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"Let knowledge grow from more to more
and thus be human life enriched."

Conifer

Conifers are woody plants so named because they bear their seeds upon hard or papery scales arranged in spirals or whorls around an axis, forming a cone. Typically, they are evergreen, upright trees and shrubs, but not all members of this botanical order, Coniferales, meet that description. Some, such as various creeping junipers, never grow more than 30 centimetres tall (about one foot). Others, such as the larches and the cypress, lose their needlelike leaves annually with the approach of autumn. Even the feature of cone bearing seems to be violated by the plum-yews and podocarps, which bear seeds in olive-like "fruits" rather than in cones, and the true yews, which enclose their seeds in a fleshy cup, called an aril. All conifers, however, bear their pollen in smaller, thin-scaled cones, each scale bearing at least two pollen sacs.

General features

Conifers have been of interest to man for several centuries, because many genera are of value as lumber-producing trees. They are important also as subjects for landscaping, for producing forests that hold high recreational value in many parts of the world, and for protecting soil from excessive erosion. The smaller species are of little monetary value except as garden specimens, but many of them are efficient in reducing erosion.

Early in human history, coniferous trees became objects of admiration because of their symmetrical growth and general beauty and important as sources of fuel and of material for construction of shelters. Various peoples held certain trees or groves sacred to their deities. The early inhabitants of India worshipped the deodar cedar and considered their groves the sacred abode of saints, sages, and prophets. The Aztecs venerated various large cypress trees in Mexico, and other peoples similarly regarded local conifers.

The wood of conifers is relatively soft, straight-grained, of even texture, readily worked, and strong under stress. It is, therefore, suitable for many purposes, from general construction, cabinetwork and interior finishing to the manufacture of boxes, crates, and scores of wooden items.

DIVERSITY

Among the smallest conifers known is *Dacrydium laxifolium*, a native of the mountains of New Zealand; mature fruiting specimens of this plant have been found that were scarcely eight centimetres (three inches) tall. Many other conifers are trailing or creeping, such as some junipers, which have been selected and horticulturally developed as ground covers less than 30 centimetres tall. Some species are shrubby, with several stems arising from the root crown, and rarely exceed eight metres (26 feet) in height. Giants of the conifer forest include *Dacrydium cupressinum*, at 55 metres tall (180 feet); redwood (*Sequoia sempervirens*), many up to 90 metres tall (300 feet) with trunks up to six metres (20 feet) or more in diameter; and big tree (*Sequoiadendron giganteum*), rarely reaching 90 metres tall but with trunks up to nine metres (30 feet) in diameter.

The tallest conifers

Most coniferous trees are pyramidal or conical when young, becoming spirelike and then rounded or flat-topped in old age. Many have columnar trunks free of limbs for considerable heights. A few can send up new shoots from stumps after the tree is cut, but most of them are killed and unable to sprout after logging or severe fires have cleared an area.

Massive buttresses support a few conifers; *e.g.*, the swamp cypress (*Taxodium distichum*) and some of the larger species of *Chamaecyparis* and *Cryptomeria*. Such buttressed trees may have a circumference fully three times as great at ground level as at two to three metres (seven to ten feet) higher on the same tree. Others have no apparent swelling at the base but may have radiating roots that anchor the trees against strong winds.

Young trees of the Lawson cypress (*Chamaecyparis lawsoniana*) and several other species have downwardly sweeping branches, the lower ones often resting on the ground at their tips. Most conifers, however, have spreading to ascending branches until the tree is quite old, at which time the top is flat or rounded and the branches, confined to the uppermost parts, mostly spread horizontally. Conifers growing near the timberline, along windswept coastal headlands, and on exposed ridges are often grotesquely twisted by the wind or by the weight of winter-long snow covers. Such stunted Alpine forests are known as elfinwood, or krummholz.

DISTRIBUTION AND ABUNDANCE

Among conifers the pine family (Pinaceae) forms vast forests in the North Temperate Zone in both the Old World and the New World. The pines themselves (*Pinus*) occur mainly in a broad band along the northern, cooler part of the Northern Hemisphere. Their southern extensions occur chiefly along mountain ranges, where they grow generally at progressively higher altitudes as they approach the tropics. Lowland pine forests occur in the southeastern parts of the United States and along parts of coastal areas of the Mediterranean.

The swamp cypress grows near coasts and along rivers and lakeshores inland throughout much of the southeastern United States. In wet or swampy areas, this tree has buttresses and upward extensions from its roots called knees; its wood is remarkably resistant to decay, which accounts for the name "wood everlasting," often applied in the lumber trade.

"Wood everlasting"

Extensive coniferous forests occur in the Rocky Mountains and in ranges paralleling the Pacific coast. Douglas fir (*Pseudotsuga menziesii*) is a valuable timber tree of this area; from northern California well into British Columbia it forms magnificent forests and constitutes the most valuable softwood tree on the continent. This area also produces trees of high economic importance among the firs (*Abies*), larches (*Larix*), spruces (*Picea*), pines (*Pinus*), hemlocks (*Tsuga*), and junipers (*Juniperus*; commonly called cedar). A considerable extent of these forested areas in the Pacific Northwest is managed and harvested by lumber companies on a continuous-yield basis. In arid to semidesert regions flanking the Rockies are vast stands of shrubby or treelike junipers which bind the soil against erosion. Nearer the Pacific Ocean, where rainfall is higher, conifers include incense cedar (*Calocedrus*), Lawson and Nootka cypresses (*Chamaecyparis*), redwood, and white and western red cedars (*Thuja*); all are valuable timber trees and several are planted as ornamentals. The California big tree grows naturally only along the western flank of the Sierra Nevada. All groves of this tree are under government protection, and their cutting is strictly prohibited.

Conifers ranging southward into Latin America include the genera *Abies*, *Calocedrus*, *Cupressus*, *Juniperus*, *Pinus*, *Picea*, and *Pseudotsuga* from the Rocky Moun-

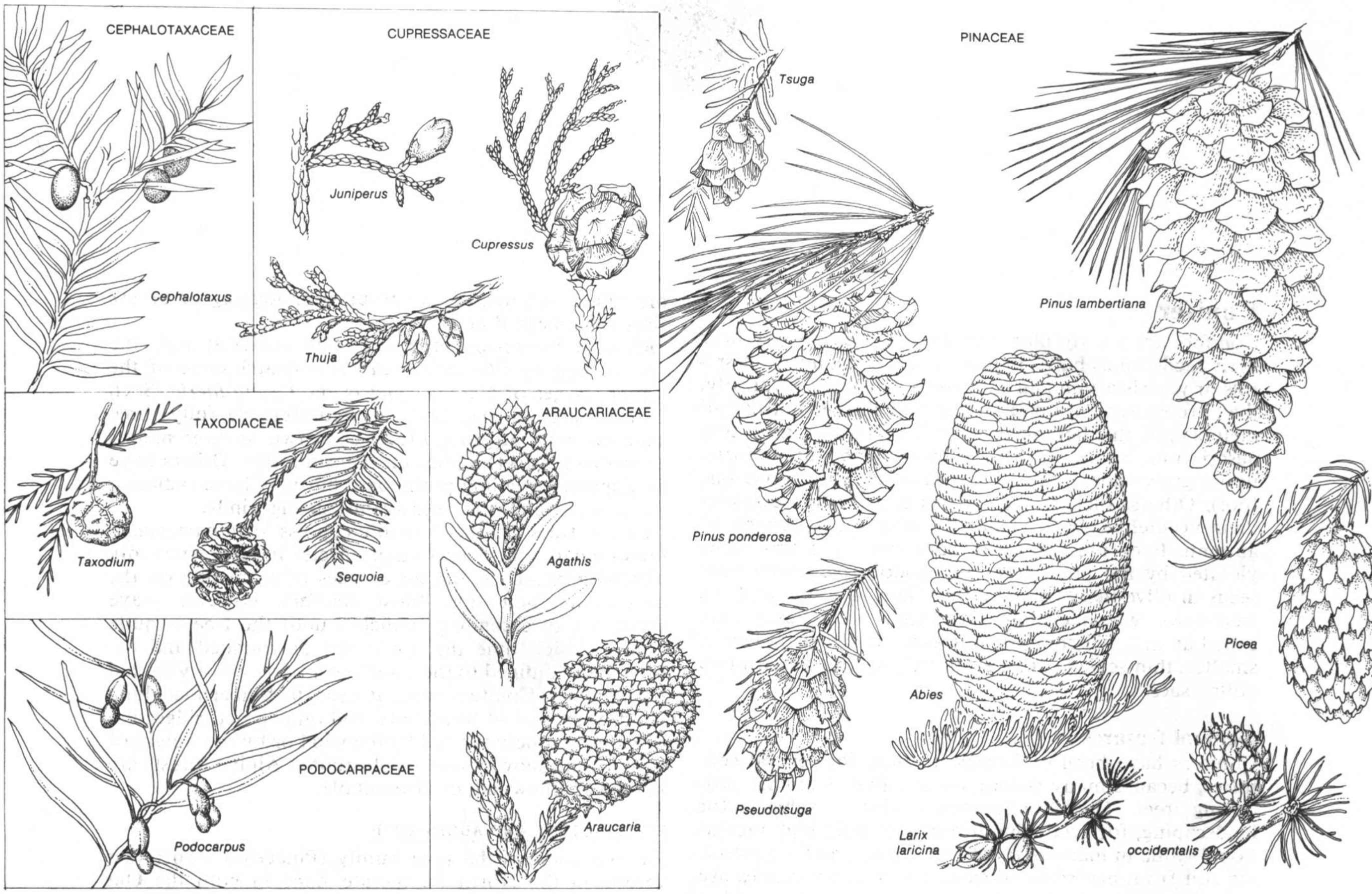

Figure 1: Conifer cones.
Drawing by M. Pahl based on *(Cephalotaxus, Podocarpus, Araucaria) Taxonomy of Vascular Plants* by G.M.H. Lawrence, Copyright 1951 by The Macmillan Company, reprinted with permission of Macmillan Publishing Co., Inc.; *(Larix laricina, Picea, Abies, Taxodium, Cupressus) Trees of North America—A Golden Field Guide* by C. Frank Brockman, illustrations by Rebecca Merrilees © Copyright 1968 by Western Publishing Company, Inc.; *(Sequoia) Illustrated Flora of the Pacific States* by LeRoy Abrams (1923), Stanford University Press; *(Pinus lambertiana, Pseudotsuga) Trees—A Golden Nature Guide* by Herbert S. Zim and Alexander C. Martin, illustrations by Dorothea and Sy Barlowe © Copyright 1956, 1952 by Western Publishing Company, Inc.

tains area and the ahuehuete (*Taxodium mucronatum*).

