Taper of some Early Palaeozoic plants

Karl J. Niklas & Harlan P. Banks

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A new method was used to measure the degree of taper of Devonian plant axes: the width w of each compression fossil (measured at distance x along the length L of each axis) was normalized with respect to the basal width w_0 of each axis w/w_0 and plotted against normalized axial length x/L. The degree of taper was taken as the slope m of the simple linear regression of $(w/w_0)^3$ versus x/L. Comparisons among m showed that different levels of branching on some specimens were statistically distinguishable, as were sterile and fertile axes from the same specimen. In contrast, sterile axes of similar rank in the hierarchy of branching from different species were found to have statistically indistinguishable degrees of taper. The degree of axial taper was observed to slightly increase over geological time, although the limited number of taxa examined make any definite conclusion unwise. Provided fragmented plant axes can be identified as belonging to a particular species, the allometry of axial taper could provide a useful method distinguishing different levels of branching in a plant body. Additionally, because the method used to quantity the magnitude of axial taper was derived from engineering theory, it may ultimately provide quantitative insight into evolutionary changes of the "mechanical design" of columnar and lateral cantilevered axes.

Key-words—Evolution, Morphometry, Allometry, Palaeobotany, Early Palaeozoic.

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साराँश

कुछ प्रारम्भिक पुराजीवी पौधों की गावदुम

कार्ल जे० निकलस एवं हारलॅन पी० बैंक्स

डिवोनी कल्प के पौधों की अक्ष की गावदुम नापने की एक नई विधि उपयोग में लाई गई है। गावदुमों की ढलानों की पारस्परिक तुलना से प्रदर्शित होता है कि कुछ प्रादर्शों में शाखाओं के विभिन्न स्तर सांख्यिकीय दृष्टि से अभिनिर्धारणीय हैं जैसी कि उसी प्रादर्श की बन्ध्य एवं अबन्ध्य अक्ष थीं। इसके विपरीत विभिन्न जातियों में विद्यमान शाखाओं के सोपान-तंत्र में उसी कोटि की अबन्ध्य अक्ष की गावदुम सांख्यिकीय दृष्टि से अनिर्धारणीय हैं। भूवैज्ञानिक काल के साथ-साथ अक्ष की गावदुम में वृद्धि प्रेक्षित की गई है हालाँकि अध्ययन किये गये सीमित वर्गकों से कोई महत्वपूर्ण निष्कर्ष नहीं निकलता। इसी विधि से खंडित पादप-अक्षों का जातीय स्तर तक अभिनिर्धारण भी किया जा सकता है। अक्षीय गावदुम के सापेक्षमितीय अध्ययन से एक पौधे की शाखाओं के विभिन्न स्तरों का अभिनिर्धारण भी किया जा सकता है। अक्ष की गावदुम अनुमापित करने की यह विधि अभियांत्रिकी सिद्धान्त से ली गयी है। इस विधि से स्तम्भीय एवं पार्श्व अक्षों की संरचना के वैकासिक परिवर्तनों का भी अध्ययन किया जा सकता है।

THE degree to which fossil plant stems are tapered is of interest for at least two reasons. First, the degree of taper provides a potential morphological criterion to distinguish among different levels of branching on the same plant or among stems from different plants. And second, the degree of taper can influence the mechanical stability of vertical and cantilevered stems. From a practical point of view, it would be desirable to distinguish among stems that come from different levels of branching on the same plant, particularly for fossil plants known only or primarily from fragmented specimens. The degree of taper is a strictly morphological feature likely to be preserved even when anatomical details are lacking for a particular fossil specimen. Likewise, the degree of taper potentially could be useful in distinguishing taxonomically among spatially or temporally contemporaneous species, although this approach likely would have limited discriminatory ability.

From the point of view of evolutionary theory, trends in the degree of taper of stems may shed light on whether plants have undergone natural selection in terms of their mechanical design. In particular,

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evolutionary trends in the tapering of stems could be evaluated in the context of the hypothesis of "economy in plant design" which argues that natural selection should favour plants that optimize the trade-off between the investment in their biomass and the level of their mechanical performance (Givnish, 1986). Engineers can construct tapered columns and cantilevered beams such that the investment of material is minimized while at the same time providing uniform strength. These objectives are achieved by means of a very precisely controlled degree of taper. If the hypothesis of "economy in plant design" is correct, then the fossil record would be expected to evince an evolutionary trend toward "optimal taper" provided that mechanical stability is important to the survival and growth of plants.

In this paper we present a method that measures the degree of stem taper. It can be applied to fragments of stems provided their lengths are sufficient to take a reasonable number of measurements. The method is derived directly from engineering practice that permits engineers to construct optimally tapered cantilevered beams and vertical columns. The method does not assume that a column or beam is optimally tapered, however. Therefore, the method can be used simply to measure the degree of taper and so has some practical benefit to the palaeobotanist interested in distinguishing among stems from the same or different plants. The method, however, does permit an estimate as to the degree to which the taper of a stem conforms to that of an optimally tapered column or beam. It can be used, therefore, to test aspects of the hypothesis of "economy in design"

MATERIAL AND METHODS

Selection of fossil species and terminology

The taxa and the identification numbers of specimens examined are given in Table 1. Whenever possible type specimens were used. However, four criteria had to be fulfilled and so the selection of specimens was limited: (1) the presence of organic connections among different levels of branching, (2) the likelihood that some axes were vertical support members for a species while others were lateral branches, (3) whether specimens were representative of species having current systematic and evolutionary importance, and (4) the stratigraphic distribution of a species. Criteria (1)-(2) were motivated by the need to draw comparisons among the allometry of taper for different levels of branching within the same plant body. It was necessary to compare the magnitudes of taper among axes whose relative positions on a plant are known in order to assess whether the allometry of axial taper could be used to identify axes from different levels of branching within the same or different fossil species. Therefore, the most intact fragments showing at least two orders of branching of fossil species were examined. Criteria (3)-(4) were needed to evaluate changes in the allometry of axial taper over evolutionary time.

