1936

The short shoots of gymnosperms

Alice Isabel Dwight

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THE LIMIT CYCLES OF CATERPILLARS

by

Alice Isabel Dwight

A Thesis Submitted in Partial Fulfillment
of the Requirements
for the Degree of Master of Science,

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Amherst, Massachusetts.

1936
Acknowledgments

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It is probable that the gymnospermous seed plants occupy the place of predominance among palaeobotanists when viewed from the standpoint of evolution. Standing as they do at the place of transition between the earlier vascular cryptogams and the recent Angiospermae, they retain a wealth of significant archaisms to which they add these modernizations which are characteristic of the present dominant world flora. And although they have, as the vast literature of the subject reveals, been a focal point for a host of detailed researches, there remains still a field for new observations, and for new interpretations in agreement with newer morphological ideas and principles.

In those genera which bear their leaves upon short shoots, or brachyblasts, they possess a striking external evidence of the play of the major phyletic principles, and it has been suggested to the writer that an investigation of the histological details of these organs with their accompanying appendages might reveal notable features which would go far to extend and make firm what are often called the "canons of comparative anatomy".

The writer has, therefore, (1) investigated the literature which pertains to the gymnospermous short shoots, (2) carried out a morphological and histological investigation of the normal, juvenile and traumatic fell ge of the gymnosperm short shoot genera, and finally (3) has been
so fortunate as to have access to the brachyclad of an undescribed species of Cretaceous pine which has served as a basis for comparison with the living forms.

Two orders of living Gnetosperms include genera whose leaves are borne on brachyblasts. One order, the Ginkgoales, is represented by its monotypic living genus, Ginkgo. The other order, the Coniferales, is much more extensive, but the short shoot or dwarf branch occurs only in Cephal, Larix, Pseudolarix, Pines and Sciadopitys.

These plants are all characterized by a condition of branch dimorphism; the cauline organs are either in the "long" or in the "short" condition. The ordinary long branch is the normal type found on all trees. The nodes are separated by considerable internodal distances, and it continues to grow forward by marked annual increments. The amount of growth varies of course in different plants, being conditioned mainly by heredity, but also by the ecological and physiological factors, such as the amount of available water, soil fertility and climatic conditions.

THE BRACHYCLAD AND ITS EVOLUTION OR THE BRACHYBLAST.

The modified and smaller branch has been given various names, such as dwarf branch, spur shoot, short shoot, or more technically, brachyblast. In contrast to the long branch, the brachyblast is characterized by greatly "telescoped" internodes or, in more technical language, by the failure of the internodes to elongate during ontogenesis. Yet many of the
genera under consideration still possess a strong terminal growing point whose meristematic activity carries them forward a little each year. The meristematic tip is generally covered with imbricated, protective scales (cataphylls) during the winter season. The growth is slight, however, and the distance between the girdles - that distance which separates one year's growth from another - is only a few millimeters at the most. In the genus *Pinus* an apical bud is usually absent in normal specimens, and the short shoots do not show yearly growth increments. The leaves on all such brachyblasts as possess a terminal bud are much congested and usually stand in a phyllotactic spiral of low gradient. In *Pinus*, however, in correlation with the absence of a terminal bud, the leaves have a verticillate arrangement.

The morphology of the brachyblast is obvious from simple inspection. It is a conical axis of limited growth. Yet, like every other plant structure, its structural features have been much debated by botanists. Even as late as 1914, H. R. Thomson (67) placed much emphasis on the morphology of the long and the short branches. Thomson points out correctly that these two branch types are not utterly distinct from one another, but that gradations between the two are frequent. This, we may add, is likewise true of various angiosperms such as species of *Prunus* and *Pinus*. Thomson regards the variation in leaf number of modern pines as an indication that the short shoot is not so highly specialised a structure as some might possibly imagine, but it is of the nature of a branch possessed of an indefinite number of fuliginous leaves. The proliferation of a
brachyblast into an ordinary branch is not unusual. Thesle cies
instances of such proliferation in Pinus sylvestris, P. ponderosa-
var. Jeffrey, P. aristata, P. Banksiana, and various other
species. In Pinus the development of the short shoot into a long
shoot is often of the nature of a traumatic reversion, because
the presence of a terminal meristem is an abnormality. The long
shoot, together with its brachyblasts, is formed normally from
a differentiation of a compound terminal bud. In Lirix, Carus
and Ginkgo, on the contrary, a terminal bud is normally present
on the brachyblast, and the development of a short branch into
a long one is not an unusual phenomenon.

It was stated above that the brachyblast or
short shoot is morphologically a cauline organ derived by a
"teleocoping", or speaking more strictly, by a failure to elon-
gate the internodes of a normal stem. This principle of abbre-
viation of a plant axis seems to be one which is fundamental
in the cormophytes. In every instance it seems to be concomitant
with some physiological adaptation or specialization. A few
examples may serve to illustrate the principle more clearly.

The well known rosette habit of certain crassu-
laceous and aizoaceous plants, or of numerous angiosperm herbs
which pass the winter in this state, is of advantage in relating
the plant either to deserts or to the physiological drought
which attends the winter in the temperate zone. Leaf congestion
on a shortened and dwarfed axis brings the plant closer to the
more humid substratum and tends to prevent excessive moisture
evaporation. The photosynthetic activity of the plant is not im-
peded by this leaf congestion, since the differential lengthening
of the petioles permits the lower ones to extend their laminae outside the area covered by those above.

The "telescoping" principle is also introduced into the winter buds of deciduous trees, and the fall of the bud scales in spring reveals the familiar "girale". Each "girale" is made up of a number of congested nodes and internodes. In the horsechestnut, for example, the elongate, decussate, diamond-shaped scars, represent the position of the petiolar bud scales which once covered and prevented the evaporation of moisture from the terminal bud.

The "telescoping" principle also plays a remarkable part in the evolution of the flower receptacle. In fact, the Englerian system of classification (2) of dicotyledonous angiosperms recognizes the chief groups of plants: (1) those whose floral members are arranged spirally upon an elevated torus, and (2) those with a cyclic arrangement of the floral members. The floral receptacle is then, in its genesis, a stem which has been compressed. In the cyclic type of flower the telescoping has proceeded to such an extreme that the torus has become a disc. As an extension of the same principle we discover that inflorescences, both of the indeterminate and determinate types, have been subject to the telescoping principle. Through the progressive series of the raceme, corymb, and umbel we arrive at the capitulum whose fullest expression is that of the composite head where the introduction of the secondary principle of division of labor leads to a curious mimicry of the simple flower. The compression of the floral axis is advantageous, since it
often facilitates insect pollination.

The tapering of the stem in each of the previous mentioned plants is evidently commensurate with some physiological advantage. One might ask, then, what benefit is derived for the gymnosperms by the gradual suppression of the spirally arranged leaves on the long shoot, and the transference of their photosynthetic function to leaves densely packed on the ends of brachyblasts. The only cogent explanation offered for the evolution of the brachyblast is that the condition exposes the foliage more effectively to sunlight, and hence the photosynthetic capacity of the plant is augmented.

The introduction of a dwarf canine organ for leaf display did not apparently at first exert any particular disturbance upon the normal foliage habit of the plant. In the larch, for example, the current season's branches carry spirally arranged primary needle-leaves as their photosynthetic members. But during the second year the food making function of the branch is entirely relegated to needles borne on the apices of short shoots, the latter being developed from conspicuous buds in the axils of certain of the leaves which clothed the branch in its first season. In the larch, too, it is of interest to note that the leaves of the short shoot are spread out in a rosette manner. In the pines, however, the brachyblast has apparently proved such an effective device for leaf display that the photosynthetic function is normally banished entirely from the leaves of the long shoot in the adult plant, and they are reduced to small grey scales. Every short shoot is borne in the axil of such a scale
leaf. The advantage gained by the development of short shoots, then, is that of improved display of foliage with an increase in the photosynthetic activity.

**Previous Observations on the Brachyblast.**

Before setting forth in detail the individual living brachyblastic genera, we may now consider various observations made by previous investigators upon plants with dimorphic branches. An examination of botanical literature did not reveal the name or data of the first individual who scientifically described or recorded in plant description the presence of dimorphic branches in the gymnosperms. The presence of long and short branches in *Larix, Cedrus* and *Ginkgo* is so pronounced that it could hardly have escaped the notice of anyone who saw the trees. The fact that the cauline nature of this dwarf organ was understood by botanists during the latter part of the last century, is clearly evident from an examination of the works of various botanists of that period. Sach's, for example, (49) recognized that short shoots in *Pinus* as well as in *Cedrus, Larix, and Ginkgo* were the result of a differentiation in the growth power of long and short branches.

Turning to palaeobotany one discovers that short shoot genera of the **Gymnospermae** are known to have been prevalent in the Mesozoic era; a few come from the Triassic, but the wealth of fossil forms pertain to the Cretaceous period. It has not yet been proved that brachyblastic gymnosperms were present in the Paleozoic, though Rudolf Florin (50) has described several Coniferae or conifer allies in deposits of the Permian period. It is
not unlikely that short shoot-bearing fossils of these plants will eventually be found in Paleozoic formations, since some of the older and ancestral Ginkgcales were characterized by their presence.

**The Phyletic Position of the Ginkgcales and Coniferales.**

In order that the plants here to consider specifically may be viewed in proper orientation, it will be well to review briefly the phyletic positions of the various groups of the Gymnosperms.

The two orders, the Ginkgcales and Coniferales, which are discussed in this paper, are now usually held to be derived from the Cordaitales, an order which became extinct at the end of the Paleozoic or the beginning of the Mesozoic era. The Ginkgcales possess several features wherein they resemble the Coniferales. It is generally held, however, that although the two groups have a common ancestor, their phyletic divergence was an early one, and the evolution of each order was along an independent line. In his recent book, "Gymnosperms, Structure and Evolution" (13), Chamberlain groups together the Cordaitales, Ginkgcales, Coniferales, and Ginkgcales as one great line of gymnosperms which he terms the Coniferophytes. This group is set off by several distinctive features from the Cycadophytes in which are placed the Cycadofilicales, Ephedraceae and Cycadales. Our present interest lies particularly with the former group, the Coniferophytes. Its ancestry appears to trace back to the great common stock of Cycadofilicales, from which the Cycadophytes likewise took their origin.
The most primitive of the Coniferales are the Cordaitales. Stellar morphology, cortical histology and seed anatomy, offer conclusive testimony to a close relationship with the Cycadofilicales which in their turn are believed to have arisen from the ferns. Though of no immediate pertinence to our thesis, one is surprised to find that Chamberlain still sets forth the heterosporous Filicales as the probable ancestors of the Gynocharaeeae. This theory has been seriously questioned by Thompson (68) who has shown in a conclusive manner that the seed plants are not heterosporous at all, and that the extreme difference in size between embryo-sac and pollen grain at the time of fertilization is a result of the rapid post-genetic growth of the former which causes it to assume a pseudo-heterosporous character. It is recommended, therefore, that the "microspore" and "megaspore" of the spermatophytes be renamed the antheridio and the gynosporo respectively. Heterospory is not a necessary concomitant of gnetophyte life cima; the Cordaitales, for example, are homosporous, yet their gnetophytes are generally sexually differentiated.

