deuterium stabilization, variable temperature, and Fourier-transform capabilities operating at 80.987663 MHz for $^{31}P$ interfaced to a wide bore (89 mm) Oxford superconducting magnet was used. Intact, incubated lenses placed in 12-mm NMR tubes were analyzed at 37°C under the following spectrometer conditions: pulse sequence, 1 pulse; pulse width, 8 μsec (45° flip angle); acquisition delay, 200 μsec; cycling delay, 250 μsec; number of scans, 4400; number of data points per free induction decay, 8192; acquisition time, 819.4 msec; sweep width, ± 2500 Hz. In addition, a computer-generated filter time constant introducing 10-Hz line broadening was applied. The chemical shifts are reported in field-independent units denoted δ (hertz per megahertz). Lens PCA extracts were analyzed as described in (*1*).


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9. The results reported represent metabolite levels present in biochemically and physiologically mature lenses excised from young adult mammals. The contribution of age as a factor in the interspecies differences cannot be completely discounted; however, the biologic ages of the animals studied are relatively close, and the markedly divergent lens metabolic differences encountered among the various species of animals are not consistent with reported differences attributable to age. As a consequence, the results reported appear predominantly to represent interspecies differences in lens metabolism, rather than age-dependent changes.

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## Lower Devonian Gametophytes: Relation to the Phylogeny of Land Plants

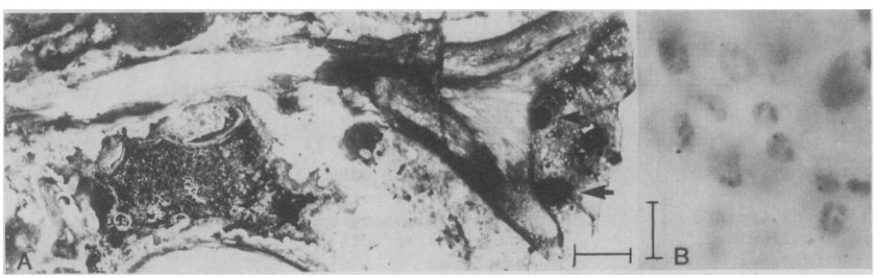

Abstract. *Three gametophytic plants now known from the Lower Devonian of Scotland and Germany show common features in their fertile parts. The morphological and anatomical structures indicate affinities to bryophytic gametophytes, although there is no evidence for a parasitic sporogonium-like sporophyte as in the Bryophyta. Several of the vascular plant sporophytes from the Rhynie Chert also have a few characteristics reminiscent of bryophytes. But these ancient gametophytes, if related to the sporophytes, indicate a closer relation of Bryophyta to Tracheophyta than would the study of sporophytes alone.*


In 1980 we described (*1*) a gametophyte with anatomically preserved tissues, gametangia, and antherozoids in different stages of development from the Lower Devonian Rhynie Chert in Scotland. We described it in detail (*2*) under the name *Lyonophyton rhyniensis* (Fig. 1). We now report a new gametophyte (Fig. 2), with anatomically preserved tissues, also from the Rhynie Chert (*3*).

Eight specimens of this new gametophyte have similar specific and generic characteristics, which are different from *Lyonophyton*. We found five gametangiophores bearing antheridia only and three bearing organs only, which we interpret as archegonia. The new gametophytes seem to form separate antheridiophores and archegoniophores. The antheridiophores exhibit the following features. (i) A round axis widens terminally into a disklike antheridiophore head. (ii) The axis and the underside of the gametangiophore head are covered with scalelike enations. (iii) The margin of the antheridiophore lacks antheridia, is thin, and seems to consist of a few upturned lobes (possibly involucral bracts). (iv) Closely spaced antheridia are borne on the convex surface of the antheridiophore. (v) The antheridia are stalked, globular, or club-shaped and mostly contain sperm (antherozoids) (Fig. 2, B and C) in different stages of development, demonstrating the gametophytic nature of the plant. (vi) The antheridia are slightly sunken or intermingled with multicellular, branched, paraphysis-like sterile tissue. (vii) A central strand of hydroids passes through the stalk of the antheridiophore and diverges into a funnel-like structure in the basal part of the antheridiophore head.

The probable archegoniophores are built similarly; the archegoniophore head may be lobed in axis-like structures, and the hydrom splits up into terete, separate strands. There are some indications that male and female gametangiophores are seated on common axes or a protocorm, as in *Sciadophyton*.

