Amber: A Botanical Inquiry

Amber provides an evolutionary framework for interdisciplinary studies of resin-secreting plants.

Jean H. Langenheim

Amber has fascinated man since he first discovered it along the shores of the North and Baltic seas in Neolithic times. He gathered it not only because it was esthetically appealing but also because he believed it possessed mystical healing and protective powers. The belief in supernatural powers of Baltic amber may be partially explained by its link with sun worship and is reflected in the Greek name for amber, *elektron*, which means "substance of the sun" (*1*). The negative electrical properties of amber and the remnants of life trapped inside it also have contributed to the belief in its mysterious nature.

Many ideas on possible origins of amber were presented in classical literature (*1*) before Pliny in his *Historia Naturalis* (A.D. 77) recognized it as a plant product "produced from a marrow discharged by trees belonging to the pine genus, like gum from a cherry, and resin from an ordinary pine" (*2*). Despite Pliny's astute observation, amber continued to be so highly esteemed as a semiprecious gem that its study and classification generally have been mineralogically oriented.

The impact of Darwinian concepts during the latter part of the 19th century led to an era of prolific study of the plants and insects enclosed in the amber. Until now, the weight of biological interest in amber has rested in the continued study of these inclusions. Recently, with new scientific perspectives and new powerful analytic tools, the age-old fascination with amber is undergoing a renaissance based on its great interest as a stable resin. In this context amber places the fundamental problems of resinous secretion in living populations into the broad perspective of geologic time.

Amber: Fossilized Resin

Relatively little significant progress has been made since Pliny's statement in characterizing amber chemically as a resin and identifying various plant sources. Most commonly the term *amber* is employed as a generic concept for all fossil resins and will be used in that sense here. However, "true amber" is considered by some (*3*) only to refer to succinite, the mineralogical species of fossil resin comprising the bulk of the Baltic Coast deposits. Amber also is frequently called a fossil "gum" because the distinction between resins and gums is not clear. For example, some plant anatomists have loosely referred to resins from angiosperms as "gums" (*4*) and the term *gum* is commonly used interchangeably with *resin* in the turpentine and copal industries (*5*). Gums chemically are hydrophilic polysaccharides which, being water-soluble, cannot become fossilized.

Resins are complex mixtures of mono-, sesqui-, di-, and triterpenoids. The terpenoids possess structures based on the linking together of isoprene (C_5H_8) units. The isoprene precursor is mevalonic acid, and the active isoprene is isopentenyl pyrophosphate which is the structural unit of all terpenoids (Fig. 1). The linking of isopentenyl pyrophosphate and dimethylallyl pyrophosphate to give geranyl pyrophosphate is the starting point for the formation of the majority of plant terpenes. The multiplicity of natural terpenoids is formed by variation in the subsequent mode of condensation. Most mono-, sesqui-, di-, and polyterpenes are a result of "head-to-tail" condensation of isoprenoid units, whereas triterpenes and tetraterpenes can be formed by "tail-to-tail" dimerization of C_{15} and C_{20} units.

Although mono-, sesqui-, di-, and polyterpenes occasionally occur among algae, fungi, and cryptogams, they are regarded as typical constituents of higher land plants. The steroids (triterpenes) and carotenoids (tetraterpenes), on the other hand, are distributed generally. Because these latter components have significant physiological functions, they have been called the "true aims of terpene metabolism" by some (*6*), whereas the other terpenoids have been traditionally considered to be secondary by-products with no metabolic function.

An understanding of the biogenetic pathways involved in the synthesis of terpenoids is of fundamental systematic importance. Substances formed by relatively simple biosynthetic processes are of less taxonomic interest than related compounds that have undergone rearrangements or other secondary changes like certain of the diterpenes. Relatively stable by-products are often the most valuable chemical substances taxonomically (*7*). In fact, the complexity of "by-products" such as plant wax hydrocarbons and resins is a positive advantage in providing taxonomic fingerprints (*8*). In addition, knowledge of biosynthetic routes may aid in detection of chemical parallelisms and convergences in evolution.

Resins are composed of volatile and nonvolatile terpenoid fractions. The volatile fraction usually consists of monoterpenes, sesquiterpenes, and some diterpene hydrocarbons; the nonvolatile fraction is primarily composed of largely unsaturated carboxylic diterpene acids and occasionally triterpene acids. Other constituents may be alcohols, aldehydes, esters, and amorphous, unsaponifiable neutral substances known as resenes. Additional nonterpenoid substances may be present in small quantities (*9*). Under natural forest conditions, the volatile fractions of most resins evaporate with varying degrees of rapidity. The remaining nonvolatile fractions can become fossilized, if they are sufficiently stable to withstand degradation and if appropriate depositional conditions are available. The possibility, however, that small amounts of volatile mono- and

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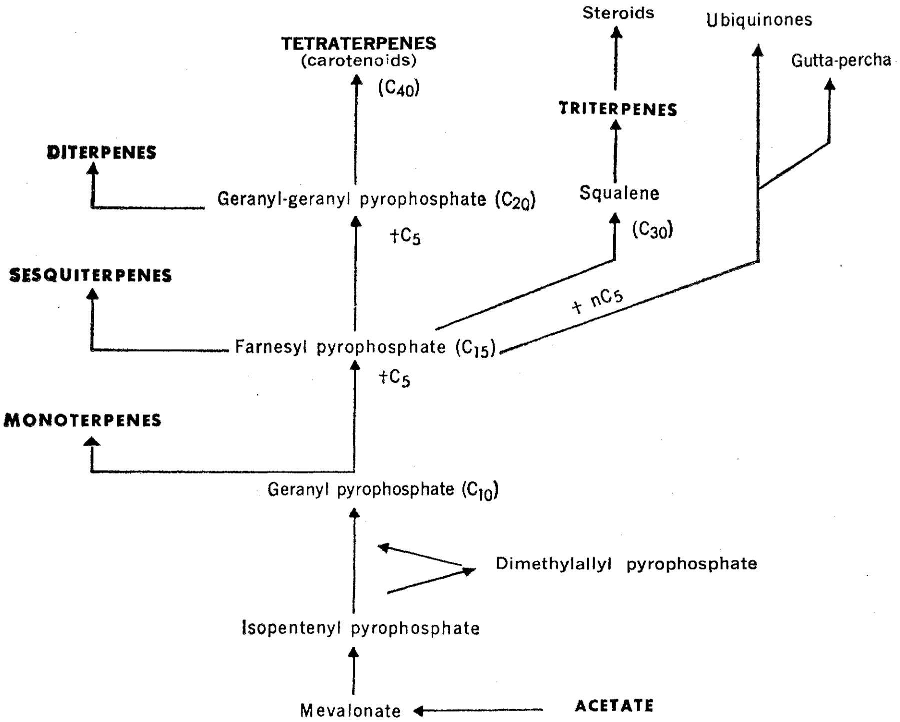


Fig. 1. Biosynthetic pathways for derivation of mono-, sesqui-, di-, and triterpenoids which comprise resins.

sesquiterpene fractions have been trapped in the nonvolatile matrix is not precluded.

Resins are synthesized in appreciable quantity by about 10 percent of the 280 plant families listed by Engler and Prantl; of 338 genera investigated, 25 percent produce resin (*10*). Among the plants, primarily trees, producing really copious quantities of resin, two-thirds are tropical. All of the genera in the coniferous families, which are primarily temperate, synthesize resins, but only the Pinaceae and Araucariaceae produce appreciable quantities. In tropical areas, the angiosperm families Leguminosae and Dipterocarpaceae are noted for their copious resin production. The Anacardiaceae, Burseraceae, Guttiferae, Styracaceae, Hamamelidaceae, Rubiaceae, Umbelliferae, Zygophyllaceae, Palmae, Liliaceae, Euphorbiaceae, Convolvulaceae, and Compositae also are prominent.

The fossilization process of resins is still not completely understood and the concept of fossilization is variously used. Resins simply buried in the soil are frequently referred to in the commercial resin literature as "fossil or subfossil" (*5*). Geologists or paleontologists, on the other hand, usually imply at least prehistoric conditions (*3*). The processes involved in fossilization of resin appear to be progressive oxidation and polymerization which presumably occur by a free-radical mechanism (*11*). The stage in these processes at which a resin is actually considered to be "fossilized," and the time interval required, have not been defined as yet.

Considerable stability in chemical structure characterizes ambers from certain populations (*12*). Coal scientists have pointed out that resins are plant products with the highest resistance to chemical attack, and suggest that the most typical stable constituents are the resin acids (*13*). Resins are resistant to the first stages of coalification, that is, the early metamorphic history of lignites. Even in low-rank bituminous coals, the resinous constituents have been so little altered that they have practically retained the composition of the parent resin (*13*). This view has been substantiated with infrared spectrophotometric studies (*14*) demonstrating that modern resins, such as that from Kauri (*Agathis australis*) as well as fossil resins from lignites and lower-rank coal deposits, show little reactivity during experimentally induced oxidation and short-time pyrolysis. Quite different spectral patterns, however, are obtained for resins from bituminous coals and it has therefore been assumed that the structure of resins probably breaks down quite rapidly with the temperature/pressure conditions in the range of those involved in the formation of the medium-volatile bituminous coals.

