The soil surface and layer of air adhering to it are heated by solar radiation during the day much more than might be expected on the basis of the low air temperature. Instead, during the night, strong irradiation can cause the soil to freeze even in summer.

Dense cushions also allow the accumulation of plant residues which would otherwise be removed by the strong winds that blow at high altitudes. These residues are slowly transformed into humus, which can provide shelter for both micro-organisms and invertebrates. The plant forming the cushion derives benefit from the increased availability of nutrients through a mass of lateral and adventitious roots which explore the soil that the plant has contributed towards forming. Not only micro-organisms and invertebrates gain advantage from these favourable micro-environmental conditions, but also other vascular plants, which come to be "hosted" in the cushions. According to recent research, a sort of "facilitating" mechanism operates in nival plant cushions, allowing various organisms to coexist within the same microhabitat, reducing inter-species competition.

Saxifraga caesia

Five different types of morphology have been distinguished in cushion plants:

1. Rosettes: dense groups of rosettes close together, from which the flower scapes emerge. Dead leaves contribute to the formation of humus. The accumulation of organic matter is never high. Various species of saxifrage and everlasting flowers (genus *Sempervivum*) form cushions of this type.
2. Creeping cushions: formed of flattened rosettes which expand on the surface by lateral branches, which may be separated by earth movements caused by cryoturbation. Fragments of broken branches contribute to vegetative propagation. These cushions accumulate only a thin layer of humus. Examples are purple saxifrage (*Saxifraga oppositifolia*) and mossy saxifrage (*Saxifraga bryoides*).
3. Tufted cushions:. they are characterised by the fact that the primary root and shoot live for only one year. The root apparatus is a mass of adventitious roots which penetrate the thick blanket of humus resulting from

Cushion of *Silene acaulis*, with *Dryas octopetala* flowering nearby

Androsace hausmannii

the decomposition of dead material within the cushion. An example is glaucous sedge (*Carex firma*).

4. Flat radial cushions: differing from previous ones by the fact that the taproot lives for longer and anchors the cushion at greater depth, this type is formed of moss campion (*Silene acaulis*) and mossy cyphel (*Minuartia sedoides*).
5. Hemispherical cushions: shoots, strictly adherent, form a rigid and compact structure, the shape of which is due to the fact that slow apical growth is accompanied by equally slow lateral growth. They are usually anchored to the substrate by a lignified, long-branched, primary root. This is the cushion type best protected against water stress, and frequently adapts to rocky environments. It is formed by several rupestral species of the genus *Androsace*, including Swiss rock-jasmine (*Androsace helvetica*).

The upper nival sub-belt is the realm of mosses and above all, lichens. Some species of moss may form cushions. Those which are capable of growing at higher altitudes include *Polytrichum piliferum*, *Grimmia donniana* and *Racomitrium lanuginosum*. Lichens of the high nival belt are mostly crusty and leafy, belonging mainly to the genera *Rhizocarpon*, *Umbilicaria*, *Parmelia* and *Lecidea*.

■ Plant species and their upper survival limit

During the early twentieth century, several botanists interested in Alpine plants went in search of the upper altitudinal limits for the growth of vascular plants. These quests were mainly in the Austrian and Swiss Alps.

Studies in the Austrian Alps demonstrated that only three species exceed 3500 m a.s.l.: Haller's fescue (*Festuca halleri*), red fescue (*Festuca rubra* s.l.) and a kind of blue grass (*Poa laxa*).

In the Swiss Alps, vascular plants can reach even higher altitudes, with five species growing above 3800 m a.s.l.: purple saxifrage (*Saxifraga oppositifolia*), white musky saxifrage (*Saxifraga exarata*), mossy saxifrage (*Saxifraga bryoides*), Alpine rock-jasmine (*Androsace alpina*) and glacier crowfoot (*Ranunculus glacialis*). The latter species held the altitude record for a long time, being found at 4276 m a.s.l. on the Finsteraarhorn in the Bernese Alps.

Recently, this record has been bettered by two-flowered saxifrage (*Saxifraga biflora*), found at 4450 m a.s.l. on the Mischabel group, on the Swiss side of the Pennine Alps.

Fauna

STEFANO VANIN · ADRIANO ZANETTI

Animals and snow

Alternating rock and snow are typical of high-altitudes

Snow and ice lying on the ground are extremely important for animals and greatly limit the structure and composition of fauna. Biodiversity is low in high-altitude environments, which are almost perpetually snow-covered or at least for lengthy periods, mainly because of the low average temperatures and scarcity of vegetation.
Snow and ice are also important here because of their capacity for mitigating extensive temperature excursions at ground level and for acting as reserves of water which is slowly released over prolonged periods. Glaciers have been determining factors in phenomena of speciation (i.e., the formation of new species) and have contributed towards faunal diversification in neighbouring geographical districts.
In Italy, there are many ecosystems and environmental conditions in which snow and ice play, or once played, an important role for fauna.

Adaptations to cold and snow. In the Alpine region, altitude determines the physical and climatic parameters on which the survival of animals and plants depends. These parameters affect factors such as: temperature, atmospheric pressure, relative humidity, solar radiation, winds, and snow cover. They are not independent; on the contrary, they are interconnected by complex relationships of cause and effect. Air temperatures in the Alps tend to fall by approximately 7°C every 1000 metres. Although precipitation is abundant in the high mountains, relative humidity is generally low because of evaporation,

Ibex (*Capra ibex*)

and the clarity of the air means that solar radiation is less well filtered. Snow cover is fundamental in the high mountain landscape which, in the Alps, assumes the characteristics of perennial snow over 2700 metres a.s.l.. This influences important ecological factors such as soil and air temperature, the formation of air currents, reflectance and humidity, which in their turn affect the structure of communities living in the area.

As well as these physical factors, biological factors, which are not independent of the former, should also be taken into consideration. The great scarcity of plants directly influences the physical variables of the system, as there is no “buffer effect” exercised by vegetation.

The biotic factors which most influence the life of arthropods in nival environments are the scarcity of trophic resources and isolation. For species associated with the more extreme environments, such as the surface of snow and ice, food resources are irregular and located mainly on the margins, where organic matter accumulates.

These resources mainly consist of pollen, fungal spores, seeds, small invertebrates, and plant and animal fragments which are transported to high altitudes by winds and air currents ascending from the valleys below. Another important food source is provided by single-cell algae and fungi which grow on the blanket of snow. Given the brevity of the summer season,

Mont Blanc (Val d’Aosta)

these food resources are not only scarce but also only available for a short period of the year.

Arthropods living in these habitats have developed adaptation mechanisms in response to these extreme physical and biological factors. Typical characteristics which indicate a specialisation to high altitudes and the nival region in particular, are reduction in body size, shortening or loss of wings, melanism, lithophily (i.e., the habit of living beneath stones), specific habits and life-cycles, and resistance to low temperatures.

Insects living in nival environments also demonstrate a high level of hydrophily (i.e., they live where there is plenty of moisture, near streams and pools) and stenothermy (i.e., they can only tolerate very narrow temperature excursions).

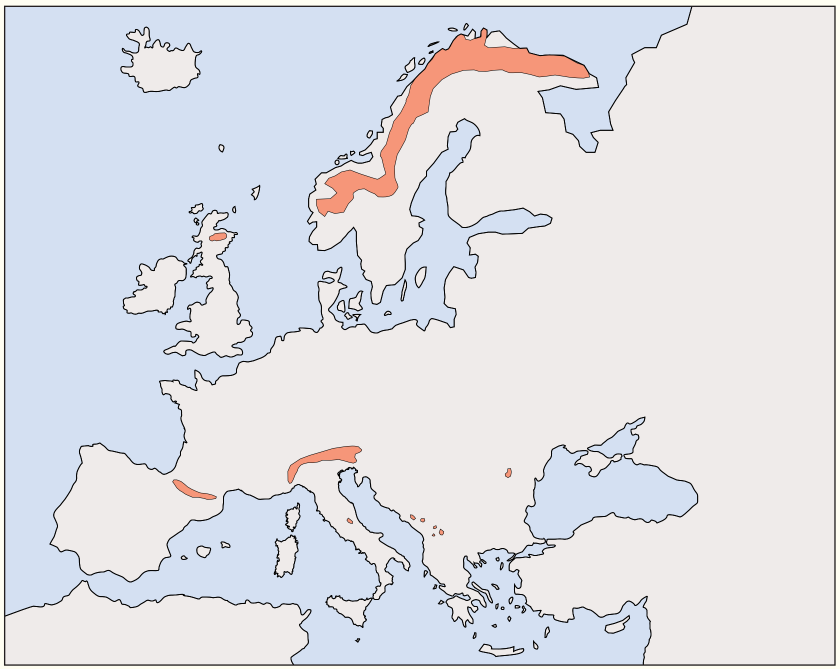
At low and medium altitudes, species vary widely in size, but this diversity is limited at high altitudes, where there is a general tendency to a reduction in body size. This is a compromise between size optimisation as a function of the short time available for growth, and the need to reach a sufficient size to be able to make use of trophic resources. Small size also means that these organisms can exploit small and irregular shaped spaces, beneath stones or in cracks, where microclimatic conditions are more favourable.

Among arthropods, there are also more dark-coloured species with increasing altitude. Dark pigmentation protects against strong ultraviolet radiation and

Maiella (Abruzzo)

Larva of *Zygaena exulans*

Adult of *Zygaena exulans*



Distribution area of *Zygaena exulans*: a typical example of boreal-alpine distribution

also enhances the ability to absorb heat, which is then slowly released during the night. Typical of this are the cases of melanism in lepidopterans living in the Himalayas.

Wind and cold play a fundamental selective role in wing shortening and/or the loss of ability to fly, together with the great specificity of certain biotopes for larval development. Examples of this phenomenon are some craneflies (tipulid dipterans), whose larvae develop in high-altitude peat bogs, and the chironomid *Diamesa steinboecki*, the larva of which is stenothermal and develops only in the very cold waters flowing from melting glaciers and snowfields.

Many carabid beetles and other predators of snow-beds are nocturnal hunters, in order to prevent dehydration during the daytime and also to avoid becoming prey themselves. For the same reason, many species discover their ideal habitat underneath stones and in rock crevices, where moisture and temperature are constant and higher than those of the external environment.

Organisms living in nival areas have also developed a series of physiological and biochemical adaptations which enable them to survive frequent sub-zero temperatures. Insects which live where cold is the selecting factor are divided physiologically into species which can avoid the formation of ice crystals inside their bodies and those which can tolerate partial freezing of extra-cellular fluids. Individuals of the same species sometimes demonstrate a tolerance to low temperatures which varies according to geographical area and environmental conditions, thus displaying both strategies. Damage due to exposure to cold is reflected at more than one level, and varies according to the duration of exposure.

At microscopic level, lowering of the temperature below freezing-point - which occurs at approximately -0.5°C in terrestrial animals - causes alterations in cell membranes, and temporary or total denaturation of proteins, with structural and metabolic consequences that modify the properties of many enzymes which are active within specific temperature ranges. At macroscopic level, all these phenomena result in reduced respiration and parallel slowing down of movements, leading to a phase called stupor or, in the absence of movement, hypothermia. Survival may be prolonged for periods of time which range from a few minutes in species not highly adapted to cold, to many months in those that are.

Species susceptible to freezing may be able to resist cold, but cannot tolerate the formation of ice in their tissues. Springtails and mites, and also many insects are examples.

Their adaptation mechanism is to lower the freezing-point of their bodily fluids, and thus prevent ice from forming. In winter, they are able to synthesise various water-soluble substances in huge quantities, which may account for up to 20% of their entire body weight. These substances include glycerol, trehalose, sorbitol, and free amino-acids, such as proline and various anti-freeze proteins. In some insects and spiders, the presence of these substances can lower the freezing-point of bodily fluids by 5-6°C. These organisms also eliminate or disguise possible nucleation points, i.e., the centres in the body around which ice crystals may form (bacteria, food, etc.), either by not eating or by emptying the intestine.
Tolerant species can cope with ice forming in their extra-cellular fluids. Various groups of animals belong to this category, including a few frogs and some insects. The bodies of these species contain cryo-protective substances (glucose, sorbitol, trehalose, etc.), the function of which is to control the size and development of ice crystals.

