The Evolution of Plants

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I. Introduction

The teaching of evolution is certainly one of the most difficult aspects of any life science course. This subject requires of the student an appreciation of the concepts of time and of change not the time durations of our own experiences (hours, days, years), rather, periods of thousands and millions of years. Geological change presents enough problems in comprehension. Rapid cataclysmic change, such as the recent volcanic eruptions of Mount St. Helens in Washington, catches our attention, but the more gradual forces of nature action of the wind and waves, slow erosion, sedimentation, continental drift can be understood only with a deeper insight. To accept the notion of long term biological change is something which requires a fair amount of substantiation, particularly when religious views seem to be in conflict with scientific thought. I believe that too frequently the student is not given sufficient opportunity to examine the evidence for organic evolution. It is difficult to appreciate such a fundamental theory of biological science when one doesn't have ample time to learn about it. The Smithsonian Institution's Museum of Natural History has recently opened an exhibit on evolution, which emphasizes the unifying aspects of the theory. In this exhibit, the effort has been made to illustrate population growth, competition, natural selection, adaptive radiation, mimicry, parallel and convergent evolution, by providing as many visual examples as space will allow. The overall effect is to understand the processes by being surrounded by the products of evolution.

This unit attempts to take a similar approach to the study of plant evolution. The topic is discussed primarily in terms of paleobotanical evidence, as well as through an examination of living plant species. The objectives of the unit are as follows:

1. to strengthen the student's understanding of the basic principles of evolution, as applied to the plant kingdom, through readings, classroom activities, and laboratory activities.

2. to develop in the student a greater awareness of the concepts of time and ecological change.
3. to consider the several methods of fossilization of plant tissues; 4. to present a brief review of the diversity of plant life, discussing some of the differences among plant in the context of evolutionary developments;
5. to provide an overview of the evolution of plants, with particular emphasis on the evolution of land plants;
6. to discuss some of the most notable of fossil plant species;

7. to familiarize the student with herbaria and with the procedures for preparing herbarium specimens. Laboratory and field activities focus on the diversity of plant life and on the examination of preserved plant remains.

Paleobotany is an area of science which can require a strong science background and very sophisticated thinking. It is not the intention of this unit to be so involved and complicated that the average student will be unable to deal with the material. The chances are small that any one of my students will become a paleobotanist, this year or in ten years' time. In presenting this material in the classroom, then, the greater emphasis is put on developing a better understanding of the concepts of time, physical and biological change, and the diversity of life.

Those changes in plants regarded as most significant are the invasion of the land, the development of seed plants, and the appearance of the angiosperms (flowering plants). The major divisions of plants will be considered in relation to their ability to survive on land, exploit ecological niches on land, and reproduce efficiently.

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II. The Concept of Time

Opinion differs among scientists as to the rate of biological evolution. The popular belief is that new species evolve as a result of a constant and gradual accumulation of genetic changes. More recently, Stephen Jay Gould and others have suggested that biological change, as with geological change, can occur in fits and starts, that there may be periods of rapid evolution followed by prolonged periods of constancy. In either case it is accepted that the phylogenetic history of a plant or animal type must be measured in many thousands and millions of years. Human experiences are measured on very short time scales seconds, minutes, hours, days, years. As we add years to our lives we become increasingly aware of the effects of time, on all aspects of our lives. We are not transformed, however, into new varieties or species of humans in the course of our lifetimes, and this is generally true of other forms of life. (Hybrids and DNA recombinants are exceptions which will not be considered in this unit.) If one can learn to think in terms of thousands and millions of years, instead of our more immediate time frames, then it becomes much easier to reach the following conclusion: that it is more difficult to imagine an organism remaining the same over one million or ten million or one hundred million years than it is to expect that organism to change over such vast periods of time.

It is suggested that students be taught an appreciation of the magnitude of time in the following two ways: first, by comparing (in a relative way) any event or earlier time with the entire age of the earth; second, by learning that small, almost imperceptible changes can add up to major changes, when given enough time. In the Teachers Institute Natural History and Biology unit "Haminid Evolution" (1979), the use of a "cosmic calendar" is discussed. This geological calendar or clock condenses the entire history of the universe into one imaginary year. The first seconds of January 1 mark the occurrence of the Big Bang, the cataclysmic birth of the present universe. The last tick of this clock on December 31 as 11:59.59 P.M. passes by, marks the approach to the present. All events in between can then be assigned a month and day, showing in familiar terms the relative time of each event. This technique is very useful in discussing the biological history of man, a genuine latecomer on the scene, in relation to other forms of life, to the age of the earth, to the age of the universe.

Let us apply this method of time keeping ta the situation of plant evolution, making the following change: January 1 stands not for the formation of the universe an event of very long ago but rather for the formation of the earth. The twelve months of our earth calendar, as we'll call it, then must span the entire 4.5 4.8 billion years generally believed to be the age of the earth. To use convenient figures, we will give Earth the benefit of the doubt and assume an age of 4.8 billion years. Dividing by 12 (months in a represents the passage of 0.4 billion or 400 million earth years. Each day on the earth calendar represents approximately 13 million years. One minute from the calendar spans 9000 actual years, and a second passes by for every 150 years of earth history.

Where does man fit on this calendar? A generous estimate for the age of Richard Leakey's KNM-ER1470 skull (Homo habilis) is 2.5 million years. This is less than 1/5 of the time covered by one of our earth calendar days. The birth of Homo can be assigned to December 31 at approximately 7:24 P.M.. That's not even yesterday! (Refer to Appendix, Figure 1.)

In the same manner the following events may be entered on the earth calendar: April 8 the oldest known biological cells (3.5 billion years old); July 1 the first primitive photosynthetic organisms (2.4 billion years old); November 18 the end of the Precambrian and beginning of the Paleozoic Era (570 million years ago); December 1 appearance of the first land plants (400 million years ago); December 21-23 true flowering plants (angiosperms) appear (135-100 million years ago); December 31 at 11:59.14 P.M. the age of the gray sandy layer of sediment at Stiles Clay Pit in Hamden, Connecticut (7,000 years ago).

It becomes apparent that plants have a much longer history than does man. In discussing plant evolution the greatest attention in this unit, and certainly the richest documentation in the fossil record, is given to the last 400 million years of time, the "month of December" during which plants achieved and improved upon life on land. Prior to this time the fossil evidence is much leaner, though certainly not totally lacking, and the conjecture is greater.