Preservation of resin through long periods of time cannot be attributed only to resistance to oxidative degradation but also to the capacity to withstand decomposition by soil microbiota. Although resins appear to be generally decay-resistant products, like waxes, sporopollenin, cutin, and lignin, differential resistance in resins from different sources is probable. Little attention has been given to soil organisms which might possess enzymes that break down the terpenoids composing resins.

Amber through Time and Space

Although ambers occur in deposits in various parts of the world, ranging in age from Carboniferous to the Pleistocene (Fig. 2), they have been reported most commonly from Cretaceous and Tertiary strata. In most instances, stratigraphic and associated paleontologic data are relatively poor so that well-determined ages are rare. Radioactive isotope age determinations of amber are not feasible since most of the samples are too old for C^{14} dating, and the presence of adequate amounts of potassium to utilize the potassium-argon method has not been demonstrated as yet. Table 1 summarizes available information regarding age, geographic location, geologic occurrence, and suggested botanical affinities for a great many of the recorded amber deposits.

Phytochemical Analyses of Ambers

Most previous chemical studies of amber have been mineralogically oriented because the purpose was to describe and classify amber as a semiprecious gem. During the 19th century, mineralogists described and named over 100 fossil resins, mostly of European origin (*15*). Because of the importance of Baltic amber, the early mineralogical studies of the Baltic deposits established the chemical and physical criteria that are still most commonly used in distinguishing all fossil resins. The noteworthy occurrence of succinic acid in Baltic amber (up to 8 percent) has been used as a primary characteristic in distinguishing two broad categories of fossil resins—the succinites yielding succinic acid and the retinites lacking it. Being nonterpenoid, however, succinic acid has been of little value in characterizing resins. Other properties also used in description of fossil resins, such as elemental composition, color, hardness, specific gravity, refractive index, and odor upon burning, are ill-suited for largely noncrystalline, complex organic materials and are insignificant to interpretation of the botanical origin.

A classification system of fossil resins has been proposed based upon gymnospermous or angiospermous origin and geologic age (*16*) but, because few definitive botanical and geological data have been available, such a system has been difficult to establish. The best evidence for botanical origin is the occurrence of amber within the wood or bark where it was synthesized. In some cases, although the amber has become disassociated from the parent tree, the resin-producing tree may be indicated circumstantially by associated plant fossils in the amber-bearing strata. However, because the specific gravity of amber is just slightly above 1, it floats in saltwater and therefore frequently occurs in estuarine or marine deposits where it probably has been transported some distance from its site of origin. In these cases, only the remnants of known resin-producing plants in the amber have been suggestive of the source.

Phytochemistry supplies other means of determining source trees. Moreover, it may give insight into the biochemical evolution within various genetic lineages by comparison of ambers of different ages as well as of ambers with modern resins. Sufficient stability of certain constituents has allowed a relationship to be established between some modern and fossil resins, despite potential changes or losses of constituents due to evolution, extinction within the lineages, or alteration in depositional and erosional environments.

A stumbling block to these comparative studies has been the relatively poor knowledge of the chemistry of resins from living populations. Only resins of economic importance, such as those of pines, have been analyzed extensively. More progress in terpenoid chemistry by both the biologist and chemist is now being made, especially as more adequate techniques have become available. Polymerized resins, being largely insoluble, are not amenable to most of the usual methods of elucidating structures of organic compounds. The analysis of whole amber and resin in the solid state by infrared spectrophotometry and x-ray diffraction gives preliminary but meaningful data.

Of the new tools available, infrared spectrophotometry has so far been most extensively used in analyzing amber (*12*). The large number of infrared absorption bands shown by modern and fossil resins offers a multiplicity of parameters from a single experiment (*12, 17*). The identity of two infrared spectra of pure compounds can be taken as proof of the identity of the compounds, but for resins, which consist of mixtures of components of relatively high average molecular weight, two restrictions must be made: (i) only the major constituents can be expected to give strong absorption bands and (ii) although absolute identity of spectra can never be expected, the presence of similarities does indicate structural similarity of the major constituents. In the polymerization of resins all simple functional groups are preserved except carbon-carbon double bonds, whereas skeletal frequencies are damped but not completely extinguished. Thus spectra of

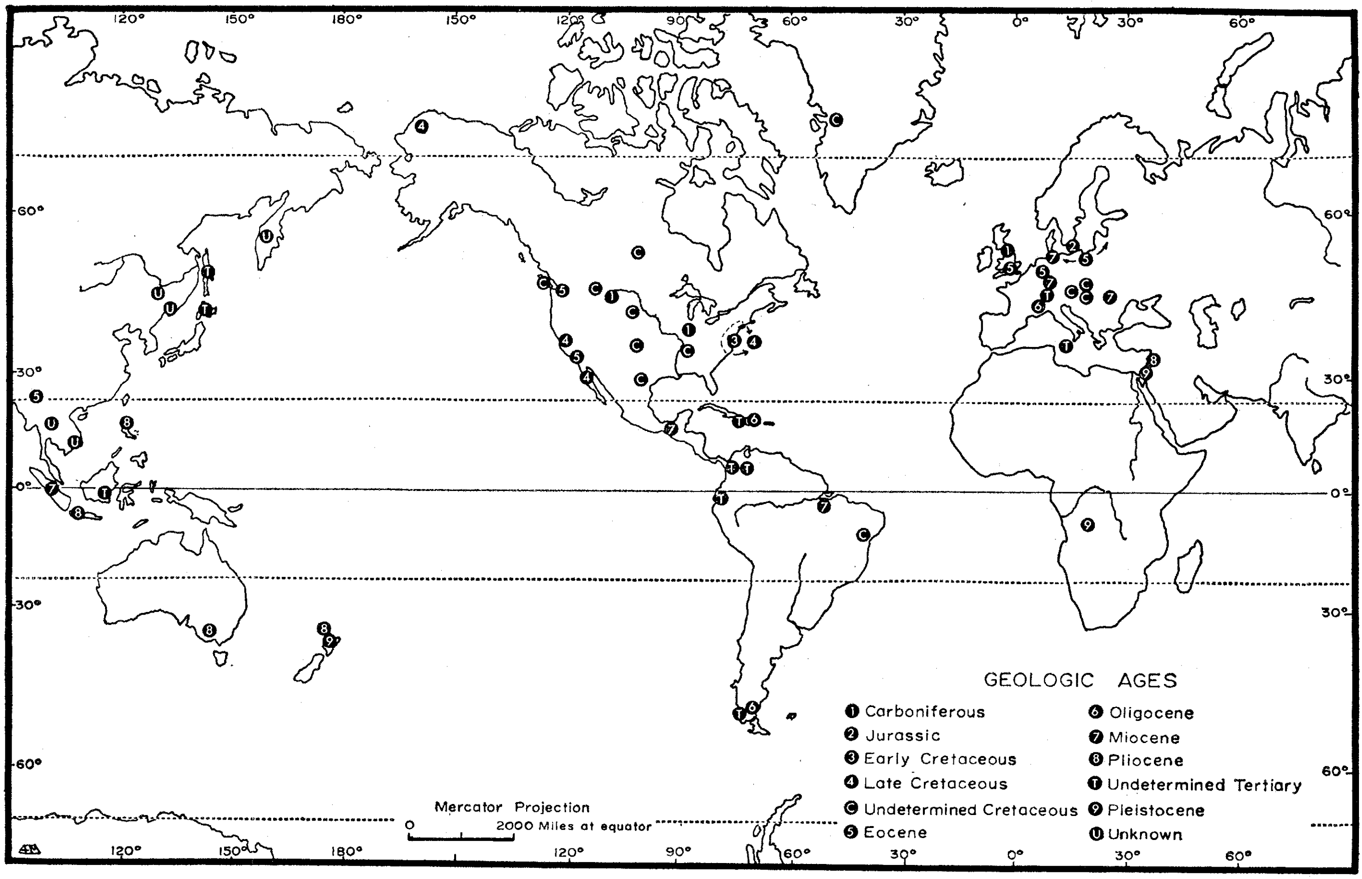


Fig. 2. Geographic distribution of ambers according to geologic age.

recent and fossil resins are often similar in that certain absorption peaks can be matched, although the intensity of these peaks is usually much weaker in the fossil resins than in the recent ones. At longer wavelengths some bands may be eliminated by either polymerization or oxidation.

All spectra, both of ambers and modern resins, show more similarities than differences in the region from 2.5 to 8 μ (4000 to 1250 cm^{-1}) where absorption bands are due to stretching and deformational vibrations of functional groups which are little affected by the intermolecular environment (Figs. 3 and 4). For example, the first absorption band at 2.9 μ (3500 cm^{-1}) is due to the stretching of hydrogen-oxygen bonds; the bending motion of these bonds causes absorption at about 6.1 μ (1650 cm^{-1}). The group of absorptions near 3.4 μ (2950 cm^{-1}) is due to the stretching of carbon-hydrogen bonds; the bending motions of these same bonds lead to absorption near 6.8 μ (1470 cm^{-1}) and 7.25 μ (1380 cm^{-1}). The prominent band near 5.8 μ (1700 cm^{-1}) is due to the stretching of carbon-oxygen double bonds, and this carbonyl band is the one where the position, intensity, and resolution show significant variation.

