MIGRATING HERD OF CARIBOU was photographed from the air as the animals rested on snow-covered ice of a Canadian lake. In the fall they migrate from the open tundra to the forested taiga, where soft snow-cover permits them to dig down to their fodder.

Animals in the Snow

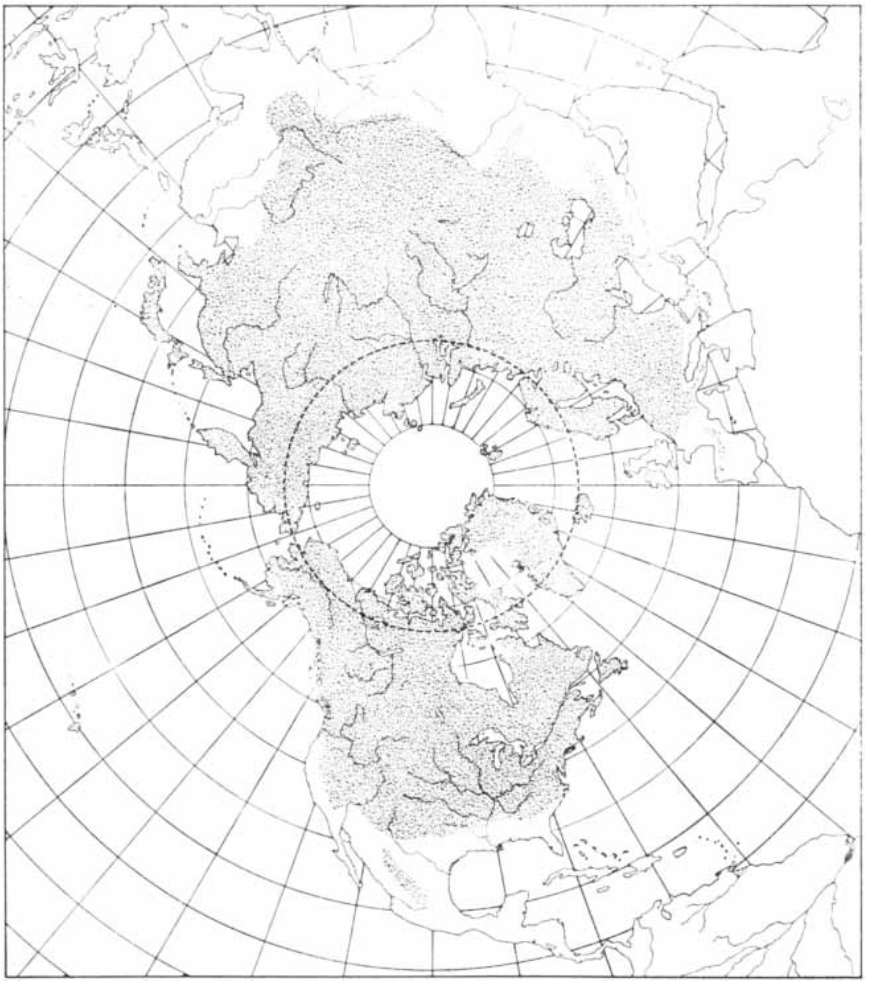
Animals that live in regions where snow persists for nine months of the year are adapted to various kinds of snow cover resulting from interaction of weather, plants and the contour of the land

by William O. Pruitt, Jr.

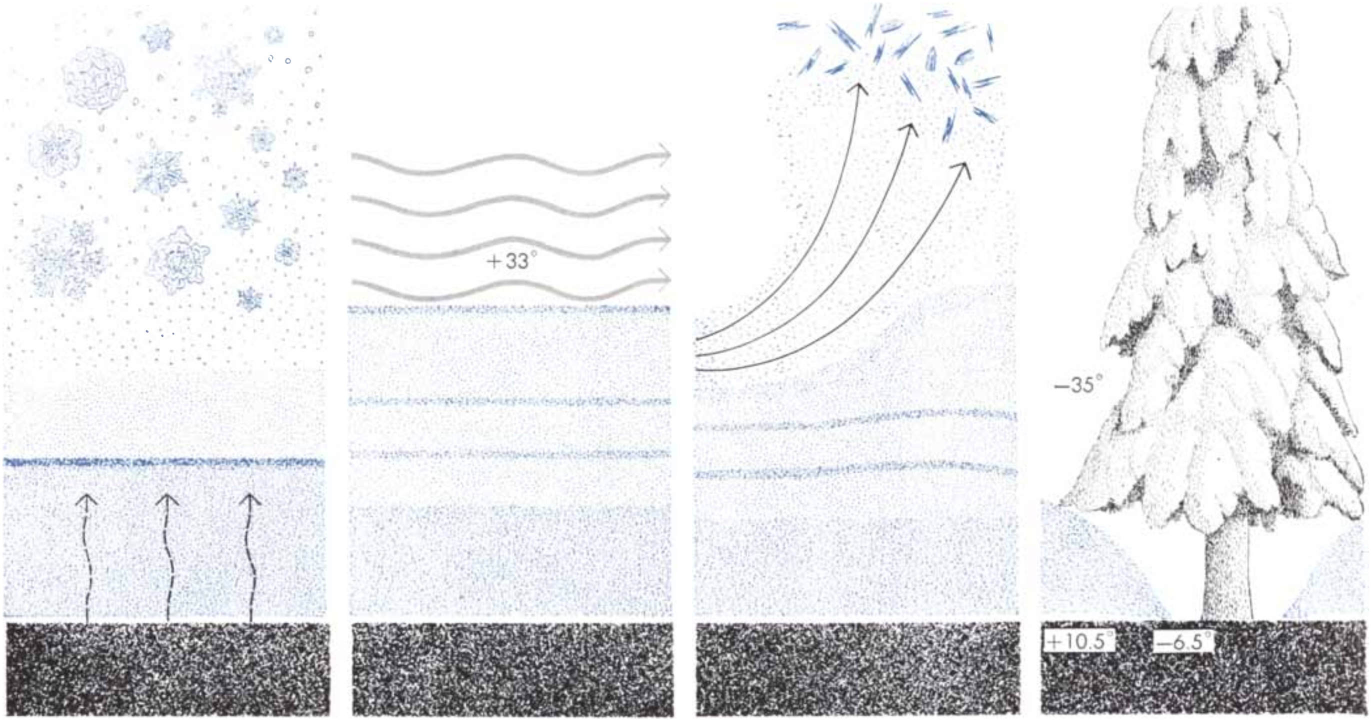
If snowflakes were rare objects, generations of graduate students would doubtless have received degrees for research into the properties and potential uses of snow. As it is, some tens of billions of these beautiful crystals of frozen water-vapor pile up in each square yard of snow of even moderate depth. In greater or lesser depth snow covers more than half of the land area of the Northern Hemisphere at some time during the year. In centers of civilization it is welcomed with shovel and snowplow; labor and equipment are speedily mobilized to clear it from sidewalks, streets, driveways, highways and airstrips. The very abundance of snow seems to have suppressed almost all but this negative interest in getting rid of it as quickly as possible. In the literature of the sciences that ought to be concerned there is little to suggest that snow is a major element in the environment of life and that it is one of life's most interesting provinces.

