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ILLINOIS BIOLOGICAL
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VOLUME XIII

PUBLISHED BY THE UNIVERSITY OF ILLINOIS

URBANA, ILLINOIS

EDITORIAL COMMITTEE

JOHN THEODORE BUCHHOLZ
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CHARLES ZELENY, Chairman

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ILLINOIS BIOLOGICAL MONOGRAPHS

Vol. XIII

No. 3

EDITORIAL COMMITTEE

JOHN THEODORE BUCHHOLZ

FRED WILBUR TANNER

CHARLES ZELENY

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EVOLUTION OF FOLIAR TYPES, DWARF
SHOOTS, AND CONE SCALES OF PINUS

With Remarks Concerning Similar Structures in
Related Forms

WITH THIRTY-TWO TEXT-FIGURES

BY

CLIFTON CHILDRESS DOAK

CONTRIBUTION FROM THE BOTANICAL LABORATORY OF THE
UNIVERSITY OF ILLINOIS

ACKNOWLEDGMENT

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I. INTRODUCTION

A. REVIEW OF LITERATURE

Since the dawn of botany as a science, the Gymnosperms have been of special interest; and the genus *Pinus*, because of its wide distribution, its economic importance, and its highly specialized dwarf shoots, has probably attracted more investigators than any other genus among gymnosperms. Hundreds of special papers dealing with this subject have appeared, the most important of which will be cited in connection with the special topics of which they treat. Numerous general works either include *Pinus* or deal with this genus alone. A modern and nearly complete list of the general works will be found in *A Handbook of Coniferae*, by Dallimore and Jackson (24).^{*} Since the present paper deals with both the foliar and axial systems of pines, much of this extensive literature has either a direct or an indirect bearing on the present problem.

Some of the most important early works in the field of pines were done by Lambert (50) and Engelmann (30) from whose works early literature lists may be obtained.

The embryo and cotyledons have been the subject of special studies or have been included in the works of Goethe (40), Richards (72), Engelmann (30), Daguellion (23), Tubeuf (93), Masters (57), Buchholz (13, 14), and others.

The seedling stages were treated by Menge (62), Beissner (5), Masters (57), Hill and DeFraine (41), and numerous others, while the buds and bud scales have been made the objects of special investigations by a long list of workers including Schumann (80), Lord Avebury (54), and Masters (57).

The interpretation of the cone scales has been the subject of a controversial and almost endless literature. Some of the chief contributors in this field are Robert Brown (12), Alexander Braun (11), Baillon (2), Sachs (75), Willkomm (101 and 102), Celakovský (20), Schleiden (78), Parlatore (68), Velenovský (97), Von Mohl (99), Strasburger (87), Aase (1), Saxton (76), and a host of others.

The literature dealing with the dwarf shoot is not so extensive. Important morphological contributions have been made, however, by Masters (57), Thompson (91), Schneider (79), and a few others, while important contributions from the fossil records have been made by Jeffrey (46) and Seward (81).

^{*}Numbers following names of authors refer to items in the Bibliography at the end of this paper.

B. THE PROBLEM

During the accumulation of the mass of literature now available much has been learned of the genus *Pinus* and its affinities. Much of this information, however, exists as detached fragments. The great need is for consolidation, supplementary investigation, and re-interpretation. With these needs in view the present work was undertaken. As the investigation progressed it became obvious that a detailed study of the ontogeny and morphology of the entire axial and foliar systems would contribute materially to a better interpretation of the phylogeny and affinities of the genus. The problem as thus broadened involves consideration of a highly

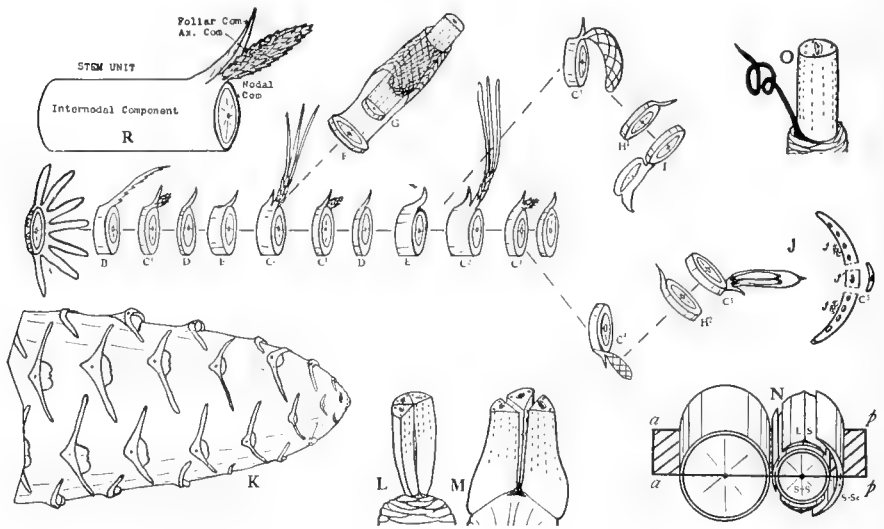


FIG. 1.—Stem units of a pine (and miscellany).

- A. Cotyledonary units.
 B. Simple-leaved juvenile unit.
 C. Fertile units.
 C¹. Branch bud unit.
 C². Dwarf shoot unit.
 C³. Staminate cone unit.
 C⁴. Ovulate cone unit.
 C⁵. Seed scale unit.
 D. Bud scale unit.
 E. Sterile bract unit.
 F. Sheath scale unit.
 G. Functional leaf or needle unit.
 H¹ and H². Involucral scale units.
 I. Microsporophyll unit.
 J. Megasporophyll unit.
 K. Semi-diagrammatic view of a stem tip during deposit of fertile units. The subtending scales have been removed in order to show the young dwarf shoots.
 L. Diagram of denuded dwarf shoot of *P. Strobus* showing base of growing leaves. The sheath scales have been removed.
 M. Same showing mature leaves and well-formed "pulvinus."
 N. Diagram of axial plane passing through both the long shoot and the dwarf shoot. Lateral and subtending scales are also shown.
 O. A two-needled dwarf shoot with one of the needles aborted.
 R. Diagram showing components of a fertile stem unit.

specialized, polymorphic branch system and an even more highly complex system of specialized structures which are the morphological equivalents of leaves.

Since the acceptance of the idea that the fascicle is borne on a dwarf shoot, it has been known that pines exhibit an extreme case of dimorphism of the vegetative branches. The possession of specialized, deciduous, dwarf shoots in contradistinction to the long shoots, is now universally accepted as the chief distinguishing character of the pines.

The modified branches which serve as axes for the staminate and ovulate cones respectively are not of the same order and are not, therefore, homologous.

According to the widely accepted "Brachyblast Theory," the seed scale also represents a modified branch; hence the branches of *Pinus* are not dimorphic but polymorphic, there being a total of five types as follows: (1) long shoot; (2) dwarf shoot; (3) staminate cone axis; (4) ovulate cone axis; and (5) seed scale axis.

In addition to this complex branch system, there are developed in the course of the ontogeny of each pine tree at least eleven types of specialized leaf structures. These were in part described by Engelmann (30), who recognized seven types exclusive of the sporophylls. Dufrenoy (27) pointed out the fact that in some ancestors of pine, the undifferentiated leaves likely served the triple functions of spore formation, carbon assimilation, and protection of the meristematic tips. By way of specialization to serve one of these functions or some combination of them, the organs here listed, in order of their ontogenetic appearance, have evolved.

1. Cotyledons (Fig. 1 A).
2. Simple, primary or juvenile leaves (Fig. 1 B).
3. Bud scales (Fig. 1 D).
4. Sterile bracts of the main axis (Fig. 1 E).
5. Fertile or subtending bracts of the main axis.
 - a. Subtending branch buds (Fig. 1 C¹).
 - b. Subtending short shoot (Fig. 1 C²).
 - c. Subtending staminate cones (Fig. 1 C³).
 - d. Subtending ovulate cones (Fig. 1 C⁴).
6. Fascicle sheath scales (Fig. 1 F).
7. True or needle leaves (Fig. 1 G).
8. Involucral bracts for the cones.
 - a. For staminate cones (Fig. 1 H¹).
 - b. For ovulate cones (Fig. 1 H²).
9. Microsporophylls (Fig. 1 I).
10. Cover scales or bracts for the seed scales (Fig. 1 C⁵).
11. Megasporephylls (Fig. 1 J).

The scope of the problem as outlined here is so broad that the present paper must necessarily include numerous separate short investigations undertaken either to supplement and round out data already available or to bridge the gaps between bodies of existing knowledge. In the light of these investigations, the author hopes to summarize and re-interpret some of the controversial questions raised by the work of other investigators. Obviously, too, any consideration of phylogenetic relationships must involve other genera, both paleontological and extant.

C. MATERIALS AND METHODS

The materials for this study were taken from pines of about thirty-five species gathered from widely separated points throughout the United States and neighboring islands. Many European and Asiatic forms which are now growing under cultivation in America are included. The most detailed studies were made on *P. sylvestris* L., *P. Laricio* var. *austriaca* End., *P. cembroides* var. *monophylla* Voss., *P. taeda* L., *P. Pinaster* Ait., *P. palustris* Mill., and *P. Strobis* L. In all of these species the observations extended over either two or three growing seasons.

Seeds, buds, and other parts were dissected under a binocular dissecting microscope; and those parts which the binocular revealed as being of possible histologic interest were later imbedded and sectioned.

For the major subdivisions of the *Coniferae*, the writer has followed the classification used by Coulter and Chamberlain (22). The specific names of the various pines have been taken from Dallimore and Jackson (24).

D. DEFINITIONS OF TERMS

A *stem unit* is considered in this paper to be an internode, together with the node and nodal appendages at its distal extremity (Fig. 1 R). It consists of an allotted portion of a stem (internodal component), a poorly defined node, a modified or unmodified leaf (foliar component) which may or may not subtend an axillary outgrowth (axillary component). A unit without an axillary component is said to be *sterile*.

The term *node* is used in its usual sense; but since the term *multi-nodal* has been used (see Shaw, 82) to describe the annual growths which show more than one period of deposit in a single season, the term is retained in this sense even at the risk of some confusion. It is to be remembered, however, that the term *multinodal* refers not to a plurality of nodes but to a plurality of periods of deposit.

In the literature the terminal bud of the dwarf shoot, because of its position with reference to the needles, has been termed the *interfoliar* bud in which sense the term is here retained.

The term *dwarf shoot* is applied to the modified branches which in the literature are often called by various other names such as spur shoot, short shoot, and brachyblast. The term *fascicle* is reserved for the tuft of needles on a dwarf shoot and is thought of as being separate from the sheath of scales (*fascule sheath*) around the needles.

By *deposit* is meant the instant of earliest recognition of a primordium.

The term *bud scale* is used in its restricted sense and is applied to those closely spaced, sterile-axiled, scale-like, primary foliar organs which serve only as protective cover for the buds.

By *extension* is meant the enlargement of a structure to its final size (second growth phase). The *year's growth* is that portion of a long shoot of which the units are extended during a single growing season.

The term *perforation* is applied to the growth of other parts through a scale (Fig. 11 C, C', and D'). The term *axial plane* is applied to a plane passing through the long axes of both a dwarf shoot and the long shoot to which the short shoot under consideration is attached (Fig. 1 N, a-p).

A primordium formerly present but no longer appearing is considered to have been *suppressed*; if the rudiment appears and is then lost without differentiation of vascular tissues, the structure is said to be *incorporated*. If the structure represented by a primordium loses its identity as a separate organ but, as a constituent of a connate structure, differentiates a separate vascular supply, it is considered to have been *welded* into a now *compound* structure.

The seed scale can be shown to consist of more than one foliar unit; for this reason the term *sporophyll* is applied to the morphological spore-bearing leaf which forms only a part of the seed scale. The term *seed scale*, therefore, is reserved for the entire seed-bearing structure.

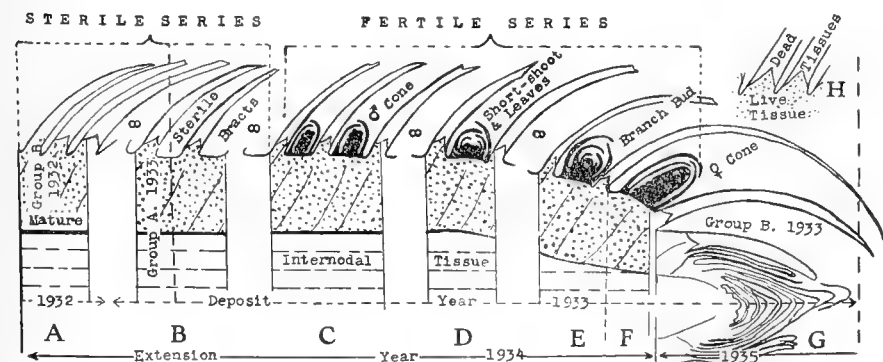


FIG. 2.—Diagram of a compound winter bud of pine, showing condition of units, order of deposit, and order of extension.

II. THE VEGETATIVE LONG SHOOT

A. SIMPLE LEAVES OF THE LONG SHOOT

The order of appearance of the various units which make up a pine tree has been given above. We shall now consider each type of unit in the light of the observations made during the present study. The first leaves to appear are always of the simple type. These are usually glaucous and, with the exception of the cotyledons, have toothed margins (Fig. 5 C and Fig. 6 C) even in species whose functional leaves are entire. They are broadened laterally, especially at their bases. They are keeled and never grow for long periods from zonal meristems, as do the regular needles, but mature all their tissues at approximately the same time. Simple leaves are not confined to the vegetative long shoots but occur also on dwarf shoots and even on the cone axes. In the course of the present work, during which hundreds of branches were examined, a close watch was kept for possible simple leaves. Numerous cases were found which, when analyzed, fell under one of the types listed below.

1. *Cotyledons*

The first simple leaves to appear are the cotyledons about which there has accumulated an extensive literature. It is generally agreed that the cotyledons are conservative in characters and, since they themselves are simple, are indicative of a simple-leaved ancestor for the genus *Pinus*.

As early as 1817 Goethe (40) argued that if a leaf is not to be thought of without a node or a node without a bud, the cotyledons, since they are leaves, mark the first node of a plant. He accounted for their cyclic arrangement and sterile axils by assuming a phylogenetic loss of both internodes and axillary buds. The essential correctness of these interpretations is borne out by the occasional assumption of a weak spiralled arrangement as reported by Buchholz (13, 14), or by the occurrence of buds in the axils of the cotyledons as found by Richards (72).

In following the early ontogeny of the cotyledons, Buchholz (13) has shown that the meristem of the stem tip arises in the embryo before the cotyledonary primordia are laid down. This differentiation of meristem for the plumule marks the beginning of the long shoot, and the appearance of the cotyledonary primordia upon it marks the beginning of its first foliar appendages. In the papers just cited, Buchholz shows that two or more cotyledonary primordia often "fuse" and give rise to a single cotyledon (Fig. 7 C, D, E, and F). He describes broad cotyledonary primordia of possible double nature and also undoubted double primordia which, without leaving a trace of their former bivalence, develop into simple structures. My own investigations have revealed similar processes

in *P. taeda*. They are probably of common occurrence among other polycotyledonous forms. Buchholz and Old (16), in their work on embryos of a close relative of *Pinus*, express the view that the cotyledonary tubes observed by Hill and DeFraime (41, 42) in the seedling stages of *Cedrus atlantica* were produced by intercalary growth during germination. The degree of adhesion attained in the formation of such tubes indicates that fusions can occur either early or late in cotyledonary ontogeny and that the union can be either complete (primordia incorporated) or partial (structures welded).

In order to bring about incorporation the primordia are deposited as is normal for growing points. Meristematic activity, however, instead of being confined to these—which would result in the production of separate organs—spreads laterally and recedes toward the base until all the intervening and subjacent tissues are involved. Two or more adjacent primordia are thus lifted up by a common (intercalary) growth. At first the resulting compound structure has as many growing points as there were constituent primordia. Some of the points, however, are soon incorporated and their separate identity is lost. Hence the mature organ is usually univalent, and there is no trace of the double or triple nature of its early ontogeny. From such evidence obtained in work on the embryos of *P. Banksiana*, Buchholz concludes that there is in this species a distinct tendency to reduce the cotyledons.

That this phenomenon is not confined to *P. Banksiana*, and that the incorporation of one organ by another is not always complete, is shown by the frequent occurrence of double, bivalent, or welded cotyledons as described by Hill and DeFraime (41, 42).^{*} These workers show that the union may involve a part or all of the cotyledons, the latter condition producing a hollow cylindrical cotyledonary tube. Such tubes were reported as occurring regularly in five species of pines and in several other gymnosperms.

Since the results just described are nothing more than different expressions of the same fusion phenomenon, it is significant, but not surprising, that double cotyledons and occasional cotyledonary tubes are found in the same species. What is more significant is that, for those pines (*P. contorta* var. *Murrayana*, and *P. montana* var. *gallica*) showing both fused cotyledons and occasional cotyledonary tubes, the total number of maturing cotyledons is far lower than occurs in pines generally. Of

^{*}Curiously enough these workers interpreted the partly divided cotyledons as evidence that, by division, the dicotyledonous condition, which they held to be primitive, was giving rise to polycotyledony. As pointed out by Coulter and Chamberlain, however, the partly fused condition can be used with equal force to show that by fusion of members the primitive polycotyledonous condition is giving rise to the condition of dicotyledony. The fact that primordia were observed to fuse, not only in *Pinus*, but in several other polycotyledonous genera, makes it probable that polycotyledony is primitive and dicotyledony derived, which is the view of the present writer.

all species studied by Hill and DeFraine, the prevailing cotyledonary numbers ran -12-11-10-9-9-8-7-6-4-4-4, and yet the number occurring in the two pines which showed both these conditions was in each case four, the lowest number in the series. These facts are strongly suggestive of *fusion and incorporation as the means by which the reduction to this low number has been accomplished*. This is in keeping with the theory of a generalized tendency toward reduction which Coulter and Chamberlain (22) have set forth for all gymnosperms.

It is apparent that the ontogeny of adjacent cotyledonary or other primordia can follow any one of three courses. The usual course is for each primordium to grow into a separate structure; this, of course, involves no reduction. Either of the other methods, however, results in fewer mature organs than beginning primordia. If, by intercalary growth, two or more primordia are lifted on a common structure, as described above, and each constituent later differentiates its own vascular supply, the effect is to produce a reduced number of organs which are clearly bivalent, or connate, as are the cotyledons of a cotyledonary tube. However, since the vascular supply to pine cotyledons is usually simple, this cannot be the means by which cotyledonary reduction is being accomplished in *Pinus*.

The third possibility involves reduction by elimination of primordia through *complete incorporation* as described above.

The tendency toward the elimination of foliar primordia by *meristematic recession* and *incorporation* is not confined to the cotyledons but manifests itself at many points in the ontogeny of a pine tree, and, as will be shown later, it is by this process that the stem tip and extra leaf primordia are eliminated from the dwarf shoots of *P. cembroides* var. *monophylla*. The fusion of parts of the Abietineous cone scale and the elimination of parts from this structure are also explainable on similar grounds. For these reasons it is not alone the *evidence of reduction* but also the *manner of reduction* which assumes importance in the present paper.

2. Juvenile and Traumatic Simple Leaves

Above the cotyledons the seedlings of all pines are at first clothed with simple leaves, as shown by Menge (62), Coulter and Chamberlain (22), and many others. The simple leaves are spirally arranged along the long axis, a character which is held in common with all *Abietineae*.

The simple leaves are followed eventually by scales and other specialized foliar organs (Fig. 1). The early botanist rightly attached significance to this sequence and used it as an argument for the derivation of specialized leaves from the simple type. Beyond the seedling stages,

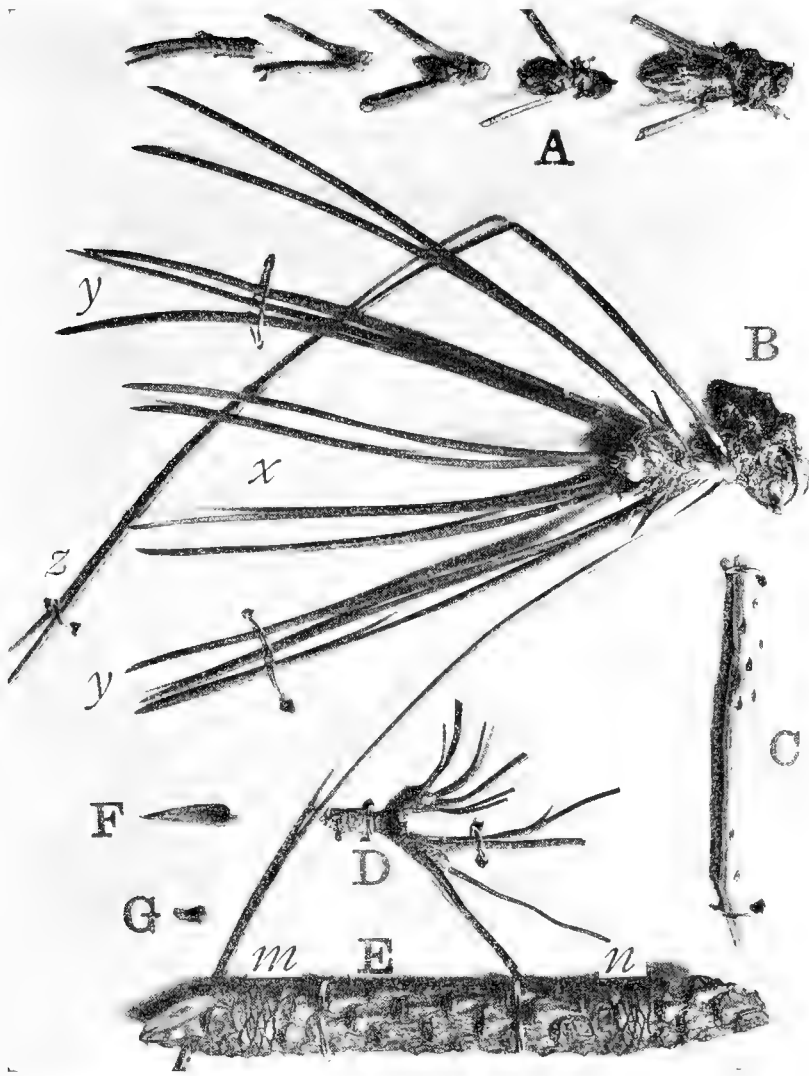


FIG. 3.—Proliferated dwarf shoots (and miscellany).

- A. Interfoliar buds of *P. Laricio*.
- B. Proliferated fascicle of *P. Laricio* with simple subtending leaves, withered original needles (*z*) and three-needled fascicles (*y*).
- C. Xylem cylinder from a young twig showing naked portion in position of former bud scale scar.
- D. Interfoliar buds of *P. Strobus*.
- E. An annual growth node of *P. Laricio* showing scars of the different units; *m* and *n* represent bud scale scars.
- F. Simple green leaf from *B*.
- G. Shed lateral scale from *B*.

simple leaves occur most commonly as responses to traumatic and nutritional stimuli (53, 54). An extensive examination of almost any pine material, however, will reveal a few spontaneous simple leaves for the transformation of which no known cause can be ascribed.

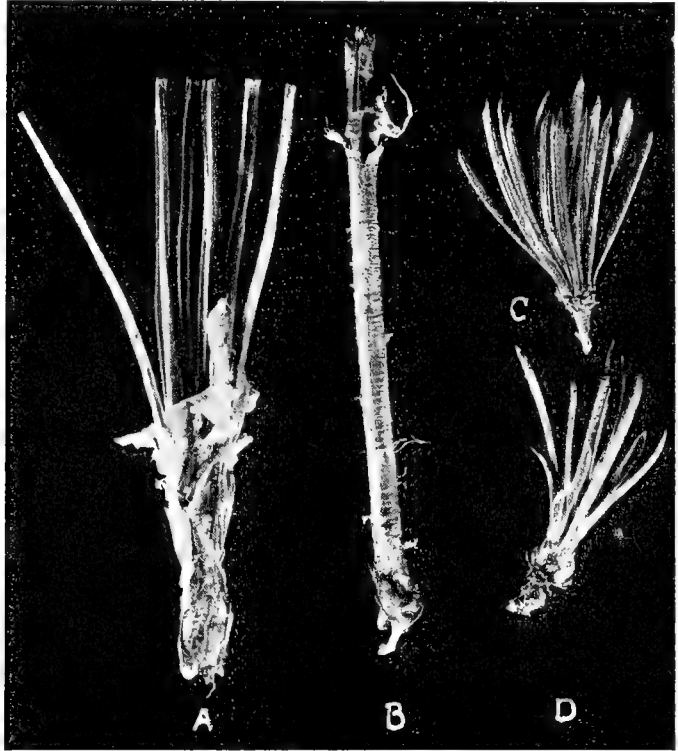


FIG. 4.—Dwarf shoots.

- | | |
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| A. Six-needled dwarf shoot from <i>P. palustris</i> . | C. Normal dwarf shoot from <i>Cedrus</i> . |
| B. Normal three-needled dwarf shoot from <i>P. palustris</i> . | D. Abnormal dwarf shoot from <i>P. palustris</i> . |

During the first year of the present work several hundred buds were removed from trees in the vicinity of Urbana, Illinois. The twigs from which the terminal buds were removed usually responded in one of two ways. They either pushed out and extended the units in the lateral buds which ordinarily would have remained dormant, or they proliferated new branches from the old dwarf shoots (Fig. 3 A and B). Often new branches came from both sources.

In those cases involving the forced extension of a dormant bud, the subtending foliar components, which had for a time served as resting primordia, seemed during this service to have had the future behavior of their tissues fixed, because after extension these in all cases formed scales

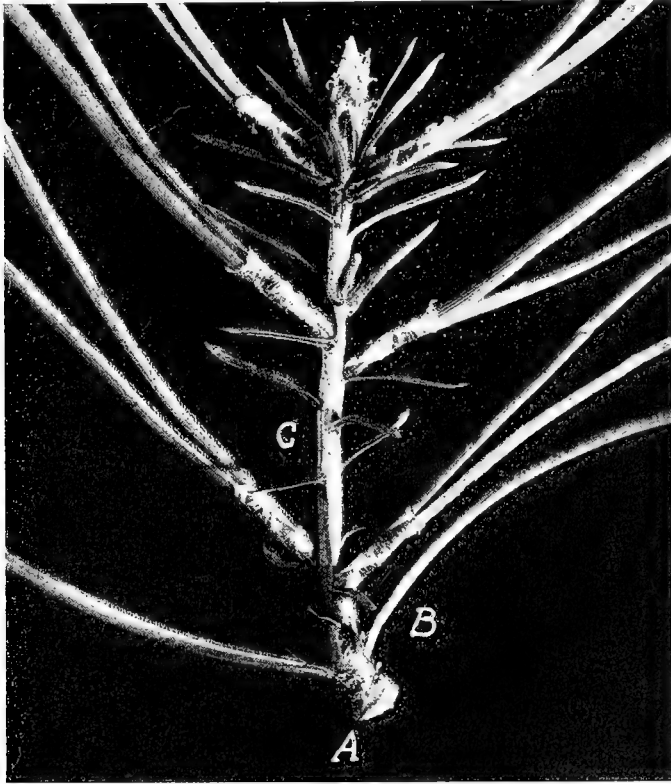


FIG. 5.—Proliferated dwarf shoot of *P. pinaster*.

A. Dwarf shoot.

B. Withered original leaves.

C. Simple green leaves with
toothed margins.

of the usual type. As previously reported by Lloyd (53), those subtending structures which were deposited and extended during the same season were, however, transformed into simple leaves (Fig 3 B and F and Fig. 5 C). Those cases in which a proliferation grew from the old dwarf shoots will be further described under the section dealing with the growing point.

It is a common observation that pines, when heavily fertilized, irrigated, or otherwise subjected to unusually favorable conditions, will pro-

duce simple leaves. Sometimes this occurs naturally (Büsgen, 17; Goebel, 38), especially in southern climates. So frequently does it occur in *P. cubensis* which grows on the Isle of Pines, surrounded as it is by the warm waters of the Caribbean, that at one time efforts were made to set up a new species (Rowlee, 74) based upon this character.