■ Living with snow: winter invertebrates

Apart from many species of arachnids, springtails and insects, occasionally stranded by cold or early snowfalls, which may be found on the blanket of snow, some characteristic species regularly live in this environment. Animals which are active during winter may be found under, above, or within the snow. Some of these, such as ciliates, rotifers and springtails, feed on micro-organisms which live on or just below the surface. Micro-organic production is the first step in the food chain which forms during winter in snow-covered areas. The higher ecological levels of the chain are composed of invertebrates such as mites and spiders, and also by vertebrates such as birds and small mammals, which may eat all kinds of food during winter.
Springtails or collembolans, together with mites, are the arthropods which tolerate cold best. Their massive presence often colours the snow purple or red, depending on species. In order to move with agility among the snow crystals, some species, like *Isotoma hiemalis*, undergo a morphological change to their legs between summer and winter. This phenomenon is known as cyclomorphosis; in spring, when the snow melts, the animal resumes its former shape.
Many types of collembolans may be found in snow at the base of tree trunks and in bushes. Springtails, like other invertebrates which are active during winter, use these breaks in the blanket of snow to pass from the surface to the space beneath. This space is the gap of 3-5 cm created by irregularities of the ground where, because of plant fragments between ground and snow layer, the microclimate is totally independent of the exterior. Snow is an excellent insulator. Beneath 20 cm of fresh snow, the temperature is constant and close to zero, moisture content is high, and there is no air movement. External temperatures may even fall below -30°C, humidity is low, and strong winds may blow. The air composition beneath the snow is the same as that outside, so the presence of oxygen is guaranteed.
Collembolans active both above and beneath the snow cover are preyed upon by numerous species of spiders, which also remain active during winter in both environments, as adults and during juvenile stages. Most of these spiders belong to the family of linyphiids, which also include numerous species of the genus *Lepthyphantes*, endemic to the Alps.
The many species of chironomid midges which leave water during winter are accompanied, in both the Alps and Apennines, by some species of stoneflies or plecopterans. Many insects are active both above and beneath the snow; the best-known dipterans being those of the genus *Chionea*, accompanied by *Boreus*, belonging instead to the Mecoptera. Before going into detail on these two genera, both characterised by obviously shortened wings, it is worth noting that numerous examples of flies belonging to the family of the phorids are also found on the snow cover, there are also some winter species

Deep accumulations of snow remain even in summer at high altitude (Gran Paradiso, Val d'Aosta)

Trichocerid dipteran

of spherocerids, and just autumn or winter species of trichocerids.

The former two are families of small, dark-coloured species, usually only a few millimetres long, with larvae which develop on decomposing organic matter of either animal or plant origin. If disturbed, individuals of species belonging to these two families rapidly seek shelter among the interstices and fissures in the snow. Specimens with slim legs and long wings belong to the trichocerids, only present in Italy with the genus *Trichocera*.

In Italy, the genus *Chionea*, whose name derives from the Greek, meaning “nival”, is represented by three species: *Chionea alpina*, *C. araneoides* and *C. lutescens*. They have sturdy legs, and their wings are transformed into small scales, smaller than the halters, which are all that remain of the second pair of wings in dipterans. Their characteristic gait, like that of spiders, has led to the name *araneoides* being attributed to a species of *Chionea*. At one time, it was thought that these dipterans were active only on top of the snow, but they have also been found underneath, in the lairs of small mammals, caves, and even occasionally in cellars and food stores, especially those containing plant material. The larvae, about which little is known, feed on decomposing organic matter, mainly of plant origin.

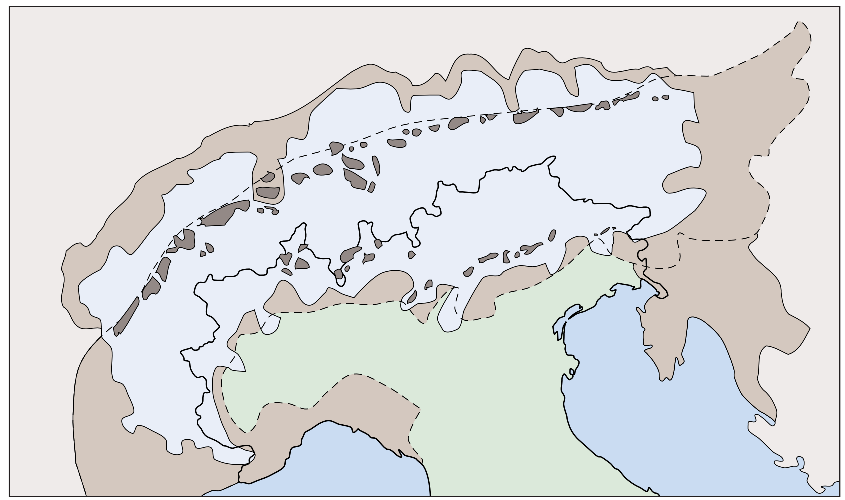
The tiny metallic-coloured *Boreus* are often associated with mosses. Adults are only active during winter and are to be found in abundance when the temperature is between 0 and +2°C. The females of this genus have slim sclerotised wings, which are modified in the males into long appendages exploited in mating. If disturbed, these insects can make sudden long jumps and then fall into a death-like state called *thanatosis*, which helps them not to be noticed by predators. Both males and females, also while mating, can often be found in large numbers on the last traces of snow in early spring, especially in broadleaf woodlands or adjacent clearings.

As well as these species, young earwigs can sometimes be found active on the snow cover, especially during the night or towards evening, while the larvae of cantharid beetles are abundant in the warmer hours. Some pseudo-scorpions, the biology of which is still something of a mystery, also move around beneath the snow.

■ Glaciers and biodiversity

Any naturalist walking through the large Alpine valleys cleaved by glacier-fed rivers has no trouble in identifying the signs of ancient glacier tongues on the rocks. Glaciers were once much more extensive than they are today, and are currently undergoing a period of rapid retreat. The valley profile, with their *roches moutonnées* or smooth rocks, on which ancient peoples often left their enigmatic cliff carvings, are all signs left by the mighty Quaternary glaciers which, in successive waves of expansion and retreat during the last million years, came into being and disappeared because of variations in the climate, in alternating hot-dry and cold-wet periods. The animal populations have also followed the climatic vicissitudes of the area, and the Ice Ages left many traces on the fauna. To identify them and understand their causes is not quite so easy because animals, unlike rocks, can migrate to colonise new territories or to escape unfavourable conditions and, in the long term, evolve and speciate (i.e., give rise to several species originating from a single one), or even become extinct.

Zoogeographers, who study and interpret the geographical distribution of animal species, have long attempted to demonstrate the current distribution areas of many species as an effect of the Ice Ages. Although this relationship has occasionally been overrated, the basic concept is still valid.



The Alps during the Würm glaciation. Blue: maximum expansion of ice; dashed line: limit of Alpine range; brown: refuge areas on margins, outside mountain range, or within it; nunataks (isolated rocks protruding from glacial ice), dark brown

Glacier on Mont Blanc massif (Val d'Aosta)

During the coldest periods of the Ice Ages, much of the Alpine range was covered by vast glaciers which ploughed across the valleys and reached high altitudes, even exceeding 2000 m in central areas. Little animal life could survive in these conditions. Only at the edges of the chain, where the glaciers were less thick, could small isolated areas - so-called "refuge massifs" - remain uncovered and maintain some biological diversity in essentially pioneering animal communities. Very ancient species of Tertiary origin also survived in these environments, favoured by the fact that the majority of foothills of the central-eastern Alps are carbonate, i.e., formed mainly of limestone and dolomitic rock. The structure and chemical properties of this type of rock give rise to soils rich in micro-cavities, which are ideal for life underground. This isolation in refuge massifs was the origin of the phenomenon of endemism.

The Alps have numerous endemic animals, i.e., species which live only in this particular area, and more especially in restricted areas in the foothills or Pre-Alps. Genera of coleopterans such as *Trechus* (ground beetles) and *Leptusa* (rove beetles or staphylinids) are fragmented into a large number of different kinds, which systematic entomologists differentiate into species or sub-species. For example, in the whole of the Alto Adige (South Tyrol) - a large mountainous territory with well-conserved environments - only four species of the genus *Leptusa* endemic to the Alps are known, but there are nine on Pizzo Arera in the Bergamo foothills alone, nine on Monte Baldo in the province of Verona, and again nine in the area of Cansiglio-Monte Cavallo in the eastern Pre-Alps.

The retreat of glaciers at the end of the last Ice Age, between 15,000 and 10,000 years ago, was instrumental in originating another model of geographical distribution, boreal-alpine, to which approximately 200 animal species living in the Alps and many fewer in the Apennines may be referred. This originated from scattered distribution areas, i.e., ones split into two or more parts, separated by large territories in which the species is absent.

Boreal-alpine species today populate far northern latitudes in Europe and often also North America, and, perhaps unexpectedly, the large mountain chains of southern Europe (particularly the Pyrenees, Alps, Apennines, Carpathians, and the Caucasus and Balkan highlands). In these cases, it is assumed that, during the Ice Ages, these species occupied continuous ranges south of the northern ice sheet, and then, as the glaciers retreated, they followed, thus fragmenting their distribution areas. Nowadays, boreal-alpine species are not strictly confined to the Pre-Alpine refuge massifs, but are also often found in the axial zone of the Alps, where habitats very similar to those of

Ptarmigan (*Lagopus mutus*)

the polar tundra are more frequent. Some of these species are currently spread throughout the Alps; others are confined to single isolated sites. For instance, there are two very widespread boreal-alpine vertebrates, ptarmigan (*Lagopus mutus*) and mountain hare (*Lepus timidus varronis*), and numerous boreal-alpine species with patchy distribution in the Alps include the staphylinid beetle *Mannerheimia arctica*, which is recorded in only two sites in the Italian Alps. This geographical isolation between northern and Alpine populations, although quite recent, has frequently led to phenomena of micro-evolution.

■ Importance of glaciers in the nival environment

Life on glaciers. Glaciers are an important component in the high-altitude environment, and influence both physical and biological parameters. The presence of glaciers in the Alps, as demonstrated by studies conducted in the Himalayas, also influences the ecosystem lower down.

Nival-glacial belt in Pennine Alps (Val d'Aosta)

The considerable volume of water which is released during melting transports with it the organic component which has been deposited by winds, or which has developed there (bacteria, micro-algae, fungi). The contribution the glacier makes to the entire high-altitude ecosystem first, and then to the belt below, is therefore not due only to water supply, but also to the organic matter dissolved in the water, which is already exploited in the first few metres by chironomid larvae. Differing ecosystems then develop, depending on the substrates over which meltwater passes or accumulates. The organic matter on glaciers and high-altitude snowfields is comprised of plant and animal fragments and nitrogen-containing molecules that the snow accumulates during its formation and deposition. The film of water on the glacier surface allows unicellular algae and fungi to develop, and they form the first element of the trophic chain on ice. These organisms, once they have been washed away, form the pabulum for filter-feeders which live in the glacier streams.

The nival environment, the altitude of which is extremely variable, depending on mountain complexes, gradients and orographical structure, is a mosaic of snow-covered areas of differing size and duration, alternating with moraine substrates, slabs of rock, glacier strips, streams and pools. Much of the life in these ecosystems therefore depends on the glaciers themselves and on patches of snow. No animals, vertebrates or invertebrates, are recorded as living exclusively on the surface of glaciers in the Italian mountains, unlike the case in other mountain ranges - for example, the chironomids of the Tibetan glaciers.

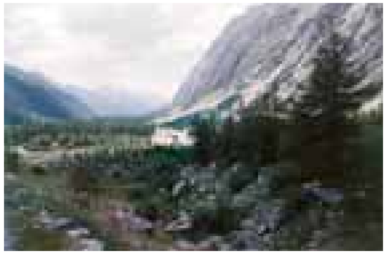
Animals of the nival environment. In common parlance, but also occasionally in ecology and zoology texts, the concept "nival environment" is associated with very diverse environmental situations.

The adjective "nival" refers to a physical factor: the presence of snow, independently of altitude or season. Snow is important for fauna, at least for small animals, in areas where a cover of 15-25 cm persists for at least 2-8 weeks of the year. This happens over much of the Alps and in large areas of the Apennines. In most cases, snow is seasonal – a fact which is not, in itself, sufficient to characterise a habitat. The adjective "nival" is therefore reserved for two environmental units dominated by the snow factor, and only marginally overlapping. The vegetation belt defined as "nival" lies above the treeline, an altitude which varies on the Alps, according to exposure and longitude, between 2700 and 2900 m. At these heights, the few animal and plant life forms are clearly influenced by low temperatures and persistence of snow. The snow cover in turn depends on the characteristics of the terrain, such as gradient and aspect, and on whether particular areas of accumulation exist, e.g., deep narrow valleys and gullies. It is also possible to speak of "nival terrains" - meaning those high-altitude areas where snow lies until the summer, as patches covering slightly sloping ground, especially in sheltered cirques ("snow-beds"). This is a particularly significant habitat in the Alps and, in a more limited way, the Apennines, because it hosts well-defined plant associations populated by well-characterised animal communities. Our description of nival fauna will mainly refer to this environment, which is common in the Alpine and the lower nival belts, but will also examine snow-bed habitats, even those lying outside the true "nival" environments - the surfaces of glaciers and snowfields, and also terrains recently exposed by retreating glaciers. The term *perinival* is used to define microhabitats around patches of snow and glaciers in the nival region and Alpine belt.