The method we used could be applied theoretically to photographs because all measurements are normalized and so have no absolute dimension. To evaluate whether the method was useful in this regard, we selected photographed specimens for measurement (Table 1).

Table 1—Fossils examined for this study along with Cornell University Palaeobotanical Collection identification numbers and relevant references. * = type specimen. ** = figured specimen. * = Buffalo Museum of Science specimen number (measurements taken from photograph**

Taxon	ID Number	References
Cooksonia sp.	199**	Banks, 1972, 1973
C. hemisphaerica	E25163***	
Crenaticaulis verruculosus	1996**, 1703(2)**, 118*, 116*, 1696**	Banks & Davis, 1969
Ibyka amphikoma	1994.14**, 186* 183*, 179*	Skog & Banks, 1973
Leclercqia complexa	2002.8	Banks *et al.*, 1972
Tetraxylopteris schmidtii	1859-3C**, 1841-15**, 1634**, 1187C**	Beck, 1957; Bonamo & Banks, 1967
Sawdonia ornata	1698	Hueber, 1971

Nonetheless, problems existed regarding the appropriate terminology to distinguish among levels of branching for species differing in their gross morphology and for which different portions of the plant body were preserved. With very few exceptions (if any), the true hierarchy of branching of any of the fossil species examined remains conjectural. The implication of homologies among branching-orders among species was avoided by using different terms to describe the branching-orders of different species. For example, "main" and "secondary" were used for the largest axes of *Ibyka amphikoma* and the lateral axes attached to them, while "sterile" was used to denote the larger axes subtending sporangia-bearing ("fertile") axes of *Tetraxylopteris schmidtii.*

Quantification of Taper

The allometry of axial taper was determined from measurements of the lateral dimension (in the plane of compression) of axes. This dimension will be referred to as axial "width", designated as w, to distinguish it from the original diameter D of uncompressed axes. Measurements of w were made with a microcaliper or with a binocular microscope equipped with an ocular micrometer. They were recorded as a function of distance x from the distal end ($x = 0$) along the entire length L of each axis. When part and counterpart fossils were available, w was measured at equivalent x and an average w for each x was computed.

The theory of elastic stability of columns and cantilevered beams treats axial taper in terms of the change in the normalized section modulus Z_n as a function of normalized axial length x/L. For a tapered or untapered cylinder with terete cross sections, the section modulus Z of each cross section is the quotient of the second moment of area I and D/2, i.e., $Z = 2I/D = \pi D^3/32$. The magnitude of D at each x was estimated based on w (see below) and used to compute Z, which was normalized with respect to the section modulus at the base of each axis Z_o, i.e., $Z_n = Z/Z_o$. Values of Z_n were plotted against x/L for each axis (Note that Z_o is a function of the cube of w/w_o since D must be a function of w).

Simple linear regressions yielded the best fit for Z_n versus x/L. The slopes m of regressions were used to determine whether the allometries of taper of different axes were statistically different. Statistical comparisons assumed non-equivalent variances, since the fossil species examined came from different populations and the morphometries of different species may differ. The modified Student's t test (Snedecor & Cochran, 1980, pp. 96-98), where t is replaced by t', was used to compare statistically values of m. Morphometries of axes were considered statistically significantly different at the 0.05 level (i.e., $t'_{calc} \leqslant t'_{0.05}$).

Estimates of original axial dimensions

Three factors made estimates of D from measurements of w difficult: (1) the matrix often obscured the lateral edges of fossil stems (in the plane of compression), (2) different plant tissues could respond to the same magnitude of mechanical force differently, and (3) tissue mechanical-anisotropy could vary as a function of L. Text-figure 1A-C illustrates some of the possible morphological consequences of these three factors. When submitted to lateral compression, a representative circular cross section through a terete axis (Text-figure 1A) will undergo lateral and vertical deformation but, dependent upon the lateral restraints imposed by the surrounding matrix, these orthogonal deformations may or may not be equivalent in magnitude (Text-figure 1B-C). If the matrix prohibits lateral expansion, then each cross section may predominantly undergo a "vertical collapse" as relatively thin-walled cells lose turgor and expel fluids and as cell walls buckle and crush together. Ultimately, each cross section may collapse completely such that its dimension orthogonal to the plane of compression becomes negligible in comparison to w. By contrast, ovalization of each cross-section can occur when the matrix provides little or no lateral restraint to tissue deformation (Text-figure 1C). This mode of deformation will occur whenever a plant axis is compressed between two plates, much like when a herbarium specimen is prepared. Under these circumstances, $D < w$ because $D + d = w$, where d is the distance to which each cross section was permitted to undergo lateral expansion.