The upper region of the spectra (8 to 15 μ; 1250 to 625 cm^{-1}) shows greater variety in pattern and differences between resins. As a kind of fingerprint this upper region is useful in grouping fossil resins which not only have similar basic structures, but which sometimes can be related to recent resins (Figs. 3 and 4). Absorption between 8 and 10 μ (1250 and 1000 cm^{-1}) is due to carbon-oxygen single bonds; it is rarely possible to assign these bands to specific structural features.

Although, in general, the absorption bands above 10 μ (1000 cm^{-1}) are still more difficult to assign, the bending motions of hydrogen atoms attached to unsaturated carbon atoms cause absorptions which yield useful information. In fossil resins, the most important of these is the sharp band near 11.3 μ (885 cm^{-1}) which can be attributed to out-of-plane bending of the two hydrogen atoms of a terminal methylene group (Figs. 3 and 4). This band, which is prominent in some fossil resins, is a feature of several resin acids, such as agathanedicarboxylic and copalic (Fig. 5), which have been isolated from recent resins. The absence of this band in fossil resin spectra, however, must be interpreted with caution, since terminal methylene groups are easily oxidized.

Amber samples from different ages and locations generally give characteristic spectral patterns (*11, 12*). A single, relatively consistent pattern may characterize an amber from a given locality. Although there is some variability, over 500 spectra of succinite from the Baltic Coast give a recognizable, repeatable pattern (*12, 17*). In other localities, such as the Alaskan-Arctic Coastal Plain, Atlantic Coastal Plain, and Baja California, the amber gives several characteristic patterns. Some spectral patterns, like those of Baltic succinite and New Zealand ambrite, appear in several geographic areas and different geologic ages (Fig. 3).

Resins are being systematically investigated from genera and species of living families whose ancestors might have produced the amber found in some of the significant deposits. As is true with the present stage of development of chemotaxonomy in general (*8*), interest centers on interrelations among genera and families. For the nonvolatile diterpene fractions of the taxa thus far investigated, differentiation of genera is usually clear. Consistent differences in the diterpene fraction among species are not common, as they are with mono- and sesquiterpene components, at least in the genus *Pinus* (*18*). Infrared spectra of the nonvolatile fraction (rosin) of the majority of species of pine duplicate the spectrum of abietic acid. The spectrum of *Pinus echinata* resin (Fig. 4) is char-

Table 1. Age, geographic location and geological occurrence, and botanical affinities of a large sample of recorded deposits of amber.

Location and geologic occurrence	Botanical affinities (and references)
Carboniferous	
Northumberland, England	Coniferales (*14*)
Upper Mississippi Valley	Coniferales (*67*)
Montana	Coniferales (*67*)
Jurassic	
Bornholm	Coniferales (*68*)
Lower Cretaceous (Albian Stage)	
Maryland (Upper Patapsco Formation)	Araucariaceae, Taxodiaceae-Cupressaceae, Pinaceae (*11*)
Upper Cretaceous (Cenomanian-Turonian; Turonian-Coniacian)	
Magothy River, Maryland (Raritan and Magothy Formations)	Araucariaceae, Taxodiaceae (*69*)
Martha's Vineyard, Massachusetts (Raritan, Magothy Formations)	(*71, 11*)
Upper Cretaceous (Cenomanian-Turonian)	
Cliffwood, Bordentown, New Jersey (Raritan Formation)	Araucariaceae (*70, 11*)
Kreischerville, New York (Raritan Formation)	Taxodiaceae, Pinaceae (*32*)
Upper Cretaceous	
St. Georges, Delaware	(*11*)
Kincora, New Jersey	(*11*)
Roebling, New Jersey	(*11*)
Harrisonville and Pemberton, New Jersey	Hamamelidaceae (*Liquidambar*) (*11*)
Cedar Lake, Manitoba	Araucariaceae (*27, 11*)
Upper Cretaceous (Turonian)	
Kuk River Drainage, Alaska	Taxodiaceae (*31*)
Upper Cretaceous (Campanian)	
Baja California, Mexico	(*72*)
Cretaceous	
Hardin County, Tennessee	(*73*)
Black Hills, South Dakota	(*73*)
Cañon Diablo, Arizona	(*73, 11*)
Terlingua Creek, Texas	(*73*)
Ellsworth County, Kansas (Kiowa Formation)	(*72*)
Peace River, British Columbia	(*74*)
Hare Island, Greenland	(*75*)
Vienna, Austria	(*73*)
Hungary	(*73*)
Switzerland	(*73*)
Bahia, Brazil (Reconcavo Group)	(*76*)
Paleocene-Eocene	
S.E. Coast, England (London Clay Formation)	Burseraceae (*77*)
Eocene	
Hukawang Valley, Burma	(*78*)

acteristic of the abietic acid type. Often 90 percent of pine rosin consists of diterpene, monocarboxylic acids, especially abietic and pimaric acids. In some pines, neoabietic, palustric, isopimaric, and levipimaric acids initially may be present, but with high temperatures and photosensitization, isomerization to the more stable abietic acid generally occurs.

Spectra of genera in the Taxodiaceae demonstrate a certain chemical heterogeneity. *Sequoia* and various species of *Taxodium* are distinct from *Metasequoia* (Fig. 4) and *Sequoiadendron*, whose spectra are relatively similar. Spectral patterns of *Agathis* (Fig. 4) and *Araucaria* are very distinctive, sometimes to the extent of characterizing species groups in *Agathis*. *Agathis australis* resin is characterized by agathanedicarboxylic acid (Fig. 5) as well as a less highly oxidized agatholic acid.

Among the angiosperm resins, spectra of three genera of the Burseraceae, *Bursera, Protium* (Fig. 4), and *Canarium,* are clearly distinguishable. In fact, species complexes are discernible among the neotropical *Bursera* and *Protium*. In the Leguminosae (Caesalpinoideae), resins of the African genera *Daniellia* and *Copaifera* are distinctive from the New World *Hymenaea* which, however, is similar to the African *Trachylobium*. Representatives of genera in the Styracaceae (Fig. 4), Rutaceae, Anacardiaceae, Hamamelidaceae, Zygophyllaceae, and others, likewise give characteristically different spectral patterns (*12*).

X-ray diffraction provides another useful technique for determining botanical origin of some ambers (*19*). In a few cases, sharp patterns of the crystalline constituents of ambers may be identical with those of modern resins. Moreover, in some of these, identification of individual constituents, such as triterpenoid alcohols characteristic of certain angiosperms, has been possible in both the modern and fossil resins. This technique provides information about individual crystalline components, whereas infrared spectroscopy indicates the functional groups and carbon skeleton of at least the major constituents of the entire, nonvolatile fraction of the resin.

Table 1 (continued)

Location and geologic occurrence	Botanical affinities (and references)
Eo-Oligocene	
Seattle, Washington (Renton Formation)	(*79*)
Eo-Oligocene; Miocene	
Baltic Coast	Pinaceae (*Pinus*) (*3, 41*)
Eocene (Domengine)	
Simi Valley, California	Pinaceae (*80*)
Eocene-Miocene	
Rhineland Brown Coals	Hamamelidaceae (*Liquidambar*) (*12, 81*) Taxodiaceae (*81*)
Oligocene	
Argentina (Patagónica Formation)	(*82*)
Dominican Republic	(*83*)
Savoy	(*73*)
Oligo-Miocene	
Chiapas, Mexico (Simojovel Formation)	Leguminosae (*Hymenaea*) (*48*)
Miocene	
Pará, Brazil (Pirabas Formation)	Leguminosae (*Hymenaea*) (*11*)
Carpathian Mountains, Rumania	(*84*)
Central Sumatra	Dipterocarpaceae (*12, 85*)
Miocene; Pliocene	
Aukland Province, New Zealand	Araucariaceae (*Agathis*) (*86*)
Pliocene	
Victoria, Australia	Araucariaceae (*Agathis*) (*30*)
Java	(*85*)
Luzon, Philippine Islands	(*85*)
Tertiary	
Medellín and Girón, Colombia	Leguminosae (*Hymenaea*) (*11*)
Magdalena, Chile	(*87*)
Guayaquil, Ecuador	Burseraceae (*Protium*) (*88*)
Northern Sicily	(*73*)
S.E. Borneo	(*89*)
Hokkaido, Inotani, Japan	(*90*)
Sakhalin	(*90*)
Haiti	(*83*)
Pleistocene	
Tel-Aviv, Israel	Anacardiaceae (*Pistarca*) (*91*)
Pleistocene-Recent	
N.E. Angola, Africa	Leguminosae (*Copaifera*) (*47*)
Unknown age	
Vladivostok	(*73*)
Siam	(*73*)
Cochin-China	(*73*)
Manchuria	(*73*)
Kamchatka	(*73*)