In certain conifers, notably *Juniperus* and *Chamaecyparis*, varieties have been established which, when propagated vegetatively, maintain the juvenile leaves throughout life. In horticultural literature these are

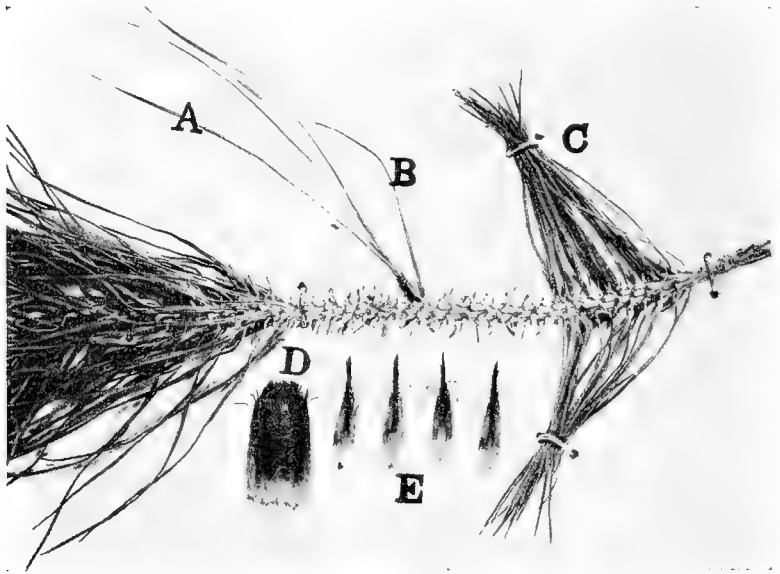


FIG. 6.—Twig from retinosporous pine (and miscellany).

- | | |
|---|--|
| A. The only fascicle on the twig. | D. Winter bud of <i>P. palustris</i> . |
| B. Simple subtending leaf. | E. Scales from same showing inter-lacing fibers. |
| C. Simple sterile leaves a part of which have been clipped away in order to show the fascicle, A. | |

spoken of as retinosporous varieties. The attempt to obtain a pine with simple leaves throughout has been only partly successful. It is not so unusual, however, to find branches or entire young trees on which the simple leaves predominate (Fig. 6). Several such trees are now growing in the greenhouses at the University of Chicago while hundreds of such branches may be found on trees growing at College Station, Texas. Hochstetter (43) describes as "incomparably beautiful" a simple-leaved variety of *Pinus* which he, for a time, was able to maintain but which unfortunately perished after a few years.

The wide differences between simple leaves in general and the foliar organs now found on *Pinus* serve to emphasize the extreme foliar specializations of the genus. At the same time the simple leaves furnish us with evidence regarding a type of leaf from which, or through which, the numerous kinds of modern and highly specialized foliar organs of *Pinus* have evolved.

B. BUD SCALES, STERILE BRACTS, AND SUBTENDING SCALES

Of the eleven kinds of foliar components mentioned above, six are scale-like. These are (1) bud scales, (2) sterile bracts of the main axis, (3) fertile bracts of the main axis or subtending scales, (4) fascicle sheath scales, (5) involucre bracts of the cones, and (6) cover scale or bracts for the seed scales. The first three of these are found on the vegetative long shoot, while the involucre bracts, fascicle sheath scales, and cover scales are borne on branches of a second order.

Like the simple leaves treated above, the scales on the main axis are primary foliar organs. Of them Büsgen (17) says:

Observation and experiment alike teach that the bud-scales and leaves actually originate in essentially similar rudiments whose later development is decided by their surroundings, i.e., their relationship to other parts of the whole shoot competing with them in growth and nutrition and to the climatic conditions.

As pointed out above the early removal of the leaves at the tip of a shoot causes buds actually destined for development the following year to extend in the year of their formation, and in this event true leaves are formed from primordia which, in the ordinary course of things, would have become scales.

This behavior is not surprising, for, as pointed out by Jeffrey (46) and Fontaine (34), ancestral pines probably had simple leaves where we now find the scale series and in addition bore fascicles similar to those now found on pines. The transformed simple leaves, therefore, may be looked upon as reversions.

The various kinds of scales present no fundamental morphological differences. The units on which they are borne are here separated into groups on the basis of (1) time of deposit, (2) amount of ultimate extension of the internodal component, and (3) presence or absence of axillary components. Because of the morphological similarities throughout the series, the description of bud scales which follows will, in most respects, apply to all of the scales in the series.

Lewis and Dowding (51) and others have given us works on the anatomy and related phases of conifer bud morphology, but the best modern summary of the literature dealing with the general subject was given by Foster in 1928 (35). As early as 1880, however, Goebel (38) called attention to the shortening of leaves and of internodes during the

winter period of such scale-free conifers as *Auracaria* and *Juniperus* and pointed out the fact that, even within a genus, we may have some forms with bud scales and others without them, as in *Podocarpus*.

During the present work, the ontogeny of the scales was followed in *Pinus taeda* L., *P. palustris* Mill., *P. Laricio* var. *Austriaca* End., *P. sylvestris* L., and *P. Pinaster* Ait. The time of deposit and the time of extension were observed. Since the putting down of new units is a growth phenomenon, the deposit of primary foliar organs, when charted, gives the typical S-shaped curve of growth (Fig. 30). The extremes are marked by sterile scales, most of which are never separated widely from each other and are, therefore, termed bud scales. Since, however, the scales for a given year's growth are in two separated age groups, these are for convenience termed, in the order of their deposit, "Group A" and

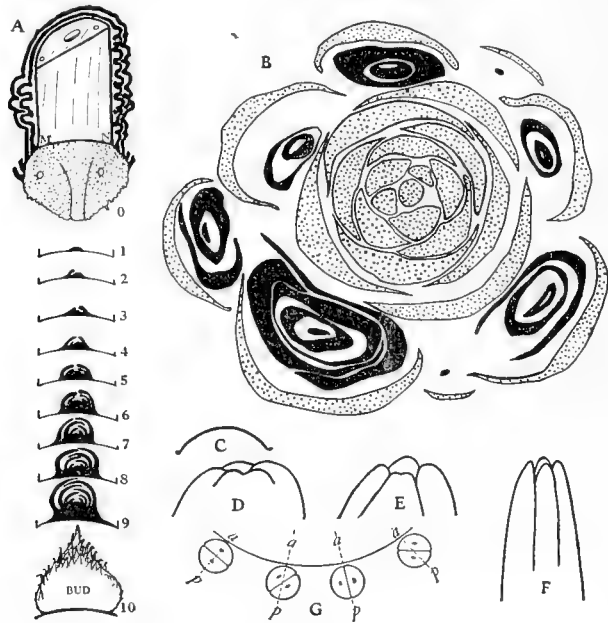


FIG. 7.—Miscellaneous.

- A. Diagram of a longitudinal section of a two-needled dwarf shoot with normal interfoliar buds in various degrees of development.
- B. Camera lucida tracing of a transverse section through the tip of a winter bud of *P. Laricio*. The black circles show the hooded nature of the scales on the lateral buds and fascicles.
- C, D, E, F. Stages in the early development of cotyledons, showing reduction in number of primordia (after Buchholz).
- G. Diagram of leaf orientation with reference to axial plane (*a*, *p*) in two-needled pines.

“Group B” (Fig. 2). Except for a difference in time sequence, the ontogeny of the bud scales is similar in the two groups. “Group A” on one year’s deposit is in series proximally with “Group B” of the previous year and distally with the sterile bracts of the main axis. The outer scales in “Group A” become dry and frayed during their first growing season. The scale blades become dead and scariosus in their outer portions but remain alive at their bases. A sharp line of demarcation sets off living tissue from dead tissue (Fig. 2 H). The scales in “Group B” spend the first winter as young tender scales or as meristematic primordia (Fig. 2 G). During the second growing season these follow through exactly the same ontogeny that has been described for “Group A.”



FIG. 8.—Young bud scales of *P. pinaster* showing the early stages of fraying.

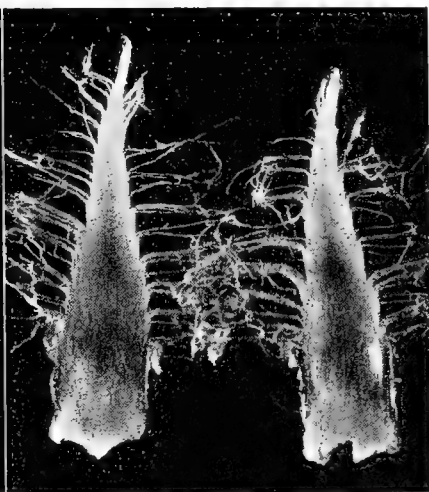


FIG. 9.—Old scale from *P. pinaster* showing method of fraying and interlocked marginal fringes.

During the second summer while maturation processes are in progress, the origin of younger and more distal units (Fig. 1 K) slowly crowds the scales in “Group B” to the base of the developing bud, where they spend the second winter (Fig. 2 A). During the early spring of their third growing season the covering of bud scales is ruptured, and the scariosus portions are either torn loose from the living base, as in the forms with deciduous bud scales, such as *P. sylvestris*, or remain attached as persistent bud scales, as in *P. palustris*.

The degree of bud scale specialization varies somewhat in the different species. The most elaborate specializations occur in species with long needles and persistent sheaths and are, therefore, well illustrated by *P.*

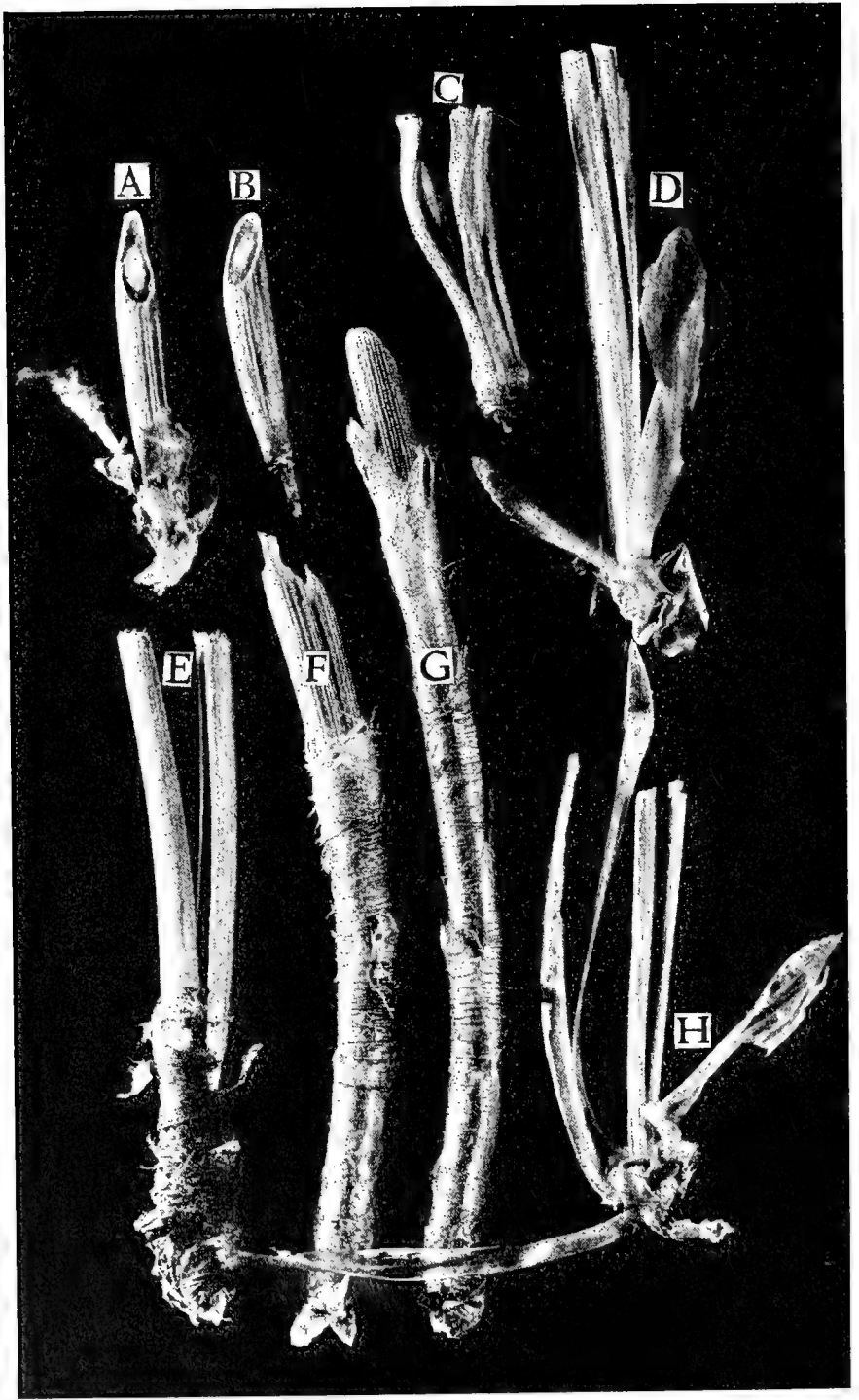


FIG. 10.—Fascicles and fascicle sheaths. (See explanation on opposite page.)

palustris (Fig. 6 D and E) and *P. Pinaster* (Figs. 8 and 9). Here the young bud scale, while still meristematic, forms a sort of hood (Fig. 11 B, C, and C') over the growing point of the stem and over all younger foliar structures. "Group A" passes these stages rapidly while "Group B" spends the first winter in the early stages of the process. Growth goes on at a more rapid rate in tissues on the margins of the hood. At this point the cellular orientation is such that, as the marginal cells elongate, a sharp angle is made with those of the scale blade (Figs. 8, 9, 11, and 12). As maturation proceeds, these marginal cells elongate enormously and become fibrous. The fibers are strong but are only loosely bound together laterally, so that, upon the deposit and expansion of the underlying structures, the resulting growth pressures rupture the older and more mature scales according to a predetermined plan. This is imposed by the nature and arrangement of the scale tissues and by the sequence of growth processes within the scale itself (Figs. 8 and 9). The angular arrangement and the fibrous nature of the tissues combine to bring about the splitting of the blade and the fraying of the overhanging hood-margin, especially along the line of angles where blade fibers and marginal fibers meet. These processes continue until the hooded condition is no longer recognizable, each separate structure having been transformed into a thin dry triangular scale with greatly frayed margin (Figs. 9 and 11 D). Upon the completion of these transformations the scale series form numerous superimposed layers of papery wrapping around the bud. The individual scales are interlocked by the tangle of tough marginal fibers, and, if loosened at their bases, they may be unrolled from the bud (Fig. 6 E) and still remain attached to each other. So tenaciously do they cling together that often a scale may be torn apart by simply pulling on the attached neighboring scales. When in position on the bud, considerable growth pressure is required to break these layers of binding material. For this reason the interlocked scales often form binding rings (Fig. 13 e) or caps (Fig. 13 f) on partly developed shoots.

The angular margins, frayed edges, and strengthening effect of the interlocking fibers were, in part, described by Lord Avebury (54), who, however, did not describe the manner of their production. Engelmann (30) and Pilger (70) also describe the delicate interwoven fringes at the

Explanation of Fig. 10

- | | |
|---|--|
| A. Dwarf shoot of <i>P. cembroides</i> var. <i>monophylla</i> cut diagonally, with sheath in place at base of needle. | D. Same with sheath in act of shedding. |
| B. Same with sheath removed, pulvinus absent. | E, F, G. Old, middle-aged, and young fascicles of <i>P. palustris</i> , showing progressive shortening of sheath by wrinkling. |
| C. Dwarf shoot of <i>P. Cembra</i> after shedding of the sheath, pulvinus present. | H. Same as D. |

margins of the scales. Dufrenoy (26) figures a fringed scale (similar to that shown in Fig. 11 D), and in describing his figure he says that the scale leaf is "strikingly similar to scale of *Cycas*; the hairs may be interpreted as sterilized ancestral ovules or stamens." The scale ontogeny proves the incorrectness of Dufrenoy's interpretation, for the fibers at the margins are neither hairs nor sterilized spore-bearing members but rather the frayed blade margins of foliar organs.

Nearly all investigators who have worked with the bud scales of pines are agreed that these scales exercise some sort of *binding effect* upon the

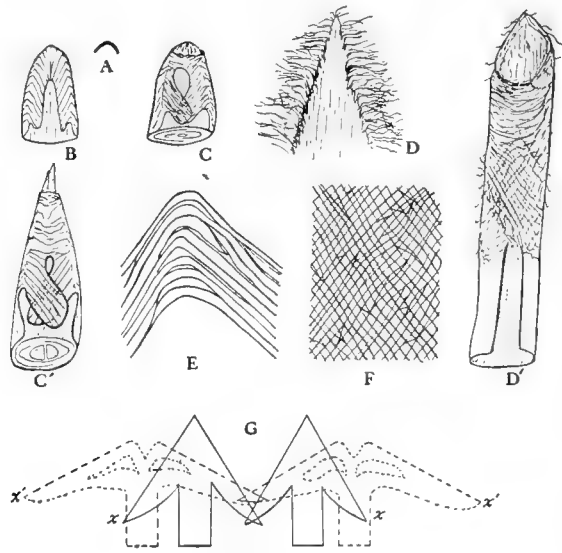


FIG. 11.—Stages in hooding, fraying, and perforation of bud scales and sheath scales.

- | | |
|---|---|
| A. Young scale primordium. | E. Cellular detail along marginal angle. |
| B. Hooded young scale with angular marginal cells. | F. Detail of overlapping fibers. |
| C and C'. Perforation of bud scales and sheath scales respectively. | G. Diagram showing how overlapping and angled margins permit expansion without disturbing the binding efficiency of bud scales. |
| D and D'. Mature bud scale and sheath scale respectively. | |

tissues within. This fact should be borne in mind, for this binding phenomenon has probably had a part to play in leaf arrangement and in the progressive reduction of the leaf number on the dwarf shoots which, while young and plastic, are enclosed within the bud.

An exaggeration of the hooding phenomenon sometimes causes the underlying growing point to push out through the crown of the hood (Fig. 11 C and C'), and, as the underlying parts are lifted up, an en-

circling sheath of fibers is left behind (Fig. 11 D') after the manner of the orchrea in *Polygonum*. Hereafter this phenomenon is termed *perforation*.

The case of the scale on the long shoot is somewhat different, for, subsequent to perforation, an increase in diameter of the encircled stem soon ruptures the encircling fibers of the perforated scale. Perforated blades and encircling fibers, therefore, represent but temporary stages in

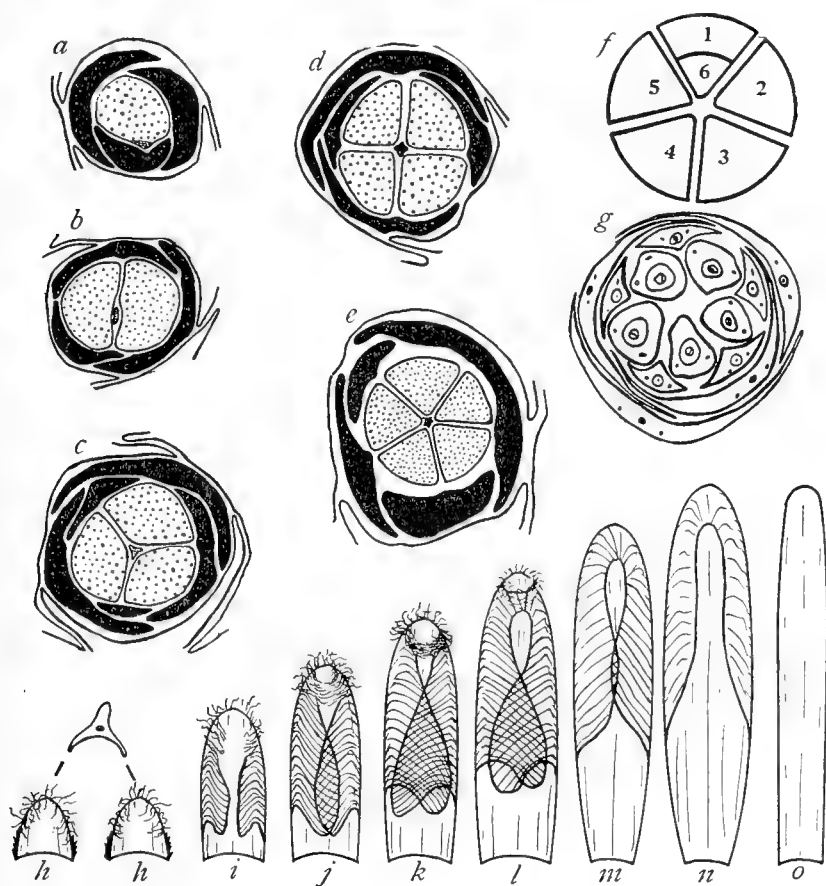


FIG. 12.—Needle shapes (and miscellany).

a, b, c, d, and e. Camera lucida tracings of transverse sections through fascicles having one to five needles, respectively.

f. Theoretical diagram of six-needled fascicle.

g. Outline of a section through a ten-needled dwarf shoot showing two whorls of five needles (after Schneider).

h to o. Semi-diagrammatic drawing of fascicle scale series at the time of perforation.

hh. Lateral scales.

i. Central scale with frayed margin.

j to l. Perforated scales.

m and n. Hooded scales.

bud scale ontogeny (Fig. 11 C and D). The insignificant increase in diameter of the dwarf shoot permits the perforated scales on it to remain as a more or less permanent encircling sheath (Fig. 11 C' and

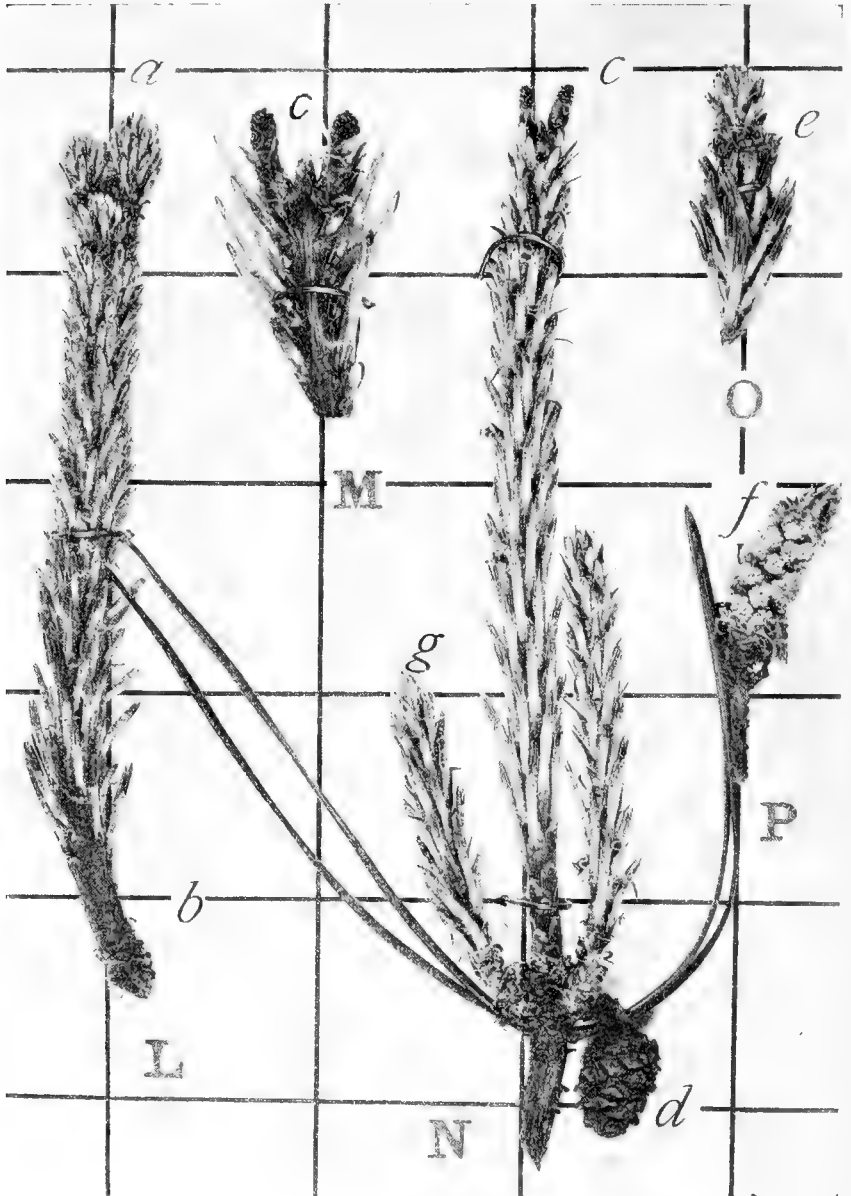


FIG. 13.—Young long shoots of *P. sylvestris*. (See explanation on opposite page.)

D') through which, by basal growth, the needles are forced as through a cylindrical die. As hinted by Eichler (29), it is this die-like action which gives the needles their characteristic cross-sectional forms (see Schneider, 79).

Except for a difference in the amount of extension undergone by the corresponding internodal components, the sterile bracts are in every way similar to the bud scales in "Group A" with which they are in direct series on the distal side.

On very vigorous shoots each year's growth usually has a number of units with extended internodal components but which are devoid of axillary buds (Fig. 13 b and Fig. 14 d to e). The sterile bracts or foliar components of these units lie between the last true bud scales and the first subtending bract. They usually remain in the bud for only a single winter. At extension of the main axis, the scarios portion is often lost and the living base alone remains. This remnant we may think of as a leaf scar or leaf cushion.

The line of demarcation between sterile bracts and the true bud scales is not a clearly defined one. After extension, the bud scales continue to occupy their crowded position at the base of the year's growth or, when shed, leave a ring of crowded scars to mark the points from which they have fallen (Fig. 3 m and n), thus dividing the twig into a series of easily recognizable annual growth segments (Fig. 15). The sterile bracts or bract scars do not remain crowded but at extension come to occupy relatively wide intervals along the base of the year's growth (Fig. 14 d to e), for at this time the two types of scales are similar and lie in continuous series at the base of the winter bud (Fig. 2 A and B). One cannot determine exactly what fractional part of the sterile scale series at the base of a dormant bud belongs to each of the two types. An approximation can be made, however, by counting the scars left on the same twig in previous years. This is made easy by the fact that most pines leave an indelible record of the various units produced on each year's growth long after their foliar components have disappeared (Fig. 3 E). In some cases the units produced in any given year can be counted with certainty

Explanation of Fig. 13

- | | |
|--|--|
| L. Vigorous shoot with laterals. | N. Long shoot with young and one-year cones and normal laterals. |
| a. Lateral long shoots developing one season in advance of the usual time. | c'. Young ovulate cones. |
| b. Naked base covered with sterile bract scars. | d. One-year ovulate cone. |
| M. Sectioned tip showing ovulate cones. | g. Normal lateral long shoot. |
| c. Ovulate cones. | O. Branch with binding ring of bud scales. |
| | e. Binding ring. |
| | P. Long shoot with staminate cones. |
| | f. Binding cap of scales. |

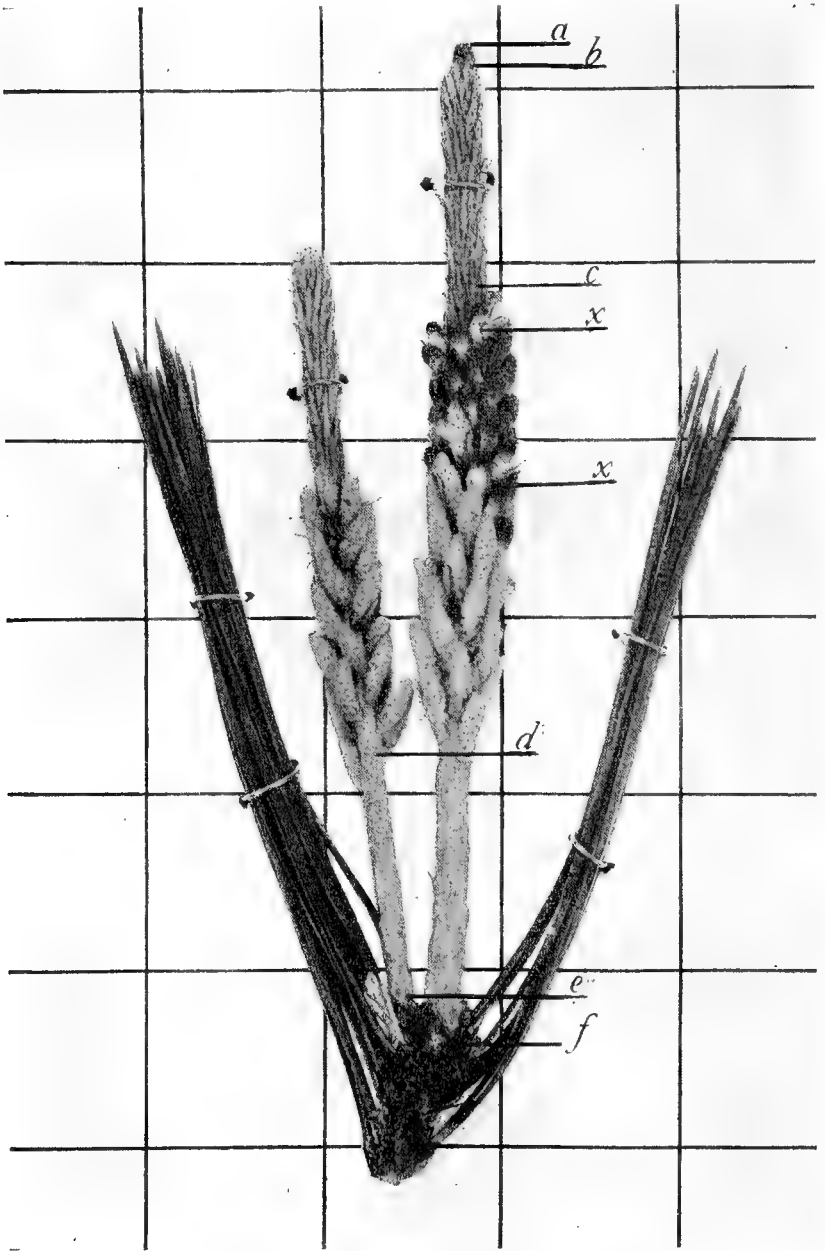


FIG. 14.—Young long shoots of *P. tonyosho*. The left branch is normal. The right branch has the staminate cone series interrupted by bisporangiate cones. (See explanation on opposite page.)

for periods in excess of a quarter of a century (Fig. 15). After the counts are made and averages taken, one may divide the total bud units in the sterile series of the dormant bud into two approximately correct groups, using for this purpose the average percentages of scales and of sterile bracts produced by the same twig in previous years.