DETAILED CONSIDERATION OF BRACHYMATA.

THE BRACHYMATA OF THE CONIFERITAE.

As the probable ancestors of the Ginkgoales and Coniferales, it is logical to suppose that the Cordaitales should exhibit a tendency toward one of branches or brachyblasts.

The Cordaitales in general were large plants often reaching thirty meters in height with their branching confined mainly to the top of the tree. The leaves were uniformly
simple, varying from two centimeters to one meter in length and usually arranged spirally on the stem. They attained their maximum representation in the Carboniferous and are said to have formed the world's first great forests. Geographically the distribution of this group was world-wide in Carboniferous time. Fossil specimens have been collected in the Carboniferous and Permian of Europe, North America, and China; in the Permian of Russia and Siberia; and in the Permo-Carboniferous rocks of India, Australia, South Africa and South America.

An inspection of the cross-sectioned coralsitean stem reveals a large pith surrounded by a ring of xylem traversed by rays, which is in turn enclosed by a broad cortex. In some specimens there is a tendency to reduce the amount of cortex and to augment the xylem. The double leaf-trace character is distinctive. The usual absence of annual rings in coralsitean woods seems to indicate a constancy in the annual climatic conditions during the Carboniferous period, though a few species of this order do show true annual growth rings. This may be a result of variable soil-moisture conditions under which the trees grew - a situation not without parallel among tropical angiosperms(13). The coralsitean stele is further distinguished by the possession of "cryptogenic" wood or centripetal meta-xylem. Many genera, however, tend to reduce the amount of centripetal xylem and finally to abolish it completely, so that a change from decenter to centerway is accomplished. The tracheidal pitting of the secondary and in multicellular, the pits usually so closely approximated that they take on a hexagonal
shape. The bordered pits are confined mainly to the radial walls of the tracheids.

All together the vascular anatomy and histology is similar to that of the Ginkgoales and Coniferales rather than that of the Cycadophytes. The archaic cryptogamic wood occurs in the conservative regions of both ginkgos and conifers; the ray character is ginkgoan and the multisieriate trachidal ritter occurs in the young root wood of Ginkgo as well as in the tribe Araceae of the Coniferales. It is, however, in the strobilar and leaf anatomy that the strongest evidence of coniferous affinities are to be found.

Homology of the Vegetative Short Shoot and Ovuliferous Scale

If one accepts the theory that the ovuliferous scale of the coniferous female strobilus is a radically altered and degenerate short shoot, one may, following the interpretation of Cordaitanthus put forward by Renault (47), see in the cordaitalian female strobilus an earlier state of the brachyblast. The ovulate strobilus of the Coniferales, as is well known, is not a simple structure like the staminate strobilus. The ovule bearing organs (ovuliferous scales) are borne in the axil of a bract. The morphology of this ovuliferous scale has been much discussed. The bract is located directly on the axis of the cone and appears to be homologous with the microsporophyll of the male strobilus. Chamberlain (13) shows two most interesting figures (page 435, figures 47-48). One is a longitudinal section through a young ovulate cone of Pinus Bankiana, the other
is a similar section through a young vegetative shoot of the same plant. At the apex of the former section, in the region of the youngest differentiated structures, the young spur shoot and the debatable ovuliferous scale appear to be histologically identical. The young ovuliferous scale might easily be mistaken for the primordium of a vegetative short shoot. In a later stage the young spur forms its sheath of scale leaves and finally a pair of needles. In the young cone, on the other hand, the more mature axillary structure produces no scale leaves, but bears two ovules on the face directed toward the axis of the cone.

Teratology likewise offers indirect evidence of the morphology of the ovuliferous scale. Abnormal specimens frequently have been collected which exhibit all transitions between vegetative and reproductive structures. Chamberlain (16) notes one abnormal cone on a Pinus species which on one side, from bottom to top, resembled a normal pine cone, and whose other face bore short shoots each with a pair of abbreviated needles.

The fact that the ovule bearing structure stands in the axil of a bract or reduced leaf, supports the view that the organ is morphologically a branch, since there is no such thing in the plant kingdom as "folium in axilla folii".

Now the female strobili of the Cordaitales, according to Renault, has the ovule borne on a short spur shoot in the axil of a leaf. Figure 1, Plate 1, a figure of Cordiaanthus, shows clearly the presence of ovule-bearing brachyblasts.
These short shoots, like those of Ginkgo, display a combination of vegetative and reproductive features. Like that of the Coniferales, the female strobilus is a compound structure. This interpretation has, however, been seriously called in question both by Bertrand (6) and later by Schoute who agreed that the cone is rather a simple strobilus. Therefore the whole ovulate structure figured by Renault is a brachyblast and is the homologue of the male strobilus which is itself only a multifoliate brachyblast. Chamberlain's figure (13) of Sarracenia lute lime likewise shows the brachyblast nature of the ovule-bearing structure. It is evident, therefore, that certain genera of the Cordaitales bore brachyblasts strictly comparable to those of Ginkgo.

Jeffrey (36) considers the vegetative short shoot to be the prototype of the ovuliferous scale, and views the living brachyblastic genera as primitive types. Whether one accepts or rejects this view, it is clear that a tendency to form dwarf organs was manifested by the Paleozoic Cordaitales, the order which is believed to be ancestral to the Ginkgoales and the Coniferales.

The Telome Theory

In 1906 Zimmermann (71) put forward the "telome theory" which has led to a reevaluation and reinterpretation of many details of cormophyte vegetative and reproductive morphology. Zimmermann considers the plant body of primitive vascular plants to be made up of units which he terms telomes. In a certain sense this is a return to the "phytomer" theory, though the "telome" is
not a morphological entity but is rather a convenient designation for the vegetative unit which lies between two adjacent dichotomies. The concept originated from the difficulty of forcing the newly discovered Devonian Psilophytales into the canons of the older organology. A plant built up completely of dichotomizing leafless axes would almost necessarily have to be called a thallophyte, yet since the axes are traversed by protostelie vascular strands, the term is hardly applicable, and a new designation is warranted for a unit which is neither a root, a stem, or a leaf. Each telome starts at the junction with another telome and ends, except in the case of terminal ones, at the starting point of the next one. These units may be either fertile or sterile. Fertile telomes are represented by the sporangium with its vascular stalk. The sterile and photosynthetic telome may be termed a "phylloid". The telomes, both fertile and sterile, are regarded as homologous.

In the light of the telome theory the old morphological battle as to the nature of the ovuliferous scale takes on quite another aspect. All cormophyte units, fertile or sterile, are homologous members or telomes. The bract and the ovuliferous scale are, then, in a fundamental sense, homologous organs. The female cone of the pine becomes, therefore, a highly specialized compound short shoot equivalent to the whole ovulate structure of Cordaites shown in Figure 1, Plate 1.

We shall delay to a later page further consideration of the significant histology of the cordaiten leaf and proceed at once to a description of the brachyblastic genera,
Ginkgo, Cephalotaxus, Larix, Sequoia and Pino.

THE BRACHYBLAST OF GINKGO.

The Ginkgoales, represented today by the monotypic genus *Ginkgo*, is an order of gymnosperms which originated at some period in the Paleozoic, reached its climax of distribution and differentiation in the late Jurassic, and since that time, has slowly run toward extinction. *Ginkgo biloba* is therefore often called a "living fossil". It is a beautiful tree which in its youth is slender and spire-like. In old age it is more sturdy and wide-spreadling. This tree exists only rarely in the wild state today; it has been recorded as growing in the China mountains. The Chinese and Japanese have always been fond of the tree. They regard it as sacred and the priests have long cultivated it in the temple gardens. The Japanese name *"Ginkgo"* means, "China country", giving direct evidence of its continental origin.

**External Morphology.**

*Ginkgo biloba* produces ordinary long branches in its current season's growth which, in their second year, form brachyblasts from the buds in the axils of certain leaves originally borne on the long shoot. The growth rate of the long branches is rapid, sometimes attaining a half meter in a year. The short shoot, however, grows very slowly, the older ones ranging from one to five centimeters in length.

The photosynthetic activity of *Ginkgo* is almost entirely carried on by large cuneate or flabelliform, often bilobed, deciduous leaves, which are borne in a spiral phyllopic
on the distal extremity of the dwarf shoot.

The brachyblasts possess a terminal bud and therefore, as stated above, they grow forward a limited amount each year, leaving behind on the short shoot stem the characteristic leaf scars and bud scale scars as records of the preceding growth. The brachyblasts branch occasionally and the branching may even take place within the main axis. It is not rare to find instances where short shoots assume a strong apical growth and push forward as long shoots.

**Histology**

A transverse section through the short shoot of *Ginkgo* shows it to be composed of a large pith surrounded by a cylinder of wood and bounded externally by a slightly functional cambium which produces a few rows of phloem cells on its outside. Cambial activity may even be sufficient to cause the formation of a very few annual rings. The primary parenchymatous cortex is broad, external to it lies a secondary cortex or periderm (multiple as the short shoot grows older) which is effective as an agent to prevent transpiration from the internal tissues. The medulla and cortex are distinguished by the presence of large vertical mucilage canals. Certain parenchymatous cells in each of these tissues enclose large crystal aruses of calcium oxalate and it is of interest to note that Jeffrey showed that the cell nucleus is enclosed by the crystalline jacket. In addition, too, the primary cortex carries many dark-colored tannin cells. The xylem is of the simple gyral-parenchyma type being composed of
tracheids and uniseriate rays. A longitudinal section shows that the tracheid possess bordered pits in single or double files on the radial walls, with transverse thickenings of proto-
cellulose, termed bars of wino or "crassiline", between the pits. The summer tracheids may bear tangential pits. A conspicuous feature of any transverse section of the Ginkgo brachyblast is the pronounced double nature of the leaf trace, a character which was established among the Corinulales.

**Histological Contrast Between Long and Short Shoots**

The contrast between the histology of the short shoot and that of the long or main branch is distinctive. Figure 2, Plate 2, represents a transverse section of the brachyblast of Ginkgo Libani, yet its general anatomical condition is similar to that of Ginkgo or Larix, and hence it may be held to represent the typical structure of an archaic brachyblast type. It shows the large pith and cortex, the small ring of vascular tissues and periderm, which have been described for Ginkgo. An examination of Figure 3, Plate 3, a transverse section of the long branch of Pinus, shows important differences.

The chief departure lies in the relative amount of cambial activity in each. The short shoot, as noted above, has a limited amount of secondary stelar tissues due to the sluggishly functioning cambium. The cortex takes up the bulk of the brachyblast tissue. The long shoot, on the contrary, exhibits normal cambial activity, and, as the figure of Pinus reveals, the xylary tissue bulk is large and shows pronounced
pronounced annual rings. The phloem is less conspicuous, while the cortex is confined to a small outer zone.

A unique reproductive feature of the Ginkgoales is the possession of swimming sperm cells such as are characteristic of the ferns.