Red deer (*Cervus elaphus*)

Snow finch in a snowstorm

The term "snow-bed" was coined by the Swiss naturalist Oswald Heer and entered the naturalist literature in the 1800s. The term indicates high-altitude biotopes in which a gentle slope, slightly concave terrain and northern exposure - all in any case receiving little sunlight - encourage snow to linger on the ground. In snow-beds, two factors influence the fauna in opposite ways, particularly invertebrates. On one hand, the short time the ground is bare reduces the period of activity of animals to between one and four months. On the other, persisting snow mitigates summer aridity and, in winter, the ground temperature remains around 0°C for a long time. In addition, beneath the blanket of snow the abundant biomass of rotting vegetation, often accumulated or moved by small mammals, especially snow vole (*Chionomys nivalis*), allows many micro-organisms to grow, particularly myxomycetes. Decomposing plant material and micro-organisms supply the pabulum for a



Complex landscape of nival belt

complex food-chain, so that snow-beds are generally the high-altitude environments with the highest biodiversity.
Botanists now identify two plant communities as being characteristic of these environments, those of nival soils on siliceous rocks (*Salicetum herbaceae*) and those on carbonate rocks (*Salicetum retuso-reticulatae*). Animal communities are also affected by the chemical structure of the bedrock, because the differing soil permeability, which increases surface aridity after the snow melts on dolomitic and, even more so, on limestone rocks, also creates deep micro-fissures which are the habitat of many endogenous species. Other factors which are important for plants, like soil pH (slightly acid on silica, almost neutral on limestone), are less of a constraint for animals.
From the zoological point of view, the snow-bed environment does not entirely overlap that identified by botanists, but often extends to communities adjoining those of dwarf willow, especially those with *Carex curvula* on silica, and those with *Carex firma* and *Seslerio-sempreviretum* communities on carbonate rocks. The presence of clay, which holds water better, can lengthen the period of favourable conditions for perinival species, especially ground-dwellers, after the snow has melted. A difference in altitude has also been observed among the nival communities of the lower and upper Alpine belt. This happens mainly on siliceous rocks, where snow-beds occupy a very wide altitudinal range because of the higher average height of the siliceous mountains in the Alps.

■ Invertebrates

All terrestrial and some aquatic or semi-aquatic animal groups are represented in Alpine nival and perinival environments. However, their description is restricted to the species which have more definite relationships with snow, i.e., those which are associated with high altitudes and which prefer damp environments like snow-beds. Xerophiles and heliophiles, i.e., lovers of dryness and bright sunlight, such as orthopterans (grasshoppers), heteropterans (true bugs) and dermapterans (earwigs), and those with a wide ecological range for which the perinival environment constitutes an occasional habitat, are not described here.

White as the driven snow

Adriano Zanetti

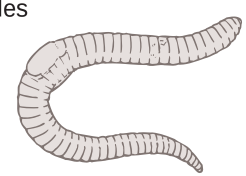
Blending in with the background is a widely-used strategy of defence and, occasionally, attack, in the animal kingdom. The term *cryptic mimicry* is often used for this adaptation. It may be in the form of homomorphism (similarity of shape) or homeochromatism (similarity of colour), both associated with particular types of behaviour, the most common being remaining completely stationary. On the white surface of snow, where uniformity is the dominant characteristic, this mimicry is displayed as homeochromatism, i.e., no colours except white. Mimicry is widespread throughout the animal kingdom, arthropods, spiders and insects being particular masters of the art. Another type of mimicry is called Batesian, which is defensive, and is based on the convergence towards distinctive colours like those of species endowed with particularly efficient defence systems. For example, this explains the similarity of many flies to bees and wasps. However, insects which live on snow (*Chionea*, *Boreus* and various beetles) do not hide by being white, and stand out clearly from their background. White colouring is the prerogative of many vertebrates living in environments which remain snow-covered for long periods. In Europe, the most striking examples are found in species inhabiting the Arctic circle, such as polar bear (*Ursus maritimus*), arctic fox (*Alopex lagopus*) and snowy owl (*Nyctea scandiaca*), but some species also live in the mountain ranges of southern Europe. In this case, white is a seasonal variation in colour, but there is also an associated geographical variation. Ptarmigan (*Lagopus mutus*) and stoat (*Mustela erminea*, see photo) are dark in summer and white in winter. The willow grouse (*Lagopus l. lagopus*) of northern Europe change colour, but in Scotland and Ireland, red grouse (*Lagopus l. scoticus*) remain dark all year. Similarly, mountain hare (*Lepus timidus*) changes colour over much of its distribution area (northern Europe and the Alps, where it's present with *L.t. varronis*), but only does so partially in Scotland and Scandinavia, and remains dark all year in Ireland and on the Fär Oër Islands. Also weasel (*Mustela nivalis*), common throughout Europe, has a white winter coat in the far north of Scandinavia and Russia. White in high-altitude species may have another adaptive significance. White fur contains many more microscopic air-filled gaps, which improve the animal's thermal isolation. This probably explains the white colouring of species which are under no threat from predators.

Platyhelminths, nematodes, rotifers and anellids. Although it was long hypothesised that platyhelminths, or flatworms, were absent from soils in the nival region, research at the end of the 1950s discovered them at heights exceeding 3000 m a.s.l.. At least three species, of which only one, *Acrochordonoposthia ramolia*, had been formally described, were isolated in soils from the Ötztal, where *Saxifraga opacifolia* grew.

In primitive soils, some nematodes and rotifers, which are highly resistant to both low temperatures and dehydration, may also be found among cushion plants and mosses. These species are anemochorous, i.e., they are dispersed by wind to colonise new substrates.

Some nematodes are also parasites on the aquatic larvae of diamesine chironomids. The species recorded in the soils of the nival region of the eastern Alps belong to the genera *Dorylaimus*, *Mononchus*, *Plectus*, *Teratocephalus* and *Tylenchus*.

The earthworm species reported at the highest altitudes is *Dendrobaena octaedra* (see drawing), found in the Zillertal (Austria) at around 3000 metres a.s.l. Specimens belonging to enchytraeid anellid families have also been recorded in the soil beneath cushion plants up to 3400 metres in the central Alps.



Arianta chamaeleon

Molluscs. The genus *Arianta* is an interesting example of molluscs associated with nival environments. *Arianta arbustorum* and *A. stenzii*, quite large species, are widely distributed in the Alps, whereas *A. chamaeleon* is only found in the south-eastern Alps, where it is also active on snow.

There are also some rare genera of the vitrinid family characteristic of nival environments: the tiny *Semilimax*, *Phenacolimax* and *Eucobresia*, with their lovely translucent spiral shells, and some species of the genera *Vitrea* and *Daudebardia* among the zonitids.

Among snails, some species of milacids reach very high altitudes and melanic (dark-coloured) individuals can be found under the stones on scree slopes. From the biological point of view, species of the genus *Arianta* at high altitude demonstrate interesting adaptations in their life-cycle: for example, *A. arbustorum* requires five years to reach maturity at 2600 m, but only two years in mountain environments at 1200 m.

Tardigrades. Many representatives of this archaic phylum related to the arthropods are found at the edges of snowfields and glaciers, among mosses or in meltwater. They survive periods of the year with adverse environmental conditions by means of a particular mechanism known as “cryptobiosis”, during which they undergo a reversible suspension of movement and an extreme reduction in metabolism. Laboratory experiments have demonstrated that tardigrades can even survive at the temperature of -272°C!

Crustaceans. There are only a few representatives of crustaceans in perinival environments, where only a few oniscoidean isopods (woodlice) are reported at high altitude.

This is mainly due to the respiratory mechanisms of these arthropods, which always require a film of water, and therefore high conditions of humidity, in order to function properly.

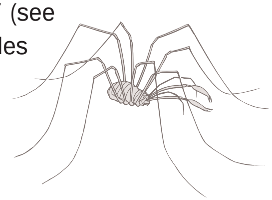
Low temperatures make this physiological mechanism inefficient. Instead, the aquatic or semi-aquatic micro-crustaceans are very interesting. They may be found among mosses, lichens, or in the interstitial environment where meltwater collects in spring. Some of these minute harpacticoid copepods, less than a millimetre long, may be considered exclusive to these environments. Until a few years ago, these species were considered to be rare but only because they were not sought in suitable sites and periods of the year. They mainly belong to the genera *Hypocampus* and *Maraenobiotus*, and probably include species still not described. The mechanism these organisms use to survive periods of inactivity (the long period of winter cold, and in summer, when these environments dry out) is unknown; presumably they enter a state of quiescence, but it is not yet understood if this means cysts or resting eggs. There are no known copepods exclusive to glaciers in Italy - like the exceptional genus *Glaciella*, discovered in tiny pools of meltwater that form during the day on the surface of the huge Himalayan glaciers.

Hypocamptus paradoxus

Aculepeira carbonaria

Spiders. Of all the non-insect arthropods, spiders are the best represented group in the perinival environment, constituting up to 50% of fauna active on the ground. They are mainly small, slim linyphiids, including numerous forms associated with cold wet habitats like the edges of snowfields and glaciers. Specimens of the genus *Troglohyphantes* may be found in detritus or under stones up to high altitudes. Their environmental preferences are similar to those of carabid beetles of the genus *Duvalius*, or of certain cholevid beetles, which are also often high-altitude perinival or cave-dwelling species. The best-represented genus of linyphiids, with six endemic species on the eastern Alps, is *Leptyphantes* which, it is hypothesised, found refuge on the highest glacier-free peaks during the Ice Ages. Two species of the genus *Leptyphantes* (*L. merretti*, *L. brunneri*), with well-defined distribution areas, have been collected at very high altitudes in the Dolomites. The gnaphosiid *Drassodes heeri* and the lycosid (wolf spider) *Vesubia jugorum* of the Maritime Alps are also considered classical components of the nival alpine area. Other species of spiders variously associated with the nival environment belong to the families of thomisids (or crab spiders), hahniids, gnaphosids (with species reaching an altitude of 3000 m), lycosids and amaurobiids.

Harvestmen are quite well represented in the perinival environment, and, together with beetles of the genus *Nebria* (*Oreoebria*), share the habit of feeding on dead animals on the snow surface. *Mitopus glacialis* reaches altitudes of over 3500 m. *Dicranopalpus gasteinensis* and representatives of the genus *Megabunus* are also associated with high altitudes. Harvestmen of the genus *Ischyropsalis* are mainly perinival, such as *I. kollari* (see drawing) in the Eastern Alps. This genus also includes troglophilous species, with an interesting ecological analogy to the ground beetles of the genus *Duvalius*.



There are no tiny mites, which have possibly the widest ecological range, living exclusively in nival environments in the Alps and Apennines. The only species which exist frequent the edges of glaciers or snowfields in the cushions of pioneer plants, in areas where organic matter accumulates, and in the few patches of soil, e.g., *Niphocephalus nivalis*. Many species of brachychthoniids live on bare ground.

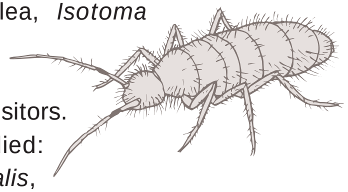
Pseudoscorpions are particularly common in forest litter, but are less well represented at high altitude. *Neobisium jugorum* and *N. dolomiticum* live under stones near melting snow in the Alps, and a close relative, probably *N. fiscelli*, in the central Apennines. *Chthonius jugorum* and *Chernes montigens* may also be found.

Diplopods and chilopods. Among the diplopods (millipedes) at high altitude, the neoatractosomatids *Trimerophorella paradisia* and *T. rhaetica* are reported as perinival. Studies of the latter have demonstrated that its biological cycle lasts for four years, and this is considered an adaptive response to the brevity of the snow-free period.

No exclusively perinival species of chilopods (centipedes) appears to exist. Some species of lithobiomorphs in the Alps regularly live in open areas at high altitude, such as *Lithobius lucifugus*, *L. muticus* and *L. schuleri*, but they are all species which are not exclusive to these environments and the associations are generally poor. There are possibly more in the high Apennines, but they are nearly always euryecious or xerophilous species of secondary pastures.

Eupolybothrus longicornis

Collembolans (springtails). The glacier flea, *Isotoma saltans*, is the only species of springtail which passes its entire life-cycle on the surface of glaciers; others are more or less occasional visitors. Perinival collembolans are little studied: *Isotomurus palliceps*, *Orchesella nivalis*, *Hypogastrura socialis* and *Ceratophysella sigillata* regularly frequent these environments. Collembolans which live on the snow surface tend to undergo demographic explosions in particular years, and they may then form extensive dark patches on snow-covered areas. This was documented in the Alto Adige (South Tyrol) during the winter of 1993-94, when *H. socialis* formed patches of up to 1000 m^2 in various locations, comprised of as many as a billion individuals.