Genera of conifers now surviving only in Eurasia and northern Africa include *Cedrus* (the mountains of northwestern Africa. Asia Minor, and the Himalayas); *Cephalotaxus* (from Korea to India); *Cryptomeria* (China and Japan); *Cathaya, Fokienia, Metasequoia,* and *Pseudolarix* (China); *Sciadopitys* and *Thujopsis* (Japan); and *Taiwania* (China and Taiwan). *Tetraclinis* is native only in the mountains of North Africa, Malta, and in a small colony in Spain. The dawn redwood (*Metasequoia*) is an especially noteworthy conifer in that it was presumed extinct and described from fossil material in the early 1940s; surprisingly, it was later found in China.

Coniferous genera common to both the Old World and the New World are *Abies, Calocedrus, Chamaecyparis, Cupressus, Juniperus, Larix, Pinus, Pseudotsuga, Thuja,* and *Tsuga.*

The largest genus of conifers

The *Podocarpus* genus, which has its centre of distribution and probably its origin in the New Zealand–Australia–New Caledonia region, has spread widely to Africa, East Asia, South America, Mexico, and the Caribbean. It is the coniferous genus with the largest number of species—more than 110—and with the only known parasitic conifer, *P. ustus,* a small shrub up to one metre (three feet) tall, which lives on the roots of another conifer, *Dacrydium taxoides.*

Callitris, confined to Tasmania and Australia, provides important timber trees and shrubs, such as *C. endlicheri,* favoured for reforestation because it grows on stony ground unfit for agriculture; even trees too small for sawlogs provide a valuable source of tannin in their bark.

Conifers are encountered less frequently in pure stands in the Southern Hemisphere. Most of them are scattered among hardwood forests or as small patches in restricted habitats. Just as *Pinus* and *Pseudotsuga* furnish a high percentage of the timber harvested in the north, kauri (*Agathis australis*), rimu (*Dacrydium cupressinum*), and several species of *Podocarpus* furnish most of the softwood lumber in Australia, New Zealand, the South Pacific insular areas, and Africa.

Australia, New Zealand, New Caledonia, and neighbouring islands support several genera of conifers of interest because of their evolutionary significance, aesthetic value, or unusual adaptations to environmental conditions; such genera are *Acmopyle, Actinostrobus, Araucaria, Athrotaxis, Callitris, Diselma, Microcachrys, Microstrobus, Neocallitropsis, Papuacedrus,* and *Phyllocladus.* Several of the above-mentioned genera produce timber trees, some in such rugged terrain that it is uneconomical to transport logs to sawmills.

South America and Africa are relatively poor in conifers. South America has two species of *Araucaria* and one species each of *Austrocedrus* and *Fitzroya,* both genera producing trees suitable for lumber in Argentina and Chile. Two other monotypic (or single species) genera, *Pilgerodendron* (Chile) and *Saxegothaea* (Chile and Patagonia), are valued, the first as timber trees, the second because it is a connecting link between the families Podocarpaceae and Araucariaceae.

Taiwan's coniferous stands

A remarkable concentration of conifers occurs on the island of Taiwan, which has native representatives from five of the six coniferous families occurring in nearly pure stands at altitudes between 5,900 and 7,300 feet. Most of the lumber-producing trees occur on rugged mountain slopes. A species of conifer discovered on the island in 1906 was named *Taiwania.*

ECONOMIC IMPORTANCE

The softwood timbers provide almost 75 percent of the commercial lumber used for general construction, mine timbers, fence posts, poles, boxes and crates, and lesser articles. During an average year, Canada, for example, produces from its coniferous forests sawed lumber valued at almost $500,000,000, pulpwood worth $650,-000,000, and paper for newsprint valued at another $600,500,000. The United States produces considerably more cut timber but less pulpwood. Europe's production is somewhat lower. Finland, Norway, and Sweden produce large quantities of coniferous logs for pulping annually without seriously depleting their forests because of their forest-management practice of cutting trees of specified age classes on a rotating schedule.

In addition to timber used in construction, the world's nations consume huge quantities of coniferous wood as fuel and in the manufacture of cellulose products, plywood, and veneers.

Coniferous trees also are the sources of valuable resins, volatile oils, turpentine, tars, and pharmaceutical products. Many of these products are used in the manufacture of varnishes, paints, greases, and soap. *Pinus* is the chief source of raw pitch, which is treated by steam distillation to yield turpentine and resin. Kauri gum, used chiefly in fine varnishes and linoleum, is obtained from accumulations on large limbs, around the bases of the trunks of *Agathis australis*, and by digging fossil gum from beneath the soil in boggy areas (these trees are native only on New Zealand's North Island, where tapping for gum has been made illegal). A similar resin, Manila copal, comes from *A. alba*, native in the Philippines (there, too, tapping or cutting of the trees is now strictly forbidden).

Natural history

LIFE CYCLE

Alternation of generations

The conifers, like all seed plants, exhibit an alternation of generations (see Figure 2) between an asexual phase (sporophyte) and a sexual phase (gametophyte). The familiar coniferous tree is the dominant, conspicuous sporophyte generation, which bears two kinds of cones, both kinds on the same tree (and thus is termed monoecious) in most conifers, on separate trees (dioecious) in a few. The smaller of the cones produces the pollen grains, technically called the male gametophytes, or microgametophytes. The larger, often woody cones bear female gametophytes, or megagametophytes, on the upper side of the cone scales. The nucleus of each living cell in a sporophyte contains a double set of chromosomes—the bodies that transmit genetic characteristics from parent to offspring—and the sporophytes are thus known as the diploid ($2n$) generation in the life cycle. Cells called spore mother cells—in pollen sacs on the male, or staminate, cones and in ovules on the female, or ovulate, cones—undergo a special cell division called meiosis, whereby two successive divisions of a spore mother cell produce four nuclei, each with half as many chromosomes as the spore-mother-cell nucleus, the haploid (n) number. Thus, the spore mother cell is the last diploid member of the sporophyte phase in the alternation of generations, and the microspores and megaspores are the first cells of the alternate, or gametophyte, phase.

In the staminate cone the microspores separate, each developing a spore coat consisting of an outer (exine) and an inner (intine) layer. In many conifers the exine balloons out to form two or three hollow wings, which increase the buoyancy of the pollen grain (microgametophyte) and facilitate transportation by air currents. Simultaneously with the formation of the wings, a series of divisions begins, which sooner or later produces two male gametes, or sex cells, ready to fertilize the egg nucleus when the latter is receptive. When the pollen is shed, each grain is usually made up of two or more prothallial cells (flattened cells with degenerate nuclei, the only remaining vegetative cells of the male gametophyte generation), a tube nucleus, and a generative nucleus. In some genera no prothallial cells form, and tube and generative nuclei develop after the pollen grain lodges in the opening (micropyle) of an ovule. Pollen grains usually are released in the spring and float long distances on air currents. Only a minute fraction of them lodge between the scales of ovulate cones; those that do may germinate and ultimately fertilize the egg nucleus. In *Pinus* and other genera that require two years from appearance of young ovulate cones to produce ripe seeds, the pollen lodges on the ovulate scales one spring, and the pollen tube grows part way toward the egg nucleus, then remains quiescent through the winter; it fertilizes the egg nucleus in the spring of the following year. In those that produce seed in one year, the processes are telescoped, and all stages from pollination to ripe seed occur in one spring–summer–autumn period.

Conifers with less obvious cones

The female strobilus (ovule-bearing structure) is an obvious cone in all members of the families Araucariaceae, Cupressaceae, Pinaceae, and Taxodiaceae, in spite of the different appearances among them. The nature of the ovule-bearing structures in *Cephalotaxus* and in the family Podocarpaceae is less apparent, but they are greatly reduced cones that have lost most of their scales and undergone fusion of remaining parts.

The ovule is that part of the ovulate cone that produces the female gametophyte (megagametophyte). The number of ovules per scale varies; a single functional one appears on each fertile scale in the Araucariaceae, Cephalotaxaceae, and Podocarpaceae. Two ovules occur on each scale in the Pinaceae, and from two to nine are found among the Cupressaceae and Taxodiaceae.

In the early stages of development, an ovule consists of a spherical or ellipsoidal mass of cells on the upper face of a cone scale. This mass is made up of food-storage tissue (nucellus) that occupies the bulk of the ovule and is surrounded by a coat, or integument, two to several cells thick. The integument is free from but lies closely against the nucellus, except at the apex, where a small opening (the micropyle) leads to the ovule.

Drawing by M. Pahl based on (A, B, C, D, E, H) B. Lloyd, *Handbook of Botanical Diagrams* (1962), University of London Press Ltd.; and (F, G) Harold C. Bold, *The Plant Kingdom*, 2nd ed., © 1964, reprinted by permission of Prentice-Hall, Inc., Englewood Cliffs, N.J.

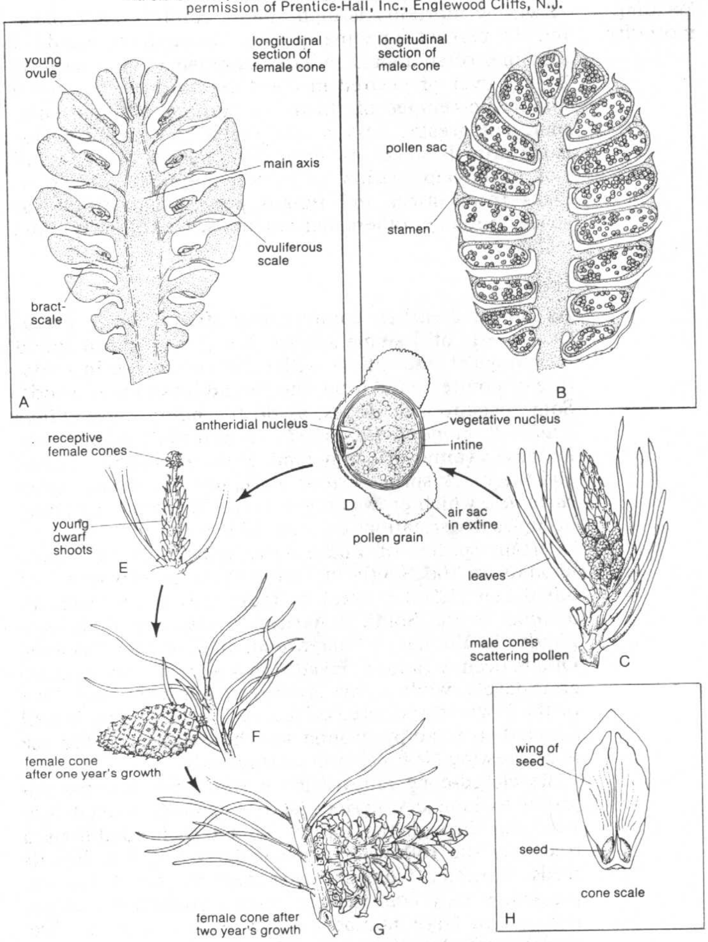

Figure 2: Reproductive structures and events in male and female cones.