**The Brachyblast of Larix.**

Turning now to the conifers we may deal first with the genera *Larix* and *Pseudolarix*, which are placed in the tribe Abietineae of the family Pinaceae. Bailey (4) includes six species and several varieties in the genus *Larix*. *Larix decidua*, the European larch, and *Larix japonica*, the Japanese larch, both in cultivation on the State College grounds, were examined in connection with the present study.

*Pseudolarix*, the golden larch, is native to Formosa and northeastern China. This genus, like *Larix*, possesses deciduous foliage, but on the basis of its anatomy, Jeffrey (33) places it nearer *Abies*. We were unable to obtain material of *Pseudolarix*, but main features of the brachyblast are said to be similar to those of *Larix*.

**External Morphology**

Figure 4, Plate 3, illustrates the foliar conditions of *Larix*, whose long shoots are notable in the fact that during the first year of growth they carry spirally arranged, slender, green leaves which perform the photosynthetic function. In the axils of certain of these leaves stand prominent buds.
which develop into short shoots during the second season. The primary leaves of the long shoot fall at the end of the first season, leaving their leaf bases as recurent leaf cushions on the long shoot.

The brachyblasts of *Larix*, like those of *Ginkgo* possess a terminal bud and therefore they grow forward slowly each year. The total length of the short shoot seldom exceeds one to one and one-half centimeters. Since the cambium, if present, is practically non-functional, the short shoot does not increase in diameter. The long shoot, however, possesses a normal and functional cambium and hence the secondary wood of the long shoot shove up around the unthickened brachyblast base, wrinkling its cortex, and finally sealing in its xylem. At the terminus of each brachyblast thirty to fifty slender needle leaves arranged in a spiral phyllotaxy are borne annually. *Larix* is unique in being the only native conifer which is deciduous. "Girdles", composed of the scars of the bud scales of a given year, are visible on both long and dwarf shoots. The annual increment of the brachyblast is recorded by the length of the inter-girdle areas. Between the girdles stand many diamond-shaped leaf scars, each showing in its center a single leaf trace imprint. The failure of the short shoot to elongate in any but the slightest degree causes the internodal distance between leaf scars to be much reduced. In consequence, an inter-girdle area of greatly approximated leaf scars exhibits a "mosaic of leaf prints". Short shoots of *Larix* often proliferate and grow forward as long shoots; they may also branch.
Figure 5, Plate 5, is a somewhat magnified view of a Larix short shoot, showing the relation of the short shoot to the main axis, as well as the distal arrangement of the foliage. Figure 6, represents several short shoots of Larix in a state of dormancy, and reveals the presence in each of conspicuous terminal bud.

**Histology**

A histological examination of the Larix short shoot in cross section shows a relatively large, stellate pith containing many tannin cells, a small cylinder of wood and phloem, a large primary cortex and an extensively developed stele. Almost all the xylary cells are arranged in radial rows and hence must be secondary in origin. The activity of the cambium is slight, since the diameter of the short shoot is equal throughout its entire length. Any extensive functioning of the cambium would give a conical shape to the brachyblast. The xylem is composed of tracheids and uniseriate rays. A cross section of the basal region of the brachyblast reveals, at least in some specimens, a partial ring of xylary resin canals located radially in the cylinder of wood. The phloem consists of only a few rows of crushed cells. The cortex contains several large resin canals. The leaf traces appear single when first detached from the stipe. In the cortex, however, the trace takes on a significant double character. The two bundles are separated by only one or two rows of parenchyma cells, so that the print on the foliar scar appears single.
The Genus Cedrus.

The genus Cedrus, like Lirix, is placed in the tribe Abietinae, and includes three closely allied species, C. atlantica, C. libani, and C. libani. These trees are native to North Africa, Asia Minor and the Himalayas. The only species at our disposal is C. libani, the Faith Ceder of Lebanon. The specimen was obtained from the Arnold Arboretum, where the tree is now being successfully grown.

External Morphology

The brachyblast of Cedrus resembles that of Lirix in size and in general appearance. Each dwarf branch possesses a terminal bud, the activity of which leads to a slight yearly increase in the length of the short shoot. The terminal bud is often accompanied by a smaller accessory bud. If both terminal and accessory buds become functional a branching of the brachyblasts occurs. Branching of the short shoots is more frequent in Cedrus than in the other genera. The girdles of bud scale scars tend to be more distinct than those of Lirix. The long shoots during their first year of growth bear spirally arranged green leaves, a condition comparable to that of Lirix.

The leaf cushions are absent from the primary leaves of the long shoot, and do not seem to be persistent as they are in Pinae and Lirix. They are evident for a few years, but are finally obliterated by the stretching of the cortical layers. Each brachyblast bears twenty-five to thirty spirally arranged green needles. These leaves are more stiff and glabrous
than those of *Larix*, and are not shed annually.

**Histology**

The transverse section of the brachyblast base of *Cedrus*, Figure 2, Plate 2, has been already referred to in the consideration of the general histological structure of the short shoot. The pith contains many tannin or resin cells. The xylem is enclosed by a band of phloem, the latter considerably more extensive than the width of this tissue in the preceding genera. The cortex, like the medulla, has many tannin or resin cells. The development of the periderm is considerable. Resin canals are present in the cortex, but xylary resin canals are absent. As in *Larix*, the leaf trace is single when detached from the stele, but it soon assumes a double character in the cortex. The two bundles are likewise separated as in *Larix* by only one or two rows of parenchyma cells.

**THE BRACHYBLAST OF PINUS.**

**External Morphology**

We come now to the focal point of our whole inquiry, the consideration of the brachyblast system of the genus, *Pinus*. They represent the organ in such a reduced and simplified condition that, without examination, one might not realize that it is strictly homologous with the conspicuous spur shoots of *Ginkgo, Larix* and *Cedrus*.

Each dwarf branch of the yellow pine, for example, several of which are shown in Figure 7, Plate 3, is borne in the
axil of a reduced gray or brown scale-leaf. Its needles are inclosed proximally by a basal sheath which is to be regarded as an investiture of persistent bud scales, such is the condition in the hard pines. The soft pines, on the contrary, are distinguished by deciduous sheaths. The bud-scale investiture at the base of the short shoot of the hard pines appears to be an interesting retention of the protective scales which cap the winter buds of the less reduced conifers. They would seem to be of slight ecological importance because the imbricated leaf scales of the long shoots now assume the protective function for the undeveloped brachyblasts during the winter season. Their persistence in hard pines may be of value in preventing the needles from drooping laxly downward. The soft pines, which have dispensed with the sheath, have the proximal portion of the needles well stiffened, in contradistinction to the succulent lax tissue which occupies the same position within the sheath of the hard pines.

The number of leaves present on a brachyblast is normally constant for the species. *Pinus strobus*, for example, is characterized by five fascicular leaves, *P. rigida* by three, *P. sylvestris* by two and *P. monophylla* by one. Variation from the normal number of fascicular leaves has probably been recorded for practically every species of pine, yet leaf number is one of the most stable criteria used in the classification of pines.

The living species of pines under normal conditions do not possess a terminal bud on the brachyblast, but it is of particular interest to record our discovery that in apparently normal short shoots of *Pinus jeffreyi*, a tiny vegetative
point occupies the space between the three fascicular needles. In a cross section through this region, Figure 5, Plate 4, it shows itself as a minute triangular area of meristematic tissue. Doubtless similar conditions occur in other pines and it would not be difficult to prepare a series showing all stages from *Pinus Jeffreyi* to full obliteration of the "punctum vegetationis".

It is, however, when we consider the response set up by traumatic stimuli, that we have some of our clearest-cut evidence which testifies as to the ancestral state of the pinean brachyblast. We have observed that when the leader of the yellow pine, *P. rigida*, is killed by the activity of the white pine weevil, *Pissodes strobi,* (which also attacks our native species other than the white pine) (22), some of the brachyblasts become much swollen at the base, and proceed to develop a terminal bud which may grow forward into a long shoot. It is regarded as a distinctly reversionary feature incited by traumatism.

It is a notable condition that a greater than usual number of fascicular leaves occur in almost every species of pine. In the case of *P. rigida* we have counted as many as eight borne on a single brachyblast.

**The Geological History of the Pinus Brachyblast**

Before investigating histologically the brachyblast of *Pinus*, it seems advisable to see what fossil evidence reveals regarding the general ancestral condition of the brachyblast in this genus.

It has already been observed that certain
representatives of the ancestral Cordaitales of the Carboniferous
had definite brachyblasts. Figure 1, Plate 1, a view of a long
branch with its accompanying short shoots of Cordiogranthus shows
best the nature of the brachyblast of these plants.

Several fossil conifers have been discovered
which bear brachyblasts.

Rudolf Florin (23) recently has added consider-
ably to our knowledge of the conifers of the Palaeozoic. Among
them is Walchia, which, according to Florin’s description, ex-
hibits short shoot structures in the female cone. Each of the
bracts of Walchia bears in its axil a short shoot with spirally
arranged scales, the upper of which are fertile. This discovery
has an obvious bearing upon the much debated morphology of the
female strobilus of Pinus.

Jeffrey (94) describes a fossil araucarian
from the Triassic which bore brachyblasts and which he has design-
nated as Woodworthia arizonica. Each dwarf branch of this speci-
men is axillated by a leaf trace which, unlike the condition in
modern araucarians, is not persistent. Branching of the short
shoots also occurs and four or five branches are sometimes repre-
sented on the surface of the trunk. We have already spoken of the
branched character of the short shoots which is frequently present
in Ginkgo, Larix, and Cedrus. No leaf traces are emitted from the
cylinder of the short shoot in its passage through the wood of
the main axis. In Ginkgo, as has been noted, the brachyblast may
branch within the wood of the parent axis. Woodworthia differs
also from Ginkgo in the absence of annual rings in the short shoot. The xylem is typically araucarian in organization. The pitting is of the closely approximated *Araucarioxylon* type.

Another araucarian conifer characterized by the presence of brachyblasts and discovered in the Lower Cretaceous deposits of Staten Island, was named *Araucariocytis* (32).

The possession of brachyblasts by extinct araucarian genera is significant in an attempt to determine the phylogenetic relationship of the various members of the Coniferales, but this consideration is hardly pertinent to our present investigation.

Brachyblasts are likewise exhibited by various fossils of abietineous affinities.

*Pityites Solmai*, Seward (52) is known both from its foliage shoots and its cones. Its brachyblasts are like those of *Larix* or *Cedrus* and are covered at the base by persistent leaf scales. The long needles resemble the leaves of *Pinus*.

*Pitycladus*, Mathewst (52) includes branches bearing multifoliolate short shoots similar to those of *Larix* and *Cedrus*. Scott figures *Pitycladus longifolius* as a scale-covered brachyblast bearing seven or eight long needle-leaves. *Pitycladus Schenki*, Seward, is a specimen which shows long branches bearing leaf cushions and short lateral shoots with scale leaves at the base, and in some cases the short shoots had tufts of needles.

