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STROBILAR COMPLEXITY IN DEVONIAN SPHENOPSIDS

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THE SCANTY DIRECT evidence of Sphenopsids in Devonian formations appears in sharp contrast with the extensive knowledge of Sphenopsids in Coal-Measures time. With the exception of the remarkable Pseudoborniales from the Upper Devonian of Bear Island, that has formed until now a distinct class, our best source of information is the Proto-Articulatae from Middle Devonian of Norway, Germany, Spitsbergen, and Belgium.

Yet recently a new Sphenopsid cone, *Eviostachya hoegi* Stockmans from the Upper Devonian of Belgium, has been described (Leclercq, 1957). The cone was 5.5 cm. long and 0.8 cm. wide. The observations based on 31 compressions and one petrification have afforded the opportunity of a combined study of the morphology and the anatomy of the cone, including the sporangiophores's stalk and the mode of division of the latter. The peduncle that supported the cone and the axis of the cone had a triquetrous strand of solid wood. The sporangiophore at its very base had an isocetes triangular bundle which further up divided into three strands that became tangentially elongated. Near the apex each strand divided again into three minute bundles which supplied nine segments. The whole organization revealed combining characters of Sphenophyllales and Hyeniales, rather than affinities with Calamitales.

The following features of the cone indicated Sphenophyllales affinity: a triquetrous strand of solid wood without pith in the peduncle and the axis of the cone; superposed whorls of six sporangiophores attached in three pairs; constriction at regular intervals marking the position of the whorls. At the same time, *Eviostachya* undoubtedly approached the Proto-Articulatae in its terminal pendulous sporangia, and in the absence of bracts between the fertile whorls.

This very distinct type of strobilus had sporangiophores with a trisected elaborate head. Each sporangiophore supported nine segments disposed in two circles: an inner circle made of three short segments bearing nine sporangia, and an outer circle consisting of six long segments bearing 18 sporangia; altogether 27 sporangia when none aborted. Spiniform appendages were inserted at the point where the segments curved down; the appendages fixed on the short segments were the longest, stoutest, and most erected.

It is a striking fact that a complex cone such as *Eviostachya* should occur at so ancient a horizon as the Upper Devonian. Such a peculiar circumstance led us to look at the morphology of the Proto-Articulatae from a new point of view.

To serve as a base of comparison with the new species that will be described, a

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short summary of the present state of knowledge of the Proto-Articulatae is given. They were flourishing mostly in Middle Devonian time. So far three genera have been distinguished, *Hyenia*, *Calamophyton*, and *Hyeniopsis*.

The habit of *Hyenia sphenophylloides* Nathorst (1915) and *H. elegans* Kräusel and Weyland (1926, 1929) is known; the plants had a stout horizontal rhizome from which upright shoots, scarcely dichotomized, arose individually. The leaves were several times divided in more or less regular dichotomy. *H. elegans* had a fertile shoot that consisted of sporangiophores which dichotomized *once* forming *two single* arms curved down with two to three elongate anatropous sporangia at the end of each arm.

The habit of *Calamophyton* is still unknown. The most completed specimens consisted of a stout erect main axis which branched initially into a few axes of very much the same size, some of which were dichotomized. The leaves were once to several times divided (Kräusel and Weyland, 1926, 1929). The fertile twigs were much like those of *Hyenia*. The sporangiophores dichotomized *once* forming *two single* arms with the tips recurved and each bore one anatropous sporangium on *Calamophyton primaevum* Kräusel and Weyland (1926, 1929) and two pendulous sporangia on *C. renieri* Leclercq (1940).

An abundance of *Calamophyton* collected in the Lower Givetian of Belgium offered an opportunity to define accurately the morphological features of the sporangiophore in a new species, *Calamophyton bicephalum* Leclercq and Andrews (1959). The holotype is a fertile branch system that reproduced the general habit of the genus. Several sporangiophores have been carefully dissected under the binocular, and they appear branched in an upper and a lower segment at a point about one-third of the way between its point of attachment and its apex. Each segment was erect and rigid. It supported three short side-stalks fixed at two different levels, the first stalk usually being given off at a lower level than the two others that appear to be given off simultaneously. Each stalk bifurcated in two short pedicels which bore an anatropous sporangium hanging over towards the twig axis. Most frequently the erected rigid segment of the sporangiophore ended in a short irregular dichotomy. As a whole the sporangiophore in *C. bicephalum* bore twelve sporangia, when none of them aborted, and it was a three-dimensional organ. The leaves were also three-dimensional appendages.

Fertile specimens of *Hyenia* have not been found frequently. The German type-specimens described by Kräusel and Weyland (1926, 1932) since World War II are no longer available. Another specimen found in Belgium (Leclercq, 1940) confirms the usual rhizomatous habit of the genus; yet it differs from the Germans' in a rather striking fashion, in that the distinctive terminally fili-form appendages prolonged the sporangiophore. In that peculiar feature, the Belgian *Hyenia* had more in common with *Eviostachya hoegi* than the other species. The reinvestigation of that unique specimen formerly described as *H. elegans* is in the course of completion. Though found *in situ* it is not very well preserved, for in the course of embedding the sporangiophores have been disturbed from their initial position. Nevertheless, selected sporangiophores on part and counterpart were uncovered; they have shown: sporangiophores given off *by pairs*, apparently three pairs in a whorl; successive whorls superimposed; sporangiophores apparently trisected; two anatropous sporangia at the end of each arm; conspicuous filiform erected appendage, single or dichotomized, fixed where the arms or stalks bent down. According to these peculiar features, a new specific name is proposed: *Hyenia complexa*.