Ovulate cones begin to develop in the fall, remain quiescent during winter, and have ovules ready for pollination in late spring. At this time the ovulate cones spread the tips of their scales apart, allowing pollen grains wafting on the breeze to sift among them. The ovules often have a small drop of liquid at the mouth of the micropyle at this time; pollen grains entrapped in the droplet are drawn toward the top of the nucellus as the liquid evaporates. The pollen tube then digests its way through the nucellus toward the archegonium, a flask-shaped structure in which the egg cell is developing. The pollen tube forces its way into the archegonium and extrudes its contents into the egg cell. A male-gamete nucleus soon fuses with the egg nucleus. The fusion of the male and female gametes is a complex process that produces two diploid nuclei in the earliest stage of the embryo. The two nuclei constitute the first cell generation of the next sporophyte generation in the alternation cycle.

SEED DEVELOPMENT

The rate of development accelerates markedly after fusion of the gamete nuclei. A complicated set of events follows, and several embryos are established. This condition, called polyembryony, is universal among conifers, but competition among the several to numerous embryos generally results in elimination of all but one; only rarely do two or more viable embryos develop in a single seed. The seed may be shed soon after maturity or, in closed-cone pines, may remain inside the cones on the tree from several to many years (as long as 30 years in *Pinus radiata*, *P. attenuata*, and *P. muricata*). Most conifers shed their seed at the end of the summer in which fertilization occurred.

Seeds that are shed in the fall lie dormant through the winter, and only about 20 percent of an average seed crop germinates with the arrival of spring.

Seedling mortality

Seedling mortality is high among conifers—approaching 100 percent for some species. Although thousands of seedlings often appear in early summer on land recently burned-over or cleared in construction projects, only a minute percentage of them live through the first summer. The greatest loss is attributable to drought during early growth stages, to excessive heating when in full sun, to the depredations of browsing animals, and to attacks from insect and fungus pests. Competition for space eliminates others, particularly when the early stand is dense.

ECOLOGY

As indicated earlier, conifers may often occur as extensive forests of a single species, but they are also found in ecological associations with other conifers or in a mixture of conifers and deciduous, broad-leaved hardwoods. Some occupy arid slopes, as do the piñon pines (*Pinus edulis*, *P. monophylla*, and *P. quadrifolia*); others grow in dense swamps or boggy land, as do the swamp cypress and the black spruce (*Picea mariana*). *Dacrydium araucarioides*, which grows only in New Caledonia, generally occupies dry situations on serpentine rocks.

Certain species of *Podocarpus* grow only in Alpine habitats in the Southern Hemisphere at elevations of 5,000 feet (1,500 metres) or more above sea level: *P. andinus* in the South American Andes and *P. macrophyllus* in Yünnan, China, are adapted to such habitats. Others occupy rain-drenched slopes and canyons at moderate levels, while a few grow near sea level only. One of the lowland species, *Podocarpus dacrydioides*, is well adapted to swampy ground and holds promise for use in reforesting New Zealand swamplands.

The closed-cone pines listed earlier have become adjusted to long dry periods and irregularly spaced fires sweeping through the forests. Under such conditions a tree may die following a particularly hot fire, but its seeds, protected from excessive heat by the closely appressed, woody cone scales, remain unscathed and are released in large numbers a few weeks after the fire, thereby reseeding the ash-enriched terrain.

Other conifers are tolerant of very low temperatures. Those that grow at timberline and near the Arctic Circle are undamaged by temperatures that drop to about −45° C (−49° F). In contrast, many conifers in the Southern Hemisphere—*e.g.*, tender species of *Araucaria*, *Dacrydium*, and *Podocarpus*—cannot survive even light frosts.

Hazards to conifers

Coniferous trees, like other trees, suffer from violent storms, destructive fires, and man-caused disturbances such as stream diversion, dam building, wasteful logging, and ill-advised agricultural exploitation. In recent years serious injuries have been inflicted by air pollution, in many areas bringing about the death of pure stands of such conifers as white pine. Smelter fumes are particularly injurious and have caused denudation of large areas of conifer forest. Areas cleared to provide agricultural land sometimes result in excessive soil erosion, so the land as well as the forest is destroyed.

Numerous insects and fungi may be extremely destructive of conifers. The white-pine blister rust is a serious menace in North America, and attempts to control it by eradicating the alternate hosts, the gooseberry and currant bushes (*Ribes* species generally), have been only partly successful. Bud-boring insects damage shoots, and other insects attack needles, the bark, and the wood. Under constant, often virulent attacks, conifer forests—especially pure stands, because of the ease with which disease and insects spread through such stands—have suffered greatly.

Form and function

THE ROOT

Many conifer seedlings develop a strong taproot after germination and retain it throughout the life of the tree. Others, especially trees growing in waterlogged soil, send out shallow lateral roots, the taproot dying shortly after the spreading roots are established. All conifers develop short roots from their main laterals or taproots. These short roots, which branch profusely, are the absorptive organs; they are abundantly supplied with mycorrhiza, fungi in a biological relationship with the root cells, which assist in absorbing dissolved minerals.

The internal anatomy of conifer roots is fairly uniform. No bark-forming tissue is apparent in the young roots of conifers. A cross section a short distance back of the tip of a young root shows an epidermis one cell thick, from some cells of which stubby root hairs grow outward. Interior to the epidermis is a layer of cortex, several cells thick, with many of the cells containing mycorrhiza, while others may contain starch grains, oil droplets, and other food reserves. A central strand of tissue comprises the vascular elements of the root, and its outermost sheath of cells, the endodermis, separates the vascular bundles from the cortex. Resin ducts are often seen in the roots.

Functions of the tracheids

Soon after the initial tissues become established—that is, the phloem, the tissue that functions in transporting foods manufactured in photosynthetic regions to other parts of the plant, and xylem, the woody parts of the water vascular system—arcs of cambium (dividing) cells become differentiated in the general ground tissue (parenchyma) and add secondary xylem cells to the woody part of the root and new phloem cells exterior to the cambial arcs. This activity soon fills the regions between the arms of protoxylem and produces a rodlike body of xylem consisting mostly of tracheids—long, slender cells with pointed ends and with perforations (bordered pits) in their thickened walls. The tracheids soon become empty conducting elements, having lost their contents during the deposition of thickenings on their walls. These empty elements serve two functions: mechanical strength and transportation of water with its dissolved mineral salts upward from the roots.

Vascular rays, present in roots in which secondary xylem has been deposited, consist of cells usually arranged in thin plates or bands one cell thick and several to many cells high that run radially from the xylem outward through the phloem. In many conifers the rays consist of thin-walled parenchyma cells only. In other conifers some rays have modified tracheids along the upper and lower margin, with the parenchyma cells constituting the central part of the strip. The number of rays increases as the stem or root grows in diameter.

THE SHOOT

The seedling shoot (hypocotyl) has the vascular tissues arranged in the same manner as in a root at its lower end, then has a transition region in which parenchyma cells come to occupy the centre of the vascular complex and above which the vascular elements are arranged as in stems. Stomates ("breathing holes") occur in the epidermis of the hypocotyl but are fewer than on leaves.

The growing tip of a conifer stem differs from that of its root in lacking a protective cap, lacking root hairs, and in possessing cells that are potential buds a short distance back of the apex.

A cross-section slice of a two-year-old stem shows an epidermis, usually ruptured at intervals by slit openings called lenticels, which permit the exchange of gases between the interior and the air outside. The centre of a cross section of a young stem consists of thin-walled unspecialized cells, the pith, with patches of xylem (usually three to five) constituting the primary xylem. Exterior to the outermost xylem elements is secondary xylem, which at first consists of discrete bundles but very shortly forms a cylinder of tracheids interrupted only by the medullary rays—rays that run from the pith outward. New vascular rays develop as the stem grows in diameter. Outside the ring of xylem is the cambium, which functions exactly as in roots, cutting off xylem elements to the interior and phloem elements to the exterior.

Resin ducts

Scattered through the xylem in several conifer genera, particularly in *Agathis*, *Larix*, *Picea*, *Pinus*, and *Pseudotsuga*, are resin ducts running longitudinally in the secondary xylem, each surrounded by small, thin-walled cells that exude resin (pitch) into the duct; it is these ducts that supply resin when the tree is tapped or the bark injured. Also present in the xylem of many conifers are scattered parenchyma cells that retain their contents for some time after the adjacent tracheid elements are empty. Parenchyma cells are much shorter than tracheids, have blunt ends, and have simpler perforations in their walls. The vascular and medullary rays in conifers are usually one cell wide and a few cells high (when viewing them in tangential sections of the stem). All conifers that normally have resin ducts in their xylem have occasional fusiform rays; *i.e.*, rays that are spindle shaped in tangential view, several cells wide and three to six times as high as wide. Running longitudinally through the central part of many fusiform rays is a resin duct similar to those parallel to the tracheids. As in roots, the vascular and medullary rays in many conifers are composed of parenchyma cells only. A few, such as *Sequoia*, at times develop ray tracheids along the upper or lower margins or in both positions. Some conifers that normally lack resin ducts—*e.g.*, *Abies*—may develop some in the vicinity of injuries.

LEAVES

Most conifer leaves are relatively narrow (several times longer than wide), usually have stomates arranged in longitudinal rows along either side of the single vein, or vascular bundle, and have a protective waxy cuticle. The vein, in all except a few genera, consists of one or two centrally located strands of vascular cells surrounded by a few parenchyma cells, outside of which is the endodermis. Between the endodermis and the epidermis are parenchyma cells, special transport cells (forming transfusion tissue) along the flanks of the strand, and, exterior to these latter cells, the palisade cells packed with the green-pigment bodies, or chloroplasts, that carry on photosynthesis. Some conifers have cylindrical palisade cells; others, as in *Pinus*, have almost spherical ones with deep folds in their walls, thus increasing the surface through which exchange of gases takes place. Immediately under the epidermis are strands of varying size and thickness composed of rigid, thick-walled cells; the strands constitute the hypodermis, a tissue that adds mechanical strength and stiffness to the leaf. Resin ducts, usually numbering from one to five in most species, vary in length and location, depending upon the species.

Needle-like and scale-like leaves

The leaves of many conifers—especially pines, firs, and spruces—are long and stiff and hence are called needles. Leaves of others—cypresses, cedars, *Calocedrus*, *Chamaecyparis*, and *Cryptomeria*, for example—are smaller and scalelike and have much of their length attached firmly to the twig, with only their tips free. Scale leaves are arranged along the branch in pairs or threes, with alternate sets at right angles to each other so as to form four to six distinct longitudinal rows. In some species the scale leaves take two forms: a longer pair set in one plane and a shorter pair, less spreading and appressed to the twig, set in the other plane, an arrangement that often results in fanlike, flattened branchlets, as in the cedars. In contrast, species with scale leaves all of similar size usually have leafy twigs that are circular in cross section.

Pinus bears two kinds of needles: simple, solitary ones set spirally on the branch of very young seedlings and longer, stiffer ones borne in bundles of two to five on a short stub, or spur branch, with each such bundle ensheathed at its base by papery scales. Each bundle persists from two to 20 years, depending on the species; then the entire spur branch falls, carrying the needles with it.

