

## Division Rhyniophyta - Upper Silurian to Middle Devonian

Among the oldest convincing fossils of early vascular land plants are those of the Division Rhyniophyta. The members of this division consist of: (1) simple axes with cuticle, stomates, epidermis, cortex and a terete (circular) centrarch xylem (xylem development occurs from the center of the stem to the periphery), without well-developed appendages or roots; (2) simple, isotomous branching systems to anisotomous, dichotomous, pseudomonopodial systems with up to four or five orders of branching, whole plants rarely exceeding ten centimeters; (3) sporangia globose to almost reniform (kidney-shaped) with longitudinal dehiscence; (4) spores with sporopollenin and distinct trilete marks on their proximal side from their placement in the tetrad. These contain the most morphologically primitive plants as well as the oldest, suggesting that morphological complexity diversified from the simplest parenchymatous forms during the middle to upper Silurian periods. Likely the Rhyniophytes disappeared when their derivatives modified to more complex forms and diverged from this primitive assemblage.

Selected members of this division include:

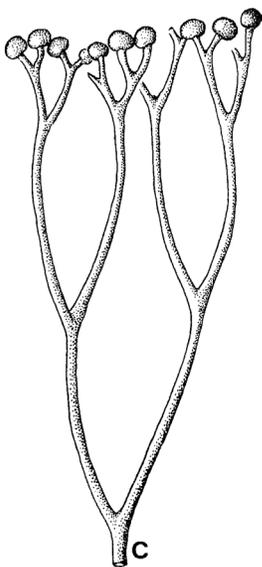
*Cooksonia*  
*Steganotheca*  
*Uskiella*  
*Rhynia*  
*Aglaophyton*  
*Horneophyton*  
*Taenioocrada*  
*Hedeia*  
*Ranalia*  
*Yarravia*

terminal dichotomies: *Hostinella*  
gametophytes of Devonian age:  
*Sciadophyton*  
*Lyonophyton*

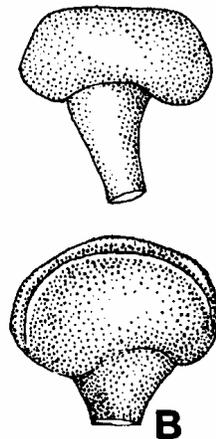
also:  
*Nothia*  
*Hicklingia*  
*Dutoitea*  
*Eogaspesia*

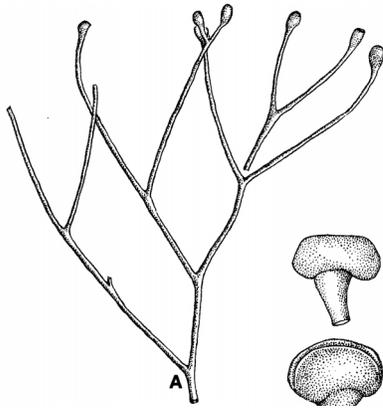
### Noteworthy Representatives

*Cooksonia* - Middle Silurian to Middle Devonian



Plants of *Cooksonia* are small, slender, freely dichotomizing axes few cm in height in the most primitive species consisting of a single dichotomy. The stems are slender with single, thin vascular strand in the center. The sporangia were small globose to reniform in shape, with terminal, longitudinal sporangia. Tracheids were not found in fertile axes originally, but were found in similar vegetative axes. Little is known of their vasculature, but tracheids appear to have annular thickenings. Although there are usually only a few orders of branching, up to four orders of branching occur in some Lower Devonian (Emsian) specimens. Many sporangia are short and wide, almost reniform, with longitudinal dehiscence. Spores are smooth with a trilete mark. Oldest specimens appear to be middle Silurian (Wenlockian) in age (420 MYA).



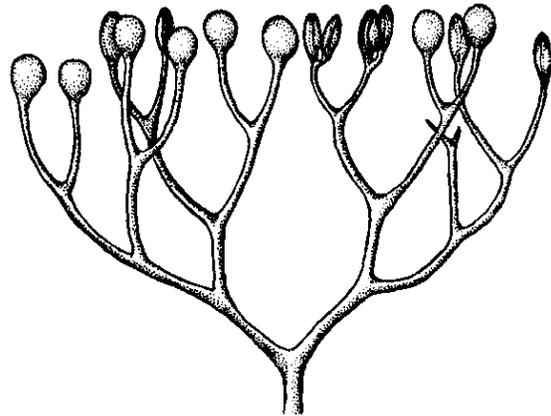


*Steganotheca* - Upper Silurian

*Steganotheca* is a somewhat more complex appearing plant than *Cooksonia*, with greater branching and an overall bushier appearance. Axes are isotomous axes, 5.0 cm tall. Sporangia are terminal with tapering walls and apparently terminal dehiscence. The central strand seen in compressions suggests a vascular cylinder. The nature and identification of tracheids in this genus has, however, never been described.