Grasping the magnitude of the long history of earth is helpful in understanding evolution. It is equally helpful to consider that gradual, minute change can have a major cumulative effect, given sufficient time. A good way ta develop this understanding of time is by using examples of plant migration. Many types of animals, particularly the vertebrates (fish, turtles, birds, and mammals) are known by our students to undergo seasonal migrations. Plant species have been shown to migrate over much greater periods of time, as a passive response to climatic changes. Dispersal by animal carriers may contribute to such migrations.

As an example, during the Eocene Epoch (60-40 million years ago) the plant life of eastern Oregon was characteristic of a subtropical climate. Over the course of a two million year period, as the Oregon climate shifted to temperate and tundra-like, these plant species migrated to an area approximately 2000 miles southward, being succeeded by Arctic flora, which were undergoing their own southward migration. As H.P. Banks suggests, assuming a migration rate averaging just over 5 feet per year, distribution of the tropical species would extend one mile further to the south each 1,000 years. At a constant rate of migration, these plants would be displaced 2,000 miles to the south, to a then-favorable subtropical climate, within 2 million years. The student should work out the simple mathematics of the problem to see this for himself.

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III. The Concept of Change Geological History

Being receptive to the teaching of evolution also requires an appreciation of the concept of change. The 4.54.8 billion years of the earth involve great alteration of geography, geology, and climate. These changes of the earth's appearance and character can be discussed in a variety of ways: development of an atmosphere, formation of land surfaces and continental drift, variation in sea level, sedimentation, mountain-building, volcanism, seasonality, glaciation. Sedimentation, the buildup and solidification of material which has settled out from marine and fresh waters, provides a record of the earth's history. Sedimentary rocks formed over the past 570-600 million years suggest that three different eras be recognized, the Paleozoic, Mesozoic, and Cenozoic. All time prior to the start of the Paleozoic is referred to as the Precambrian. Our earth calendar shows that the Precambrian accounts for 9/10ths of the entire history of the earth. The three eras mentioned above are divided into 12 geologic periods, and some of the periods are further broken down into epochs. For example, the Cenozoic Era, which spans the period of 70 million years ago to the present, is divided into Tertiary and Quaternary Periods. Sedimentary evidence suggests that the Tertiary (70 to 1 million years ago) was characterized by continental uplift, extensive mountain building, gradual changes in climate including cooling and drying trends, and a corresponding diversification of plant and animal life. (see Appendix, Figure 2.)

The epochs of the Tertiary are the Paleocene, Eocene, Oligocene, Miocene, and Pliocene, and each can be considered in terms of its characteristic climates, geography, geological activity, and biological makeup. Similarly, the Quaternary is divided into Pleistocene and Recent Epochs, spanning the last 1 million years. The Pleistocene was a time of major periods of glaciation in North America, four periods of cooling of most of the continent and burial under advancing ice sheets, separated by periods of glacial retreat and warming of the climate. The most recent retreat of the ice sheets occurred a scant 11,000 to 12,000 years ago.

It is not being suggested that students memorize the geologic chart in their study of plant evolution. That is an activity which is best left undone. It is, however, important for the student to learn something of the natural forces which shape the earth. It is important to realize that the New Haven of today is not the same as the New Haven of fifty years ago. By initially focusing on short term natural or man-made alterations of an area, visible over the course of a generation or less, a study of more gradual change is made easier.

Being provided with a chart of the geologic periods and completing sections of the chart can help to reenforce one's appreciation and awareness of change. The lesson gained does not have to do with what was going on during the Devonian or the Mississippian, but rather with the understanding that the earth, its physical and biological components are in a constant state of flux. Some changes are very slow, others are rapid and dramatic, but change there is.

In a later section of this unit the student makes comparisons between the environments of an area separated by a span of 300 million years. The plant life and climate of a typical lowland coal swamp of the Carboniferous are compared with the vegetation and climate of a present deciduous hardwood forest. It is this type of activity which best emphasizes the levels of change undergone through time.

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IV. Paleobotanical Evidence The Formation of Fossils

The history of plant life on earth is studied through an examination of living forms, as well as of fossilized plant remains from the past. In the next section of this unit the major divisions of plants, both living and extinct, are briefly described. Let us now consider the various ways in which plant fossils have been formed. Paleobotany is the science that studies fossilized plant material. Fossils the word means 'extracted from the earth' or 'dug up' are produced through a combination of physical and chemical processes acting on the remains of organisms. Most plants are rapidly decomposed after dying, and in this sense plant fossils are rare. Many plant types grow in areas where preservation is unlikely, such as in uplands; sedimentary deposits are usually required for fossils to form. Soft parts are especially prone to decay. In spite of the odds being very much against any individual plant being preserved, there are many localities throughout the world where fossil plants are abundant.

Plant matter is protected from rapid decomposition by burial in sediment, soon after death. Clay, mud, sand, and suspended particles in the oceans, freshwater lakes and streams, and swamplands are capable of being deposited around plant tissue. Burial in volcanic ash will also protect plant remains. Sedimentary deposits, like clay and sand, undergo compression and solidification in time to yield shales, sandstones, and limestones. It is in this sedimentary rock that one looks for fossils.

Different processes of preservation result in the following types of fossils:

1. compactions These are fossils found in peat, brown coals (lignites), and other soft sediments. The plant remains, frequently seeds and fruits of the Tertiary or younger, are entirely of original organic material. They are three-dimensional fossils which have been somewhat flattened and reduced in volume. As with living plant tissue, compactions can be sectioned and examined microscopically for cellular structure.