To our way of thinking snow would seem principally a hindrance to the locomotion and food-getting of animals. The onset of winter is the occasion for spectacular southward migrations of birds and mammals. But many creatures, by anatomy and behavior, have become adapted to survive in snow cover that may persist for nine months of the year. Some have developed snowshoes or stilts that permit them to move freely above the snow. Others have found refuge beneath the snow cover and there have occupied a dark, damp and silent world with a constant climate warmer than that of the world above.

The biologist who sets out to study the role of snow in the life history and distribution of animals must first learn something about snow itself. A snow cover is by no means simple and homogeneous. The snow cover varies greatly in texture and structure from place to place and presents sharply contrasting environmental situations. On this diverse subject the wisest instructors are the subarctic Indians and the Eskimos. Long ago they fashioned quite different technologies to take advantage of the special properties of the snow cover in the regions they inhabit. They each succeeded, for example, in making snow do the service of the wheel. On the wind-hardened snow of the open Arctic tundra the Eskimo sled, or "komatik," rides

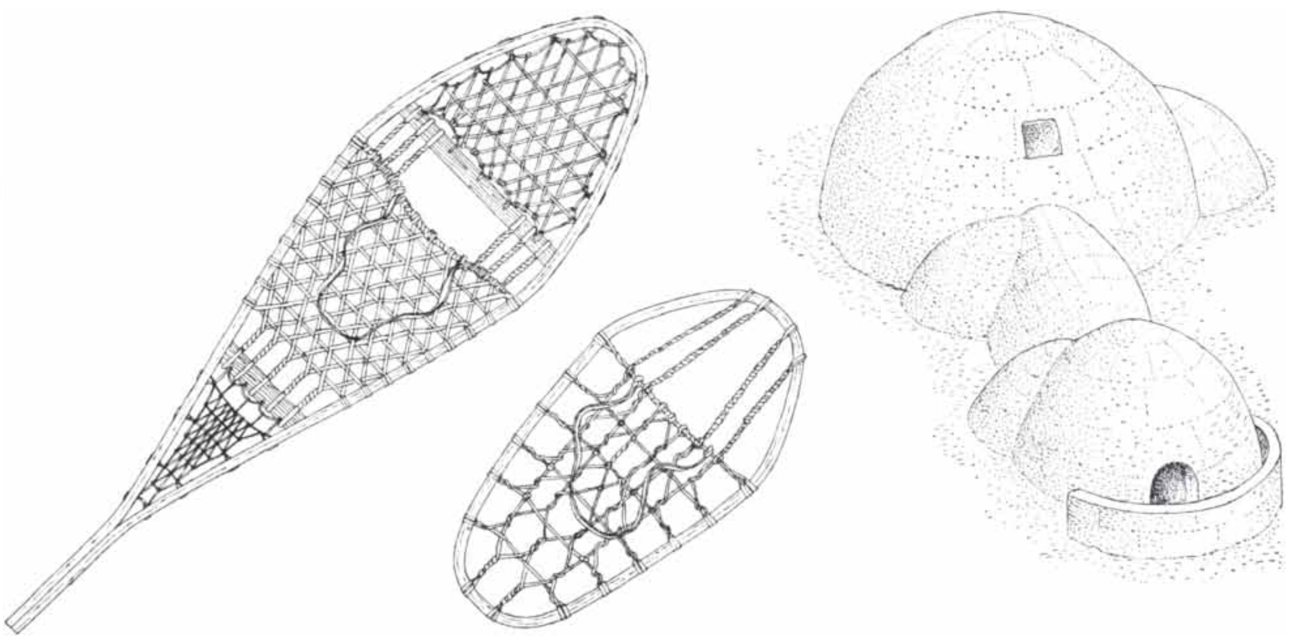


SNOW COVER lies at some time in the year on more than half of the land mass of the Northern Hemisphere. The limits of the snow-covered (*shaded*) area are approximate.