Coleopterans. Coleopterans or beetles are the best-known invertebrates of the perinival environment and are therefore given a fuller description than that dedicated to other, not equally well-known, animal groups. They allow quite well-defined associations to be identified, although taxonomic difficulties and a scarcity of serious studies on communities does not permit the detail that characterises corresponding works in botany.

Carabus (Orinocarabus) pedemontanus vesubianus

Carabid beetles. Carabid beetles are the best-known dwellers of nival environments, with a quite well-described succession of populating stages.

Carabus (Platycarabus) bonellii

Among the many representatives of the genus *Carabus*, which includes large-sized species, the representatives of the two sub-genera *Orinocarabus* and *Platycarabus* include perinival species which are widespread in the Alps but which do not occur in the Apennines. Species of the sub-genus *Orinocarabus* are almost all exclusive to the Alpine belt, with the only exception of *Carabus* (*O.*) *linnaei*, which is a forest species. They are particularly common and abundant in the internal regions of the Alps, but are much rarer or absent in the external massifs. There are seven species of *Orinocarabus* in the Western Alps, often split into sub-species, with slightly overlapping distribution and also associated with types of soil: *C.* (*O.*) *putzeysianus* (Ligurian and Cottian Alps), *C.* (*O.*) *fairmairei* (Cottian Alps), *C. (O.) cenisius* (Cottian and Graian Alps), *C.* (*O.*) *latreillianus* (Graian and Pennine Alps), *C.* (*O.*) *heteromorphus* (Graian Alps), *C.* (*O.*) *concolor* (Pennine and Lepontine Alps, Bernese Oberland) and *C.* (*O.*) *lepontinus* (Lepontine Alps). In the central Alps, the number falls to three, *C.* (*O.*) *silvestris*, *C.* (*O.*) *castanopterus* and *C.* (*O.*) *adamellicola*; in the eastern Alps to two, *C.* (*O.*) *bertolinii alpestris* and *C.* (*O.*) *carinthiacus*. Representatives of the subgenus *Platycarabus*, which feed on snails, are found mainly on carbonate soils, such as those of the eastern Pre-Alps. *C.* (*Platycarabus*) *creutzeri*, for example, is the most common large carabid beetle in the central-eastern Pre-Alps, although its altitudinal distribution is very wide. It usually feeds on molluscs, as does *C.* (*P.*) *cychroides*, which is endemic to a small area in the Cottian Alps. *C.* (*P.*) *fabricii*, a central and east European species, is found on the Italian Alps in restricted areas of the South Tyrol, and *C.* (*P.*) *bonellii* is the most widespread representative of the subgenus *Platycarabus* throughout the Alps, especially in more central areas, with a wide altitudinal range.

Species of *Cychrus* are even more specialised predators of snails than *Platycarabus*. The most characteristic, because of the extremely long, narrow front part of its body, is definitely *Cychrus cylindricollis*, which is often found when the snow melts in a restricted distribution area between the Bergamasque

Cychrus attenuatus latialis

Pre-Alps and Monte Baldo, further east. The species of *Nebria* of the subgenus *Oreonebria* are flat brown carabid beetles, approximately one centimetre long, with an elegant body shape, long legs and antennae. They are active by night on the snow surface, where they feed mainly on dead insects.

The most widespread in the Alps and in many sites in the Apennines between Tuscany and Emilia Romagna, is *Nebria castanea*. Many others have more limited distribution: *N. angustata* (central Alps), *N. austriaca* (a few sites in the South Tyrol), *N. diaphana* (eastern Pre-Alps, Dolomites), *N. lombarda* (Orobian Alps), *N. macrodera* (Maritime Alps), *N. ligurica* (Maritime and Cottian Alps), *N. picea* (a few sites) and *N. angusticollis* (Cottian and Graian Alps).

On melting snow, it is easy to observe individuals of *Ocydromus*, subgenus *Testediolum* (4-5 mm long). They have metallic teguments and large eyes, and run quickly over the ground even during the day. Six species are known in the Italian Alps: *Ocydromus* (*Testediolum*) *glacialis* (over most of the range), *O.* (*T.*) *jacqueti jacqueti* (Western-Central Alps), *O.* (*T.*) *pyrenaeus* (Western Alps), *O.* (*T.*) *rhaeticus* (Pre-Alps, Central Alps) and *O.* (*T.*) *julianus* (Eastern Alps). They are species with wide distribution areas, but with some ecological and biogeographical differentiation. For instance, *O.* (*T.*) *glacialis* is associated with higher altitudes, and *O.* (*T.*) *rhaeticus* is essentially Pre-Alpine in the Central Alps. Two species are present in the Apennines: *O.* (*T.*) *glacialis* and *O.* (*T.*) *jacqueti appenninus*. *Princidium bipunctatum* (Alps, Apennines) has similar ecology to the species of *Testediolum.* In the Apennines, there are a considerable number of endemic nival bembidiin carabids: *Peryphanes alticola* on the Maiella, and two *Ocys*, *O. pennisii* on Monte Gorzano and *O. tassii* on Monte Greco, which display adaptations to life in the soil.

An extraordinarily large number of endemic species of the genus *Trechus* populate the perinival environment of Pre-Alpine carbonate soils, although not exclusively. The area with the greatest diversity appears to be the central Pre-Alps, and some high-altitude *Trechus* are also found in the Apennines. The genus *Duvalius* includes carabid beetles related to *Trechus*, but more adapted to life in the soil and in underground cavities, as revealed by the small size of the eyes, loss of body colour, and lengthening of the appendages. On limestone

Pterostichus honnorati sellae

Nebria orsinii

and dolomitic Alps, especially in the east, many species of *Duvalius* can be found underneath stones where snow is melting, often at the entrance to small cavities, whereas only cavernicolous or endogenous species of this genus are found in the Apennines.

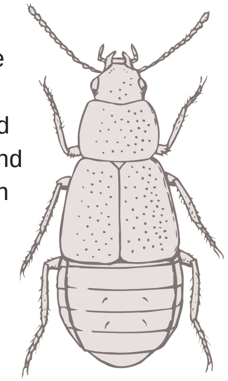
Oreonebria ligurica

During the short summer season, the carabid beetle communities populating snow-beds must face a succession of stages, corresponding to the progressive drying out of the soil. In higher areas with siliceous soils in the inner Alpine regions, species of the genus *Nebria*, subgenus *Oreonebria*, are very frequent and abundant from May-June onwards. The continuous supply of meltwater at the edges of the snow in June and July forms a “riparian” type of micro-environment. It is often very rich in carabid and staphylinid beetles, whose abundance is also favoured by the less severe environmental conditions in the gaps beneath the snow, which are improved by the activity of small mammals and the piles of plant debris they produce. An association characterised by *Ocydromus*, subgenus *Testediolum*, is found during this stage. At the end of June, immediately after the snow has melted completely, the maximum number of adult carabid beetles may be found on the ground (*Carabus*, subgenus *Orinocarabus*; *Pterostichus* sensu lato; *Amara*, and others). From July-August onwards, on the progressively drying soil, the community becomes enriched by increasingly xerophilous species. These are predators, or have mixed dietary regimes. Representatives of the genus *Amara*, such as *A. quenseli* and *Cymindis vaporariorum*, are characteristic of this stage. In the central-eastern Pre-Alpine areas with carbonate rocks, carabid beetle communities are richer in species, thanks to a set of environmental and zoogeographical factors. *Oreonebria* and *Testediolum* are less abundant, species of *Platycarabus* dominate instead of *Orinocarabus*, and *Trechus* and *Duvalius* are frequent.

In the Apennines, the areas with true perinival communities are mainly the high central massifs. The species start appearing earlier in the season, and *Oreonebria* is substituted by *Nebria (Nebria) orsinii* and, locally, by *Leistus glacialis*, which occupy the same niche, feeding on dead insects on the snow. *Nebria posthuma* appears later, and associations with *Cymindis vaporariorum* are occasionally found.

Stenus glacialis, with characteristic mobile lower lip

Staphylinid beetles. These beetles are characterised by their short wing-cases and very mobile abdomen.
They represent one of the groups of terrestrial invertebrates with the most divergent adaptive radiation.
The vast majority are carnivorous, and are to be found both in the soil and in temporary environments with plenty of decomposing materials: for example, in the mountains, on cattle dung.
Staphylinids, or rove beetles, are well represented in the Alpine environment by species mainly associated with specific soil types, being especially abundant in more highly evolved soils with alpenrose thickets or green alder, but they may also be found in extreme situations on pioneer land.
There are numerous perinival species in dwarf willow communities, high-altitude meadows and plant communities of mountain avens (*Dryas octopetala*), where they most often prey on invertebrates such as springtails and dipteran larvae, but they may also have particular, many still unknown, habits. For example, *Aleochara* species are parasites on dipteran pupae.
Many staphylinid beetles appear early on the edges of melting snow, where they are associated with carabid beetles, in particular bembidiines (*Testediolum*) and trechines. Some *Philonthus*, like *Ph. frigidus* (found in the Alps and some sites in the Apennines) and representatives of the subgenus *Kenonthus*, are typical of these ephemeral associations. *Stenus*, with its large eyes and mobile lower lip, which is used for capturing springtails, are more often low-altitude riparian species, but are also quite well represented in Alpine environments, with a clear preference for the perinival level. *Stenus glacialis* probably reaches the highest altitudes, up to approximately 2500 m in the Alps, and is replaced in the Abruzzo mountains by the related *S. abruzzorum*. A conspicuous number of small wingless species, with a marked tendency to be endemic, populate the Alps and north-western Apennines (*S. cottianus*, *S. kahleni*, *S. focarilei*), central Pre-Alps (*S. areolatus*, *S. guglielmomontis*), eastern Pre-Alps (*S. liechtensteini*, *S. cavallomontis*) and Tuscan Apennines (*S. bordonii*).



Two representatives of the enormous sub-family of the aleocharines, *Atheta tibialis* and *Aleochara heeri*, are considered strictly perinival - they are always abundant and active in springtime around melting snow. Rarer and difficult to spot are the small species of *Alpinia*; wingless and not very active, they are widespread in the Balkans and, in Italy, are found in the Eastern Alps and Pre-Alps (*Alpinia montiscanini* on Monte Canin and *A. rosai* on Monte Cavallo, both in Friuli) and Apennines (*A. italica*), and some *Oxypoda*, in particular *O. densa*.
The most characteristic staphylinid beetles of the nival environment in Italy are probably two representatives of the genus *Mannerheimia*, small shiny, broad, flat omaliines. *Mannerheimia arctica* (see drawing), with boreal-alpine distribution, has only ever been found at the high Stelvio Pass and in a second site, yet to be confirmed, near Braies in the South Tyrol. In the Stelvio area, it is found regularly on moraine soils and under stones among dwarf willows, but the population is considered to be in grave danger. *M. aprutiana*, endemic to the central Apennines, is another lapidicolous (stone-dwelling) species living at high altitudes (2500 m on the Corno Grande of Gran Sasso, and 2700 m on Monte Amaro in the Maiella).
Representatives of the genus *Deliphrosoma*, similar to *Mannerheimia* but larger, which belong to the group of autumn species, are associated with snow. *D. macrocephalum* may be found on the Alps wandering on the snow at high altitude after the first snowfalls; on the Apennines *D. platyophthalmum* has similar ecology. *Acidota cruentata*, and more especially *D. algidum*, are also habitual visitors to the snow surface, but are associated in particular with the mountain belt. The very large genus *Leptusa*, with approximately one hundred species almost all endemic to the Alps and, more sporadically, the Apennines, is typical of the Alpine communities, but its members, generally associated with soil, can rarely be considered perinival. Among these, the almost blind and depigmented species of the subgenus *Typhlopasilia*, in particular *Leptusa stoeckleini*, are widespread from the Lessini Hills to Monte Grappa.
Recent research on staphylinid beetles in a perinival environment of the southern Balkans has demonstrated exceptional species diversity in this habitat, often with astonishing adaptations. Traces of this Balkan fauna have remained in the high-altitude Apennines. This has been proven by two species of the genus *Emmelostiba*, recently described in Abruzzo (*E. rosai* on Gran Sasso, *E. kappi* on the Maiella), and it is probable that further research in the central-southern Apennines will lead to the discovery of yet others.

Chrysomelid beetles. The chrysomelids or leaf beetles, convex, short-bodied phytophagous and include many high-altitude species closely associated with environments where dwarf willows grow. They are therefore undoubtedly characteristic of the snow-bed community, although the adults do not necessarily make their appearance when the snow melts, and they are therefore not typical perinival species. *Phaedon salicinus* is found in the western-central Alps on *Salix retusa. Gonioctena nivosa*, a boreal-alpine-pyrenean species, is associated with *Salix retusa* and *S. herbacea*, and *Chrysomela collaris*, which lives on various types of willow in northern Europe, is exclusive to high altitudes in the Alps.