One conifer, *Phyllocladus*, carries on photosynthesis in leaflike flattened branchlets, its true leaves being minute scales that fall soon after they appear. *Sciadopitys* has two anatomically identical leaves united side by side and borne at the tip of a minute spur that is formed in the angle of a temporary scale leaf and the twig.

Leaves of most species of *Podocarpus*, those of *Cephalotaxus* and *Cunninghamia*, and some species of *Araucaria* are intermediate between needles and scale leaves. They usually are oblong to broadly linear, stiff and leathery, and often have sharp ends. They are spirally arranged, but some of them have twisted bases so that they appear to grow on opposite sides of the twig. Some have several veins running from base to apex rather than a single, middle vein. Several genera in the family Taxodiaceae bear leaves on lateral branchlets that function through one to several seasons, then shed the entire branchlet. *Taxodium* and *Metasequoia* shed such branchlets annually, leaving the trees bare during the dormant season; while *Sequoia* and *Sequoiadendron* retain the branchlets several years and are evergreen.

In some conifers, stomates are confined to the lower surface of the leaves, but in others they may occur on all surfaces with a concentration on the undersurface.

GROWTH AND BIOLOGICAL PRODUCTION

Conifers require a much lower concentration of mineral nutrients than is needed by food crops. Minute quantities of iron are essential, and traces of zinc and several other minerals are needed. (Zinc deficiency caused considerable loss among plantations of Monterey pine [*Pinus radiata*] during the early phases of reforestation in Australia.) Potassium-deficiency symptoms appear in young conifers only when concentration of that mineral falls below four parts per million, and calcium deficiency occurs only when that mineral drops below three parts per million. Mineral deficiencies sometimes produce no apparent symptoms other than reduction in rate of growth, but changes in colour are often indicative of a low level of vital nutrients. Nitrogen deficiency—as might occur in low wetlands—stunts seedlings and causes their leaves to turn yellow; phosphorus-deficient plants turn purple; and potassium and iron deficiencies cause loss of chlorophyll in conifer leaves.

Nearly 50 species of fungi enter into symbiotic relationships with the roots of conifers as mycorrhiza. Mycorrhiza may afford some protection against pathogenic fungi, and they definitely assist the conifer host in drawing up certain minerals and increase the rate of absorption of water from relatively dry soils.

Most conifers are able to carry on photosynthesis in low light intensity; thus, young plants can survive under rather shady conditions and in light near the blue end of the spectrum. Many conifers carry on photosynthesis more efficiently than broad-leaved hardwoods because their needles have a relatively higher concentration of chlorophyll. Conifers in cool areas continue photosynthetic processes at temperatures as low as −6° C (about 21° F); few flowering plants can approach such a performance. Conifer seedlings grow at maximum efficiency under long-day photoperiods—light for 15–20 hours daily—but cease growing when the 10-hour days of autumn begin. Of course, different photoperiod reactions occur, depending upon the latitude and on species adaptation to environmental factors normal to their respective habitats. Furthermore, growth of conifers is most rapid under conditions of warm days and cool nights, with the greatest growth occurring among those subjected to the greatest differences, within their tolerances, between day and night temperatures.

Conditions for maximum growth

Not only is there an annual growth rhythm, resulting in annual growth rings, but there is also a strong daily rhythm, with more shoot elongation occurring at night than during daylight hours. In semi-arid regions, where precipitation during the growing season often is in the form of brief but violent rainstorms, several growth rings may form in a conifer during a single summer. Such alternate growth surges and low activity are directly correlated with the intermittent rains but lag appreciably behind the actual occurrence of the storms. Where the water supply is uniformly high and the temperatures uniformly warm, however, conifers produce almost no visible growth rings, since growth is fairly uniform.

Physiological factors associated with the initiation of cone production are puzzling, but genetic factors are definitely involved. The average age of first cone formation of 60 conifer species is 5.2 years. A few species produce some ovulate cones at two years of age; others, such as the sugar pine (*Pinus lambertiana*), bear no cones until 25 years old. A number of species have a nonproductive period of several years between the first crop of cones and the next. Among many conifers seasons of high seed production alternate with seasons of low production.

Longevity and senescence are equally difficult to understand. The ability to root from cuttings appears to decline with age. The terminal shoot of a tree four or five years old roots easily when cut and placed in a rooting medium. In contrast, a cutting from the top of a pine tree 200 years old will not root, even if treated with potent growth-promoting substances. The conifers with the longest life-span discovered to date—and the oldest plants in existence—are the bristlecone pines (*Pinus aristata*), growing at 11,000 feet (3,400 metres) above sea level in the White Mountains of California and similar areas in Nevada, Utah, Colorado, and northern Arizona and New Mexico. Ages of almost 5,000 years have been determined by counting growth rings in borings taken from the thick trunks of these gnarled and twisted trees. Conifers that produce tall, sturdy trunks rarely attain ages one-half as great.

The oldest plants

Seeds of conifers vary greatly in viability (ability to germinate) and in longevity. The seeds of pines in the subgenus *Haploxylon*—typified by white pines—lose their viability very rapidly if stored at room temperature, much faster than do those of the subgenus *Diploxylon*, or yellow pines, under similar conditions. Seeds of all conifers that grow in temperate climates or in sub-Arctic areas retain their viability best if stored at a temperature of about 5° C (41° F). Seeds of closed-cone pines have remained viable up to 30 years when contained within the cones held on the trees; they deteriorate rapidly, however, after they are released from the protective cones. Some conifer seeds germinate more rapidly when subjected to at least a short period of illumination, others do best if left in light throughout each day, and a few react favourably to short periods of illumination with red light.

CHEMICAL COMPOSITION

The chemistry of pines is more thoroughly known than that of any other conifer because of the great amount of investigation conducted by industries that utilize pine products.

Cellulose is a component of cell walls in all higher plants, including conifers; lignin occurs in xylem, or wood, and is more complex in its structure. Coniferous lignin differs from the lignin of broad-leaved angiospermous trees in giving no reaction to a test for the chemical syringaldehyde.

The hemicellulose present in conifers can be made to yield such sugars as xylose, mannose, arabinose, galactose, glucose, and rhamnose and the urinelike uronic acids. Conifer wood yields only 15 to 20 percent of hemicelluloses, compared with 20 to 30 percent in angiosperm wood.

The sugar pine exudes a sugary substance that the American Indians used as food and medicine. First named pinite, later pinitol, it has been found in the wood of six species of pines in the subgenus *Haploxylon* but not in the wood of any of the pines of *Diploxylon*.

Polyphenolic compounds occur in the wood of many conifers, but percentages of separate phenols vary greatly from sample to sample. Some polyphenols are abundantly present in the heartwood, or nonliving core, of conifers, with only minimal fractions of them in the sapwood, bark, needles, cones, and pollen grains.

As much as 50 percent of the weight of conifer seeds is fat, which constitutes the main food reserve for the embryo; the fats are mainly triglycerides of unsaturated fatty acids such as oleic, linoleic, and linolenic, predominantly the second. Seeds of pines growing in northern areas contain somewhat higher percentages of unsaturated fats than do those of trees from southern, warmer areas.

Waxes present in the bark, on needles and twigs, and in the pollen of some conifers often impart a whitish or bluish "bloom." These waxes generally are classified as estolides and are made up of long chains of polyesters of hydroxy acids.

Volatile oils

Volatile oils occur in the leaves, twigs, wood, and to a lesser degree in the bark of conifers. They usually constitute only about 0.5 percent of the fresh weight of the material processed. The chemical composition and relative volatility of these oils vary greatly, that obtained from needles being different from that from the twigs and older stem wood in the same tree.

Tall oil, a mixture of substances obtained as a by-product of paper-pulp manufacture, is used chiefly in the manufacture of soaps and greases.

Oleoresins present in many conifers form the basis of the naval-stores industry in several parts of the world. Droplets of oleoresins occur chiefly in cells surrounding the resin ducts in the sapwood. When the resin canals are severed or ruptured, the pitch seeps through the wound and may be collected in a suitable receptacle. Raw oleoresin can be separated into two main components, turpentine and rosin, the relative percentages of which vary considerably among the pitch-producing pines and other conifers. Oleoresins also collect in pockets in the bark of several species of *Abies*, although the wood of this genus lacks resin ducts. Each "blister" must be tapped individually, and the product, Canada balsam, is produced in small quantities and has limited uses.

Venetian turpentine, used mainly in artwork, is an oleoresin taken from the heartwood of the European larch (*Larix decidua*) by boring a hole in the lower trunk, allowing the pitch to accumulate, and collecting it periodically. The annual production is very low, usually not over two ounces of pitch per tree per year.

Oleoresins obtained from stumps and collected by tapping living trees yield rosin generally composed of about 90 percent diterpene resin and acids and up to 10 percent of nonacid compounds. The steam-volatile fraction of oleoresins from pines, called turpentine, is a complex of about 30 chemical constituents.

Evolution and paleontology

ANCESTRAL CONIFERS

The geological history of the conifers began in the Carboniferous period (about 345,000,000 years ago). The

"Form genera" of the Voltziaceae

earliest conifers represented in the fossil record have been lumped, for convenience, in the family Voltziaceae, of uncertain relationship to still earlier groups of plants (see Figure 3). Within the Voltziaceae several "form genera" (those based on a general type of organ, such as a leaf, a twig, unidentifiable beyond these general lines) have been included in a newly proposed genus, *Lebachia*, and one older genus, *Walchia*, the latter retained to include all leaf-bearing twigs in which stomatal characters cannot be determined.

Lebachia, a straight, upright tree with a slender trunk of unknown height, appeared first in the late Carboniferous time (about 300,000,000 years ago) and became commoner and more widespread later. Both staminate and ovulate cones of *Lebachia* were cylindrical and were borne singly at the tips of twigs on the same tree.

In the Permian Period (from 225,000,000 to 280,000,000 years ago) occurred *Ernestiodendron filiciforme*, vegetatively similar to *Lebachia* but evolutionarily advanced over *Lebachia*. A further evolutionary advance is shown by *Pseudovoltzia liebeana*. It had two kinds of leaves, spirally arranged, those at the ends of the younger branches being long, linear, and flattened, while those on the older branches were shorter, more slender, and incurved. Scales of the ovuliferous cones were arranged spirally but had a flattened, five-lobed appendage axillary to each bract except the basal two or three. These appendages have been interpreted as having arisen by fusion of five ovuliferous scales such as those in *Lebachia*, their terminal parts still free, and a loss of the ovule from at least two of the five scales. Continued reduction, or fusion, through a greater part of the scales, plus loss of one more ovule, could have resulted in an ovulate cone scale similar to those now possessed by many modern conifers.

The foregoing series of fossils presents a clear line of development from ancestral forms to the immediate predecessors of modern conifers. This evolutionary line apparently developed rapidly during the Mesozoic Era (from 65,000,000 to 225,000,000 years ago), but few fossils of that age are adequately preserved, so it is difficult to follow advances in later differentiation.