At its distal end, the sterile bract series is continuous with the staminate cone series (Fig. 14); but if, as is often the case, the latter is omitted, then direct contact is made with the dwarf shoot series (Fig. 13 L and N). The first fertile scale in either orthostich or parastich usually marks the beginning of the fertile series, which, from that point to its end, remains unbroken. This is not always the case, however, for staminate cones may intrude themselves into the dwarf shoot series or vice versa.

A similar overlapping is found between sterile bracts and cones and also between sterile units and fascicled units. These interruptions are not always confined to the borderline between series. In *P. palustris*, and less frequently in other species, interruptions by the intrusion of one or several units of a different type occur well up in the body of a series. This is especially true of the intrusion of sterile units into the dwarf shoot series. Such gaps occur most frequently on the ventral surface of horizontal twigs (Fig. 16 A). Gaps in the various fertile series are especially frequent on those twigs on which the scale leaves have been replaced by simple leaves (Fig. 5).

The fertile units of a given year's growth, save for the presence of axillary outgrowths, are similar in every way to the extended sterile units described above; and the accompanying scales are in every detail like those already described.

Before leaving the general subject of scales, it is probably worth while to restate the chief points in regard to these organs. It seems certain that regardless of type the scales have developed from leaves of a simple nature. The main peculiarities of pine scales, in comparison with the scales of other plants, are bound up with the phenomena of hooding, fraying, and perforation, the results of which permit the scales to exert binding pressures upon the organs growing within them. *Pinus* is also peculiar in that all the primary foliar organs are normally scale-like.

Explanation of Fig. 14

- | | |
|--------------------------------|--------------------------------------|
| a to b. Normal ovulate cone. | xx. Bisporangiate cones in staminate |
| b to c. Dwarf shoot series. | cone series. |
| c to d. Staminate cone series. | d to e. Sterile bract series. |
| | f. Bud scale scar. |

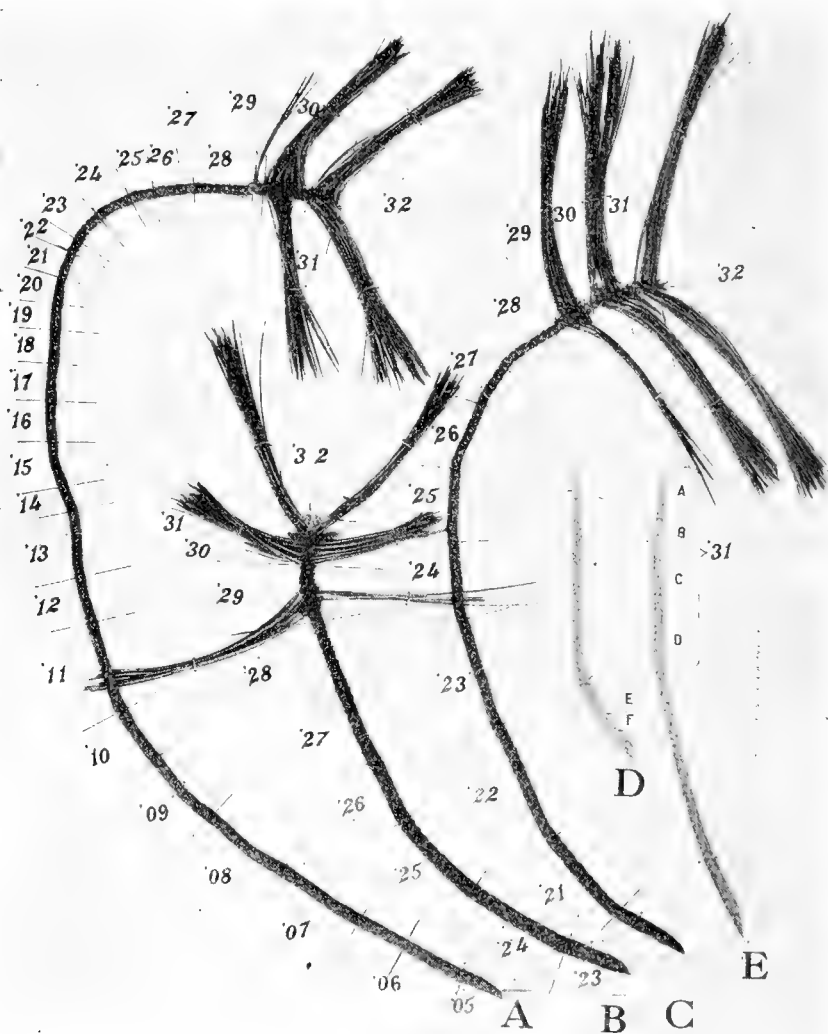


FIG. 15.—Twigs of *P. Laricio* from the north (Illinois) and of *P. palustris* from the south (Texas) with dated annual growth nodes.

- A. Twig of *P. Laricio*, normal except for 1929, a year in which the terminal bud was destroyed. Subsequent growth came from a lateral bud.
- B. Twig of *P. Laricio*, normal except for shortening of internodes and

- leaves of 1930 due to transplantation of the mature tree in the winter of 1929.
- C. Normal twig of *P. Laricio*.
- D and E. Stripped twigs of *P. palustris* showing multinodal growth for 1931.

C. HOMOLOGIES OF THE AXILLARY SHOOTS

Turning now from the foliar to the axillary components on the vegetative long shoot, we find these to be of four types, viz., staminate cones, dwarf shoots, branch buds, and ovulate cones. The staminate cones and dwarf shoots fall naturally together in one group, and the branch buds and ovulate cones comprise another.

The staminate cones and dwarf shoots are alike in origin and in position. They have determinate growth and are deciduous. Each is clothed at the base with a series of thin scales. Without a clear borderline between them, the cone and dwarf shoot series lead directly into each other. These facts make it clear that in *Pinus* the axis of the staminate cone and that of the dwarf shoot are of the same order and are as nearly homologous as it is possible for fertile and vegetative shoots to be.

Near the end of a year's growth and terminating the orthostiches of fertile units on the long shoot, one to several branch buds occur. These usually deposit their basal scales during their first season (Fig. 2 E). The fertile units for their first year's growth are deposited during the second season, and extension of their first year's growth occurs during the third season (Fig. 13 g). On vigorous shoots this program can be shortened (Fig. 13 a), in which case the lateral long shoots are seen as lateral extensions of the year's growth upon which they are borne. In this position they are strikingly suggestive of young ovulate cones which not only occupy similar positions (Fig. 13 a and c) but originate at the same time in the ontogeny of the year's growth. The presence of secondary dwarf shoots (brachyblasts or seed scales) upon their axes mark the cones as modified long shoots, as does also the frequent proliferation of their growing points into long shoots. These evidences make it clear that the ovulate cones and the lateral long shoots are of the same order and that the ovulate cone, therefore, should be looked upon as a modified long shoot.

D. NORMAL ANNUAL GROWTH OF THE VEGETATIVE LONG SHOOT

Without attempting to analyze the complex of physiological conditions upon which the regular sequence of events within a pine bud is dependent, the story of seasonal bud behavior is briefly outlined below:

Upon the return of favorable growing temperatures following the winter rest, the internodal tissues of the bud units (Fig. 2) are first to spring into vigorous activity. Although the other parts (dwarf shoots, sheath scales, needles, etc.) seem ready to grow, something seems to inhibit them. Only the cones are able to compete with the internodal cells as the latter enter actively into their long delayed grand period.

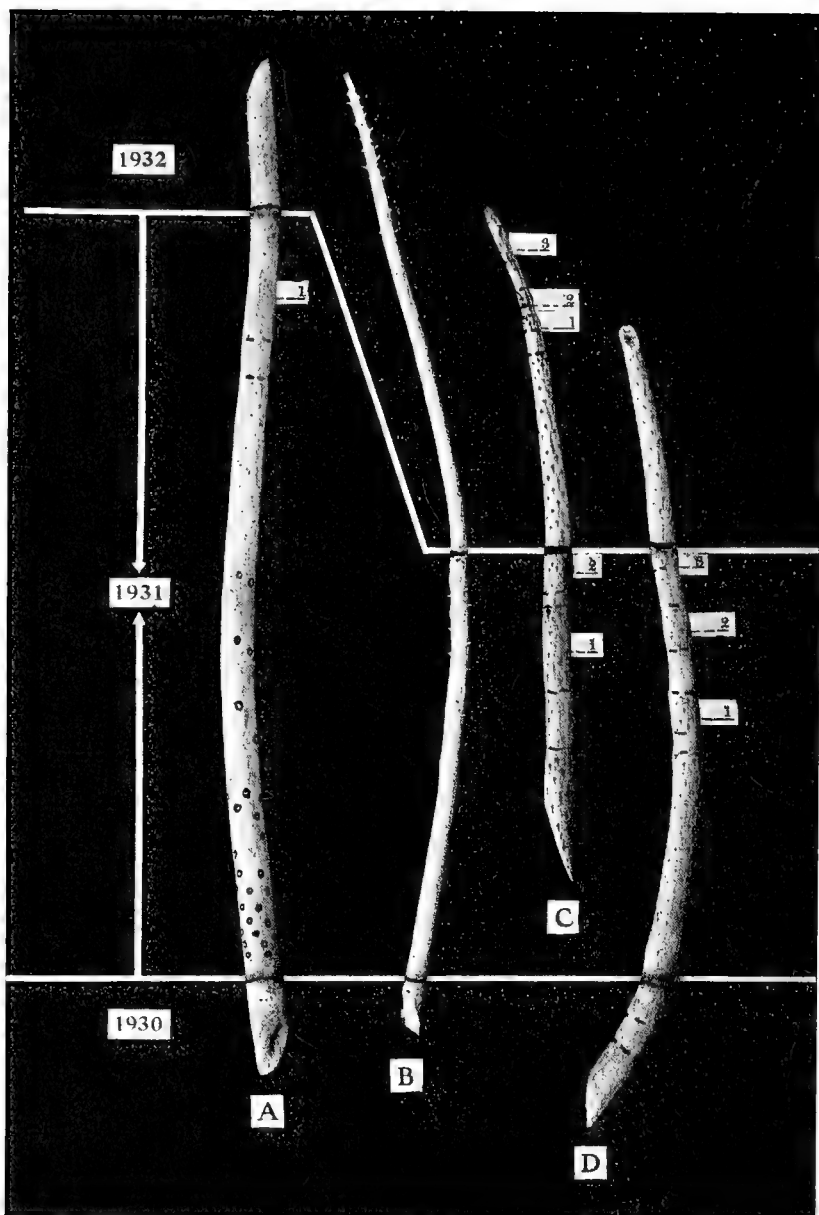


FIG. 16.—Stripped twigs showing annual growth nodes.

- A. Ventral surface of a twig of *P. palustris*. Inked circles show blanks in the dwarf shoot series. The series was continuous on the dorsal side.
- B. Twig of a white pine from Massachusetts.

C and D. Multinodal twigs of *P. palustris* from Texas. The numbered segments represent successive fertile series deposited during the years indicated.

As the internodal tissues pass the crest of their grand period and begin maturation, the tissues of the dwarf shoots and of their foliar organs (sheath scales and needles) spring into vigorous activity. These, as pointed out by Küster (49), all spend the winter in approximately the same developmental stage. As the outermost scales of the sheath begin to mature, the needles in their turn become the conspicuous extension organs. Their growth is accelerated for a time, but, as the summer approaches, it becomes slower and more irregular.

Soon the distal portions of the scales and leaves become matured and growth becomes confined to narrow basal zones. While active growth is still in progress, the matured portions probably carry on their full share of photosynthetic and protective work respectively. While leaf, scale, and cambial growth are still active, the deposit of new units is begun at the growing point of the long shoot. This manifests itself first by a slow addition to the sterile primordia already present at the tip of the axis ("Group B" of previous season). As the growth processes become more rapid, fertile units are deposited (Fig. 1 K). On slowly growing twigs the fertile series usually begins with pollen cones followed by short shoots. The cones may, however, fail entirely. On vigorous twigs pollen cones are seldom deposited, and in this event the first units in the fertile series are dwarf shoots.

The time sequence for both deposit and extension is somewhat variable, depending upon the species, the latitude, and the season. The different species in a given locality start activity at approximately the same time and at first run parallel courses. As summer progresses, the species which mature their needles early (usually those with short needles) advance more rapidly and begin the deposit of new units, while the species with long needles are continuing the growth of these organs. As fall approaches, however, the species with long leaves and a proportionately greater photosynthetic area are accelerated in their processes; and, by the onset of the winter rest, all have attained corresponding growth stages.

E. ABNORMAL ANNUAL GROWTH OF THE LONG SHOOT

1. *Multinodal Annual Growth and Summer Shoots*

In case the season of deposit is interrupted by a hot dry period followed later by rains and a return of favorable conditions, a so-called multinodal year's growth is produced. These multinodal shoots are especially frequent in southern pines and are more likely to occur in some species than in others. This behavior was observed most commonly in *P. palustris* growing at College Station, Texas. Indeed, multinodal growth in this case was more the rule than the exception (Fig. 16 A, C, and D).

It was found that by stripping the bark from a year's growth the separate series of fertile units could be displayed to good advantage. This is made possible by the fact that those portions of the wood from which sterile bracts are stripped appear smooth. The woody cylinders leading to the dwarf shoots, however, clearly mark the points from which these structures grew (Fig. 20 D and E).

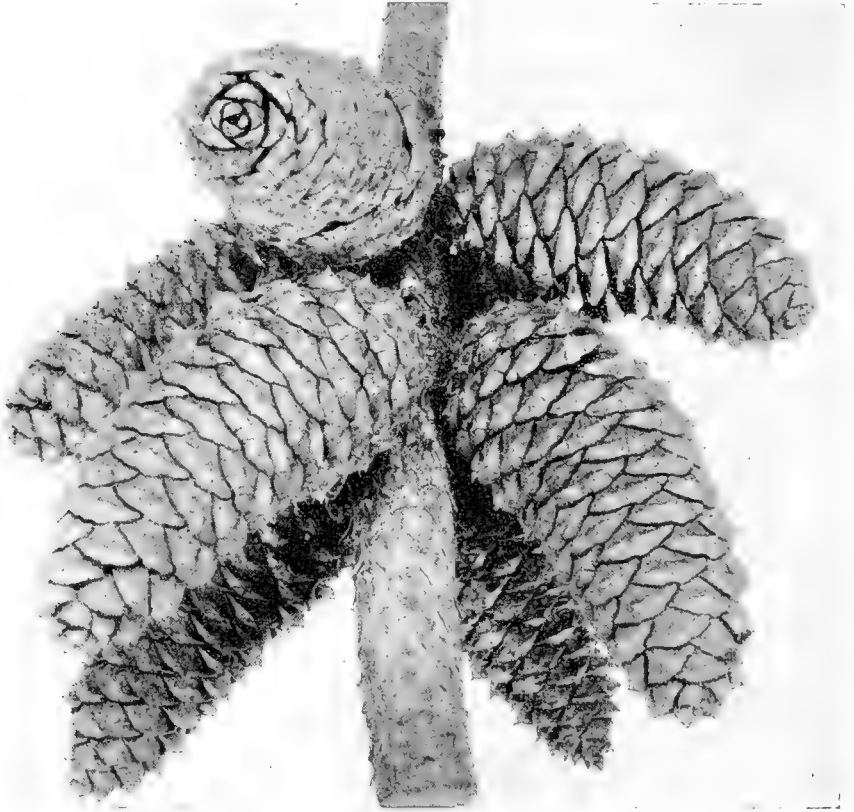


FIG. 17.—Two sets of mature cones of *P. taeda* produced in the same season as a result of multinodal growth.

In each case of multinodal growth, as conditions become unfavorable, the twig behaves exactly as if ceasing deposit for the year. The dwarf shoot series gives way to the usual number of lateral buds (and ovulate cones, if these are to be produced), after which the regular series of scales ("Group B") is deposited. When favorable conditions return, the dwarf shoot series is resumed and continued until again brought to a similar close. This process may be repeated a second or even a third time in a single summer (Fig. 16 C and D).

Multinodal shoots are related to the so-called summer shoots which sometimes result when the season is unusually long and the break between favorable seasons is marked. In this case the units which are deposited in the early period may be extended in the fall or late summer of the same year in which they were deposited. This occurred on many twigs of *P. palustris* and *P. pinaster* at College Station, Texas, in the summer of 1932.

2. Lateral Cones

If, as pointed out by Shaw (82), the multinodal twig under consideration is producing ovulate cones, those that close the first fertile series will be in the so-called lateral position, while those closing the last series will appear to be either terminal or sub-terminal. Actual terminal cones are extremely rare. Masters (57) says that they are never really terminal. Cases of actual terminal cones are on record, however, these having been described by Tubeuf (93) and Worsdell (104).

The production of two to several sets of cones on the same year's growth is common as shown by Mayer (59) and Gates (37). In the course of the present work numerous cases of this type were found, most of which occurred on trees from stations in Texas. Figure 17 shows such a specimen which produced, at the upper end of the first fertile series, a set of four cones and several branch buds. These were followed by numerous sterile scales and finally by a second series of dwarf shoots which again was terminated by four cones, making a total of eight, four of which were in the lateral position and four in the so-called terminal position. Each set of these cones occupied the same relative position with reference to a fertile series of units, the nature and order of which was determined by external conditions. As pointed out by Mayer (59), the so-called lateral cone, in the light of these observations, becomes a matter of ecologic interest rather than a fixed taxonomic character.

3. Intrusion of Ovulate Cones into Staminate Cone Series

Several young trees of *P. tonkyosho* were observed in which ovulate cones had partly or completely replaced the staminate cones. These trees produced, in what ordinarily would have been the pollen cone series, staminate cones at the base, bisporangiate cones* in the middle, and ovulate cones at the top (Fig. 14 x). The plants which produced this curious arrangement grew as a border planting and had evidently been heavily fertilized. A somewhat similar grouping of cones has been reported by Fujii (36), who says that up to a certain stage the cones may

*Of these cones more will be said in the section dealing with the seed scale, where their transitional scales will be discussed.



FIG. 18.—Abnormal long shoot and dwarf shoot of *P. pinaster*.

A. Long shoot with dwarf shoots in place.

B. Dwarf shoots from A, showing over-developed interfoliar buds and the relation of leaf length to bud size.

be developed into pollen or ovulate types, depending upon nutritional conditions. Similar bisporangiate cones have been reported by Righter (73) and by Meehan (60). The latter has even proposed a "law of sexuality" for the conifers, in which he holds that the "sex" is determined by the vigor of the twig upon which the cones are borne.

The replacement of other fertile units by ovulate cones expresses itself variously (Fig. 19 D). Sometimes the physiological condition is such that all the axillary outgrowths are replaced by ovulate cones. This condition has been reported by Keslercanek (48), Mullins (63), Witmack (103), Tubeuf (94), and others. As many as ninety-six ovulate cones have been found in series on a single twig.

4. *Abnormal Axillary Bud Development*

Another case of abnormal annual growth involved several twigs of *P. pinaster* growing at College Station, Texas. For some reason the growth of dwarf shoots on these did not stop at the customary point but proceeded in each case to make a long dormant bud (Fig. 18). Since these abnormal short shoots were borne at all axils, the long shoot, although little modified, may be looked upon as being abnormal in its secondary product. A similar twig has been reported for *Abies* by Tubeuf (94), who states that they are of frequent occurrence in this genus. This observation is interesting in that it is suggestive of a latent ability of *Abies* to produce branches in the axils of all its leaves. This suggestion is further strengthened by the fact that members of this genus often produce dwarf shoots as shown by Masters (57), or proliferate the seed scales into shoots as shown by Stenzel (86) and others:

III. THE REPRODUCTIVE LONG SHOOT, OR OVULATE CONE AXIS

A. PRIMARY FOLIAR ORGANS

Near the point of attachment to the main axis, the ovulate cone produces several sterile units which bear scale-like foliar components, or involucre bracts (Fig. 1 H²). Morphologically these are very similar to the scales already described for the main axis. They are broader, however, less frayed at the margins, and are probably never perforated.

Higher up on the cone, fertile units are borne. The axillary component of each fertile unit is the much-discussed seminiferous scale. The primary foliar component of these fertile units is the cover scale (Fig. 1 C⁵). In the pines it remains small and woody and is sometimes partly fused against the seed scale. That these structures are indeed leaves,

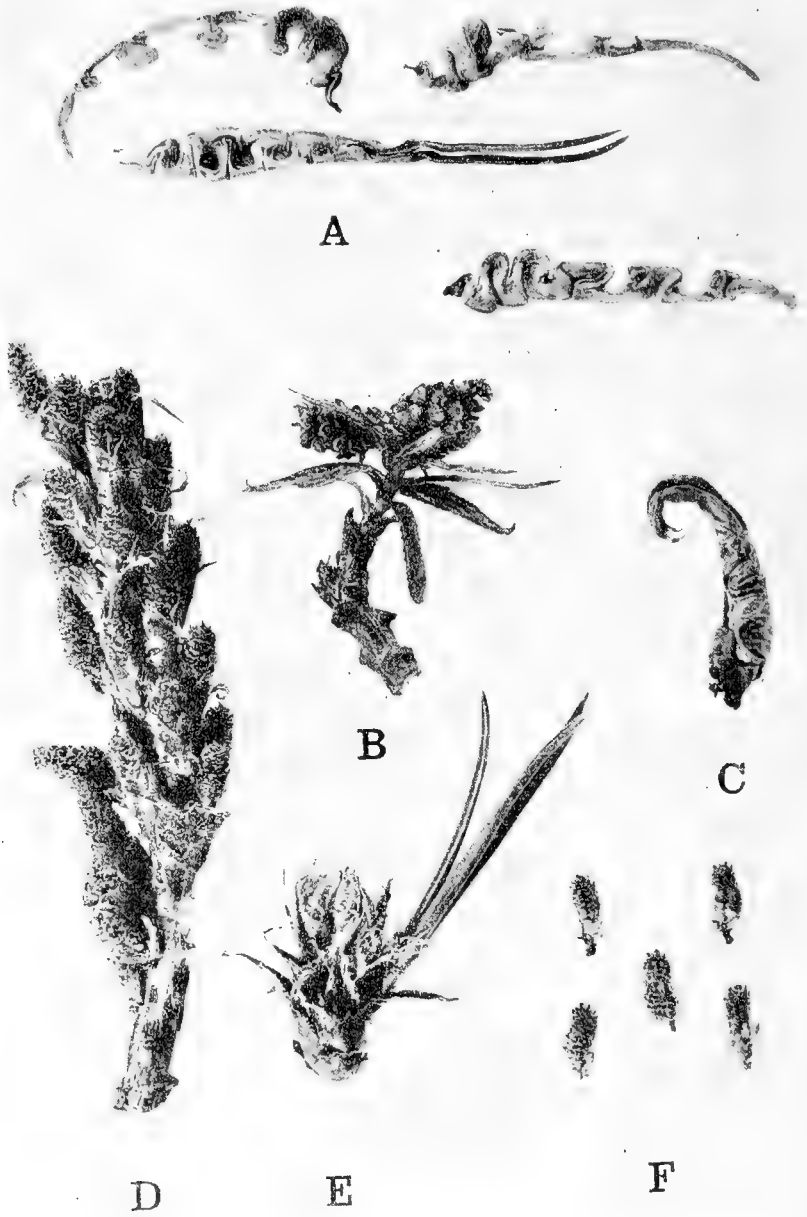


FIG. 19.—Miscellaneous. (See explanation on opposite page.)

at least in *Abies*, has been shown by Willkomm (102). In *Larix*, as was pointed out by Masters, they grow into functional leaves (Fig. 24 G).

As shown by Aase (1), the vascular strands from the cone axis to the bract and seed scale vary somewhat, depending upon whether one examines the tip, the middle, or the base of the cone. The middle or functional region tends, however, to give off bundles to bract and seed scale exactly as the vegetative long shoot gives off bundles to the subtending scale and the short shoot (Fig. 23 A and J).

B. GROWING POINT

On the cone axis the tip meristem usually is transformed entirely into woody vestiges which give no evidence of an earlier latent ability to continue into foliage-bearing branches. However, as shown by Masters (57), Thiselton (89), Stenzel (86), Willkomm (102), Tubeuf (95), and others, and as I have observed in several relatives of *Pinus*, indeterminate growth of the cone axis is not uncommon. Masters (55) and others have described proliferated cones in *Larix*, a genus in which these cones seem to occur most frequently. During the present work several such cones were found growing on *Larix europæa* at Urbana, Illinois. Coulter and Chamberlain (22, p. 414) express the opinion that certain gymnosperms, like *Torreya*, have evolved beyond the stage of the compound strobilus by simply proliferating the cone axes and then transforming all the scales, save one, into leafy shoots.

Certain proliferated cones of *Abies* which were described by Willkomm (102) so closely resembled the precociously proliferated branch of *Pinus pinaster* (Fig. 18) described above, that for comparative purposes a few of Willkomm's figures are here reproduced (Fig. 29 z and z'; Fig. 32, parts 7, 8, and 9). A comparison of these figures will reveal the fact that the subtending scale of the pine shoot has its counterpart in the leaf-like cover scale on the *Abies* twig. The lateral scales on the dwarf shoot of the pine twig (Fig. 25 C) correspond in position to the leaf-like lateral expansions (megasporophylls) on the secondary shoots of the proliferated *Abies* cone. The tip buds of the two are, of course, homologous; and no doubt the fascicle sheath scales and needles which

Explanation of Fig. 19

- | | |
|---|--|
| A and C. Needles from bound fascicles of <i>P. palustris</i> . | D. Staminate cone series of <i>P. tonyosho</i> largely replaced by ovulate cones. |
| B. Abnormal shoot of <i>P. pinaster</i> with simple leaves and staminate cones. | E. Bud of <i>P. Laricio</i> with one fascicle developing one season in advance of its normal time. |
| | F. Bisporangiate cones of <i>P. tonyosho</i> . |

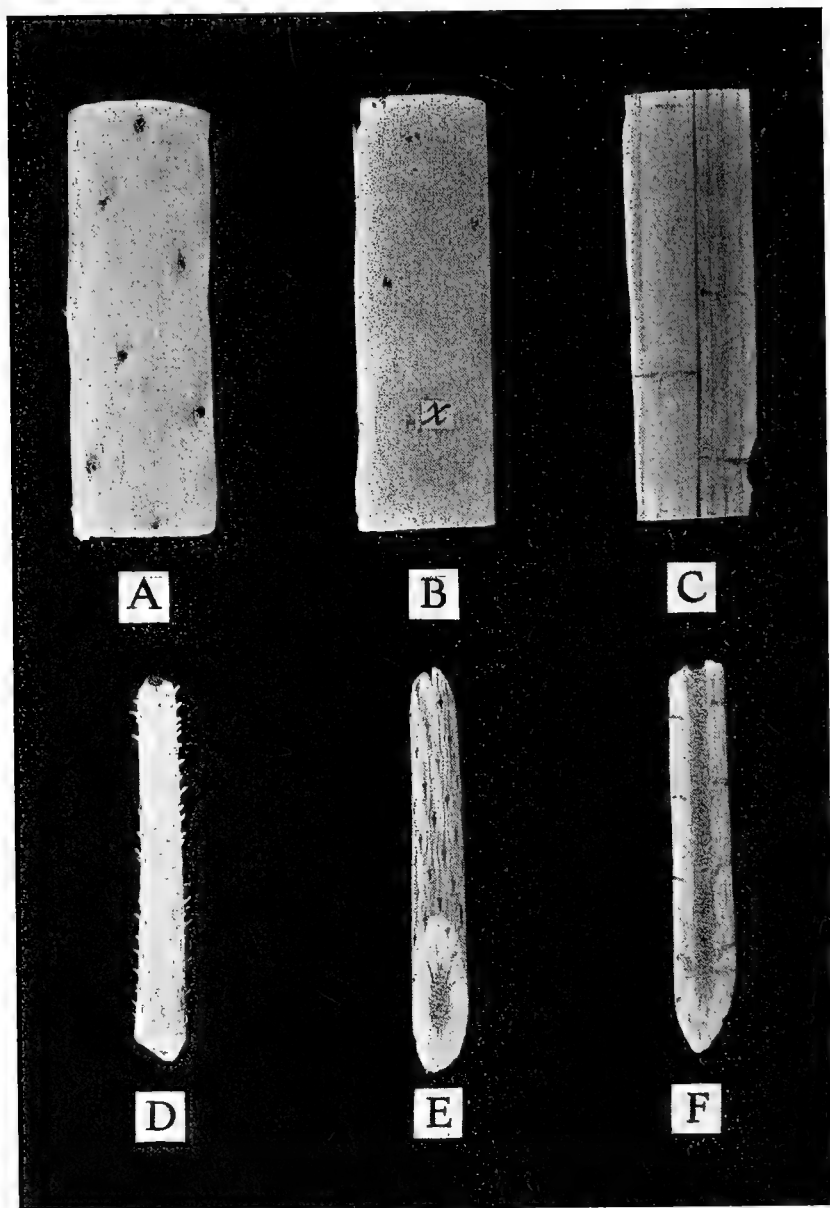


FIG. 20.—Comparative studies of the woody cylinders of *Taxodium distichum* and *Pinus palustris*.