Provided that the mode of deformation (vertical collapse versus ovalization) can be determined for a particular specimen, the relative correspondence between the magnitudes of w and D can be crudely estimated. In the case of pure vertical collapse, $D \approx w$, although tissue dehydration may result in D being slightly greater than w. In the case of pure ovalization, the mensuration formula for the circumference of an ellipse C_e can be used to infer the magnitude of D:

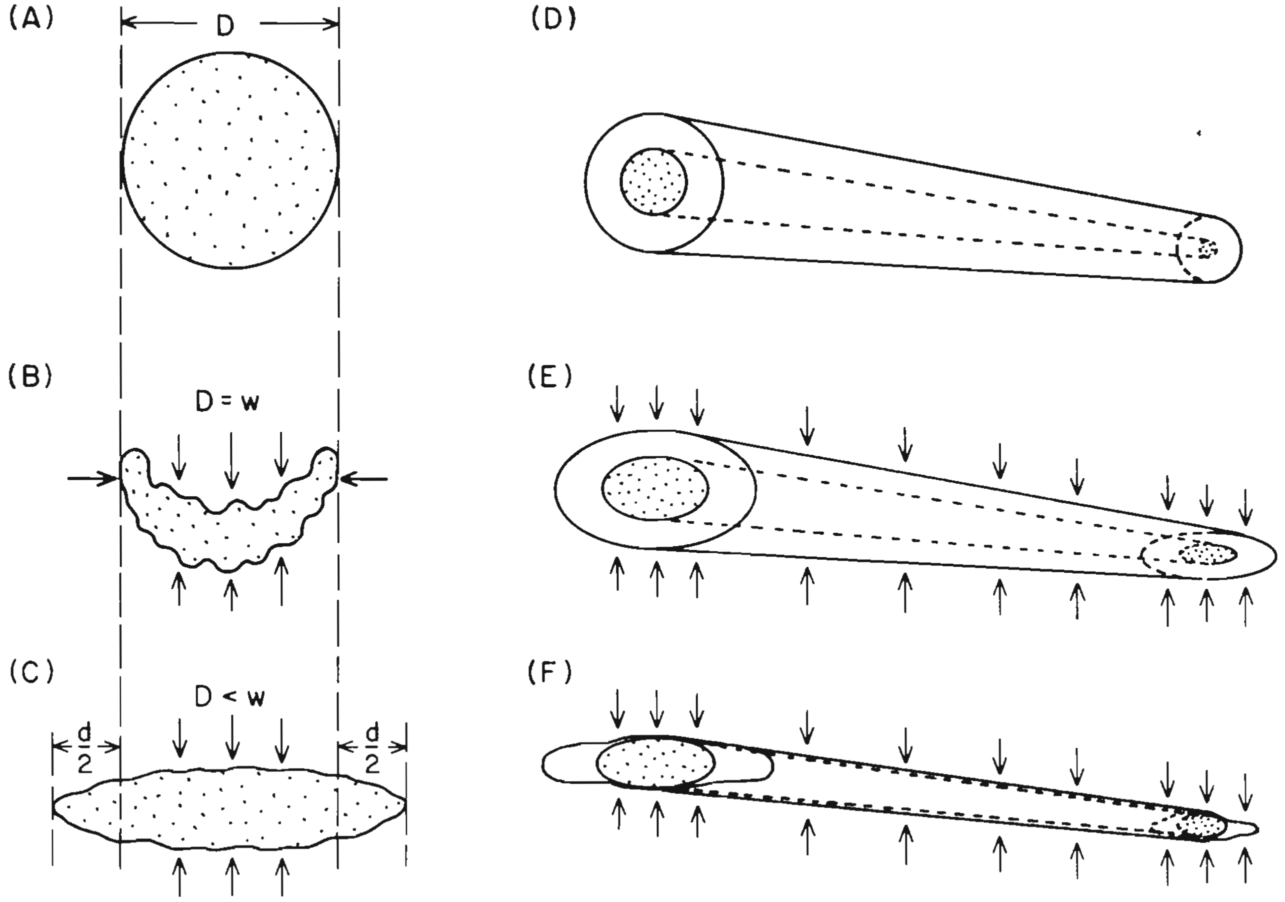
$$C_e \approx 2\pi \left(\frac{a^2 + b^2}{8}\right)^{1/2}, \qquad \text{Eqn. 1}$$

where a is the major axis (the lateral dimension) and b is the minor axis (the vertical dimension) of each elliptical cross section. Setting the original circumference ($C = \pi D$) of each terete cross-section equal to C_c and solving for D yields the formula

$$D \approx 2 \left(\frac{a^2 + b^2}{8}\right)^{1/2}, \qquad \text{Eqn. 2}$$

Noting that $a \doteq w$ and that the magnitude of $b - 0$ as either the magnitude of compression increases or the tissues of an axis progressively deform under a constant compressive load, the extreme case is seen to be $D \approx 0.707$ w, i.e., measurements of w can over-estimate the magnitude of D by as much as $\approx 29\%$.