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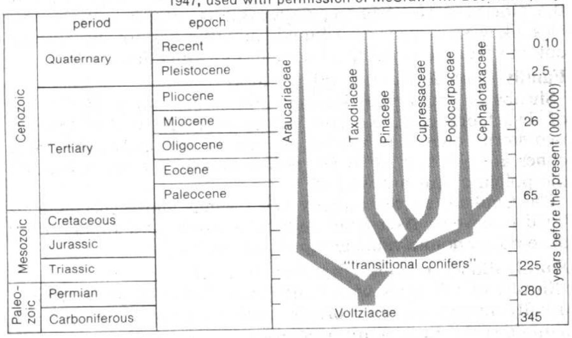

Figure 3: Conifer dendrogram.

FOSSILS OF CONTEMPORARY CONIFERS

It is difficult to identify any modern coniferous genera with fossils older than those from the Cretaceous Period (from 65,000,000 to 136,000,000 years ago).

Early in the 20th century, some botanists argued that the family Pinaceae represented the most primitive stock of the coniferous evolutionary sequence and were followed by the family Araucariaceae. The general opinion has become that both families are descendants of an ancient stock—possibly going back to the *Pityeae*—that they represent two lines that became differentiated in the Middle and Late Mesozoic and that the present segregation of the two—and other families of the Coniferales—is chiefly the result of the extinction of intermediate, Mesozoic types. The conifers as a group reached their zenith in the Middle Cretaceous and have been declining ever since. The angiosperms have been more successful in the never-ending competition among organisms and have come to dominate the floristic scene.

The decline of the conifers

The diagram in Figure 3 of the theoretical lines of descent among the gymnosperms shows the presumed general routes of evolution followed by the different branches of the groups in geologic time.

The oldest fossil referred to the family Araucariaceae with reasonable assurance is *Araucarites delafondii* from the Permian of France. It consists only of triangular cone scales that had separated from the cone axis, with each scale bearing a single seed on its undersurface.

Extensive deposits containing *Araucarioxylon* and *Woodworthia* wood occur in North America, the most famous being those in the Petrified Forest National Park in Arizona. No cones are attached to the petrified logs, but the tracheids have pit characteristics of *Araucaria*, and there is no doubt about the relationship. Several species of *Araucarites* occur in Cretaceous sediments in Alabama, New Jersey, North Carolina, South Dakota, and Wyoming.

Excellent fossil cones of *Proaraucaria mirabilis* came to light in volcanic ash, probably Eocene in age (from 38,000,000 to 54,000,000 years ago), in Patagonia. These cones differ from modern *Araucaria* cones in having a deep cleft between the tips of the bract and the ovuliferous scale, a condition similar to that found in modern members of the Pinaceae. Only one seed appears on a scale, and the structures of both scale and seed strongly resemble those in the *Eutacta* section of *Araucaria*.

Cone scales of *Agathis* are fairly common in Cretaceous and Tertiary sediments. The first specimens found were *A. borealis* from Arctic deposits, but subsequently others were found in Cretaceous rocks along the North American Atlantic coastal plain. Cones of *Protodammara speciosa*, of similar age but slightly smaller than *Agathis borealis*, were obtained in New York.

The plum-yew family (Cephalotaxaceae) is represented by fossils of foliage and seeds that resemble those of *Cephalotaxus*, in Lower Cretaceous beds in Alaska, South Dakota, and Virginia.

A fairly recent family, the cypresses (Cupressaceae), is represented by undisputed fossil specimens of several genera in Upper Cretaceous and Tertiary sediments, including *Callitris*, *Thujopsis*, *Thuja*, *Juniperus*, and *Chamaecyparis*.

Fossils of the pine family (Pinaceae) may extend back into early Mesozoic times, but definite relationships of the genera are hard to establish. *Prepinus*, consisting of needlelike leaves on short shoots, were found in Lower Cretaceous formations in New York. Internal structure of these leaves suggests that *Prepinus* is an ancestral form of *Pinus*, possibly linking the pines, true cedars, and larches. Some undisputed *Pinus* cones and seeds are known from Cretaceous rocks of Greenland, Maryland, South Dakota, Virginia, and western Canada, and cones were found in Lower Cretaceous deposits in Europe. Fossils of various pine structures, including pollen, first appear in Eocene rocks and become abundant in Miocene (about 7,000,000 to 26,000,000 years ago) and Pliocene (from 2,500,000 to 7,000,000 years ago) formations from widely scattered localities.

Fossil remains belonging to *Abies*, *Cedrus*, *Keteleeria*, *Pseudotsuga*, and *Tsuga* have been found in Miocene and Pliocene beds. *Picea* occurred in the Lower Cretaceous of Belgium but did not appear in North American fossil floras until Miocene time, and *Larix* seems not to have appeared in the fossil record until the Pleistocene Epoch, about 2,500,000 years ago. Leafy shoots that might have been precursors of either *Cedrus* or *Larix* came from Jurassic rocks (of 136,000,000 to 190,000,000 years ago) and were called *Pitycladus*.

Three different types of wood with characteristics of the Pinaceae, but without attached cones or leaves, have been found in abundance and now are generally assigned to three form genera—*Cedaroxylon*, *Piceoxylon*, or *Pinuxylon*—which replace earlier names. Altogether, about 200 different "species" presumed by their authors to belong to the Pinaceae have been described.

The earliest known representative of the family Podocarpaceae was found in the Lower Jurassic (about 190,000,000 years ago) of New Zealand and in India. The

The earliest known podocarps

Podocarpaceae and Araucariaceae competed for dominance in the Southern Hemisphere at this time, and fossils belonging to *Dacrydium* and *Podocarpus* lines have been found in Middle Jurassic rocks of Antarctica. Other fossil representatives of these genera occurred throughout Cretaceous and Tertiary times in Argentina, Chile, South Africa, India, Australia, and Tasmania. *Phyllocladus asplenioides*, found in Eocene deposits in New South Wales, and other fossils resembling *Phyllocladus* have been found in Cretaceous rocks in Nebraska, New York, and Greenland.

Some Mesozoic fossils named *Elatides* were first placed in the Pinaceae but now are considered closer to the family Taxodiaceae. *Elatides williamsonis*, from Middle Jurassic strata in Yorkshire, is the most ancient of the unquestioned Taxodiaceae. Its staminate cones had scales with pronounced stalks and broadened, triangular terminal expansions set almost at right angles to the stalk. The ovulate cone scales bore two to five small ovules near the juncture of the stalk and the expanded terminal part. This fossil probably was closely related to *Cunninghamia*, or it might have been intermediate between *Cryptomeria* and *Sequoiadendron*.

The fossil predecessors of *Sciadopitys* go back to Lower Jurassic beds of New Jersey and Norway, to the Lower Jurassic of Sweden, and from Jurassic to Cretaceous in Greenland.

Fossils of *Sequoia*, *Metasequoia*, and *Taxodium* have been hard to differentiate when cones were not among the leaves and twigs. Much of the *Sequoia* and *Taxodium* material of Eocene age is now known to be *Metasequoia*. It is possible that some petrified tree trunks still standing in the Yellowstone National Park may be those of *Metasequoia*.

Genuine *Taxodium* fossils are abundant in Tertiary deposits of North America, Europe, and Asia; fossils uncertainly referred to as *Glyptostrobus* occur in the Lower Cretaceous of Greenland, and more positively determined ones come from Eocene rocks in North Dakota, the Miocene of Oregon, and from several other Tertiary localities; *Cryptomeria* has been found in Tertiary beds in Great Britain and from Upper Cretaceous strata in Japan; *Athrotaxis* has been recorded from the Lower Cretaceous of Patagonia and questionably from Czechoslovakia; *Cunninghamia* has come from the Upper Cretaceous of Japan, and pollen grains of this genus were found in the Green River shales of Eocene age in Colorado and Utah.

Classification

DISTINGUISHING TAXONOMIC FEATURES

The foremost identifying feature of the conifers is the cone, which has already been discussed in earlier sections. Another equally important character resides in the chromosomes. Not only the number but also some of the structural characteristics of conifer chromosomes are remarkably stable and may serve as taxonomic guides. Three basic series of chromosome number occur among the conifers: an 11 series in the Cupressaceae and Taxodiaceae, a 12 series in the Cephalotaxaceae and Pinaceae, and a 13 series in the Araucariaceae. The Podocarpaceae, obviously more evolutionarily versatile than the other families, has no fewer than four basic numbers in its various genera: 12, 13, 19, and 20 having been determined. (The last two numbers in this diverse series probably arose through the fusion of one or two chromosomes, followed by duplication of the entire set.) The chemical characteristics of various resins, turpentines, and other substances are important factors in the classification of conifers. It is already known that terpenoid characteristics of the heartwood of the Cupressaceae are quite different from those of the Pinaceae and that those of the Araucariaceae and Podocarpaceae have distinctive chemical divergences. Phenolic compounds in the haploxylon pines are markedly different from those of the diploxylon pines.

Arrangement of families, genera, and species according to morphological, anatomical, chemical, and ecological characteristics is not too difficult. But construction of a phylogenetic classification that shows lines of evolutionary derivation is a far more difficult task because of the incomplete nature of the fossil record.

ANNOTATED CLASSIFICATION

The taxonomic scheme given below is based upon characters, mostly visible, that are used in formulating what is called a key, or horizontal, rather than phylogenetic, classification.

ORDER CONIFERALES

Creeping shrubs to giant trees, all of which bear staminate, or pollen-producing, cones and most of which bear ovulate, or seed-producing, cones (exceptions: Cephalotaxaceae and Podocarpaceae). The largest order of gymnosperms, with about 50 genera and more than 500 species, found in all parts of the world.

Family Araucariaceae

Shrubs and trees with cone scales flattened, overlapping, and usually numerous and bearing bracts, at least in young cones. A single seed on each ovulate scale. Leaves are mostly leathery or their bases leathery and the free part curved.

The Araucariaceae consist of 2 genera only, *Agathis*, with 21 species, and *Araucaria*, containing 14 species distributed among 3 sections of that genus, based on characters of leaves, cones, seeds, and methods of germination. Section *Colymbea* has broad, flattened, rigid leaves, large cones about 20 cm long, seeds with only 2 cotyledons, and hypogeal germination (*i.e.*, the seed and cotyledons remain under the soil throughout germination and establishment of the seedlings). Section *Eutacta* has awl-shaped, less rigid, smaller, curved leaves, smaller cones (usually less than 10 cm long), seeds with 2 to 4 cotyledons, and epigeal germination (*i.e.*, the cotyledons are pushed above the surface of the soil upon germination). Section *Intermedia* has awl-shaped, only slightly rigid juvenile leaves but broad, flat, rigid adult leaves, cones intermediate in size, 2 to 4 cotyledons, and epigeal germination. The family is completely limited to the Southern Hemisphere in its natural distribution.

