been reported from the Lummelundagrottan Cave (Gislén & Brinck 1950). The two species must be classified in the same way in Norway as in other parts of Europe, i.e. as habitual trogloxenes.

Diptera

Only four species have been identified in our material (Table 11). In addition there are specimens from four genera that could only be identified to the generic level. Rather large numbers of Diptera were trapped, but unfortunately the specimens were so badly preserved in most of the pitfall-traps that the material was unsuitable for identification.

Of special interest is the record of *Speolepta leptogaster,* a mycetophilid species not

Fig. 13. *Scoliopteryx libatrix* hibernating in the upper level of Svarttjernsgrotta Cave No 1. Photo: S.E.L.

Table 10. Number of individuals of Lepidoptera species from Norwegian caves. For symbols see table 3.

Species	Caves South Norway Gam	Fin	Sva	Tot.
Geometridae:				
○ *Triphosa dubitata* L.	-	-	2	2
Plusiidae:				
○ *Scoliopteryx libatrix* L.	1	1	2	4
Number of species	1	1	2	2
Number of individuals	1	1	4	6

previously recorded in Norway, neither in epigean nor hypogean localities. This species was found in the Bevergrotta Cave, which has a rather numerous population (>100 individuals observed). Both adults and larvae have been found all year round in this cave (Fig. 14). *S. leptogaster* is a typical cavernicolous insect in most European countries, and is also found in Algeria and USA (Wolf 1934—38, Dixon 1974, Hazelton 1975, 1977, Strouhal & Vornatscher 1975), often regarded as more numerous in hypogean than epigean conditions. It is widely distributed in caves, both in the dark zone and in the threshold zone, and is characterized as a typical troglophile. Although a few adults have been recorded from epigean conditions in England, it seems there only to breed in hypogean localities, natural or man-made (Jefferson 1983). The Norwegian population is certainly troglophilic, and should perhaps rather be regarded as troglobitic.

Rhymosia fasciata has been recorded from caves in Belgium (Leruth 1939), Germany, the Netherlands (Wolf 1934—38) and England (Dixon 1974, Hazelton 1975), and is characterized as a habitual trogloxene. *Heleomyza serrata* has been reported from most European countries and USA (Wolf 1934—38, Dixon 1974, Hazelton 1975, 1977). It has previously been recorded from the Hammarnesgrotten Cave in North Norway (Natvig 1923), and from South Sweden (Gislén & Brinck 1950). In other parts of Europe both species are described as habitual trogloxene to troglophile. *H. brachypterna* has been recorded in Austria (Strouhal & Vornatscher 1975) and USA (Wolf 1934—38). *R. fasciata* and the two *Heleomyza* spp. often occur

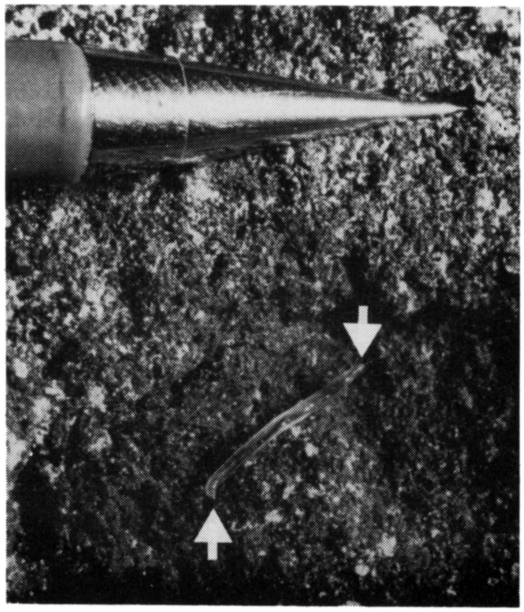


Fig. 14. Larva of *Speolepta leptogaster*, Bevergrotta Cave, South Norway. Photo: S.E.L.

Table 11. Number of individuals of Diptera species from Norwegian caves. For symbols see table 3.

Species	Caves South Norway Bev	Sva	North Norway Kal	Tot.
Mycetophilidae:				
◑-●? *Speolepta leptogaster* (Winnertz)	13	-	-	13
○ *Rhymosia fasciata* Meigen	-	2	-	2
○ *Exechiopsis* sp.?	-	1	-	1
○ *Mycetophila* sp.	-	-	1	1
○ *Exechia* sp. (*parva* Lundström?)	-	1	-	1
Heleomyzidae:				
○ *Heleomyza serrata* (L.)	1	-	1	2
○ *H. brachypterna* (Loew.)	-	2	-	2
Culicidae:				
○ (probably *Culex pipiens*)	-	1	-	1
Number of species	2	5	2	8
Number of individuals	14	7	2	23

in subterranean environments like the runways and dens of small rodents. Both *Heleomyza* spp. in Norway have to be regarded as habitual trogloxenes, belonging to the parietal association, even if they are sometimes found in the dark inner zone.

CONCLUDING REMARKS

A total of 70 (+ 2—3) species of invertebrates has been recorded in our studies of Norwegian caves. 19 species are characterized as troglophiles, while all the other must be regarded as trogloxenes, several of them habitual trogloxenes, most of them accidental ones. No true troglobitic species has been recorded till now, perhaps with the exception of *Speolepta leptogaster* which may be a troglobite under the Norwegian climatic conditions. Together with the additional species recorded by Hippa et al. (1984 a, b, 1985 a, b, 1986) in the Jordbrugrotta and Grønligrotta Caves, a total of 84 species has been recorded in Norwegian caves.

The Norwegian fauna of cavernicolous invertebrates registered till now is rather poor compared with the cave fauna in other European countries, even when compared with the fauna of caves in South Sweden. This is partly due to the low level of research activity hitherto in the speleobiological field. But probably more important is the fact that the caves are situated further to the north than most other European caves with a more severe and harsher present climatic regime. Multiple glaciations during the Pleistocene period must obviously have had implications for the faunal history of our caves, with less suitable conditions prevailing during long periods of glaciations. It is therefore tempting to assume that the caves may have been completely water-filled and hence unsuitable for terrestrial animals.

However, Castleguard Cave penetrates almost 11 km underneath the Columbia Icefield, Banff National Park, Canada (Ford et al. 1983). The main cave is air-filled (vadose) and suggests that caves may remain hospitable for terrestrial and aquatic fauna through periods of almost complete ice-cover. The glacial situation is very similar to the conceptual model of a glacial ice-cover resembling that of Greenland to-day. The crucial point for faunistic relicts is therefore the extent of ice-cover during each of the Pleistocene glaciations (Nesje et al. 1988), and the indication of other biological relicts (see discussion in Mangerud 1973). The existence of Acari (C. Pugsley, p.c. 1984) and cavernicolous crustaceans (Holsinger et al. 1983) in Castleguard Cave raises the possibility that such faunistic relicts may be found in Norway too. One of the purposes of our future research is to investigate this possibility.

The registration of the Norwegian speleofauna is just beginning. An intensified regional survey needs to be carried out on a year-round basis in order to draw a more valid general picture of the Norwegian speleofauna and its ecology.

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