Considered solely from the point of view of the organization of the sporangiophore, Upper and Middle Devonian Sphenopsids were remarkably elaborate; the sporangiophore as a whole produced 27 sporangia on *Eviostachya hoegi*, 12 on *Calamophyton bicephalum*, very probably 12 also on *Hyenia complexa*. Compared with the two latter, the great peculiarity of *Eviostachya* consisted of the tangentially expanded trichotome head of the sporangiophore, formed by the robust curved segments which however were not fused in a scale, and the two concentric circles of sporangia. Moreover it was differentiated in a distinct cone.

With their complex sporangiophores, *Calamophyton bicephalum* and *Hyenia complexa* differed outstandingly from the other known species. Did they represent differentiated species within their respective genera, or the typical organization of the two genera cleared off on the base of a better preserved material and the use of a new technique of uncovering? In any case it appears that a reinvestigation of the old material so far described is desirable.

The strobilar complexity of the Upper and Middle Devonian Sphenopsids undoubtedly throws a new light on the Proto-Articulatae. It becomes evident that forerunners with less modified sporangiophores should have preceded in time the advanced Proto-Articulatae. In relation to this, it is of interest to mention compressions found in the Lower Devonian of west Siberia that might have belonged to a precursor of the Articulatae. The new plant named *Protohyenia janovii* Ananiev (1957) consisted of fragmentary sterile and fertile shoots, the external aspect of which was ribbed; the ribs did not alternate at the nodes. The leaves were segmented by successive irregular dichotomies and showed a marked tendency to an arrangement in superposed verticils.

The most remarkable feature of the plant was in the terminal position of the pair of erected sporangia located at the tip of each segment of the divided lateral appendage. In form and in size, the latter was like the sterile leaf and it is possible that both organs were homologous. Ananiev tends to interpret the ribbed surface of the axis as being in relation with a probable triangular or stellar shape of the stele. On the other hand, the Russian author interprets five twigs disposed more or less parallel on the rock as suggesting a rhizomatous habit.

The affinity, suggested by the author, of *Protohyenia janovii* with *Hyenia* could be justified on the basis of the plant having a ribbed axis and a tendency to a verticillate disposition of the dissected leaves. Yet as long as the anatomy of *Protohyenia janovii* is not known, and the way the leaf-bundles are given off, some possibility remains that the plant should have analogy with primitive types of Ferns.

The discovery in the Lower Devonian of an undoubtedly Sphenopsid plant bearing terminal erected pairs of sporangia should be of primordial importance, as showing a precocious type of sporangia preceding the bending down of the segments and pendulous position of the sporangia. Such a view has been argued by W. Zimmerman (1938, 1952) in his "Telome Theory." We do not yet possess sufficient data for attempting to trace such a line of evolution. However in relation to this, it is of interest to mention that in Belgium, *Calamophyton* and *Hyenia* remains have been found at the lowest part of the Couvinian, which represents the base of the Middle Devonian (Stockmans, 1940). This fact foreshadows the finding of Proto-Articulatae's precursor in the Lower Devonian.

In seeking to understand the facts, it appears that the fructifications of the Devonian Sphenopsids hitherto described seem to approach the Sphenophyl-

lales more than the Calamariales in most of their characters. They give an impressive view of the advanced structure already reached in Devonian times by that synthetic race of plants which was flourishing in the Coal-Measures time. On the other hand, they project the root of the Articulatae much farther back in Early Palaeozoic.

THE PHYLOGENETIC SIGNIFICANCE OF DICHOTOMOUS VENATION IN ANGIOSPERMS

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INTRODUCTION

MORPHOLOGICAL SURVEYS HAVE revealed the persistence of primitive types of tracheary elements, carpels, and stamens in certain members of the Ranales and have thus contributed to a better understanding of the phylogenetic trends of specialization of these structures in the angiosperms (3, 14). In contrast, theories and opinions differ widely in respect to the origin and phylogeny of the foliage leaf. Was the prototype of the angiospermic leaf a dichotomously veined appendage which originated, like the megaphylls of ancient ferns and pteridosperms, from an overtopped system of "cauloids" or "telomes"? Some authors, e.g. Hallier (9), Lam (12), and Van der Hammen (10), maintain that "traces of ancient dichotomies" may still be seen in the pattern of branching of the *main veins* in the leaves of certain modern angiosperms. Bugnon (6) concluded that foliar vein dichotomies represent an "atavistic tendency." Other authors, however, on various grounds, completely reject the telome concept as an explanation of the origin of the foliage leaves in angiosperms (13, 15).

Many years ago, Sinnott and Bailey (19) proposed the idea that the primitive type of leaf in angiosperms was a three-lobed, palmately veined appendage attached at a trilacunar node. They also postulated that if a palmate venation pattern is primitive, the angiosperms probably arose from a coniferous rather than a cycadean stock. However, in a recent paper Bailey (4) has re-evaluated the accumulated evidence from nodal anatomy with particular reference to the assumed primitiveness of the trilacunar node. His survey shows that a large proportion of angiospermic cotyledons, as well as the foliage leaves of certain primitive ranalian genera, are vascularized by two independent traces associated with a unilacunar node. He concludes that this type of nodal vasculature, which commonly occurs in the lower Pteropsida, is probably primitive in the dicotyledons and that it is no longer possible to derive *all* unilacunar nodes from trilacunar ones. Certain plants illustrate that reduction from the trilacunar to the unilacunar type of node has occurred, but the factors responsible for such reversible changes in evolution are obscure at present.

A sadly neglected aspect of the phylogeny of vasculature in angiospermic leaves is the systematic study and interpretation of venation patterns (7, 18,