# THE GROWTH HABIT OF *LEPIDODENDRON SERRATUM* FELIX*

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**ABSTRACT**

The question as to whether all of the species of the paleozoic genus, *Lepidodendron*, were arborescent with secondary growth or whether some of them may have been of vine or semi-herbaceous habit with only primary tissues, has been investigated by observation of over 200 specimens of *Lepidodendron serratum* Felix.

None of the over 200 specimens (many of which reached an apparent maximum diameter of 10 cm) exhibited any form of secondary growth either vascular or periderm. In addition, one specimen showed a distinctive asymmetrical form, with the stele occupying a marginal position and all of the leaf traces leading to leaf bases localized on the side of the stem opposite the stele. This type of anatomy is directly comparable to that found in the stems of many living lianas and along with the strong evidence for lack of secondary growth seems to indicate that *L. serratum* was a " lax, flexuose " plant as originally postulated by Felix.

*LEPIDODENDRON serratum* was established by Felix (1952) on the basis of numerous specimens found in coal balls from the Fleming coal of Middle Pennsylvanian age from southeastern Kansas. All of the stem fragments Felix observed were quite small, the largest reaching only 43 × 16 mm. in diameter. He also noted that, "— often almost entire coal balls consisted of tangled masses — of *L. serratum* associated with a varied flora " and that, " not a single specimen with secondary vascular or cortical development was present ". On the basis of these characteristics he suggested that the plant may have been of " lax, flexuose " growth rather than arborescent.

Eggert (1961), however, cites considerable evidence that the presence or absence of secondary tissue development in *Lepidodendron* is only an indication of the age of the specimen and is useless as a taxonomic or morphological indication. He points out that in the various species typically exhibiting secondary xylem (*L. vasculare*, *L. scleroticum*, *L. brevifolium*, etc.) that small branches are still frequently encountered in which secondary growth is lacking. His viewpoint of *L. serratum* is, accordingly, that the specimens so far described by Felix "— represent relatively small branches of the crown of some relatively large plant ".

Since the initiation of our National Science Foundation supported program of large scale coal ball cutting, we have collected and cut over 5,000 lbs. of coal ball material from the Kansas Fleming coal with the result that the apparent abundance of *L. serratum* noticed by Felix (1952) has been substantiated and hundreds of specimens have been exposed. These specimens range from a seeming maximum (as represented by 8 specimens all of almost identical size) of 100 mm. × 40 mm. down to hundreds of small branches 2 mm. or less in diameter. As described by Eggert (1961), the presence or absence of a pith in the stele appears related to size with the larger steles having a large medullary area while the smallest branches are characterized by their protostelic structure. The steles of the largest specimens average 15 mm. in diameter with the maximum radial thickness of the exarch primary xylem being 2 mm., while the protosteles of the numerous small branches average ·4 mm. in diameter.

In addition to the size range described above, one specimen of particular interest has been discovered which shows a strong bilateral symmetry. In transverse sections the stem measures 14 mm. × 10 mm. with it's

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stele being within 1 mm. of one side of the stem and all of the leaf traces and leaf bases departing from the opposite side of the stem (FIG. 1). The similarity of this anatomical pattern to that found in living lianas and rhizomes (where the stele is often in an asymmetric position on the side of the axis nearest the substrate or support) lends support to Felix's (1952) concept of a vine-like growth habit for the species. This concept is strengthened further by the fact that our several hundreds of specimens, revealing those of much larger dimensions than previously described, are still characterized throughout by the complete absence of any secondary tissues. It accordingly seems desirable to describe the species more fully, based on the extensive new material, in order to bring out what appear to be the true features of the plant. This will be done by describing in detail the two new growth forms mentioned above, i.e. (A) The stems of apparent maximum size; (B) The asymmetric stem of possible rhizome or liana nature.

(A) *Stems of apparent maximum size*: As Eggert (1961) has pointed out there seems to be good evidence that the carboniferous lycopods were characterized by determinate growth throughout their ontogeny. The remarkable uniformity in overall diameter of the numerous steles of *Lepidophloios kansanus* with abundant secondary xylem seems to indicate that not only were they representative of the older (more basal) parts of the stem but that the growth of the stele and extra-stelar stem tissues were as limited to a certain maximum as was the development of the plant as a whole. Similarly the several hundred specimens of *Lepidodendron serratum* observed, while consisting in large part of small branches, included a total of 8 axes of large size which were remarkably uniform in their overall dimensions. As shown in Fig. 4 these stems were always characterized by having been subjected to lateral compression prior to being embedded in the coal ball sediments and in this form have the average transverse dimensions of $100 \times 40$ mm. The stele in each specimen measured an almost identical 15 mm. in diameter (in its uncompressed form) including a pith of 11 mm. diameter and a thickness of 2 mm. for the primary xylem. Phloem and the distinctive inner cortex shown in the specimen illustrated in Fig. 1 were not preserved in any of the large axes but the homogeneous outer cortex averaged 20 mm. in thickness. In none of the 8 large specimens (or the hundreds of smaller ones) were there any signs of secondary growth, either vascular or periderm.