Amber of Gymnospermous Origin

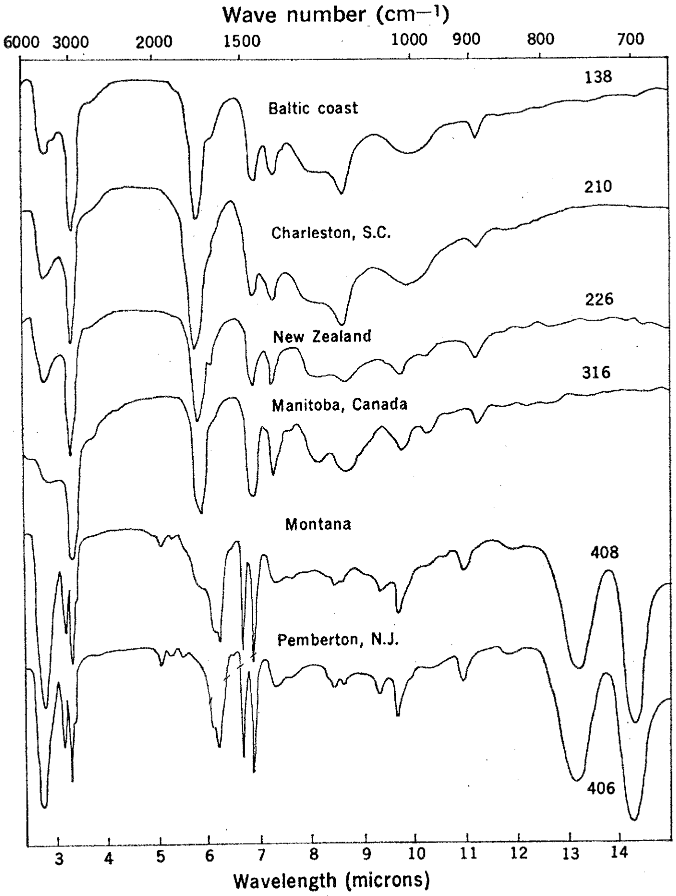
The earliest evidence for synthesis of resin is among gymnospermous plants. Only those belonging to the Coniferales are known to have produced resin, although members of the extinct Cordaitales probably did also. These arborescent Cordaitales, together with seed ferns, constituted the bulk of seed plants in Carboniferous coal forests. In the secondary wood of *Cordaites* and *Mesoxylon*, thin-walled ray cells sometimes contain a "dark, resinous material" (*20*). Also in *Cordaites* "gummy material" occurs in the pitch and "secretory sacs" traverse the parenchyma cells of the primary cortex. Because these resinous-appearing materials have not been isolated from the cells, it has not been possible as yet to determine if they are true resins.

The earliest evidence of a specialized resin receptacle are the pockets or canals in the outer petrified bark of *Araucarioxylon arizonicum* in the Triassic Chinle Flora from Arizona (*21*). No amber is known from the Permian and Triassic and relatively little from the Jurassic and Early Cretaceous. Since these are periods during which the modern genera of conifers differentiated (*22*), amber from coniferous sources might be expected. The only well-documented Early Cretaceous amber occurs in Maryland in strata associated with pollen from members of the Podocarpaceae, Araucariaceae, Pinaceae, and Cupressaceae-Taxodiaceae complex (*23*).

Amber is relatively common in the formations along the Atlantic Coastal Plain, where it usually is associated with lignitic remains of Araucariaceae, Taxodiaceae, Cupressaceae, or Pinaceae (*24*). Araucariaceous pollen and cones have also been described from several of these Cretaceous deposits (*25*). The wood of *Araucarioxylon* is considered very similar to that of modern species of *Agathis* and *Araucaria* (*26*). Infrared spectra corroborate the araucarian origin for amber from some of these localities (*11*). These spectra are similar to some of those of Cretaceous amber from Manitoba, Canada, and to Late Tertiary ambrite from Auckland Province, New Zealand. The Manitoban amber has been transported a long distance from its origin so that there are no associated plant fossils. Some of the Manitoban amber is similar chemically to Cretaceous walchowite from Europe (*27*), which may be derived from *Dammaraphyllum* or other araucariaceous sources (*28*). Ambrite is assumed to have derived from *Agathis australis.* This species is noted for its copious production of resin which has been collected for commercial purposes from the soil, where it has accumulated through generations of forests (*29*). All of the spectra discussed above are similar to those of resin from living *Agathis australis* and *Agathis labillardieri,* but not other species of *Agathis* and *Araucaria.* Araucarians disappeared in the Early Tertiary in the Northern Hemisphere and their distribution is now restricted to the Southern Hemisphere. Florin (*22*) has questioned the occurrence of *Agathis* and *Araucaria* in the Northern Hemisphere during Cretaceous times, although his evidence was based strictly upon cones. Certainly the similarity of the spectra of various North American Cretaceous ambers with that of numerous resin samples of *Agathis australis* suggests a very close relationship.

Tertiary amber from Australia and New Zealand was probably also derived from *Agathis.* Evidence such as *Agathis* leaves embedded in the amber, associated fossil *Agathis* wood, and the presence of agathic acid in the amber have supported this source for Pliocene amber from Victoria, Australia (*30*), as well as that from Pliocene or possibly Late Miocene lignites in Central Otago, New Zealand.

The prevalence of *Sequoia, Metasequoia,* and *Sequoiadendron*-like remains associated with Late Cretaceous and Early Tertiary amber suggests that some of it may be derived from these taxodiaceous plants. Late Cretaceous amber from the Alaskan-Arctic Coastal Plain occurs with such a predominance of megafossils of *Sequoia, Sequoiadendron*(?), and *Taxodium* that it may well have been derived from taxodiaceous trees growing close to lakes or coastal swamps (*31*). Also, amber from Kreischerville, New York, was associated with taxodiaceous or cupressaceous lignites (*32*). Taxodiaceous and cupressaceous ambers from several of the Early Tertiary European brown coals have been reported, their derivation being substantiated by associated wood specimens such as *Cupressinoxylon, Taxodioxylon,* and *Juniperoxylon* (*33*). Infrared spectra of ambers from the North American localities mentioned, however, differ from those of resins of present-day *Sequoiadendron, Metasequoia,* or various species of *Taxodium.* There is a general resemblance but not a close relationship to *Sequoia.* Despite lack of good correlation of infrared spectra of these ambers with some modern taxodiaceous resins, it seems highly probable that some are from this source because the Taxodiaceae are chemically heteroge-



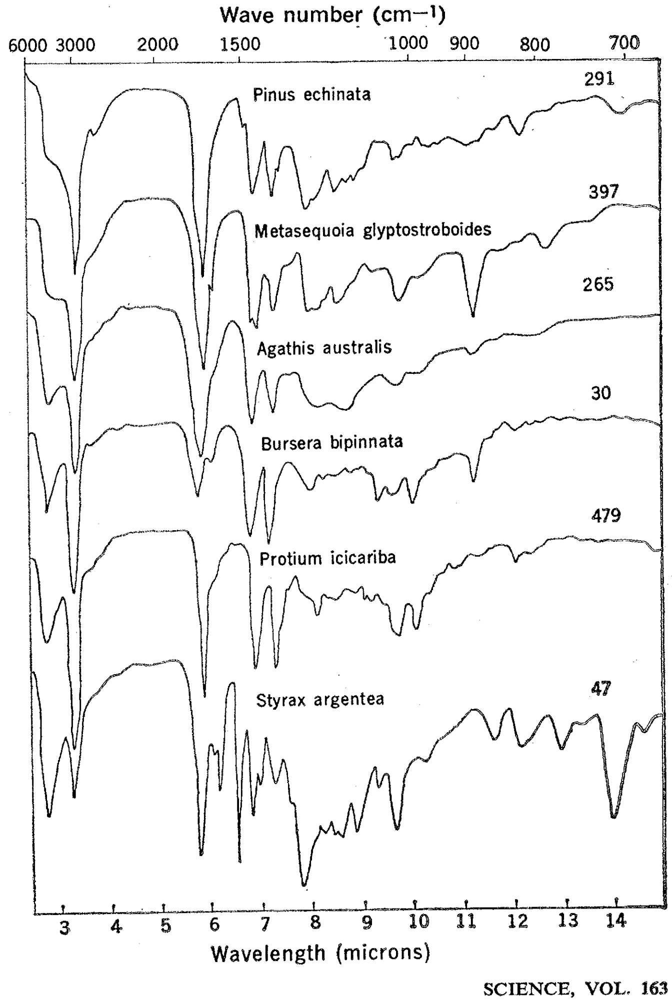
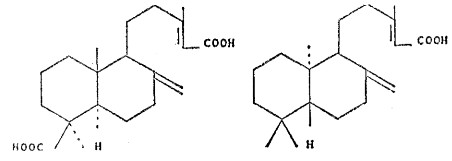


Fig. 3 (above). Infrared spectra of representative ambers from six sites. Fig. 4 (right). Infrared spectra of the nonvolatile fraction of resins from extant populations of six species.

nous (*34*). Thus, fossil taxodiaceous resins are likely to be highly variable and interpretation of resins from this source must await more studies from extant sources.