However, "pure" vertical collapse and ovalization are idealized as shown in Text-figure 1B-C because it is assumed that the original circumference of the undeformed cross section is "conserved" during fossilization. Also, plant axes typically evidence transverse and longitudinal



Text-figure 1—Possible geometric alterations attending the vertical compression of a terete axis. **A-C.** In transection, vertical compression of an originally terete axis (A) with diameter D can result in a compression fossil whose lateral "width" w equals D if the surrounding sediment provides lateral support or in a fossil whose w is greater than D if the sediment provides little or no lateral support. **D-F,** Dependent upon the extent to which an axis is anatomically heterogeneous, lateral compression of a terete axis (D) can lead to equivalent (E) or non-equivalent ovalization of transections along axial length. D = original axial diameter, w = lateral ("width") dimension of compression; d = w - D.

anatomical heterogeneity and tissue mechanical anisotropy (i.e., the magnitudes of orthogonal strains are not equivalent for equivalent magnitudes of stress). Thus, each cross section through a real plant axis may fold upon itself such that its deformed circumference is substantially less than its original circumference. Also, transverse and longitudinal deformations of tissues differing in mechanical properties or relative volume fraction are likely not be uniform. Some of the possible consequences of these phenomena are shown in Text-figure 1D-F which illustrates a simple two-phase (stiff "core"and less stiff "rind") anatomy compressed in a matrix permitting cross-sectional ovalization. A tapered rind of relatively thin-walled tissues (open area) is drawn around a tapered core of relatively thick-walled tissues (stippled area). Because the magnitudes of taper of the core and rind differ, the volume fraction is contrived to decrease acropetally along the length of the hypothetical axis. When submitted to a compressive lateral load, the magnitudes of deformation of the two tapered cylinders of tissue will differ, resulting in a compressed axis whose sequential cross sections will have variously related magnitudes of w and D. Under these circumstances, unless anatomical details are preserved, there is no legitimate method to retrieve estimates of D from empirical measurements of w. If, however, one of the tissues in the axis is relatively stiff (e.g., the core) such that its circumference is conserved, then the external D of the axis (core plus rind) can be estimated by the construction of dimensionless ratios relating the cross-sectional distortion of the stiffer tissue to that of the less stiff tissue (see Niklas, 1984, p. 489). Clearly, this method of extrapolation requires that some anatomical details are available.

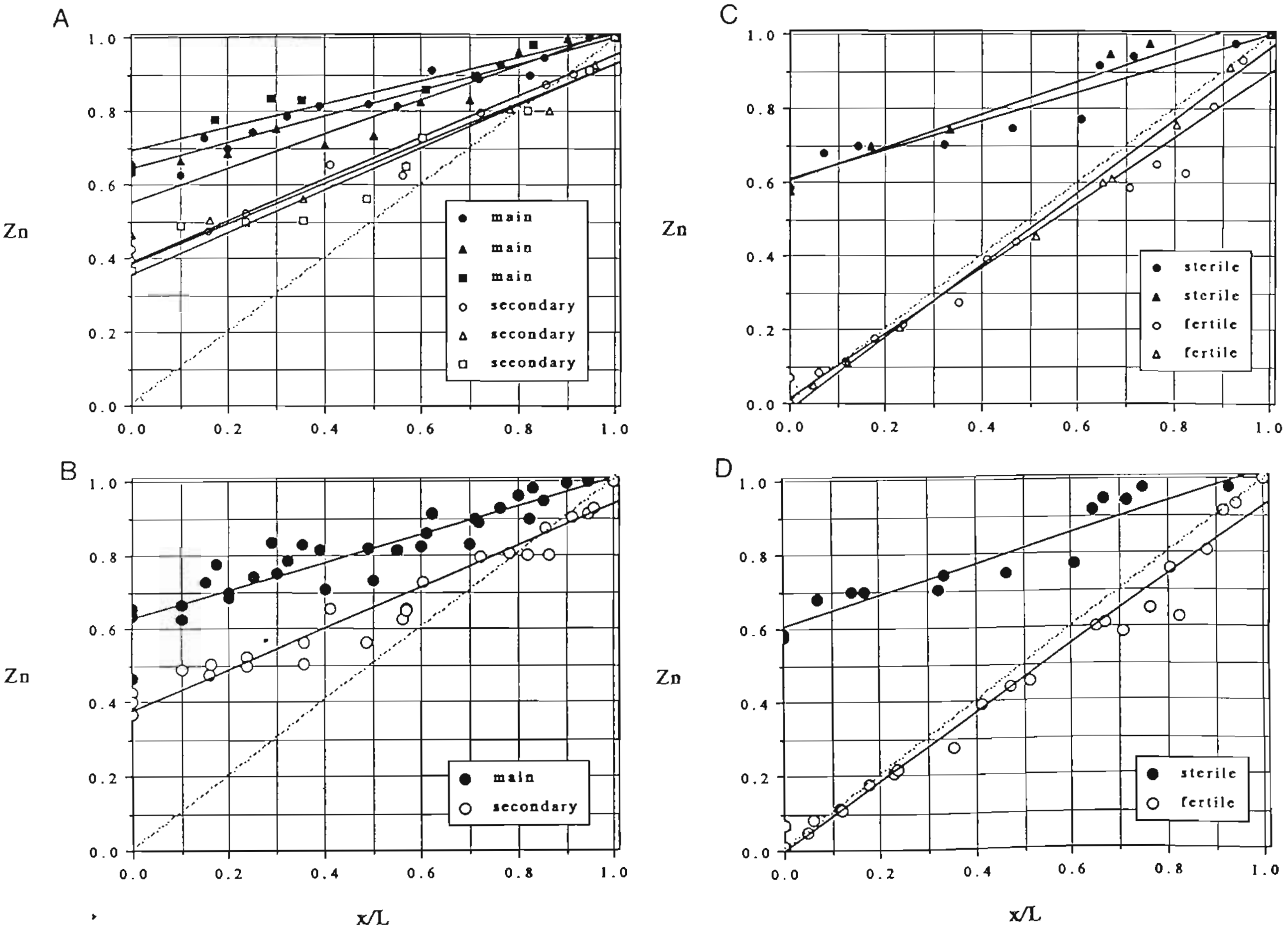
Fortunately, some anatomically preserved specimens were available for most of fossil species selected for study. Based on these petrified specimens, the relative mechanical anisotropy of constituent tissues (primary vascular and ground tissues) submitted to compressive loadings could be inferred. In those cases where anatomical details were insufficient, it was assumed that the error in estimating D from w was uniform along the axial length of each specimen. This assumption is probably legitimate for relatively short axes and for those consisting exclusively of primary tissues. It should be noted that the normalization procedure used to quantify the allometry of axial taper (Z_n versus x/L) will tend to reduce the influence of non-uniform error in estimating D from w.