Other significant species of chrysomelids are *Chrysolina latecincta*, which lives on *Linaria alpina*, often on scree slopes near glaciers, and *C. relucens*, common in only two Italian Alpine sites, in the Urals, along the coastline of the White Sea and in Siberia. *Oreina (Frigidorina) frigida* is a representative of the genus which is most often to be found in high-altitude snow-beds. Although not rigorously nival, three *Oreina* species of the subgenus *Protorina*, associated with several *Doronicum*, are found on the Alps, in particular the Eastern Alps, whereas *Oreina sybilla* is endemic to the central Apennines.

Curculionid beetles. Weevils, or curculionid beetles, are characterised by the shape of the head, which is elongated in a rostrum. They represent a huge group, but the nival environment is not particularly suitable for them, because of their phytophagous feeding habits and a general preference for warm environments. This does not stop numerous species from being found more or less exclusively at high altitudes on snow and, if further research is undertaken, it is probable that other species new to science will be discovered.

Perinival curculionids over-winter mainly in the adult state and are active when the snow melts, in some cases from early May. They belong to two families of the group found in Italy, the apionids and the curculionids *sensu stricto*. Most high-altitude species have a diet of roots or can be found amongst mosses, but few have larvae living above ground.

Osellaeus bonvouloiri is an apionid worthy of mention. It lives between 2000 and 3000 m a.s.l., and is usually associated with *Saxifraga oppositifolia*, a pioneer plant which populates ground recently abandoned by glaciers. In these environments, the typically shaped *O. bonvouloiri* is almost the only beetle to be found. On the eastern Pre-Alps, a distinct subspecies associated with *Saxifraga caesia* lives on Monte Baldo.

Many species of curculionids live at high altitudes, but few are exclusive to nival environments. The species of *Oreorhynchaeus* associated with snowbells are particularly emblematic, but the representatives of *Otiorhynchus* especially characterise high-altitude communities. Some species like *Otiorhynchus tener* and *O. nubilis* of the Western Alps are found in areas where the snow melts in late summer, although they can also be seen in the soil of cool meadows. Many other Alpine and Apennine *Otiorhynchus* are considered perinival *sensu lato*. *O. abruzzensis* frequents high altitudes on the Gran Sasso, and *O. praetorium* lives between the roots of *Saxifraga aizoides* at above 2000 m on the Monti della Laga. *Dichotrachelus* is a curious high-altitude curculionid, identifiable by its keeled wing-cases with strange club-shaped bristles. Species which reach very high altitudes include *D. meregallii* in the Eastern Alps, found almost as far up as 3000 m, and numerous other species frequent high cirques after the snows have melted. The larger species are associated with the saxifrages, the smaller ones live amongst the mosses growing on rocks. Some Lombardy and Veneto *Dichotrachelus*, although not reaching such high altitudes as those in the Western Alps, are also usually found in perinival dolinas.

Other high-altitude curculionids of the Alps more or less closely associated with the nival environment are representatives of the genera *Lepirus*, *Pelonomus*, *Brachyodontus*, *Orthochaetes* and *Trachystyphlus*, the latter with a species also found in the Apennines.

Holes in snow allow small insects to reach the surface

Shrunken snow-bed in a debris cirque

Scarabeid beetles. High altitudes are often frequented by many scarabeid beetles living on the dung of cattle grazing the Alpine meadows, and many of these coprophages are considered to be Alpine species. However, few scarabs are truly associated with perinival environments. Among those which are, representatives of the subgenus *Neagolius* of *Aphodius* are particularly significant. They have homogeneous biology, about which, however, very little is known, and they almost certainly eat decomposing plant material instead of dung, as most of their congeners do. Their presence may be favoured by snow voles collecting plant litter beneath the snow. Species of *Neagolius* are associated with the Alpine belt, between 1800 and 2300 m a.s.l., and are characterised by such highly pronounced sexual dimorphism that some specimens of the female sex have been described as entirely different species. The females of some species are wingless or short-winged, depigmented, and may lead underground lives. The males are attracted by the whiteness of snow patches and, curiously, by the smell of tobacco smoke. The species of *Neagolius* have rather limited distribution areas in the Alps and Apennines: *A.* (*N.*) *amblyodon* populates the Italian slopes of the Cottian and Graian Alps, *A.* (*N.*) *ligurius* the Ligurian and Maritime Alps, *N. penninus* is endemic to the Pennine Alps, *A.* (*N.*) *limbolarius* and *A.* (*N.*) *montanus* the Dolomites and Veneto Pre-Alps, and *A.* (*N.*) *pollicatus* the Julian Alps and Veneto Pre-Alps.
The distribution of *N. schlumbergeri consobrinus* is rather particular. It lives in the Orobian Alps, and the Lombardy and Veneto Pre-Alps, and there is an isolated population in the Apuan Alps. Instead, the central-southern Apennines, from Monti Sibillini to Pollino, is home to *N. schlumbergeri samniticus*.
Agolius has similar ecological characteristics to the subgenus *Neagolius*, *A. (A.*) *abdominalis* of the Alps and northern Apennines being represented over most of the Alps by *A. (A.*) *abdominalis abdominalis*, whereas *A. (A.*) *abdominalis emilianus* lives on the Apennines in Emilia Romagna.

Byrrhid beetles. The byrrhid or pill beetles are ground-dwelling beetles, which mostly feed on mosses. They are oval in shape, with robust teguments and, if disturbed, enter thanatosis, i.e., fake death, assuming a posture with their legs tucked along their body so that they resemble seeds. They are often abundant at high altitudes, but the few exclusively perinival species on the Italian Alps are nearly all endemic: *Simplocaria jugicola* lives only on some peaks in Piedmont, *S. nivalis* is exclusive to massifs in the provinces of Trento and Brescia, *Byrrhus focarilei* lives on the spurs of Presolana near Bergamo, and *Curimopsis carniolica* is reported on some peaks in the Carnian Alps (Friuli Venezia Giulia).

Dipterans. Although the collembolans is the taxonomic group with the largest number of individuals in the nival zone and at high altitudes in general, the greatest species diversity appertains to the dipterans. Despite the fact that most dipterans arrive from valley bottoms and lower altitudes, transported by the wind and ascending currents, a relevant and extremely variegated proportion is formed of species which actually live at high altitude. As the nival zone is a complex environmental mosaic, with alternating areas of rock, morainic substrates, snow patches, screes, etc., there are several habitats in which dipterans may live. The many glacier streams which flow through these areas allow the larval development of many nematocerans, including simuliids and chironomids, mainly of the genus *Diamesa*, with some short-winged species.

Most dipterans in this altitudinal belt feed on decomposing organic matter and fungi during the larval stage, although there are a few predatory and parasitic species - for example, some tachinids. A determining factor for larval development, together with the availability of organic matter, is the presence of moisture. In areas where these conditions are found, such as small mountain peat bogs or in gullies and fissures, numerous specimens of tipulids (craneflies) can be found, with names evocative of this environment (e.g., *Tipula glacialis*).

Besides the conspicuous tipulids, the smaller sciarids and mycetophilids are also numerically important. The former include some species with shortened wings, which can be found among cracks in the soil and have larvae which feed on decomposing organic matter; the latter eat the fungi growing in these areas.

Examples of ephydrids of the genus *Scatella* can also be found close to damp areas, with their characteristic brown wings with light-coloured markings, and empidids. In the nival belt and among the last green alder bushes of the Alpine belt, flights of bibionids of the genera *Bibio* and *Dilophus* can be seen. The males of these species swarm together in vast numbers, while the females, which are also able to fly, can more often be found on grass stalks or among branches. The larvae of these species also feed on decomposing, especially plant, organic matter.

According to the well-known Italian dipterologist Mario Bezzi, the nival environment may be defined as that of the anthomyids: dipterans of the size and build of house flies, of which the genera *Delia* and *Zaphne* may be seen in abundance on poppy flowers colonising scree slopes or stationary on boulders, soaking up the heat of the sun. It should be noted, however, that Bezzi's use of the term "nival" refers to the vegetation belt and not only perinival environments. According to the same author "…[the nival area] is distinguished by the absolute predominance of anthomyids and the almost complete lack of syrphids and acalypterans, which are very frequent in the regions below", and "a given fauna may be termed *nival* when more than half its species and more than three-quarters of the individuals belong to the anthomyids".

The adults of this family, the larvae of which are prevalently saprophagous, fly in search of the few flowers growing in the nival belt and they rest on them, clinging on by their strong claws if the wind rises. Although less numerous, there are some syrphids, coloured yellow and black, the majority belonging to the genus *Syrphus*.

Some species of empidids, which mate close to snow patches, have particularly interesting behaviour. The male of these species, belonging to the genus *Rhamphomyia*, before mating, presents an offering of prey to the female, usually a nematoceran dipteran that he has caught.

Boreal-alpine species like the sphaerocerid *Crumomyia setitibialis*, found on the Marmolada massif in the Dolomites, are particularly interesting from the biogeographical point of view. The species, generally considered nival, such as the genus *Chionea*, which is wingless and often active on the snow, have a wide altitudinal range, being found from mountain to Alpine belts.

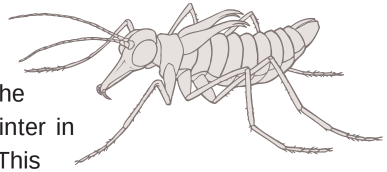
Chionea lutescens

Animal populations at high altitudes on the Apennines

The greater height of Alpine peaks compared with Apennine ones is not the only reason for fewer high-altitude species along the backbone of the Italian peninsula. Their lower altitude actually allowed the Apennine chain to conserve many of its original fauna during the first Pliocene-Quaternary ice ages, when many thermophilous species of the Alps had already been decimated and residual populations were only to be found in isolated areas of refuge between which any possibility of gene flow had been interrupted.
It was only during the most recent Würm glaciation that glaciers formed down the entire Apennine ridge, as far as Pollino but, after this dramatic period of impoverishment, there was no faunal reservoir left. This might have been available from any sufficiently near southern mountain chain, which could offer the Apennines suitable colonisers for the highest habitats as they became free of ice. The Alps fared better, because during the post-glacial period they were reached by temperate-cold populations which, at the height of the Ice Age, had found refuge on the Pyrenees, in the Balkans, or in Italy, along the Apennines. Thus, although the post-glacial northward return of temperate-cold fauna which had survived in southern refuges originated many cases of boreal-alpine distribution, there are very few species with scattered distribution which, besides the northern European populations, also included a contingent on the Apennine summits. Against at least two hundred animal species with scattered distribution in both Scandinavia and the Alps, there are very few boreal-Apennine species: one of these is the grasshopper *Aeropus sibiricus*. Species absent from northern Europe but found on both the Alps and the highest Apennine massifs are much more common.
As well as numerous insects, this type of distribution is that of such vertebrates as Alpine newt (*Triturus alpestris*), common frog (*Rana temporaria*), snow finch (*Montifringilla nivalis*), Alpine chough (*Pyrrhocorax graculus*) and snow vole (*Chionomys nivalis*).
Towards the end of the Pleistocene, approximately two million years ago, the Apennine chain - previously formed of a series of islands and archipelagos - finally linked up with the Alps and, therefore, with the extensive mountain system extending, with few gaps, from the Pyrenees as far as the high ranges of central Asia. This geographical link-up enabled large-scale faunal migrations which, although more than once interrupted by climatic events during the Quaternary, led to the major affinities between high-altitude fauna in the Apennines and that living in similar environments elsewhere. The level of differentiation between populations depends both on the zoological group in question, and on the antiquity of the reciprocal isolation between the inhabitants of each mountain range. Thus, whereas Abruzzo chamois (*Rupicapra rupicapra*) is differentiated from its Pyrenean cousin only at subspecies level, the differences between the Pyrenean and Apennine populations of many groups of insects are clear enough to lead to the identification of separate genera.

Alpine choughs (*Pyrrhocorax graculus*)

Forficula apennina



Mecopterans. On the surface of the snow, at high altitude but also in mountain woodland, it is not difficult to come across the peculiar *Boreus hiemalis* in autumn and winter in the Alps and some sites in the Apennines. This insect possesses various extravagant characteristics. It looks like a scorpion fly, but its wings are atrophied and, in the male, have the purpose of holding the female during mating. Its head is elongated in a rostrum with which it feeds on moss fragments and dead insects. The boreids have a circum-boreal distribution which includes the cold regions of Eurasia and North America.