2. compressions and impressions When fine-grained sedimentary deposits containing dead plants are subjected to the extreme weight of overlying strata, so that the air and water are driven out, compressions and impressions may form. The plant matter, usually leaves but also trunks, stems, and roots, is reduced to a "thin carbonaceous film" or is "coalified." This method of fossilization is also known as carbonization. If a two-dimensional positive image is formed, it is called a compression. In this case the only original organic matter left of the leaf or stem is the thin layer of carbon. Negative images, or imprints, are called impressions. They are also two-dimensional, but they are lacking in any original material. Those compressions which have remnants of waxy leaf cuticle can give thin peels suitable for microscopic examination. Leaf venation is evident. The cellular structure of underlying remains can be detected. Some deformation of the plant does occur. Compressions and impressions are not necessarily found in concert.
________Among the more abundant of sedimentary deposits containing compressions and impressions are the coal deposits of the Carboniferous Period. In the case of coal formation, the coal itself, which we call a fossil fuel, consists of vegetable matter too altered to yield recognizable fossils. The well-known fossils of the Carboniferous swamps come from the clay and silt deposits above and below the coal layer. Hard coal (anthracite) is in fact the end product of a series of physical and chemical processes which convert peat first into lignite, then into soft, or bituminous coal. When considering energy production and use, it should be realized that anthracite burns cleaner and hotter than soft coals, and is in

3. petrifactions In some sedimentary deposits the surrounding water is high in mineral content; silica ($SiO2$) or Calcium Carbonate ($CaCO3$) may be present, but also iron and manganese oxides. These salts precipitate out of solution and collect inside any plant matter present. The plant matter may be replaced during mineralization, but usually cell cavities are filled, enclosing the original plant material. Thin sections from throughout these three-dimensional fossils reveal beautifully preserved cell structure under the microscope. Striking colors result from the presence of the oxides. The best-known petrifactions are the "petrified woods", particularly those of the Petrified Forest in Arizona and of Yellowstone National Park. These are coniferous trees of the Triassic.

Silicified or petrified woods are not the only examples of petrifactions. The coal balls of the Carboniferous, which contain well-preserved material from the lowland coal swamps, are also products of this type of fossilization.

4. casts and molds These fossils actually consist of no original plant material, and they show no cellular structure. They are, though, very useful and accurate renditions of surface structure or internal layering of wood and bark. When a root or stem trapped in sediment decays away, the surrounding deposits may be solid enough to retain their shape. The mold which results solidifies as a faithful copy of the exterior surface of the solid plant part. If the cavity left behind is then filled with new deposits, a cast is produced, identical to the original plant. Many times molds and casts occur together. Plants commonly preserved in this fashion are the roots and wood of treelike club mosses and horsetails. The bark of these plants occurred in several layers, and casts very different in appearance may actually come from the same plant. The dinosaur tracks common to the red sandstone of the Connecticut Valley are molds and casts left behind from creatures which walked in clay and mud deposits.

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V. The Diversity of Plant Life The Major Divisions of Plants

In this section the major divisions of plants and the basic characteristics of each type of plant will be listed. Some comparisons will be made between extinct species and present day forms. But first, some mention should be made of our understanding of the origin of life on earth and the major events which must have taken place prior to the arrival of the land plants. The oldest known life consists of forms of bacteria, blue-green algae, and green algae, all of which probably resided in salt water environments. Earlier this summer an announcement was made of the 1977 discovery of the oldest known biological life. U.C.L.A. paleobotanist J. William Schopf and an international team of scientists had delayed announcement of the find for three years, while extensive tests were run on these filaments of cells to determine their age, chemical makeup and microscopic appearance. The studies convinced the group that this cellular life existed little more than one billion years after the earth's formation. The findings also suggest that a period of organic evolution took place much closer to the origins of the planet than previously realized. The 3.5 billion year old cells are near-identical in appearance to some present day bacteria, and more primitive forms must have preceded them.

Much additional evidence of life from approximately half a billion to three billion years ago has been gathered in the past 15 years, most notably by Elso S. Barghoorn of Harvard and by Schopf. The 3.2 billion year old chert of the Fig Tree formation in Transvaal, South Africa contains spherical microfassils named Eobacterium. Chert (a flintlike or quartz-like rock) from the Gunflint formation in western Ontario, dated to 2.0 billion years ago, contains filamentous structures resembling present day blue-green algae. This is believed to be early evidence of photosynthetic activity. These above-mentioned microfossils were found chiefly during the examination of stromatolytes, dome-shaped layered deposits of material found in various regions of the world, which are a type of organosedimentary structure. The stromatolytes were formed by the action of early life. They are the indirect evidence of early life, rather than consisting entirely of fossilized life. They do, as mentioned, contain some actual remnants of life. Stromatolytes are comparable in form to the algal mats produced under certain conditions today.

Bacteria and blue-green algae have a prokaryotic organization. Their cells lack true nuclei, because of the absence of a nuclear membrane. The cellular unit of plants and animals is the more advanced eukaryotic cell, in which nuclear material is set off from the cytoplasm of the cell by a nuclear membrane. Eukaryotic cells first appear in the fossil record in the 0.5 billion year old Bitter Springs charts, also in Australia's Northern Territory. These cells are evidently photosynthetic and they most closely resemble the green algae. The eukaryotic organization achieved 500 million years ago led to rapid evolution of multicellularity in plants and animals, and most significantly to life on land. By 400 million years ago a number of distinct plant types had begun to appear. Since then each group has experienced diversification and varying degrees of success. There have been dominant plant types throughout this time, and there have been a number of extinctions. Some of these developments are listed below.

Thallophytes: algae These eukaryotic plants, which ore classified primarily on the basis of color (green. goldenbrown. brown, red) lack true roots, stems, and leaves. Their aquatic environments hove o stability not offered to plants living on land. The niches occupied by today's algae ore

in many ways the same as those filled by the green algae of 500 million years ago.

fungi The decomposers of the plant world, fungi have been found in the fossil record in deposits as early as the Rhynie charts of the Middle Devonian. As with the algae, much remains to be learned about the early forms of these non-green plants and their phylogenetic histories.

Bryophytes: mosses and liverworts These plants possess a greater specialization of tissues than is found among the thallophytes. True roots do not exist, but the mosses and liverworts have distinct leaf-like forms. Their fossils are quite rare.