RESULTS

Morphometry of Taper

The axial tapering of specimens of *Ibyka* and *Tetraxylopteris* (Table 1) are plotted in Text-figure 2. The data and simple linear regression curves for Z_n versus x/L from six axes of *Ibyka* are shown in Text-figure 2A-B, while those from four axes of *Tetraxylopteris* are shown in Text-figure 2C-D. (similar but closed and open symbols are used to indicate the data for individual specimens). A dashed diagonal line is provided on each graph to indicate the isometric relationship between Z_n and x/L for an optimally tapered beam with uniform strength in bending.

The data plotted in Text-figure 2A-B are from three specimens of *Ibyka*, each of which had a large axis (identified as "main") bearing at least one sterile lateral axis (identified as "secondary"). Trends in the data suggested that each of the three main axes was less tapered (more prismatic) than its corresponding secondary axis. Simple linear regressions of the data supported this impression; regression formulas for the three main axes were

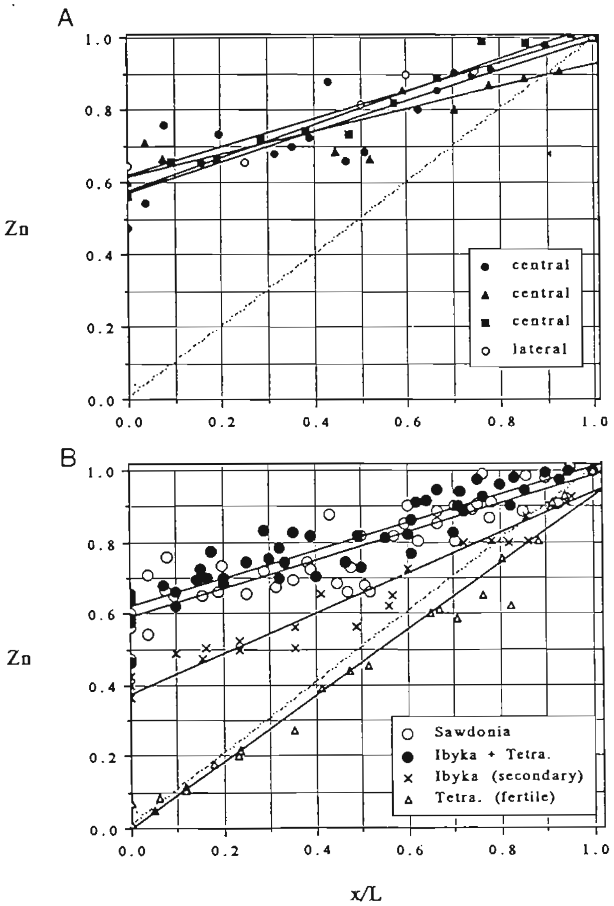


Text-figure 2—Normalized section moduli (Z_n) versus normalized length of axes (x/L) of *Ibyka amphikoma* (A - B) and *Tetraxylopteris schmidtii* (C - D). Dashed diagonal line shows the predicted slope m of an "optimally" tapered beam (m = 1). Linear regression equations for regression curves of actual data are provided in the text. **A.** Regression curves for data from three individual "main" and three individual "Secondary" axes. **B.** Regression curves for pooled data from A. **C.** Regression curves for data from two individual "sterile" and two individual "fertile" axes. **D.** Regression curves for pooled data from C.

$Z_n = 0.646 + 0.356\ x/L$ ($r^2 = 0.947$), $Z_n = 0.549 + 0.466\ x/L$ ($r^2 = 0.902$), and $Z_n = 0.694 + 0.319\ x/L$ ($r^2 = 0.908$), while those of the corresponding secondary axes were $Z_n = 0.393 + 0.563\ x/L$ ($r^2 = 0.968$), $Z_n = 0.385 + 0.549\ x/L$ ($r^2 = 0.964$), and $Z_n = 0.354 + 0.579\ x/L$ ($r^2 = 0.944$). A comparison between the x ± SD of slopes of main and secondary axes (0.380 ± 0.076 and 0.564 ± 0.015, respectively) yielded $t' = 4.08$, which is statistically significant at the 1% level, i.e., the average magnitude of taper of the three main axes was statistically distinguishable from that of the three attached secondary axes. Main and secondary axes were also statistically distinguishable based on the y-intercepts of linear regressions (analyses not given). The regression formulas for the pooled data from the main and secondary axes of *Ibyka* were $Z_n = 0.627 + 0.381\ x/L$ ($r^2 = 0.861$) and $Z_n = 0.375 + 0.565\ x/L$ ($r^2 = 0.954$), respectively. The allometry of taper of both main and secondary axes, therefore, deviated from that of an optimally tapered cantilevered beam; Text-figure 2B reveals that the section moduli of *Ibyka* axes were larger than those of an optimally tapered beam.

