EEB 171: Collections of the Peabody Museum
Professor Leo Buss

Reconstructing *Calamites*: Building Giants from Fragments

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ABSTRACT

The height of the arborescent sphenopsid *Calamites* is reconstructed in this study based on patterns observed in its closest extant relative, *Equisetum*. Notable similarities in the anatomy, development, and phylogeny of *Calamites* and *Equisetum* suggest that the morphology of extant *Equisetum* can predict the morphological features of *Calamites*. Analyzing measurements of specimens from five different species of *Equisetum* show that there is a strong correlation ($R^2 = 0.7037$) between midpoint diameter and stem height. However, since *Calamites* possessed a secondary xylem that is frequently lost in fossil specimens, it was necessary to further evaluate preserved calamitean organic material. This material, from coal ball specimens, was measured and analyzed to determine whether a relationship existed between total stem diameter and pith diameter. A strong positive correlation was found between the latter and the former ($R^2 = 0.8584$). This relationship was used to predict the total diameter of *Calamites*, which was subsequently used to predict its height. The predicted height of *Calamites* ranges from 9 to 34 meters. Although the large difference in size and morphology between *Equisetum* and *Calamites* raises questions about the overall reliability of the procedure, nonetheless this study proposes a valid and practical method for reconstructing the hidght of *Calamites*.

INTRODUCTION

The complex wetland communities of the Carboniferous Period, approximately 290-260 million years ago, were the first truly structurally modern ecosystems and are some of the best understood in paleobotany (Greb, *et al*., 2006). The economic importance of coal has led to an abundance of information about the flora of the Pennsylvanian coal-forming period of the Upper Carboniferous (Greb *et al*., 2006). Yet despite a plethora of fossil specimens, understanding the plants they represent remains a complicated process. A prime example is *Calamites*, an arborescent sphenopsid prevalent during the Carboniferous Period that has fascinated scientists from the advent of paleobotany in the late eighteenth century (Eggert, 1962). Most fossil specimens are incomplete, due to fragmentation both through natural processes during their lives and during decomposition, and it is impossible for scientists to observe the plant in its original environment (Daviero and Lecoustre, 2000); thus, the accumulation of knowledge is necessarily a slow process contingent on discoveries of more complete specimens. The discovery of new fossil exposures and better-preserved specimens allow the refinement of previous inferences. The cylindrical pith casts of *Calamites*, for example, were originally thought to be representations of the outer surfaces of the stems (Janssen, 1939). It is now recognized that the pith casts were formed as sediment filled the central cavity and solidified before the more resistant xylem tissues decomposed, and reflect only the internal morphology of *Calamites* (Taylor and Taylor, 1993).

Fossil remains of *Calamites*, the primary resource in studying this extinct horsetail, are preserved in a variety of manners. Today, the term *Calamites* is used to refer to an array of preservation modes, including “impressions, compressions, and pith casts of the external surface of stems or of the central canal or pith” (Taylor and Taylor, 1993, p.320). As is the case of most plant fossils deposited during the Carboniferous, *Calamites* fossils were formed from organic material, frequently fragmented, that was deposited in swamps, mires, or levee banks that was subsequently covered by sand or mud and later compressed by subsequent sediment into thin layers of coal (Cleal, 1988). The term compression refers to a specimen where coalified tissue is still present; an impression lacks this tissue but leaves an imprint in the rock. Pith casts, which are mold-cast modes of preservation, are formed when the the internal part of the stem (pith) decays and is filled by sediment which is then mineralized; the tougher xylem later decays more slowly and is subsequently filled in by distinguishably different sediments (Taylor and Taylor, 1993). Coal balls, a rarer mode of preservation in which minerals in solution permeate the organic material before it is coalified, are vital resources in studying *Calamites*, as they preserve details of cell structure that are lost in compressions and impressions (Cleal, 1988). Coal ball peels are used to study these details; the fossilized organic material is transferred to clear, cellulose acetate sheets (Rothwell, 2005). The coal ball preserves the *Calamites*'s secondary xylem and serves as a source of evidence otherwise destroyed in the typical preservation process. The accumulation of fossil specimens in all these modes of preservation constitute a vital foundation for the process of widening scientific understanding of *Calamites*.