A. Stripped twig of *Taxodium* showing the projecting ends of branched dwarf shoots.

B. Same with surface layers removed.

C. Same in radial section.

D. Stripped twig of *Pinus* with the woody cylinders of the dwarf shoots projecting.

E. Same but older.

F. Same in radial section.

cover the bud in *Pinus* find their counterparts in the basal scales which cover the bud of *Abies*.

When it is remembered that the abietineous cone is a conservative structure and that the pine twig just described is only an exaggerated phase of a condition which occurs normally in this genus, one is impressed with the probability that some ancestor of *Abies* had dwarf shoots and that the present form of the genus has been attained by secondary loss of these structures. This view is further strengthened by the observations of Tubeuf (94) who found occasional vegetative twigs of *Abies* with buds in the axils of all their leaves.

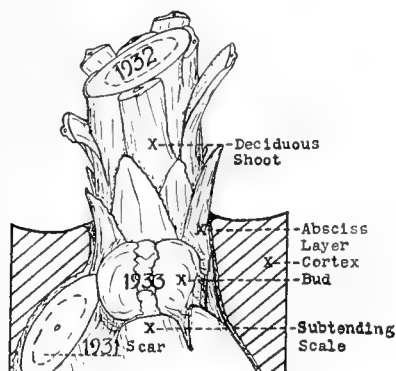


FIG. 21.—Diagrammatic drawing of the imbedded dwarf shoot of *Taxodium distichum*, showing the relation to successive deciduous shoots.

The tip meristem of another cone described by Willkomm had proliferated a long branch of ordinary vegetative type, the lower one-third of which had produced some axillary tissues corresponding in position and texture to the seed scales with which they were in series. These tissues filled up the space between the subtending leaf and the main axis, thus making the base of the latter concrescent (Fig. 29 x and x'). Since the seed scale is a dwarf shoot, this evidence suggests the possibility that the origin of concrescent leaves in conifers was associated with the disappearance of dwarf shoots from their axils.

In summary it may be said that exceptions to the rule of determinate growth of cones occur with sufficient frequency to convince us of their latent power of becoming indeterminate. The nature of these exceptions shows clearly that the megasporangiate strobilus is a compound structure and, therefore, its axis is equivalent to a long shoot and its scales are equivalent to dwarf shoots.

IV. THE EVOLUTION OF THE LONG SHOOT

A. THE VEGETATIVE LONG SHOOT AND ITS FOLIAR ORGANS

If we may assume that some remote macrophyllous ancestor of *Pinus* was devoid of resting buds and had both monomorphic branches and monomorphic leaves with no delay between deposit and extension (Fig. 29 a), then the steps in the evolution of the long shoot of *Pinus* with its characteristic, scale-like, primary leaves, its compound bud, and its well-marked annular growth-nodes, would seem to have been as follows:

1. Adaptation to temperate climates with seasonal climatic changes required protection of the meristematic tips. The plant met this need by a delay in the onset of the grand period of growth, thus bringing more and more foliar organs to overlap and protect the growing point.

2. The recurring need for protection during certain seasons (winter or drought) alternated with seasons of active vegetative growth and thus tended to fix the protective function on certain of the leaves on the long axis. These became specialized in this work and were transformed into scales. The remaining leaves on the long axis remained crowded within the scaly cover during unfavorable conditions and were later extended as food makers. The scales with their protected content of embryonic units thus formed a simple bud (Fig. 29 c and d).

3. A still further delay, both in the time of deposit of units of the main axis and the time of extension, led to a further telescoping of parts until all the primary leaves became scale-like; and the rudiments for the lateral units were produced before leaving the bud, thus leading to the formation of the *compound bud* (Fig. 2) which limited and shaped the growth of the enclosed short shoots.

4. The periodic extension of the compound buds gave rise to the characteristic annual growth nodes of the long shoot (Fig. 15) as already described.

B. THE OVULATE LONG SHOOT, OR CONE AXIS

That the steps leading to the compound ovulate strobilus closely paralleled those leading to the formation of the compound winter bud is attested, first, by similar vascular units (Figs. 23 A and H) and, secondly, by the same arguments which were used earlier in this paper to support the homology of lateral long shoots and ovulate cone axes. The cogent fact that their secondary outgrowths (dwarf shoots and cone scales) run such close parallels is also suggestive of a parallel in the evolution of the long shoot and the cone axis.

The steps leading to the compound strobilus were taken at a time when the ancestors of *Pinus* were perhaps at the Cordaitan level. So re-

mote was that period that little fossil evidence of the course of this evolution has as yet been found. If the supposed parallel between vegetative and fertile long shoots is an actual one, then the compound strobilus must have resulted from internodal shortening of a fertile long shoot which bore numerous simple fertile shoots at its nodes. In a manner analogous to that by which numerous dwarf shoots were brought together to form the compound bud, this shortening brought together the numerous simple strobili, or primitive seed scales (Fig. 32, parts 1, 2, and 3) into a compound strobilus. Just as pressures within the compound bud *limited, shaped, and displaced* the sheath scales of the dwarf shoot, so the formation of the compound strobilus *limited, shaped, and displaced* the sporophylls on the simple strobili.

V. THE VEGETATIVE DWARF SHOOT AND ITS FOLIAR ORGANS

Turning now from the cone and the more or less generalized long shoot to a consideration of the shortened and highly specialized dwarf shoot, we find that its primordium is put down in the axil of the scale

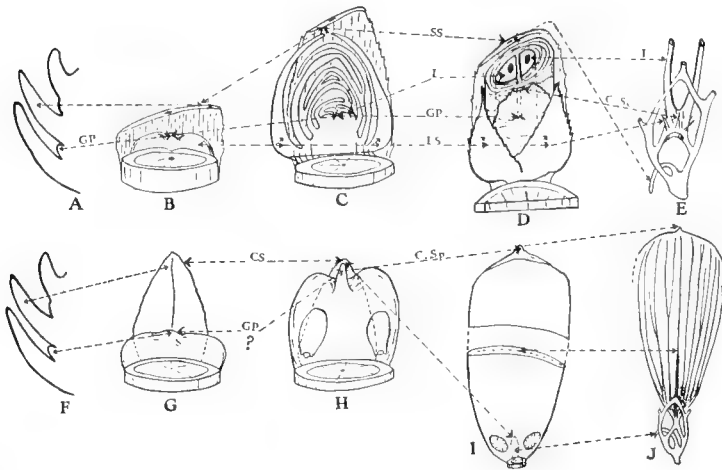


FIG. 22.—Diagrams showing corresponding structures as they appear during the development of the dwarf shoot and seed scale of *Pinus*.

A to E. Stages in the development of the dwarf shoot and its vascular supply.
F to J. Corresponding stages in the development of the seed scale.

SS. Subtending scale.
GP. Growing point.
L. Leaf.
LS. Lateral scale.

CS. Cover scale.
CSc. Central scale.
CSp. Central sporophyll.

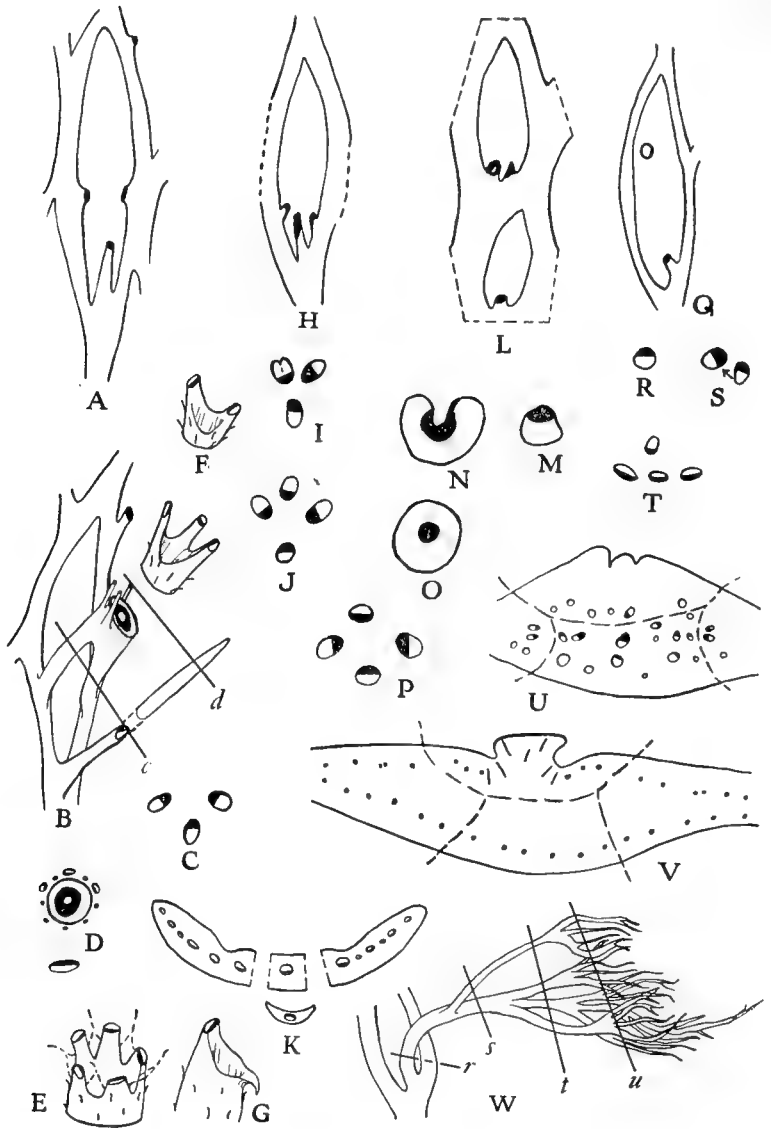


FIG. 23.—Diagrams of vascular structures showing the writer's views with reference to the relationships existing between the dwarf shoot of *Pinus*, the cone scale of *Pinus*, and the cone scale of *Araucaria*.

A. Supply to dwarf shoot and subtending scale of *P. Banksiana* (redrawn from Aase).

B. Same as A, but with supply to sheath scales and needles added.

C and D. Transverse sections through vascular supply to three-needled dwarf shoot. The bundles to the lateral scales and the central scale are exaggerated for emphasis.

(Continued on opposite page.)

primordium in mid-summer (Fig. 1 K and Fig. 30). The young dwarf shoot primordium gains rapidly the rudiments for all its sheath scales and for its functional leaves as was shown earlier. All these structures are extended during the season following their deposit.

A. SHEATH SCALES

1. Morphology

In all pines examined, the three most proximal of the foliar organs on the dwarf shoot were regularly and definitely placed with reference to the axes of both the long and dwarf shoots. The first two were always on opposite sides of a plane passed through the long axes of both the dwarf shoot and the long shoot (Fig. 1 N and Fig. 25 C), and the third was directly between the two axes and was bisected by their common plane. Hereafter in this paper this plane will be spoken of as the *axial plane*; the first two scales on the dwarf shoot will be called the *lateral scales*; the third scale will be termed the *central scale*.

The lateral scales are opposite each other, thickened at the base, keeled, and exhibit little or no intercalary growth. They are seldom perforated but are often serrate on the keel, and in other characters they are set off sharply from the papery sheath scales which follow them (Fig. 22 D and Fig. 12 hh).

Granting that the two lateral scales represent successive foliar organs on the dwarf shoot, it follows that the internode between them has been lost and that the scales have been displaced from their phyllotaxic positions. This view is supported by the fact that if we begin far enough

Explanation of Fig. 23 (Continued)

- E. Supply to five-needled fascicle showing in dashed lines the location of the supply to the inner circle needles when present (drawn from Schneider's description).
- F. Supply to two-needled fascicle.
- G. Supply to the one-needled fascicle showing vestige of bundle to the aborted leaf as found in *monophylla* (from Schneider's description).
- H. Supply to typical cone scale and bract (modified from Aase's drawing of *P. maritima*).
- I and J. Transverse sections through *H* at different levels (redrawn from Aase).
- K. Diagram of final distribution of the four bundles seen in *I*.
- L. Diagram of supply to lowest scales and bracts on typical cones of *Pinus* (redrawn from Aase's figure of *P. Banksiana*).
- M, N, O, and P. (Redrawn from Aase's figures of *P. Banksiana*).
- Q, R, and S. Supply to scale of *Araucaria Balansi* (modified from Aase).
- T. Diagram of principal bundles in scale of *Araucaria*.
- U. Subdivision of bundles in sterile scale of *A. Balansi* (modified from Aase; dashed lines separating branches of principal bundles supplied from her description).
- V. Diagram of a cross section of *Agathis vitiensis* (modified from Eames).
- W. Diagram of ramifications of bundles in scale of *Araucaria*.

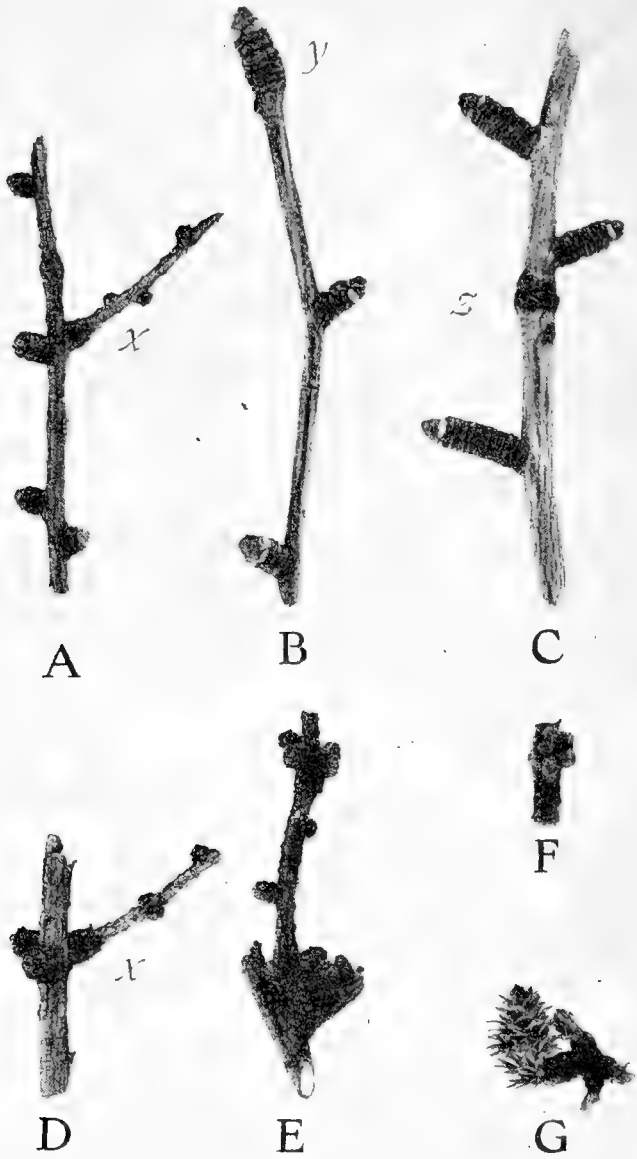


FIG. 24.—Dwarf shoots of *Larix* and *Ginkgo*.
(See explanation on opposite page.)

distally on the dwarf shoot, the angle between successive foliar organs regularly conforms to a two-fifths phyllotaxy; but, as the lateral scales are approached, the displacement becomes evident (see arrows in Fig. 25 C).

The central scale is displaced to a less degree and more closely resembles in form and texture the regular sheath scales. The differences separating it from the other scales would perhaps not justify the assignment of a special name to it, but, as will be shown later, the central scale has had a homologue in the evolution of the sporophylls to form the cone scale and demands, therefore, both a special name and special notice.

In addition to the lateral scales and the central scale, there is deposited on the young dwarf shoot a series of scale primordia which show little or no displacement. These are the regular fascicle sheath scales.

All the scales spend the winter in the meristematic condition (Fig. 25 F).

Spring growth (extension) begins almost simultaneously in all of these young scales, but maturation is in acropetal succession. This results in a constantly increasing length of scale from the proximal to the distal end of the fascicle scale series (Fig. 12 h to o).

In their later ontogeny, the scales follow through the processes of hooding, fraying, and perforation as described for the bud scales earlier in this paper. Here, however, these processes, especially perforation and the reverse growth of the marginal cells, are far more pronounced than in the bud scales already described. The situation is complicated still further by the development of intercalary meristems at the bases of the sheath scales by which these continue growth after perforation has been accomplished. Because the dwarf shoot undergoes such limited secondary increase in thickness, the sheath ordinarily encircles the base of the needles from which the scales may be slipped off one by one without being split.

With several superimposed layers of papery scales overlapping them and hindering their elongation, it is not surprising that pine leaves have developed needle-like points for perforating these layers. There is obviously a close correlation between the complexity of the sheath and the

Explanation of Fig. 24

- | | |
|--|---|
| A. Twig of <i>Larix curopcea</i> . | C. Normal <i>Ginkgo</i> twig showing wide interval between successive dwarf shoots. |
| x. A dwarf shoot which later extended to make a long shoot. | z. Bud scale scar. |
| B. Long shoot of <i>Ginkgo</i> . | D. Same as A. |
| y. A portion of the long shoot failed to extend, thereby making a dwarf shoot. | E and F. <i>Larix</i> twigs with repeatedly branched dwarf shoots. |
| | G. <i>Larix</i> cone growing from one member of a four-parted dwarf shoot. |

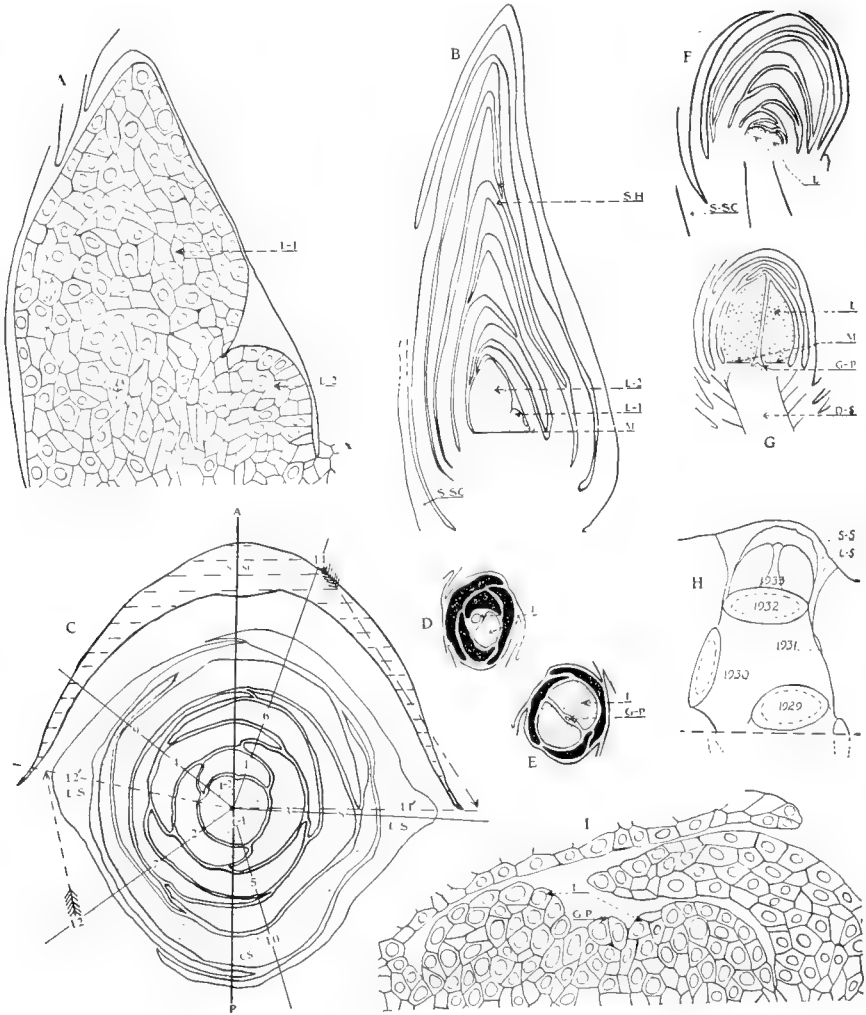


FIG. 25.—Comparative studies of the early development of leaves in *P. cembroides* var. *monophylla* and *P. Laricio*.

- A. Camera lucida drawing of a longitudinal section of the leaves of *P. cembroides* var. *monophylla* soon after the beginning of spring growth.
- B. The same less highly magnified and showing the hooded scales and other related structures.
- C. Camera lucida tracing of a transverse section through the developing fascicle of *P. cembroides* var. *monophylla* showing the rudimentary second leaf, the phyllotaxy, and the displacement of the lateral scales.
- D and E. Cross sections of dwarf shoots from *P. cembroides* var. *monophylla* and *P. Laricio* at stages corresponding to B and F, respectively.
- F. Longitudinal section of winter dwarf shoot of *monophylla*.
- G. Longitudinal section through young leaves of *P. Laricio* in a stage of development comparable to that shown for *monophylla* in B.
- H. Diagram of imbedded winter bud of *Taxodium distichum*.
- I. Double leaf primordia of *P. cembroides* var. *monophylla* in winter condition.

development of horny and otherwise highly specialized points on the needles of *Pinus*.

Meehan (61) speaks of a "membrane" on *P. monophylla* which he says is present at the beginning of needle growth. By releasing this membrane Meehan thought that he could influence the number of needles on the dwarf shoot. Without doubt the structure referred to was nothing more than the multiple cover of sheath scales.

Collectively, the scales form a binding sheath for the fascicle of leaves. By reenforcing the point made weak by the basal meristems, the sheath makes possible the long-continued growth of the needles. In this respect the fascicle sheath is analogous to the encircling leaf sheath of the grasses.

The effectiveness of the sheath as a strengthening splint may be easily demonstrated by simply removing it from fascicles on which the leaves are actively growing. In this case the leaves fall limp, hang in a pendulous fashion, become dried at the base, and soon break off. The drying gives evidence of a secondary function of the sheath, i.e., the prevention of excess evaporation from the young parts which are as yet unprotected by a cuticle.

Once the needles are mature, the zonal meristems are lost. Mechanical and epidermal tissues are formed for parts within the sheath, and consequently its strengthening function is no longer required. This is evidenced by the fact that in many pines the sheaths are deciduous, falling away at the maturation of the leaf bases or soon afterward. Indeed the fascicle sheath, by obstructing the light from the basal portion of the leaf, becomes positively detrimental in that it appreciably reduces the photosynthetic area of the leaves.

2. Methods of Scale Removal

Pines have evolved several mechanisms for removing this obstruction. In some species the fascicle scales are more or less stiff and are weakly attached at their bases and have only a few of their distal scales perforated. As long as the needles are growing rapidly, the tissues within the encircling fibers are in the first phase of growth. The cells of such tissues are small, and consequently the total diameter of the encircled leaves is small. As elongation slows down and the maturation zone reaches points nearer and nearer the base, there comes a time when the enlarging basal portions of the leaves expand within the encircling fibers until the jacketing sheath is broken apart. Near the basal point of attachment an absciss layer is now formed from which the scales are soon broken by the movement of the leaves in the wind. The scales leave a bulging cushion or scar at points from which they fall away. When the

scales have been shed, the needles are left exposed to the light and air for their full length.

In *P. excelsa*, *P. flexilis*, and many others the scales are stiff and weakly attached at the base as described above, but the few perforated scales are more or less proximal in position. In this case the functional leaves, when mature, develop a special basal enlargement (Fig. 10 C and Fig. 1 L and M) which breaks the encircling fibers. The expansion of these structures forces the scales sharply outward and breaks them off, leaving the mature dwarf shoot entirely free of scales (Fig. 10 D, H, and C).

A third method of ridding the fascicle of its scaly sheath is found in *P. cembroides* in which the scales and leaves mature simultaneously. After maturation the former become brittle and dry. Upon drying, they warp and break and thereby expose the leaf base to the light. Since the breaking is not at a predetermined point, a ragged rosette of papery scale bases is left. These remnants become smaller and smaller until after a time their obstruction to light and gases is negligible (Fig. 10 A).

As a rule the pines with persistent sheaths have more scales, and these are perforated to a far greater extent than is the case in pines with deciduous sheaths (Fig. 10 E, F, and G). As the enclosed portions of the needles mature, the encircling scales are frayed sufficiently to accommodate the increased diameter of needles; and the sheath, although remaining unbroken (Fig. 11 D'), is shortened until finally two-thirds or three-fourths of the originally covered portion of the leaves lies exposed.

3. Scale Number per Dwarf Shoot

In view of the possibility that the fascicle scales for the various species of pines would show numerical differences, as had been found by Engelmann (30) for the involucre scales at the base of the staminate cone, scales from the fascicles of each species and variety studied by the writer were counted and tabulated (Table 1). The extreme range is from seven, a minimum for *P. albicaulis*, to twenty-three, a maximum for *P. Torreyana*. The widest range in any one species is found in *P. palustris*, which, because of the uniformity in samples taken from several trees growing at College Station, Texas, was selected for testing the variation in scale number from place to place over the geographic range of a species. Samples taken from each of nine stations show that, on the whole, the numbers are related; but the samples taken from College Station, Texas, are far higher. Those samples from Foxley, Alabama, however, are lower than was anticipated. The cause of this wide variation may be due either to climatic conditions or to varietal differences within the species.

The widest range found among the fascicles of a single tree was in *P. rigida*, on which there seemed to be a difference in the scale number in fascicles taken from the various parts of a year's growth. This was observed also in a sample of *P. palustris* from Beaumont, Texas. The latter specimen had a summer shoot, and the fascicles which grew on this had a scale number which was less than that for the fascicles on the regular year's growth.

In order to test the variation in the scale number with reference to the position of the fascicles on the year's growth, vigorous twigs of *P. pinaster*, with a minimum of thirty fascicles on each year's growth, were selected; and ten fascicles from base, middle, and top, respectively, were removed and the scale number counted. No conspicuous differences were found (Table 2).

From the uniformity existing in the seven trees of *P. sylvestris* from Urbana, Illinois, the five trees of *P. taeda*, and the twenty-six trees of *P. pinaster* from the region around College Station, Texas, one would be tempted to conclude that the trees of a given species growing under similar conditions have a rather uniform scale number. Contradictory evidence, however, is afforded by *P. Laricio*, *P. Strobis*, and *P. montana*.