Family Cupressaceae (cypresses)

Prostrate to upright shrubs and trees with cone scales usually expanded at their tips and meeting at their edges (not overlapping), numbering usually 3 to 12 per cone; bracts not visible externally. Ovules, containing the seeds, are borne erect. Leaves are scalelike, in pairs or threes; they may be spirally arranged in juvenile forms of certain species.

The cypress family consists of 18 genera and 130 species: *Juniperus* leads with about 60 species, distributed widely in the Northern Hemisphere, *Cupressus* is second with 21 species likewise widely distributed, and the rest of the genera contain from 1 to 13 species each and range less widely.

Family Cephalotaxaceae (plum-yews)

Shrubs or small trees having single seeds borne at the tips of dwarf branches. No cone scales normally visible (one or two sterile ones may appear at base of the seed). Staminate cones are globular or ovoid, pollen sacs 3 to 9 per scale, and the pollen grains are winged.

The Cephalotaxaceae family has 1 genus and 7 species confined to eastern Asia from Assam to Korea and Japan. They have no economic value except as ornamentals

Family Pinaceae (pines, firs, spruces, etc.)

Shrubs to tall trees with cone scales flattened, overlapping, usually numerous, and bracts evident. Two seeds on each ovulate scale. Leaves are needlelike.

The Pinaceae is the most diverse of all the living coniferous families: it includes 10 genera and more than 200 species; *Pinus* alone has about 100 species (some botanists recognize only about 80) divided between 2 subgenera, *Haploxylon* and *Diploxylon*. *Haploxylon* pines, in which each needle has only 1 vascular bundle and usually 5 needles on a dwarf shoot, are called white pines; their wood is usually softer than that of the other subgenus. *Diploxylon* pines, whose needles have 2 vascular strands side by side within the endodermal sheath and mostly in bundles of 3 (3 on a dwarf shoot), have wood that contains more resin than does that of the white pines and is harder, the heartwood being slightly yellowish, hence the common name yellow pines. Many pines bear large, edible seeds that have high nutritive value and are used commercially. The smaller edible seeds of other pines are consumed by animals in large quantities.

Among the other genera of the Pinaceae, *Abies* has almost 50 species, widely distributed in the Northern Hemisphere. *Cedrus*, with 4 species in the Atlas Mountains of North Africa, Asia Minor, and the Himalayas, and *Cathaya* and *Keteleeria*, with 2 each, are both native in China. *Larix* has 10 species in the Northern Hemisphere. *Pseudolarix* contains 1 species, in eastern China. *Pseudotsuga*, with 5 species and an additional variety, occurs in western North America, Japan, and China. *Tsuga* has about 10 species, in the Northern Hemisphere. *Picea*, with 31 species, is widely distributed in temperate regions of the Northern Hemisphere.

Family Podocarpaceae

Prostrate shrubs to tall trees having single olive-like seeds borne at the tips of dwarf branches. No cone scales normally visible. Staminate cones cylindrical, with two pollen sacs per scale, and the pollen grains not winged.

This predominantly Southern Hemisphere family consists of 7 genera collectively possessing approximately 150 species. *Podocarpus* surpasses *Pinus*, having more than 110 species distributed throughout the greater part of the Southern Hemisphere and extending well into the Northern Hemisphere in Asia and as far north as Mexico and the Caribbean in North America. *Dacrydium* is second in the family, with about 20 species, centred in the New Zealand-New Caledonia area but extending to Chile, the Philippines, and Malaysia. Two genera, *Microcachrys* and *Saxegothaea*, each consists of a single species of limited range; the former native in Tasmania and the latter native in southern Chile and western Patagonia. The other 3 genera are: *Acmopyle*, with 3 species in New Caledonia and Fiji; *Microstrobus*, with 2 species confined to New South Wales and Tasmania; and *Phyllocladus*, with 6 species in New Zealand, New Guinea, Tasmania, Borneo, and the Philippines.

Family Taxodiaceae

Shrubs and tall trees with cone scales usually expanded at their tips and meeting at their edges (not overlapping), numbering usually 3 to 12 per cone; bracts not visible externally. The ovules are inverted (in contrast to the condition in the Cupressaceae). Leaves are linear to awl-shaped (scalelike on adult branches of *Sequoiadendron*) and spirally arranged on branchlets.

The Taxodiaceae include 10 genera, 6 of which have only one species. *Taxodium* and *Athrotaxis* consist of 3 species each, and *Cunninghamia* and *Taiwania* each have 2. It would seem probable that the 6 monotypic genera are approaching extinction. They are *Cryptomeria* (Japan); *Glyptostrobus* (south China); *Metasequoia* (interior China); *Sciadopitys* (Japan); *Sequoia* (western coastal United States); and *Sequoiadendron* (western flanks of the Sierra Nevada in California).

CRITICAL APPRAISAL

Classification of the conifers has been debated vigorously for more than a hundred years and is still being studied critically. Significant advances have been made in the understanding of the lines of descent and the familial relationships among the conifers. One of the most important of these advances was that made by the Swedish botanist, Rudolf Florin, who, in 1951, clarified the line of descent from *Cordaites*, a gymnosperm that has been extinct since about the end of the Permian, to *Lebachia*, thence through *Ernestiodendron*, *Pseudovoltzia*, and *Ullmannia* to the earliest genera of the conifers, and who detected the homologies between Cordaitean inflorescences and the ovulate strobili of modern conifers. As a result, it is no longer doubted that the one-seeded structures of Cephalotaxaceae and Podocarpaceae are homologous with the apparently vastly different woody cones of *Araucaria* and *Pinus*.

Advances in knowledge of conifer relationships

A particularly vexing problem is the proper disposition of the yews (family Taxaceae). Earlier they were considered, along with the pines (Pinaceae), as the only two groups within the order of conifers. Later investigations, however, have led to the separation of the yews as a distinct order, Taxales, equivalent in rank to the Coniferales (see GYMNOSPERM).

The problems encountered in aligning, relating, and separating the genera and species included within the six families of conifers are extremely complex. Such details can be found only by consulting a fairly large number of research papers and books. Such a task would require using interdisciplinary approaches, data derived from microscopic as well as macroscopic features, and the consultation of chemical, physiological, and ecological sources. The brief bibliography below holds clues to more extensive literature dealing with such specialized and divergent subjects.

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(I.L.W.)

Connecticut

One of the six New England states, Connecticut is located in the northeastern corner of the United States. In area it is the third smallest state in the nation, with 5,009 square miles (12,973 square kilometres), and ranks among the most densely populated. It lies athwart the great urban-industrial complex along the Atlantic Coast, with Massachusetts on the north, Rhode Island on the east, Long Island Sound (an arm of the Atlantic Ocean) on the south, and New York on the west.

An overview of the state

Connecticut, with its many beaches and harbours, its forest-clad hills, and its village greens that are often surrounded by houses that date from the 17th and 18th centuries, represents a special blend of modern urban life, rustic landscape, and historic sites. It is a highly industrial and service-oriented state, and its per capita income and value added by manufacture are among the highest in the nation. The strength of its economy lies in a skilled working force, much of it fabricating products that have been manufactured in Connecticut since the products were invented.

As might be expected, the population of more than 3,000,000 residents is heavily urban. The state has no single large city, however, and the intense crowding characteristic of many urban areas is not found in Connecticut. On a national scale, it continues its long tradition of being a prosperous state, with in-migration attracted by the good employment opportunities, excellent educational facilities, and pleasant living conditions for the majority of its people. (For related topics, see the articles UNITED STATES; UNITED STATES, HISTORY OF THE; and NORTH AMERICA.)

THE HISTORY OF CONNECTICUT

Colonization. In contrast to many of the other New England areas, relations between Indians and the early settlers in Connecticut were good. Trading posts were established along the Connecticut River by the Dutch from New Amsterdam and by the English from the Plymouth Colony, but the first permanent European settlers in the state came from the Massachusetts Bay Colony to the middle Connecticut Valley during 1633–35 and to the Saybrook–New Haven coastal strip during 1635–38. In 1665 the Connecticut River settlements and the New Haven Colony were united, and the general outline of the state emerged, although its borders were not finally demarcated until 1881, more than 200 years later. The New Haven Colony was unsuccessful in an attempt to settle Delaware Bay, and the united Connecticut Colony, despite its charter provisions, lost its claim to a strip of land extending to the Pacific. Following the American Revolution settlers from Connecticut, with claims in the Midwest, were among the first to move into an area that became known as the Western Reserve, now northeastern Ohio.

Land claims

Political, economic, and social maturation. The political development of the colony began with the Fundamental Orders of Connecticut (1639), a civil covenant by the settlers establishing the system by which the river towns of Windsor, Hartford (now the capital), and Wethersfield agreed to govern themselves. The orders created an annual assembly of legislators and provided for the election of a governor. This was superseded by the royal charter of 1662, a liberal document that provided for virtual self-government by the propertied men of orthodox faith in the colony. It served Connecticut well until it was replaced by the state constitution adopted in 1818, a document that after being amended many times was replaced by a new constitution that was adopted in 1965, reflecting the more complex needs of contemporary government. The Congregational Church was disestablished by the constitution of 1818.

Connecticut remained an agricultural region of farms with a few small urban areas—Hartford, New Haven, New London, and Middletown—until the early 19th century. The economy began to change, however, after 1800 when textile factories were established, and by 1850 employment in manufacturing outnumbered that in agriculture. The shift to manufacturing had been aided by the inventive genius of a number of Connecticut residents. Eli Whitney, well known for his invention of the cotton gin, developed the idea of machine-made parts for guns. An order for muskets from the federal government enabled him to build a musket factory in Hamden. The principle of interchangeable parts, adapted to clock manufacturing by Eli Terry of Plymouth in 1802, rapidly became basic to all manufacturing.

The economic, social, and political innovations that emerged in the 19th and 20th centuries were often resisted at first, but eventually they were accepted. Slavery, first attacked by legislation in 1784, was not abolished completely until 1848. The constitution of 1818 granted suffrage to men with certain property qualifications, but women's suffrage came only through federal enactment in 1920.

THE NATURAL AND HUMAN LANDSCAPE

The natural environment. *Surface features.* Essentially a rectangle in shape, 100 miles (160 kilometres) west to east and 50 miles north to south, Connecticut covers the southern portion of the New England Upland. It contains three major regions: the Western Upland, the Central Lowland (Connecticut Valley), and the Eastern Upland. The northern part of the Western Upland, often called the Berkshire Hills, contains the highest elevations in the state, about 2,300 feet (700 metres) in the northwest corner. It is drained by one major river, the Housatonic, and numerous tributaries.