Fossils, however, are not the only source for inferences that can be made about extinct species. In *Calamites*, much of the understanding of its ontogeny and morphology is based on study of the extant horsetail *Equisetum*. Noting "manifest Equisetaceous affinities" (Scott, 1920, p.70) led scientists to classify *Calamites* in the same order (*Equisetales*) as present-day *Equisetum*, which is the only extant member of the family *Equisetaceae*. Comparing a range of fossil specimens of *Calamites* to modern *Equisetum*, Eggert (1962, p.119) observes that the anatomy of *Calamites* "is strikingly similar in its general features to that of extant species of *Equisetum*." He further notes, "as numerous authors have pointed out, the plant probably developed much like *Equisetum*" (p. 122). Thus, in his authoritative inquiry into the overall ontogeny and morphology of *Calamites*, the developmental processes he identifies are supported by observation of similar processes in *Equisetum*. Furthermore, these also form the basis for the hypotheses he makes about processes that cannot be confirmed by the fossil record. The evident similarities between the two genera provide a crucial source of information in studying extinct these plants.

Still, there are at least three major differences between *Calamites* and *Equisetum*. The first two "involve the much larger size and the presence of secondary stellar and cortical tissues in the fossil forms" (Eggert, 1962, p.100). Estimates of the calamitean height fall into a range from 5 meters (16.4 feet; e.g., Greb *et al*. 2006) to 24.4 meters (80 feet; e.g., Niklas, 1996). *Equisetum*, on the other hand, is significantly smaller, and falls between 12.9 cm (*E. scripoides*) and approximately 8 meters (*E. giganteum* and *E. myriochaetum*), though these latter are acknowledged as being exceptionally tall for the genus (Hauke, 1963). The secondary xylem observed in *Calamites* is simply not present in *Equisetum*. This woody secondary xylem was at least 12.0 cm thick (Taylor & Taylor, 2003) and would have been essential for stability at the heights to which *Calamites* is estimated to have grown (Spatz, *et al*., 1998). The third major difference is the presence, in *Equisetum*, "of a ribbed peripheral ring of collenchyma or unlignified sclerenchyma with a high structural Young's modulus" (Spatz *et al*., 1998). The differences between *Equisetum* and *Calamites* do not invalidate the use of *Equisetum* as a model; however the stuctural differences must be carefully considered when extrapolating from modern *Equisetum* to *Calamites*.

This paper reconstructs the overall height of *Calamites* based on a nuanced understanding of the similarities and differences between *Calamites* and extant *Equisetum*. The observations and inferences made by other researchers indicate that both the anatomy and development of *Equisetum* and *Calamites* are similar. Thus, relationships in *Equisetum* may be used to predict the morphological aspects of *Calamites* that cannot be determined from fossil evidence, such as the height of the intact plant. By adjusting the findings for the known differences between the two species, this study takes into account their potential confounding effects, such as the absence of measurable secondary xylem in pith casts. The validity of the predicted height derived from these methods is to be credited to the degree that the assumption of equivalency between *Equisetum* and *Calamites* is valid.

MATERIALS AND METHODS

Nine herbarium specimens representing five species of *Equisetum* were measured. These specimens were borrowed from the Yale Peabody Museum's Herbarium collection and were comprised of specimens originating from the herbariums of Yale University (YU) and the Connecticut Botanical Society (CBS), consisting of YU.008066 (*Equisetum variegatum)*, YU.007861 and YU.007858 (*E. hyemale*), CBS.01012 and CBS.01014 (*E. flaviatile*), YU.007717 and YU.007718 (*E. sylvaticum*), and YU.007645 and YU.007643 (*E. arvense*). Stem length, stem diameter, number of ribs, internode length, and average internode length of each sample were measured to +/- 0.1 cm using a ruler. The stem length was determined by measuring each specimen's cauline axis, the length of stem that is above ground, from the first internode above the root growth and including the strobilus. The stem diameter was measured at the middle of the internode that was equidistant between first internode and the tip of the strobilus. The number of ribs was determined by counting the visible vascular ribs of that same internode. Finally, the internode length was determined by measuring each segment between nodes, as identified by the indented circumferential ring on the stem from which the branches originated. These internodes were averaged to derive the average internode length.