Although the numbers involved leave much to be desired, it is a striking fact that when grouped according to needle number in a fascicle, the two-needled pines usually have twelve scales (Fig. 31 A), the three-needled pines fifteen (Fig. 31 B), and the five-needled pines ten (Fig. 31 C). Sixteen of the thirty-two species counted, including all of those in which the total number of fascicles counted ran above three hundred, had nodes which fell at either ten or at fifteen scales per fascicle (Fig. 31 G). These numbers are equivalent to four and six turns of the phyllotaxic spiral, respectively, and are twice and three times the basic leaf number for *Pinus* as determined by Schneider (79). It is probable that further counts will show a clear-cut tendency to stabilize the scale number at ten, fifteen, and possibly at other multiples of five.

It should be pointed out that the pines with deciduous sheaths are uniformly low in scale number and that for those with persistent sheaths the scale number is high. The scale number per fascicle seems to increase with the length and diameter of the needles, the highest number being found in *P. Torreyana*, which has needles unusual as regards both length and diameter. The second highest numbers were found in the long-leaved pine, *P. palustris*.

It is too early to attempt final conclusions in regard to scale numbers and their significance, and yet there seems to be a definite relation between scale number and the deciduous habit, and between scale number and length of leaves, and possibly between scale number and leaf number.

TABLE 1.—NUMBER OF FASCICLE SCALES FOR THE VARIOUS SPECIES OF THE GENUS PINUS (Concluded)

Species	Variety	Local-ity*	Needle-Sheath num-ber condi-tion†	Trees stud-ied	Scale numbers													Modes							
					7	8	9	10	11	12	13	14	15	16	17	18	19		20	21	22	23	Av.		
Pinaster A.		C.S.T.	2	26	25	198	234	191	34	15
ponderosa D.	Jeffreyi	J.P.M.	3	1	4	11	8	7	17
ponderosa D.	pendula	J.P.M.	3	1	7	18	4	15
ponderosa D.	scoparium	J.P.M.	3	1	1	4	13	5	16
ponderosa D.	?	J.P.M.	3	1	10	17	3	15
ponderosa D.	?	U.I.	3	1	2	22	3	14
ponderosa D.	?	E.P.C.	3	1	1	16	22	11	11
pungens L.		J.P.M.	2	1	8	3	9	5	12
resinosa S.		J.P.M.	3	1	6	37	13	12
rigida M.		S.N.V.	3	1	1	4	12	28	27	21	8	1	15
sinensis L.		J.P.M.	2-3	1	5	13	13	12
Strobus L.		U.I.	5	1	3	15	36	43	3	12
Strobus L.		U.I.	7	1	5	11	3	9
Laeta L.		U.I.	2	1	13	168	309	10	10
Thunbergii P.		N.T. &	3	5	4	17	6	3	13	96	76	4	15
Tonyosho P.		J.P.M.	2	1	4	25	3	12
Torreya P.		D.I.	2	1	11
virginiana M.		Cal.	5	1	2	19	10	2	22
Total		J.P.M.	2	1	1	97	339	780	466	492	393	381	558	434	194	98	145	17	11	10	2	2	10

*Meaning of locality abbreviations:

- A.M. Arizona Mountains
- A.T. Alpine, Texas
- B.T. Beaumont, Texas
- Cal. California
- C.F. Chattanooga, Fla.
- C.S.T. College Station, Texas
- D.I. Dundee, Illinois
- D.I.N.Y. Dana Island, N. Y.
- E.P.C. Estes Park, Col.
- F.A. Foxley, Ala.
- G.P.M. Gulf Port, Miss.
- J.P.M. Jamaica Plains, Mass.
- K.S. Kingston, S. C.
- L.C.A. Lake Charles, L.
- M.M. Missouri Mountains
- N.T. Navasota, Texas
- P.F. Persacola, Fla.
- S.A.F. St. Augustine, Fla.
- S.N.Y. Syracuse, N. Y.

†D = Deciduous sheath. P = Persistent sheath.

TABLE 2.—VARIATION OF SHEATH SCALE NUMBER WITHIN THE SPECIES *P. pinaster*

Tree No.	Part of year's growth counted	Scale number per sheath				
		13	14	15	16	17
1	Bottom.....	1	5	4
	Middle.....	2	6	2
	Top.....	...	9	1
2	Bottom.....	...	3	7
	Middle.....	2	7	1
	Top.....	4	6
3	Bottom.....	...	5	3	2	...
	Middle.....	...	7	3
	Top.....	...	3	7
4	Bottom.....	3	7	...
	Middle.....	10	...
	Top.....	1	9	...
5	Bottom.....	8	2	...
	Middle.....	1	9	...
	Top.....	1	2	7
6	Bottom.....	...	3	4	3	...
	Middle.....	2	4	4
	Top.....	2	6	2
7	Bottom.....	...	4	4	2	...
	Middle.....	3	3	4
	Top.....	1	9	...
8	Bottom.....	1	5	4
	Middle.....	3	5	2
	Top.....	...	8	2
9	Bottom.....	...	1	4	5	...
	Middle.....	1	9	...
	Top.....	2	8	...
10	Bottom.....	...	4	6
	Middle.....	...	4	5	1	...
	Top.....	...	3	7
11	Bottom.....	...	5	3	2	...
	Middle.....	...	5	5
	Top.....	...	4	6
12	Bottom.....	...	3	5	2	...
	Middle.....	...	7	3
	Top.....	...	3	7
13	Bottom.....	1	5	4
	Middle.....	1	8	1
	Top.....	...	9	1
14	Bottom.....	...	4	6
	Middle.....	2	8
	Top.....	5	5
15	Bottom.....	8	2	...
	Middle.....	4	6	...
	Top.....	3	3	4
16	Bottom.....	1	4	5
	Middle.....	...	3	5	2	...
	Top.....	2	5	3
17	Bottom.....	5	5	...
	Middle.....	10	...
	Top.....	1	9	...
18	Bottom.....	...	4	3	3	...
	Middle.....	3	4	3
	Top.....	1	8	1
19	Bottom.....	...	1	4	5	...
	Middle.....	2	8	...
	Top.....	4	6	...
20	Bottom.....	...	5	5
	Middle.....	2	5	3
	Top.....	...	5	5
Totals.....		24	177	191	175	33

It may be more than a coincidence that the species with the most regular scale number (*P. sylvestris*, Table 1) is also the species which shows the most regular leaf arrangement (Table 4).

4. Axillary Structures

Tubeuf, in his classification of the buds of pines, mentions "buds in the axils of the sheath scales" but gives no detailed account of having found any in this position. In the dwarf shoots of *Cedrus* and *Larix*, axillary branching is not uncommon (Fig. 24 E, F, and G).

During the course of the present work, branched dwarf shoots were occasionally found in *Pinus*, but these seemed in every case to be due to fasciation rather than to branches having arisen from the axils of any of the scales on the dwarf shoot. The units on the dwarf shoots may, therefore, be looked upon as essentially sterile.

B. FUNCTIONAL LEAVES, OR NEEDLES

Immediately upon the completion of the sheath scale series on the dwarf shoot, there are deposited as many leaf primordia as are normal for the species. These primordia, after crowding each other and the tiny growing point of the dwarf shoot into the dome-shaped space beneath the hooded scales, become inactive and remain so until spring (Fig. 2 D and Fig. 25 F).

1. Time of Deposit

At the beginning of the present work some doubt was entertained as to whether these irregular structures were the leaf primordia or simply young scale primordia which in the spring would be followed by the deposit of true leaves. Their distinctive shapes and arrangement suggested that they were different from the scales, but it was thought that perhaps this was a consequence of their terminal position and the space relations under the hood of sheath scales. It is true that certain investigators, notably Goebel (38) and Küster (49), called them leaves; but little or no proof was offered to support these statements.

In order to get evidence on this point, counts of sheath scales were made on both the old and the new fascicles from the same shoots. In *P. Laricio*, *P. taeda*, and *P. Strobus*, which are representative of the two-, three-, and five-needled pines, respectively, the primordia on a young winter dwarf shoot exceed the number of scales on the mature dwarf shoot. The excess is approximately equal to the number of leaves characteristic of the species, plus one (Table 3). This indicates that not only are all scales and all needles present during the winter rest but that the growing point of the dwarf shoot is also present as a separate elevated

primordium. Both microtome sections (Fig. 25 F) and direct daily observations, made at the time of resumption of spring activity, have confirmed these conclusions.

The cells which are present in the resting primordium evidently enter the second phase of growth along with the tissues of the sheath scale, but there is considerable delay in extending beyond the sheath. This is due to the fact that the sheath growth is synchronized with leaf growth,

TABLE 3.—COUNTS OF SHEATH SCALES ON OLD AND NEW FASCICLES

Species	Average number of scales on 100 old fascicles	Average number of primordia on 100 new fascicles	Difference	Number of leaves plus one (growing point)
<i>P. Laricio</i>	10.52	13.61	3.09	3.00
<i>P. taeda</i>	15.27	19.38	4.11	4.00
<i>P. Strobus</i>	11.28	17.52	6.24	6.00
<i>P. cembroides</i> var. <i>monophylla</i>	10.75	14.00	3.25	2.00

TABLE 4.—LEAF ORIENTATION WITH REFERENCE TO AXIS OF DWARF SHOOT

Species	Tree				
		A	B	C	D
<i>P. Banksiana</i>	1	2	23	0	7
	2	0	6	28	15
<i>P. densiflora</i>	1	31	45	2	7
	2	20	7	0	8
<i>P. Laricio</i>	1	7	16	7	49
	2	5	30	20	35
	3	11	15	32	44
<i>P. montana</i> var. <i>Mughus</i>	1	35	5	45	22
<i>P. Murrayana</i> Eng.....	1	6	5	1	20
<i>P. Pinaster</i>	1	60	18	20	6
	2	18	14	5	35
	3	32	9	17	9
<i>P. pungens</i>	1	11	13	8	21
<i>P. resinosa</i>	1	0	8	30	22
<i>P. sinensis</i>	1	50	7	0	8
<i>P. sylvestris</i>	1	99	1	0	0
	2	2	2	112	2
	3	60	9	0	0
	4	100	4	0	4
	5	43	37	0	16
<i>P. Thunbergii</i>	1	6	17	19	8
<i>P. virginiana</i>	1	0	25	7	1
<i>Total</i>		598	316	353	339

and for a time the sheath expands to accommodate the growing leaves within.

Soon the outer portions of the needles are mature and are pushed up through the scales while the tissues of the latter are still immature. From this time on, the leaves grow from zonal meristems. The leaves grow at a far faster rate than do the sheath scales, and, since the leaves fit tightly into the sheath, this growth, as long as it continues, keeps the sheath tightly extended and the scales drawn to their full extent. As soon as the leaves are mature, the shedding and wrinkling phenomena which were described above begin.

2. Leaf Orientation

In order to determine whether or not the orientation of needles is uniform for a species, certain researches were undertaken, but because of the difficulty of determining with accuracy the arrangement of the needles on the three-needled and the five-needled species, observations were confined to the pines which have only two needles per fascicle.

A sharp razor was drawn across the base of each fascicle, severing the leaves near their points of attachment. The plane of section was perpendicular to the axis of the dwarf shoot. Since the contiguous faces of the needles form a plane surface, it was found convenient to refer this *plane of needle separation* to the axial plane which passes through the long axes of both the long shoot and the dwarf shoot (Fig. 1 N).

When a twig, with its dwarf shoots cut as described above, is viewed from the apex, the lines separating the severed needles are seen to lie at various angles with reference to the axial plane (Fig. 7 G). The orientation is not constant but is rather uniform. This is especially true of *P. sylvestris*, in which five vigorous twigs from as many different trees gave a predominance of needles with their separation planes at right angles to the axial plane (Table 4). In certain cases the predominant orientation was exactly at right angles to that found on the other trees of the same species. On those twigs which showed a wide variation in arrangement, the leaves at a given level on the stem were usually oriented in the same way.

From the limited data obtained, no important general conclusions are safe. Perhaps it is not too much to suggest that some two-needled pines tend to favor an arrangement of needles in such a way that the separating plane is either parallel with the axial plane or at right angles to it. In other species the arrangement seems to be at random.

3. Leaf Fusions

Many cases of needle fusions have been reported. In fact fusions are so common that varieties with all the needles of a fascicle fused have

been established for *P. excelsa*, *P. Strobus*, *P. sylvestris*, and others (Masters, 57). Individuals with a part of their needles fused can be found in almost every species in any season. Strasburger in his famous work of 1872, *Die Coniferen und die Gnetaceen*, (87) shows figures of fused needles of *P. pumilio*. Many other cases have since been described,

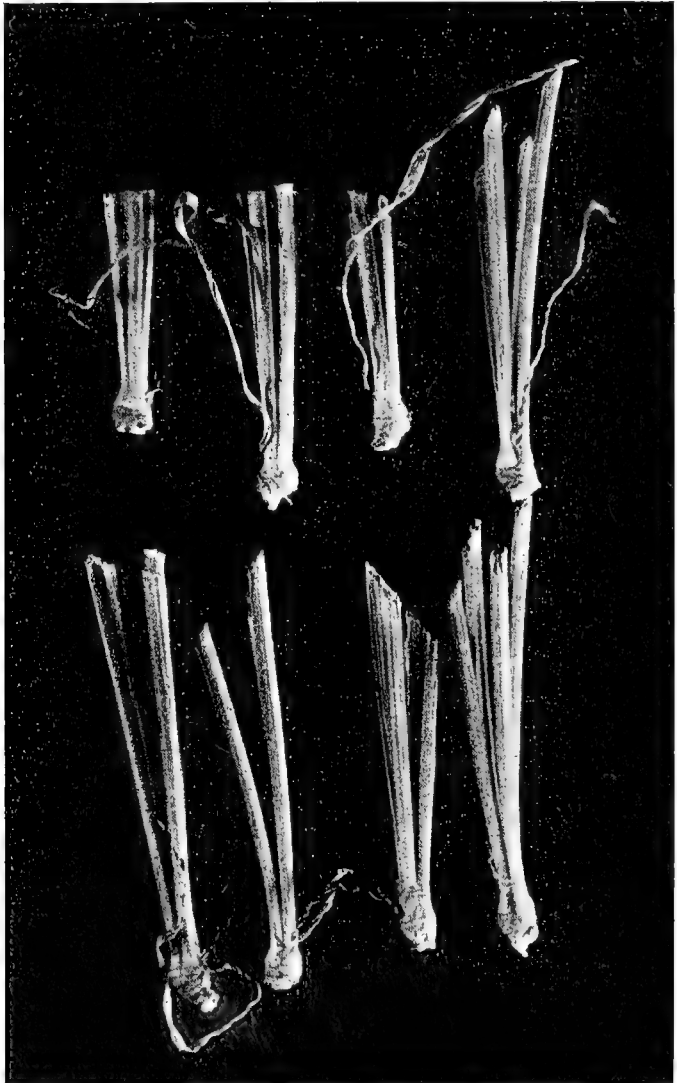


FIG. 26.—Fascicles of a normally five-needled pine with one of the needles reduced to a filamentous vestige.

and Schneider (79) has given an extensive treatment of the entire subject. Even the leaves of *P. cembroides* var. *monophylla* offer no exception to the rule of occasional fused needles. This was shown by Masters (57) who, after describing the normal univalent needle of this variety, described also the fused condition. He says: "There are always two foliar tubercles only one of which is developed. In other cases . . . both leaves are formed but remain coherent by their edges so as to appear simple." Sir Joseph Hooker (45) found this condition occurring so consistently in monophyllous leaves which he sectioned that he, without discovering the simple condition, pronounced origin by fusion (welding) as the method by which the single leaves of this variety are produced. The three needles of *P. Nelsoni* are normally attached by their inner angles (Fig. 27 v). A sample of *P. clausa* from Pensacola, Florida, showed the same feature (Fig. 27 u). Perhaps all of these fusion phenomena can be explained exactly as the welding of cotyledons was ex-

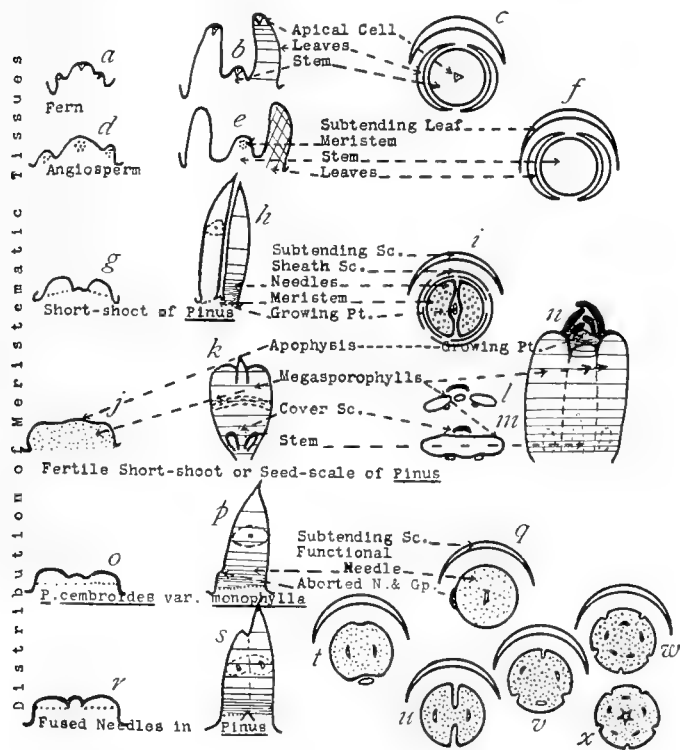


FIG. 27.—Diagram showing the author's conception of the relation between the evolution of zonal meristems and the reduction and fusion of parts on the dwarf shoots and cone scales.

plained earlier in this paper. Fusions, in general, seem to be the result of *meristematic recession* and *subsequent zonal growth*.

When the leaves of a two-needled pine "fuse," the growing point for the dwarf shoot may be crowded aside and remain unincorporated (Fig. 27 t); but in the five-needled pines in which all the needles are fused into a solid column, there can be but one place for the remnant of the growing point of the dwarf shoot, and that is at the distal end of the column. If the growing point had not been involved in the common upward growth, it would have remained at the end of the dwarf shoot; in this event the column would have been hollow instead of solid (Fig. 27 x).

Needles fused in nearly every conceivable manner have been described, and proliferated dwarf shoots are also common; yet no case has been reported in which the proliferated growing point for the dwarf shoot has been carried up on the fused leaves. According to Masters (57), such a case was observed for *Sciadopitys* by Carrière in 1857.

Schneider (79) contends that the fusion of the needles of pines is so superficial that it is a mistake to compare this condition to the congenital fusion of *Sciadopitys* leaves. He believes that the growing point of pines is never carried up on the leaves, and yet he shows that fusion in pines can go so far that the double point is entirely eliminated and the double vascular strand is enclosed in a single endodermal sheath. Both these conditions go beyond that normally found in *Sciadopitys*.

Since the seed scale is considered here as a dwarf shoot, we are not without our example of a transported and proliferated dwarf shoot in this genus; for Stenzel (86), Willkomm, and others have shown that the

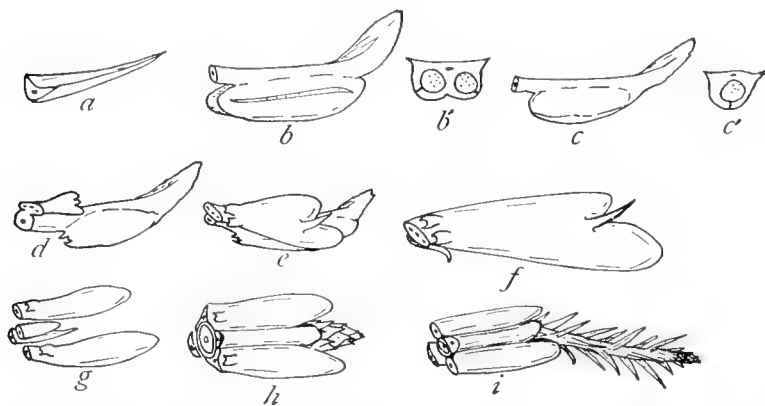


FIG. 28.—Diagram of a series of intergrading involucral bracts, microsporophylls, megasporophylls, seed scales, buds and branches found on various bisporangiate and proliferated cones of the *Abietineae*.

a, b, c, d, e, f, and g. From *Larix europea* and *P. tonyosho* examined by the author. h and i. From proliferated cones of several genera described in the literature.

growing point of the seed scale is sometimes carried up on the tip where it may make a well-developed dormant bud (Fig. 29 z and z') or even a leafy shoot (Parlatore, 68) (Fig. 28 H and I).

The sum of this evidence permits us to link leaf welding with meristematic recession and with zonal growth, and to see that the welding process can involve vegetative leaves as well as cotyledons, growing points, and other structures.

4. *The One-Leafed Pine (Monophylla)*

Since its discovery by J. C. Fremont, *Pinus monophylla*, now known as *P. cembroides* var. *monophylla* Voss., has been the subject of various morphological interpretations. In 1874 Bertrand (7) interpreted the leaf of this pine as a kind of twig, the vascular cylinder of which had opened and flattened out. In this he seems to have followed Meehan, who had previously (1872) advanced a twig theory for the interpretation of the leaves of pines in general as simply the subdivided extension of the dwarf shoot.

As pointed out by Engelmann (31) it was long considered probable that the terete leaf of *monophylla* was in reality a connate pair (Carrière, 18). Indeed, such double needles do frequently occur in this as well as in other pines. This fact led Sir Joseph Hooker (45) to a misinterpretation of the true relationship in *P. monophylla*. He says:

The anomaly of the single leaf is due to the cohesion of the two semiterete leaves of each sheath and is far from a constant character. In plants at Kew the two leaves are as often free as united and on making a transverse section it will be seen that the vascular bundle in the center of the cylinder is in fact double, and that the two parts are sometimes separated.

This misinterpretation was probably caused by the tendency toward proliferations and fusions which pines undergo when subjected to exceptionally favorable conditions. *P. monophylla* at Kew is under conditions vastly different from those of its Rocky Mountain habitat.

In 1882 Strasburger (87, p. 389) called attention to the facts that the vascular cylinder of the monophyllous dwarf shoot is open and that the needle is traversed by a simple rather than a double vascular bundle. From these facts he correctly concluded that the needle is univalent. This view had also been expressed by Thomas (90).

In 1913 Schneider (79) advanced convincing anatomical evidence of a vestigial vascular strand which is present on the rim of the opening described by Strasburger. The vestige is opposite the functional vascular bundle and in the position of the vascular strand of the second needle of two-needled dwarf shoots. Schneider correctly interpreted this as evidence of needle atrophy at this point, but since he worked with mature dwarf shoots, he was unable to find any external evidence of such atro-

phied needles. Much earlier Masters (56) had seen evidences of such an abortion. He says:

I investigated the development of the constituent parts of the leaf-bud at various stages of growth, and without going into details which are for this purpose unnecessary, I may say that the development supplied the clue which neither outward morphology nor internal anatomy sufficed to give. In point of fact, in the earliest stages examined there were always two foliar tubercles, one of which speedily overpassed the other, so that ultimately all traces of the second leaf were obliterated. . . .

The monophyllous sheath of this pine therefore owes its peculiarity to the generally arrested development of one of its two original leaves.

This observation, if substantiated with figures and detailed descriptions, would have furnished the complete story and would have prevented many later mistakes in the interpretation of the leaves of this pine. The view that the leaf of *P. monophylla* represents an aborted branch was at first adopted but later rejected by Meehan (60), who, because of further research stimulated by Newberry (65), changed over to the interpretation which holds the structure to be a single true leaf.

5. Leaf Reduction in *P. monophylla*

The presence in *monophylla* of more needle primordia on the winter dwarf shoots than ultimately come to maturity (Table 3), at once centered attention upon this variety as possibly holding the key to the manner by which the reduction in needle number in pines generally has been accomplished. Daily observations were made, and a close series of material was imbedded during the developmental stages.

As growth processes began, the growing point of the dwarf shoot and one leaf primordium (Fig. 25 D) remained inactive while the basal portion of the remaining needle began the usual meristematic activity (Fig. 25 A), pressing the differentiating point up into the crest of the hooded scales (Fig. 25 B). Soon the meristematic zone seemed to recede and to spread entirely across the top of the dwarf shoot, thus involving the inactive primordia in the general upward movement. As these were lifted into the cylindrical space within the sheath cavity, they became flattened and incorporated in the general mass of undifferentiated cells composing the functional needle. Within a short time both inactive primordia disappeared completely.

The manner by which this reduction is accomplished is strikingly similar to that by which the number of primordia is reduced during the formation of the cotyledons as previously described. Bearing in mind the suddenness with which the evidences of the manner of reduction disappear, one is not surprised that workers who examined only the mature leaves and fascicles failed to discover them.

On the mature dwarf shoots of other pines, Schneider (79) found all gradations from complete failure of a part of the needles in a fascicle to those in which the aborting needles approached the normal size and development. This frequent occurrence on nearly all pines has been amply confirmed by my own findings (Fig. 26 and Fig. 1 o). By sectioning the dwarf shoots on which these vestiges occurred, Schneider showed that in each case the atrophied trace of the vascular strand was clearly recognizable. Since he had found a similar trace on the normal dwarf shoots of *monophylla* (Fig. 23 G), he was at a loss to explain the absence of an external vestige from this variety. His conclusion was that the development had likely begun but was arrested before the rudiments became recognizable externally.

6. Leaf Reduction in Other Pines

In order to determine whether the method of reduction of the needle number observed in *monophylla* also occurs in other pines, a large number of young fascicles was examined. Many were found with needle primordia in excess of the normal number for the species under observation; but these did not occur with sufficient frequency to justify the conclusion that there would have been a later change toward a lower number, for mature fascicles with needles in excess of the normal number are common in nearly all pines. Neither microtome sections nor direct observations revealed any reduction processes in other species similar to those taking place in *monophylla*. The fact that such processes were not discovered cannot be taken as final proof that they do not occur, but rather as an indication that other methods of reduction, the evidences of which are everywhere apparent, must have accounted for most of the reduction of the needle number in pines.

The evidences that reductions in needle number have actually been going on are of such nature and number as to leave little doubt as to what the general trend has been. Summarized, these evidences are as follows:

(a) The dwarf shoot, being a specialized branch, must have evolved from a more generalized branch type. This of necessity could have been nothing other than the ordinary long shoot with its indefinite number of leaves. A rudimentary bud with partly developed leaf primordia remains as a convincing evidence of this reduction.

(b) The earliest fossil pines had numerous leaves on the dwarf shoots, indicating that the trend in leaf number has been downward.

(c) Leaf vestiges and vestigial vascular strands for aborted needles are common. The two may be associated, or the latter may be present without the former, as in *monophylla*.

(d) Varieties or specimens within a species are often found with less than the usual number of leaves, indicating that reductions are still taking place.

(e) Traumatic stimuli which would be expected to bring about a return to primitive conditions cause the needle number to be increased, marking the higher number as the primitive one.

(f) Dwarf shoots often grow into long shoots with a large number of needles; and when this occurs, the branch bears simple leaves and has other features which suggest this as a primitive branch type.

(g) It is significant that of the related plants with dwarf shoots *Cedrus*, *Larix*, and *Pseudolarix*, which have large and indefinite numbers of leaves on their dwarf shoots, have scarcely gone beyond the pine-level in any of their characters, while *Sciadopitys* and *Taxodium* with highly specialized dwarf shoots and fewer foliar organs show a complex of characters which, on the whole, are more advanced than those of *Pinus*. This suggests that dwarf shoot reduction and specialization are associated with advancement.

7. Increases in Leaf Number

It was hoped that a careful examination of the ontogeny of fascicles on which supernumerary needles were growing would, in comparison with that of ordinary fascicles, show significant developmental differences. It has long been known that the conditions at the time of deposit and extension may influence the number of needles on the dwarf shoot, for in 1899 Bothwick (9) showed *Pinus Laricio*, which is ordinarily a two-needled species, to be capable of producing dwarf shoots with three and four needles each. For this reason *P. Laricio* was chosen for determining whether or not noticeable developmental differences occur. A tree on which less than two per cent of the fascicles normally had three needles was selected for observation of the ontogeny of supernumerary needles.

The end and lateral buds distal to the annual growth which had been extended during the summer of 1930 were completely removed during the fall of 1930. One or two of the most distal dwarf shoots on each dis-budded twig, proliferated long shoots during the spring of 1931. These produced fascicles of which nearly twenty per cent had three needles each (Fig. 3 y). The ontogeny of these three-needled fascicles, however, showed nothing which in any way differed from that of pines normally producing three needles.

The increase in needle number noted above seems to point to a three-needled ancestor for two-needled pines. Similar evidence is at hand to support the view that this three-needled ancestor came down from more remote ancestors which had four and five needles.