The morphological and anatomical characteristics of *Lyonophyton* enabled us (*4*) to show that another Lower Devonian plant, *Sciadophyton*, previously believed to be a sporophyte, is probably a gametophyte (Fig. 3). *Sciadophyton* has so far only been found as impressions or compressions with conducting strands partly mineralized, but in its morphological features we see a nearly complete gametophyte. From a flat central initial structure (protocorm) axes (up to 10 cm long) radiate. It may be that all the upright subaerial axes terminate in gametangiophores which are bowl- to funnel-



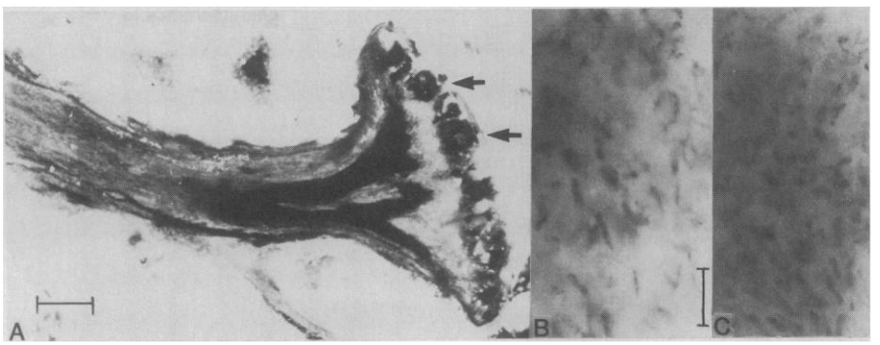




Fig. 1 (top). *Lyonophyton rhyniensis*. (A) Longitudinal section through the stalked gametangiophore showing two antheridia on the upper (inner) surface (arrows) (scale bar, 1 mm); (B) section through an antheridium with mature sperm (scale bar, 10 μm). Fig. 2 (bottom). Sections through the new gametophyte. (A) Longitudinal section through the stalked antheridiophore showing antheridia on the upper surface (arrows) (scale bar, 1 mm); (B and C) sections through two antheridia with mature sperm (scale bar, 10 μm).



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shaped and bear compressed roundish bodies (Fig. 3). The conducting strand of *Sciadophyton* is formed, at least in the stalks of the gametangiophores, of genuine tracheids.

Three different gametophytes are now known from the Lower Devonian (Siegenian-Emsian boundary, about 380 million years old). It is therefore possible to make some general comments on gametophytes and associated sporophytes from this period.

We have compared *L. rhyniensis* with bryophytic plants (*2*). Our interpretation was based on the organization of the stalked gametangiophore, conducting tissue which divided in the basal part of the gametangiophore, and, chiefly, the antheridial features. The spermatocytes in the antheridia are arranged in story-like complexes, as in bryophyte antheridia.

The new gametophyte shows further similarities with bryophytic gametophytes. Specifically the enations on the gametangiophore stalks and on the underside of the gametangiophore heads, the position of the antheridia on the upper surface of the disklike antheridiophore head, the sterile tissue among the antheridia, the involucral-like margin of the antheridiophore, and the probable archegonia on special archegoniophores allow general comparisons with the gametangiophores of some bryophytes.

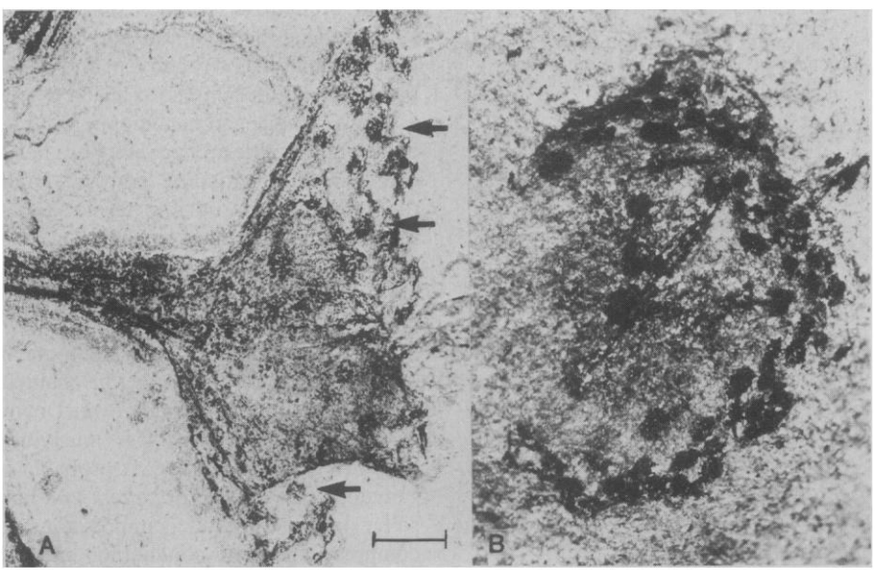


Fig. 3. *Sciadophyton* sp. (A) Side view showing an apparent gametangiophore with possible gametangia (arrows) on the upper (inner) surface of the gametangiophore (scale bar, 1 mm). (B) Top view showing possible gametangia preponderant on the margin of the gametangiophore.