Lepidopterans. At high altitudes in the Alps, in both snow-beds and the true nival belt, it is easy to observe flamboyant representatives of butterflies like brown ringlets (*Erebia*), and the more elusive moths and tiny micros in flight. Knowledge of these groups is still somewhat scanty. However, it may be assumed that high-altitude butterflies, as caterpillars, feed on one or very few types of plants (monophagous and oligophagous species). Species diversity thus depends on the variety of plants growing in the environment.
Only about thirty species of butterfly have been reported in the literature above 3000 m in the Swiss Alps. For Italy, unpublished data available at the Tiroler

Erebia pluto

Landesmuseum Ferdinandeum in Innsbruck (Austria) identify approximately fifty species. Of these, around ten are associated with cryptogams and around forty with seeding plants. There are species endemic to the Alps, boreal-alpine species, mountain species with Eurasian distribution, and migratory species. Only a few are closely associated with nival habitats. These include Alpine endemics like the psychid *Dahlica argenterae*, the geometrid *Glacies wehrlii*, and the arctiid *Holoarctia cervini*. Twenty or so species frequent both the nival belt and areas below, especially the Alpine belt. Many endemic species live in habitats dominated by vegetation typical of scree slopes and boulders of the Alpine belt. These species also reach sub-nival and nival habitats, such as *Plutella geniatella* (plutellids), various species of the genera *Sattleria* (gelechiids), and *Neosphaleroptera* (tortricids), *Catoptria luctiferella* and *Eudonia sudetica* (crambids), various *Erebia* (satyrids), particularly *Erebia pluto* and *E. gorge*, *Glacies spitzi* (geometrids) and *Discestra melanopa* (noctuids).
Species like *Eudonia vallesialis* and *Orenaia helveticalis* (crambids), *Sciadia tenebraria*, *Elophos celibaria* and *Glacies alticolaria* (geometrids), and *Standfussiana wiskotti* (noctuids) are mainly restricted to the nival belt and are only rarely found at lower altitudes. Lastly, it should be noted that only a very few species prefer dwarf willow habitats. These include the tortricids *Aterpia andereggana* and *Epinotia cruciana* and the geometrid *Pygmaena fusca*.

Erebia gorge

Marmot (*Marmota marmota*)

■ Vertebrates

Chamois (*Rupicapra rupicapra*)

All vertebrates which lead sedentary lives in the Alpine environment have relationships with snow and ice, but no species is resident in so restricted a habitat that it exclusively frequents nival lands as intended by the botanical meaning of the term, that is, mosses (polytrichaetes) or phanerogams (dwarf willow communities).

Vertebrates which live in this habitat display numerous adaptations to the prolonged snow cover.

Winter hibernation in systems of underground burrows is typical of Alpine marmot (*Marmota marmota*) - which moreover, should by origin and habitat be considered a steppe species, having originated from central Asia. Melanism, i.e., total or partially dark colour, which is found, for example, in high-altitude black salamanders (*Salamandra atra*, *S. lanzai*) may constitute a response to low temperatures, because these animals can be more efficiently warmed by basking in the sun. A thick blanket of snow frequently induces temporary altitudinal migrations in sedentary species which remain active during winter, such as some ungulates and birds.

Red deer (*Cervus elaphus*) have different winter and summer quarters, and although they only make limited journeys, they prefer broad valleys with little snow which are sunlit at midday in winter. Ibex (*Capra ibex*), typically found in summer in rocky habitats above the tree-line between 2200 and 3000 m, spends winter and spring among sparse larch, mountain pine and, exceptionally, spruce woodlands, descending as far down as 1100 m a.s.l..

Chamois (*Rupicapra rupicapra*), which has a wide altitudinal range in summer, from the mountain to the Alpine belt, moves downhill in winter, and Abruzzo chamois (*Rupicapra pyrenaica ornata*), which in summer frequents high-altitude meadows above 1700 m, is to be found during winter in precipitous woodland slopes in valleys between 1300 and 1700 m. The shape of its hooves makes this animal surefooted on snow, thanks to a fold of skin between the two toes.

Few species of Alpine terrestrial vertebrates can be considered specifically and substantially adapted to snow. Among the amphibians, Alpine salamander (*Salamandra atra*) and Lanza's salamander (*Salamandra lanzai*) are considered

Lanza's salamander (*Salamandra lanzai*)

habitual although not exclusive visitors to nival habitats. The former is widespread in the Central-Eastern Alps at altitudes of between 800 and 2800 m. The latter, described as a new species in 1988, and distinguishable from *S. atra* by subtle morphological characteristics, is endemic to the Cottian Alps. These are viviparous species, which give birth to between one and five already metamorphosed offspring.

In the scanty perinival meadows it is sometimes possible to find the small viviparous green lizard (*Zootoca vivipara vivipara*), which gives birth to fully-formed young. In these extreme environments it is constantly stalked by adder (*Vipera berus*), which seeks refuge among the rocks, grass cushions and contorted shrubs.

The snow finch (*Montifrigilla nivalis*) is a quite large Alpine song bird (17-18 cm) which has a close and constant relationship with snow. During the winter, it is easy to watch it on the snow-covered surface, often along ski slopes and, when the snow melts, it frequents the melting edges in search of invertebrates on which to feed. Characteristic of this species are its strikingly black-and-white wings, more extensively white in the male, and tail. Its bill is yellow in winter, turning black in spring. Snow finches tend to gather and walk about on the ground in lively groups. During summer, they reach higher altitudes than in winter, up as far as the snowline, and are generally to be found above the tree-line in summer, where they frequent open rocky areas. Nests are on the ground under rocks or in cracks. This bird's varied diet includes berries, buds and insects. Its distribution area covers all the large mountain ranges of Eurasia, from Spain to Mongolia. In Europe, it is widespread in the Pyrenees, Alps, Apennines and Balkan highlands. In Italy, it populates the Alps and higher mountains of the central Apennines in the Marches, Latium and Abruzzo.

Less conspicuous, but with similar habitat preferences is Alpine accentor (*Prunella collaris*). This species, of the same size as the snow finch, speckled grey-brown on the back with russet flanks, nests among bushes and rocks, and tends to congregate in small groups on the ground, where it feeds on plants and insects. It inhabits the mountains of central-southern Europe and Asia at high altitudes, and its distribution in Italy follows that of the snow finch, comprising the entire Alpine range and high peaks in the central Apennines.

Snow finch (*Montifringilla nivalis*)

Alpine accentor (*Prunella collaris*)

Ptarmigan (*Lagopus mutus*) is the snow bird *par excellence*. This grouse, just over 35 cm in length on average, turns almost completely white in winter. The feet are also covered in white down; only the tail stays black, but remains hidden when the bird is on the ground. In the male, a thin black line runs from the bill to just above the eye. In summer the male is mostly greyish-brown with white wings and belly, with a prominent red wattle over the eye. The female is also brown, but more rufous than the male.

The habitat of the species is associated with snow. Camouflaged on snow-covered ground, it can escape predators, especially eagles, but also other raptors and foxes. It lives above the treeline throughout the year, in open areas with rocks and shrubs mainly between 2200 and 2800 m. It prefers protected snow-beds, moraine soils and tracts of discontinuous herbaceous vegetation, where it finds the plants on which it feeds. These include dwarf willow, high-mountain heaths (cowberry, crowberry, Alpine strawberry-tree, creeping azalea and heather), saxifrages, and thyme, of which it eats the buds, twigs, leaves, flowers and fruit, depending on seasonal availability, plus the occasional insect.

Ptarmigan is a monogamous species and nests on the ground, where the female lays 6-8 eggs, sitting on them for three weeks. Courtship begins in May, when the male displays his tail, enlarges his wattle and sings. In late autumn, ptarmigan tend to become gregarious and form flocks of many families, which remain together until the following spring.

Ptarmigan (*Lagopus mutus*)

The geographical distribution of ptarmigan is also connected with ice and snow. The species is widespread in the cold regions of Eurasia and North America, including Greenland and Iceland, the Alps and Pyrenees, with a classical scattered boreal-alpine distribution which became fragmented after the Ice Ages.

Mountain hare (*Lepus timidus varronis*) with its white winter livery, is well-adapted to life on the snow, but is not exclusive to high altitudes. It is similar to brown hare (*Lepus europaeus*), but has shorter ears and tail and the coat colour is less contrasting. Its gait is also different: it runs a little more slowly and with less frequent and noticeable spurts of speed.

Seasonal colour change is a characteristic of mountain hare. In summer, the dominant colour of the upper parts is speckled greyish-brown, with white lower parts. Cheeks, nose and outer paws are reddish, the tips of the ears are black. In winter, this hare becomes entirely white or pale grey, but always with black ear tips. Adaptations to snow-covered environments, as well as colour, include paws densely covered with fur, strongly splayed toes and the habit of allowing itself to become entirely covered by snow during heavy snowfalls.

The geographical distribution of mountain hare includes the Alps, northern Europe as far as Poland, northern Russia, Siberia, Mongolia and Manchuria. It is uniformly distributed throughout the Alps, with populations which are attributed to the sub-species *varronis*, smaller than the typical northern

Mountain hare (*Lepus timidus varronis*)

European size. It colonises altitudes between 1200 and 3500 m, rather lower down in winter. It frequents open conifer and broadleaf woodlands, especially in summer, the shrubs of the sub-Alpine belt, Alpine meadows, and sometimes the nival belt. It is prevalently a species of dusk and the night, in general solitary. During the day, it remains in hiding-places amongst the bushes, and in winter digs burrows beneath the snow in search of food and shelter.
It is essentially a herbivorous species, feeding on herbaceous plants, especially legumes, berries and fungi. It survives the winter by eating grass and the dried shoots, roots and bark of broadleaved trees such as alder, willow and birch, conifer seeds, mosses and lichens.
The altitudinal distribution of stoat (*Mustela erminia*) in the Alps is similar to that of mountain hare, in that the species is widespread between 1000 and 3000 m a.s.l.. The stoat's slim cylindrical body, with short legs and long tail, confer on it a typical appearance which it shares with the weasel.
In summer, the stoat's coat is light brown on the back, with white underparts and the inner sides of the legs. It prefers mountain environments, although it can also be found in the lowlands in the northern parts of its distribution area. From the environmental point of view, it adapts to various conditions and lives in both wooded and open areas, although it avoids dense forests, preferring scrub, the edges of woodland, and rocky environments in order to escape

Stoat (*Mustela erminea*) in summer livery

from predators, and it may also approach mountain huts. It mainly feeds on small mammals, which it hunts throughout the day, particularly rodents such as snow vole, but also nestlings and young birds, insectivores and insects. It can, in turn, be prey to larger mustelids, foxes and raptors.
Stoat has a circum-boreal distribution, populating the temperate-cold and cold regions of Eurasia and North America. In Europe, it is widespread from the far north (except Iceland) to the large southern mountain ranges (Pyrenees, Alps, Balkan highlands and the Caucasus). It was introduced into New Zealand in the late 19th century to counter the spread of rabbits. In Italy, the species is present throughout the Alps, although scattered.
Brown bear (*Ursus arctos*) also occasionally visits nival environments but, after eating large quantities of berries and nuts in autumn, it hibernates during the winter months in a den in a rock crevice or cave, where the female gives birth, usually to twins, in January or February.
The cover of winter snow at high altitudes prevents the ground temperature from dropping too low to impede all the activities of small mammals, but it remains at around 0°C, although it may fall to below -10°C above the snow. Snow vole (*Chionomys nivalis*), the best-adapted small mammal to life at high altitudes in the Alps and Apennines, remains active throughout the winter and digs tunnels under the snow in search of arthropods and molluscs. When the snow melts, these tunnels of decomposing plant material, particularly grass,

Brown bears (*Ursus arctos*) also occasionally visit nival environments

Snow vole (*Chionomys nivalis*)

are clearly visible on the ground and may terminate in nests made of the same materials. In summer snow vole digs underground tunnels.

Snow vole is a species with Eurasian distribution, extensively found in the southern European mountains from the Pyrenees to the Alps and Apennines, on the Russian Tatra, Balkan highlands and in the Near East as far as Iran and Turkestan. In Italy, it is common all over the Alps, in the Apennines in Tuscany and Emilia Romagna, and the highest summits of the central Apennines (Maiella, Gran Sasso, Monti della Laga, Montagne della Duchessa).

Tunnels dug by voles

During the final stages of the last Ice Age, snow vole was widespread throughout the Italian peninsula but, as the temperature rose, it found refuge at high altitudes, forming more or less isolated populations which may represent different subspecies. The preferred habitats of snow vole are Alpine and sub-Alpine meadows and rocky scrub between treeline and snowline, where it often shows anthropophilic behaviour close to human settlements (shepherds' huts, mountain refuges). In some areas, it may also be found at lower altitudes, down to hill level. Snow vole is mainly herbivorous, eating grasses, roots, with the occasional invertebrate.

Alpine shrew (*Sorex alpinus*) is the only insectivore which regularly inhabits high altitudes in the Alps. Identification of these small animals is always difficult, and specialised knowledge is required to distinguish between Alpine shrew, common shrew (*Sorex araneus*) and other similar species. Alpine shrew is a tiny mammal 6-7 cm in length, widespread in Europe, where it populates the Alps, Jura, Tatra and Sudeten Mountains, the Balkan highlands and the Carpathians, with isolated populations in Germany and in the Pyrenees; in Italy, it lives throughout the Alps. Alpine shrew has a wide altitudinal range from 300 to 2000 m and above, and frequents various types of environment. At low altitude, it is to be found in damp gullies close to water; higher up it lives in woods, mainly conifer, and high-altitude open areas, preferably where there are plenty of rocky places to which it can scuttle for shelter or refuge.