Tracheophytes: club mosses Once the dominant plants of the forest (Carboniferous Period), the club mosses, also called lycopods or lycopsids, are reduced today to five genera and approximately 900 distinct species, all small and herbaceous. They possess true roots, stems, and leaves, as is true with all tracheophytes. The most common living members are Lycopodium and Selaginella, which enjoy widespread distribution. The club mosses are characterized by scale-like leaves and a dichotomous branching of the stem. During the Carboniferous the most conspicuous forms were the arborescent lycopsids, especially Lepidodendron and Sigillaria. The herbaceous Lycopodites and Selaginellites were also common plants of the period. Tree-like forms had a two-layered bark, which is well preserved in molds and casts. Their evolutionary significance lies mainly in the advances made in branching and in the development of a more complex rooting system, an example of differentiation of plant tissue. Their remains are one of the chief ingredients of coal.

horsetails These lower vascular plants, also called sphenopsids, are even more reduced in diversity today than the club mosses. Equisetum is the only living genus. The leaves are reduced in size, and the stem and cones of horsetails are characterized by the presence of ridges (nodes and internodes). The arborescent horsetails, especially Calamites, were dominant in the Carboniferous lowland swamps, and herbaceous forms (e.g., Sphenophyllum) were common. They faced the same Permian extinctions which greatly reduced the diversity of the club mosses. The present day plants continue to grow in moist habitats.

pteropsids, including: ferns These plants range from the commonly known hernaceous ferns of Connecticut forests to very large tree-like species, usually of more tropical climates. Psaronius is a 20 to 25 foot toll fern of the Carboniferous. A separate category of fern-like plant was the seed fern; these plants bore foliage typical of a fern, but they also bore seeds, a gymnosperm-like characteristic. Seed ferns were present during the late Devonian and persisted until the Permian. Medullosa is a common example from the Carboniferous. True ferns are a group of plants which appeared fairly early in the history of land plants, and they continue to adapt successfully to the earth's environments.

gymnosperms: the cycadeoids Cycadeoids were present during the early Triassic and survived until the end of the Cretaceous, when this form of gymnosperm became completely extinct. They had large, fern-like leaves, which grew from a thick, barrel-shaped trunk. During processes of preservation, leaves almost always became dissociated from trunks, and are found separately as fossils today. The trunks bear two types of scars, from the leaf bases and from the reproductive organs. Yale's Peabody Museum of Natural History has an outstanding collection of these rare fossils, most collected from the Black Hills of South Dakota by G.R. Wieland. These and other gymnosperms are seed plants.

cycads Fossil leaves of cycads are essentially indistinguishable from those of the cycadeoids. These two plant types, which also have similar short, thick trunks, are classified separately on the basis of reproductive anatomies (particularly cone structure). Some present day cycads are arborescent, an Australian species growing as tall as 60 feet.

ginkgos These plants were present during the Permian, or perhaps as early as the Carboniferous. One species remains alive today, native to remote forests of China, and planted widely as an ornamental tree. Leaves of these plants are fan-shaped, sometimes deeply lobed, and with a characteristic venation. Because the ginkgo has remained largely unchanged in appearance for many millions of years, it is referred to as a "living fossil."

conifers The conifers have been present on earth since before the Carboniferous, and they are a group of plants which once had a greater diversity than is evidenced today. The seven present day families include pine, spruce, fir, hemlock, juniper, cypress, bald cypress, and the largest forms of life on earth, the Sequoias (S. gigantea the largest plants; S. sempervirens the tollest). Conifers are usually evergreens and their leaves appear as needles. They ore more prevalent in temperate parts of the world.

angiosperms Recognized as the most advanced plants on earth, the angiosperms contribute the reproductive structure of the flower to the seed habit of life. These "covered seed" plants enclose their ovules in hollow ovaries. They are abundant and exceedingly diverse plants, with more than 200,000 species known to exist. Angiosperms first appeared as long ago os 135 million years, and they began their present dominance 70 to 100 million years ago. The two basic forms of angiosperms are the monocotyledons and dicotyledons, which are distinguished by the number of embryonic leaves, the arrangement of vascular bundles in stems and roots, leaf venation, and groupings of petals in the flowers. Angiosperm families are grouped primarily on the basis of floral structure.

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VI. An Overview of Plant Evolution Trends in Evolution

Paleobotanical work of this century has provided many clues to the evolutionary history of the plant kingdom. A detailed description of phylogenies for the major divisions of plants is beyond the scope of this unit. It is important, however, to identify some of the most significant trends in the evolution of plants, any one of which could be explored to a degree in the classroom. The following trends in evolution are judged to be of greatest significance as plants attained higher levels of complexity. a) method of energy use heterotrophic and anaerobic life forms leading to autotrophic and aerobic life forms. It is generally believed that the earth's atmosphere did not have high levels of oxygen until the evolution of photosynthetic plants. Early life forms must necessarily have existed under anaerobic conditions. They were heterotrophic forms of life, meaning that foods and necessary nutrients were obtained externally, most likely through processes of fermentation. Later, autotrophic organisms developed which could produce their own food, through the process of photosynthesis. A consequence of autotrophic life is development of aerobic life.

b) cellular organization Prokaryotic cells, with less organized nuclear material leading to eukaryotic cells, with true nuclei; unicellular life forms leading to multicellularity.

c) ecological niches occupied aquatic (marine and freshwater) forms leading to the development of the land plant. The principal obstacle to overcome was the tendency to dry out in a nonaqueous environment. Anatomical advances, such as a thickening of cell walls and a system of transporting water and minerals throughout plant tissues, were required for successful development of the land habit.

d) differentiation of plant tissues branching; evolution of roots, stems, and leaves; development of the seed. Early land plants lacked branching. Greater complexity of growth was attained by plants which had a dichotomous pattern of branching, two equal axes being formed at each fork. Ultimately, trilateral branching off a main stem evolved. The evolution of the seed is considered to be one of the most significant advances of the land plants.

e) plant size the herbaceous habit leading to the arborescent habit. It is not to be assumed that larger plants are more complex or advanced plants. It is true, in the plant world as well as the animal world, that many life forms have followed a trend toward larger and larger representatives. The club mosses and horsetails are examples of plants which achieved gigantism and dominance, only to be followed by extinction of the large forms.

f) mechanisms of reproduction spore size; asexual reproduction leading to sexual reproduction. Early land plants were homosporous; they had reproductive spores of one type, one size. An important advance in the move toward seed production was heterosporous reproduction, where two distinct reproductive cells, of differing sizes, were produced by plants. The development of sexual reproduction and of the seed allows for increased efficiency of reproduction and the increased possibility of genetic variability.

g) coevolution with animals The angiosperms have undergone an accelerated evolution during their 135 million year history largely as a response to the pressures exerted by insect predators. They have adapted to life with insects not only as a means for defense as is the case with the conifers, for example but also in ways which have increased the reproductive advantage and dispersal advantage of these plants. The wide variety of flower types among the angiosperms, and the extremely elaborate ways in which some species have coevolved with particular species of insects (orchids and wasps, for example) give ample evidence that they have attained a degree of success in exploiting their environments that has never been attained by other plant types. The two sections that follow will be most useful in the teaching of plant evolution because of the attention that they give to the concept of change over time, and to the methods of fossilization of plant tissues. It is suggested that emphasizing the differences between two ecologies widely separated in time will be more effective in teaching biological change than would the in-depth tracing of any plant phylogeny, particularly with high school students. Paleobotany and plant anatomy can become very involved disciplines, and the knowledge required to fully appreciate the modifications undergone by plants throughout their evolutionary histories is beyond the level of most high school students. Class time which concentrates on some comparisons of plant forms and ecological niches occupied by these plants, as well as on methods of locating and studying preserved plants, will be most productive in this study of evolutionary biology.