*Uskiella* - Lower Devonian

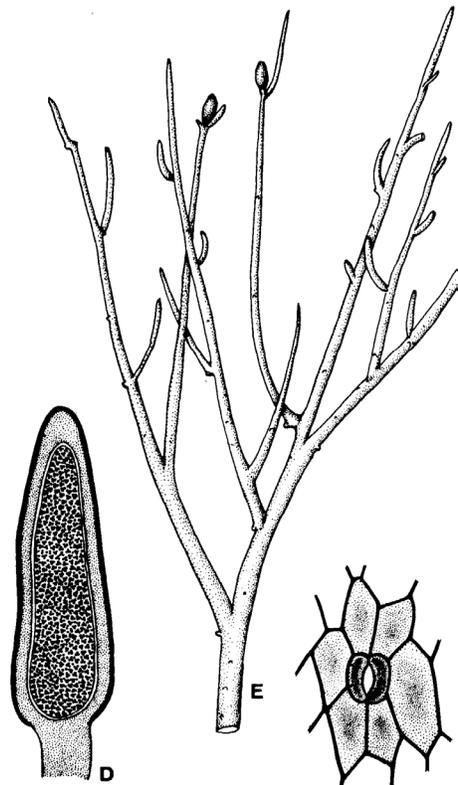
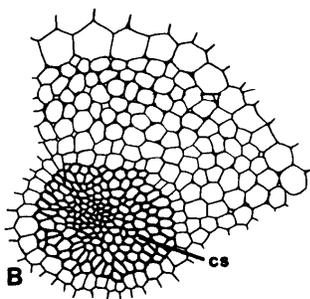
*Uskiella* has larger sporangia than *Cooksonia* and a more complex sporangial wall organization. This genus is marked by a very primitive vegetative appearance resembling that of *Cooksonia*, yet with structurally advanced sporangia. The sporangia have a longitudinal dehiscence pattern and are almost purse-like in the extent of their opening.



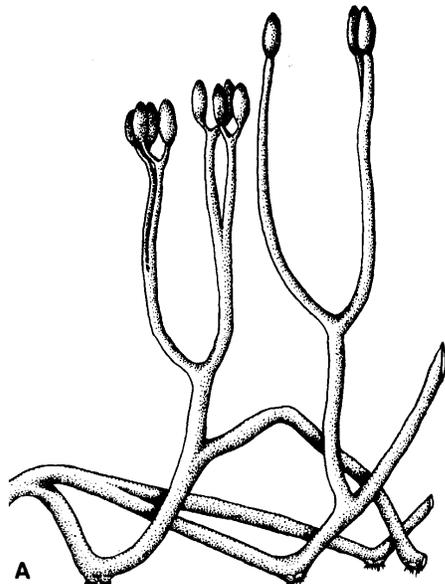
The fertile region is densely reproductive, appearing as if in transition to a telome truss.

*Rhynia* - Lower to Middle Devonian

*Rhynia* is the best described of the Devonian genera, represented by robust plants up to 50 cm tall and a clear differentiation of prostrate and upright axes. Branching is dichotomous to pseudomonopodial with elliptical sporangia terminal on short laterals. In cross section, the stems are radially symmetrical with a clearly differentiated epidermis, cortex and vascular cylinder. The thickenings of the tracheids are annular, with the smallest cells located near the center of the cylinder, indicating that the maturation of the xylem is centrarch. The xylem is immediately surrounded by thin-walled cells that may represent phloem. Guard cells, stomata and a cuticle-like layer is present on the surface of the aerial axes, strongly suggesting that these were photosynthetic surfaces. The prostrate axes contained local enlargements that appear corm-like where single-celled rhizoids occur,



presumably anchoring these plants to the underlying substrate, similar to root hairs. The sporangia are roundly elongated and have transverse dehiscence. Many examples of this plant have been anatomically preserved in the Rhynie chert of Aberdeen Scotland. This is a structurally refined plant in comparison with *Cooksonia*.