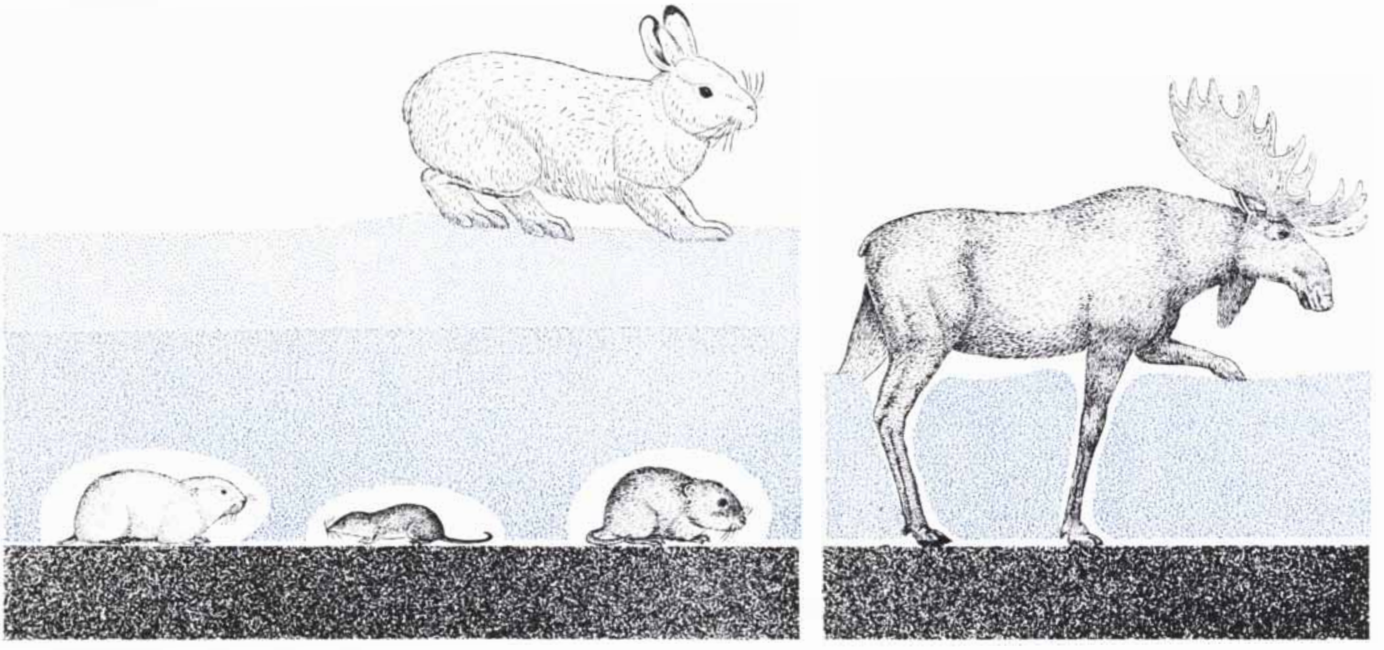


CHARACTER OF SNOW COVER varies with weather as it accumulates. The first snow is compressed by later falls (*shaded layer at left*). Warm, moist winds may thaw the top centimeter (*second from left*) which freezes to a thin, dense crust. Cold, dry winds break up the flakes (*third from left*) and lay down a "wind crust" of more densely packed snow. Trees, catching the snow in their branches, cast a "snow shadow" on the ground. The ground temperature in the shadow is lower than that under the insulating snow cover.

upon runners, and is unsurpassed in lightness, ruggedness and ease of pulling. For the thick, fluffy snows of the subarctic forest, or taiga, where the komatik would bog down, the Indians created the runnerless toboggan. The Eskimos built snug houses quickly and easily from roughly shaped blocks of the hard tundra snow, though many of them have now lost the art. To build a snow house in the soft taiga snow the Dindye or Kutchin Indians of Alaska first heaped up a huge mound, allowed it to harden or "set," and then hollowed out a cavern inside. On the snow-covered tundra the Eskimo can walk almost anywhere without sinking, but in the forest the Indians had to devise snowshoes; small ones with coarse-meshed webbing for relatively dense snow-cover and long, broad ones with fine-meshed webbing and turned-up tips for a thick cover of light snow. The rich lore of snow that underlies such ingenious adaptations is reflected in the



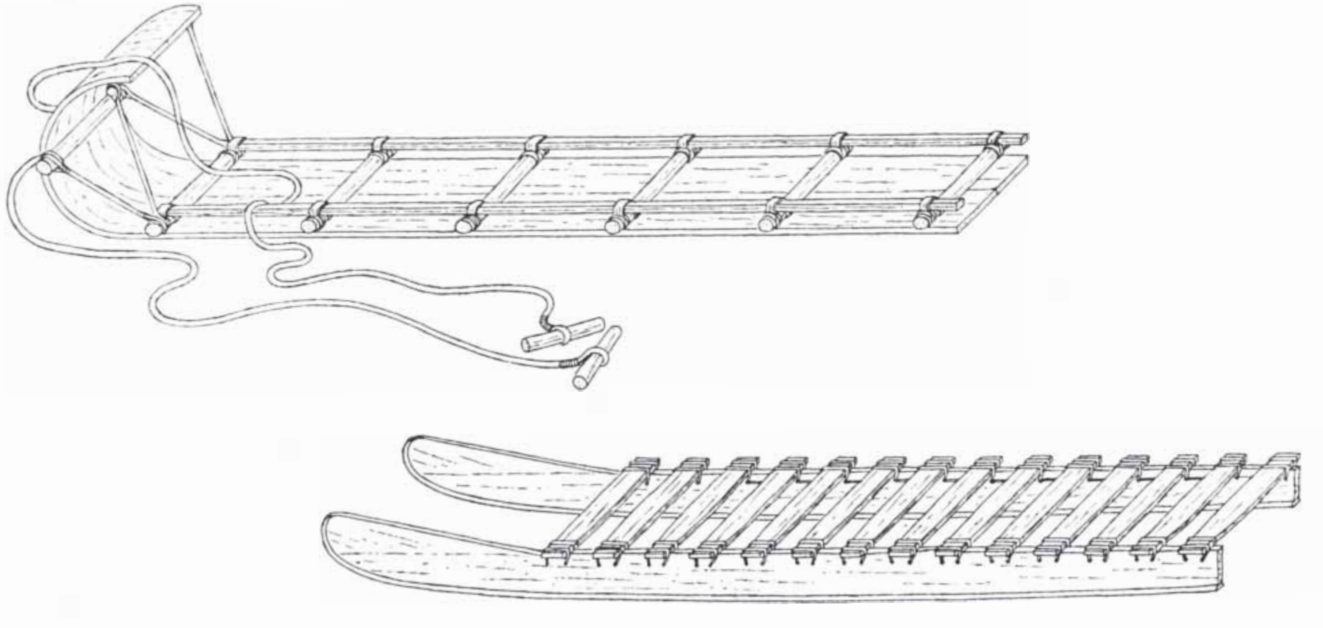
TECHNOLOGICAL ADAPTATION of Indian and Eskimo reflects the different quality of the tundra and taiga snow cover. To walk upon the light, fluffy snow of the taiga country, Indians must use snowshoes: large shoes with fine-mesh webbing for soft, deep