The Lowland Swamp Forest of the Carboniferous and the Present Day Northern Deciduous Hardwood Forest

A very effective way to apply the concepts of time and change to the study of the evolution of plants is to have the student make direct comparisons between the floras of two widely separated geologic periods. The vegetation of the Upper Carboniferous (Pennsylvanian, 300 million years B.P.) is well known for the eastern United States, and it is fairly easy to make comparisons between the flora of this period and the flora of a modern Connecticut forest. The disturbances of man in Connecticut have eliminated essentially all virgin forest in the state, but much is known about these former hemlock-hardwood forests.

The two forests should be compared on several different levels: in terms of climate, environment, and anatomical features of representative plants. Six genera of plants which characterize the Carboniferous are: Lepidodendron (an arborescent lycopsid); Calamites (an arborescent sphenopsid); Sphenophyllum (an herbaceous sphenopsid); Cordaites (a gymnosperm); Psaronius (a tree fern); and Medullosa (a seed fern). (See Appendix, Figure 3). These genera represent a cross section of the flora common to the Carboniferous, and they are the plants which were dominant and abundant during the period.

For their similar abundance and dominance in Connecticut's deciduous hardwood forests and for the similarity in the niches they fill in the forest, the following present day species are selected for the comparison: Tsuga canadensis (hemlock); Fagus grandifolia (American beech; Pinus strobus (White pine); Kalmia latifolia (Mountain laurel); Oxalis montana (wood-sorrel) ; and Osmunda cinnamomea (Cinnamon fern). Either Acer saccharum (Sugar maple) or Quercus borealis (Northern red oak) can be substituted for the beech for the convenience of using a more familiar species.

During the Pennsylvanian, which lasted 45 million years, North America experienced a succession of events in which land masses would rise and seas would abate, to be followed by subsiding lands and advancing seas. Inland seas occupied large portions of North America. In the eastern part of the continent as well as throughout the world the lowland swamp predominated. The lush vegetation of these swamps has been transformed over time into the rich coal deposits of Pennsylvania and Appalachia. Carboniferous plant fossils are numerous in layers above and below the coal, preserved by submergence.

The great height of the soft-wooded trees, the large leaves of many of these plants, and the excellent preservation of very delicate leaves all suggest that the climate of the Carboniferous was warm and moist. The climate is believed to have been tropical or semi-tropical, in marked contrast to the temperate climate and the distinct alternating seasons of today. Freezing winters didn't occur in the Carboniferous.

Significant ecological differences exist between these two widely separated periods. As mentioned, the most obvious difference is that the Carboniferous forest was a lowland swamp and the deciduous forest is on higher, drier land. The Carboniferous trees (Lepidodendron, Calamites, Cordaites) grew in close proximity with standing water. The herbaceous sphenopsid Sphenophyllum may well have grown partly submerged. An important similarity, however, between the two floras is in the niches occupied by each of the plants. Lepidodendron (up to 100 feet tall) and Cordaites (50-100 feet tall) in particular formed a broad open canopy in the forest, comparable to the heights achieved by hemlock (50-100 feet), beech (75 feet), and white pine (60-100 feet), The deciduous forest probably has a tighter canopy. Intermediate levels of growth (the understory) are formed by Calamites (to 30 feet), Psaronius (20-25 feet), and Medullosa (12-15 feet) in the Carboniferous and by the present day example of Mountain laurel (15-20 feet). Sphenophyllum was a creeping, semierect plant which grew in dense clumps. Similar niches are occupied today by Wood-sorrel and by the ferns. These common features of the plants, which are all photosynthetic plants and hence producers, should be emphasized.

It is in anatomical detail that the two floras are markedly different. The coal swamps were totally lacking in deciduous trees, which had not yet made their appearance on earth. These are the dominant plants today. The most wide-spread plants of the coal swamps were the arborescent club mosses and horsetails and the gymnosperm Cordaites. Today it is the flowering plants. Some specific differences follow. Lepidodendron species were the most imposing plants in the Carboniferous forest. These "scale trees" (arborescent lycopsids) enjoyed dominance for a period of millions of years, then became extinct during the Permian. The only surviving club mosses are herbaceous plants, growing a few inches high. Lepidodendron had dichotomous branching, two forks of equal size always forming. The bark of this tree was two-layered and thick. Growth rings are not found in the trunk and branches. Calamites was another thick-barked tree. An arborescent sphenopsid, it too found extinction in the Permian. The trunk, stems, and rhizomes were jointed and had vertical ribs, a feature found today in the herbaceous Equisetum, the only surviving horsetail genus. Calamites bore aerial roots, above-ground structures found today usually among tropical trees. Lepidodendron, Calamites, and Sphenophyllum (the herbaceous sphenopsid) were spore-bearing plants.

Psaronius, a tree fern, and Medullosa, a seed-fern, were the plants most similar in appearance to a representative plant in today's forests, the modern fern. In many respects the fronds of all three plants bear strong similarities. What is noticeably different is that Psaronius was a tree-like plant, unlike any of our ferns in Connecticut. and Medullosa belonged to a now-extinct group of plants which combined the general appearance of ferns with a seed-producing habit. Cordaites was an early gymnosperm. This tree closely resembles some of the pine family members. However, Cordaites had broad, strap-shaped leaves, not needles. Also different is the method of producing seeds, in racemes, not cones.