Eleven specimens of *Calamites* housed in the Yale Peabody Museum's Paleobotany Collections were also measured (Yale Peabody Museum (YPM) 35609, YPM 40030, 23201, YPM 45160, YPM 49147, YPM 35610A, YPM 35610B, YPM 10475, YPM 3867, YPM 711, YPM 733, and YPM 703). These specimens represent a variety of preservation modes, including compressions, impressions, and pith casts. Measurements of length, diameter, circumference, number of ribs, ribs per centimeter, internode length, average internode length, and number of nodes were made to +/- 0.1 cm using a ruler. The length measured was the length of the specimen, though there were no fossilized specimens of complete plants. The diameter, on flattened specimens, was measured as the width at the midpoint. On pith casts, diameter was measured at the widest point. The circumference was measured only in pith casts and determined by encircling the specimen with a wire and recording the length of wire used. The number of ribs was recorded in flattened specimens by counting the visible ribs across the width at the midpoint of the specimen. In pith casts, it was determined by counting the number of ribs on the surface area of half the circumference, when this area was visible. When this was impossible, the number of visible ribs was recorded and a measurement of the visible counted area was taken. The ratio of ribs per centimeter was also calculated in order to control for differences between these measurements. Internode length was measured on specimens that contained more than one node. When multiple internode lengths could be determined, these lengths were averaged to derive a single characteristic internode length for the sample. Finally, the number of circumferential scars indicating the presence of a node (Daviero and Lecoustre 2000) was counted.

Several specimens of *Calamites* that retained their wood were measured. These included three coal ball peel slides, YPM 44755 (with two measured specimens), YPM 3877, and YPM 2582, and one coal ball YPM 49674. In the slides, diameters along the major and minor axes of the total sample, as well as the for the pith, were measured to (+/- .1 cm). The total measurements were determined by measuring from the external edge of the darker brown coloring (the wood) at the widest points of axes perpendicular to each other. The pith measurements were measured from the cessation of the darker coloring across the light colored center (the pith) at the corresponding axis of the total measurement. The total stem diameter and the pith diameter of the coal ball was measured at the widest point.

RESULTS

Table 1 shows the measured morphological parameters for modern *Equisetum*. These parameters were examined for relationships that could be used to predict morphology in *Calamites*. Combinations of these variables were plotted; the most convincing relationship was that of diameter and length. A plot of the *Equisetum* diameters and their respective length showed a positive correlation (Figure 1). Linear regression shows a linear relation ship of stem length, L_e, and total diameter, d_{total}, with a correlation of $R^2 = 0.7037$.

$$L_e = 79.867d_{total} + 16.049$$

In order to use this relationship predictively, however, it was necessary to determine the true diameter of the *Calamites* specimens. Because most fossil specimens represent only the pith, it was necessary to determine whether a relationship between the amount of secondary xylem and the amount of pith existed in order to estimate the total diameter of all the *Calamites* stem specimens. This analysis was based on measurements taken from the coal ball peel slides and coal ball (Table 2). The coal ball peel slides and the coal ball stem were preserved in an ellipse due to the diameter deformation (lateral expansion) related to compression. The diameters of circles with equivalent areas were then calculated and used as an estimate of the unflattened total and stem diameters of the specimen. The diameter for the slide specimens was determined by solving for the area of the total ellipse and the area of the pith ellipse, using the formula $A=\pi ab$, where A is area, a is the major axis, and b is the minor axis. These areas were then solved for the diameter by equating $A=\pi ab$ and $A=\pi r^2=\pi(d/2)^2$. Thus, true diameter $d = 2\sqrt{(ab)}$.

A strong linear relationship, $R^2 = 0.8584$, was observed (Figure 2) between the pith diameter, d_p, and the total diameter, d_{total}.

$$d_{total} = 2.4019d_p - 0.0461$$

Therefore, to determine the overall height, it is necessary to first determine the total diameter of the specimen. By substituting the function for d_{total} into the equation for L_{eq}, the total diameter can be included in the overall predictive function.