ADAPTATION TO SNOW is achieved by three principal routes. The varying hare has developed "snowshoes" and so travels on top of the snow. The moose is able to manage fairly deep snow on its long "stilts." Smaller animals such as the lemming, shrew and vole *(left to right)* live under the snow, finding there a damp environment with a relatively constant temperature that never falls far below freezing. The heat loss due to the high surface-to-volume ratio of these small animals would cause them to perish above the snow.

languages of the northern peoples. Each of these languages offers concise words to designate particular aspects of snow which in English call for cumbersome descriptive phrases [*see glossary on page 66*]. I have found many of these words more suitable than the "official" meteorological terms for specifying snow conditions in their relationship to the life of animals that inhabit snowy regions.

The variations in snow cover begin with the formation of the snow as it falls. In temperate and cold-temperate climates, as atmospheric moisture sublimes directly from the vapor to the solid state, the snowflake builds up as a six-armed star or hexagonal plate with a thickness of about .1 millimeter and a diameter ranging from one to five millimeters. Through aggregation as they fall, such snowflakes may form extremely complex structures. In the arctic or sub-



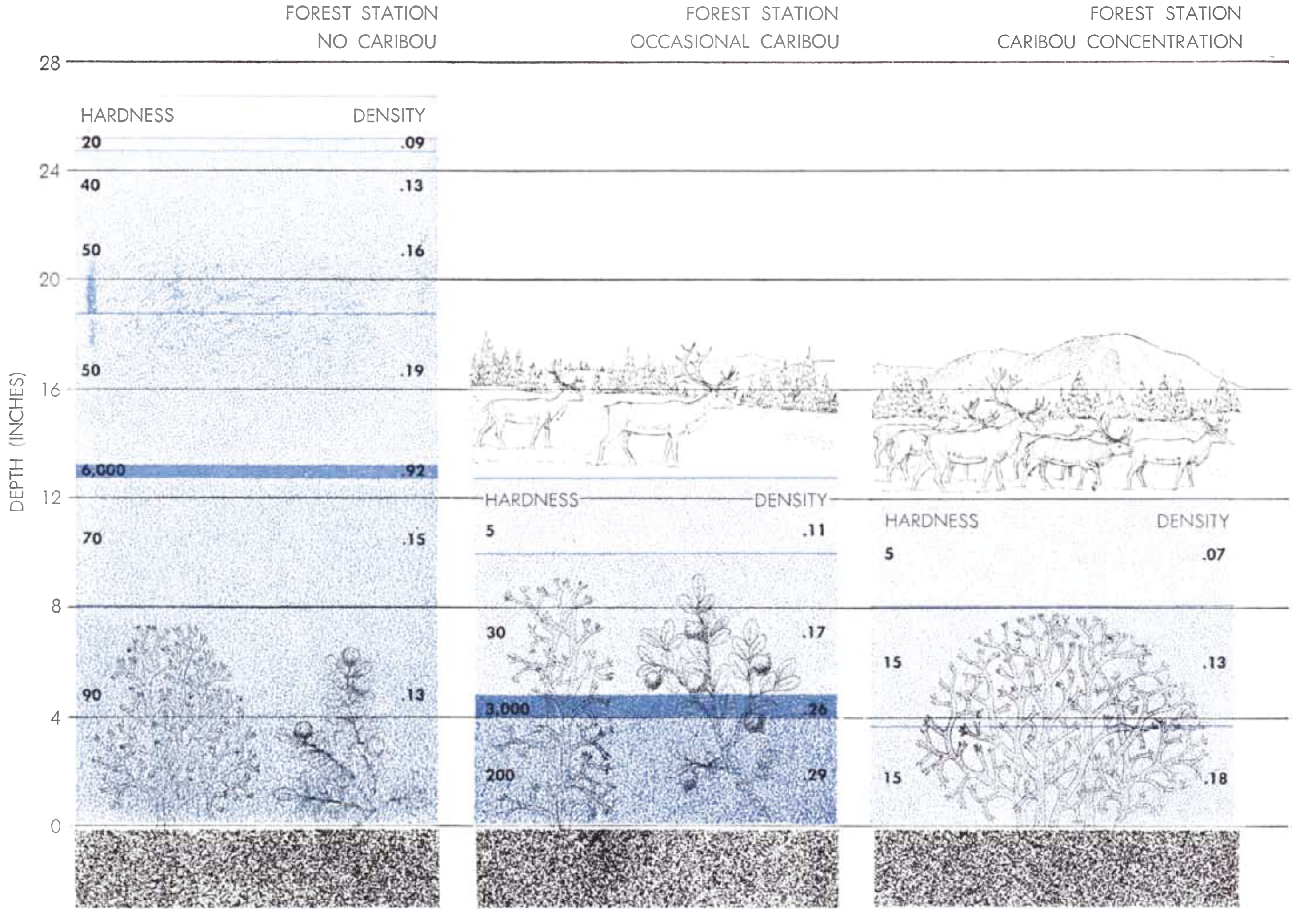
snow; smaller shoes with wide-mesh webbing for denser snow. From roughly carved blocks of hard, dense tundra snow Eskimos build igloos. The Indian toboggan is adapted to the soft taiga snow; the Eskimo "komatik" rides on runners on top of tundra snow.

arctic, snow falls more frequently as needles or tiny prisms, ranging in length from .1 to three millimeters and in diameter from .01 to .2 millimeter. From the moment they come to rest on the earth or upon snowflakes that have preceded them, the delicate stars and flakes change their shape.