Physiographic regions

The Central Lowland is different in character, being a downfaulted block of land, approximately 20 miles wide at the Massachusetts border and narrowing as one progresses toward the sea, which it meets at New Haven. It is filled with sandstone and shale. Periodic volcanic activity pushed immense quantities of molten rock to the surface and produced the igneous deposits of the central valley. These layers of sandstones and traprock have been faulted, broken, and tipped so that there are numerous small ridges, some reaching as high as 1,000 feet above their valleys. Within the lowland, the Connecticut and other rivers have eroded the soft sandstones into broad valleys.

The Eastern Upland resembles the Western in being a hilly region drained by numerous rivers. Their valleys come together to form the Thames River, which reaches Long Island Sound at New London. Elevations in this area rarely reach above 1,300 feet. In both uplands the hilltops tend to be level and have been cleared for agriculture.

Climate. In Connecticut's moderate climate, winters usually average slightly below the freezing level (32° F, or 0° C) and the state receives from three to five feet of snow each year. Snow may remain on the ground until March, but more commonly mild spells and rains that occur during the winter melt it so that the ground is bare. Summers average between 70° and 75° F (21° to 24° C), with occasional heat waves driving the daytime temperatures above 90° F (32° C). Precipitation, averaging from three to four inches (75 to 100 millimetres) per month, is quite evenly distributed. The coastal portions have somewhat warmer winters and cooler summers than does the interior, while the northwestern uplands are high enough to have cooler and longer winters with heavier falls of snow. Perhaps the most marked characteristic of Connecticut's weather is its changeability. Cold waves and heat waves, storms and fine weather can alternate with each other weekly or even daily. The statement of Hartford resident Mark Twain "If you don't like Connecticut weather, wait a minute" has become a widely appropriated and adapted proposition.

Vegetation and animal life. Originally, Connecticut was a forested region. The few Indian clearings, the swampy flood plains, and the tidal marshes accounted for about 5 percent of the total area. It is part of the mixed deciduous and coniferous forest of the eastern United States. The southern two-thirds is largely an oak forest. The northern border belongs to the northern hardwood region of birch, beech, maple, and hemlock. A few higher elevations and some sandy sections support a coniferous forest. Virtually all of the primeval forest has been cut, and the current woodland that covers two-thirds of the state is a mixed forest.

The animal life when the first settlers arrived included deer, bear, wolves, foxes, and numerous smaller species, such as raccoon, muskrat, porcupines, weasels, and beaver. Deer are still found in the less densely settled regions, but in general the larger animals have been severely decimated. Most birds are migratory, but chickadees, blue jays, and the immigrant English sparrows are year-round residents.

Patterns of human use. Most regions in Connecticut are not clearly defined, although Fairfield County in the southwest section is uniquely oriented toward New York City, serving as a major "bedroom suburb" for many commuters. With two of the state's largest cities, Stamford and Bridgeport, the region is the fastest growing area of the state. The northwestern and northeastern quarters are less densely populated areas. They have some agriculture, but most residents there, as elsewhere in the state, work in the manufacturing cities and towns along the rivers.

Connecticut's small towns represent a territorial concept that is equivalent to a township in other parts of the country. Within each town, a town centre is surrounded by the town hall, schools, churches, usually a village green, a number of houses, and often a tiny business district with several stores. Elsewhere within the town, other hamlets may contain similar communal gatherings. If the hamlet is on a stream, the houses often cluster around a red brick factory that was erected in the 19th century to run its machinery from a waterwheel in the river. Such mill villages are to be found throughout the state, although many of the factories have been abandoned. Farmsteads and cultivated fields once lay between such small population nodes, but the roads connecting these villages have become sparsely lined with rural, nonfarm homes.

Rural and urban settlement

City status in Connecticut is determined not by population but by vote of the residents to change their governmental system from a town meeting to a city form. By 1980 there were six towns in Connecticut with more than 50,000 people and one city with fewer than 10,000. All of the larger towns and cities are manufacturing centres, some of which originated as mill towns and grew with their factories. The power source changed from water to steam and later to electricity, and often the products manufactured have changed to fill the needs of a new economic and social structure, but each city and town prides itself on the uniqueness that often is associated with its products.

THE PEOPLE OF CONNECTICUT

The ethnic mix. The Algonkin Indians, the original occupants of Connecticut, comprised about 16 separate tribes with some 5,000 to 7,000 members. The first European settlers were English, coming directly from England or by way of the Massachusetts Bay Colony. During the 17th and 18th centuries population growth occurred primarily through an excess of births over deaths; immigrants, mainly from the British Isles, arrived at a rather slow rate. At the time of the first U.S. census, in 1790, Connecticut had a homogeneous population, about 90 percent of which was of English ancestry. Blacks were a minor element in the population, accounting for about 2 percent in 1790.

Patterns of immigration

The immigration of the Irish, beginning in the 1840s, and of French Canadians after the Civil War, continued throughout the 19th century. Later in the 19th century the primary sources of foreign immigration shifted to southern and eastern Europe—Italy, Poland, the Austro-Hungarian Empire, and Russia. Each immigrant group tended to congregate in certain parts of the state. Thus New Haven and its suburbs are populated largely by descendants of Italian immigrants; Poles are concentrated in the Naugatuck Valley, and the French Canadians live in the northeast. The immigration of blacks into Connecticut after World War II showed the same tendency. By 1980 blacks comprised almost 7 percent of the state's population, with more than two-thirds of them living in the five largest cities. New Haven and Hartford were more than 30 percent black. Puerto Ricans have moved to Connecticut from New York City, especially into Stamford and Bridgeport.

Demography. From 1790 to 1840 the state's growth rate hovered between 4 and 8 percent per decade. Connecticut was—considering its small size and its limited agricultural resources—quite adequately filled. During the 19th century thousands of Connecticut residents, especially the young, migrated to better agricultural lands in the western part of the country; their places were taken by newcomers from Europe. The state's population growth passed the national rate in 1900 and did not fall below it until the 1970s.

For more than 300 years the distribution of Connecticut's people has reflected the region's changing economy and resources of the land. Settlement began in the middle Connecticut Valley, where the soils were good, and on the coast, where maritime activities, trading, and fishing supplemented the living that the settlers were able to derive from the land. The upland areas were not fully occupied until the late 18th century, yet by 1790 the population was fairly evenly distributed across the state. Towns with better agricultural lands or with other resources—marine or mineral—had denser populations. During the 19th century the rise of waterpowered manufacturing attracted young people from the agricultural upland towns to the growing mill towns, and virtually all of the upland towns lost population. Towns with better assets for manufacturing grew rapidly.

The movement of people and industry into the cities dominated the population movements until 1920. Since then Bridgeport, Hartford, and New Haven, the three largest cities, have had a general movement of population to the suburbs and to the former agricultural hill towns.

THE STATE'S ECONOMY

An economic overview

Sources of income. The foundation of Connecticut's economy is manufacturing, which employs about one-third of the state's work force. In addition to such military products as helicopters, submarines, aircraft engines, guns, and ammunition, it makes thousands of items that are sold on a worldwide basis. Among the items that have been manufactured in Connecticut by long tradition are pins, clocks, silverware, sewing machines, Winchester rifles, and many brass products. Historically, mining was important; but the last iron mines closed early in the 20th century, and the state's high ranking in value added by manufacture is due mainly to the import of nearly all raw materials. Only sand, gravel, and stone are still produced within the state.

Since 1870, agriculture has declined in importance, and it is a relatively minor element in the economy. The precipitous decline in the number of farms resulted in the enactment of a farmland preservation program. Connecticut's farms produce substantial quantities of milk, eggs, poultry, and vegetables for local consumption and one important export crop, shade-grown tobacco, used mainly for cigar wrappers.

Except for the oyster industry and the historically important whaling industry, commercial fishing has never been very important in the state. The oyster industry has been attempting a comeback from the devastation that was caused by natural elements and pollution of the coastal waters.

Connecticut often is referred to as the nation's insurance centre and Hartford as The Insurance City. Marine insurance was the first concern of Connecticut companies, and eventually the coverages that they offered expanded to many forms of casualty insurance. Some of the largest insurance companies of the United States are based in Connecticut.

Labour legislation

Economic management. To correct abuses in the free enterprise system, Connecticut has had to enact numerous regulations. The first child labour law was passed in 1842, but it was ineffectual; for 30 years after its passage hundreds of children continued to work long hours in the textile mills. A labour department was set up by the state government in 1873, and since then hundreds of laws and regulations have been enacted to control working conditions. The length of the working day, minimum wage rates, equal pay for equal work, and similar protective regulations have been passed. State departments supervise banks, insurance companies, and the public utilities, and in 1959 the Department of Consumer Protection was organized to consolidate several existing agencies. Labour unions are strong and may be given partial credit for the high wages and good working conditions characteristic of most factories. There is also an active association of manufacturers.

Transportation. Connecticut's railroad network is a basic link in the Boston–New York City transportation pattern. The first railroads were constructed to bring the produce of the agricultural interior to Connecticut ports. Each of the larger river valleys—the Housatonic, Naugatuck, Connecticut, Willimantic, and Quinebaug—supported its own railroad. The line along the shore was completed in 1852. Until 1930 the railroads flourished with the expanding Connecticut economy, but highway competition for passengers and products reduced railroad traffic severely. Most of the river lines have dropped passenger service; freight service continues on some, but on others it has been abandoned. Service on the New York–New Haven Line has deteriorated despite its heavy use as a commuter facility between southern Connecticut and New York City. Limited-access highways crisscross the state, but they are concentrated in the densely settled coastal and Connecticut Valley regions. Connecticut pioneered this new type of road. The first section of the Merritt Parkway, from New York to near Milford, opened in 1938 and often is acclaimed as one of the most scenic and best designed of these highways.

Bradley International Airport, north of Hartford, is the major airport, but there are many other airports throughout the state that offer regional services. The port of New Haven is one of the largest in New England, and the U.S. Coast Guard Academy is located in New London.

ADMINISTRATION AND SOCIAL CONDITIONS

Structure of government. *State level.* Connecticut's state government is headed by a strong governor who is elected for a four-year term. The governor initiates legislation, prepares the state budget, appoints department heads, and can veto individual items of an appropriation bill.

Connecticut's General Assembly met biennially until the adoption of a constitutional amendment in 1970 provided for annual legislative sessions. The 187 members are elected for two-year terms. The 36 senatorial districts are approximately equal in population. The House of Representatives was originally based on towns, with each town, regardless of size, having at least one representative. The 1965 constitution reapportioned the lower branch so that it also is based upon population.

The judicial system

The state's judiciary is headed by the Supreme Court. Superior courts were formed in 1978 by a merger of the courts of common pleas and the juvenile courts. The justices of the Supreme Court and of the superior courts are nominated by the governor and appointed by the General Assembly for eight-year terms. Probate judges are elected on partisan ballots for four-year terms.