Members of the Pinaceae have classically been considered to be the source of "amber." This preconception has resulted from the assumption that the source of Baltic amber (succinite) was several species of pine and possibly spruce, included within a single specific concept, *Pinus succinifera* Conw. (*35*). The presence of droplets of amber in the resin canals in the xylem parenchyma of wood of the pinaceous type has provided the most convincing evidence for this source (*36*). The occurrence in the amber of pinaceous needles, a few female cones, and numerous male fructifications has also been used in supporting this derivation. There are, however, numerous other coniferous inclusions (*35*), including 18 species of seven genera of the Cupressaceae. Specimens of *Thuja* actually exceed those of pines in abundance of foliage remains.

Chemical evidence for this pinaceous origin of Baltic amber has not been presented as yet. The most important single, defining chemical property has been the presence of succinic acid, but pines today are characterized by abietic and pimaric acids. Infrared spectra of Baltic succinite display a characteristic pattern that remains remarkably consistent (*17*). This pattern occurs not only in the Eo-Oligocene amber along the Baltic Coast, but from other ages in different geographic areas, such as Cretaceous amber from Manitoba, Canada, two Cretaceous localities along the Atlantic Coastal Plain (Fig. 3), Eocene amber from Halle, Germany, and Miocene amber from Japan. Such similarity in spectra has been assumed to imply a similar botanic source (*11, 12*). This spectral pattern, however, is not similar to that of any modern pine resin. Considerable change in the chemical composition of the resin during evolution of the pines might possibly explain the lack of correlation. However, the spectrum of *Agathis* is the most similar to that of Baltic amber of any modern resin investigated (Fig. 3). Also agathalene (1,2,5-trimethylnaphthalene), a diterpene of the agathic acid type, has been reported from Baltic amber (*37*). Amber with a typical succinite spectrum from Halle, Germany, is associated with woods possibly of the Araucariaceae (*38*). Since no araucarian remains have been described from the Baltic deposits, this source has never been considered. Nonetheless, these associated araucarian properties suggest that the Baltic trees with typically pinaceous-type wood were derived from an araucarian stock, or one which was common to both araucarians and pines. The isolation recently from *Pinus lambertiana* (*39*) of lambertianic acid, which belongs to the same series as agathic acid, also indicates a possible chemical relation between resins of pines and of araucarians. Indeed, the chemistry of these resins appears likely to provide evidence bearing on the phyletic relationships between the pines and the araucarians.



Agathanedicarboxylic Copalic

Fig. 5. Structural formulas of the diterpene resin acids, agathanedicarboxylic and copalic.

The eastern Baltic deposits are so large that they have been mined commercially on a large scale since the mid-19th century and still are in operation today. The almost inexhaustible quantities of amber and the frequent occurrence of large-sized pieces have raised questions as to how trees could have produced so much resin. Because pines do not commonly exude, or at least accumulate, this quantity of resin "naturally" today, Conwentz (*35*) proposed that the entire forest of amber-producing trees had been infected by some unique pathological condition that he called "succinosis." This concept of a "sick amber forest" was so masterfully presented by Conwentz that only a few investigators (*40*) have suggested that Baltic amber accumulations could have resulted from normal production of resin. They thought that pines, dominant in forests over extensive areas for several million years, could account for the large quantities of resin found in the Baltic deposits. None of these investigators, however, gave attention to the enormous quantities of resin produced and accumulated under apparently normal forest conditions by either araucarians or various angiosperms in tropical habitats, despite the fact that a tropical, or at least subtropical, environment had been suggested for the Baltic amber-producing forests (*41, 42*). All in all, the evidence for Baltic amber being derived from pines, closely related to those we know today, remains unconvincing.

Furthermore, the apparent rarity of amber of pinaceous sources from any geographic locality is puzzling since fossil pine wood and needles are relatively common. Pine resins of a modern type may be susceptible to microbial attack, because masses of them do not accumulate in the soil as do those of many araucarians, legumes, dipterocarps, and others. Oxidative degradation or dehydrogenation of the resin acids also may have occurred. For example, the fossil hydrocarbon reficite has been identified as a dehydropimaric acid, which thus may have been of pinaceaus origin (*19*).

Amber of Angiospermous Origin

The source of most amber appears to have been coniferous until the Tertiary period. One exception during the Late Cretaceous is the genus *Liquidambar* (Hamamelidaceae). Amber samples from Late Cretaceous deposits in New Jersey and Montana give infrared spectra that differ from those of most other fossil resins in lacking a well-defined carbonyl group (Fig. 3). The distinctive pair of bands at 13.3 μ and 14.3 μ (750 cm^{-1} and 700 cm^{-1}) is clear evidence for the presence of mono-substituted benzenoid rings. This structure has been ascribed to *Liquidambar* because it contains cinnamic acid and styrene (*43*). This indicates a composition similar to that of siegburgite, which occurs in the early Tertiary brown coals along the lower Rhine, where *Liquidambar* was a prominent component in the *Myrica-Cyrilla* moor and *Sequoia* woods (*44*) which formed these coals.

X-ray diffraction analyses (Fig. 6) have indicated an angiospermous origin for Tertiary amber from three localities, that is, Highgate copalite from the London Clay Flora, glessite from the Baltic Coast, and guayaquillite from Ecuador (*19*). In each case, the amber contained a crystalline triterpenoid alcohol, α-amyrin. This alcohol is characteristic of various species within the genera *Canarium, Protium*, and *Bursera* in the Burseraceae and *Amyris* in the Rutaceae.

The affinities of the Eocene (or

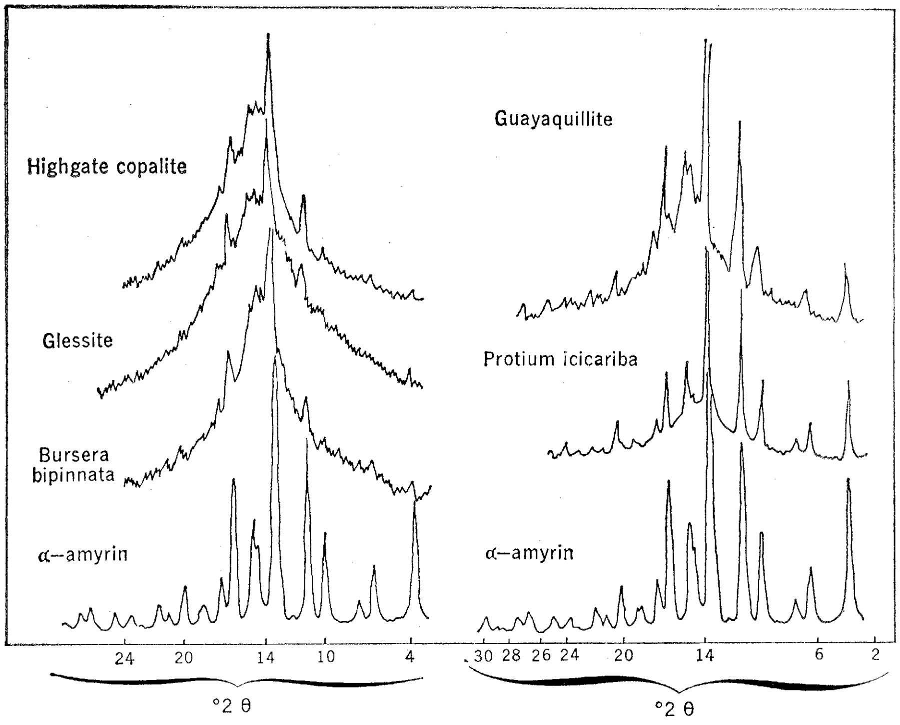


Fig. 6. Comparison of x-ray diffraction patterns of the ambers Highgate copalite and glessite with modern resin from *Bursera bipinnata* and the amber guayaquillite with modern resin from *Protium icicariba*. All of these spectra of fossil and modern resins are similar to that of α-amyrin. [After J. Frondel (*19*)]

Paleocene) London Clay Flora are predominantly tropical, most of the flora being allied to genera inhabiting present-day tropical or montane rain forests in Indo-Malaya (*45*). Since burseraceous fossil seeds occur in the London Clay Flora, the source of Highgate copalite had been suggested as either *Protium* or *Canarium*, which are known to produce large quantities of resins in the Paleotropics. The indication of α-amyrin by x-ray diffraction analyses has substantiated a burseraceous source but has not indicated the genus involved.

Glessite, a rare variety of Eo-Oligocene amber occurring with the common succinite along the Baltic Coast, has been attributed by some to a pinaceous source (*36*), but others have thought that it was chemically similar to "benzoin," in the Styracaceae, or to the modern myrrh (*Commiphora*) in the Burseraceae (*46*). The presence of α-amyrin again supports a burseraceous origin, and points to the possible significance of Indo-Malaysian floral affinities during this period of the widespread Tethys Sea.