The genus *Pityoxylon* was established to include coniferous fossil woods which possess both horizontal and vertical resin canals. Almost all of the plants characterized by wood of
the *Pityoxylon* type bore brachyblasts.

*Pityoxylon anomum*, Holden (17) bore short shoots much larger than the ordinary pine. The ligneous features of this fossil are extremely like those of *Praecinus*, a well known fossil which will be described below. All of the leaves of *Pityoxylon anomum* are borne on brachyblasts, none being persistent on the long branches. The brachyblast medulla also has aggregations of sclerenchymatous tissue, a feature characteristic of hard pines.

Certain fossil types so closely resemble the modern pines that they are placed in the genus *Pinus* or *Praecinus*. Miss Holden (22) describes the Cretaceous *Pinus praecleropilosa* of Cliffwood, New Jersey as probably the earliest form possessing all the characters of the modern hard pine. An association is shown of both primary and fascicular leaves, the latter of which are borne on brachyblasts subtended by a foliar trace. The short shoots are much larger than those of modern pines, yet these structures never have shown annual rings such as sometimes occur in *Ginkgo*.

Bailey (3) describes a fossil pine which he designates *Pinus acsuatuensiformis*. The short shoot has no axillating leaf trace. Anatomically it shows a combination of both hard and soft pine characters. It has the tangential pitting and the smooth ray tracheids of a soft pine, and the sclerified pith of a hard pine. Another similar fossil, *Pinus succinifera*, Gothan, of the Tertiary shows likewise a blend of *Hanloxyloon* and *Diploxylen* characters.
In 1868 appeared a classical paper by Jeffrey (35) in which he described a coniferous fossil which seems to be the direct ancestor of the modern pines. The specimen was discovered in the Cretaceous deposits of the Androscott clay pits on Staten Island, and since it is regarded as the progenitor of Pinus, it was appropriately named *Pseudipinus statenensis*. Figure 5, Plate 5 is an external view of the brachyblist of *Pseudipinus statenensis*. It is clearly a somewhat bulky short shoot which is distinguished by the presence of a considerable number of fascicular leaves. In the basal region are scars which represent the former position, not of foliage leaves, but of bracts. An important feature of this short shoot is the presence of a terminal bud, whose presence permitted the organ to increase slightly in length. The phenomenon of cladoptosis was already established in this archaic pine ancestor and is the characteristic method through which the modern pines lose their old foliage.

In 1888, following the discovery of *Pseudipinus statenensis*, two more fossil short shoots were found in the Cretaceous clays of Gay Head, Martha's Vineyard, Massachusetts (36). Jeffrey regards these brachyblistas as closely allied to the first specimen and designates them as *Pseudipinus viticentensis*. They differ from the condition of *Pseudipinus statenensis* in that their wood contains numerous resin canals in two or more rows, and in the absence of sclerotic nests from the pith. The preservation was not good enough to show details of the leaf anatomy which is so marvelously exhibited in *Pseudipinus statenensis*.

Stopes and Kershaw (53) have described a fossil
from the Upper Cretaceous of Japan which they consider closely allied to Jeffrey's *Praunus*, and have consequently named it *Praunus jarmacicus*. Although this specimen has a multifoliate brachyblast, it shows several important features in its leaf anatomy which differ considerably from those of *Praunus stonestanensis*.

A consideration will now be given to the three-needled short shoot of a Cretaceous pine which as yet has never been described botanically. The specimen was found by Professor Jeffrey in the Kreischerville deposits. A slide bearing cross sections of the fossil was presented by the finder to Doctor R. E. Torrey, and is introduced here with Professor Jeffrey's permission. Figure 10, Plate 5 shows a cross section through the entire short shoot. The specimen is obviously from a typical three-needled pine, but unlike any known living pine it bears a strong terminal bud and not a mere apical meristem such as we have figured for *Praunus Jeffreyi*. Figure 10 shows three small leaves within the normal three-leaved fascicle; they have just been differentiated from the bud. The histology of this fossil will be discussed in subsequent pages.

**Histology**

Like the short shoots of *Ginkgo*, larch and cedar, the short shoot of a pine possesses a small core of wood. This is all that remains of the bulky xylem of the ancestral branch.

A cross section of the tiny cylinder shows a continuous ring of xylem when taken far down on the short shoot.
Figure 11, Plate 6, represents the cross section of the basal region of the short shoot of *Pinus Banksiana* and it shows the vascular tissues forming a complete ring. The stalk of the dwarf branch soon disintegrated above into a set of fibrovascular bundles which enter the leaves. In *P. strobus*, for example, five bundles are present in the short shoot base, since each leaf in the white pine has but a single fibrovascular bundle. Figure 12, Plate 6, illustrates the condition of *P. sylvestris*, in which four vascular strands are present, grouped into sets of two each. This figure shows that two of the bundles have not yet become completely separated from each other. *P. rigida* or *P. Jefferyi*, three-needled pines, have six fibrovascular bundles which also tend to arise in pairs, since each of the three leaves has two bundles. Several rows of phloem cells lie outside the xylem of each vascular strand. Around each vascular bundle are cortical cells which, a short distance farther up the leaf, are replaced by the characteristic transfusion tissue and mesophyll of the foliar organ. The cortical cells of the basal region of the leaf and short shoot of *P. sylvestris* are peculiar in that the inner cells have lignified walls and have large perforations or pits on the horizontal walls. Cortical resin canals are usually present in the basal cross section of a short shoot, but are not as numerous here as in the leaves.

**Cladostemia**

The brachyblasts of *Pinus* are distinguished from those of *Ginnsa*, *Larix* and *Cedrus* by the phenomenon of cladop-
The leaves of Ginkgo and Larix are shed annually from the short shoot. Cedrus retains the fascicular leaves two or three years before dropping them. In Pinus, however, the whole short shoot becomes detached from the main stem when the leaves are shed. P. Strobus retains its short shoots two years before cladoptosis occurs. P. sylvestris retains its leaves for three years, while in P. austriaca the brachyblasts do not become detached until the fourth season.

Cladoptosis is not an uncommon phenomenon in the plant kingdom. A rather complete survey has been made by James Stark on the shedding of branches and leaves in the Coniferae (66). Stark points out that in cladoptosis one is dealing with a situation in which one morphological unit (shoot) behaves physiologically like another (leaf). He calls attention to the fact that many of the Cupressinae, such as Thuja, Libocedrus, Guercus, and Sequoia exhibit cladoptosis in the deciduous nature of their leafy twigs. In Pinus the branch (short shoot) which is shed, is somewhat more limited than the general leafy twig which is shed in the Cupressinae.

In this detail we have another of those curious analogies which accompany the assumption of the leaf function by branches. Thus the extreme type of cladophyll, as in Eucalyptus, takes on the shape and full physiology of the leaf; it gives up its apical growth and its chlorenchyma shows a dorso-ventral differentiation.

In Pinus the brachyblast behaves like a foliar unit and has taken on the deciduous habit of the leaf itself. In
Panius remarkably the unifoliate brachyblast is to all intents and purposes a single leaf. One is led into a false line of evolutionary speculation by such curious facts to which the theory of orthogenesis alone seems to offer any tangible key.

The short shoot or ectophyll.

In any turn next to the curious tree, Sciadopitys verticillata, of the tribe sciadopiineae. The genus is native to southern Japan, but is now cultivated in the United States as an ornamental tree. Each short shoot is reduced so extremely that it shows little except a long needle with a deep groove on its dorsal (abaxial) face. This needle is believed to be the fusion product of two originally separate leaves, which united apparently along their ventral and lateral faces. The core of wood of each brachyblast is reduced almost to complete obliteration. No attempt was made to obtain microscopic sections of this region. The brachyblasts are arranged in verticils on the long branch and each arises from the axil of a scale.

Culinary of brachyblasts.

Such are the facts which relate particularly to the structure of the brachyblast cauline axis apart from the detailed histology of the foliar scales. We have, we think, established the following points:

1. The brachyblasts of Ginkgo, Larix and Cedrus are obviously more complex in organization than those of even the most complex species of Panius. At the same time they are clearly derivative from the long shoot and in spite of their
abbreviated length and limited radial growth they possess the normal complement of the long branch, such as scaly terminal buds, growth from an apical meristem, slight cambial development, and secondary cortex. They may branch or even grow into long shoots.

3. With the living pines extreme regression has been introduced and the brachyblast is assuming the character of a deciduous foliar member. Yet it still retains the bud scales, apical meristem (well formed in *Pinus Jeffreyi*) and develops a small axis of secondary wood. Trausatis often converts its apical meristem into an apical bud.


**THE CYCLOPINEANS AMONG ANIMALS AS A RELATIVE HISTOLOGICAL UNITS**

Before advancing to study the more recent matter of leaf histology it may be well to discuss briefly the criteria which comparative morphology considers most valid in its attempts to establish evolutionary affinities and sequences.

Jeffrey (37, 38) has formulated certain canons of comparative anatomy which he holds to be pertinent in such evolutionary interpretations. He has appropriately designated these criteria as the "5 R's of comparative anatomy." They are
the phenomena of retention, reversion and recapitulation. These three, together with whatever paleontological evidence is available, constitute the main criteria which the anatomist employs in the attempt to establish the phyletic position of a given specimen.

The doctrine of conservative organs or retention is based on the fact that certain regions of a plant, such as the leaf, reproductive axis, root or sporangium, often possess, to a greater or lesser extent, some feature not known in the stem or progressive part of the plant. In the ancestral plant type, however, the given feature was present even in progressive organs of the plant. Jeffrey (38) cites as an example the leaf anatomy of the Cycadales, where the fibrovascular bundles of the foliar organs are distinguished by the presence of centripetal xylem. The stem, however, is distinctly endarch. The Paleozoic Cycadofilicales, which are generally held to be ancestral to the Cycadales, are characterized by the presence of centripetal xylem in the bundles of both the stem and the leaf. The presence of centripetal xylem in the foliar strands of the living cycads, according to the doctrine of retention, helps to establish the relationship of the modern cycads to the Paleozoic Cycadofilicales.

Reversionary phenomena often follow upon traumatic stimuli. The Abietineae, for instance, are sometimes divided into two series, the Pinea and the Abietae. The Pinea are distinguished by the possession of both horizontal and vertical normal resin canals in the wood; the Abietae, on the contrary, have no normal resin canals at all in the secondary wood, though they
occur in the conservative organs. In *Cephalocaulis*, however, after injury, resin canals are found in both horizontal and vertical planes. In *Abies* itself vertical resin canals appear in wounded areas. The inference is that the pinean condition is the one ancestral to the abietean. Traumatic stimuli do not always cause reversionary features to appear. A correlation with the condition of conservative organs and with fossil evidence is necessary before a traumatic feature can be definitely termed reversionary.

The third principle is that of recapitulation. A terse statement of this law is that "ontogeny recapitulates phylogeny". The Hyatt-Cope school of Neo-Lamarckians, of the late nineteenth and early twentieth century, did much toward the development and clarification of this principle. Hyatt (30) states the law in the following words: "In the young, stages are found, the equivalents of which are to be sought in the adults of the ancestral types". The principle is too well known to require labored development here, though it is not so generally understood that plants as well as animals present numerous illustrations of the law.