Dr. Charles F. Hottes, of the University of Illinois, called attention to an unusual specimen of a two-needled pine (*P. Laricio*) which he had observed over a period of years. This tree was found to be covered with thousands of young twigs which clothed the trunk to a height of twenty or more feet. These twigs remain from one to a few years, then die off, only to be replaced by others of a similar nature. A detailed examination of some of these twigs revealed astonishing irregularities in needle number. To illustrate this point a description of a single twig will suffice.

In the spring of 1932 the twig in question appeared as a five-needled dwarf shoot. This shoot soon proliferated a branch with numerous units, the foliar components of which were simple with axils mostly sterile. The axils of five of these simple leaves produced dwarf shoots, and in each case these had five needles each instead of the customary pair

TABLE 5.—DISTRIBUTION OF FASCICLES HAVING VARIOUS NUMBERS OF NEEDLES FROM TWIGS OF ONE TREE

Number of needles	Number of fascicles	Percentage of total
1	0	0
2	100	23
3	281	64
4	2	0.45
5	56	13
6	0	0

characteristic of the tree from which the branch was taken. The same twig continued growth in the spring of 1933. This season it made a growth four or five inches long, which was covered throughout with simple leaves. The axils of these leaves bore dwarf shoots, each with three needles.

A representative sample of similar unusual twigs from the same tree was gathered, and the fascicles were picked at random until a hundred normal (two-needled) fascicles had been counted. In order to obtain this number, 439 fascicles were counted. Among these the needle numbers per fascicle were found to be distributed as shown in Table 5.

The most remarkable feature was the paucity of four-needled fascicles in comparison with five-needled fascicles. The latter, although more remote from the normal, occurred twenty-eight times as frequently as the former. This suggests five as the basic leaf number and confirms the view at which Schneider arrived from a consideration of the anatomical evidence.

8. Factors Determining Leaf Number

As shown by Eichler (29), the cylindrical space within the sheath determines the cross sectional form of the needle. Needles which grow alone on dwarf shoots are circular in cross section. Sections of those grown in pairs, threes, fours, and fives make up halves, thirds, quarters, and fifths of circles, respectively (Fig. 12 a to e). Since fascicles with one, four, or six needles are relatively rare, there must be some biological reason for this numerical discrimination.

Since the sheath plays such an important rôle in shaping the cross sectional form of the needle and in making possible its unique zonal growth, one naturally turns to this organ when seeking the element of survival which has been responsible for this *trend toward certain fixed numbers*.

It was hoped that the phyllotaxic arrangement of the scales on the dwarf shoot and the arrangement of needles within the sheath would throw some light upon the probable reasons for these facts. The leaves themselves are cyclic, but the phyllotaxy of the other foliar structures on the dwarf shoot, to which series the leaves undoubtedly belong, follow the 2/5 scheme. It then becomes clear that, with the progressive shortening which was necessary in order to eliminate the internodes and produce the cyclic position, the complete elimination of the internodes from two turns of the phyllotaxic spiral would bring *five* needles into a cycle. A sixth needle, if included, would fall in line with number one and a seventh in line with number two, and so on, thus setting up interference and unequal competition within the limited space afforded by the sheath (Fig. 12 F). Doubtless the phyllotaxic arrangement, coupled with the crowding of the needles within the sheath, constitutes the major factor responsible for the preponderance of five-needled species in the genus *Pinus*.

Why the reduction should have continued below the number five is a matter for speculation. The evidence indicates that the decrease below five must have been a gradual one, the loss of needles being one by one. If this be true, the immediate forerunner of *P. monophylla* had two needles and that of *P. Laricio* and other two-needled pines had three, while that of *P. palustris* had four and so on. Prior to the attainment of the five-needled condition the reduction must have been at first erratic. As the internodal shortening proceeded and the cyclic arrangement was attained, the needles at first must have tended to stabilize at two or more whorls of five needles each, those of the outer whorl alternating with those of the inner whorl (Fig. 12 g). Ample anatomic evidence to support this view is given by Schneider (79) (Fig. 23 E).

The number of needles per fascicle varies considerably with the species and with conditions. Schneider gives a table showing these variations in a number of common species.

In seeking to ascertain the reasons for the fact that four-needled and six-needled types have proved to be less stable than those with three, two, or five needles, it was observed that in perforating the covering of sheath scales, the entire fascicle of needles pushes up as a single organ of thrust. The immediate need is for an efficient perforating organ, for the leaves must escape from the sheath before their photosynthetic work can begin. Any arrangement of needles which permits displacement at this critical stage reduces the combined efficiency and disfavors the survival of the dwarf shoot whose leaves have such an arrangement. In three-needled and five-needled fascicles, the planes of separation between the needles will permit little or no lateral movement, for each needle is wedged against the two neighboring ones; and the planes of separation are discontinuous at the central angle (Fig. 12 c and e). This is not the case in fascicles with four needles, for here each separating plane extends from side to side and permits lateral movements of the component needles (Fig. 12 d). This might possibly displace one or more young needles and prevent their united action as organs of thrust in perforating the sheath.

A search was made for evidences which would throw light upon this possibility. *P. palustris*, which has a complex sheath of many scales and which in addition occasionally produces fascicles with four needles, was selected as favorable material for a test. A search was made for those fascicles from which the needles had failed to escape or from which they had escaped with difficulty. These proved to be extremely rare. Since they usually remain on the tree for only a short time, one must examine large quantities of late spring or early summer material if fascicles with crumpled and bound needles (Fig. 19 A and C) are to be found in number. In order to find nine fascicles of them, approximately 100,000 fascicles were examined. From the same trees from which these were obtained, 5,000 fascicles were selected for determining the needle number in normal fascicles. Of the 5,000, only nine had four needles each. All of the others had two and three needles. In other words, approximately one normally developed fascicle in five hundred had four needles. Among the fascicles with bound needles, however, three in nine had four needles each. This is one in three as compared with one in five hundred for the fascicles with free needles.

Although these results are suggestive, the question of whether or not the leaf arrangement, which in its turn is a function of the leaf number, is an important factor in penetration, and consequently in survival, will await the gathering of more extensive data.

9. Vascular Supply to the Leaves

As shown by Schneider (79) and confirmed by Aase (1), the vascular supply to the dwarf shoot arises as two bundles which soon unite to form a complete vascular ring, from which arise the small bundles to the various scales. At the top of the ring the bundles to the leaves arise (Fig. 23 B). It makes little difference whether we are considering the hard pines in which the bundles to the leaves subsequently divide or the soft pines in which one "full bundle" without dividing supplies a single leaf. In either case we may, by combining the vascular supply from a unit of the long shoot with the vascular supply in a dwarf shoot, get an arrangement such as is shown above.

C. MERISTEMATIC TIP, OR BUD OF THE DWARF SHOOT

1. *Abnormal (Proliferated) Interfoliar Buds*

Distal to the needle attachment and resting at the tip of the dwarf shoot, the more or less inactive growing point for this modified branch is usually to be found. From the works of Schacht (77), Dixon (25), Masters (57), Penzig (69), and others it has long been known that under certain circumstances these growing points may continue activity and grow into long shoots (Fig. 5). Sections through the fascicles showing the normal unproliferated growing points were figured by Strasburger (87).

Dufrenoy (26) points out that the old functional leaves on a proliferated branch serve the proliferated branch in a manner analogous to that in which the cotyledons serve the young seedling. This is unquestionably a fact; for the original leaves at the base of such proliferated branches (Fig. 3 z) usually fall away at the close of the first year, while on the same tree the leaves on normal non-proliferating dwarf shoots may remain for four or five years. The increase in diameter of the dwarf shoot may disturb the vascular supply to the original leaves, or it may be that the expansion of a bud within causes the sheath to choke the leaves at their tender bases, resulting in death. The analogy to cotyledons seems to offer the best explanation for the death of the original leaves, for in proliferating branches a food gradient is evidently set up from old leaves to young primordia. This is shown by the arrest of growth in the leaves of branches proliferating before the maturity of the original leaves, in which case there is a direct relation between the size of the proliferated bud and the length of the accompanying leaves (Fig. 18 b).

During the course of the disbudding experiments that were previously mentioned, it was found that in *P. Laricio* var. *Austriaca* one hundred per cent of the disbudded twigs could be made to proliferate from the tips of some of their dwarf shoots, usually the most distal ones. Indeed

so regularly does proliferation occur in this species that it is possible to prune back half or more of the annual growth of each twig each season, thereby producing a small dense tree suited to rock gardens or to other plantings of limited space. On such a tree all the branches represent proliferated dwarf shoots. Just such a tree has been maintained for years at the Horticultural Rock Garden at the University of Illinois.

The disbudded twigs of *P. Strobus* proliferated twigs from their interfoliar buds to a far less extent than those of *P. Laricio*. In *P. Strobus* not more than one twig in a hundred proliferated at all, and this, during the first summer following disbudding, took the form of a scale-covered bud. In *P. Laricio* branches were often pushed out immediately without the intervention of dormant buds. Schneider (79) found that *P. Strobus* proliferated more readily than did *P. sylvestris*. Since *P. sylvestris* is more like *P. Laricio* than it is like *P. Strobus*, this observation may be taken to be the reverse of what would be expected. Very likely the ability to proliferate will be found to depend upon the age and vigor of the tree, but the writer's observations indicate that, other circumstances being equal, pines with persistent fascicle sheaths proliferate more readily than those with deciduous sheaths.

2. Normal (Non-Proliferated) Interfoliar Buds

Voluminous and interesting is the literature on proliferated dwarf shoots, but no extensive researches have been made into the normal nature and frequency of occurrence of bud rudiments on those normal dwarf shoots which never proliferate. It is true that Bothwick (10) has written a short paper on this subject, but he leaves the impression that these "interfoliar" buds occur on all of the dwarf shoots and that they are more or less invariable in make-up. Other writers dismiss the subject with but a word. Jeffrey, in his exhaustive comparison of *Prepinus statenensis* with modern pines (47), leaves the impression that although the buds are present on modern pines, they soon disappear. He says of them: "The growing point of the short-shoot [of *Prepinus*] persisted indefinitely and did not disappear at an early stage, as in the living representatives of the genus." Other modern botanists seem to be of the opinion that such buds do not normally occur. Torrey (92), summarizing the evolution of the brachyblast, says: "Modern pines rarely have more than five needles, and have completely lost the terminal bud." In the light of these views the question of frequency, distribution, and variation of these interfoliar buds was undertaken.

A preliminary investigation showed that on some dwarf shoots no trace of the tip meristems is to be found (Fig. 7 A). When present, these growing points grade from minute simple domes of meristematic

TABLE 6.—CONDITION OF INTERFOLIAR BUDS

Species	Locality*	Tree	Number of needles	Sh.	0	1	2	3	4	5	6	7	8	9	10
Armandi.....	J.P.M.	1	5	D	30	10
Banksiana.....	J.P.M.	1	2	P	28	2
Cembra.....	D.I.N.Y.	1	5	D	0	5	10	5
Cembra.....	D.I.	2	5	D	15	1
Cembra.....	J.P.M.	3	5	D	31	10
clausa.....	P.F.	1	2	P	5	..	5	4	1	2
densiflora.....	J.P.M.	1	5	P	25	6
excelsa.....	D.I.N.Y.	1	5	D	35	22
flexilis.....	J.P.M.	1	5	D	20	30
flexilis.....	E.P.C.	2	5	D	10	5	5	2
flexilis.....	?	1	5	D	10	30
Koraiensis.....	J.P.M.	1	5	D	15	15
Lambertiana.....	V.I.	1	2	P	5	1	2	4	1
Laricio.....	V.I.	2	2	P	12	13	16	7	3
Laricio.....	V.I.	2	105	P	9	11	11
Laricio.....	V.I.	2	4	35	13	1	1
Laricio.....	V.I.	2	6	12	6	25	4	1
mitis.....	M.M.	1	5	P	17	15
monticola.....	J.P.M.	1	2	P	45	2
murryana.....	E.P.C.	1	2	P	0	3
Pinaster.....	E.P.C.	2	2	P	14	1	12	4	4
Pinaster.....	C.S.T.	1	3	P	6	11	10	11	16	3
ponderosa.....	J.P.M.	1	3	P	1	6	3	11	6	2
ponderosa.....	E.P.C.	2	3	P	0	0	3	11	5	2
ponderosa.....	J.P.M.	3	3	P	0	0	0	3	2	3
ponderosa.....	J.P.M.	4	3	P	0	0	0	1	23	1
resinosa.....	J.P.M.	1	3	P	7	6	3	5
rigida.....	D.I.N.Y.	1	3	P	5	7	4	1
rigida.....	J.P.M.	2	3	P	0	0	5	15	3
sinensis.....	J.P.M.	1	2-3	P	2	10	21	13	6	1
Strobilus.....	J.P.M.	1	5	D	50	3	2
stylvestris.....	V.I.	1	2	P	65	24	11
stylvestris.....	V.I.	2	2	P	76	21
stylvestris.....	V.I.	3	2	P	115	8	27
stylvestris.....	V.I.	4	2	P	119	21	7	13	3
taeda.....	C.S.T.	1	3	P	35	80
Thumbergii.....	J.P.M.	1	2	P	0	0	2	10	15	1
virginiana.....	J.P.M.	1	2	P	49	2

* The locality abbreviations are the same as in Table 1.

tissue through buds with varying numbers of secondary (foliar) primordia to well-developed scaly buds (Figs. 7 A). The latter grade off without a separating line into types already described as proliferated. There was some indication that the buds grew from year to year without being actually extended to form branches. For this reason the observations made to determine the normal interfoliar buds were always made on fascicles which were in their second year of growth.

In order to make the necessary observations, the fascicle sheaths were removed and the needles spread apart under a dissection microscope. An estimate was made of the number of secondary scales present on the primordium. Eleven classes were made. Those on which there was a complete absence of primordia were tabulated under zero (Table 6). Those on which dome-shaped growing points were present but which were without secondary scales were placed in class one. Those with a small number of scale primordia were classified according to the estimated number of their scales into classes two to nine. All others, regardless of the degree of development, were placed in class ten (Fig. 7 A).

No species was found in which growing points were entirely absent from all of the dwarf shoots. As would be expected they are less developed on the pines which have deciduous sheaths; for in order to be able to dispense with the sheath, meristematic activity in the entire fascicle, including the intercalary zones of the needles, is cut short. This arrest undoubtedly affects the adjacent tissues of the interfoliar bud. The shedding of the sheath exposes the growing point to the sun and drying air. This exposure has an adverse effect upon the bud's further development. These facts, in part, account for the usual low state of the growing point on the white pines and for the fact that proliferations for these have been so rarely reported in the literature. They explain at the same time the low percentage of proliferation obtained from the disbudded branches of *P. Strobus*.

In order to determine whether or not the interfoliar buds continue to grow over a period of years, *P. pinaster*, because of the fact that its dwarf shoots are deciduous only after several years, was selected for study.

In the fall of 1932, large numbers of fascicles were gathered from each year's growth for the years from 1928 to 1932, inclusive, approximately equal numbers being taken from each year's growth. These collections were repeated for each of several twigs from each of several trees. In order to eliminate the human element, fascicles of each age were placed in separate paper bags; the bags were then dated with concealed numbers; and after the fascicles had been thoroughly stirred, the

bags were drawn at random. The condition of 100 primordia from each bag was determined (Table 7).

The results obtained from these counts showed little evidence of any growth except for the first and possibly the second years. Buds from fascicles which were two years old were better developed than those from three, four, and five-year fascicles. Since bud parts once formed cannot

TABLE 7.—ANNUAL GROWTH OF INTERFOLIAR BUDS OF *P. pinaster*

Year	0	1	2	3	4	5	6	7	8	9	10	Mode	Average	Age in years
1928.....	...	3	10	3	48	30	6	1	4	4.20	5
1929.....	...	2	3	16	66	13	1	2	4	4.11	4
1930.....	9	13	58	15	1	4	4	3.98	3
1931.....	4	12	18	28	32	5	1	1	...	6	4.91	2
1932.....	10	37	41	9	3	4	3.58	1

be lost and since any differential shedding over the course of years would tend, by elimination of the most weakly developed fascicles, to raise rather than lower the average bud condition, we must account for the high average on 1931 (second year) fascicles by assuming that during that year conditions for bud formation were more favorable than in the years immediately preceding.

D. BRANCH AND LEAF FORMS IN FOSSIL AND MODERN RELATIVES OF PINUS

In selecting a series of fossils with which to illustrate the steps in the probable evolution of the dwarf shoot, the task is not an easy one, for some think that pine-like characters have at times been held in common with other plants which are not abietineous. Jeffrey (47) for example says: "The occurrence of linear leaves in fascicles is in itself no real evidence of Abietineous affinity." While admitting that in some instances it might have been possible to select better representatives from the endless number of fossil relatives, the following will, nevertheless, serve our purpose.

1. *Pityites*

When one reads a summary of fossil Abietineae such as is given by Seward (81, Chapter 48), he is impressed with the difficulties of separating these plants into the various fossil genera. Because of these difficulties, Seward proposes the group name *Pityites* for abietineous fossils which cannot with confidence be referred to a more precise position. The difficulties created by the interblending of characters is well illustrated by *Pityites Solmsi*, the long shoots of which were made up of units with

short internodal components. The foliar components fell off and left persistent bases such as are met with in modern pines. The dwarf shoots were clothed at the base with scales and bore numerous (10 to 20) long needles. It is unlikely that any of the scales completely encircled so large a number of needles. If perforation occurred at all, the encircling fibers must have been broken early, and any supporting work was due either to rigid bases or to fibrous entanglements along the adjacent scale margins. The cones of this plant resembled those of *P. Strobis* or *P. excelsa*.

Some of the dwarf shoots of *Pityites Solmsi* were branched as in *Larix* (Fig. 24 E, F, and G) and *Cedrus*, the latter of which it resembled, though the greater length of needles is more in accordance with that of recent species of *Pinus*.

2. *Prepinus statenensis*

Probably the best-known fossil relative of modern pines was described by Jeffrey (46), who includes in the summary of his paper the following important conclusions:

The name *Prepinus* is proposed for this type in the belief that it is the direct ancestor of *Pinus*.

The Abietineae are the oldest living family of the Coniferales.

Pinus is the oldest living representative of the Abietineae.

From the excellent figures and the clear descriptions furnished by Jeffrey, several significant facts in regard to the morphology of this interesting fossil are manifest.

The dwarf shoot was deciduous, as is evidenced by a single annual ring associated with resin canals which were occluded by tyloses. The sheath scales were numerous, and at least the basal ones were shed, leaving marks very similar to those left where the scales of modern pines break away from a living base. Most of the scales were not deciduous, and, although there is no evidence of perforation, the crowded and angular leaves show clearly that the sheath exerted sufficient pressure upon the leaves to shape them into the available space within the sheath cavity. The reduced and distorted growing point on the dwarf shoot gives a similar testimony regarding growth pressures. The presence of a scale-like protective cover around the growing point, marks this as a bud belonging originally to a different year's growth from that of the rest of the dwarf shoot. The elongated angular leaves suggest growth from zonal meristems, and yet the continuation of resin ducts to the very base, as in the simple leaves of modern pines, hints that zonal meristems were probably less specialized than in modern pines.

The leaf trace in *Prepinus statenensis* remained undivided, resembling in this respect species of *Pinus* belonging to the section *Strobis*, *Cembra*, etc.

3. *Fossil Pines of Modern Types*

Existing in the same forests with *Prepinus*, there were pines of modern type, as shown by Jeffrey (46), who figures a transverse section through the base of a quadrifoliar dwarf shoot of one of these. This specimen, even to such details as leaf arrangement, leaf shape, and nature of sheath scale, could pass for a pine of today. The double vascular bundle in the leaves of this specimen marks it as a hard pine.

Detached leaves from bifoliar dwarf shoots of both hard and soft pines were also found in the same beds.

Solms-Laubach (84) described leaves of a *Pinus-like* plant from the Upper Jurassic or Lower Cretaceous of Bell Island. This plant had leaves which were oval or circular in outline and had the typical infolding of the walls of the mesophyll as do modern pines and cedars. The shape of the leaf made it strikingly like the leaf of *monophylla*. Solms-Laubach described the vascular bundle as being single; this would make the plant all the more like *monophylla*. Seward (81), after having examined some of the material, could find no convincing proof of the singleness of the bundle. He points out the fact that a second bundle may sometimes be absent in individual leaves of species normally possessing them. In speaking of this species, Seward says: "It affords an interesting example of an Abietineous type in all probability of Upper Jurassic age, exhibiting a remarkable resemblance to certain recent species especially *Pinus monophylla*."

Under the name *Pityocladus*, Nathorst (64, p. 62) describes branches similar to those of *Pityites Solmsi* and of *Prepinus*. Their occurrence as detached fossils suggests the possibility of their being deciduous, while the presence of leaves on some but not on others suggests the possibility of indifferently deciduous leaves on the dwarf shoot. This is just as one would expect in a form which was transitional between deciduous leaves and deciduous shoots.

4. *Taxites*

An interesting species, which Seward (81) says was first described by Nathorst as *Taxites longifolius*, shows an association of flattened and elongated leaves with scale-covered dwarf shoots. The leaves were from one to five or more millimeters in breadth and were borne in fascicles of eight or more. Such plants have been found at numerous widely separated points. Leaves of this type may be looked upon as hesitating between the abandonment of blades and the establishment of zonal meristems.

5. *Pityophyllum*

Seward (81, p. 380) says:

This name [*Pityophyllum*] is applied to detached leaves of needle-like form like those of recent pines, or to long linear leaves broader and flatter than the needles of *Pinus*. Some of the specimens referred to this genus are very similar to the leaves of *Keteleeria*. In a few cases the leaves are still attached to a dwarf shoot, but usually they occur as detached specimens. The genus is met with in Rhaetic strata but is especially abundant in Jurassic floras and persists through Cretaceous and Tertiary rocks. The leaves generally described under this generic term are broader and flatter than such leaves as those of *Pityites Solmsi* and recent Pines, and the presence of a fine transverse wrinkling on the lamina is a characteristic feature. *Pityophyllum* is employed for both the narrower and broader forms, and includes specimens which in all probability belong to Coniferes of more than one family. Some are certainly Abietaceous but the flatter and broader forms bear a closer resemblance to the leaves of some species of *Podocarpus*.

6. *Modern Relatives*

The morphology of the dwarf shoots of *Cedrus*, *Larix*, and *Pseudolarix* is comparatively simple and well understood. The situation in *Taxodium*, however, is more complex. Here the portion of the dwarf shoot which is homologous to the dwarf shoot of pines is partly imbedded and may be exposed by stripping away the bark (Fig. 20). These dwarf shoots branch repeatedly from lateral buds which occur at the base of the current growth (Fig. 21).

The resulting deciduous shoots are homologous to a proliferated dwarf shoot of pine and not to the ordinary dwarf shoots as interpreted by Bernard (6). It is as if the dwarf shoot of pines should produce a lateral bud in the axil of one or both of the lateral scales and then form the absciss layer just distal to this point, later imbedding this basal remnant with its bud in the cortex of the primary branch. The following spring the lateral bud again repeats the process. Such behavior on the part of *Taxodium* accounts for the yearly crop of deciduous branches, while the production of more than one lateral bud leads to branching of the dwarf shoot and eventually to the tufts of deciduous twigs which are so characteristic of the old branches of members of this genus.

If *Sequoia* and related plants have abandoned regular annual branch-fall in favor of a more or less continuous branch-fall as hinted at by Bernard (6), it may be that in such plants the homologue of the dwarf shoot now lies imbedded at the base of the lateral branches. It is conceivable that this has been one of the ways by which the dwarf shoot has been eliminated from some members of *Pinaceae*.

These findings are difficult of exact interpretation; but for our purpose it is sufficient to point out that the forms which were characteristic of Jurassic and Cretaceous time and which persisted through the

Tertiary had leaves and dwarf shoots, each of a type through which those of modern pines must, of necessity, have evolved.

The sum of these findings calls to our attention forms with large and indefinite numbers of scales as well as large and indefinite numbers of functional leaves on the dwarf shoots, forms with indifferently deciduous leaves, with indifferently bladed leaves, with indifferently developed zonal meristems, with fascicle sheath scales serving partly developed supporting functions, dwarf shoots with partly suppressed growing points, tufts of functional leaves which approach the whorled condition, and flattened fascicled leaves unshaped by sheath pressures. Plants with these features grew side by side with others which, at this early period, had evolved characters that we now associate with the most advanced of modern pines. In short, the fossil record when combined with the better-known story of the short shoots of modern forms presents a fragmentary but readable history of the evolution of the dwarf shoots of *Pinus*.

VI. EVOLUTION OF THE VEGETATIVE DWARF SHOOT AND ITS FOLIAR ORGANS

A. LITERATURE

In treating the gymnosperms as a whole, Coulter and Chamberlain (22, p. 406), under the heading of "Evolutionary Tendencies among Gymnosperms," call attention to the fact that, "A general tendency expresses itself throughout a great group, and has to do with the transition from ancient to modern forms, rather than with the breaking up of the group into several phylogenetic lines." Certain of the tendencies to which they have called attention need be mentioned here. Their conclusion in regard to "the most obvious tendency to reduce the cotyledons to the fixed number two" has been mentioned earlier in this paper.

In discussing the tendencies of the leaf, Coulter and Chamberlain say:

It seems clear that the most ancient gymnosperms were large-leaved forms, from which the small-leaved conifers were derived and yet small-leaved pteridophytes may have been more ancient than large-leaved ones. If this be true, the appearance of small leaves among conifers is the reappearance of an ancient feature and not its retention.

Coulter and Chamberlain make no mention of internodal shortening as a general tendency, and yet this change must have accompanied the transition from macrophyly to the microphyly. Large-bladed leaves on short crowded nodes such as we find on modern pines is inconceivable. In order to prevent light interference, bladed leaves on dwarf shoots require long petioles as in *Ginkgo*. Indeed, Fankhauser (33) found a close similarity between the anatomical structure of the petiole of *Ginkgo* and

the leaf of pines. Masters (57) thinks that pine needles represent the petiolar remnant of such a leaf. The macrophyllous leaves of *Ginkgo* necessitate a sparse distribution of the dwarf shoots along the twigs (Fig. 24 B and C). These are often more than 100 times as far apart as the dwarf shoots of pines. Whether the extreme internodal shortening in the ancestry of *Pinus* occurred during or after the acquisition of microphyly is a debatable point, but it is certain that the short internodes did not precede the loss of broad blades.

Additional quotations from Coulter and Chamberlain are advisable:

The leaves of gymnosperms may be used to illustrate a structure that exhibits no general evolutionary tendency, but responds more or less directly to the conditions of living. The most ancient gymnosperms possessed ample, fernlike leaves, and under appropriate conditions this type of leaf persisted, as in the tropical cycads of today. The conifers, however, have developed a very different type of leaf, one that was well under way among the Cordaitales, and which reaches an extreme expression in small and rigid needles or conrescent scales. . . .

It would be interesting to know the conditions in which needles and conrescent disks were established: but in the absence of any such knowledge, the sharply contrasted geographical distribution of Cycadales and Coniferales may suggest that the conditions of change were associated with the evolution of the land areas and of the climate of temperate regions.

Because of the close relationship between the various components of a stem unit, it is preferable to treat the evolution of the foliar and the corresponding internodal component together. In the light of evidences already cited, an attempt is made to outline the steps as we interpret them.

B. STEPS IN THE EVOLUTION OF THE DWARF SHOOT AND FUNCTIONAL LEAVES

1. Before the advent of branch dimorphism the forerunners of the dwarf shoots must have been simply the leafy secondary branches (Fig. 29 a). Since these were in no way different from the long shoots, the production of simple buds as described for them applied also to the laterals, thus crowding the first year's growth of the lateral shoots into simple, scale-covered, axillary buds (Fig. 29 c). Upon extension these at first must have made ordinary long shoots.

2. Further shortening involved units other than those bearing bud scales and produced a dwarf shoot with shortened annual growths (Fig. 29 f). At this level in dwarf shoot evolution, the possibility of becoming a long shoot likely depended upon position as in *Larix* and some other modern forms. The most distal branches were favored, and they alone had the opportunity to grow into shoots of unlimited growth. The remaining shoots were miniature replicas of their more favored fellows. In such crowded positions the leaves, in order to prevent light in-

terference, must have been either linear as in *Cedrus* or else lifted on long petioles as in *Ginkgo*. A reduction or loss of blades, therefore, probably paralleled this early development of the dwarf shoot. From this point the evolution of the dwarf shoot seems to have followed more than one course. We shall concern ourselves only with that leading to *Pinus*.