Conservation and management

GIUSEPPE MUSCIO · MARCELLO TOMASELLI · STEFANO VANIN · ADRIANO ZANETTI

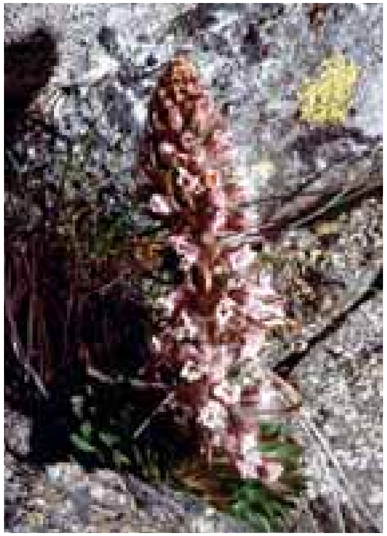
■ Conservation problems of nival flora

Alpine ecosystems, especially those at higher altitudes, are fundamentally unstable and at risk of alteration. This is mainly for geomorphological reasons, due to the continual remodelling of mountainsides by the weather. Exceptions are the plant communities growing in the fissures of rocky cliffs, where evolution can proceed practically undisturbed for very long periods, and thus act as refuge habitats for very ancient vascular plant species.

The intrinsic weakness of high-altitude ecosystems is further accentuated by the effects of global climate change which, as is widely known, is giving rise to a general warming of the air and of the Earth's surface. The consequences of this process in terms of the floristic composition of nival plant communities, already documented in ongoing research by Austrian and Swiss scientists in the Alps, will be the upward migration of more thermophilous species. In turn, the most significant phytogeographical effect of this will be that microthermal nival species, which are unable to compete with the expansion of the more aggressive thermophilous species, will become rarer and risk extinction. It is obvious that a strategy of conservation of the "original floristic purity" of nival phytocenoses, to counter changes caused by global warming, is above all a political problem, to be managed at world level, and that to undertake merely local preventive measures is a senseless operation.

A real menace to high-altitude ecosystems, which instead can be efficiently countered with local preventive or conservation measures, is the proliferation of infrastructures to serve the skiing industry. The construction of ski-lifts and building of ski-slopes often involve devastating work of stripping and excavation, as the vegetation cover is removed from huge areas. Seeds of native herbaceous species should always be used for restoration of these areas, in order to recreate vegetation as similar as possible to the original flora. Excavations also usually alter the local hydrogeological equilibrium: this can be fatal for the survival of Alpine ecosystems, such as mountain peat bogs and snow-beds, which rely on the availability of large quantities of water in the soil.

Tourists frequently exploit the highest altitudes (Mont Blanc, Val d'Aosta)



The ancient king (*Saxifraga florulenta*)

Apennine primrose (*Primula apennina*)

Some typical species of Alpine and nival ecosystems are included in protected species lists. The best-known of these, in Italy, is that produced by the Italian WWF Association, in collaboration with the Italian Botanical Society. Some bryophytes of snow-beds appear on this list, such as the liverwort *Marsupella brevissima*, and the mosses *Kiaeria falcate* and *K. starkei*, which are designated as threatened species.

Flowering plants include the ancient king (*Saxifraga florulenta*), an endemic plant with distribution confined to shady siliceous crags of the Maritime Alps, and Apennine primrose (*Primula apennina*), endemic to the north-facing arenaceous rocks in the western Apennines between Tuscany and Emilia Romagna.

The ancient king and Apennine primrose were added as priority species to the 1997 updated list of the European Union 1992 Habitat Directive and confirmed in subsequent lists (1997 Regional Red List, 2001 Red List of Italian Flora).

No Alpine or nival phytocenoses are designated as priority habitats in the Habitat Directive, EEC 92/43.

Non-priority habitat types include siliceous and carbonate debris, marked 61.1 and 61.2 in the Corine Code, and 8110 and 8120 in the Nature 2000 Code, respectively, and siliceous and carbonate rocks (62.2 and 62.1 in the Corine Code, and 8220 and 8210 in the Nature 2000 Code).

■ Effects of human activities and climate change on fauna

The nefarious effects of man's existence and his works on high-altitude environments are not so glaring and deep-seated as they are on the plains and along the coasts. There are a number of reasons for this, including the obvious difficulty of access, and many high-mountain areas are now also protected. The integrity of high-altitude environments, particularly nival ones, is nonetheless exposed to numerous threats, both global and local.

The causes of climate change and the bearing that human activities have on it are debatable, but the reduction in the extent of glaciers and ice-fields is clear for all to see, and anyone who has regularly or occasionally visited the mountains over recent decades will have direct experience of this. But the retreating glaciers have less influence on fauna than the shrinking snow-fields and frequent repetition of unusually hot summers with long dry periods, and the consequent water stress which endangers small populations in restricted habitats. Moreover, a rise in the treeline would radically transform the vegetation in many sites and consequently the animal populations which live in them.

The presence and activities of man are the factors which have most effect on high-altitude ecosystems and therefore on animal communities. Much may be written about the influx of ski installations. Artificial snow, on which

Temporary pool formed by meltwater (Central Apennines) environmentalists focused their attention some years ago, may have an impact, but it is infinitely less than that of the construction of ski-slopes, with their accompanying large-scale movements of soil to make their shape more regular. The modifications of the ground and vegetation that these operations involve is followed by alterations in the structure of the fauna, especially those which live in the soil. Although biotic diversity may even occasionally increase, the number of ecologically valuable species with small distribution areas decreases, in favour of those which are more widespread and less demanding. The threat constituted by the skiing industry, which is always localised, is in any case much less than that of the changes caused by the progressive abandon of high-altitude Alpine pastures, with the disappearance of the habit of summer livestock grazing. It is difficult to imagine precisely how the Alps and Apennines would (or will, perhaps) appear without livestock on high pastures, and what the faunal structure would be in areas where meadows have been replaced by shrubs, or even, with climate change causing the rise of vegetation belts, by woodland.

■ Climatic variations

The previous sections have briefly decribed the risks faced by the nival environment: analysing the problem from a wider perspective, the question of the survival of this habitat must be inserted in what has been defined as “global climate change”. The figure on page 29 gives a broad overview of general climate trends. However, to limit the scope of the problem to a simple rise in temperature caused by the “greenhouse effect” would be too restricting. For example, man also modifies the climate by destroying forests or creating artificial lakes. What might appear as just a small scar, such as the destruction of a wood to make way for a ski-slope or livestock pastures and fields, also has an effect on the climate.

It is undeniable that the greenhouse effect plays the most significant role: in the last few hundred years, the rise in temperature has been approximately 0.6°C per century, but in the most recent decades this has increased to around 2°C per century. The last few years spanning the millennium have also been amongst the hottest ever recorded, in Italy too.

It is these hot summers which are among the most significant factors that have led to the shrinking of glacier-covered areas and perennial snows. Future scenarios are depicted in different ways according to the various schools of thought, but it is clear that the hypotheses of advancing either towards a drier climate or towards an ice age are not incompatible. The two are connected, because it is possible for a phase of warming to be followed by a brief ice age, caused by modifications of ocean currents, and then to return to an even hotter phase. The result would be significant variations to coastlines and often very rapid mutations in the extent of ice and snow deposits, which are in any case destined, in the medium-short term, to be reduced on a global level and, in Italy, to shrink or almost entirely disappear. Global warming will involve significant climatic variations: a rise in sea level, an increase in temperatures on a regional scale (but with lowering in some areas), and a rearrangement of regional rainfall patterns, with substantial changes in their intensity, more frequent extreme events, and altered distribution of phenomena like winds, storms and hurricanes. Signs of these are already apparent.

Little has been done until now to arrest the advance of the greenhouse effect, and what has been done is merely a drop in the ocean. Even if the agreements reached in the Kyoto protocol were to be rigorously applied by all signatories, this would not be sufficient to restore natural temperature patterns: the percentage of atmospheric carbon dioxide (one of the gases responsible for the greenhouse effect) is destined to double within a century if no interventions are made and, in the most optimistic hypothesis of the Kyoto protocol being adhered to - something that is still a long way off - CO_2 will have increased by a mere 50%!

Canin glacier (Friuli Venezia Giulia) in 1989: note clear signs on mountain of ice level a few decades previously; this glacier is now even smaller

Icehouses and ice wells

Icehouses and ice wells are the last remaining testimonies to what was, in the past, originally a business activity, when ice or snow was gathered and preserved in winter and then sold in summer. It was used in many different ways, but mainly for preserving food and preparing cold drinks. The collection and sale of “natural” ice began to die out in the early twentieth century, with the appearance of the first refrigerating plants and factories, although it did continue until the middle of the century in some regions.
In Catania, for example, the snows of Mount Etna were considered a precious asset and used to make the famous sorbets or to cool wine: the sale and use of snow were banned after the Second World War for health reasons.
Snow and ice were generally stored inside stone buildings built for the purpose, although there were areas where, quite simply, accumulated pressed snow was conserved inside natural crevices or fractures in the rock.
In some cases, when conditions made it possible, the ice deposited inside natural caves was used directly; this was possible especially in Alpine areas, where many caves preserve both winter snow and fossil ice (see box on pp. 47-48).
The construction of an icehouse involved the digging of a pit 5-10 metres deep, rectangular, square or round in shape depending on the region, and generally lined with stone. The upper part of the building, usually one or two floors, was built with blocks of stone, and the roof, made of slabs or blocks, was sometimes covered with earth. The entrance preferably faced north.
Icehouses were used for preserving snow, rolled to the building in the winter months as large snowballs, or gathered in sacks and baskets. It was then compacted with shovels or poles, until ice formed. Inside the icehouse, layers of ice 20, 30 or 40 centimetres deep were accumulated, alternating with layers of straw. Ferns, leaves or hay were also used to separate the layers and for insulation. The ice was cleaned before being stored, to remove any foreign bodies which might have made it melt faster, as well as lower its value. Immediately prior to being sold, it was cut up with axes and saws, and purified using special tools (a procedure called “shaving”).
Icehouses were common everywhere, but one particularly interesting detail is that snow was also gathered in notoriously torrid areas like the plains in Apulia. Icehouses are still to be found dotted around the countryside in the Murge and Salento, though collecting and storing snow ceased at the end of the nineteenth century, when the first artificial ice-making plant in Lecce began production. Similarly, the *Domos de sa Nie* in Sardinia ceased to be functional when imported ice from Norway became cheaper.
In some regions, ice rather than snow, was gathered directly, and then stored in “ice wells”. In the Lessini Hills and the Trieste karst, for example, ice which had formed in the coldest periods (December and January) in specially built artificial basins fed by a dense network of channels conveying rainwater, was cut up into blocks. At times of maximum production by each of the dozens of ice wells in the Lessini Hills, one-and-a-half tons of ice were transported by special wagons into town every day. The ice from areas in the Trieste karst was even exported to Egypt. In some regions, selling ice was an important and high-earning business, often managed by private individuals, but sometimes controlled by monopolies which contracted out the work (as in the case of Sardinia and the Spanish government).

Ruins of an icehouse in Salento (Apulia)

Busa dal Giaz cave (Paganella, Trento): columns of ice were cut and sold

Suggestions for teaching

MARGHERITA SOLARI

■ Tracks in snow

Marmot tracks, with marmot in background

- Aims: to recognise the tracks ("spoor") of animals and understand their importance for identifying the fauna, to develop capacities for observation and comparison
- Level: schoolchildren of 8-13 years of age.
- Equipment: literature, manuals for identifying footprints or "spoor" and tracks; equipment for field trips: notebook, ruler, magnifying-glass, camera.
- Collaboration: perhaps an expert for field trips.

PRELIMINARY STAGE

1. Introduce the work in class: discuss with students the species of animals they have seen most often; compare with species shown in textbooks as being most common in the study area; emphasise how difficult it is to see shy or nocturnal animals and how to detect their presence by the traces they leave.
2. By means of class discussion, analyse the types of traces which an animal may leave: footprints, tracks and signs, food leftovers, droppings, regurgitated pellets, feathers or fur, bark-stripping, etc.
3. Encourage individual observation and description of some types of footprints in drawings and photographs, examining elements useful for it: shape of outline, size, presence of toes (1or 2; 3 in front and one at the back; 4 or 5), presence of claws; tracks of animals walking, trotting, running, and jumping.