Specimen	**Length (cm)**	**Diameter (cm)**	**# Ribs**	**Avg Internode length (cm)**	**Ribs/cm**
YU.008066 (*E. variegatum)*	36.6	0.2	6	4.0	30.0
YU.007861 (*E. hyemale*)	85.5	0.8	14	6.4	17.5
YU.007858 (*E. hyemale*)	25.0	0.1	3	1.8	30.0
CBS.01012 (*E. flaviatile*)	62.0	0.8	7	2.7	8.8
CBS.01014 (*E. flaviatile*)	87.0	0.5	9	3.3	18.0
YU.007717 (*E. sylvaticum*)	30.0	0.3	6	3.5	20.0

YU.007718 (*E. sylvaticum*)	34.5	0.2	8	2.6	40.0
YU.007645 (*E. arvense*)	19.6	0.1	4	1.5	40.0
YU.007643 (*E. arvense*)	27.8	0.3	5	1.9	16.7

Table 1. Measurements of *Equisetum.*

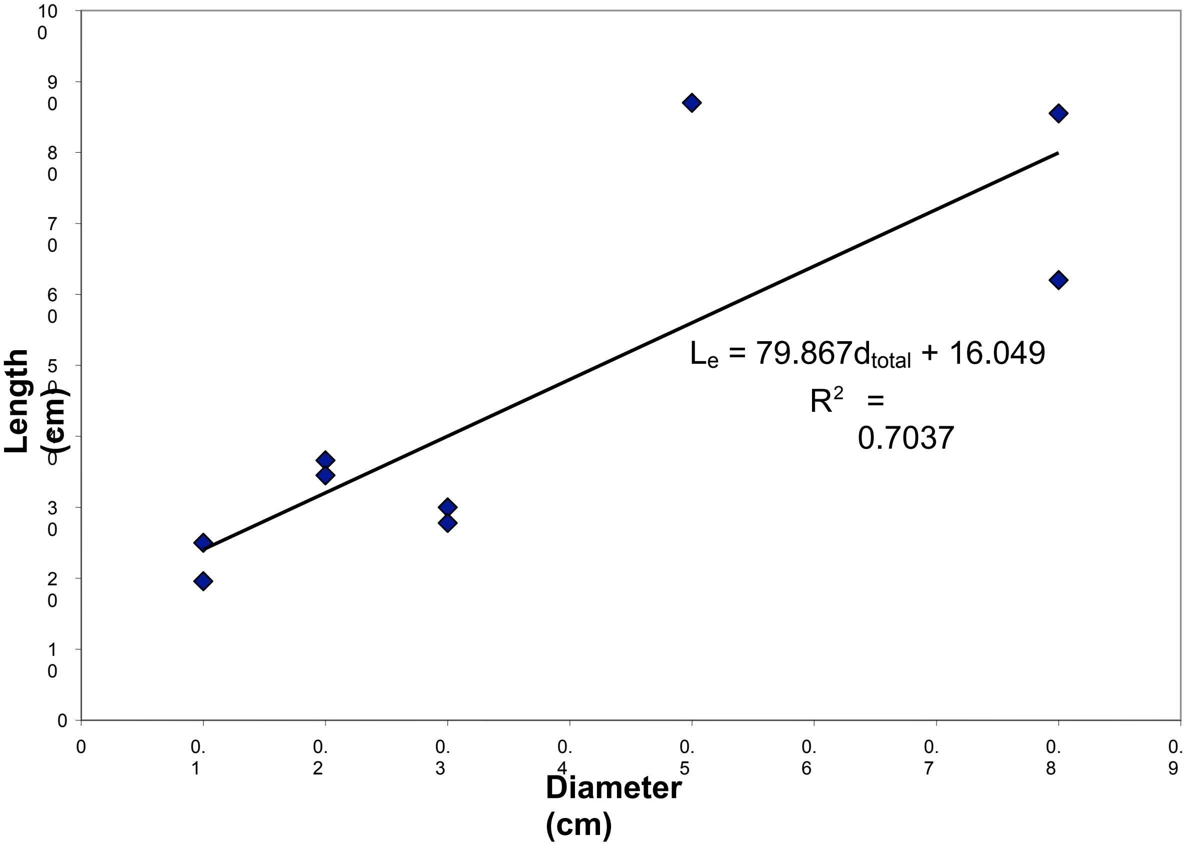


Figure 1. Diameter vs. length in *Equisetum*.