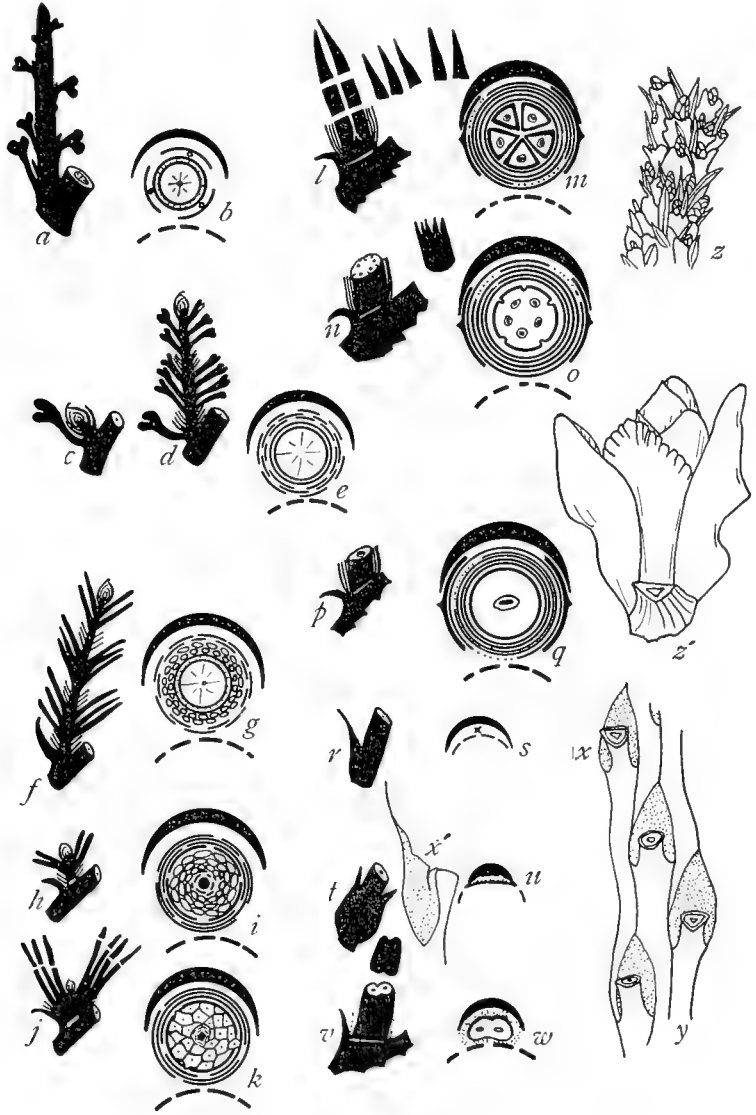


FIG. 29.—Diagrams showing the author's conception of the chief steps in the evolution of the dwarf shoot.
(See explanation on opposite page.)

3. Further shortening crowded the leaves, even after extension of their short internodes, back within the cup (forerunner of the sheath) formed by the old bud scales. This protected the leaf bases from mechanical and insect injury, and from drying, thus permitting the basal cells to remain tender and meristematic. The acquisition of zonal meristems gave the power of continued growth, thus permitting an adjustment of needle size to the season. This overcame the handicap imposed by the acquisition of compound buds, for in these the number of units for a given season is unchangeably fixed during the season prior to their functioning, so that the leaf number cannot be adjusted to later changes in climatic conditions. With the advent of basal meristems it became possible to limit or to increase the photosynthetic area without changing the leaf number.

Crowding of the leaves within the cup or sheath limited tip growth of the dwarf shoot to a single annual growth; consequently these shoots soon fell behind and were shaded off. Branch-fall came to have survival value, and the deciduous habit became fixed. With the establishment of branch-fall, it became poor economy to store much food in the dwarf

Explanation of Fig. 29

- | | |
|---|--|
| a. Hypothetical early ancestor with monomorphic branches and monomorphic leaves. | o. Same in transverse section. |
| b. Section of the same showing subtending leaf in black and the position of the primary stem in a broken arc. | p. Dwarf shoot of <i>Pinus cembroides</i> var. <i>monophylla</i> . |
| c. Simple axillary bud. | q. Same in transverse section. |
| d. Lateral branch showing well-marked annual growth. | r. Simple sterile leaf as in <i>Larix</i> . |
| e. Transverse section of same showing bud scales surrounding the stem. | s. Transverse section of same showing sterile axil. |
| f. Twig similar to <i>d</i> , but with leaves crowded and blades lost. | t. Concretescent scale leaf as in <i>Cupressus</i> . |
| g. Transverse section of same showing leaf bases within the circle of bud scales. | u. Transverse section of same. |
| h. Twig similar to <i>f</i> , but further shortened and deciduous (white line represents absciss layer). | v. Dwarf shoot of <i>Sciadopitys</i> showing loss of sheath and fusion of needles. |
| i. Transverse section of same showing sheath scales specialized for support. | w. Transverse section of the same. |
| j. Twig similar to <i>h</i> , but further shortened. | x and x'. Exterior and sectional view of a reduced axillary seed scale on a proliferated shoot from the cone of <i>Abies</i> (after Willkomm). The tissues of the reduced scale render the base of the leaf concretescent. |
| k. Transverse section of the same showing crowded angular leaves and reduced interfoliar bud. | y. Proliferated shoot from cone of <i>Abies</i> (after Willkomm). |
| l. Dwarf shoot of <i>Pinus</i> . | z. Portion of a twig similar to <i>y</i> except the seed scales are well developed and each bears a bud at the tip (after Willkomm). |
| m. Same in transverse section. | z'. Single unit from <i>z</i> but more highly magnified (after Willkomm). |
| n. Dwarf shoot of <i>Pinus</i> with fused needles. | |

shoots or to use materials in the construction of woody parts soon to be lost. Further elongation of the leaves at the expense of the shoot was the natural consequence. The tendencies toward leaf extension and shoot shortening were thus accentuated.

It is extremely unlikely that these early dwarf shoots acquired at once any of the highly specialized features such as perforated scales or whorled leaves. For this reason we would postulate for this stage in the evolution of the dwarf shoot, a short, weakly, deciduous branch whose basal bud scales supported several close spirals of leaves of the typical conifer type and whose tip formed a poorly developed scale-covered bud for the following year's growth. To put the case in other terms, this stage in the evolution of the dwarf shoot was approaching the *Prepinus* level (Fig. 29 j and k).

4. We have only to assume the continued shortening of internodes in order to arrive at the condition found in *Prepinus statencensis*. Here the deciduous habit was well established and the interfoliar bud reduced and crowded out of shape. The sheath scales were highly specialized and evidently exerted sufficient pressure upon the enclosed leaves to shape these to the cylindrical space within the sheath.

5. The compound winter bud on the long shoot had several far-reaching effects upon the dwarf shoots which in their early stages came to be enclosed within it. This enclosure relieved the scales of the dwarf shoot of the work of meristematic protection, this function having now been taken over by the primary (subtending) leaves. The scales on the dwarf shoot were thus left free to exercise their newly acquired function of leaf support. Hooding, fraying, perforation, zonal growth, and the various means for shedding the sheath now came as adaptations to the supporting function. The young buds for the dwarf shoots were crowded together within the compound bud, where competition for space was keen. Growth pressures were exerted upon the meristematic secondary shoots; their proximal scales (lateral and central scales) were displaced and flattened, and certain leaf arrangements were favored.

6. The delay which was responsible for the compound winter bud necessitated the almost simultaneous extension of the main twig, of all the dwarf shoots, and of the leaves. This in turn necessitated the formation of all these structures out of stored foods. The limited amount of growth possible from this source tended to shorten still further the internodes on the primary axis, to bring the dwarf shoots into interference with each other, and to put an additional premium upon a long-continued growth of the needles.

7. Further specialization of the sheath scales, especially the advent of perforation, increased the binding efficiency of these organs. The

leaves were crowded and their corresponding internodes shortened to extinction, and the needles were brought into the cyclic position. The cyclic arrangement necessitated a limitation of leaf number to harmonize with the phyllotaxy, and dwarf shoots with five needles or with some small multiple of five needles were favored. The acquisition of these features together with a continuation of the reduction of the interfoliar bud marked the advent of the true pines (Fig. 29 l and m).

On occasional dwarf shoots in nearly all pines and in the so-called monophyllous varieties in several species, meristematic recession involves all the leaves in a common upward growth, producing a single structure from the welding or cohesion of several leaves (Fig. 29 n and o). This carries the evolution one step beyond that attained by the group as a whole. With reference to its tip meristem and functional leaves, at least one related form, *Sciadopitys*, became stabilized at this level. In this genus an additional reducing step has been taken, for *Sciadopitys* has eliminated the scales of the fascicle sheath.

8. In some respects one variety (*monophylla*) of *P. cembroides* carries the reductions beyond the point attained in *Sciadopitys*. Here the recession involves the incorporation of extra leaves into a single functional one with but a vascular vestige of the other contributing member. Thus is produced the most highly specialized condition found in the vegetative dwarf shoots of any modern pine (Fig. 25 A; Fig. 29 p and q). The sheath, although still present in *monophylla*, is here reduced in number of parts and in complexity of scales.

9. There is some evidence in support of the view that shoot reduction has at some time in the past gone far beyond the point now found in either *Sciadopitys* or in *P. cembroides* var. *monophylla*. The reduction of dwarf shoots to the point of extinction is not inconceivable. If this has been the course of evolution, we should not be surprised to find fossil plants with pine-like characters but with extremely reduced phylloclads in the axils of simple leaves, or simply a proliferation of axillary tissue to produce an adhesion of leaf and stem. Following the production of such a reduced structure, the next step would be the complete loss of the axillary outgrowth. Thus by the complete elimination of dwarf shoots, pine-like ancestors may have given rise to other genera such as are now described as having monomorphic branches (Fig. 29 r, s, t, and u).

C. EVOLUTION OF THE LEAF MERISTEMS

The important steps in the phylogeny of leaf meristems which we find in pines appear to have been as follows:

1. Apical as in ferns (Fig. 27 a, b, and c). Buchholz (15) has shown that this condition is still retained in the early embryos of pines.

2. Grouped or general as in most simple leaves.
3. Basal as in the needle leaves of pines (Fig. 27 g and i).
4. Sub-basal as in *P. cembroides* var. *monophylla*, in fused pine needles, and in the seed scales (Fig. 27 j to x).

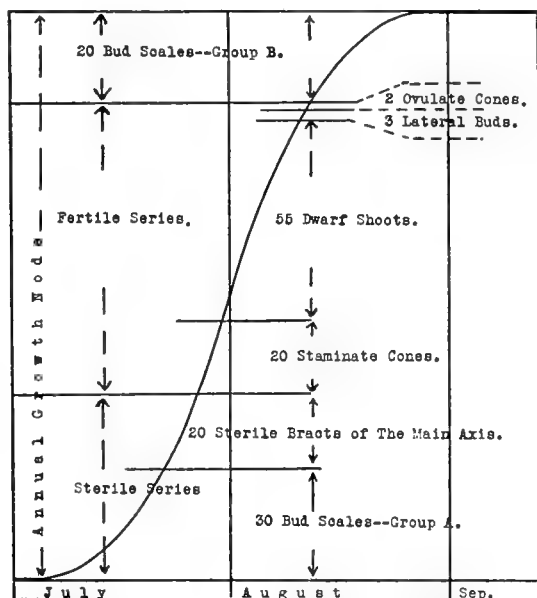


FIG. 30.—Annual curve of deposit of units on the long axis.

VII. THE OVULATE DWARF SHOOT, OR SEED SCALE

A. VOLTZIA AND THE PRIMITIVE TYPE OF SEED SCALE

Numerous fossils have been described which throw some light upon the structure of the primitive abietineous cone scale, but our discussion will be confined to the single excellently preserved specimen of *Voltzia Liebeana* which Walton (100) figured (Fig. 32, parts 4 and 5) and described in 1929.

Voltzia was obviously a conifer, the seed scale of which was woody, flattened, multisporophyllate, and transitional between the greatly reduced seed scales of modern conifers and the simple strobili (Fig. 32, parts 1 and 2) out of which the scales of both *Voltzia* and modern conifers must have evolved.

On Walton's specimen the leaf-like cover scale was unmistakably present. The constituent sporophylls of the branch-like seed scale were five in number. The first pair were opposite each other, and in both shape and position resembled the lateral scales of the vegetative dwarf shoot. Although somewhat crescent-shaped in cross section (Fig. 32 *cs*), these lateral sporophylls had their seed-bearing surfaces turned away from the cover scale and toward the axis of the compound strobilus of which they were originally a part.

The individual sporophylls each bore a single seed, which is the exact number found on the sporophylls* of members of both the *Abietineae* and *Araucarineae*.

The central sporophyll of *Voltsia* occupied a position exactly corresponding to that of the central scale on the vegetative dwarf shoot of *Pinus*. It was more flattened than the lateral sporophylls and was not folded, a fact which shows that the direction of pressure was along the axial plane. The apex of the central sporophyll was directed upward. The long axis, while lying in the axial plane, paralleled that of the main axis of the compound strobilus. If the central sporophyll had an opposing mate on the cover-scale-side of the axis, this was so much reduced that it remained hidden by the cover scale.

The two sporophylls that remained were flattened, sterile, and laterally placed. They occupied the concavities formed by the folding of the lateral sporophylls.

During fossilization of Walton's specimen, the growing point of the scale was hidden in such a way that the presence of a terminal-bud-vestige was left uncertain. Our experience with dwarf shoots in general and with cone scales in particular leads us to believe that a terminal bud of some kind must have been present. Reason demands the presence of such a growing point, at least during the early stages, for we cannot conceive of the presence of five well-developed foliar organs without assuming an axis out of which their early primordia were developed. We have a choice, then, of assuming the presence of an axis on the mature scale or its absence due to incorporation during the development of the scale.

With this brief description we shall leave *Voltsia* for the moment and return to it in connection with the treatment of the evolution of the cone scale of conifers in general.

B. DEVELOPMENTAL MORPHOLOGY OF THE NORMAL SEED SCALE

The early developmental stages of the seed scale are amply treated by Strasburger (87, Plate V) who makes a comparative study of them as

*The morphological sporophyll is here referred to. It is not to be confused with the seed scales.

seen in many conifers. He, from a study of the normal anatomy and development, arrives at the brachyblast interpretation of the seed scale.

In the present work the similarities between the early stages in the development of the dwarf shoot and the corresponding stages in the development of the cone scales were found to be striking (Fig. 22). The bract or cover scale for the latter, as pointed out by Strasburger (83), is without question homologous to the subtending scale of the former. Both give rise to axillary outgrowths (Fig. 22 A and F) which, because they grow from the axils of homologous organs, are themselves homologous. In both cases these axillary outgrowths in their turn give rise to a pair of simultaneously appearing lateral primordia (Fig. 22 B and G) which, by the same rule, are homologous. In other words, *the megasporophyll of the seed scale is homologous to the lateral scales of the fascicle sheath.*

The primordia for the lateral megasporophylls are more robust and appear earlier in the ontogeny of the axillary outgrowth than do the lateral scales of the fascicle sheath (Fig. 22 B and G). In *Pinus*, simultaneous meristematic activity in all three primordia of the cone scale lifts the triple-pointed structure upward until the center member finally ceases meristematic activity and matures all its tissue, thus becoming the apophysis (Fig. 22 H and I).

The lateral sporophyll primordia differentiate vascular strands and become the two flattened lateral extensions of the seed scale, and each bears a single ovule. The three fused structures collectively make up the seed scale (Fig. 28 g and f).

Since in its early stages the median member resembles the growing point of the dwarf shoot, Strasburger interpreted it as the axis of the dwarf shoot. The unquestioned presence of this structure demands that, regardless of whether it be interpreted as a true axis or as a third sporophyll or as some other structure, some disposition be made of it; for, while differentiating its own vascular supply, it becomes welded in as an integral part of the connate seed scale. The question yet to be settled, however, is whether the primordium and the vascular strand subsequently differentiated represent vestiges of a foliar or an axial structure. Discussion of this point will be deferred until all contributing evidences have been presented.

C. ABNORMALITIES OF BISPORANGIATE CONES

Ordinarily the cones of members of the *Abietineae* are monosporangiate, but numerous descriptions of exceptions may be found in the literature. Stenzel (86) found on one occasion in *Picea excelsa* Link:

. . . . androgynous cones, in which the male organs usually occupied the base and the female the upper part; more rarely were the male scattered amongst the

female; and still more rarely did the male form a middle zone with female above and below. Some of the bracts bore pollen-sacs.

Miss Holmes (44) describes, in one of the latest articles on this subject, a bisporangiate cone of *Tsuga canadensis* which was without transitional scales. She gives a partial summary of the literature dealing with the subject and points out the fact that similar cones have been found in most abietineous genera.

In the spring of 1932, the present writer discovered seven bisporangiate cones of *Larix europea*, most of which showed scales of various transitional and deformed types. These were carefully removed in order from the base of the cone upward, and a serial record was made of the characters of each scale.

Although bisporangiate cones in this species are not new (Bartlett, 4), it was hoped that the series of transitional scales would reveal some evidences of the morphology of the abietineous seed scale. When the scale records for the individual cones were arranged in parallel, certain very suggestive trends were apparent. Before this material could be assembled for publication, hundreds of bisporangiate cones of *Pinus toyosho* (Fig. 14) and two cones of *P. Laricio* were discovered.

After numerous specimens of the pine material had been examined and serial records of the transitional scales on each had been made, most of the scales were observed to fall naturally into the classes which had already been made for *Larix*. The same general trends were observed here as were recorded for that genus.

The following description will be clearer if the reader will refer frequently to the series of accompanying diagrams (Fig. 28). In most cases scales of the following types were found on each cone examined and in approximately the order given:

1. At the base there were the usual involucre bracts which on normal pollen-producing cones precede the microsporophylls. In *Larix* these are green and in appearance closely approach the functional leaves (Fig. 24 G; Fig. 28 a).

2. Next in series followed the normal microsporophylls with their characteristic paired and abaxial pollen sacs (Fig. 28 b and b').

3. As the region of transition was approached, there was a strong tendency toward reduction and final disappearance of one of the pollen sacs while the remaining one tended to assume a median position (Fig. 28 c and c').

4. At about this level the pollen sacs began to produce rudimentary micropylar apparatus (Fig. 28 d) and otherwise to assume the appearance of ovules, while various aborted structures began to appear in the axils of the microsporophylls.

Above this level the behavior became far more erratic. Every conceivable type and combination of abnormal cover scale and seed scale were found. Some types appeared but once, and many others could not be fitted into any series. Most of the types, however, fitted into the regular series and were repeated on cone after cone.

Continuing our description of the regularly recurring types we have:

5. Nearly normal microsporophylls bearing micropylar apparatus on each sporangium and with rudimentary seed scales in the axils of the sporophylls, as shown in Fig. 28 (d), except with two microsporangia instead of one.

6. Cover scales with bladed portions similar to those appearing on the microsporophylls and at the same time bearing single median ovules on their abaxial surfaces and normal seed scales in their axils.

7. Leaf-like cover scales with two-lobed fleshy sterile seed scales in their axils.

8. Leaf-like cover scales with axillary structures consisting of fleshy seed scales divided to their bases (Fig. 28 g).

9. Forms similar to those described above (paragraph 8) but with the median member obviously welded into one of the members of the divided scale.

10. Forms similar to those described above (paragraph 8) but with blade-like expansions on some of the constituent megasporophylls.

11. Normal-appearing seed scales, the ovuloid structures of which were full of pollen.

12. Cover scales which in color and texture were identical with the seed scales and in some cases bore normal-appearing ovules on their abaxial surface. In one case the cover scale was so much like the two members which constituted the seed scale that had it not been for the point of the apophysis, it would have been impossible to determine which pair in the trio belonged to the seed scale. In other words, the cover scale was in the latter case transformed into a normal megasporophyll.

13. Finally the transitional zone and irregular structures gave way to normal cover scales which bore normal seed scales in their axils (Fig. 28 f). From this point to its apex, the cone was then, as a rule, normally ovulate.

The general impression gained from this array of material is that during the period of deposit of cone units, some physiological upset reversed the trend of development. Sporophylls which ordinarily would have produced two microsporangia began by stages to approach the megasporophylls in texture, in product, and in number of sporangia, and during the course of transition produced every conceivable transitional form. If, as suggested by Fujii (36), the sporophylls are at first indifferent as to type and their course is later determined by nutritional con-

ditions, the present observations are just as would be expected of a series of sporophylls formed during a period of nutritional change.

From the standpoint of the interpretation of the seed scale, it is significant that the number of sporangia per sporophyll becomes reduced to one, and that this assumes a median position at the same time that the microsporangium is acquiring micropylar apparatus and other characters ordinarily associated with ovules. The inference seems clear: the microsporophyll in *Pinus* has a pair of sporangia, while the megasporophyll has but a single sporangium. This is further attested by the presence of but a single ovule on the abaxial side of those cover scales which assume the color and texture of the seed scale. This is especially noteworthy since these cover scales were in direct series with normal microsporophylls and they in turn with leaf-like involucre bracts.

It is also significant that, at a stage during which the megasporophylls that ordinarily fuse to form the seed scale are remaining free from each other, many of them develop expanded blade-like tips, indicative of their foliar nature.

Of further significance is the fact that various constituents, which ordinarily fuse to make the seed scale, can be found as single, double, or triple rudimentary elevations, and that only two of these bear ovules.

If only one ovule is present, the point of the apophysis can usually be seen fused against the side of the unilateral scale as would be expected if one of the sporophylls had failed while the other had in the usual way become fused with the median member. If two ovules are present, they are on a scale that approaches the normal, i.e., double-pointed and flattened, or else they are on the divided halves of such a scale—indicating that the sporophylls normally fuse, but at times fail to do so.

Occasionally these divided scales have between them at their bases a third rudiment, which, with reference to the cover scale, occupies a position approaching the axillary. Since in no case this central structure bore either an ovule or a bud, the material afforded no direct evidence as to whether the central structure represented the shoot axis as proposed by Strasburger or a third and sterilized sporophyll as proposed by Celakovský. The position of this structure could not be used to argue alone for its cauline nature; for, as will be shown later, this argues equally as strongly for its sporophyll nature.

From the sum of the evidence certain facts seem indisputable. It is clear that in *Pinus* there are three parts which normally fuse to make the seed scale. Of these, the two lateral members normally bear one ovule each.* The third or median member normally makes the apophysis.

*The fact that one ovule per sporophyll seems to be normal for *Pinus* does not preclude the possibility that some members of the *Pinaceae* may have sporophylls which are multiovulate; otherwise we would have to assume an incredibly large number of sporophylls in the scales of such forms as *Sequoia* and *Cupressus*.

It is sterile, axillary in position, and therefore represents either an axis or a sterilized central sporophyll. The cover scale is foliar and is homologous to the microsporophyll; it may or may not be involved in the fusion of parts. The ovulate cone, as this evidence testifies, is a compound structure; and the seed scale is, therefore, a modified short shoot, or brachyblast.

D. ABNORMALITIES OF MONOSPORANGIATE AND PROLIFERATED CONES

It is remarkable how other teratological forms of an entirely different nature from those summarized above force us to similar conclusions with regard to the nature of the seed scale. I refer to what is commonly called proliferated cone scales. The persuasive power of these structures is well illustrated by the fact that Willkomm (102), despite his previous adherence to the placentation theory of Schleiden and of Sachs, from a study of proliferated cones of *Abies*, came to agree with the brachyblast interpretation. Botanists in general have tended to adopt this view, and in numerous instances it has been such proliferated cones which provided convincing evidence of the correctness of the theory. The literature list of such proliferated cones is a long one. It includes the following:

- Parlatore—*Pinus Lemoniana* (68).
 Oersted—*Picea* ? *Larix* sp., *Pinus montana* (67).
 Sperk—*Cunninghamia*, *Cupressus lusitanica* (85).
 Stenzel—*Picea excelsa*, *P. alba*, *Tsuga Brunoniana* (86).
 Willkomm—*Picea excelsa* (102).
 Velenovský—*Larix* (97).
 Caspary—*Spruce* (19).
 Celakovský—*Spruce* sp. ? (21).
 Noll—*Larix* sp. ? (66).
 Engelmann—*Sequoia*.
 Braun—*Taxodium*, *Cryptomaria*, *Glyptostrobus* (11).

In spite of this array of evidence, not all modern botanists agree upon the brachyblast interpretation of the seed scale. Jeffrey (46), for example, apparently considers the evidence inadequate. He says (p. 337):

The view sometimes advanced that the ovuliferous scale in the Abietineae consists of a fused pair of foliar structures has apparently no evidence in its favor. It is as clearly a single leaf as is the microsporophyll.

The axillary structures which Willkomm (102) found on proliferated cones of *Abies* may be taken as representative (Fig. 19 z and z') of the scales on proliferated cones in general. This material and that found on my own bisporangiate cones of *P. tonyosho* are supplementary, for while

the former shows transitional stages between foliage leaves and cover scales, between cover scales and microsporophylls, and between microsporophylls and megasporophylls, the latter shows transitional stages between the sporophylls and true leaves and between the apophysis and the central constituent of the scale (Fig. 28 e and h).

In order to weld every link in this chain of metamorphosis from leaves through bracts, microsporophylls, and megasporophylls finally to the welded scale, it is only necessary to review the marvelous array of structures described by the workers cited above. A complete review of all the tell-tale individuals in the perfectly blending series is out of the question. We must be content with a partial description of a few representative specimens. The descriptions are taken largely from Worsdell's (104) excellent summary of this subject. He says:

In 1876 Stenzel described a cone in which in the axil of the bract a leafy bud arose, whose first two leaves were harder and browner and more erect than those of the ordinary vegetative shoot, and resembled more the seminiferous scale; they were directed somewhat towards the axis; the following pair of leaves were median, anterior and posterior [Fig. 32, pt. 20]. No ovules were to be seen. The pair of larger first leaves were often fused with the small leaves of the bud. He [Stenzel] concludes that 'the seminiferous scale of the Spruces consists of the first two leaves of an otherwise undeveloped branch arising in the axil of the bract, these leaves being fused by their posterior margins, and thus having their dorsal side directed towards the axis of the cone, and bearing each on this side an ovule.'

He [Stenzel] also possessed at this time a proliferated cone of *Picea alba*. The buds in the axils of the bracts bore, besides the two seminiferous scales fused by their posterior and gaping at their anterior margins, a posterior and an anterior scale, and one or two inner scales. In some cases the seminiferous scale was so completely fused with the anterior bud-scale as to form a single flat scale as seen from the front, but in reality its posterior margins were represented by two low ridges, visible from the inside, which did not, as in other cases, extend as far as the posterior bud-scale. As regards the characteristic projection or 'Dorn' on the seminiferous scale of *Pinus*, which Strasburger thinks is an axis, it may represent either the place of fusion of the posterior margins of the seminiferous scale, or the posterior bud-scale.

It is significant that this description of a proliferated scale could, with a few minor changes, pass for a description of the scale of *Voltzia*, for the "anterior bud-scale" here referred to is clearly equivalent, not only to the central sporophyll of *Voltzia*, but to the whole series of anterior structures shown as S' in the sketches comprising Fig. 32. The presence of "one or two inner scales" makes the resemblance to *Voltzia* almost complete.

The same kind of sports as those in *Picea* occur in *Tsuga Brunouiana*. In the latter plant, the posterior bud-scale is often as well developed as the anterior one, so that the parts of the bud all come to be united laterally into a woody structure. The axis of the bud is often more elongated into a leafy shoot.

Here again we have parts similar to those in *Voltzia* but with a pos-

terior mate for the central scale and with a well-developed terminal bud for the brachyblast.

Casparry and Oersted found cones of more than one genus which in many respects were like the bisporangiate cones of *P. tonkysho*, described earlier in this paper. Many of their cones, however, had additional developments in the form of buds on some of the central members. They thus furnished convincing evidence of the branch nature of such scales.

In the proliferated *Sciadopitys* cones described by Masters, the seed scales were replaced by the regular double needles which are generally admitted to be brachyblasts. Masters concludes: "Whatever be the nature of the so-called leaf of *Sciadopitys* [Fig. 32, part 15], it must be essentially the same as that of the seed scale of *Abietinae*."

Velenovský in 1888 described a cone of *Larix* on which one axillary bud "bore ovules on the lower surface of all its leaves" (Fig. 32, parts 1 and 2).

Certainly such proliferated scales, by the very frequency of their occurrence, argue strongly for the brachyblast interpretation of the abietineous cone. Of this, Celakovský seems to have been fully aware. In this connection, Worsdell quotes him as follows:

In the *Abietinae* the seminiferous scale is "a symphyllodial structure, consisting of three fused appendages (two in *Picea*) of an axis, of which the two lateral are fertile carpels (reduced to sporangia) fused together to form the 'crista' of the seminiferous scale, while the third median leaf—the median knob of the first rudiment—remains sterile, and either aborts or, fused with the two other fertile carpels, forms the keel and mucro (in *Pinus*)."