Besides these three principles, the comparative anatomist considers whatever fossil evidence is available. If the paleontological knowledge coincides with the facts gained by the retentive, reversionary and recapitulatory phenomena, a sound conclusion can be made concerning the problem. If the fossil evidence is not cogent with the other, then either the inductive reasoning is faulty or other factors are present which must be taken into
consideration.

The "3 H's of comparative anatomy" have stood the test of time and are now generally accepted by morphologists of the twentieth century as valid criteria.

An examination of the brachyblasts of the Pinaceae reveals that this family illustrates a remarkable single line regression from a complex to simple organization (65). Although the evolutionary tendency for the gymnospermous brachyblasts as a whole is regressive, it is obviously impossible to think of Ginkgo, Larix, Cedrus and Sciadopitys as forming a single orthogenetic or phyletic series. The series is best interpreted not only as one of regression, but also as a step series. A step series may be defined as one in which the evolutionary condition of an organ in one phyletic line sets it in a definitely lower or higher position than the condition of the same organ in another phyletic line. When the phyletic lines are numerous the variations of such organs may give the false effect of a true genetic series. It is probable that every "phyletic line" ever determined is of the nature of a step series. It is to be noted that within this step series, there is present in the Pinaceae, a well-marked regressive orthogenetic series. The following is an attempt to set forth as a step series, the phyletic relationship of the various brachyblast genera or species considered in this paper:
Ginkgo (large, deciduous leaves; terminal bud) A

Larix (many needle-like, deciduous leaves terminal bud) E

Cedrus (many needle leaves; shed every 2-4 years; terminal bud) C

Proximus (many needle leaves; cladoptosis; terminal bud) D

E. Strobus (5 leaves per brachyblast; cladoptosis; no terminal bud) {1}

E. quadrifolia (4 leaves; cladoptosis; no terminal bud) {2}

E. rigida (3 leaves; cladoptosis; terminal bud recalled by traumatic stimuli) {3}

E. terminosa (2 leaves; cladoptosis; no terminal bud) {4}

E. monophylla (1 leaf; cladoptosis; no terminal bud) {5}

Sciadopitys (2 completely fused leaves on a much reduced brachyblast; no terminal bud; condition perhaps equivalent to Figs monophylla) N

Stage "A" may be much more primitive than stage "B" or "E". Yet it can scarcely be said, after an examination of the morphology of each, that "A" is the genetic ancestor of "B" or "E". The similarities which exist rest upon common ancestral source. The different lines of the series often parallel one another, and convergences are often introduced which confuse the problem. In this series, for example, the Larix and Cedrus short shoots show considerable superficial resemblance, yet several anatomical features exist which indicate their divergence.
The Pinaceae, as noted above, illustrate remarkably well, a regressive orthogenetic series from the complex brachyblast of the fossil precursor, Pseudotsuga, to the much reduced one-leaf short shoot of *Pinus murrayana*. The results of an application of the "3 R's" to the Pinaceae are cogenet with paleontological discoveries.

**LEAF MORPHOLOGY AND HISTOLOGY.**

Having considered in some detail the organology and histology of the short shoot axis, we may now proceed to an examination of the leaves of those genera of gymnosperms which bear brachyblasts.

It has already been pointed out that the adult functional foliage of these plants is largely confined to dwarf cauline organs. Yet different conditions are often to be noted in the juvenile and the traumatic foliage, and the fossils likewise have an interesting story to tell in this connection.

The seedlings of these plants, of which *Pinus* may be taken as a typical example, are in fact distinguished by the absence of brachyblasts, and the photosynthetic function is performed by slender needles which are arranged in a spiral phyllotaxy on the main axis of the plant. They are sometimes spoken of as primary or primordial leaves. Brachyblasts appear later, developing from buds in the axils of certain of the primary leaves. Some species of *Pimus* develop their brachyblasts on the seedling inside an age of two or three years, but many do not develop them until they attain an age of four or five years. In correlation with the appearance of brachyblasts, the primary
leaves show a progressive reduction and, on older parts of the plant, are seen reduced to brown or grey scales which sublend the short shoots but which are no longer capable of photosynthetic activity. In other words, like the bracts which sublend the pedicels of an inflorescence, they become mere functionless retentions from an earlier state of functional activity.

The seedling leaves of Ginkgo are cuneate-flabelliform and are traversed with dichotomizing veins like those of the adults. But unlike the adults they are deeply bilobate or even repeatedly cleft. That this is a significant recapitulatory feature becomes evident when we consider the leaves of the fossil forms, Ginkgoniphilus and Balera, which are widespread in Eocene and Tertiary rocks. The extinct genus Balera (62), for instance, possesses a leaf so extremely shredded, that it resembles the archaic archeopterid ferns and appears to be little removed from the fundamental dichotomizing telomes system of the Psilophytales. The leaves of the long branch are likewise distinguished by a deeper lobation than are those of the brachyblanf. This is as it should be - the long branch and its foliage representing the more archaic state whence the short shoot is derived.

It is a matter of common observation, that as a result of traumatic stimulation, long acicular primordial leaves appear on old branches of Pinus. The writer has observed the presence of these leaves on suckers which developed from the base of a freshly cut stump of Pinus rigida, where they attained a length of approximately four and one-half centimeters. In some cases the primordial leaf developed at points where no bracky-
blast was present. These leaves were fully formed and were functional photosynthetic organs. The writer also obtained, from the Forest Nursery of the Massachusetts State College, a twelve or fifteen year old specimen of *Picea pungens* which was rather stunted, presumably the result of insufficient nourishment, or perhaps of some injury during its transplanting. Certain brachyblasts on this plant were likewise subtended by well-developed primary leaves and, moreover, several branch termini were abnormal in that they possessed spirally arranged primary leaves in whose axils no brachyblasts had yet developed. This latter condition recalls the conditions of the first year's growth of the long branches of *Larix*. It has been noted that in *Larix* and * Cedrus*, Figure 4, Plate 3, the part of the stem representing the current season's growth is characterized by the presence of spirally arranged primary leaves, and that during the second year brachyblasts develop from buds in the axils of certain of these leaves. The primary leaves are shed at the end of the first year and in consequence, photosynthetic activity is later confined entirely to the foliage of the brachyblasts.

The Japanese have succeeded in fixing the juvenile foliage character of various conifers by propagating branches of young seedling plants. Plants which do not obtain sufficient nourishment often tend to retain the juvenile foliage. The species which have usually been the subject of these experiments among the Japanese belong in the genera *Thuja* and *Chamaecyparis* (4).

Paleobotany may next be investigated in an
attempt to determine the relative prevalence of primary and brachyblastic foliage on the ancient Coniferae. It has already been pointed out that fossil remains of brachyblasts have been discovered in the Cretaceous and Triassic deposits of the Mesozoic. In a few cases short shoots and primary foliage have been found on the same branch. Fontaine (44), for example, describes certain remains, which he refers to Heer's Jurassic genus Lentostrbus, as having both fasciculate leaves and others which are arranged spirally at intervals on the main branches. The latter, he tells us, are comparable to the primary leaves found in the seedling, and occasionally as a result of injury in living pines. Miss. Holdan, in her article on the Cretaceous Pitveylia from Cliffwood, New Jersey (25) has described for Pinus protosclerocystis a condition in which the leaf traces are not wholly confined to an axillary position but are likewise quite numerous in the pith. She interpreted this condition as an indication that the leaves of this conifer were of two sorts: those borne directly on the main axis as they are in the seedling, and those borne on short shoots. Yet Florin (93) in his description of various Palaeozoic genera of Coniferae reports the presence of only primary foliage in the specimens which he inspected. There is good evidence, however, that among the Cordaitales, the primitive and putative ancestors of the conifers, brachyblast-bearing genera were already present. In general in fossil conifers, primordial foliage has been much more prevalent than leaves borne on brachyblasts.
Paleontological evidence, then, together with the juvenile and the traumatic foliar conditions of the living gymnosperms, seems to indicate that the original type of functional foliage was borne upon long shoots and that the relegation of foliage to the brachyblasts is of secondary origin. This is cogent with the idea expressed at the opening of this paper, that the introduction of brachyblasts into gymnosperms was a secondary feature, which led to improved leaf display and augmented the photosynthetic capacity of the plant.

**THE MICROPHYLLY OF CONIFEROUS LEAVES.**

Coniferous leaves, both of the primary and short shoot types, are often small and acicular and at first glance this suggests that their ancestry is to be sought among the microphyllous races of the past, such for example as the dendroid Lycopodiaceae, and Professor Seward (55) has actually suggested such a derivation. How the small leaves of the Lycopodiaceae have been regarded as modified emergences and as fundamentally distinct from the vascular foliar "periphytes" of the ferns. Yet the vascular anatomy of the stem and the structure of the reproductive parts contradicts Professor Seward's opinion and forcibly suggests that the gymnosperms arose among the megaphyllous ferns. And indeed, not all gymnosperms are microphyllous. The Cordaitales, ginkgos, araucarians and podocarps often possess large paddle-shaped blades.

It seems, then, only logical to regard the needle-leaf as derived phyletically by reduction from an ancestral
megaphyllous condition. The idea may be expressed more technically by stating that the coniferous leaf is coenogenetically microphyllous but palingenetically megaphyllous. Seeking an ecological explanation for this assumed reduction one can find it in the progressive refrigeration which has modified the climate of the northern hemisphere so greatly since Mesozoic time. A race of evergreen trees must face the austere drought of winter and must cut down evaporation. Reduction in leaf area results in the prevalent microphyll of the Coniferae.

If one accepts Zimmermann’s telome theory (71), however, the whole argument as to the fundamental question of microphyll or megaphyll disappears, for then the minute leaf of the Lycosodius is nothing but a single telome, while the megaphyllous leaves may be interpreted as greater aggregations of telonomic units.

It is not the object of this paper, however, to argue these theories. The pertinent fact is that the apparent coenogenetic microphyll is closely related to the xerophytic nature of the coniferous leaf.

XEROPELLY OF CONIFEROUS LEAVES.

The xerophilous features of the coniferous leaf can be best shown by a discussion of the anatomy of a typical pine needle such as that shown in Figure 16, Plate 7, which represents a transverse section of the median part of the fascicular leaf of *Pime rigida*. The leaf is covered by a thickened cuticle which is effective in preventing the escape
of moisture from the internal tissues. Beneath the cuticle lies the epidermis, a single layer of sclerenchymatous cells. Internal to the epidermis is a hypodermis of one or two rows of sclerenchymatous cells. The hypodermis at intervals projects inward as sclerenchymatous ridges for four or five rows in thickness. Both these tissues have a mechanical function, but they likewise tend to prevent transpiration from the internal tissues. The stomata of coniferous leaves are sunk in longitudinal grooves on both the inner and the outer faces of the leaf. Sunk stomata are likewise characteristic of desert plants which are highly modified for the xerophytic life. The tissue just inside the hypodermis is the chlorenchymatous photosynthetic layer, and it is composed of two to four rows of large cells distinguished by infolded walls and termed "rosette cells". The whole tissue may be spoken of as plicate mesophyll. The mesophyll is separated from the inner vascular region by a well-defined endodermis. Inside the endodermis lies a broad tissue which completely surrounds the two fibrovascular bundles. This layer, highly characteristic of gymnospermous leaves, constitutes the transfusion tissue. In Pingu it consists of parenchyma cells mixed with other cells which bear bore red pits on their horizontal anticlinal and lateral walls and must, in fact, be regarded as tracheidal in nature. The transfusion tissue constitutes an important water storage and conductive region. It seems probable that it may be correlated with the xerophytic nature of these leaves, since an efficient water storage and conductive
tissue must be an advantage at least in northern Conifers which are subject much of the year to a condition of physiological drought.