Specimen	Axis A – total (cm)	Axis B - total (cm)	Axis A - pith (cm)	Axis B - pith (cm)	Total diameter (cm)	Pith diameter (cm)
YPM 44755 (1)	0.7	0.5	0.3	0.1	1.2	0.4
YPM 44755 (2)	1.4	0.6	0.6	0.2	1.8	0.7

YPM 3877	0.6	0.4	0.4	0.2	1.0	0.6
YPM 2582	1.6	1.1	1	0.6	2.7	1.5
YPM 49674					5.5	2.0

Table 2. Measurements of *Calamites* coal ball peel slides and the coal ball (YPM 49674).

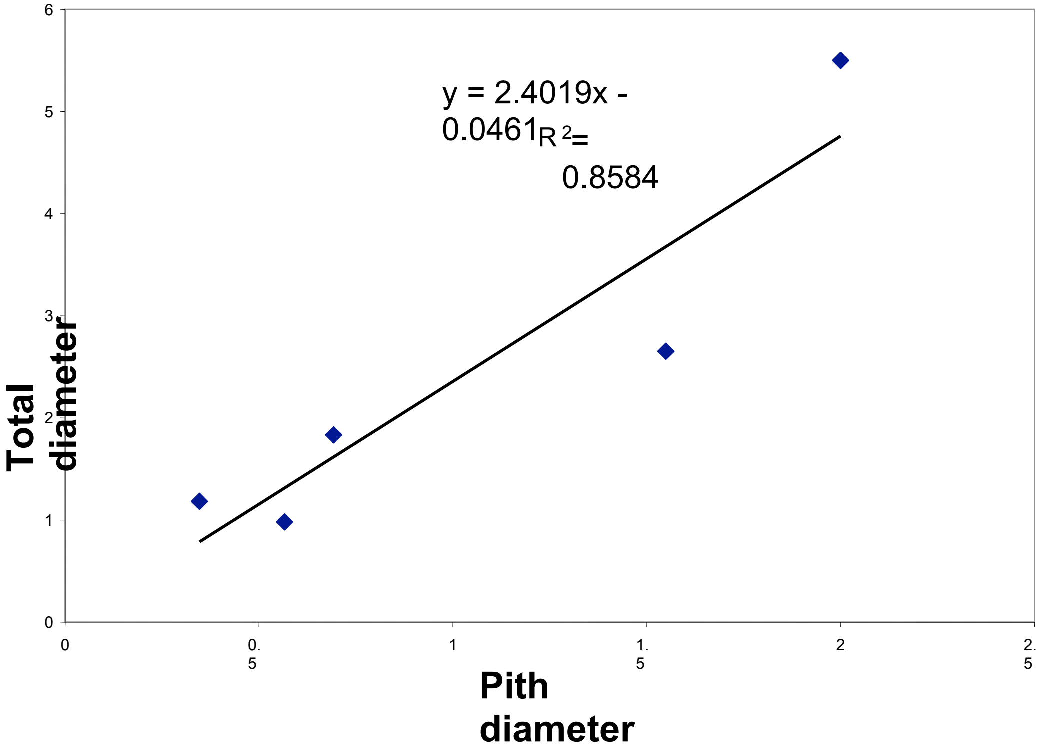
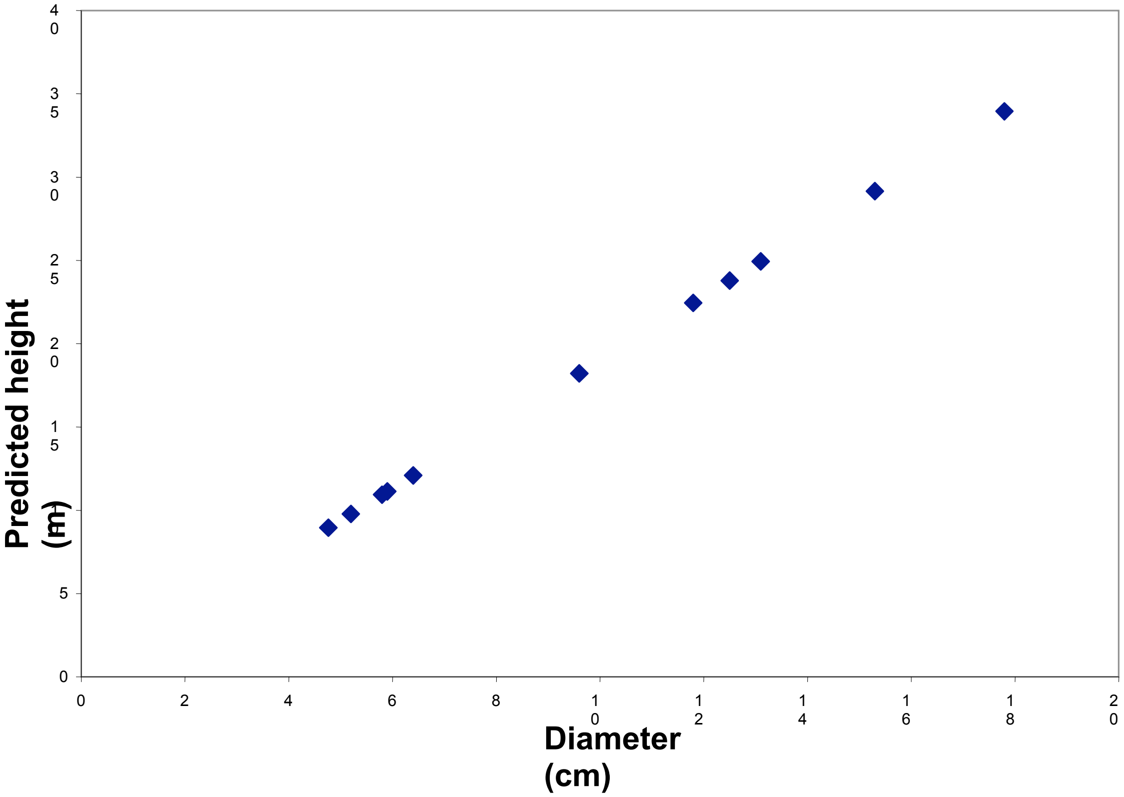