The numerous spirally arranged leaf traces form a conspicuous pattern as they follow a steeply ascending path from their point of origin on the exarch protoxylem strands of the stele to the leaf bases due to the lacunae formed by the usual disintegration of the parichnos parenchyma occupying the abaxial position of the bundle (FIGS. 3, 4). While this tissue is nearly always lacking in the mature specimens, it is clearly evident in the unusually well preserved specimen shown in Fig. 1. That this tissue is of the nature of parichnos parenchyma and not phloem is demonstrated by longitudinal sections showing the cells to be nearly isodiametric to only slightly retangular. Thus the dearth of recognizable phloem in the paleozoic lycopods remarked upon by other investigators (ARNOLD, 1960) is again emphasized in the present material of *Lepidodendron serratum*.

The leaf bases of the large specimen shown in Fig. 4 are illustrated in the tangential section of the stem seen in Fig. 5. They are diamond-shaped and lack the tapered, serrate margins Felix (1952) listed as part of his original species diagnosis. The present evidence would seem to indicate that the tapered, serrate leaf base is only characteristic of the smaller stems and branches; these features, along with the " numerous small, epidermal emergences " being lost in the maturation of the older main stems.

(B) *The asymmetric stem or " rhizome "*: This unusual form of *Lepidodendron serratum* axis is illustrated in Figs. 1 and 2. It measures $1{\cdot}0 \times 1{\cdot}4$ cm. in transverse section with the small primary siphonostele being asymmetrically positioned within 1 mm. of one side of the stem. The stele itself is $1{\cdot}3 \times 1{\cdot}8$ mm. in transverse section with exarch primary xylem 0·3 mm. in radial thickness surrounding a central, parenchymatous pith. It is enclosed in a compact parenchyma of small rectangular cells which merges outwards into a homogeneous parenchyma of larger isodiametric cells referred to here as the inner cortex. This is separated by a sharp line of demarcation from the outer cortex which is also composed of isodiametric, but thicker walled cells. The peripheral tissues of the outer cortex form a dark coloured margin due to the black, opaque contents of the somewhat more compact cells.

Leaf traces with well preserved abaxial parichnos parenchyma (which is very similar in appearance to the inner cortex tissue) lead from the marginal stele to the opposite side of the axis where they enter the typical *L. serratum* type leaf bases shown in Fig. 2. The leaf bases are limited to the side of the stem opposite the marginal stele.

The specimen was 8 cm. in length with over 6 cm. of this distance being characterized by the asymmetric, bilateral symmetry shown in Fig. 1. At a space of around 1 cm. above the section shown, the outer cortex became 1/3 again as thick as shown while the diamond-shaped leaf bases (similar to those shown on the left side of the stem in Fig. 4) became free from the cortex lobes. There was a gradual tendency for the stele to move into a more usual central position in the terminal 2 cm. of the fragment as if at this point the " rhizome ", or twining stem, were turning upwards or away from it's substrate to assume an erect or radially symmetrical type of growth.

*Discussion* — It is obviously more difficult to prove the absence of a structure than it is to prove its presence. The irrefutable proof of the former could only be achieved through complete knowledge of all parts of the plants involved through all stages of their ontogeny whereas the latter requires but a single section possessing the tissue in question. Accordingly while the " indisputable evidence " demanded by Eggert (1961) for the acceptance of the lack of secondary growth as a specific character in the paleozoic lycopods may never be possible, we feel that the present study of *Lepidodendron serratum* fully satisfies the main objections to the concept in previous works. First, the present description is not based on just " small branches " but includes the 8 large specimens described above which are nearly 3 times the size of any previously described specimen and apparently represent the stem's maximum development. Second, the over 200 specimens observed over a period of 15 years of collecting Kansas coal ball plants have all consistently shown only primary tissues. Third, the type of stem anatomy illustrated in Fig. 1 seems only explainable in terms of similar structure in modern day climbers or semi-prostrate plants.