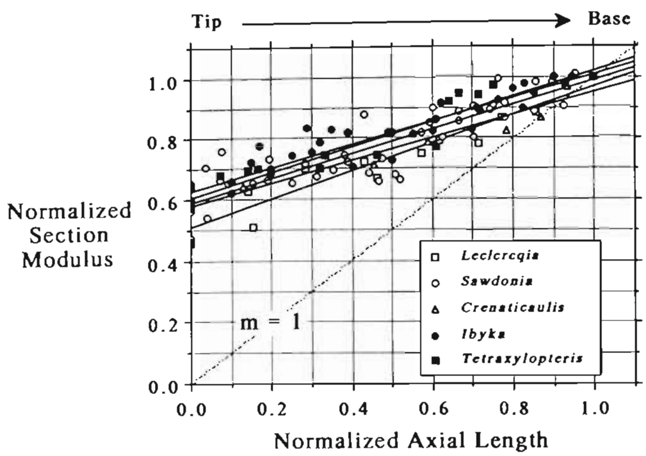
Text-figure 2C plots the data from two specimens of *Tetraxylopteris*, each of which had a main axis (designated as "sterile") bearing at least one fertile axis. The simple linear regression formulas for the sterile axes were $Z_n = 0.609 + 0.394\ x/L$ ($r^2 = 0.903$) and $Z_n = 0.605 + 0.448\ x/L$ ($r^2 = 0.953$), while those of the two fertile axes were $Z_n = 0.013 + 0.888\ x/L$ ($r^2 = 0.967$) and $Z_n = 0.013 + 0.978\ x/L$ ($r^2 = 0.995$). The difference in the taper of sterile and fertile axes was statistically distinguishable at the 1 per cent level. Regression of the pooled data from the sterile and fertile axes (Text-figure 2D) yielded the formulas $Z_n = 0.607 + 0.415\ x/L$ ($r^2 = 0.916$) and $Z_n = 0.001 + 0.927\ x/L$ ($r^2 = 0.978$). The latter was taken as evidence that the relationship between Z_n and x/L was nearly isometric ($m \approx 1$).

Data from three central axes and the only lateral axis of sufficient length for study from *Sawdonia* are plotted in Text-figure 3A. Simple linear regression of Z_n versus x/L for the central axes yielded $Z_n = 0.570 + 0.426\ x/L$ ($r^2 = 0.762$), $Z_n = 0.616 + 0.312\ x/L$ ($r^2 = 0.786$), and $Z_n = 0.576 + 0.457\ x/L$ ($r^2 = 0.957$), while that of the one lateral axis was $Z_n = 0.618 + 0.392\ x/L$ ($r^2 = 0.936$). Regression of the pooled data from the three central axes yielded $Z_n = 0.586 + 0.399\ x/L$ ($r^2 = 0.808$). All of the regressions of data from *Sawdonia* had formulas whose slopes deviated significantly from an isometric Z_n versus x/L relationship.



Text-figure 3—Normalized section moduli (Z_n) versus normalized length of axes (x/L) of *Sawdonia ornata* (A) and comparisons among data from *Sawdonia*, *Ibyka amphikoma*, and *Tetraxylopteris schmidtii* (B). Dashed diagonal line shows the predicted slope m of an "optimally" tapered beam (m = 1). Linear regression equations for regression curves of actual data are provided in the text. **A.** Regression curves for three individual "central" and one "lateral" axis of *S. ornata*. **B.** Regression curves for pooled data from central and lateral axes of *S. ornata* (see A), pooled data from "main" and "sterile" axes of *I. amphikoma* and *T schmidtii* (Ibyka + Tetra.), pooled data from "secondary" axes of *I. amphikoma*, and pooled data from "fertile" axes of *T. schmidtii* (see Text-figure 2).

Text-figure 3B provides comparisons among the data sets from *Sawdonia*, *Ibyka*, and *Tetraxylopteris*. In this figure, the data from the central and lateral axes of *Sawdonia* were pooled and compared with the pooled data sets from the main and sterile axes of *Ibyka* and *Tetraxylopteris*. A t'-comparison indicated that the morphometries of taper of central/lateral axes of *Sawdonia* and the main/sterile axes of *Ibyka/Tetraxylopteris* were indistinguishable based on the slopes of regression curves. However, once again, the average taper of the secondary axes of *Ibyka* and the fertile axes of *Tetraxylopteris* were distinctly different from the other categories of axes plotted in Text-figure 3B. These relationships were interpreted as circumstantial evidence that "central", "lateral",



Text-figure 4—Normalized section moduli (Z_n) versus normalized length of axes (x/L) of three zosterophyllophyte-lycopod genera (*Leclercqia*, *Sawdonia*, and *Crenaticaulis*), *Ibyka amphikoma*, and *Tetraxylopteris schmidtii*. Dashed diagonal line shows the predicted slope m of an "optimally" tapered beam (m = 1). Linear regression equations for regression curves of actual data are provided in the text. For further details, see text.

"main", and "sterile" axes may be mechanically analogous orders of branching in the plant bodies of these three fossil species, while "secondary" and "fertile" axes constitute two separate categories of branching.