Figure 2. Pith diameter (cm) vs. total diameter (cm) in coal ball peel slides and coal ball.



Thus, the function to determine height is

Figure 3. *Calamites*: Pith diameter (cm) vs. predicted height (m).

ces to

$$H_c = 191.833d_p - 19.731$$

where H_c is the estimated hight of *Calamites*.. The heights as found by this function are represented in Figure 5 and lie in a range of 8.947-33.949 m.

DISCUSSION

The height range of approximately 9-34 meters proposed by this paper is generally consistent with the heights given in other estimates for calamitean height, which range from 5-24.4 m (Table 3). However, the maximum exceeds previous prediction by as much as 10 meters. The wide variation in predicted heights, not only between other authors but within these results, requires explanation. Because other authors have not provided details of their methodology these cannot be accounted for in the

Author	Predicted *Calamites* Height
Greb, *et al*. (2006)	5 meters minimum
Daviero & Lecoustre (2000)	10 meters minimum
Hickey (2003)	15 meters
Janssen (1945)	50 feet (~15 meters)
Langford (1958)	50 feet (~15 meters) minimum
Raven, *et al*. (1999)	18 meters minimum
Taylor & Taylor (2003)	20 meters
Niklas (2003)	80 feet (~24.4 meters) maximum

Table 3. Other authors' predicted *Calamites* heights.

analysis; obviously, the reasons for differences between the predictions in this paper and those given in other studies cannot be completely enumerated. However, there are many concrete considerations that must be accounted for in evaluating the results of this paper, including concerns regarding potential sources of error in both data collection and methodology.