Miss Stopes, in an article on the xerophytic character of the gymnosperms (57), puts forward the view that the xerophytic nature of conifer leaves is not due to inherited adaptations or dry conditions, but is the result of the histological structure of the wood. She points out that gymnosperms, with tracheids their only means of water conduction, are incapable of sending a rapid flow of the water through the wood, as can the angiosperms with their efficient vessels. Hence the plants must set strict limits to their leaf surface and to their transpiration. As a result, even in a mesophytic forest, the individual gymnosperms are continually in want of water, and the result is the assumption of xerophytic foliage, which acts as a check against undue loss of moisture.

Professor Groom, however, has shown that Miss Stopes’s theory does not hold in the case of Larix which has a rapid transpiration current.

Turning, on the other hand, takes a definite stand and asserts that the soil upon which coniferous forests occur varies widely, yet it is always physically or physiologically dry, a fact which harmonizes with the xerophytic structure of the conifer leaf.

Perhaps the xerophily and microchlyly cannot really be attributed to any one factor, but is rather the result of a combination of those mentioned above.
HISTOLOGY OF THE FASCICULAR LEAF.

Since the pine leaf is representative of coniferous foliage, and exhibits features which may be profitably compared with fossil types, we turn now to consider the leaf structure of several species of Pinus. The histological details of the needles of Larix and Cedrus are not radically different, and do not warrant separate description. Likewise the leaf anatomy of Sequoia really has little in common with the acicular leaf, whose story is the main focus of interest here. Acicularity, with its curious internal idioblasts and peculiar sunken stomata represents an aberrant type of coniferous leaf and need not be considered in detail.

Figure 13, Plate 7, representing the sectioned leaf of Pinus rigida may again be used to represent a typical condition for the tissues in a medullary cross section of a fascicular pine leaf.

The epidermis and hypodermis have been already referred to in connection with the xerophytic nature of the coniferous leaf. They consist of sclerenchymatous tissues whose function is mechanical and protective.

The mesophyll, however, is of interest because of its peculiar rosette cells and its phyletic significance. In Figure 14, Plate 7, these cells are shown under higher magnification. Each shows a number of flanges which project into the cell cavity. Haberlandt (26) points out that every polyhedral or rosette cell of the mesophyll consists of a number of branches, each of which resembles a palisade cell in shape, and
he sees in the mesophyll of Pinus a superficial resemblance to the true palisade tissue of angiospermous leaves. The physiological significance of these infolded walls is linked with an augmented photosynthetic capacity of the leaf. It is known that the chloroplasts in a given mesophyll cell tend to assume a peripheral position or to spread out on any wall projection. Hence the physiological advantage of the flanged type of photosynthetic cell consists mainly in the fact that a larger internal surface is provided for the display of chloroplasts, though it likewise increases the area available for gaseous interchange with the environment. The increase in number of chloroplasts that is made possible by the presence of these flanges of the mesophyll cells is considerable. Haberlandt remarks that if the internal surface of a cell devoid of flanges be reckoned as equal to one hundred superficial units, the corresponding value for the rosette cells of Pinus sylvestris would range from one hundred and fifteen to one hundred and thirty-five units.

In longitudinal section (Figure 15, Plate 8) the mesophyll closely resembles normal palisade tissue, though a slight change in focus reveals the irregular shape of the constituent cells.

Resin canals are conspicuous inclusions of the mesophyll. The magnified view of the mesophyll, Figure 14, includes the transverse view of a resin canal. The typical resin canal is lined by a layer of secretory resiniferous cells which in their turn are inclosed by a sheath of one or more rows of accessory cells. The number of resin canals present in the
given coniferous leaf is usually constant. *Cupressus Libani*, *Larix laricina*, *Pinus Strobus*, *P. ponderosa* and *E. Jeffreyi* all are distinguished by the presence of two resin canals. *P. sylvestris* is characterized by nine and *P. nigra* by ten of these schizogenous spaces.

If, however, in contradistinction to a median section, we cut the fascicular leaf through its basal part, we find a strikingly different condition which for some reason does not seem to have been noted by anatomists, or, at any rate we have found no reference to it in the literature. The basal mesophyll cells of a fascicular leaf such as that illustrated by *Pinus Banksviana*, in Figure 16, Plate 6, are distinguished by an entire absence of cells which show ridges or flanges projecting into the cell cavity. The units of the parenchyma are not infolded but possess normal cell contours. Figure 17, Plate 9, shows these simple parenchymatous cells under higher magnification. If this figure is compared with Figure 14, the contrast between the two mesophyll types is striking. An examination of a longitudinal section of the fascicular leaf of *P. sylvestris* revealed the fact that the simple parenchyma extended upward for seven tenths of a millimeter into the body of the leaf before it was replaced by the plicate mesophyll. In fact the basal cross sections of the leaves of eight pine species examined revealed in each case a mesophyll which consisted of simple parenchymatous cells. The fascicular leaves of *Cupressus* and *Larix* likewise show basal simple parenchyma, but higher up it is replaced by plicate mesophyll which extends to the terminus
of the leaf just as it does in Pinae. The phyletic significance of these facts will be discussed later.

It is important to note here, however, that the basal region seems to be the first part formed in the ontogeny of the leaf, and from the basis of the biogenetic law this detail assumes significance. In some Coniferae, such as in Larix, it has been noted that an intercalary type of growth occurs, but even with intercalary development, the basal leaf region seems to be the first formed, the intermediate growth starting slightly above the first formed leaf tissue.

Grant Allen (1) has argued that the basal portion of a leaf is of greater phyletic age than the more distal region. He cites instances in which the primitive color of the petal is retained in the basal region of the member, while the new and more highly evolved colors appear first on the margins. He shall later give palaeontological evidence which tends to substantiate the theory that the simple parenchyma of the leaf base is truly an index of the greater phyletic age of this portion of the leaf.

The single layer of cells which bounds the mesophyll internally (Figure 13) is the endodermis. K. berleman (25) suggests two physiological functions for the endodermis: (1) it restricts translocation to certain definite parts, and prevents the premature escape of substances which travel in the vascular bundles; (2) it affords mechanical protection to the conducting strands. In transverse section certain lignified areas known as Ca. pary's bands are conspicuous on the radial and sometimes on
the tangential walls of the endodermal cells. Figure 11, Plate 6, shows the longitudinal aspect of the endodermis. The Casparian bands appear continuous except where perforated by well defined pits.

The area which lies inside the endodermis and surrounds the vascular bundles of the leaf is a curious zone which has been termed the transfusion tissue. In a typical coniferous leaf such as that of *Pinea*, this tissue consists of ordinary parenchyma interspersed with short, squat tracheidial cells which typically bear bordered pits on both the longitudinal and horizontal anticlinal walls. The walls of the tracheidial cells are generally lignified and stain bright red with safranin, but sometimes, as in *Pinea*, they resemble ordinary parenchyma cells and take the blue haematoxylin stain, a detail which suggests that they are cellulose-walled. They are, however, devoid of protoplasmic contents. Figure 18, Plate 9, shows a typical instance of the transfusion tissue, in cross section, revealing the presence of cells with bordered pits on the transverse walls, and other parenchymatous cells which show large nuclei. In figure 18, representing the longitudinal section of a leaf, it is shown the nature of the transfusion tissue in its radial aspect.

The cells of the transfusion tissue of *Larix* and *Cedrus* are always lignified, stain bright red with safranin, and usually bear small bordered pits on the walls. The transfusion tissue of *Ginkgo* differs from that of the other genera in that the cells show reticulate thickenings instead of bordered pits. We have noted in an apical section of the f asciculate leaf of *Larix*
also that certain of the transfusion cells bear reticulate thickenings.

Since this tissue has been so extensively studied, it is of interest to review briefly some of the observations and theories which have been set forth concerning its origin and function.

Transfusion tissue was first noted by Carsten in 1847, and studied carefully by Frank in 1884.

Van Mohl, 1871, (67) gave it the present designation of "transfusion tissue". Van Mohl also studied it in Taxus and observed that as one moves from the leaf base toward the apex, the xylem of the vascular strand gradually changes into transfusion tissue. He also cited its presence in Podocarpus and Cymus.

Many students believe that transfusion tissue is merely modified parenchyma. Lignier and Jeffrey, however, hold that at least in Cymus, the tissue is the remains of obsolete side veins. Another and similar hypothesis correlates the presence of transfusion tissue in gymnosperm leaves with a lack of vein ramifications in these leaves. Coniferous leaves, it is to be noted, for the most part, possess but one or two vascular strands.

The French botanist, Van Tieghem, maintains that the transfusion tissue is a part of the pericycle surrounding the bundle.

Finally Goodall (70) in 1857 put forth a theory
of the origin of transfusion tissue which has gained considerable favor among morphologists. He holds that this tissue is derived from the centripetal xylem. In an investigation of the cotyledons of *Ginkgo biloba*, he noted small scattered tracheids in the position of normal centripetal xylem and observed, furthermore, that they graded into cells with a greater diameter and with thickened reticulate markings on their transverse or horizontal anticlinal walls. But reticulate thickenings, as we have noted, are characteristic of *Ginkgo* transfusion tissue. In *Cycas revoluta* Worsdell noted a similar transition between small elements near the protoxylem and other larger cells which bore bordered pits on their transverse walls.

Bernard (7), like Worsdell, believes the transfusion tissue to be derived from the centripetal xylem. He goes a step beyond Worsdell, however, when he concludes that if the transfusion tissue of the *Cycadeaes* is derivative of the centripetal xylem, it then follows that the same tissue in the *Cupiferales* also originated from centripetal xylem. Bernard demonstrated clearly the origin of this tissue in *Agathis laranthi-Falina*.

We have noted already that the bordered-pitted transfusion cells of the *Pinus* leaf are interspersed with parenchyma, and that their reaction to stain gives evidence that their walls are chemically of cellulose rather than lignified. There is evidence to believe that they are in a process of conversion to the parenchymatous state and that the parenchyma cells among them have already suffered complete transformation.
This is a situation which is evidently analogous to the conversion of certain tracheids of the stem into wood parenchyma, a phenomenon which is widespread among the Coniferae (23).