The taiga snow, on which my work has centered, may best be visualized as an emulsion of air and ice, with the volume of air far exceeding that of the ice. New-fallen taiga snow may have a specific density only 5 per cent of that of water. Beneath the snow cover, as a rule, the soil is warmer than the air through which the flakes have fallen. Heat and moisture therefore flow upward from the soil through the snow. These temperature and vapor-pressure gradients play a crucial role in the history of the cover. Through sublimation, molecules of water leave the attenuated tips and corners of the flakes below and attach themselves to the tips of flakes above, which are colder because they are farther from the soil. In this process the larger and more massive flakes also grow at the expense of the smaller and more delicate ones. Eventually the bottom layer of the cover assumes a coarse granular structure, the so-called depth hoar—"pukak" in the language of the Kobuk valley Eskimos of Alaska. The snow particles next to the ground may in time be completely eroded away, leaving a vacant space with fragile, lattice-like walls and roof.

As the cover thickens with successive falls, its lower layers are compressed. Each snowfall, originating in a unique sequence of meteorological events, is somewhat different from all others. Thus each layer is made of a different type of flake or grain and has a different thickness, hardness and density. The passage of a warm, moist air-mass, bringing thawing temperatures and perhaps even a light rain, will increase the moisture content and density of the uppermost centimeter or so of snow. The succeeding cold air-mass will freeze the moisture, and the snow cover will now possess a hard, dense top-layer, or even a crust of ice. This layer may be buried by subsequent snowfalls. If it is dense enough, it may be impervious to the passage of air and water vapor and so will cause a change in the steepness of the moisture and heat-flow gradients in the cover. Marked fluctuations in the air temperature during the accumulation of the cover will thus set up complex gradients and a succession of ever changing densities and hardnesses within.

Later in the winter a windstorm may sweep over the snow. Reaching down through the sheltering spruce trees of a taiga the wind picks up the surface flakes and tumbles them about, abrading their delicate points and reducing the flakes to shattered remnants. With their smaller size and simpler outlines, the particles nest more closely together, forming a hard, dense layer. If this reworking of



DISTRIBUTION OF CARIBOU is determined by the character of the snow cover. The hardness of the layers in the cross sections of snow is measured by the weight (in grams) that can be supported by a square centimeter of the snow. The density is relative to water;

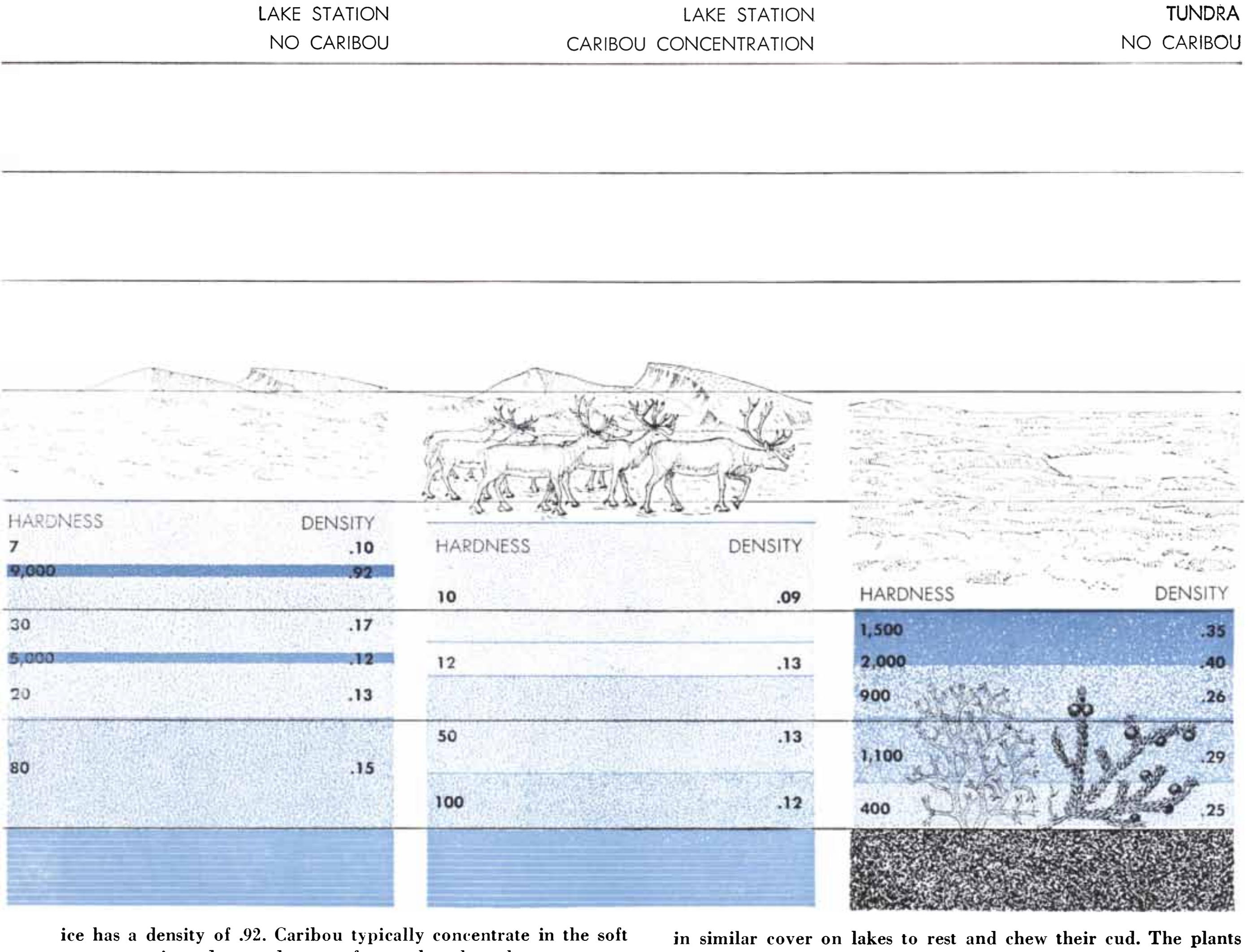
the cover is confined to the surface, it forms a "wind slab." If it involves the entire depth of snow, as happens regularly on the tundra, the cover is transformed into a hard, dense mass ("upsik") capable of supporting the weight of a fox, wolf, caribou or man.