Potential error in data.—A significant potential source for error is the small sample size. The survey of *Equisetum* used only nine specimens and was limited to five species; a more representative sample would include many more specimens. This would minimize the impact of the variation among individuals both within and between species. Beyond mere numbers, increasing the sample size in terms of species and age would also increase the representativeness of the results. This is imperative in using extant species as models because the the limited availability of fossil specimens will always severely restrict the available fossil data. The fragmentation of fossil specimans makes it virtually impossible to determine species and age for a particular specimen. There are thought to have been at least 30-40 species of *Calamites* (Leo Hickey, personal communication), yet it is extremely difficult to differentiate them from the fragments in the fossil record. As is observed in *Equisetum*, there may have been considerable height variation between these species, as well as differences in the relationships between diameter and height. Increasing the sample size to include all extant species of *Equisetum* would be a step toward including all possible relevant information. Including a wider range of ages among specimens is also essential in this endeavor. Obviously, plants vary in size depending on age and stage of growth. As there is no way to determine the specimen's age from the fossil specimens or coal balls, including a variety of specimen ages ensures that the resulting predictions are generally reliable across a population of mixed ages.

The analysis of the secondary xylem within *Calamites* would likewise benefit from a larger sample size. Five measurements from four different sources may be inadequate to quantitate the true relationship. The conclusion that the relationship between total diameter and pith diameter is linear was based on measurements from a limited number of specimens, yet it is possible that larger samples would reveal that the relationship is logarithmic or even exponential.

Because of the small size of the *Equisetum* specimens and the preserved *Calamites* organic material, more precise measurement techniques would result in a more accurate predictions. This study employed a standard centimeter ruler with 10 millimeter markings per centimeter. However, it was frequently noted that the specimens were so small that many measurements did not adequately reflect differences in size. For example, many *Equisetum* leaves were marked as 0.1 cm in cases where they were clearly between 0.0 cm and 0.1 cm. Other leaves that were between 0.1 and 0.2 cm, but closer to 0.1, were also marked as 0.1. Because *Equisetum* was used to predict the height of something much larger, accuracy on the smaller scale is especially important for precise predictions of height. More accurate instruments such as digital calipers would produce measurements accurate in the micrometer range. Digital image analysis of coal ball peels would produce more accurate delineation of the boundary between the secondary xylem and the matrix and of the boundary between pith and secondary xylem. This would not only allow more accurate measurements, but might allow many more samples to be processed as well.

In addition, the locations at which some measurements were made are potentially confounding. In this study, the diameter of *Equisetum* was measured at the midpoint of the specimen. However, other authors have suggested that it is the basal diameter that is most strongly correlated to length in *Equisetum* (Daviero, *et al.*, 1996). Therefore, the midpoint diameter may not be as strongly predictive of overall height as the basal diameter. However, in the context of this study, this may not be such a large concern. Because it is impossible to tell what part of the tree the fragmented fossils belonged to, measuring the midpoint of *Equisetum* may most accurately reflect this uncertainty. In *Equisetum* it is recognized that the stem diameter is largest at the base of the stem and "decreases after the first proximal one-sixth of the stem length evaluated in the number of internodes" (Daviero, *et al.*, 1996). Thus, the unknown location of the fossil specimens with respect to the overall stem may be more likely to be represented by the midpoint than the basal diameter.

Potential error in methodology.—A more fundamental question is whether the method used by this paper can be expected to accurately predict the height of *Calamites*. The basic assumption underlying the method used in this paper is that modern *Equisetum* develops in a manner that is similar to *Calamites*. However, considering the evolutionary distance between them, this is not necessarily the case. *Equisetum* is believed to "have diverged—or arisen by anagenesis—in the Tertiary from an older genus, *Equisetites*, which dates to the mid-Permian" (Des Marais *et al.*, 2003, p. 737). While it has been suggested that there was "an ancient relationship between Equisetaceae and Calamitaceae" (Des Marais *et al.*, 2003, p. 747), there is no direct link as has been established between *Equisetites* and *Equisetum*. Thus, the notable differences between *Equisetum* and *Calamites* may ultimately be more revealing than their similarities. There is obviously no way to observe the growth and development of *Calamites* and its development; although hypotheses can be made regarding the process of growth, their certainty is necessarily limited. It is difficult to know whether other characteristics in *Calamites* are indeed represented in *Equisetum*. It is accepted that common characteristics are likely to be ancestral, i.e. represent homology; when dealing with morphological characters, however, the possibility of convergent evolution (homoplasy) must be considered. The traits *Equisetum* ultimately carried may be significantly different from those found in *Calamites*.