The only tissues which remain to be discussed are those which constitute the fibrovascular bundles. Bundle number, first of all, is one criterion used in the differentiation of hard and soft pines. The *Pinus* of soft pines are constant in the possession of a single vascular strand. Figure 18, Plate 10, a median transverse section of *P. strobilus*, may be considered to represent the typical condition of a soft pine. Figure 19, the median cross section of *P. rigida*, represents the condition in the *Pinus* or hard pines. Histologically the bundles of these two groups are identical. *P. strobilus* exhibits the following features. A few smaller tracheid-like cells of the endarch primary xylem, lie on the margin of the bundle which is directed toward the two inner faces of the triangular leaf. Developed centrifugally from these through cambial activity lies the secondary cells. On the outer face of the xylem is the phloem, composed mainly of parenchymatous cells. The bulk of the xyleary tissue is therefore of secondary origin and since the needles remain on the tree for several years, the sluggish cambium builds up a considerable arc of wood and phloem. According to Verschaffelt's theory that the transfusion tissue is a derivative of the centripetal xylem, the vascular bundle of *Pinus* can no longer be considered as endarch, but must necessarily be classified as exarch. One or two uniseriate rays are usually present in the xylem and phloem of each bundle.
Some transverse sections of pine leaves show a considerable number of fibrous cells located around and between the vascular strands. Figure 16, Plate 8, the basal region of *P. Banksiana*, shows a considerable development of these thick-walled cells. The fiber cells apparently tend to strengthen the leaf mechanically. *P. Banksiana* also is the most northern American pine and the fibrous cells may perhaps be correlated with the general small size and tough, fibrous and xerophytic nature of the leaf. *P. sylvestris*, which also has a northern distribution in Europe and Asia, shows considerable development of similar tissue.

It has been noted above that the number of vascular bundles in a leaf is a taxonomic criterion. Several other features of the leaf are used in classifications of the species of *Pinus*. Since resin canals are numerically constant for a given species, they have been included in some keys. Stomata, too, on the basis of their number and location on the surfaces of the leaf is another factor of taxonomic value. Leaf shape, is a characteristic feature. If the fascicle has ten needles, each leaf in the cross section is hemispherical; the individual leaf of a three-needled fascicle tends to be triangular in section with the outer surface of the leaf curved as an arc and the median inner angle approximately 120°. The fascicular leaf of *P. Strobus*, which has a quinquefoliate brachyblast, is also triangular, but the angle formed by the two inner sides of the leaf is only about 75°; the unifoliolate, brachyblast leaf of *P. ponderosa*, on the other hand, is terete.
Blind retina (61), in an attempt to reconstruct a working key for the various types of primitive eye structure present, employ among other cases, the characteristics and characteristics of strata, microfossils, and the vascular system along with the shape of the individual P. reversionis leaf.

THE STRUCTURAL HISTOLOGY LEAF

It has already been noted that on the young branches, the boundary to a certain by rounded scale leaves, the functional botanist of the P. reversionis leaf, it was observed, however, that in the case of most in the species, traumatic stimulation induced the formation of functional remaining leaves. This is apparently a revolutionary process. It is of interest to examine such a leaf to determine any deviation from the histology of the mature leaf as constructed.

Figure 17, Plate 10, represents a basal transverse section of the mature fully-grown primary leaf of P. reversionis. The simple parenchyma tissue of the mesophyll shows clearly. The most marked difference, however, is the fact that the vascular strand of the primary leaf is simple, whereas that of the fascicular leaf of the same species is considerably double, another notable feature of the mature leaves of this species in this basal section.

A section of a short distance above the base, on the other hand, shows similar morphologies in a well-developed stele. The vascular strand, however, parallels a couple
The epidermal layer of *E. marina* is thicker than that of *E. radiata*. A simple epidermis exists in contrast to the double leaf tissue in the freshwater leaf.

**The Epidermal Layer.**

The epidermal cells are some long, rather connective tissue, present among the epidermal cells of *E. radiata*. A simple epidermis is present in the freshwater leaf. The superficial leaf cells of *E. marina* are a histological condition essentially the same as the epidermis of the freshwater leaves. The superficial leaf cells are of intermediate size, typical of many transitional forms. The superficial leaf cells of the freshwater leaf may be of intermediate size, typical of many developmental forms. The superficial leaf cells are clearly visible through the epidermis. These leaf cells are primary leaves which show that these angiosperms have

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we are dealing again with the same occurrence as before the previous findings that we have already noted in the case of a cone of the juvenile type, but, unlike the remaining part of the adult branch, the primary leaves of the branch internodes have taken over a new function of protection for the developing bud.

**Botanical Studies on Young Coniferous.**

The above considerations on the leaf anatomy have been gained by comparative study of the adult type of branch or coniferous leaves, and all studies can therefore be to observe the non-pertinent type, yet, it is provisionally assumed which may be seen by this organ. In a sense a bill exists for the evolutionary capacity of such plants, as noted to botanists by the determination of the small leaves will have very direct light on the condition of the modern coniferous leaf.

It has been noted that the reduction leaf shows histological features which relate it to evergreens. *Chamaecyparis nootkatensis* has been described by Stiebe (4) and the leaf anatomy is representative for coniferous leaves. Figure 11, Plate 11, is a transverse section of the leaf blade of *C. nootkatensis*. The external zone of the leaf is limited into a palisade layer above and a spongy layer below the palisade zone. The differentiation between the two layers is not distinct in the transverse section as shown of Figure 11. The leaves being at moisture are surrounded by the soft wood. The spongy zone is strengthened, particularly in the region of the spongy zone by transverse veins of xylem tissue. The parenchyma area is not surrounded by other which
is entirely centripetal in its development and which merges on both its flanks with thick-walled cells possessing small cavities and bearing bordered pits on their walls. Outside this layer lies another tissue which consists of cells with thinner walls and larger lumina; the walls of these latter cells are also border-pitted. The two layers inclose the phloem as well as the xylem completely. Now these two layers of pitted tracheidal cells, which enclose and are intimately associated with the fibrovascular bundle, constitute a double sheath of transfusion tissue. Sometimes a third group consisting of a few clear cells with thin walls and elongated transversely, are present between the vascular bundles, and since they seem to merge with the outer sheath of transfusion tissue, they are sometimes designated as accessory transfusion tissue. It is notable that, unlike Ficus, the transfusion tissue is composed entirely of tracheidal cells with no admixture of parenchyma. The inner transfusion sheath, from its position on the flanks of the bundle, supports Herend's theory that transfusion tissue is derived from the vanishing centripetal xylem. Since this layer presumably appeared first in evolution, it is termed the "primitive transfusion tissue". The outer transfusion sheath is considered by Miss Stopes to be derived from the parenchyma of the leaf mid-rib, and hence this layer may be designated the "peridesmic transfusion tissue". The third or accessory transfusion tissue may have had a separate development from the mesophyll of the leaf, and may be called "mesophyll transfusion tissue". The leaf anatomy of Corallina principiosa, then, is distinguished by a complexity of transfusion tissue, the innermost
sheath of which is very likely a derivative of the centripetal xylem.

We turn next to the foliar histology of *Praehinus*, the putative progenitor of the modern genus *Pinus*. Figure 22, Plate 11, shows a cross section through the needle cluster of the multifilicate brachyblast of *Praehinus asterophyllus*, Jeffrey (35). The section does not include all the fascicular leaves, since some of these were lost in the process of fossilization. As we noted in the previous descriptions of the brachyblast, that *Praehinus* is distinguished from modern pines by the persistent terminal bud. The presence of a large number of fascicular leaves in *Praehinus* causes them to assume a polyhedral shape in contrast to modern pines where the restricted number of fascicular leaves leads only to a plano-convex or a triangular cross section. The presence also of a great number of reduced enclosing scales would seem to indicate, since scales are morphologically leaves, that even a greater leaf number characterized the short shoot of some unknown ancestor of *Praehinus*. In Figure 23, Plate 13, the polyhedral character of an individual leaf is shown to better advantage. The details of the leaf anatomy are best revealed by a more highly magnified portion of the leaf, as shown in Figure 24, Plate 14. Beneath the epidermis, which is strengthened by hypodermal ridges, lies the mesophyll, the cells of which are distinguished by a complete absence of infoldings of the wall. Two resin canals are characteristically present in a leaf. The mesophyll, because of the entire absence of resin canals, grades directly into the transfusion tissue. This tissue is obviously
extensive and needs careful study. As in *Gnetites microphyllus*, the transfusion tissue of *Pseudotsuga* may be divided into an inner sheath of thick-walled cells with small cell cavities and an outer zone of thin-walled cells with large lumina. Likewise it shows no parenchyma interspersed with the tracheidal cells. The fibrovascular bundle is single as in the soft pine, *P. Strobus*. Below the xylem lies a cavity left by the phloem which did not withstand fossilization. The xylary condition is reasonable among pine needles since it can be discerned that a large amount of centrifugal wood is present. In Figure 34, the centripetal elements are present as the upper xylary cells which, starting at about the center of the xylem, pass with a slight enlargement of their lumina toward the dark band of tissue which is the inner transfusion sheath. This figure shows the orientation of the centripetal cells as well as their relation to the inner sheath. The centrifugal xylem is not seriated, nor does it come into direct contact with the transfusion tissue except on the flanks, since ventrally the phloem separates it from the transfusion tissue. A longitudinal section of the leaf reveals more completely the nature of the transfusion sheaths. The inner thick-walled cells show bordered pits, are much elongated, and present, in fact, a certain resemblance to true trachoids. The outer sheath is made up of cells with much thinner walls which show little longitudinal elongation. The latter are covered like the with larger bordered pits. The intimate relation of the centripetal xylem to the inner transfusion cells serves to increase the resemblance of the
leaf of *Praxinellus* to the corallitean condition. The inner transfusion tissue of *Praxinellus* may be considered as equivalent to the innermost layer of the same tissue of *Cordaites principale*, both answering to "primitive transfusion tissue" of Corda, while the outer sheath in each case may be termed the "peridesmic" sheath. Jeffrey considers the presence of centrifugal xylem, the extensively developed transfusion tissue, the absence or poor development of an mesarchis, and the simple parenchymatous character of the mesophyll, as primitive leaf features and as we have seen already, his thesis is sustained by the application of the phyletic canons of research to the study of living pines.

The leaf histology of Stope's *Praxinellus integrifolia* (58), taken from the Upper Cretaceous deposits of Japan, resembles *Praxinellus integrifolia* in the presence of the resin canals in the leaf, hypodermal ridges of sclerenchyma beneath the epidermis, polyhedral shape of the leaf resulting from the multifoliate condition of the brachyblast, and a broad zone of transfusion tissue. The vascular strand, however, is double, being divided by an intruding strand of the inner thick-walled sheath, and the vascular strand shows likewise an entire absence of centrifugal xylem. The mesophyll of this fossil is somewhat crushed and Stope observes that if the cell walls are unfolded, the feature is not very clearly manifested.

Several other articulated fossil leaves exhibit notable histological details.