As the snow whispers down through the spruce trees, a significant portion of it remains caught in the branches. The snow that clings to the trees ("qalí") often accumulates in quantities sufficient to bend and break mature spruces. Indeed, there is evidence that in the interior of Alaska breakage by qalí initiates the cycle of forest succession that gives the taiga there its characteristic mosaic of evenly aged stands of spruce interspersed with stands of variously aged willow, alder and aspen. With so much snow caught in the branches of the spruce there develops around the base of each tree a bowl-shaped depression in the cover, called a "qámaniq." The soil may be bare at the trunk, and the snow gradually increases in depth outward from the tree. At the tips of the branches the "snow shadow" ends, and the depth of the snow increases abruptly.

As the days lengthen in the spring, sunlight striking down through the trees melts the top layer. Upon freezing at night, the soggy surface forms a "sun crust," or "siqoqtoaq." In high altitudes and latitudes, where the coming of spring brings lengthening periods of intense sunlight with the air temperature still far below freezing, the surface flakes are transformed into long vertical spicules, called ablation needles or "qulu."

For most birds and several of the larger mammals the snow cover means deprivation of food supply. Their behavioral response to this ecological challenge is to flee the country that is so ideally suited in the spring and summer for their reproductive period, the most vulnerable in their life cycle. Investigation has shown that in most cases these animals can withstand the prevailing winter temperature of the regions they abandon, if they are provided with sufficient food. It must therefore be their inability to procure food from under the snow that induces their mass exodus. Among birds the migratory species are principally insect-eaters and ground-feeders; among mammals the most notable migrators are the elk and the gregarious caribou.

I have found that the winter distribution of caribou is quite precisely regulated by the character of the snow cover. Most of them abandon the tundra and its hard-packed snow-cover in the autumn and migrate to within the tree line. Aerial surveys of wintering bands of caribou, combined with on-the-spot analyses of the snow cover, show that these animals concentrate where the snow is soft, light and thin, permitting them to dig through it easily to uncover the food below. These areas are bounded, as if by a fence, by areas where the snow is hard,



ice has a density of .92. Caribou typically concentrate in the soft snow-cover in and around spruce forests, but they also congregate in similar cover on lakes to rest and chew their cud. The plants across the bottom of this illustration are not drawn to scale.

ENGLISH	KOBUK VALLEY ESKIMO (ALASKA)	DINDYE (FORT YUKON, ALASKA)	CHIPEWYAN (NORTHERN ALBERTA)
SNOW	ANNÍU	ŽA	SIL(CH)
SNOW THAT COLLECTS ON TREES	QALÍ	DÉ-ŽA	DE-CHÉN-KAY-SÍL(CH)
SNOW ON THE GROUND	APÍ	NON-KÓT-ZA	SIL(CH)-DE-TRÁN
DEPTH HOAR	PUKAK	ŽAI-YA	YATH(K)ÓNA
WIND-BEATEN SNOW	UPSIK	SETH(CH)	SIL(CH)-T(CH)RÁN-AL
FLUFFY TAIGA SNOW		THEH-NÍ-ZEE	YATH-THEY-YÉ-REE-LAY
SMOKY SNOW OR DRIFTING SNOW	SǏQÓQ	ZA-HE-ÁH-TREE	NIL(CH -SEE-NI-(K)OTH
SMOOTH SNOW SURFACE OF VERY FINE PARTICLES	SALUMÁ ROAQ		
ROUGH SNOW SURFACE OF LARGE PARTICLES	NATATGÓNAQ		
SUN CRUST	SIQOQTOAQ	ŽA-ES-ČH(A	NA-HÓ-T(CH)RAN
DRIFT	KIMOAQRUK	ZA-KÉ-AN-É-HAE	YATH-NÉE-ZUS
SPACE FORMED BETWEEN DRIFT AND OBSTRUCTION CAUSING IT	ANMANA		
SHARPLY ETCHED WIND-ERODED SNOW SURFACE (SASTRUGI OR SKAVLER)	KAIOGLAQ		
IRREGULAR SURFACE CAUSED BY DIFFERENTIAL EROSION OF HARD AND SOFT LAYERS	TUMARÍNYIQ		
BOWL-SHAPED DEPRESSION IN SNOW AROUND BASE OF TREES	QÁMANǏQ	(ZH)E-QUIN-ZEE	DAY-CHEN-YATH-DO-DEE
SNOW DEEP ENOUGH TO NEED SNOWSHOES		DET-THLO(K)	YATH-THAY-T(R)ÁN-AI(CH)-HÁ
SPOT BLOWN BARE OF SNOW		SI(CH)	OH-BÉH
AREA OF DEEP SNOW THAT PERSISTS PERHAPS ALL SUMMER		ZA-KAY-TAK-KOK	YATH-THAY-(ÁN)

TERMINOLOGY OF SNOW is enriched by precise words from Eskimo and Indian languages. Each word specifies a snow condition that often requires a full phrase in English.

dense or thick. The critical hardness, expressed in terms of capacity to bear weight, seems to be around 60 grams per square centimeter. The corresponding specific density ranges upward from 16 per cent of that of water to that of ice (which of course has a density somewhat less than that of water), and the fence-forming depth of snow is about two feet [*see illustration on preceding two pages*]. In the course of a winter the caribou herds may be seen to move about in accord with the shifting of the fences of unsuitable snow.