Local government and politics. Below the state government are 169 local units called towns. Legally, they are creations of the state, with their rights and responsibilities set out in state statutes. There is, nonetheless, a long-standing and intense tradition of local autonomy. These local governments maintain roads and provide elementary and secondary education and police and fire protection. Larger municipalities also provide water and sewage facilities and other services. The original form of government was based on the town meeting, at which the citizens elected selectmen to run the town between the annual meetings. As populations increased and problems of administration became more complex, other systems were substituted. Most larger communities have opted for a city form with an elected mayor and council. Some smaller communities have elected mayors; some have town or city managers. Many towns have retained the town meeting or have substituted the representative town meeting.

The social milieu. *Education.* From the earliest days, every town has been required to maintain public elementary schools and, as the town grew in size, secondary schools as well. Connecticut is renowned for its private schools and colleges. Yale University, in New Haven, is regarded as one of the world's great universities; and other institutions, such as Wesleyan University in Middletown, have national recognition. Public higher education has expanded considerably. The community college system, founded in 1965, had 12 colleges by 1980. Also under the control of the state are five technical colleges, four state colleges, and the University of Connecticut, with its main campus in Storrs.

Health and welfare. The community and the state have become increasingly involved in health and medical care. Most people live within 10 miles of hospital services, and doctors and other medical personnel are numerous. There are many community health clinics in addition to the advanced medical centres of the University of Connecticut at Farmington and of the Yale–New Haven Hospital. In relation to most states, Connecticut provides generous welfare benefits. Departments for the aged and for children and youth services have been established to meet the special needs of communities.

Urban redevelopment. Despite inner-city blight and abandoned housing, progress has been made by urban redevelopment programs in Connecticut's larger cities. Urban renewal programs in New Haven during the 1950s and 1960s became a prototype for the nation. Much work in rehabilitating urban areas remains to be done, however, especially in residential neighbourhoods.

Government involvement. The state government has provided increasing funds to local governments for the many social programs that are operated. Although Connecticut has an income tax, the government relies to a great extent on high sales and business taxes for revenue. In 1977 the state government was reorganized, consolidating authority in 20 executive and two administrative departments in order to make these departments and the many unaffiliated agencies more accountable to public officials.

State agencies

CULTURAL LIFE AND INSTITUTIONS

Preservations. Connecticut provides a variety of landscapes: rocky headlands, beaches, forested hills, and, perhaps most attractive, the small towns around their tree-dotted village greens. Throughout the towns, hundreds of houses dating from the 17th and 18th centuries are preserved by more than 100 local or national historical societies.

Numerous sites important in Connecticut's past or associated with illustrious individuals are maintained by state or private organizations. These include the Putnam Wolf Den in Pomfret, Mt. Riga Furnace in Salisbury, Ft. Griswold State Park in Groton, Old New-Gate Prison and Copper Mine in East Granby, the Mark Twain Memorial home in Hartford, the Tapping Reeve House and Law School in Litchfield, and the (William) Gillette Castle State Park in East Haddam. Perhaps the best known is Mystic Seaport in Mystic, where a small New England seaport has been recreated with all its ships and shops. The outdoorsman can tramp the many miles of trails and camp in one of the 30 state forests, covering more than 130,000 acres (52,500 hectares), or in one of 88 state parks, comprising some 30,000 acres.

The arts. Recreation in another form is provided in the fine arts. Art exhibitions are held annually in many cities, a number of which have art galleries and museums. The best known are the Yale University Art Gallery, the Wadsworth Atheneum in Hartford, and the New Britain Museum of American Art. Symphony concerts and concerts by smaller groups are presented regularly in the larger communities. Several educational institutions have public concerts throughout the year. Repertory companies operating in or near resort areas in the summer include Westport County Playhouse in Westport and the Oakdale Musical Theatre in Wallingford. The American Shakespeare theatre in Stratford, the Long Wharf Theatre in New Haven, and the Goodspeed Opera House in East Haddam are well known. The Yale School of Drama was, at its founding in 1925, the first such school at an institution of higher learning. Southwestern Connecticut is also within easy reach of the vast artistic resources of New York City.

The performing arts

Communications. There are about 25 daily newspapers in the state, including two university papers. By 1980 few cities had both morning and evening papers, but almost 60 towns supported weekly papers. There are 75 AM and FM radio stations and nine television stations. Most of the state's residents also can receive television broadcasts originating in New York, Massachusetts, or Rhode Island; and Boston and New York City newspapers are widely distributed.

Prospects. Vigorous efforts have been made to improve living conditions throughout the state. Many citizens and groups have given attention to preservation of the state's natural landscape, and laws controlling air and water pollution have been passed by the legislature. Plans for development and conservation have been made to provide a framework for the state's future.

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(J.B.Ho./I.J.S.)

Connective Tissue, Human

The connective tissues are a heterogeneous group of tissues derived from the mesenchyme, a meshwork of stellate cells that develop in the middle layer of the early embryo. They have the general function of maintaining the structural integrity of organs and providing cohesion and internal support for the body as a whole. The connective tissues include several types of fibrous tissue that vary only in their density and cellularity, as well as more specialized variants ranging from adipose tissue through cartilage to bone. The cells that are responsible for the specific functions of an organ are referred to as its parenchyma, while the delicate fibrous meshwork that binds the cells together into functional units, the fibrous partitions or septa that enclose aggregations of functional units, and the dense fibrous capsule that encloses the whole organ, collectively make up its connective-tissue framework, or stroma. Blood vessels, both large and small, course through connective tissue, which is therefore closely associated with the nourishment of tissues and organs throughout the body. All nutrient materials and waste products exchanged between the organs and the blood must traverse perivascular spaces occupied by connective tissue. One of the important functions of the connective-tissue cells is to maintain conditions in the extracellular spaces that favour this exchange.

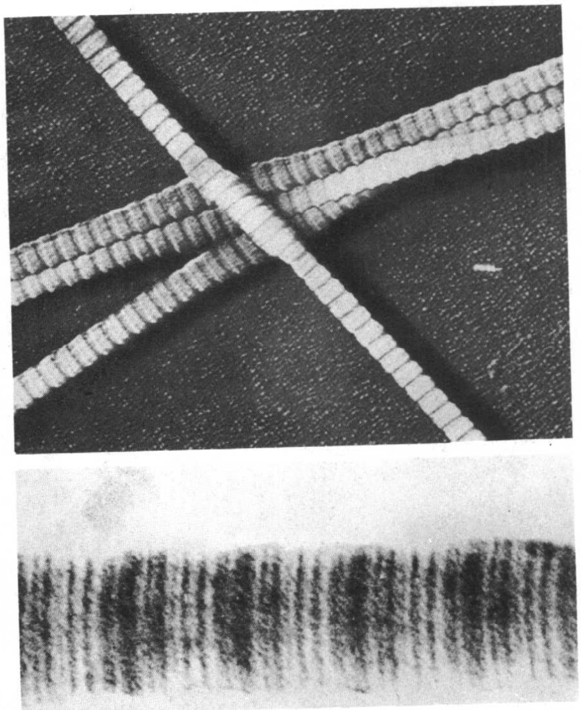
Some organs are suspended from the wall of a body cavity by thin sheets of connective tissue called mesenteries; others are embedded in adipose tissue, a form of connective tissue in which the cells are specialized for the synthesis and storage of energy-rich reserves of fat, or lipid. The entire body is supported from within by a skeleton composed of bone, a type of connective tissue endowed with great resistance to stress owing to its highly ordered, laminated structure and to its hardness, which results from deposition of mineral salts in its fibres and amorphous matrix. The individual bones of the skeleton are held firmly together by ligaments, and muscles are attached to bone by tendons, both of which are examples of dense connective tissue in which many fibre bundles are associated in parallel array to provide great tensile strength. At joints, the articular surfaces of the bones are covered with cartilage, a connective tissue with an abundant intercellular substance that gives it a firm consistency well adapted to permit smooth gliding movements between the apposed surfaces. The synovial membrane, which lines the margins of the joint cavity and lubricates and nourishes the joint surfaces, is also a form of connective tissue.

COMPONENTS OF CONNECTIVE TISSUE

All forms of connective tissue are composed of (1) cells, (2) extracellular fibres, and (3) an amorphous matrix, called ground substance. The proportions of these components vary from one part of the body to another depending on the local structural requirements. In some areas, the connective tissue is loosely organized and highly cellular, in others its fibrous components predominate, and in still others, the ground substance may be its most conspicuous feature. The anatomical classification of the various types of connective tissue is based largely upon the relative abundance and arrangement of these components.

Collagenous and reticular fibres

The fibrous components are of three kinds, collagenous, elastic, and reticular fibres. Most abundant are the fibres composed of the protein collagen. The fibrous components of loose areolar connective tissue when viewed with the light microscope appear as colourless strands of varying diameter running in all directions, and, if not under tension, these have a slightly undulant course (see photo). At high magnification, the larger strands are seen to be made up of bundles of smaller fibres. And the smallest fibres visible with the light microscope can be shown with the electron microscope to be composed of multiple fibrils up to 1000 Å in diameter. These unit fibrils are cross-striated with transverse bands repeating every 640 Å along their length.



(Top) Electron micrograph of four collagen fibrils shadowed with metal to increase their contrast and reveal their periodic 640-Å cross striation. (Bottom) In a more highly magnified electron micrograph of a collagen fibril stained with phosphotungstate, the cross striation can be resolved into several distinct bands which depend upon the arrangement of the tropocollagen molecules within the fibre.
By courtesy of (top) J. Gross, (bottom) B.R. Olsen

Extracellular fibres. Collagen is of commercial as well as medical interest because leather is the dense collagen of the dermis of animal skins preserved and toughened by the process called tanning. Fresh collagen dissolves in hot water, and the product is gelatin. Under appropriate conditions, collagen can be brought into solution without chemical change. The fundamental units in such solutions are slender tropocollagen molecules about 14 Å wide and 2800 Å long. Collagen appears to be secreted in this form by the connective-tissue cells called fibroblasts, and the tropocollagen molecules assemble extracellularly to form striated collagen fibrils. By an alteration of the physicochemical conditions, tropocollagen in solution can be induced to polymerize with the formation of cross-striated fibrils identical to native collagen, thus simulating in the test tube the process of assembly that is believed to take place during fibrogenesis in the living organism. Analysis of the structure of collagen by X-ray diffraction has shown that the tropocollagen molecule consists of three side-by-side polypeptide chains—linear combinations of a number of amino acids, which are subunits of proteins—each in the form of a left-handed helix. These three left-handed helices are further twisted around one another to form a major right-handed helix. Upon chemical analysis, the amino-acid composition of collagen is found to be unique in its extremely high proline content (22 percent) and in the fact that one-third of the amino acid residues are glycine. It is the only naturally occurring protein known to contain hydroxyproline and hydroxylysine. Two of the three polypeptide chains comprising the tropocollagen molecule are similar in amino-acid composition, while the third is distinctly different. In the tissues, the collagen fibrils are believed to be held together by a polysaccharide component that has not been fully characterized.

Reticular fibres are distinguished by their tendency to form fine-meshed networks around cells and cell groups, and by virtue of their property of staining black because of adsorption of metallic silver when they are treated with alkaline solutions of reducible silver salts.