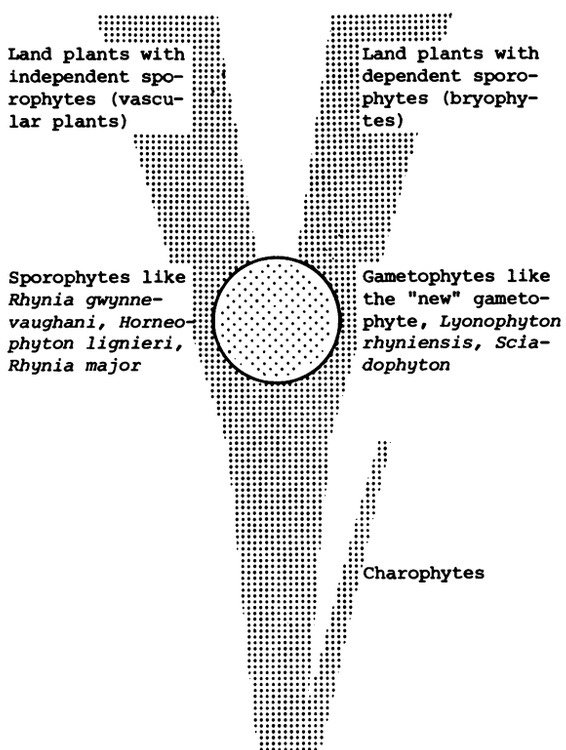


Fig. 4. Suggested phylogenetical position (circle) of Rhynie Chert plants after anatomical characteristics.

The antheridia of *Lyonophyton* and of the new gametophyte are large, produce tens of thousands of spermatoids, and are characterized by multicellular massive stalks. At least the antheridial jacket of *L. rhyniensis* is built up by two layers, and the spermatogenous tissue is arranged in story-like complexes. It may be that the antheridial formation of *Lyonophyton* and the new gametophyte did not follow that of living vascular plants, where a surface cell divides into a jacket mother cell and a primary spermatogenous cell. However, there seems to be some evidence that the spermatogenous tissue of these gametophytes is histogenetically formed at a later stage, like that in some bryophytes. Both gametophytes also show some similarities with pteridophytic gametophytes.

The organization of *Lyonophyton* gametangiophore stalks might be compared with that of axillary gametophytes such as the Psilotales. The general morphology of the antheridiophore head of the new gametophyte bears some resemblance to that of some lycopsid gametangiophores. After considering all morphological and histological features, we suggest that these gametophytes are closer to bryophytes than to pteridophytes. *Lyonophyton rhyniensis*, with its free antheridia, reminds us of gametangiophores of eubryoid bryophytes, and the new gametophyte, with its probably sunken antheridia and sunken archegonia, shows similarities to marchantoid or anthoceroid bryophytes. A specialized comparison of these gametophytes with living ones, bryophytes as well as pteridophytes, including a taxonomical valuation, is not yet possible.

In the Rhynie Chert the gametophytes are associated with some physiologically independent sporophytes such as *Rhynia major* (*5*), *R. gwynne-vaughani* (*5, 6*), *Horneophyton lignieri* (*5*), *Asteroxylon mackiei* (*7*), and *Nothia aphylla* (*8–10*). The situation of *Sciadophyton*, a probable gametophyte from the Lower Devonian (Siegenian) of the Rheinisches Schiefergebirge, is similar in general, although its habitat was different (floodplain). Horizons with an autochthonous and monospecific *Sciadophyton* vegeta-

tion alternate with horizons containing an autochthonous and monospecific sporophyte vegetation (*11*). The sporophytes—the sporophytic nature is demonstrated by sporangia—show naked, roundish, and rare dichotomously branched axes which are more than 25 cm long. Many botanists, such as Bierhorst (*12*), Bold, Alexopoulos, and Delevoryas (*13*), and Taylor (*14*), regard sporophytes like *R. major*, *R. gwynne-vaughani*, *H. lignieri*, and *N. aphylla* as vascular plants and place them at the base of vascular plant evolution. Other botanists, such as Hébant (*15*) and Watson (*16*), mention bryophytic characteristics of *R. gwynne-vaughani* and *H. lignieri*.