*Pinites (Pinites) sibiricus*, Scott (13) has taken
from the Upper Jurassic or Lower Cretaceous deposits of Bell Island, Franz Josef Land, and first described by Solms-Laubach. The shape of an individual leaf is almost round and hence resembles externally that of *P. amabilis* or *Calpurnia*. The bundle is single and is enclosed by transfusion tracheids, the whole being sheathed by a single layer of thick-walled cells. The mesophyll, however, approximates that of modern pines, and possesses photosynthetic cells which have distinct infoldings of the cell walls.

**Pinus vaccinoides**, Stapes (59), from the Upper Cretaceous of Hokkaido, Japan, evidence various histological features which are strikingly modern and is hence rightly given the same genus name as the modern pines. The mesophyll has distinct rosette cells, the vascular strand has all the xylem developed centrifugally, but the transfusion tissue is not as well formed as in modern pines, and is distinctly set off from the mesophyll by a well defined endodermis. This specimen, like *Pityites cirrhata*, resembles *P. amabilis* to some extent. The histology of *Pinus vaccinoides* and *Pityites cirrhata* is very similar.

We come now to the consideration of the undescribed three-needle pine, which was discovered at Arlecdonville, in the Cretaceous strata from which *Pinus* and *Calpurnia* are included to Preiss or Jeffrey himself for the material which forms the basis for the following description. Figure 10, Plate 5, shows a transverse section of the entire shoot. On the outside, the fascicular leaves are enclosed by several of the
scales which make up the bract, blad sheath. It presents a terminal bud, just like *Prasinus*. In our figure the terminal bud shows three smaller leaves inside the large outer particular leaves, each small leaf being placed in a position alternating with a large leaf. The cells of the three small leaves show as yet little histological differentiation. A higher magnification of an adult leaf, such as that of Figure 18, Pl. to 16, reveals several features of exceptional interest. The epidermis, on the outer face of the leaf, is strengthened by hypodermal ridges of sclerenchyma. The mesophyll, even in sections taken well above the basal region shows a distinctly simple character of the parenchyma cells; in other words, rosette cells are entirely absent. resin canals, if present, are not distinctly revealed. As in *Prasinus*, the mesophyll merges directly with an outer broad zone of transfusion tissue, some of these large-ribbed cells show well-preserved bordered pits on their horizontal anticlinal walls. Internal to the transfusion zone lies a dark band of small cells which are comparable to the inner or primitive transfusion sheath of the fossil leaves described above. The vascular strand, however, like that of *Prasinus japonicus*, Stipes, becomes double by the intrusion of a tongue of the inner transfusion tissue. Of the components of the vascular strand itself, the xylem alone is preserved; the soft phloem cells have disintegrated leaving but a cavity to represent their former position. The xylem is entirely centrifugal in its development and is mostly of secondary origin.
The descriptive histology of a considerable number of unattached pine needles is likewise to be found in the literature.

The mesophyll usually consists of simple parenchymatous cells, though the exceptions were noted in which the mesophyll has typical rosette cells like those of the modern Coniferae. This in no way militates against the theory that simple parenchyma preceded plicate parenchyma. The introduction of a given feature into certain geologic series of a race by no means coincides in time with its development in other closely related series. Hence we may interpret the presence of rosette cells in the mesophyll of the Jurassic-Cretaceous Pityurus marginatus and Pityurus bobrium as a precocious introduction of a detail which has become a dominant feature of the photosynthetic tissue in the modern representatives of Pinus.

The leaves of Jurassic-Cretaceous pines differed, then, from modern pines in the following features:

1. A greater development of the translucence tissue.
2. A differentiation of this tissue into an outer layer of wide lumened, slightly elongate cells and an inner layer of small, thick walled elongate cells.
3. An absence of parenchymatous cells in the translucence tissue.
4. A general absence of infolding of the cell walls of the mesophyll.

Praepinus, in addition, exhibits other features
which must be regarded as primitive, such as:

1. A multifoliate brechylast.
2. Presence of centripetal wood.
3. A single fibrovascular bundle.

**Comparison of Fossil and Modern Coniferous Leaves.**

From a comparison of the histological conditions of the modern fascicular coniferous leaf with its juvenile, traumatic and retentive stages, and with the available fossil evidence, we are justified in drawing the following conclusions.

Since the basal part of the coniferous leaf is held to represent its phyletically oldest region, it is not strange that it retains the single parenchymatous condition of the mesophyll which is dominant in fossil types and which, in general, is held to be the primitive condition for this photosynthetic tissue.

The absence or poor development of an endodermis in the basal region of the juvenile and subtending leaves, and in the terminal bud scale, seems to coincide also with the archaic condition manifested by *Pseudocedrus* and by many Cretaceous representatives of *Pinus*.

The presence of a single vascular strand in the various primary leaves of *P. viridis*, the fascicular leaves of which have a constantly double leaf trace, may be regarded as a condition retentive of the single strand condition, found in *Pseudocedrus* and certain other fossil pines. It is probable, however, that the double character of the leaf trace was developed relatively
early in the geological history of the pine, since coniferous leaves with both single and double bundles are well represented in Cretaceous deposits.

The presence of parenchyma in the transfusion tissue of modern pines is in direct contrast to the wholly tracheidal character of the equivalent tissue in the fossils.

CONCLUSIONS.

The preceding study which has been made on the gynospermous short shoots, both of modern and fossil types, together with the histological examination of the foliage of these plants, has resulted in several definite conclusions which constitute a connected and logical evolutionary story.

1. The brachyblast is a dwarf cauline organ derived by the "telescoping" of a long branch, and hence in primitive types such as *Ginkgo*, *Larix*, and *Cedrus*, it exhibits transitions to the long branch condition.

2. The history of the gynospermous short shoot throughout is that of a regressive orthogenetic series. This is best expressed among the *Pinaceae* in which a well defined series can be traced from the Cretaceous *Pinus* to the living *Pinus monophylla*.

3. The ancestral pine short shoot, such as that borne by *Pinus*, was polyphyllous and possessed a terminal bud. As shown by an undescribed three-noded fossil pine of Kreischerville, this latter condition was retained after
the leaf number had become definitely reduced to three.

4. Normal short shoots of the modern pines are distinguished by a definite number of verticillately arranged leaves, and by the complete absence of a terminal bud. A small meristematic vegetative point may occur, however, and under abnormal conditions it may become functional as an apical bud.

5. The three-needled short shoot of *Pinus* from the Kreischerville Cretaceous deposits, illustrates the primitive histological details of the pine leaf such as the absence of an endodermis, the extensive development of the double transfusion zone, and the absence of infoldings of the walls of the mesophyll cells.

6. The basal region of the fascicular leaf of pines, retains the phyletically primitive feature of simple parenchymatous mesophyll.

7. The primary leaf of *Pinus*, in addition to the lack of infoldings of the mesophyll cells in the basal region, shows also the absence of the endodermis in this region, as well as a persistently single leaf trace throughout its entire length.
LITERATURE CITED


Figure 1. - *Cornulinaea*: Longshoot bearing beads on definite branches. (After Berry.)
Figure 2. - Cernea Libani: transverse section of the base of short shoot. The simple leaf traces are seen in the cortex which surrounds stele with its narrow zones of wood and phloem. A definite cork layer is present. The dark cells of the cortex contain resin. x 40

Figure 3. - Pinus species: transverse section of the long shoot. The shoot is some eight years old. The resin lacunae, resin canals and cortical resin canals are notable. x 10
Figure 4. - *Larix decidua*: external view showing the foliar condition for the first two years growth. (After Torrey.)

Figure 5. - *Larix decidua*: external view of a single short shoot, highly magnified. (After Torrey.)

Figure 6. - *Larix decidua*: external view of several short shoots in the bud condition. (After Torrey.)

Figure 7. - *Pinus resinosa*: external view of several brachypods showing their relation to the long shoot. (After Torrey.)
PLATE IV

Figure 6. - Plate J: transverse section of short shoot bud showing the presence of an apical meristem. Only a single leaf section is represented entirely. x 50
Figure 9. - <i>Picea rubens</i>. - <i>Abietinula</i>; external view of branch (<i>blast</i>), x 40. (After Jeffrey.)

Figure 10. - Unidentified <i>Cryptomeria</i> pine; transverse section of branch (<i>blast</i>). Sections of three large (<i>pine cone</i>) needles are shown. In the middle is the sectioned a lateral bud with the three well-formed needle-prickings, x 40.
Figure 11.—Pinus Bungeana: transverse section of basal region of prophyllart, x 30.

Figure 12.—Pinus ayisi: transverse section of median region of prophyllart at the point where the vascular bundles are leaving the stele, x 30.
Figure 13. - Rimia rigidula: transverse section of median region of foliole. The peripheral epidermis is bounded inwardly by a single row of anodermal cells within which lies the transfusion tissue encircling the vascular bundles. x 40.

Figure 14. - Rimia rigidula: transverse section of mesophyll, highly magnified. The reticulate character of the mesophyll cells is clearly evidenced. In the middle of the figure lies a resin canal. At the extreme right and several cells of the endodermis at this level become seen a few transfusion transflorescence x 300.
Figure 15. - Pinus sylvestris: longitudinal section of fascicular leaf. x 50.

Figure 16. - Pinus Banksiana: transverse section of basal region of fascicular leaf. The mesophyll of this figure is to be compared with that of Figure 13 and 14, Plate VII. x 50.
Figure 17. - Pinna Baccifera: Transverse section of basal mesophyll, highly magnified. The cells, unlike those of Figure 16, Plate VII, bear no plications. x 560.

Figure 18. - Pinna rigida: Transverse section of transfusion tissue, highly magnified. The cells are clearly of two sorts - empty ones which bear bordered pits and are tracheidal, and protoplasmic ones whose function is probably that of starch storage. At the left an arc of the endosperm is included in the photograph. x 550.
Figure 19. - *Pinus strobus*: transverse section of median region of fascicular leaf. The single strand feature is evident. X 30.

Figure 20. - *Pinus rigida*: transverse section of basal region of trichastically produced primary leaf. The brachyblast leaves of this plant carry two vascular strands but the more arachide primary leaf is haploxyloid. X 40.
Figure 21. - *Gymnosporangium pruinatum*: transverse section of leaf. (After Torrey.)

Figure 22. - *Pyrinia stellata*: transverse section of a group of fasciculate leaves. x 10. (After Jeffrey.)
Figure 23. *Pseudina stamenopsis*; transverse section of a single fascicular r leaf, x 64. (After Jeffrey.)

Figure 24. *Pseudina stamenopsis*; transverse section of a portion of a fascicular leaf. This figure shows more clearly the centripetal primary xylem, the double transfusion sheath and the scanty simple chlorenchyma which appear in the photograph above. (After Torrey.)
Figure 2.5. - Unusual 3-needled Cretaceous pine, transverse section of a single leaf. Like *Picea* this needle carries the double transversal sheath and the scanty simple chlorophyll. It is diploxylic but centripetal xylary elements are absent. The selenia has decayed completely. The triangular cork lobe above the needle is a fragment of an immature leaf from the terminal bud (cf. Figure 19, Plate IV). Portions of the other needles are likewise visible. Below are seen fragments of the sheath scales. x 40.
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