The Stiles Clay Pit of Hamden

The Quinnipiac Valley has extensive deposits of red clay, laid down between 11,000 and 12,000 years ago during the close of the last glacial period. Our region of Connecticut is famous, in fact, for its New Haven clay, which has been quarried for brick manufacture for more than 125 years. Up until the last several years this area was the site of a major quarrying operation. Clay pits were dug in the meadowlands bordering the Quinnipiac River, and the Stiles Corporation brickyards with their kilns were located nearby. Many of the earlier buildings in town were built of the locally manufactured bricks. Bordering the marshes along State Street, from New Haven to North Haven, the deposits of clay lie between 15 and 20 feet below the present land surface and well below sea level. The clay varies in thickness, due to differential erosion of the deposits more than 7,000 years ago, but various estimates of the thickness of the clay range from a minimum of 3 to 20 feet to a maximum of more than 75 feet. Close examination would reveal that the clay actually is made up of many distinguishable layers, called varves. Each varve was laid down during post-glacial time in the course of one year, the clay material that precipitated out in the winter freezes being different in appearance from the summer silts. For this reason it is known as varved red clay. There is reference in the literature to a count of 364 varves in one 17 foot thick section of exposed clay.

In order to get to the clay, workmen had to remove the covering layers of material, which were deposited in more recent millenia. In the 1800s and early 1900s they dug manually; steam shovels were used later. The upper deposits are the ones of interest to the paleobotanist, because they are rich in compacted, semi-fossilized Plant matter. The outdoor laboratory of the Stiles clay pits has received the attention of the Yale scientific community since the early 1900s. As quarrymen labored for the important clay deposits, gealogists and ecologists studied the exposed overlying strata and their contents. At certain depths the following macroscopic plant matter has been uncovered: leaves of many types, twigs, nuts and seeds, cones, stumps and lags, some of them quite sizable, and remains of salt marsh plants and peat. Microscopically, many types of pollen are found. A cursory examination of the sediment is all that is needed to realize that there are several distinct layers present and that the geological conditions under which organic and inorganic materials were deposited varied. A summary of the geological events of this region follows.

Between 10,000 and 15,000 years ago, in late-glacial and post-glacial times, a freshwater lake had formed at the mouth of the Quinnipiac River. As the glacier slowly retreated, a mass of ice broke off, became stagnant, and dammed up river water as well as its own melting water. These deep, muddy waters were responsible for the thick buildup of the clay. During the gradual warming period which ensued, the glacial ice eventually disappeared and the ponded waters were restored to a river system. There may have followed several thousand years during which silt and sands were deposited, only to be eroded away along with some of the underlying clay.

Today a four foot layer of coarse sandy material lies immediately above the red clay. It has been dated, through radiocarbon testing of an entrapped log, to 7,000 years before present. There is no indication that this sand was deposited under salt water conditions. Rather, the freshwater river, moving at a rate fast enough to carry along fairly heavy sand particles is responsible for these deposits. Logs and stumps are found throughout this layer and also in the four foot layer of finer gray sand above, apparently deposited by more slowly-moving waters. There are also layers in which nuts and seeds are common, or thicknesses of matted leaves. These important fossil-bearing strata are now located 10 to 18 feet below the surface. It is this material which shows the early stages of fossilization.

Found in this “basal alluvium” are the remains of wood, leaves, and reproductive structures of beech (the predominant species of tree), hemlock, hickory, pine, oak, and buttonwood. The logs present are not in their natural positions but instead were washed into the area, where they sank and became buried. The remnants of shrubs and of a number of herbaceous plants are also contained in the sandy layers. These findings are suggestive of a shallow stream or river environment, surrounded by a beech forest. In the upper portion of the fine sandy layer maple is found, indicating that the region changed over to a freshwater marsh for a period of time. A log in this upper layer of sand is radiocarbon-dated to 3560+80 years B.P.

All material lying above the sand is peat, and it forms a layer approximately 10 feet thick. The peat contains remains of Spartina and Phragmites, grasses. This is salt water tidal marsh vegetation, and it indicates that for the last 3,500 years the region was at sea level, and that the tidal conditions had killed off all freshwater trees, shrubs, and herbs. The peat accumulated slowly from succeeding growths of marsh grasses. The balance between sedimentation and submergence of the land (or a rising sea level) had shifted to conditions which persisted until recently.

When man intervened and constructed a dike and railroad bridges downriver, the now-protected area changed over to a freshwater marsh habitat, characterized by the growth of Typha (cattail). It is now referred to as an estuarine freshwater marsh. The same species growing 3,000 to 7,000 years ago in the area of the Quinnipiac River are found in the surrounding area today. A walk through the thickets that lie south of the clay pit turns up wild grape vines and raspberry canes, whose seeds are preserved in the clay pits. Beech trees, maples, and oaks also make up the thickets.

Today the New Haven clay is no longer quarried in Stiles clay pit. A series of quarried and abandoned pits are found to the east of State Street, filled up with water. The most recent site to be dug is now being used for landfill, meaning that it is a garbage dump. It will eventually revert to marshland or be filled in above sea level. Presently below sea level, the pit is protected by a dike from the nearby tidal waters and it is continually being pumped of water that seeps in from the uplands, just as it was pumped during the brickmaking period. One expanse of the pit remains where a 14 foot high cross section of the peat and sandy layers can be seen. The brick clay now lies out of view.

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VII. Unit Outline and Sample Lesson Plans

I. Introduction.

____Lesson 1: (2-3 days) Introduction to the study of plant evolution—evolution the unifying theory of biology. (a review, making use of slides & photographs)

II.The Concept of Time

Lesson 2: Preparation of an Earth Calendar
(2 days)
Lesson 3: Plant Migration Time

(1 day)

III. The Concept of Change Geological History

Lesson 4: (1 day) Ecological Change (a brief review of the effects of wind, waves, erosion, volcanic action, earthquakes)

Lesson 5: Preparing a Chart of the Geological Periods (2 days)

IV. The Diversity of Life The Major Divisions of Plants

Lesson 6: Slides: The Diversity of Plant Life (Set #1) (2 days)

Lesson 7: Preparing Herbarium Specimens

(2 days)

Lesson 8: A Trip to an Herbarium

(1 day)