The diversity of the paleozoic lycopods, emphasized by the great variety in their reproductive structures (ABBOTT, 1963), lends weight to the possibility that they also may have shown as great plasticity in adapting themselves vegetatively to the various growth niches of their environment. Accordingly it seems as reasonable to assume that there were semiherbaceous forms as well as those in which the growth pattern was essentially that of a shrub or vine as to insist that they were all arborescent. Certainly the profuse branching (which is more monopodial than " unequal dichotomy ") originally stressed by Felix (1952) and substantiated in this study strongly implies a scrambling semi-bushy plant. Also there is considerable, as yet unpublished, evidence that *Lepidodendron serratum* bore a small cone of the *Lepidocarpopsis* (ABOTT, 1963) type which is quite distinct from the usual *Lepidocarpon* and *Lepidostrobus* fragments making up the Kansas coal ball flora. Since descriptions of most the fossil plant species are based on a few scattered fragments, it is probably inevitable, as well as desirable, that the original species diagnoses be emended as more complete information becomes available. Accordingly the following emended diagnosis is given here.

*Lepidodendron serratum* Felix, emend.

Exarch primary body; secondary xylem development and periderm lacking; small branches with long tapering leaf bases with serrate margins and with numerous epidermal emergences; serrations and emergences lacking in mature stems; smallest branches protostelic; others siphonostelic with a homogeneous pith of thin walled cells 3 times as long as broad, no tracheid-like cells appearing in the pith; leaf traces mesarch with prominent lacunae usually representing the abaxial parichnos strand; cortex of 2-3 zones, usually only the outer well preserved; branching frequent, characterized by an unequal dichotomy; some stems characterized by an asymmetric, marginal position of the stele.

*Locality and Horizon* — Strip mine of the Pittsburg and Midway Coal Company, Cherokee County, Kansas; Fleming Coal, Cherokee group, Des Moines Series, Middle Pennsylvanian.

*Type Specimens* — WCB707, WCB798 and UCB815 Washington University, St. Louis. K.U. 1156, 1260, 844, and 373, University of Kansas, Lawrence.

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## EXPLANATION OF PLATES

PLATE 1

1. Transverse section of asymmetrical (rhizome ?) stem. st, stele; *t*, leaf trace with abaxial parichnos strand. × 9. K.U. 373 p 11.

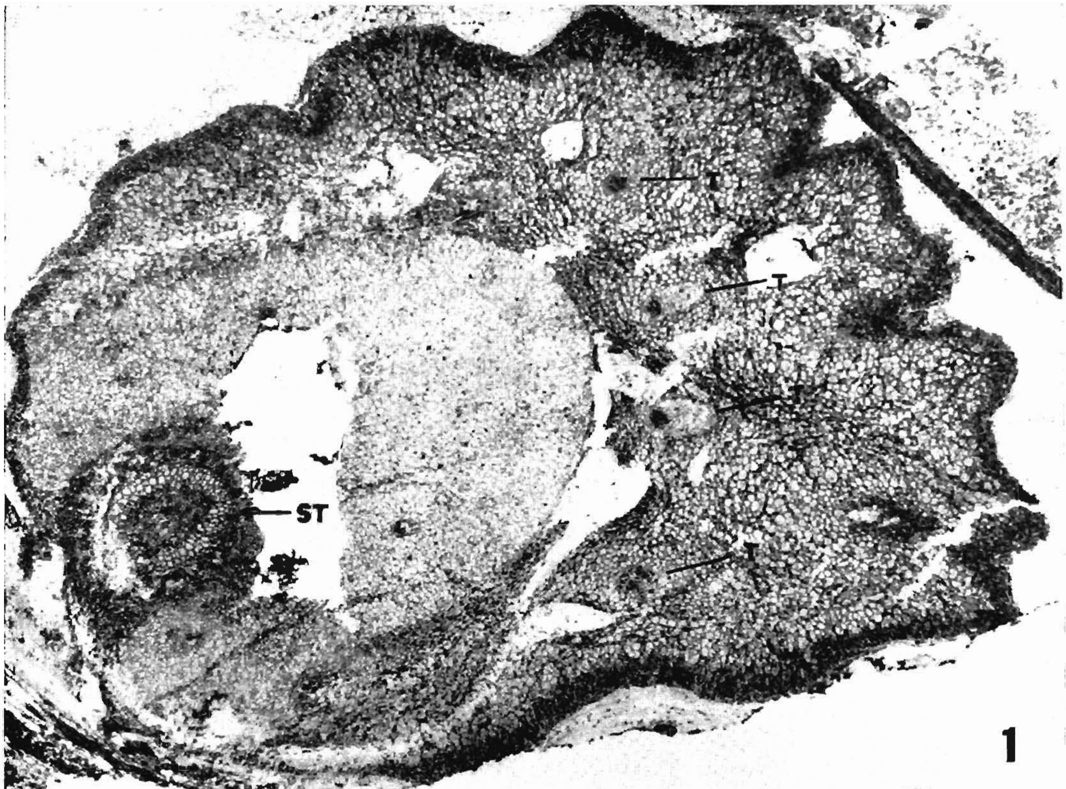
2. *Lepidodendron serratum*. Tangential section of asymmetric stem shown in fig. 1 taken through leaf cushions on side of stem opposite the marginal stele, i.e. right side as illustrated. × 9. K.U. 373 p 21.