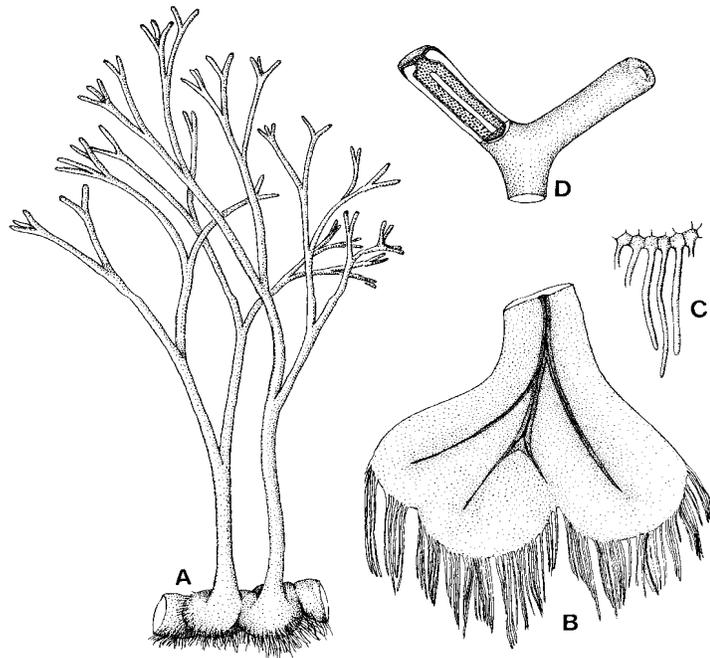
*Aglaophyton* - Lower Devonian

*Aglaophyton major* is the name given to the less robust axes of *Rhynia* found in the Rhynie chert and was the suspected gametophyte of *Rhynia gwynnevaughnii*. This genus has many of the same characteristics of the former, but the dichotomous nature of the branching is not masked and the sporangia clearly on terminal axes, not overtopped as in *Rhynia major*. Presumably, these are both less derived features, reflecting a more similar design to *Cooksonia*.

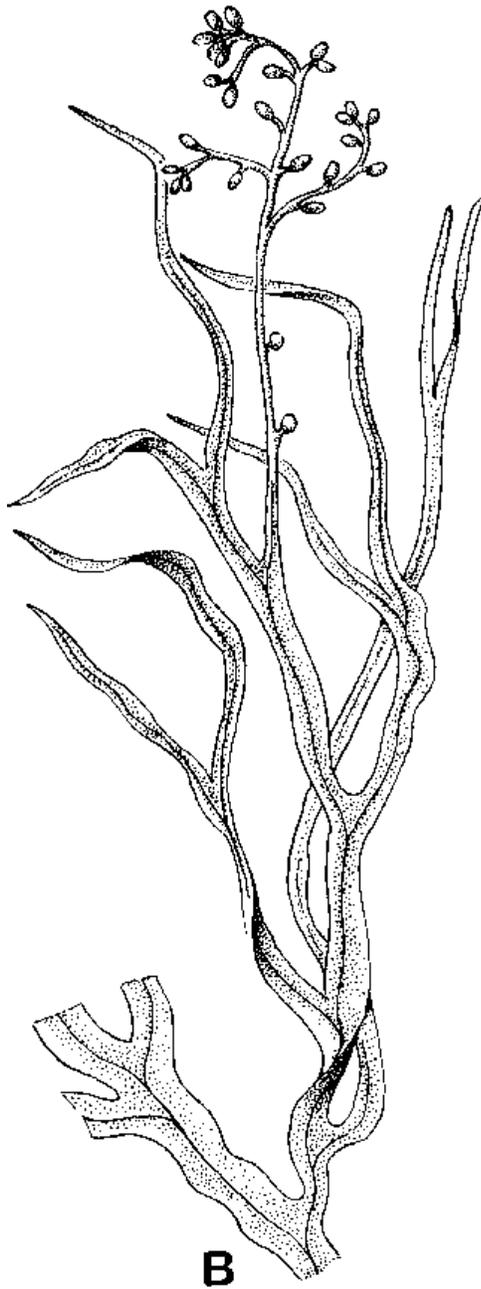
**Rhyniophyte diversity - the origin of the columella, flattened axes, synangia and fertile telome truss**

*Horneophyton* - Lower Devonian

*Horneophyton* consists of freely-dichotomizing axes with distinct aerial and prostrate systems. The anchoring system in *Horneophyton* is clearly corm-like with unicellular rhizoids attached at the base. The sporangia are particularly noteworthy because they appear to be sunken into a vegetative axis for protection, and the center is occupied by a columella, which is a typically bryophytic characteristic. Although it is unclear whether this species could represent the origin of bryophytes, it is certainly consistent with some of our expectations.