Comparisons among sterile (?main vertical) axes

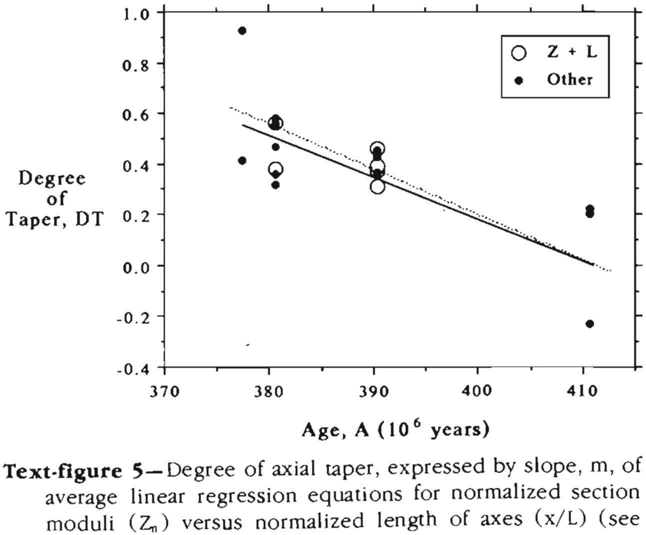
Some of the taxa examined were known to produce secondary tissues (e.g., *Tetraxylopteris*) while others were known to be composed exclusively of primary tissues (e.g., *Sawdonia*). The data from sterile axes that we believed to be the main vertical support members for each specimen were co-plotted in an effort to determine whether tapering was more pronounced in axes evincing secondary growth. Text-figure 4 provides comparisons among the taperings of sterile axes of *Tetraxylopteris, Ibyka, Leclercqia, Sawdonia,* and *Crenaticaulis.* The slopes and y-intercepts of the various regressions curves shown in Text-figure 4 were statistically indistinguishable among these specimens. These data were interpreted to indicate a basic uniformity in the degree of taper of sterile axes, regardless of the presence or absence of secondary tissues.

Atypical taperings

The majority of specimens examined evinced an acropetal decrease in axial girth and therefore the slopes of the linear regression of Z_n versus x/L for these specimens were positive. Exceptions to this generality were seen for all six of the axes measured from a photograph of a specimen of *Cooksonia* (designated *hemisphaerica*, stored in the Buffalo Museum of Science; see Table 1) and for three zosterophyllophyte and three lycopod specimens just beneath bifurcations of axes (data not presented). Each of the six axes measured from a photograph of the Buffalo Museum specimen tapered basipetally, i.e., the width w of these axes decreased toward the base of each axis. As a consequence, the slopes of the linear regressions of Z_n versus x/L for these axes were negative as was the average slope (see Text-figure 5). In the case of six bifurcated zosterophyllophyte or lycopod specimens, the subtending axis to each bifurcation tapered acropetally but then increased in lateral dimension (over lenghts of from a few millimeters to two centimeters, dependent upon the specimen) until the point at which the two subtended axes on each specimen morphologically departed. For these six specimens, the degree of taper could not be determined in terms of regressions of Z_n versus x/L since no reliable measurements of regression slopes or y-intercepts were possible.

Changes in axial taper as a function of geological age

The degree of taper evinces a slight tendency to increase over evolutionary time, although the degree



Text-figure 5—Degree of axial taper, expressed by slope, m, of average linear regression equations for normalized section moduli (Z_n) versus normalized length of axes (x/L) (see Table 1), versus geological age of specimens. Data for zosterophyllophyte-lycopod genera ("Z + L") and for *Cooksonia* spp., *Cooksonia*-like specimens. *Ibyka amphikoma* and *Tetraxylopteris schmidtii* ("Other") are distinguished by symbols (see insert). Solid linear regression curve is for a regression of all (Z + L + Other) data points (n = 20); dashed regression curve is for regression of "Other" data points (n = 6). Negative value for degree of taper indicates a basipetal decrease in girth; positive values of degree of taper indicate an acropetal decrease in girth. Linear regression equations are provided in text.

of taper of lycopods and zosterophyllophytes appeared to change little as a function of geological age. These trends in the data are suspect, however, because of the comparatively few taxa for which reliable measurements could be made (n = 6) and because the data from *Cooksonia* and *Cooksonia*-like specimens likely weighted regressions due to the lack of data from Lower Devonian plant fossils. The average slopes of simple linear regressions of Z_n versus x/L for each category of axis listed in table 1 are plotted in Text-figure 5 as a function of geologic age. Each taxon is represented in this figure by as many different categories of axes as could be distinguished on the basis of the degree of taper, e.g., *Tetraxylopteris* is represented by two data points ("sterile" and "main"). Thus, regressions are biased by taxa that possess many levels of branching since each level of branching is represented by a datum. Linear regression of all the data yielded the regression formula: $DT = 6.28 - 0.015\ A$ ($r^2 = 0.567$, $n = 20$), where DT is degree of taper and A is age (in 10^6 years). Regression analyses of the data from zosterophyllophytes and lycopods ("Z + L") and from the remaining taxa ("Other") yielded $DT = 3.75 - 0.009\ A$ ($r^2 = 0.261$, $n = 4$) and $DT = 6.24 - 0.015\ A$ ($r^2 = 0.563$, $n = 16$), respectively.