This view has not been given the attention that it deserves; for, if the "anterior bud-leaf" mentioned by Velenovský is a constituent of the normal seed scale, it follows that the middle member of the three primordia on the young cone scale (Fig. 22 G) is not the primordium for the axis but rather the primordium for the central sporophyll. The growing point of the axis either has been completely suppressed or is incorporated into the central sporophyll.

There are some who, in spite of the frequent recurrence of these atavistic forms and the regularity of arrangement of their parts, still hold that such structures are meaningless abnormalities. This view is hardly tenable, for structures which occur regularly on plants of many genera and yet maintain a more or less constant form can hardly be called monstrosities, especially when early fossil forms like *Voltzia Liegeana* bring direct evidence to support the view that the observed forms represent true reversions. Careful comparison with *Voltzia* causes the doubt regarding the meaning of separated multifoliate parts of the seed scale to disappear, and the presence of buds and branches at the tips of the cone scales to become fraught with evolutionary meaning.

E. VASCULAR SUPPLY AND THE SCALE OF ARAUCARIA

In summarizing her description of the vascular supply to the cone units of *Pinus*, Aase says, "In all cases four bundles result, the lower supplying the bract [cover scale], the remaining three the scale [seed scale]." In similar terms we might summarize Aase's findings with reference to *Araucaria* by saying that, in all cases four bundles result, the lower three supplying the bract, the remaining one the scale (Fig. 23 Q to V). If the four bundles are homologous throughout, it simply means that in *Araucaria* the two lateral sporophylls instead of the central one have been sterilized, reduced, and welded into the scale. In keeping with the greatly exaggerated size of the cover scale in *Araucaria*, the lateral scales, although fused with a common structure consisting of four parts, apparently derive their vascular supply from the sides of the bundle leading to the cover scale (Fig. 23 U, V, and W).

With the idea that the functional sporophyll in *Araucaria* represents the central sporophyll, Celakovský would agree, but not to the welding in of the lateral sporophylls. Worsdell says of Celakovský's opinion in this matter: "In the Araucarieae where the seminiferous scale, bearing a single ovule, is obviously not a compound but a single organ, *the scale consists solely of the leaf* or its sporangial representative, the first leaf pair of the axillary bud being entirely absent."

Eames (28) in 1913, in a paper on *Agathis*, summarized the seed scale situation in general and concludes that, in origin, it is compound in all Coniferales; with reference to the group under special investigation he says, "Even within themselves the Araucarineae show a complete series from a form with strobilar units of a distinctly double nature to one most simple through reduction."

Sinnott (83) is of the opinion that both podocarps and araucarians have evolved from ancient abietinean stock and that the epimatium of podocarps, the ligule of araucarians, and the scale of Abietineae are all homologous structures and vestiges of axillary shoots. He thinks the simple scale of the podocarps has arisen either from the fusion of the two constituents of the abietinean scale or by the abortion of one of them. This derivation of the araucarian scale and of its one functional sporophyll component is not the same as that suggested by Celakovský; for to derive the single functional sporophyll directly from a *Voltzia-like* ancestor by sterilization of the lateral sporophylls is quite a different thing from deriving first the abietinean type of scale and then, out of this, by further reductions, deriving a simple scale with a single functional sporophyll. Sinnott's interpretation would make the functional sporophyll of *Araucaria* the homologue of one of the lateral sporophylls, while that of Celakovský would make it the homologue of the central scale.

VIII. EVOLUTION OF THE OVULATE DWARF SHOOT, OR SEED SCALE

A. LEADING INTERPRETATIONAL THEORIES

Although a brief restatement of the principal views relative to the morphological interpretation of the cone scale will probably help us to see the significance of the contributions made in the present paper, it would not be profitable for us to discuss in detail the numerous interpretations which have been placed upon this structure, for they are amply treated by Radais (71), Worsdell (105), Coulter and Chamberlain (22), and others.

The leading theories have been:

1. A calyx, Linnaeus (52).
2. An open carpel, Robert Brown (12).
3. A placental or ligular outgrowth from the cover scale, Schleiden (78), Sachs (75), and Willkomm (early works, 101).
4. Two fused leaves of an axillary branch or two leaves fused against the side of the axillary branch, Alex. Braun (11), Von Mohl (98, 99), Strasburger (87 and 88), Willkomm (late works, 102), Velenovský (97), Celakovský (20), Noll (66), Thiselton (89), Saxton (76), and a number of others.
5. The first and only leaf of an aborted axis, Van Tiegheim (96) or a simple axillary megasporophyll, Jeffrey (47).
6. A chalazal outgrowth from the ovules, Bessey (8).

In the formulation of this array of theories, nearly every known branch of botanical science has contributed arguments for or against the various views. The chaotic condition of the whole problem serves to emphasize the fact that the final solution cannot be expected to come from isolated bits of information but rather from the accumulation of evidences from many fields, and by a new evaluation of the old evidences from all fields.

By a careful examination of the list of interpretations given above, it will be seen that following the discovery of gymnospermy (1827) only a small group of workers have interpreted the cover scale as being equivalent to the sporophyll. These may be grouped together, for they would make the seed scale a simple sporophyll and the entire cone a simple strobilus. All the other interpretations would make the cover scale a subtending bract and the entire cone a compound strobilus. In all the theories in the latter group, the seed scale is interpreted as a *secondary axis of limited growth and, therefore, a dwarf shoot* (brachyblast).

The differences between the various interpretations in this group arise in the effort to decide *just how short this ovuliferous short shoot really is.*

Is it so short that the axis fails entirely and only a single sporophyll appears on the spot where the shoot disappeared, or is it just short enough for the true axis to put in its appearance and then produce in turn one, two, or more foliar organs? After all, these are but questions pertaining to the extent of shortening, and the various interpretations, excepting those of Sachs and Bessey, are seen to be not very different one from the other.

Had the various workers proposing these theories observed the comparative ontogeny of seed scale and vegetative dwarf shoot, had they seen an abundance of integrating scales and sporophylls, had they been acquainted with *Voltzia Liebeana* as described by Walton, and had they taken into account the vascular anatomy as described by Aase, Eames, and Sinnott, there is little doubt that all would have been united upon the brachyblast interpretation. None, then, would have felt constrained to

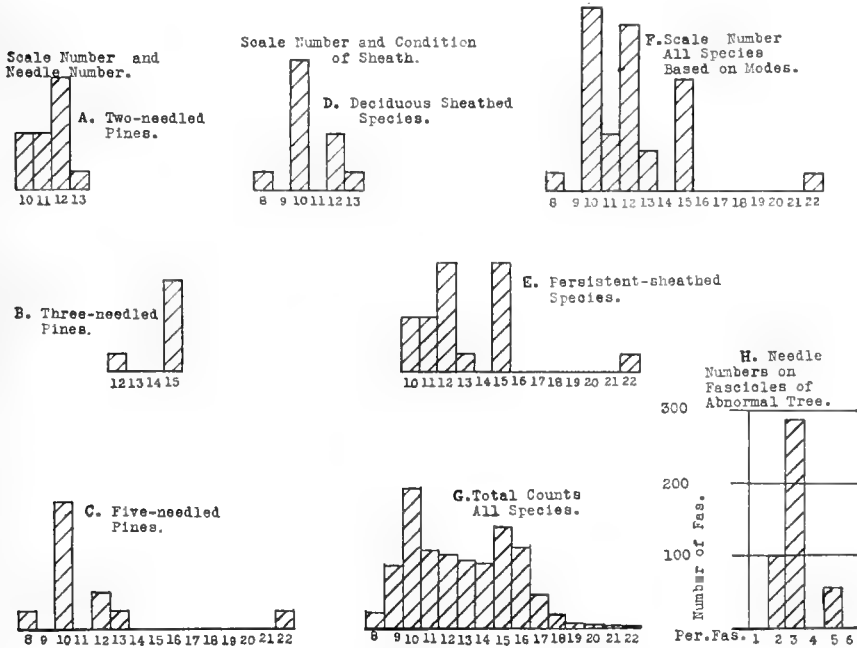


FIG. 31.—Graphs showing fascicle scale numbers in relation to needle number and persistent and deciduous sheaths.

- A. Scale numbers on the fascicles of two-needled pines.
- B. Same for three-needled pines.
- C. Same for five-needled pines.
- D. Scale number on the fascicles of pines with deciduous sheaths.
- E. Same for pines with persistent sheaths.
- F. Scale number on all species based on nodes.
- G. Scale number on all species based on total counts.

defend a set number of sporophylls as having been retained by all conifers, but instead would have been free to admit of variations in number of constituent sporophylls in the seed scale. In *Araucaria* this number is made up of one functional sporophyll with vascular remains of two others; in *Abietinac* it is made up of two functional and a single vestigial sporophyll with frequent reversions to more; in *Voltsia* the number is three functional and two vestigial. The whole range of forms marks out tendencies which point unmistakably to lost forms with a large and indefinite number.

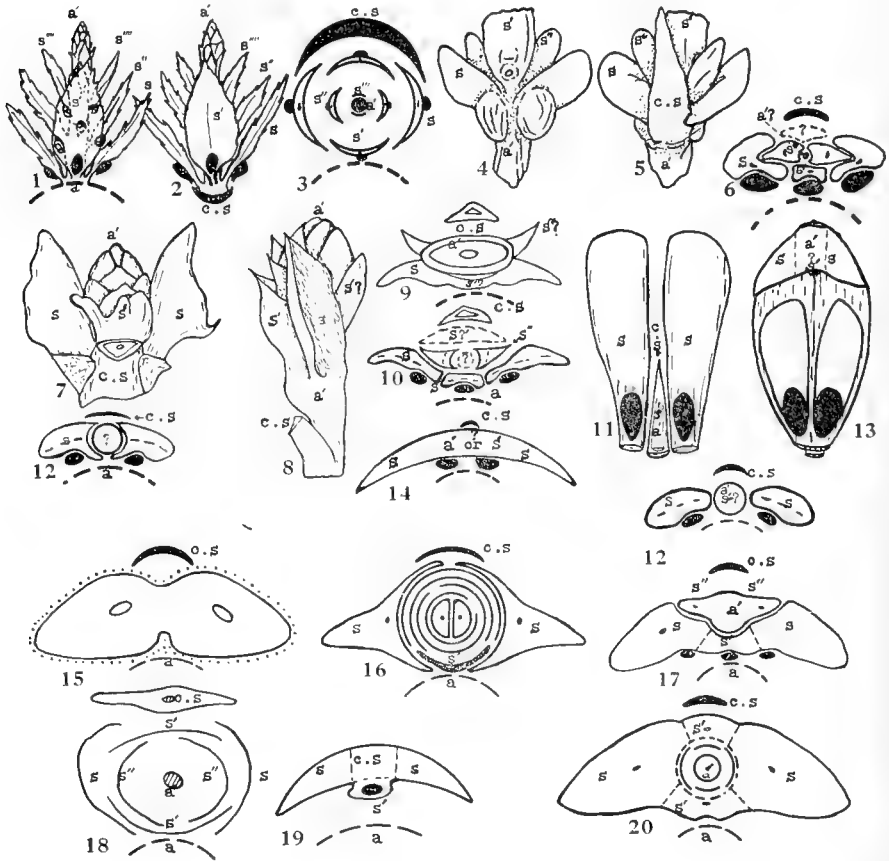


FIG. 32.—The author's conception of the chief steps in the evolution of the cone scale. The lettering throughout is uniform, *a* representing the cone axis and *a'* the axis of the simple strobilus or cone scale, *c.s.* the bract or cover scale, and *s*, *s'*, *s''*, etc., the various sporophylls. (See explanation on opposite page.)

B. SUMMARY OF STEPS IN CONE SCALE EVOLUTION

In order to see how the seed scale may have been phylogenetically produced, one has but to assume a repetition here of processes known to have taken place in other parts of such plants as the pine.

1. The same foliar reduction processes which have for geological ages been operating on the vegetative dwarf shoot of *Pinus* and related forms have operated also upon the ovulate dwarf shoot, reducing its foliar organs (sporophylls) to a single functional pair.

2. The same internodal shortening (to disappearance), which brought cotyledons and functional leaves into cyclic positions, and the lateral scales of the vegetative dwarf shoot into positions opposite each other, has, in an analogous manner, brought the first foliar pair on the ovuliferous dwarf shoot into basal positions directly opposite each other.

3. The same pressure between subtending leaf and main axis which flattened the base of the dwarf shoot and displaced the three most proximal of its attached foliar organs, has here flattened and displaced the sporophylls.

4. The same meristematic recession which involved in a common intercalary growth the adjacent cotyledonary primordia on the embryo, the adjacent leaf primordia on fascicles of fused needles, the adjacent leaf and growing point primordia on the dwarf shoots of *monophylla*, has here again produced a compound ("fused") organ.

5. The same process of incorporation by maturation, which eliminated extra cotyledonary growing points from the embryo, and extra leaves as

Explanation of Fig. 32

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| <p>1 and 2. Front and back views of the hypothetical early simple strobilus.</p> <p>3. Transverse section of the same.</p> <p>4 and 5. Front and back views of <i>Voltzia Liebana</i> G. (redrawn and relabelled from Walton).</p> <p>6. Probable transverse section of same with the shed seed and the axis supplied.</p> <p>7, 8, and 9. Back, side, and sectional views of typical cone scales from the proliferated <i>Abies</i> cones described by Willkomm (redrawn and relabelled from Willkomm).</p> <p>10. Same but with axis reduced, fused parts separated, and with seed supplied.</p> <p>11. Scale of <i>Pinus tonyosho</i> which by the failure of the usual fusions shows the separated constituents of the scale.</p> | <p>12. Transverse section of the same.</p> <p>13. Mature seed scale of <i>Pinus Lambertiana</i>.</p> <p>14. Transverse section of the same.</p> <p>15. Diagram of section through base of the double leaf of <i>Sciadopitys</i> showing the absence of central and lateral scales.</p> <p>16. Diagrammatic section through base of dwarf shoot of <i>Pinus</i>.</p> <p>17. Diagram of Sperk's abnormal scale of <i>Cunninghamia</i> as described by Worsdell.</p> <p>18. Diagram of Caspary's abnormal abietinean scale (relabelled from Worsdell).</p> <p>19. Diagram of araucarian scale.</p> <p>20. Diagram of a scale from Stenzel's abnormal cone of <i>Picea</i> (from his description).</p> |
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well as a superfluous growing point from the dwarf shoots of *P. monophylla*, has here eliminated extra sporophylls and the growing point of the ovulate dwarf shoot.

From forms with numerous widely separated sporophylls displayed in simple strobili, the evolution of the cone scale gave rise to forms with successively shorter and shorter axes and with fewer and fewer sporophylls.

Voltzia with its fertile lateral pair of sporophylls, its fertile central sporophyll, and its sterile vestiges of more distal sporophylls, represents but a step in the shortening and reduction processes.

From *Voltzia*-like forms, evolution followed two lines. In one case, reduction and fusion of parts and the sterilization of the lateral sporophylls gave rise to a single-seeded scale containing but one functional sporophyll which, however, became an integral part of an apparently simple seed scale as in *Araucaria*. This superficially simple seed scale has been derived from the welding of the bract, two sterilized lateral sporophylls, and a functional central sporophyll.

In the line leading to the *Abietinae* the *retention, modification, and welding* of the primary pair or lateral sporophylls together with the sterilization of, and in some cases the loss of, the central sporophyll, gave rise to the scale as we now find it in this group.

C. ADVANTAGES OF THE BRACHYBLAST INTERPRETATION

This view has the following advantages:

1. It is in keeping with the views held by the most careful workers in the field.
2. It brings into harmony many of the apparently conflicting views of previous workers by showing these views correct as far as they go; for in the absence of complete information regarding the details of development, partial interpretations should be regarded as incomplete and not necessarily as incorrect.
3. By this view the two most characteristic structures found in *Pinus*, i.e., the dwarf shoot and the seed scale, become homologous and explainable by the same evolutionary tendencies.
4. It accounts for all the primordia which appear in the axil of the cover scale.
5. It homologizes the microsporophylls and megasporophylls as well as the axes upon which these are borne.
6. It is in agreement with the finding of buds, dwarf shoots, and leafy shoots in the axils of the cover scales and makes intelligible the widespread occurrence and regular form of these structures.
7. It lends meaning to the divided, partly-fused, and triple-pointed scales on bisporangiate and proliferated cones.

8. It derives the abietineous and the araucarian cone scales from a common type and points to known structures to explain the vascular anatomy of both.

9. It makes intelligible the finding of single ovules on the lower surfaces of foliar constituents of axillary buds and explains why, when the bud is suppressed, the two lower sporophylls "orientated themselves" with reference to the axis (Velenovský, 97).

10. It lends eloquence to the otherwise discordant *Larix* cone described first by Velenovský, one scale of which bore "besides the two fleshy placental lobes, five other fleshy ovule-bearing scales," and makes this scale and the short statement about it speak clearly for the branch origin of the scale.

11. It is in keeping with the finding of multisporophylled seed scales in early fossil gymnosperms and points, for the origin of both araucarian and abietinean cones, to a type the existence of which is well established.

12. It fixes well-marked tendencies which will account for the conditions found in the cones of *Sequoia*, *Cupressus*, and *Taxodium* without involving additional processes; for a continuation of internodal shortening coupled with meristematic recession would certainly soon involve the primordium of the subtending scale (cover scale) in the common upward movement and in the fusion. It is conceivable that incorporation by maturation might also apply to this primordium, thus accounting not only for the fusion of seed scale and cover scale but also for the disappearance of the latter from those forms in which little or no trace of it can be found.

IX. THE PHYLOGENY OF THE PINACEAE

No doubt the members of the family *Pinaceae* have had a common ancestor, and since the *Abietineae*, the oldest tribe in this family, show a strong leaning toward dwarf shoots, it is likely that the common ancestor had dwarf shoots. This is evidenced by the fact that four of the nine genera in the *Abietineae* (*Pinus*, *Cedrus*, *Larix*, and *Pseudolarix*) have this feature. In *Cedrus*, *Larix*, and *Pseudolarix* the dwarf shoots are of a rather generalized type, and on the whole the associated characters are primitive.

Three of the eight genera in the tribe *Taxodineae* (*Sciadopitys*, *Taxodium*, and *Glyptostrobus*) have dwarf shoots, and in every case these unquestionably represent extremes of dwarf shoot specialization. These are on the whole associated with more advanced characters than are the dwarf-shoot-bearing members of the *Abietineae*. The more advanced tribe of *Cupressineae* has ten or eleven genera with no vegetative dwarf shoots among them. The evidence suggests that the common

ancestor of all *Pinaceae* had spur shoots of a non-specialized type and that such branches have been lost from most of the genera and have become highly specialized in the majority of those which have retained them.

We find ourselves projecting the established evolutionary trends of *shortening, recession, elimination, and meristematic fusions* against the background of the *Pinaceae* and inquiring as to what characters would show in a line of plants in which the tendencies to reduce the dwarf shoot had brought this structure to the vanishing point towards which we have seen it so steadily carried. One has but to strip the dwarf shoots from a pine in order to see what type of plant would be produced by the loss of these organs. Our hypothetical plant can then be constructed by applying to this "disbranched" pine the tendencies already well established.

The leaves of such a plant would certainly be microphyllous, even scale-like (Fig. 29 r and s), as occur almost universally in the family *Pinaceae*. The axils would be for the most part sterile, and those which remained fertile would produce long shoots with probably an occasional reversion to the dwarf shoot condition as found in *Abies*, *Pseudotsuga*, etc. Conservative portions of our hypothetical plant, especially when wounded or otherwise unduly stimulated, would be expected to show some trace of the ancient dwarf shoot character, as do the seed scales of all *Abietineae* cones and the cone axes of proliferated individuals from many genera. The trend toward internodal shortening would no longer be hampered by the necessity of keeping the dwarf shoots properly distributed. This shortening, if continued, would lead to the complete elimination of internodes, thus producing opposite and cyclic leaves just as we find in the *Cupressineae*. With the axillary shoot eliminated and the primary leaf alone remaining, further fusions by intercalary growth could do nothing except to produce adnation of the primary foliar organ with the internode of the primary axis. Indeed the presence of a trace of the old dwarf shoot meristem in the axil would be expected to favor such a course (Fig. 29 x, x', and u). This would produce a conrescent leaf as in certain members of the *Cupressineae* (Fig. 29 t and u).

It is clear that, instead of describing a hypothetical plant, our description fits well the features associated with higher members of the family *Pinaceae*. So numerous and varied are the points of agreement that on a basis of dwarf shoot evidence alone, we can safely assume that evolution of the *Pinaceae* has been from a common ancestor with generalized dwarf shoots as in *Cedrus*, through forms with more and more highly specialized dwarf shoots as in *Prepinus*, *Pinus*, *Sciadopitys*, *Taxodium*, etc., to forms from which the dwarf shoots have been eliminated as in *Abies*, *Pseudotsuga*, etc., and finally to forms with opposite and conrescent leaves as in *Cupressus*.

For phylogenetic purposes it is unsafe to consider dwarf shoots, or cone scales, or any other single structure alone. One should rather consider all the known characters of the organism with which one is working. Sinnott's work on *Podocarpus* (83) well illustrates this fact. He effectively compares the characters of the *Abietineae* and *Podocarpineae* to support the derivation of the fruiting structures of the latter from the cone scale of the former and to argue for connecting these two groups on the phylogenetic tree. The mass of evidence would support such a connection, and yet we prefer to leave open the question of where to connect the line leading to the *Podocarpineae* until we know more definitely whether the single functional sporophyll of *Podocarpus* represents the central sporophyll or one of the lateral sporophylls.

In nearly all forms the evolution of the vegetative dwarf shoot and that of the ovulate short shoot have gone hand in hand. Forms like *Larix* and *Cedrus* have primitive short shoots associated with relatively primitive seed scales; *Sciadopitys* and *Taxodium* with highly specialized short shoots have advanced cone scales; and forms like *Cupressus*, *Juniperus*, and *Araucaria*, from which the dwarf shoots have been lost, have the most highly specialized cone scales found among the members of the *Pinaceae*.

From this general agreement between the evolution of the dwarf shoot and the seed scale, only *Picea*, *Tsuga*, *Abies*, and *Pseudotsuga* are out of line, for these forms, although devoid of short shoots, still possess seed scales which are at the *Pinus* level. Since the bulk of characters for these plants is primitive, it is necessary to assume that while advanced in one character they have remained primitive in many others.

Our conclusions with reference to phylogeny are: that the *Araucarineae* and the *Abietineae* separated early from a common ancestor; that there is some doubt as to which of these lines gave rise to the *Podocarpineae* and *Taxodineae*; that among the *Pinaceae*, *Cedrus* and *Larix* are low, *Prepinus* and *Pinus* intermediate, *Sciadopitys* and *Taxodium* high, and *Cupressus* the highest in position.

X. SUMMARY

1. A study is made of the axial and foliar systems of about thirty-five species of pines and of a few related plants.
2. The constituent units of the tree are described in their order of appearance.
3. The ontogeny of the cotyledons supports the view that polycotyledony is a primitive character and that fusions, incorporations, and reductions mark advances.

4. The natural and abnormal occurrence of simple leaves is treated, and their artificial production through wounding is demonstrated.

5. In the ontogeny of the bud scales it is shown that the interlocking fringed margins are the product of several factors including a hooding of the primordium, an angular arrangement of the marginal tissues, and the expansion of underlying parts which in some cases actually perforate the overlapping scales.

6. A technique is described whereby the number of bud scales and of sterile bracts can be approximately determined prior to extension of the buds which contain them. This technique is utilized in following the time of origin of units within the bud.

7. The bud scales are divided into groups "A" and "B" based upon the time of origin and upon the amount of extension of their respective internodes.

8. The expansion of the winter bud into the annual growth is described.

9. Normal and abnormal sequence of deposit is followed, and evidence is given supporting the view that the so-called lateral cone is an ecologic rather than a fixed character.

10. The staminate cone axis is considered homologous to the dwarf shoot, and the ovulate cone axis homologous to the long shoot.

11. Seed cones with proliferations and abnormal sequence of units are described, and the nature of their abnormalities is used to support the theory that they represent modified long shoots.

12. The ovulate cone is considered a compound strobilus, and the cone scale a simple strobilus.

13. The origin of concrescent leaves is associated with the disappearance of dwarf shoots from the primary axes.

14. The ontogeny of the dwarf shoot and of its foliar organs is given in detail and the following facts established in regard to them:

a. The first two scales are laterally placed, opposite each other; and the first three are distinct from the other scales.

b. The encircling sheath is produced by the perforation of the scales and the exaggerated overlapping of the scale margins.

c. The dwarf shoot spends the winter rest in full possession of all of its foliar structures including the needles.

d. Both scales and needles grow from basal (zonal) meristems.

15. In the pines which have deciduous fascicle sheaths, the shedding of the scales involves the loosening of the cohering portions and the detachment of the scales from the shoot. These steps are accomplished differently in the different pines.

16. The pines with persistent sheaths crumple these until they cover

only one-fourth to one-third as much of the leaves as when fully extended.

17. The scale numbers per fascicle from representative samples of thirty-two species and several varieties have been counted and the results tabulated. The numbers are too variable to be of much taxonomic value, but certain tendencies are manifest, notably the tendency to stabilize the scale number at either two or three times the basic leaf number (2×5 or 3×5).

18. The early ontogeny of the leaf is given, and its manner of perforating the overlying sheath is shown.

19. The orientation of the needles within the sheath is not a constant character but in some species approximates constancy.

20. The needles are found to fuse in various ways.

21. Fusions are linked with internodal shortening and meristematic recession.

22. The ontogeny of the dwarf shoot of *Pinus cembroides* var. *monophylla* is essentially like that of other pines except that only one of the two original leaf primordia comes to maturity, the other needle, together with the growing point of the dwarf shoot, being usually incorporated into the functional leaf but without differentiation of vascular tissues. Similar incorporations were not found in other pines.

23. Dwarf shoots on disbudded branches showed an increase in the number of leaves, thus marking the reduced number as a derived character.

24. The basic leaf number of needles is five. This is equivalent to two turns of the phyllotaxic spiral.

25. A theory of interference is advanced to account for the tendency toward stabilization at five needles.

26. Inefficiency in perforating the sheath scales has probably disfavored stabilizations of pines with four needles.

27. A growing point or interfoliar bud is present between the needles of most of the dwarf shoots in all the species included in the study.

28. The degree of development of these buds depends both upon the species and upon the conditions of growth. They develop least in the pines which have deciduous sheaths.

29. Disbudding of the long shoots induces proliferation of some of the interfoliar buds on the more distal dwarf shoots.

30. Numerous abnormal (bisporangiate) cones of *Pinus* and *Larix* are described in which the ovuliferous scales show non-fused and transitional conditions which, in general, support the brachyblast theory.

31. The brachyblast theory of the cone scale is strengthened by the fact that the early ontogeny of the dwarf shoot proves to be almost identical with that of the cone scale and by the fact that the three most

proximal and most regularly placed scales on the dwarf shoot all have similarly placed counterparts on the cone scale.

32. The two sporophylls on the seed scale correspond to the lateral scales on the dwarf shoot.

33. Some of the fossil relatives of *Pinus* are reviewed.

34. The dwarf shoot of *Pinus* is found to be homologous with the persistent basal (imbedded) portion of the shoots of *Taxodium*, the deciduous portion of which corresponds to proliferated pine fascicles. It is pointed out that a discontinuation of the habit of seasonal branch-fall may have given rise to forms like *Sequoia*, in which the true homologue of the dwarf shoot of *Pinus* may have disappeared simply by being imbedded and by having its habit of shedding discontinued.

35. Most of the unique vegetative characters in *Pinus* can be directly or indirectly attributed to influences incident to the formation of the compound bud. This structure relieved the sheath scales from the work of meristematic protection and permitted specialization along other lines. It necessitated the almost simultaneous development of many structures from stored food and exerted shaping pressures upon the enclosed immature dwarf shoots.

36. Tentative steps in the evolution of the leaf meristems of pines are presented as follows: (a) apical, (b) grouped, (c) basal, and (d) sub-basal (in certain special cases).

37. The early common ancestor of the *Pinaceae* probably was macrophyllous and had monomorphic branches.

38. The formation of dimorphic branches accompanied the transition to microphyllly, and the development of the two was probably interdependent.

40. The disappearance of the dwarf shoots and a continuation of the tendencies toward internodal shortening are postulated as explanations for the appearance of abietineous forms with opposite, whorled, and concrescent leaves.

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