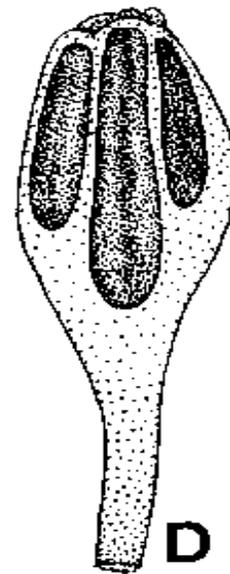
*Taeniocrada* - Lower Devonian to Upper Devonian



*Taeniocrada* is an abundant possible rhyniophyte which remains noteworthy because of its unusual flattened nature. It is this type of elaboration at the margins of the axis that may have formed the first primitive adaptations of the photosynthetic surface to gain an advantage over the otherwise strictly terete competition. Interestingly, this is not simply an extension of a lateral lamina, but a flattening of the whole axis. Although the formation of lamina would have been more efficient, it was not seen in the rhyniophytes. This is suspected to have been aquatic based on its distribution in the rock matrix with emergent reproductive areas. The sporangia of this plant were terminal on dichotomous recurved branches.

*Yarravia* - Lower Devonian

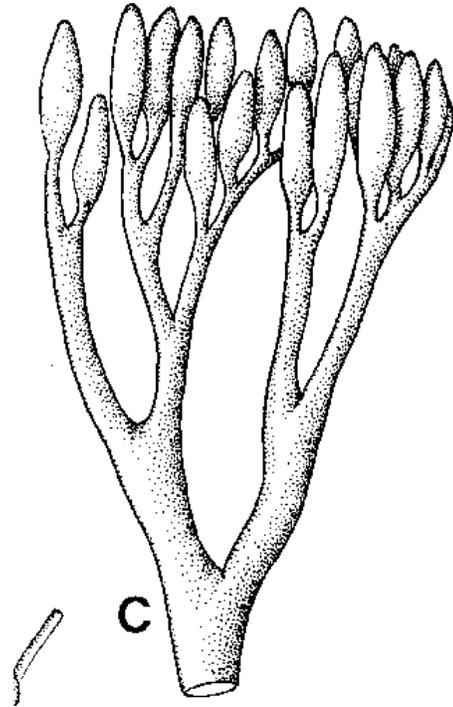
*Yarravia* is another possible rhyniophyte that is noteworthy because of its degree of reproductive advancement. The most remarkable characteristic is the presence of synangia composed of five or six fused sporangia at the tip of a branch, which is particularly interesting in context with the synangiate sporangium of *Psilotum*. If synangiate sporangia are remarkably advanced, it seems interesting that this advancement was made by the Lower Devonian. Truly, if this plant is a rhyniophyte, it is difficult to describe the



presence of synangia as an advanced characteristic in the overall scheme of vascular plant evolution.

*Hedeia* - Lower Devonian

The most interesting feature of *Hedeia* is the degree to which the sporangia are gathered at tips branch clusters forming fertile telome trusses. This grouping provides evidence for a differentiation between the reproductive and vegetative regions of the plant, reflecting a specialization of function and affords protection for the fertile regions. Eventually, it would be expected that sterile trusses might provide less costly protection, but this is a modification only weakly present in the rhyniophytes.



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**Gametophytes of the Devonian**

The gametangium-bearing gametophyte genus *Lyonophyton* occurred as a contemporary of *Rhynia*, *Aglaophyton* and *Horneophyton* and was first described in the same famous Rhynie chert. It consists of upright axes with bowl-shaped gametophores containing antheridia on the inner surfaces of the lobed rim and archegonia in the bowl (C, D). The genus name *Sciadophyton* is assigned to compression fossils of similar gametophytes (A, B), although it is unclear whether they are different. These are about the same diameter as the stems of *Aglaophyton major* with which there appear to be vegetative similarities. The sporophytes emerging from these outwardly resemble *Taeniocrada* and *Zosterphyllum*. Given the fragmentary nature of the fossil record, reconstructing the gametophytes of the other genera will be difficult and require considerable luck in collecting the right specimens.