V. Paleobotanical Evidence The Formation of Fossils
Lesson 9: The Stiles Clay Pits 7,000 Year Old

(2 days) Plant Remains Lesson 10: How Fossils are Formed

(1 day)

VI. An Overview of Plant Evolution
Lesson 11: (1-2 days) Language used in the study of plant evolution (Slides: The Yale Peabody Museum of Natural
History The Paleobotany Collection) (Set #III) Lesson 12: Slides: Plant Evolution The Fossil Evidence

(3 days) (Set #II)

Lesson 13: The Teaching Collection of Fossil Plants
Lesson 14: (3 days) Comparing a Carboniferous Forest with a present day Deciduous Hardwood Forest. (Trip to a local Hardwood Forest)
VII. Conclusion.
Lesson 15: Review and Evaluation of Unit

(1 day)

Sample Lesson Plans

Preparing Herbarium Specimens
(materials: vasculum (optional); garden clippers; notebook; plant press; herbarium sheets; Elmer's glue; needle & thread; labels; field guide to trees.)(Suggested trees: Red oak, White oak, Sugar maple, Silver maple, Elm, Beech, Ginkgo)

Procedure:
More than 250,000 different species of plants have been named and described by botanists, and estimates of the total number of plant species on earth run to 800,000 or more. Obviously, many plants in various parts of the world have not yet been properly described. Botanists have developed a system for preserving and describing plants collected in the field. Specimens are located and the different parts of the plant are removed for drying. Large structures, such as wood samples, fruits, and cones, are

usually just stored in boxes. Smaller, flat structures. including branches and leaves. receive more specific treatment.

You will be following procedures for collecting and preparing plant specimens. The 'herbarium sheets' which you make will be useful to others in identifying and describing plants.

A. Collecting specimens from trees.
(In the field . . .) Select one of the trees in the area and describe the appearance of the tree. Make note of the following: height, overall shape of tree, diameter of trunk near ground level, color and appearance of bark, position of branches. Make simple sketches or drawings of the tree or its parts. These drawings will be helpful to you when you return to the laboratory to identify the tree. Collect a leaf sample from the tree, looking for a small branch which has leaves in good condition (not chewed up or damaged). Do not select leaves which are very large or very small for the tree. Also collect any fruit, cone, or nut samples that may be found on the tree. If you have a vasculum, put the leaf samples inside it to help prevent drying out.
B. Pressing the leaves.
A stem with 2 to 4 good leaves on it is best to use. Place the sample in a spread out position between the sheets of newspaper, which in turn go between sheets of blotter paper and corrugated cardboard. When your specimens and those of the others have been put in the press, it is strapped together tightly. Herbaria usually prop the plant presses over enclosed hot plates to speed the drying process. . . . After 1 2 days, check the specimens for dryness and flatness.

C. Preparing the herbarium sheets.

Herbarium sheets come in a standard size 12" x 17". Place your dried specimen on the paper. gluing it to the paper with small amounts of Elmer's glue. If the branch is somewhat thick, it may be necessary to sew it onto the sheet at several points. This is a technique which requires an amount of skill, but give it your best try. Use the guidebook and your notes from the field to identify the specimen. Record the following information on the label: Date, Record No., Location, Description. Common Name, Botamical (Latin) Name. Family, Collected by———.

The Stiles Clay Pit of Hamden, Connecticut

(Laboratory materials: Walks and Rides in Central Connecticut and Massachusetts, Longwell & Dana; Stiles Corp. bricks; Diagram: The Stiles Clay Pit (cross section); prints of Stiles Clay Pit; sample material from the different levels of the pit; tree stump (3,500 5,000 yr. old); samples of matted leaves; chemicals: $HNO3$ (dil) and glycerin.)

Procedure:

1. Read Longwell & Dana, "To The Clay Pits And Brickyards Of Quinnipiac Valley," pp. 120-122, the day before the lab period.

2. Define the following word: varves -

3. Compare the 75 yr. old brick from Stiles Brickyards with the newly-made brick. In what ways do they differ in appearance? The brickyards operated from 1854 until 2-3 yrs. ago.

4. Study the cross sectional diagram of the pit. At what depths would you expect to find semi-fossilized plant parts?

5. In the room are jars containing samples gathered from depths of 1, 6, 14, 17, and 20 feet. Describe the color & appearance of each sample; describe briefly any plant parts in each jar.

6. Study the peat layer from the pit. How thick is this layer in the pit? Spend the next 5 minutes removing plant matter from the peat, trying not to break the leaves, etc.. Describe what you remove & compare it with herbarium sheets for Spartina, Phragmites, and Typha. a) write common names for each of these plants; b) can you identify any of the fragments?

7. Examine the section of hemlock stump & count the tree rings to determine the age of the tree when it died. Stumps & logs from the pit were not found in upright positions, but rather lying on their sides. What does this tell you about where the trees were growing and how they got into the area of the pit?

8. Obtain a sample of matted leaves. These leaves were found at a depth of 13 1/2 ft., as shown on the diagram. Using scalpel or tweezers, pry into the edae of the leaf mat & expose a clean-looking inner surface of leaves. Repeat 2-3 times, until you have a thin layer of matted leaves. Now soak the leaves in dilute nitric acid to separate off individual leaves for study. (NOTE TO THE TEACHER: CAUTION HNO3 is a very caustic chemical & must be handled carefully. If your students are not experienced in handling acids, perform this step prior to class.) When the individual leaves are loose, gently lift them out, rinse in water, & set them aside. Did any seeds float to the surface? If so, save them. Make sketches of 3 of the leaves. Compare the leaves & sketches to the ff. herbarium sheets: American beech; Sugar maple; Buttonwood; American elm; birch sp.; White oak; Basswood. Pay particular attention to the overall shape of the leaf & the pattern of leaf veins. Can you now identify any of the leaves isolated from the leaf mat? Are they in any way different from the corresponding herbarium specimens? Carefully transfer any whole separated leaves to the glycerin container & clean up all laboratory materials.