Guayaquillite, of unknown but probably Tertiary age from deposits in Ecuador, also contains α-amyrin. Although there are no associated plant fossils, a burseraceous source such as *Protium* is supported by the fact that several species, for example, *P. heptophyllum* and *P. icicariba*, produce large quantities of resin in Ecuador today. Infrared spectra of guayaquillite are somewhat similar to those of resin from *P. icicariba* but differ from those of numerous other Central and South American species of *Protium*.

The infrared spectrum of an impure, "earthy" amber from Miocene beds in central Sumatra is strikingly similar to that of present-day *Shorea*, in the Dipterocarpaceae (*12*). Although no associated plant fossils substantiate this origin, members of the Dipterocarpaceae are among the most likely sources from these areas, as the resin is not only produced in large quantities under natural conditions, but accumulates in the soil.

Samples of amber from northeastern Angola, dating from 8000 B.C. to a possible Pleistocene age, give spectra that resemble species of *Copaifera*, a member of the subfamily Caesalpinoideae of the Leguminosae (*47*). *Copaifera* is a genus noted for its copious resin production, particularly in Africa. Discovery of amber deposits is to be expected in Africa, which has numerous resin-producing genera. At present, it represents a significant geographic gap in location of amber deposits (Fig. 2).

The most complete set of correlative data to substantiate botanical origin of amber has been assembled for the Neotropical leguminous genus *Hymenaea*. Amber from *Hymenaea* occurs in Tertiary deposits in Mexico, Colombia, and Brazil (*11, 48*). *Hymenaea,* like *Copaifera,* belongs to the subfamily Caesalpinoideae; its center of distribution is in the Brazilian Amazon Basin (*49*). Among the 27 species of *Hymenaea, H. courbaril* is known for the most abundant secretion of resin. It has an extremely wide range of distribution, occurring in all of South America except Argentina, Uruguay, and Chile, on most of the islands of the West Indies, and along the Pacific drainage throughout Central America to Central Mexico.

Infrared spectroscopy has been particularly useful in studying amber derived from *Hymenaea*. The spectra of the majority of samples of amber from Chiapas, Mexico as well as those from Girón and Medellín, Colombia, and Pará, Brazil, are similar to those of resin from modern *H. courbaril* (*49*). The spectra of both the resin of *H. courbaril* and these ambers are in accord with the expectations raised by the gross structure of the diterpene copalic acid (Fig. 5), reported to be a component of *H. courbaril* resin (*49*). These spectra also do not resemble those of other potential amber producers, such as *Styrax, Amyris, Protium, Bursera, Myroxylon, Guaiacum,* and *Pinus* (*49*; Fig. 4). Remarkably consistent spectra were obtained from samples of *H. courbaril* from various populations in Mexico, Guatemala, Dominica, Costa Rica, Guyana, Venezuela, Brazil, and Ecuador. Such minor differences as do occur over this wide geographic range may reflect ecotypic variation in the population.

These slight differences in resin spectra shown through the distribution of *H. courbaril* also are reflected in the spectra of the amber from different localities. The spectra of the Chiapas amber are more closely related to spectra of modern *H. courbaril* resin from populations in Mexico and Guatemala than to those of resins from more southerly populations (Fig. 7). Moreover, the spectra of amber from Girón and Medellín, Colombia, are most similar to those of *H. courbaril* resin from Guyana, and the amber from Pará, Brazil, is more comparable to resin from Brazil than from other areas.

Although the spectra of all of these ambers closely resemble that of resin from *H. courbaril,* more differences occur in the Mexican amber than in the others (Fig. 7). For example, the broad band at 14.2 to 14.4 μ (695 to 705 cm^{-1}), due to unassigned skeletal vibrations, has disappeared in the amber as a probable consequence of polymerization. The 11.3 μ (885 cm^{-1}) band, which is assigned to $=CH_2$ out-of-plane deformation of terminal carbon-carbon bonds, decreases as would be expected if the $=CH_2$ became oxidized. The attendant formation of new carbon-oxygen bonds would also account for the slight shift of the absorption maximum near 8 μ (1250 cm^{-1}). These changes, however, are not noted in the samples from Colombia and Brazil. It is probable that the Chiapas amber is older than the others, and thus may have undergone more polymerization than those from Colombia and Brazil. Evidence for greater oxidation may reflect either depositional or erosional conditions.

The occurrence of *Hymenaea* leaflets and possibly sepals and pollen in the amber (*49*) provides corroborative evidence for *Hymenaea* as the source of Chiapas amber. Moreover, *H. courbaril* secretes large quantities of resin that accumulate in the soil around the tree. This accumulation in the soil from trees growing adjacent to a depositional environment aids in the incorporation of the resin in the geologic record. In Mexico today, *H. courbaril* grows commonly along rivers that enter the ocean in mangrove-fringed estuaries. Analysis of the pollen in the Chiapas amber-bearing beds indicates that much of this amber was deposited in such an estuarine environment with abundant mangrove vegetation of considerable complexity at or close to the site of deposition (*50*).

Physio-Ecology of Present Resin Producers

Determination of the botanical sources of amber, although it may also have phylogenetic implications, is only a prelude to other evolutionary considerations. The development of resin-secreting systems and the role of environmental conditions in controlling the synthesis, secretion, and accumulation of resins are central to an understanding of their evolutionary significance.

Resin is produced in parenchyma cells that usually line rounded pockets or cysts and elongated canals. These containers may arise by either schizogeny, lysigeny, or both. Schizogeny involves the separation of cells, which round off and increase their intercellular spaces to produce pockets or canals, of which the secretory cells form an epithelial layer. Lysigeny results in the formation of cavities from the breakdown or disintegration of secretory cells. These resinous secretory cavities may occur in parenchyma tissue in any part of the plant, although their location varies with each species.

Although during the early 20th century (1900–1936) Tschirch, Stock, Frey-Wyssling, and others (*51*) extensively investigated the mechanisms of discharge of resins from cells and the anatomical development of the secretory system, we still are far from understanding these problems. The cellular site where resins are synthesized is as yet unidentified. For example, only in *Pinus pinea* has the ultrastructure of resinous secretory cells been examined (*52*). A working hypothesis was suggested that the sequence of enzymatic reactions producing the resinous terpenoids begins inside the plastid or on the plastid membranes and continues on the endoplasmic reticulum membrane. If this is so, the biosynthesis of these resinous terpenoids would have many features in common with that of animal steroids.

Confusion still dominates the issue regarding the necessity of injury and disease in inducing the development of the secretory pockets and canals, and particularly those formed lysigenously. In some plants, such as *Styrax* and *Liquidambar,* resin seems to be produced from lysigenous cavities primarily following injury. In others, such as members of the Leguminosae, Diptero-

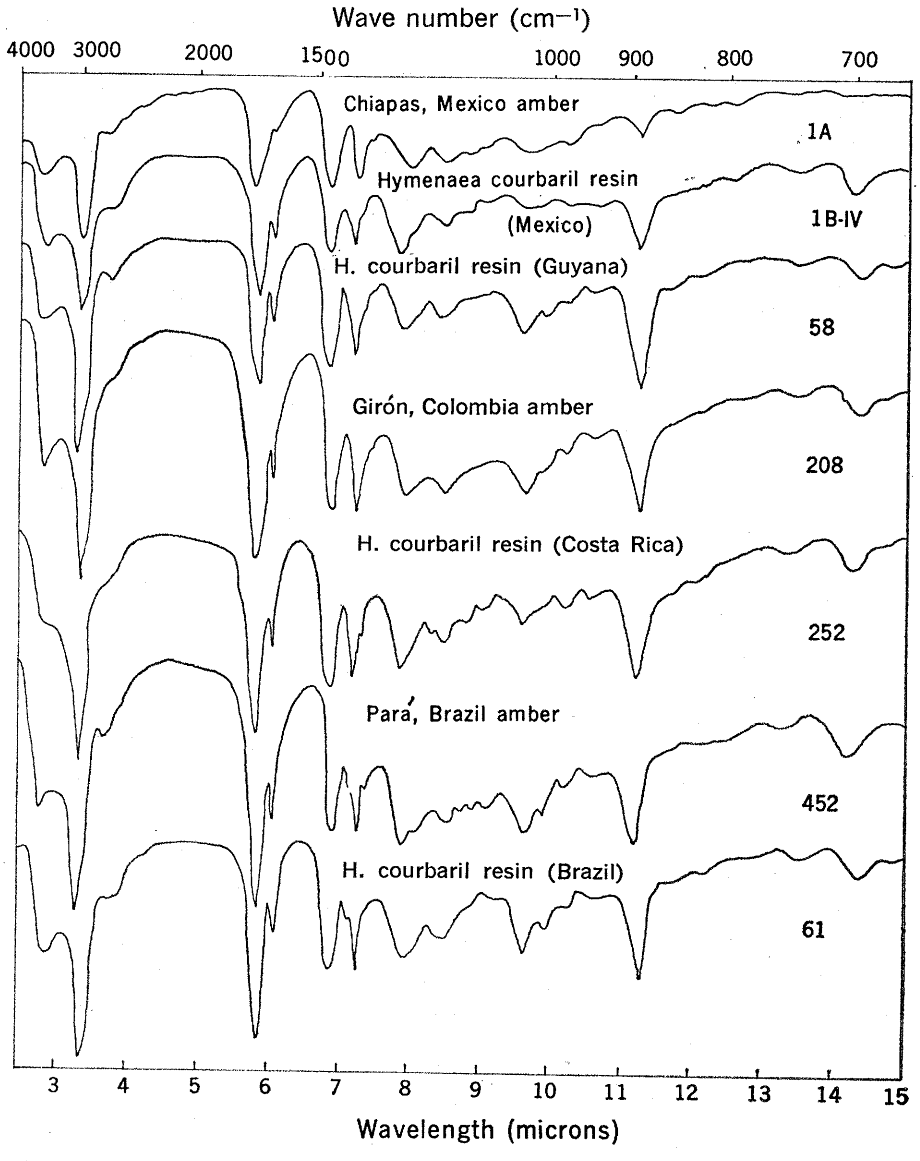


Fig. 7. Comparison of infrared spectra of amber from three sites with resins from extant populations of *Hymenaea courbaril* from our sites.