Val Veny (Valle d'Aosta)

Ungulate tracks

Mountain hare tracks

FIELD TRIPS

4. Field trips to the country to observe the prints of animals; outing after a snowfall to compare students' footprints on fresh soft snow, beaten snow, frozen snow, prints left after walking or running (apply mathematical models to determine size, speed, etc.).

CLASSWORK

5. Study a snowfield environment, compare it with that of a glacier, and analyse physical and chemical aspects. Individual research by students on animals living on the edges of snowfields (vertebrates leave their footprints, e.g., marmot, ibex, chamois, ptarmigan, mountain hare, etc. but micro-mammals who dig tunnels also leave traces). Further study on salient points of interest of the various species, and their habits in particular.

7. Recapitulate data collected in class; study some characteristic species, with further analysis of prints, tracks, and other signs.

8. Summarise the data on a board, with a drawing of the animal, its footprint to scale, the period of the year when the animal is active, and its habits (if visible by day or not, etc.).

9. Draw conclusions in class

■ Metamorphosis of snow in snowfields

- Aims: to develop capacities for observation and analysis, knowledge of the formation and metamorphosis of snow, ability to interpret natural phenomena through the laws of physics.
- Level: students of 14-17 years.
- Equipment: relevant literature.

Note: the suggestion is limited to studying the metamorphosis of dry snow.

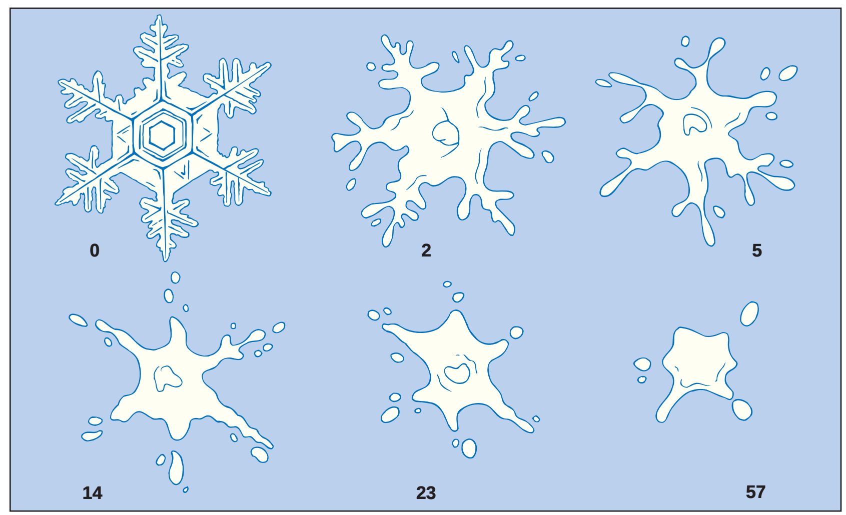
PRELIMINARY STAGE

1. Introduce work in class: illustrate the concepts of vapour tension and over-saturation with examples, perhaps in the laboratory (vapour condensation in a conical cooling flask, etc.).

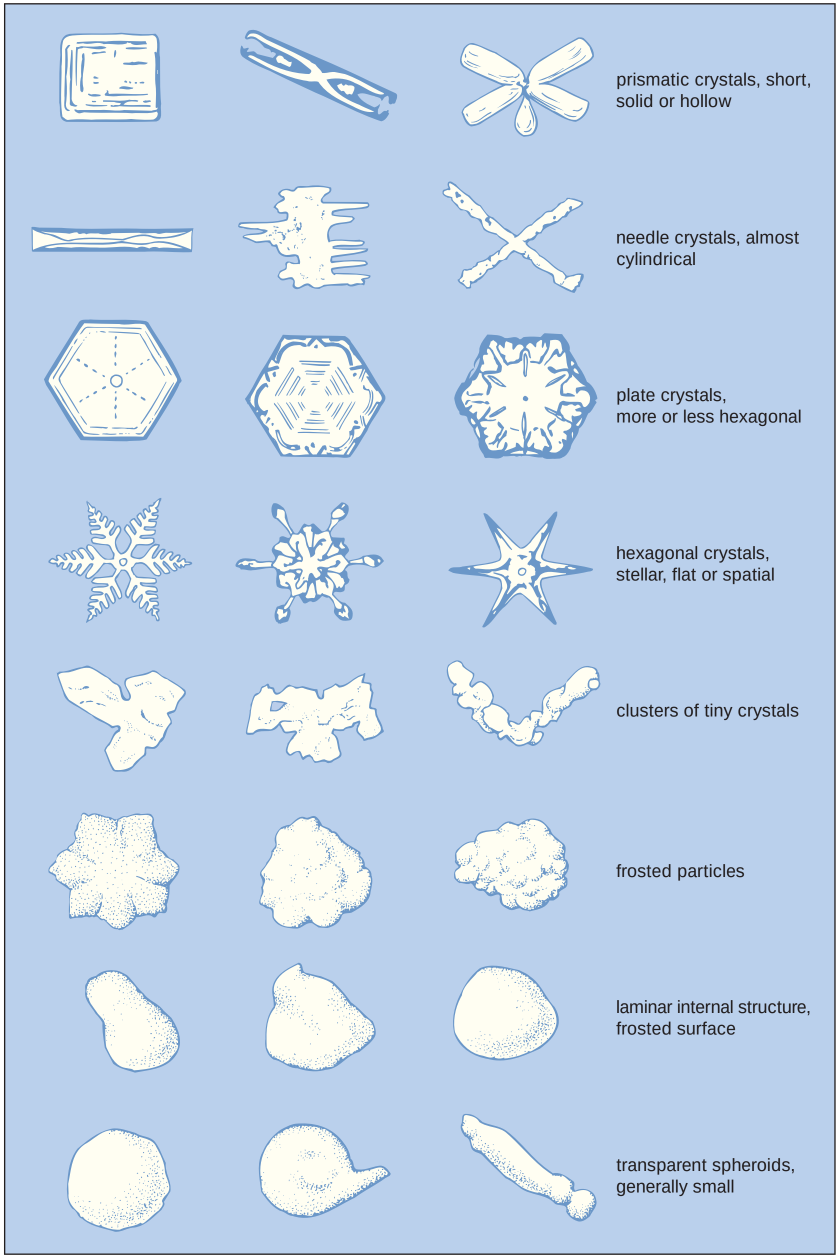
2. Involve students in a discussion on the mechanisms of formation of rain and snow; analyse the structure of the first ice crystals which form in the atmosphere; illustrate the hexagonal symmetry of ice crystals; compare geometric shapes with other natural shapes of the inorganic (permafrost soil polygons, basalt lava columns, etc.) and organic world (dendrites of ammonite shells, leaf symmetries, etc.).

CLASSWORK

3. Study the various shapes of fresh snow crystals (columns, etc.). Crystal



Snow crystal metamorphism at constant temperature over time (numbers indicate days)



Geometric model of ice crystal growth

shape depends on temperature and vapour tension: in general, little excess vapour favours slow growth, which leads to the formation of crystals in columns, whereas higher density favours more rapid growth, and complex-shaped spatial dendrites are generated. Note the fact that any shape of snow crystal may fall on any mountain range (although there is some diversity, and the snow cover in maritime climates appears to be more stable than elsewhere).

4. Study the metamorphic processes which begin immediately after crystals are deposited, due to changing environmental conditions: metamorphosis is due to the fact that fresh snowflakes in a blanket of snow are in an environment with much lower values of over-saturation than those of the atmosphere in which they were generated; this favours sublimation, with loss of water molecules from the surface of the crystal, especially from the points in which vapour tension is highest, i.e., branches and accentuated convexities. Illustrate the speed of metamorphosis, which is slower for rounded crystals with a low surface/volume ratio, and faster for dendrites.

5. Introduce the concept of compaction and later metamorphosis of snow in snowfields over the following months, caused by thermal gradient, temperature, and overloading pressure due to accumulated layers of snow (this may be generalised by stating that the sublimation process of crystals in deeper layers generates vapour which rises to the surface, and then cools and condenses around grains in the upper layers, where the vapour tension is lower).

6. Analyse the physical factors which influence the process of metamorphosis: when the thermal gradients in snow layers are high, with high temperatures and large spaces between the grains, the process is rapid and leads to the formation of angular multi-faceted grains, with steps and striations, generating, at depth, what are known as “deep frost”, composed of goblet grains. When conditions are the opposite, the process is slow and generates rounded shapes; bridges form between the grains, thus “cementing” the blanket of snow, a process which occurs less often with large geometrical grains. Altitude influences all these factors, as rarefied air accelerates recrystallisation.

7. Discuss the adhesion mechanisms of various layers of snow at different stages of metamorphosis, and their cohesion with layers of fresh snow. Mention the possibility of avalanches generated by the collapse of a deep or surface layer in given conditions.

8. Draw conclusions about the physical factors and the laws of mathematics which govern some aspects of nature.

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Glossary

> Alliance: in phytosociology, a grouping of closely related associations.
> Angiosperm: flowering plant.
> Anophthalmous: without eyes.
> Anthropophile: organism which regularly lives in or near environments created by man.
> Association: basic unit of vegetation characterised or differentiated by a given floristic composition.
> Biotic (factor): in an ecosystem, a factor determined by the presence or activity of organisms.
> Brachypterous: (insect) with abnormally small wings, flightless.
> Calcicole: organism associated with substrates with high calcium content (carbonate soils).
> Chamaephyte: a woody plant typically carrying overwintering buds at the tip of twigs or branches, 10-50cm from the surface of the ground.
> Circadian: activities which are carried out over a period of aboutr 24 hours
> Circum-boreal: species whose distribution area is limited to high latitudes in the northern hemisphere.
> Coenosis: association of organisms living in the same environment.
> Coprophage: animal that feeds on excrement (usually of mammals).
> Cryoclastic: process of disaggregation of rocks (cracking, shattering) caused by freeze-thaw cycles.
> Cryonival: referring to phenomena typical of cold climates; correlated to ice and snow.
> Cryo-protective: protecting against freezing.
> Cryptogam: plant that reproduces by spores.
> Deflation: transport by winds of small granules, soil particles and/or other small debris.
> Denaturation: alteration in the structure of a protein, which does not change its composition or amino-acid sequence.
> Depigmentation: reduction or total disappearance of pigment usually seen on the external surface (exoskeleton, skin) of an animal, often associated with life underground.
> Dicotyledon: angiosperm with two embryo leaves and broad adult leaves with branching veins.
> Diploid: organism with two identical chromosome sets in each cell.
> Dormancy: inactive phase during which growth and developmental processes are deferred.
> Edaphic: pertaining to soil.
> Endemic: species with a distribution area restricted to a particular geographic region.
> Endogeal: animal whose entire life-cycle is conducted in the soil.
> Frost wedging or gelifraction: fracturing of rock by expansion caused by water freezing in planes of weakness or in pore spaces
> Geliturbation: propensity of rock to breakdown by gelifraction.
> Hygrophilous: growing in or preferring moist habitats.
> Insolation: amount of solar radiation reaching the Earth’s surface.
> Lapidicolous: animal that lives or regularly seeks refuge beneath stones.
> Lithology: study of the physical, chemical and structural characteristics of rocks.
> Metamorphic rock: aggregate of minerals formed by re-crystallisation (without fusion) of pre-existing rocks after changes in pressure and/or temperature.
> Monocotyledon: angiosperm with one embryo leaf and adult leaves with parallel veins.
> Nival: pertaining to snow.
> Pabulum: organic material regularly eaten by an animal species.
> Pedogenesis: process of soil formation.
> Phanerogam: plant whose reproductive organs are easily visible as either flowers or cones.
> Phylum: major animal classification unit, below kingdom and above class.
> Phytocoenosis (or plant community): association of different species living together in the same ecosystem.
> Phytophage: animal that feeds exclusively on plant material.
> Pleistocene: the first of two epochs of the Quaternary era, from approx. 1.8 million to 10,000 years ago.
> Quaternary: period of geological time, covering approx. the last 1.8 million years.
> Relict: residual geographical distribution.
> Retuse: (leaf) with a rounded or obtuse apex with a slight notch.
> Rosette: flattened, rose-like group of leaves at the base of the stem.
> Saprophage: organism which feeds on decomposing organic material.
> Solar radiation: amount of energy the sun irradiates in space, evaluated at 5.2 1024 kcal per minute.
> Stenothermal: unable to tolerate a wide temperature range.
> Symbiosis: two species living together; one cannot exist without the other.
> Taluvium (pl. taluvia): hill-slope deposit containing a mixture of coarse, rocky debris and finer particles.
> Temperature excursion (annual): difference between average temperatures of the hottest and coldest months.
> Tetraploid: organism with four times the haploid number of chromosomes.
> Thanatosis: defensive behaviour, in which an animal feigns death in order to avoid danger or to escape a predator.

> Thermophile: organism which grows best at relatively high temperatures.
> Vascular plant: plant (ferns or seed-bearing) containing conducting (or vascular) tissue.

List of species

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