In contrast to the caribou, the moose is an exemplar of anatomical adaptation. Its long legs reach down through the snow cover to the firm ground beneath and carry its belly well above the surface. When the snow cover attains a thickness of about three feet, however, stilts no longer suffice. At such times the moose packs the snow in trails or "yards." The alternative to the stilt is the snowshoe, and the classic example of this adaptation is the oversize feet of the varying hare (*Lepus americanus*). But wherever the hardness and density of the snow fall below a critical level, the hare too turns to packing the snow to form regular trails and runways.

Temperature as well as snow cover is an important factor determining the behavior of animals in the northern winter. Only the larger mammals—the hare, fox, wolf, lynx and moose—are metabolically able to withstand the extremes of cold and live above the snow surface. Smaller mammals such as shrews, voles and lemmings have such a small body mass with respect to their heat-dissipating body surface (and such comparatively inefficient fur) that their metabolism cannot maintain normal body temperature. Their survival in the subarctic winter climate is made possible only by the behavioral adaptation that causes them to seek shelter under the taiga snow cover.

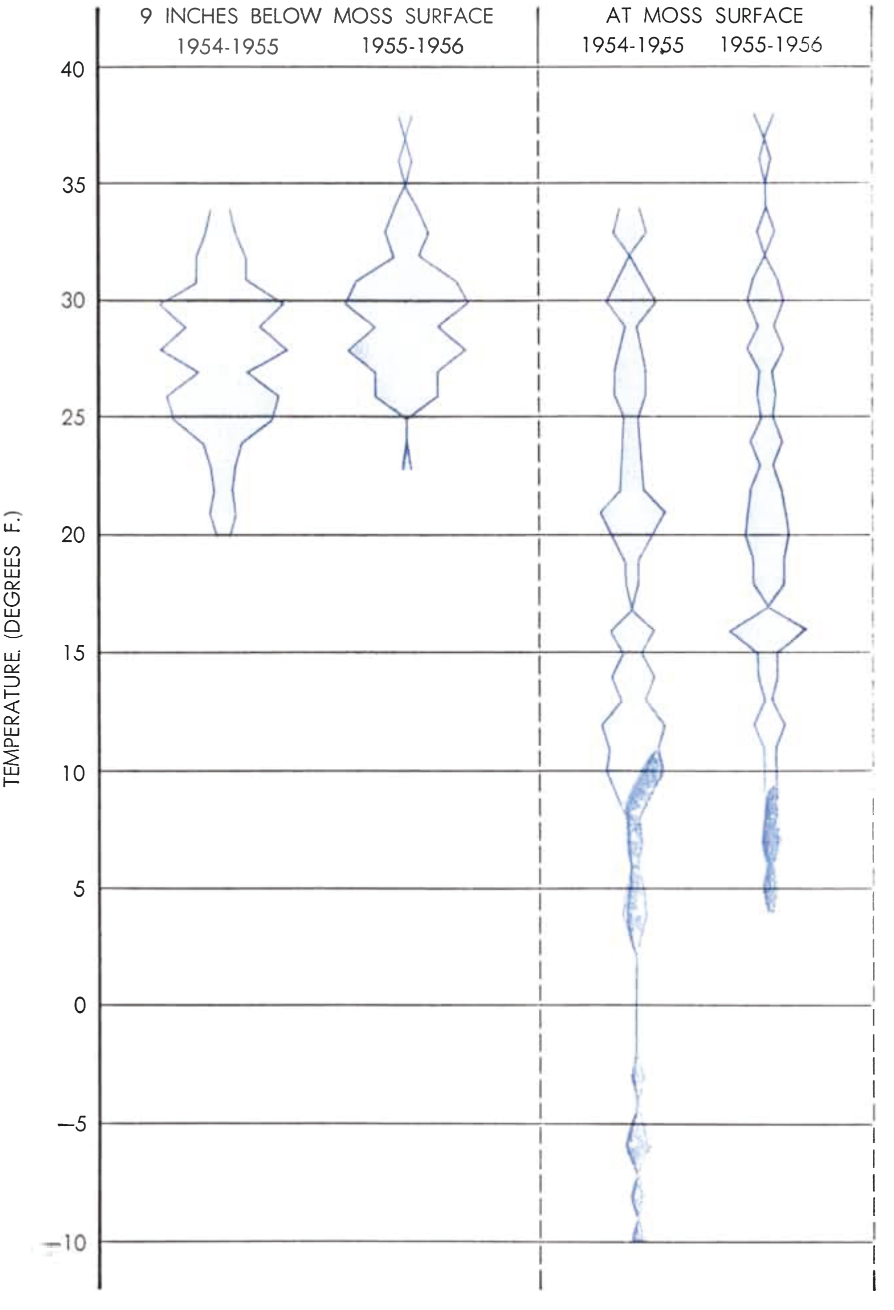
The snow is such an effective insulator that the temperature of the mossy floor of a mature spruce forest seldom drops below 20 degrees Fahrenheit, even though the air above may fall to 50 and 60 degrees below zero F. In the interior of Alaska I was once unable to detect any temperature change during a period of nine days at a spot in the forest floor under a cover of two and a half feet of snow, even though the air temperature above fluctuated between 24 degrees above and 28 degrees below zero F. Freshly fallen fluffy snow has a thermal conductivity of only .0002 calorie per square centimeter per second through a gradient of one degree centigrade. Thus vegetation, small mammals and hibernating or pupating insects are protected from the violent temperature changes that characterize the climate above the snow cover.