The hydroids of *R. major* or *N. aphylla*, the creeping rhizoid-bearing "rhizomes" of *R. major*, *R. gwynne-vaughani*, and *H. lignieri*, or the columella in *H. lignieri* sporangia might be bryophyte-like characteristics. Our bryophyte-like gametophytes from the Rhynie Chert seem to revalorize these features. Moreover, the axes of, for instance, *R. major*, the most simply constructed sporophyte of the Rhynie Chert, show generally the same organization as the gametangiophore stalks of our Rhynie Chert gametophytes. Conducting tissue (hydroids and phloem-like cells) is surrounded by a simply constructed parenchymatous cortex, which is enclosed by an epidermis with stomata (without accessory cells) and a cuticle. Satterthwait and Schopf (*17*) described a phloem-like tissue in the axes of *R. major* with pores in the lateral cell walls. The gametangiophore head of every specimen of the new gametophyte contained similar tissue above the hydrom. *Lyonophyton rhyniensis* has stomata without accessory cells and double-layered antheridial walls. The stomata are comparable with those of *R. major* or *R. gwynne-vaughani*, and the double-layered antheridial walls might be compared with the many-layered sporangial walls of Rhynie Chert sporophytes (*12*).

On the basis of the phylogeny of single characteristics, some sporophytes, foremost *R. major*, and the gametophytes of the Rhynie Chert seem to exhibit a similar level of development. We might even suspect some taxonomical relationships, but there is no concrete evidence for such.

The bryophytic characteristics of the Rhynie Chert sporophytes do not have to be based on direct taxonomical relationships to genuine bryophytes. These characteristics, and the sporophyte-like characteristics of our gametophytes, might be remnants of a plant group which preceded both bryophytes and pteridophytes (Fig. 4). The mere fact of its geologic age puts the Rhynie flora close to the evolutionary roots of land plants. Our investigations suggest that consideration of sporophytes and their evolution only may lead to misinterpretations of phylogenetic relationships. The investigation of Devonian gametophytes puts our understanding of the phylogenetical development of the land plants into a new perspective.

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## Control of Vascular Contractility by the Cardiac Pacemaker

Abstract. *Rhythmic contractile activity, synchronized with pulsatile pressure changes, was recorded from rabbit aorta in vivo. The contractions were locked in frequency to the pulsatile activity of the heart even when the heart was electrically paced to rates as high as 600 cycles per minute; termination of cardiac contractility resulted in their elimination. When the atria and ventricles contracted at different rates, the pulse-synchronized contractions were locked to the atrial rate. Excision of the right atrium, but not the left, resulted in the abolition of pulse-synchronized contractions. It is concluded that a common pacemaker controls cardiac and vascular contractility, coordinating events in the two tissues.*

Although contractions can be elicited from the smooth muscle component of the large arteries by various stimuli (for instance, neural transmitters, hormones, and membrane depolarization) (*1*), the fundamental question of whether the vessels undergo rhythmic activation during the cardiac cycle was, until recently, unresolved. Classically, the large arteries were described as passive elastic tubes whose viscoelastic elements were periodically distended by pulsatile pressure changes (*2*). However, several studies indicated that the vessels may produce rhythmic tension changes during the cardiac cycle. Hysteresis in aortic pressure-circumference (*3*) or pressure-diameter (*4*) relations suggests that the aorta imparts energy to the blood. A possible explanation for this phenomenon is that active contraction of the smooth muscle wall occurs during each systole. Heyman and co-workers (*5*) measured the phase relation between the pulse wave as recorded simultaneously extra- and intra-arterially. A neurally dependent leading by the extra-arterial event was observed. This phase shift was attributed to rhythmic activation of the smooth muscle component of the arterial wall.

Recently, we bypassed the blood flow through sections of large arteries in rabbits in vivo. When mechanical activity was measured under these conditions, we found that the aorta and the carotid, femoral, and coronary arteries show rhythmic contractions which oscillate at the same frequency as the pulsatile activity of the heart (*6–8*). The observed phase-locking between the tension and pulse pressure changes, with an increase in tension being temporally correlated with the upstroke of the corresponding pulse wave (*8*), suggests the term pulse-synchronized contractions (PSC's). The PSC's were shown to be produced by neurogenic activation of the smooth muscle component of the arteries, with the neural signal responsible for activation conducted caudally, away from the heart (*6*). The PSC's remained frequency-locked to the heart rate, even after drug-induced perturbation from the rest-


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