Thus, the most cautious predictions of calamitean height are those that attempt to minimize this uncertainty. Given the concerns both with the scrutability of the fossil record and the representativeness of *Equisetum*, it is necessary to approach a reconstruction of *Calamites* from a third perspective: mechanics. Spatz *et al.* (1998) investigated the biomechanical characteristics of *Calamites* based on values found for the equivalent characteristics of living plants, for example, using biomechanical characteristics of several species, including *Equisetum*, to derive a modulus of elasticity for *Calamites*. A variety of hypothetical situations with varying wind loads and weights were explored, including a comparison with the Euler buckling length the authors calculated for the

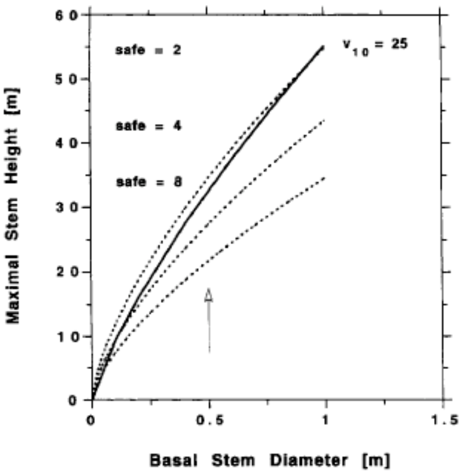


Figure 4. The maximal height of a reconstructed hollow-stemmed sphenopsid, from Spatz, *et al.* (1998). The solid line represents the maximum height with steady wind loads of 25 m/s 10 m above the ground in open terrain. The broken line represents the Euler buckling length with safety factors of 2-8. The arrow represents the typical basal diameter of *Calamites*' stems, .5 m.

stem, to determine the viability of the reconstructed height. Spatz *et al*. (1998)'s method predicted "the maximal height of a tree extending to the top of a dense canopy as a function of the basal diameter of the stem" as can be seen in Figure 4 (Spatz *et al*., 1998, p.75). The values derived from their methods provide a further insight into the range of predicted heights given in this paper. The range of total diameter from the *Calamites* in this paper was 11.4 – 42.7 centimeters (as determined using this paper's function for total diameter based on pith diameter), a range below the "typical" basal diameter provided by Spatz *et al*. (1998). Although the authors provide no precise values for comparison, after examining the graph illustrating their maximum height (shown in Figure 4), it appears that the range of 9 – 34 meters proposed here exceeds the corresponding maximal heights even under conditions of low wind stress. Although these calculations are based on assumptions about factors such as density of the trees, tensile strength of the wood, and the strength of the rhizomal support networks, it is telling that Spatz *et al*. ultimately provided a fairly liberal estimate of the maximal height. That the reconstructed height range as found in this paper exceeds even this estimate is undeniably significant.

However, this factor alone does not invalidate the range predicted in this study; rather, it suggests that the technique used to predict the height must be refined. The values of this paper exceed Spatz *et al*. (1998)'s predictions by only a few meters at either end of the range. This may reflect the inaccuracies of sample size and measurement in this work rather than a fundamental difference in the predictions. Additionally, the range given here follows the same basic trajectory as the maximum height range. That this paper predicts a height so close to those of Spatz *et al*. (1998) suggests that it has captured an essential element in the reconstruction of *Calamites*. Although this maximal height range is by no means in and of itself conclusive, ultimately, comparing the results with the mechanics of *Calamites* provides a compellingly concrete procedure to determine the accuracy of the method and the results.

CONCLUSION

In the uncertain process of reconstruction, this study succeeds in filling an obvious gap. While many authors have reconstructed calamitean height, few have published their methodology. In doing so, this paper not only contributes to a fuller understanding of the factors that must be considered in a height prediction, but provides a means to test the underlying assumptions and accordingly refine this method. Comparison of the 9 – 34 meter heights predicted in this paper to a previous mechanical study suggests that this range is likely to be somewhat high. However, this fact alone does not contradict the usefulness of this inquiry. Rather, it suggests that further studies utilizing this method may succeed in predicting feasible and cautious values for *Calamites* heights.

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