Small mammals disappear below the surface in the autumn when the snow cover has built up to a depth of about six inches. The temperature of the moss and the soil at this time ceases to follow the fluctuation of the air temperature. A. N. Formozov, the distinguished Russian naturalist, has observed the same threshold in the activity of small mammals of the taiga in the U.S.S.R. In the cycle of the seasons the period between the onset of subfreezing temperatures and the development of the snow cover to the critical thickness undoubtedly gives shrews, voles and lemmings their severest trials.

Although the temperature under the snow cover remains stable from day to day, the temperature of the forest floor varies strikingly from place to place. One would expect, for example, that the qámaniq under the snow shadow of the spruce would be cold spots. I have found this to be true: With the air temperature at 25 degrees below zero, the soil temperature one inch below the surface was 2.5 degrees below zero at the base of a tree and 9.5 degrees above zero just beyond the qámaniq. Later in the winter, with the air temperature at 33 degrees below zero, the temperatures were respectively 6.5 below zero and 10.5 degrees above zero. The activity of the small mammals under the snow reflects this pattern of temperature at the forest floor. Sampling of the population by means of live traps under the snow shows that red-backed voles avoid the qámaniq in favor of those parts of the home range under full snow-cover. The Russian worker N. V. Bashenina has recently shown that carbon dioxide gas sometimes accumulates under a taiga snow cover in concentrations sufficient to cause voles to construct "ventilator shafts" up through the snow. At the openings of these shafts the voles are exposed to predation by owls. Formozov believes that it is this habit of the vole that permits certain species of owls to survive the subarctic winter.

Since snow is an excellent insulator against sound, the winter environment of the voles and shrews is silent. It is also dark, because a one-foot snow cover transmits only 8 per cent of the incident light and a two-foot snow cover only 1 per cent. The air beneath the snow is calm and essentially saturated with moisture. Hovering between 15 and 25 degrees above zero for most of the winter, the temperature varies quite slowly. The subnivean environment is thus strangely removed from the subarctic winter above the snow, with its brilliant days and moonlit nights, its relatively sudden and violent temperature changes, its winds and forest noises. By diverse bodily and behavioral adaptations the small mammals of the taiga are able to utilize this environment and survive the northern winter. Without the snow cover the region would be deprived of most of its mammals.

There is one mammal, the familiar red squirrel (*Tamiasciurus hudsonicus*), whose size and weight place it just between the two groups that live respectively above and below the snow. When the deep cold of the subarctic winter settles over the spruce forests of the Alaskan interior, the red squirrels shift the locus of their activity from the trees above the snow to subterranean tunnels below. For weeks at a time no red squir-



UNDER-SNOW TEMPERATURES recorded through two winters at an Alaskan station show the relative stability established by the insulation of the snow. The horizontal dimension of the colored areas indicates the frequency with which each temperature occurred.

LAKE SNOW, contoured like sand dunes by the wind, has a relatively high density due to abrading and breaking up of the snowflakes, which permits them to pack closely together.

TAIGA SNOW, sheltered from the wind, tends to be light and fluffy and clings to the branches of spruce trees. Beneath the trees at left can be seen the snow shadow or "qámaniq."

rels will be seen in the forest. The critical temperature that sends them from the environment of the moose, fox and lynx into the environment of the shrew and red-backed vole seems to lie between 25 and 30 below zero.

We are indebted to Formozov for a scheme that classifies mammals on the basis of their adaptation to snow. Those animals that are unable to adjust to snowy conditions he calls chionophobes, from *chiōn*, the Greek word for snow. In North America the pronghorn antelope, the wild turkey and the opossum belong to this category. Chioneuphores are animals such as the shrew, fox, vole, moose and elk, which can survive in snowy regions. The small, select group of animals such as the varying hare, the North American caribou and the varying or "hoofed" lemming, which possess definite adaptations for snow and are limited to snowy regions, are known as chionophiles. This ecological classification has great possibilities as a tool in zoogeographic studies and should also underlie all wildlife management programs in snowy regions.

In Alaska the distribution of the snow cover very closely follows the known distribution of glacial ice during the Wisconsin age, during which the last extensive glaciation occurred in North America. Formozov has noted a similar relationship between regions of heavy snowfall in the U.S.S.R. and the region occupied by the Dnieper and Don lobes of the glacial ice during the Würm age, which corresponds to the Wisconsin. Undoubtedly the snow-producing conditions that attended the opening of the Pleistocene Epoch contributed considerably to the wholesale extermination of the earlier Pliocene mammals. We may find here an explanation for the disappearance of such mammals as the mammoth, mastodon, antelope, and of certain species of musk ox in North America and the woolly rhinoceros and the "Irish Elk" in Europe and Asia. These animals may have been chionophobes, tied to environments that were cold but had little snow. As their semiarid arctic prairies retreated poleward before the advance of the taiga, with its deep soft snows, the doomed chionophobe species may have been trapped behind such barriers as the glacial Lake Agassiz, which reached across North America from Ontario to eastern Saskatchewan. Or they may have been caught in *cul-de-sacs* of suitable environmental conditions surrounded by ever constricting fences of unsuitable snow.

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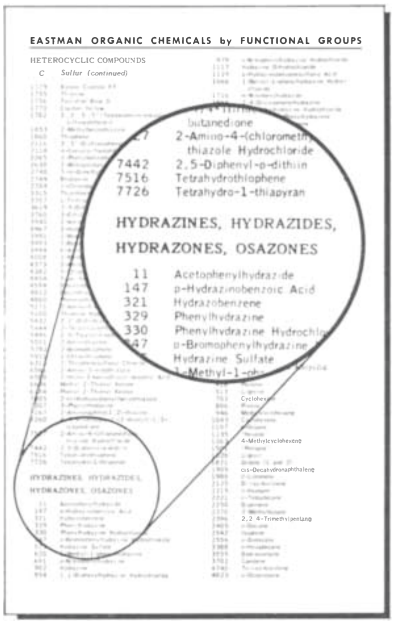
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