carpaceae, and Anacardiaceae, pockets which originate schizogenously can later be enlarged lysigenously (*51*). In these cases, secretion occurs initially through the epithelial cells, and then an even larger production occurs from surrounding cells that break down. Lysigenous cavities, nonetheless, do originate *de novo,* as in *Citrus* and *Eucalyptus,* where the developing cavities may be recognized in the meristem (*53*). In the leguminous *Copaifera,* lysigenous cavities originate in isolated pockets in the wood parenchyma but later are increased in size by merging with cavities in the medullary rays. The result is resin cavities frequently of enormous dimensions, apparently not initiated by external injuries (*9*).

Because of the prominence of *Hymenaea* as a resin and amber producer in Central and South America, we are studying the development of the secretory system and the conditions which control resin production and accumulation in *H. courbaril.* Soon after seed germination, schizogenous pockets form in cortical and medullary tissue of the epicotyl and in the stem (but not the root) portion of the hypocotyl as well as in the developing leaves (Fig. 8A). In branches, spontaneous secretion of resin occurs from schizogenous pockets close to the periderm (Fig. 8B). As the branch enlarges, these pockets persist until bark formation finally obliterates them. Resin is then produced from cells forming lysigenous cavities in the cambial zone.

In the mature tree, which can reach a height of over 55 meters and a diameter of more than 2 meters, the resin seems to issue from vertical fissures in the bark, which may develop due to tension during rapid growth. The generally smooth bark is sometimes interrupted by rugose patches composed of these fissures (Fig. 8C). If a cut is made into either the trunk or the root of the mature tree, the viscous resin exudes slowly from the area of xylem differentiation in the cambial zone (Fig. 8, D and E). Lysigenous pockets form initially and then these coalesce to produce enlarged cavities. Thus, as in *Copaifera,* resinous cavities of very large dimensions may be produced. From these, probably, are secreted the large masses of resin which may hang from the trunk or accumulate at the base of the tree. Large accumulations of resin that appear where branches join trunks have been shown in some trees to be associated with tangential splits in the cambium caused by strong bending or torsion of the trunk. In *Picea* similar cavities generally appear in the spring with the initiation of springwood when the cambial zone is especially broad (*54*).

Local populations of *Hymenaea courbaril* in the same regions in Mexico and Brazil (*49*) have been noted by commercial resin collectors for their exceptional yields. At present, it is not possible to sort out genetic from environment factors which influence resin yield. It seems likely that yield in *H. courbaril* is determined genetically, as has been demonstrated for several species of pine, that is, *Pinus palustris, P. caribaea,* and *P. elliottii.* Certain individuals yield two and one-half times as much resin as the average tree of the same size growing under similar conditions (*55*). In breeding experiments on the variation and inheritance of resin yield capacity in *P. elliottii,* this trait not only varies highly among individual trees but is more strongly inherited than most biological traits (*56*). Although selection was made mainly for resin production in these experiments, the high resin-producing strain also yields about 12 percent more volume growth (wood

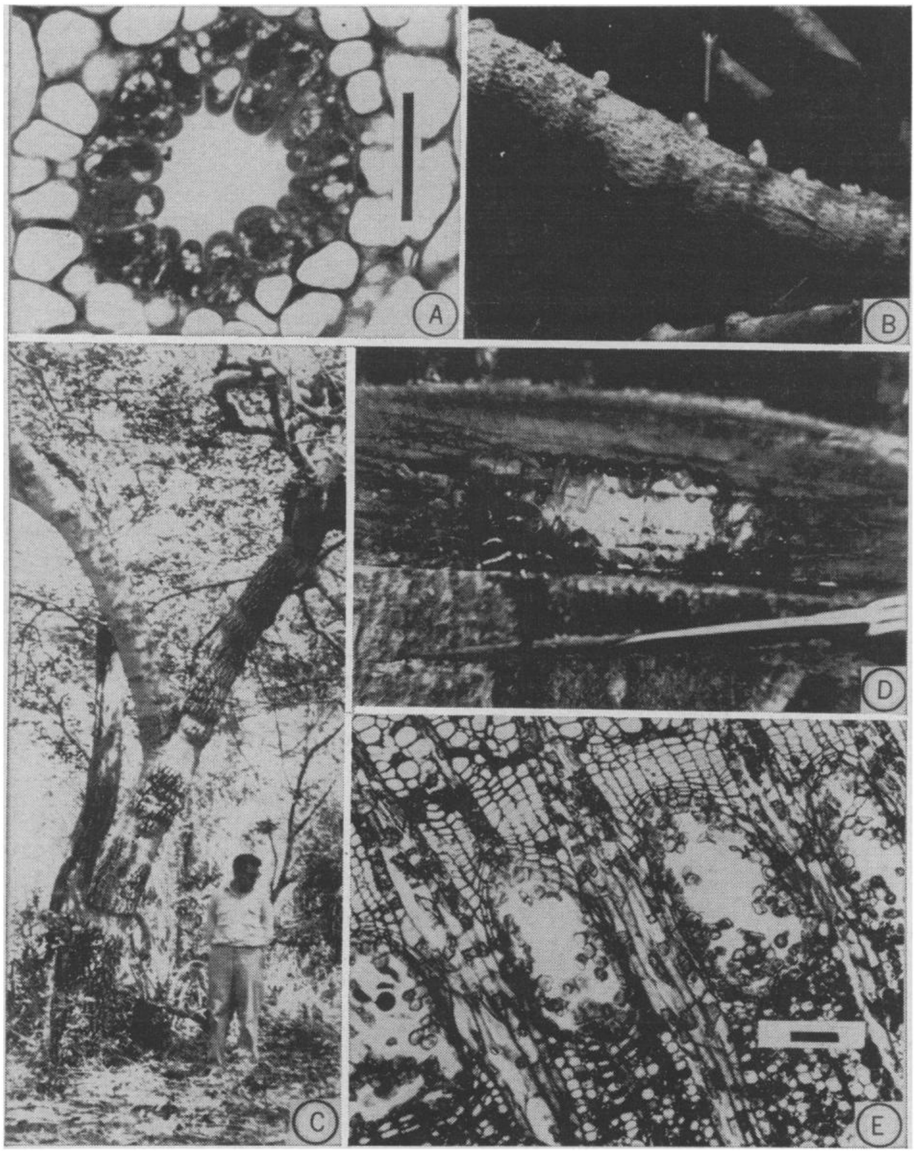


Fig. 8. Resin synthesis and secretion in *Hymenaea courbaril.* (A) Resin pocket in pith of petiole from year-old plant (Mexico) showing densely cytoplasmic secreting cells. Line scale is 50 μ. (B) Branch (Guerrero, Mexico) showing spontaneously exuded balls of resin. (C) Small tree (Guerrero, Mexico) with rugose patches of vertical fissures from which resin issues. (D) Cut in trunk of mature tree (Villa Colón, Costa Rica) showing viscous exudation of resin from cambial zone. (E) Lysigenous pockets developed in cambial zone of mature tree (Belém, Brazil). On left, coalescence of pockets forms enlarged cavities. Line scale is 50 μ.

production) than normal strains. Moreover, the quantity of resin synthesized is directly proportional to the size of the crown (*57*).

Hymenaea courbaril occurs through a wide range of climatic and edaphic conditions. The largest, most vigorous trees, growing under high moisture regimes and on fertile soils, appear to produce the largest quantity of resin. Thus, superimposed upon genetic capacity, apparently conditions that contribute to higher growth rates may increase resin synthesis. It is possible that certain physiological races or ecotypes may display a particularly high photosynthetic efficiency which would increase capacity to synthesize resins. Experimental studies on *Mentha piperita* (*58*) have demonstrated that monoterpene metabolism is controlled by daytime photosynthesis and nighttime utilization of photosynthate.

Raison d'Être of Resins

Shortly after the recorded advent of arborescent plants (approximately 300 million years ago), some evolved a specialized mixture of terpenoid compounds which is secreted into a specialized, correlatively developed anatomical system. What is the reason for being of these resinous terpenoids? Do they serve some physiological function in metabolic processes, some ecological, adaptive function in protection against injury, or both?