DISCUSSION

Based on a comparatively limited number of measurements taken from a very few Devonian plant fossils, we feel that our method to quantify the degree of taper of fossil stems warrants further study and wider systematic application. Among its merits, this method permits the degree of taper to be computed even for comparatively fragmented specimens. Since taper is a morphological feature, specimens lacking anatomical details can be treated in the same manner as specimens for which anatomy is preserved. Another merit is that axes believed to represent different levels of branching within the same plant or from different plants can be directly compared both graphically and quantitatively. Finally, the method has the virtue that the manner in which taper is quantified can be interpreted in the context of the biomechanics of presumed columnar vertical stems and horizontally cantilevered lateral branches. This may be useful in attempts to discern whether evolutionary patterns exist that are adaptive in terms of the mechanical roles of stems and branches. Based on the limited data presented here, however, we feel that specific conclusions about the manner in which taper varies among different levels of branching in the taxa examined are unwarranted. We also feel that definite conclusions cannot be drawn concerning whether evolutionary trends exist in the degree of taper for Devonian plants. Some of our findings warrant comment, however, and are discussed below.

With the exceptions of a *Cooksonia hemisphaerica* specimen (for which measurements were taken from a photograph) and three bifurcated axes of zosterophyllophyte and three axes of lycopod specimens, every plant axis examined showed some degree of acropetal tapering regardless of whether secondary growth was present or not. The majority of observations is consistent with the fact that tapering can occur in the organs of extant species without benefit of secondary growth, although these organs are typically determinate in their growth in length. The determinate stems of inflorescences of numerous species and the petioles of pinnately compound leaves lacking secondary growth typically taper in girth (see Silk, Wang & Cleland, 1982; Niklas, 1991) while virtually all stems with secondary growth taper to some degree (McMahon & Kronauer, 1976; Bertram, 1989). In this regard, the pronounced taper of some fertile lateral axes, like those of *Tetraxylopteris*, was not surprising, particularly since these organs are determinate in growth and possess some secondary tissues. Likewise, the tapering of sterile, presumably main support axes of *Tetraxylopteris* is explicable on the basis of an increase in axial girth due to secondary growth. Surprisingly, however, the most robust axes of *Sawdonia*, *Leclerecqia* and *Crenaticaulis* tapered in like manner to those of *Ibyka* and *Tetraxylopteris* despite the fact that secondary growth is believed or known to be absent among the former three genera while no evidence exists to suggest that these three genera were determinate in their growth in length. Diffuse and persistent cellular division or enlargement of ground tissue cells could produce tapered indeterminate axes lacking secondary vascular growth. Similar phenomena have been reported for *Psilotum nudum* (Niklas, 1990) and for some species of palm (Rich, 1986). The developmental mechanism responsible for the tapering of axes of zosterophyllophyte and lycopod genera such as *Sawdonia*, *Leclerecqia*, and *Crenaticaulis* deserves special study.

The taperings of the Utica *Cooksonia*-like specimen and those of some bifurcated zosterophyllophyte-lycopod specimens yielded regressions with negative slopes, in the former case, or unmeasureable slopes, in the latter cases. These exceptions to the majority of observed patterns of taper highlight that the method presented here is sensitive to morphometric variations in axial girth.

In the case of bifurcated axes, a regional expansion of axial girth toward the distal end of the subtending axis on each specimen is not uncommon among fossils. When pronounced, however, the degree of taper cannot be adequately measured by our method since regression of the normalized section moduli versus normalized axial lengths is non-linear and so has no unique slope. A modified method to treat specimens with this morphology is being explored. The *Cooksonia*-like specimen illustrates that taper can be basipetal and that this "reversed" taper can be compared at least graphically with specimens evincing the more typical acropetal taper. The significance of a reversed taper is unclear and warrants further study.

In terms of its functional significance, tapering in the girth of stems can be advantageous under certain circumstances (Leiser & Kemper, 1973). Tapering can minimize the magnitudes of bending stresses experienced in vertical stems or cantilevered branches as a consequence of self-loading. This can be advantageous in plant organs that are anatomically similar throughout their length, as when secondary growth is lacking or poorly developed, because primary tissues typically deform under lower stress levels than do secondary tissues. Tapering can also distribute the magnitudes of bending stresses more or less evenly throughout vertical and cantilevered support members (Timoshenko & Gere, 1961). Once again this is mechanically advantageous in organs that are more or less anatomically homogeneous along their length. Also, provided that the degree of taper is optimized, the quantity of material (biomass) invested in the construction of stems and branches can be minimized. For these and other reasons, axial tapering provides mechanical benefit and may have been under selective pressure to evolve early in the history of plants that grew vertically on land. Visual inspection of the regression of axial tapering versus geological time (Text-figure 5) suggests that the degree to which some axes taper, particularly fertile determinate lateral branches, increased over the course of time. This warrants further investigation and will require detailed study of the manner in which tapering differs among the various branching levels of individual fossil plant species as well as extensive comparisons among the most tapered axes from a variety of species that are contemporary in geological time. Based on our limited data, we suspect that the main columnar axes that provide the bulk of mechanical support for each early Palaeozoic plant will evince a conservative degree of taper, particularly among species that are indeterminate in vertical growth, whereas the degree of taper will increase as higher levels of branching are studied within each plant or as geologically younger plants are examined. The degree of taper, therefore, will be size- and time-dependent and allometric analyses will be required to permit comparisons among taperings for different scales of organ-size and for organisms for different periods of time.

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