PLATE 2

3. *Lepidodendron serratum*. Transverse section of medium-sized branch showing unequal dichotomous (monopodial) branching, wide primary cortex with lacunae associated with leaf traces. × 4. K.U. 1156B.

4. *Lepidodendron serratum*. Transverse section of large mature stem with wide primary cortex. × 1.5 K.U. 1156A.

5. *Lepidodendron serratum*. Tangential section through leaf bases of stem shown in Fig. 4. × 3. K.U. 1156A.


ST
T
1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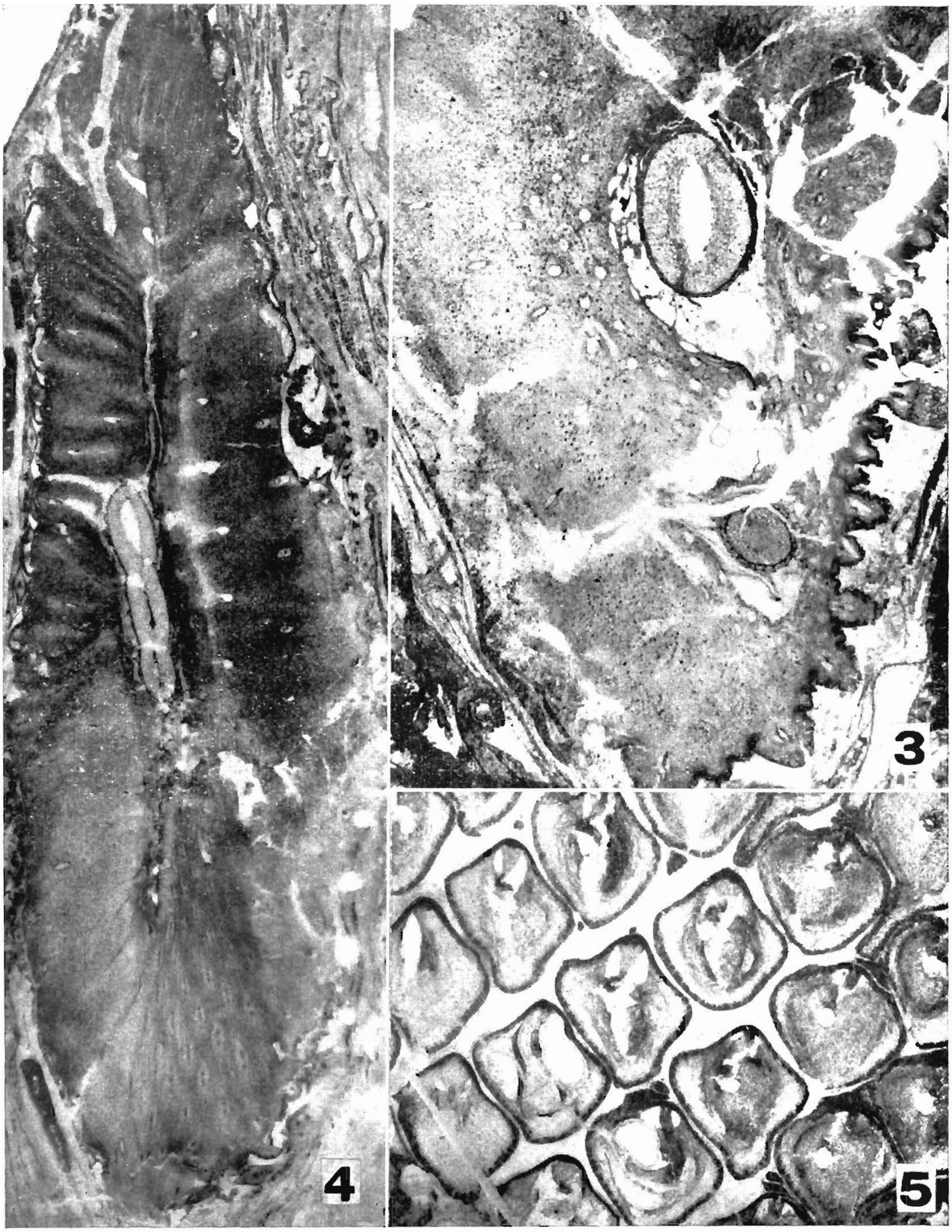
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