The traditional view has held that these terpenoids were end products in a copiously productive metabolism and only represented ways of disposing of excess acetate. They were thus considered "indifferent ballast" that formed slowly and irreversibly (*59*). It has been pointed out that the terpene compounds found in the lower plants, that is, at early stages of plant evolution, such as phytol of chlorophyll, gibberellin, carotenoids, and steroids, are predominantly those with physiological significance. Only the phylogenetically more recent higher plants produce, beyond the physiologically necessary terpenoids, significant amounts of mono-, sesqui-, and diterpene compounds.

However, as these lower terpenoids are being studied biochemically and physiologically, their participation in metabolism becomes increasingly apparent. For example, metabolic turnover of monoterpenes in *Mentha* has been demonstrated (*58*) and has led to the suggestion that other supposedly inert secondary products are subject to dynamic metabolism. Resin from *Larix* has been shown to have an apparently inhibitory effect on growth in the wheat coleoptile (*60*). Pine resin also has been found to act as a growth inhibitor in high concentrations but acts as a synergist in stimulating growth in low concentrations (*60*). Quantitative differences in resin acid composition in various tissues of *Pinus elliottii* have been suggested as possibly differentially influencing growth response in these tissues (*61*).

Most commonly the evolutionary significance of resins has been attributed primarily to protective adaptation against injury and disease inflicted by insects and fungi. Physiologists generally have tended to dismiss this interpretation (*51*), indicating that it was simply an outgrowth of a Darwinian overemphasis on purposeful adaptation. Some entomologists, on the other hand, believe that the habits of insects have evolved reciprocally with the biochemical characters of plants, pointing out that most secondary plant substances possess characteristic odors or tastes that may elicit sensory reactions in insects. Fraenkel (*62*) proposes that the raison d'être of secondary products in plants is to either repel or attract insects. He assumes an initial development of an unspecialized chemical response by plants to insect attack. Subsequently, in some cases, certain compounds developed more specific repellent effects. In others, a host preference arose when a given insect species by genetic selection overcame the repellent effect and the substance then could become an attractant, for example, to induce feeding or to aid in locating a breeding site.

The effect of resins in either repelling or attracting some insects has been investigated to a limited degree. For example, high exudation pressures of resin, under the influence of water supply, have been shown to control bark beetle attacks (*63*). Insect-induced crystallization of *Pinus strobus* resin provides resistance to attack (*64*). Various volatile terpenes of *Pinus ponderosa* differ specifically in their toxic effects upon bark beetles (*65*), and hence upon the resistance of the trees to attack. Specific volatile terpenes in *Pseudotsuga menziesii* resin, however, have been shown to attract various bark and timber beetles to favorable breeding material (*66*). Differences were shown to exist in the attractive power of different mono- and sesquiterpene constituents of Douglas fir resin for different species of bark beetles (*Dendroctonus*). Also freshly-cut trees may be invaded by certain species of bark beetles virtually within minutes of cutting whereas other species preferred the deterioration products of dying trees.

The Future for Amber-Resin Studies

Investigations of amber are now being revitalized through new scientific perspectives accompanied by utilization of sophisticated analytical tools. Viewing amber as fossilized resin, that is, a complex of plant terpenoids, rather than as a mineral, provides an evolutionary framework for chemosystematic and physio-ecologic studies of resin-secreting plants.

Since the chemical composition of resin is genetically controlled, all constituents may be useful chemosystematically in living plants. The volatile mono- and sesquiterpenes have been helpful not only with species determinations but in discerning ecotypic differentiation and hybridization in some conifers and probably will prove to be so in angiosperms. Although only the nonvolatile fractions are available in ambers for comparison with modern resins, these are sufficiently stable in certain genera and families to be helpful systematically. Nonavailability of the usual methods of organic chemical analysis, because of insolubility of the resins, has been overcome by techniques such as infrared spectrophotometry and x-ray diffraction. Although these methods have provided taxonomic fingerprints, mass spectrometry may offer a better potential means of elucidating actual structures of constituents of resins.

The chemical composition of a resin, its resistance to oxidative degradation and microbial attack, the amount synthesized, secreted, and accumulated, as well as the availability of a depositional environment, all determine the probability that resin will be preserved as amber. Among the gymnosperms, members of the Araucariaceae, and, among the angiosperms, members of the Leguminosae, Burseraceae, and Dipterocarpaceae have given us the closest ties between fossil and modern resins. They thus are likely to be the most profitable families in which to study the various evolutionary aspects of resin production. In addition, however, study of some ambers themselves may be of evolutionary import. Coniferous ambers offer an opportunity to assess biochemical evidence for phylogenetic relationships, because most conifers not only produce some resin but also have had a long geologic record. Overlooked small occurrences of amber, especially if they are associated with identifiable fossil woods or other plant material, might supply illuminating data. Small quantities of amber probably have been frequently overlooked in rock outcrops, since previous interest in amber has been primarily in either sufficient quality or quantity for its use as a gem or for the striking organic remains trapped in the resin.

Carefully oriented studies of biosynthesis are needed to understand the development of the resinous secretory process. We still know little of the cellular site of synthesis of mono-, sesqui-, and diterpenoids as well as of the conditions controlling the morphogenesis of the secretory containers. The predominant occurrence of resin producers in tropical habitats emphasizes the need for experimental investigations of the conditions inducing synthesis, secretion, and accumulation of resins. Factors that increase photosynthetic efficiency may well be involved in selection of physiological races with a high capacity for resin synthesis. Interdisciplinary studies in biochemistry, physiology, morphogenesis, and ecology may be necessary to determine whether the terpenoids comprising resins serve a metabolic, physiologic role or an ecological, protective one, or both. Physiologists have traditionally dismissed a physiological role for these lower terpenoids, but recent radioactive tracer investigations and growth regulator bioassays suggest that the constituents of resins at least are turned over metabolically and may just possibly serve in some regulatory capacity.

In assessing the ecologic role of resins, it is obvious that the various components of resins may function differently. It has already been shown that some constituents specifically repel certain insects while others attract them. One component may be fungicidal whereas another may successfully plug a wound. In some populations, resins may not serve as a specialized protective or attractive mechanism. It is predicted, however, that increasing evidence will be shown of intimate plant-insect and plant-plant relationships based on these terpenoids. Again, research will probably be directed toward the tropics where these interactions appear to flourish.

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Editing a Scientific Encyclopedia

Planning and preparation of the *International Encyclopedia of the Social Sciences* are recounted.

David L. Sills

The thousands of "encyclopedias" written since the age of Greece and Rome have two attributes in common. They have all claimed to provide a comprehensive survey of knowledge (either all knowledge, or one branch of knowledge), and they have all been based upon some explicit or implicit scheme for classifying knowledge.

In their other attributes encyclopedias vary widely. Most of them are multiauthored, but a number of great encyclopedias have been written by one man. Most are multivolumed, but a number of important one-volume encyclopedias have been published. Most present the articles in alphabetical order, but this fairly modern practice is by no means universal even today.

Because of the claim to be comprehensive and the explicit or implicit schemes used for classification, the study of encyclopedias provides a vast (and largely untapped) opportunity for research into both the history of science and the sociology of knowledge—the study of the relation between the characteristics of a society and the origins and nature of what it considers to be "knowledge." Consider the most famous encyclopedia ever produced, the 17-volume *Encyclopédie* edited by Diderot and D'Alembert. The very fact that it was prepared, to say nothing of its contents, is often taken as an indicator of the broad social and intellectual movement called the Enlightenment. The aim of the *Encyclopédie* was to treat all subjects, those related to social arrangements no less than those of the physical environment, in terms of a rational, scientific approach—nothing was to be considered too sacred to be questioned by the rationalist iconoclasts of the Enlightenment.

The *Encyclopaedia of the Social Sciences* was edited by two economists, E. R. A. Seligman and Alvin Johnson, and was published in 15 volumes by the Macmillan Company between 1930 and 1935. It reflects the prevailing notion of the late 1920's and early 1930's that social ills can be cured if knowledge from the social sciences is both widely dispersed among the public and is brought to bear on these ills; it also reflects the fact that the social science most highly developed at that time was economics (largely pre-Keynesian). The historicist insight that the *Encyclopaedia* is a document of its time, not simply a compilation of more or less obsolete articles, is in part the result of the effort to create a new encyclopedia of the social sciences.

The recently published *International Encyclopedia of the Social Sciences*, (*IESS*) was published in April 1968 in 17 volumes by the Macmillan Company and the Free Press. As its editor, I am presumably well qualified, perhaps overly qualified, to tell its story. Nevertheless, I have handicaps, some self-imposed and some that I cannot avoid. In spite of Watson's example in *The Double Helix* (*1*), I am not willing to expose all the conflicts and frailties that are part of the story, even though many of these are an essential component of the sociology of knowledge. Also, my account can be only a partial one because I obviously did not know everything that was going on. Each of my fellow editors has his own story to tell, as do many of our contributors. Finally, this is only a partial story because we *encyclopédistes* of the 20th century, no less than those of the 18th, constitute part of the data that some future sociologist of knowledge will analyze if he studies the *IESS*. The

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