Plant Evolution: The Fossil Evidence (Slide Set II & worksheet)

slides #1,2: Fossil hunting. These people are searching layers of sedimentary rock for plant fossils. How do you think these rock layers were formed?

slide #3: Fig Tree microfossils. This stratum of rock in South Africa is one of the oldest known formations of rock on earth, dated to 3.2 billion yrs. ago. Describe the microfossils contained in this rock.

slide #4: Gunflint chert, stromatolytes. Stromatolytes are believed to be the fossilized evidence of plant growth from many millions of yrs. ago. This stromatolyte may have been produced by the growth of bluegreen algae, simple photosynthetic plants. The rock is 2.0 billion years old.

slide #5: Gunflint chert, spore-like bodies & filaments of blue-green algae. How old was the earth at this time?

slide #6: Reconstruction Middle Devonian plants. This slide shows the way a forest of 375 million yrs. ago may have looked. This & the ff. slides are of plant life from the Paleozoic, Mesozoic, & Cenozoic Eras, which span the past 570 million yrs. These more recent times are much better known than the Precambrian time of the first several slides.

slide #7: Devonian alga. By the Devonian period a variety of simple plants lived on land. Water plants, such as algae, continued to be successful, though. This alga is one example of a Devonian thallophyte.

slide #8: Psilophyton. This vascular plant from 390 million yrs. ago is important because of the branching that arises from the main stem. It is a more complex type of branching than earlier plants had. What is a vascular plant?

slide #9: Devonian lycopod, Archaeosigillaria. This plant is of a different type from Psilophyton. What structures did the plant have that Psilophyton lacked?

slide #10: Archaeopteris. This plant is called a progymnosperm. It was one of a group of plants which gave rise to the gymnosperms, of which many examples are alive today. Name some plants which have needles.

slides 11-13: Reconstruction Carboniferous forest. We will compare this 300 million yr. old forest with one of today. First, let's take a closer look at the plants growing here.

slides 14-19: Lepidodendron reconstruction, cast & mold, roots, cones. This lycopod (club moss) was a tree which grew to be 100 ft. tall. Describe the bark of the tree. What caused the diamond-shaped 'scars' on the tree?

slide #20: Sigillaria reconstruction. In what ways was this club moss similar to Lepidodendron?

slides 21-24: Calamites reconstruction, stem anatomy foliage. This plant is a giant arborescent sphenopsid, or horsetail, which grew to 30 ft. or more. What does the word "arborescent" mean? (Hint: Arbor Day) The club mosses & horsetails reproduced by spores, not seeds. What other plants, living today, produce spores?

slides 25,26: Sphenophyllum, reconstruction & fossil. Unlike the plant Calamites, this horsetail is an herbaceous plant. What does "herbaceous" mean?

slide #27: Equisetites, Stuttgart Germany.

slides 28,29: Psaronius, reconstruction & foliage. These leaves (fronds) are very similar to those of some present day plants. Name the plants.

slides 30,31: Medullosa reconstruction & foliage. This fern-like plant produced seeds.

slides 32,33: Cordaites reconstruction & foliage. The tree shown here is a forerunner of today's conifers. In what ways are its leaves different from conifer leaves, however?

slide #34: Reconstruction Mesozoic Era. Name the types of plaits shown in this reconstruction.

slide #35: Specimen Ridge, Yellowstone National Park. These are among the best-known fossil plants. What are they?

slides #36,37: Petrified tree, cross section of wood. What are you able to see in this fossil?

slide #38: a mid-Jurassic Ginkgo fossil foliage.

slide #39: Metaseguoia, a fossil conifer.

slide #40: Proaraucaria, fossil cones. Gymnosperms are plants with "naked seeds." Where in the cone are the seeds located? Why are they called "naked"?

slide #41: Pinus fossil, the cone.

slides #42-45: Cycadeoidea, reconstruction, trunk, polished lateral cross section, longitudinal section, collecting cycadeoids. This extinct plant lived 150 million years ago. The Peabody Museum at Yale has one of the finest collections of cycadeoid fossils in the world. Can you tell the difference between the leaf scars & the scars left by the reproductive organs?

slide #46: Reconstruction Tertiary forest.

slide #47: tree cast, Oregon cascades.

slides #48-50: angiosperms: Astranium, Sassafras, Ulmus. Flowering plants have been the dominant plants on earth for 100 million years or so. What type of reproductive structure is produced by a flower? Fossils are produced as compactions, compressions & impressions, casts & molds. What type of fossil is the Ulmus leaf?

slides #51, 52: Generalized climatic zones, Late Eocene-Early Oligocene & Late Oligocene Early Miocene.

slide #53: Cartoon, "South America Secedes" (continental drift)

The Earth Calendar

In order to improve one's perspective on the magnitude of geologic time, a special earth calendar is devised. The entire 4.8 billion year history of the earth is condensed into one calendar year. The following events can then be plotted:. January 1 the formation of the earth

April 1 chemical evolution is occurring

April 8 the oldest known biological cells appear

May 1 the prokaryotic cell Eobacterium Fig Tree formation, Transvaal, South Africa

July 1 the first primitive photosynthetic organisms (filamentous blue-green algae) Gunflint Iron Formation, western Ontario (Gunflint chert)

October 15 in addition to filamentous blue-green algae, there are green algae (the first eukaryotic cells) Bitter Springs Formation, Northern Territory, Australia

November 18 beginning of the Paleozoic Era. End of the Precambrian

November 18-22 sudden and dramatic appearance of diverse marine plant and animal life

December 1 first (Vascular) land plants

December 4 the diversification of lycopsids. first leaves. advent of the seed and of arborescence.

December 6-10 the Pennsylvanian lowland coal-swamp forests (carbonif.)

December 10 seed ferns become extinct

December 11-14 extensive Permian extinctions (arborescent lycopsids and sphenopsids disappear).

December 17-21 the Jurassic: conifers, seed ferns, and cycads dominate

December 21-26 the Cretaceous: dominance of the gymnosperms. Cycadeoids become extinct. First angiosperms appear.

December 23 angiosperms begin dominance over all other plant types.

December 25 the modern angiosperm genus Platanus traces back this for

December 30-mid Dec 31 the Miocene: diversification of herbs

December 31 7:24 P.M. the appearance of man (Richard Leakey's KNM-ER1470, Homo habilis)

December 31 8:18 P.M. many subtropical plants of North America become extinct.

December 31 11:58.40 P.M. varved red clay has been deposited along the Quinnipiac River Basin.

December 31 11:59.14 P.M. sedimentation of coarse gray sand above the New Haven red clay.

CD : - Blu
- musique Zaïroise
- Destiney Child
- Muray !

Water
onions
Tooth paste