This supports the theory that the capability for a high rate of glutamine synthesis in livers of ureosmoregulating fish may be directly related to production of urea.

Leech *et al.* (*23*) reported that glutamine was not detectable in the blood of the shark *Squalus acanthias* during various starvation periods. If ureosmoregulatory fish in general do exhibit a very low blood glutamine level, the utility of their having a high tissue glutamine synthetase activity becomes at once obvious.

The ornithine-urea cycle has been considered to be a route for detoxification of ammonia in typically ureotelic vertebrates (*8*). Our findings are consistent with this view. But, for the group of animals that retain urea for osmoregulation, we emphasize that urea synthesis serves not only to detoxify ammonia, but also represents an economical physiological adaptation that makes osmoregulatory use of the glutamine synthetase and the ornithine-urea cycle pathway. The assimilation of ammonia by glutamine synthetase and subsequent glutamine-dependent synthesis of urea would support the osmoregulation of these species and would provide a route for excretion of nitrogen (ammonia) through loss of urea via the gills and kidney of ureosmoregulators.

Our study suggests that glutamine synthesis may be the initial step in assimilating ammonia for subsequent synthesis of urea in marine, ureosmoregulating species of fish. Our findings and those of Anderson (*22*) in the accompanying report are mutually supporting.

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Devonian Gametophytes with Anatomically Preserved Gametangia

Abstract. *The oldest anatomically preserved and physiologically apparently independent gametophytes are described from the Lower Devonian of Scotland. These gametophytes have upright, leafless axes with terminally borne, bowl-shaped gametangiophores. The antheridia are stalked and their walls are multicellular. The archegonia are clustered in groups on common bases.*

In the course of phylogeny of the Tracheophyta the gametophytes were reduced to effect only sexual reproduction. Therefore today in the Tracheophyta the sporophyte is dominant in size as well as in life-span and is the typical assimilating "green" plant. The gametophytes are very reduced in size and simplified in shape and structure. In the Bryophyta the gametophytes are the longer living and more differentiated generation; the sporophytes are physiologically more or less dependent on the gametophytes, to which they remain attached throughout their life-span. It was hoped that Devonian gametophytes would provide clues to the phylogenetic development and early ancestors of the land plants. Prior to the present discovery, however, all that had been found with any certainty among the ancient land plants was the sporophyte generation. It seemed that the gametophyte generation either did not exist as independent plants or failed to be fossilized.

Evidence of gametophytes was to be expected in the silicified fossil peat near Rhynie in Scotland. The Rhynie Chert has been placed in the Lower Devonian, at the Siegenian-Emsian boundary (*1*), for the last 15 years. The plants in the Rhynie Chert are preserved with cellular structure. It was from this material that Merker (*2*), Lemoigne (*3*), and Pant (*4*) claimed to find evidence of gametophytes. They interpreted parts of *Rhynia gwynne-vaughanii* as gametophytes. Previously, these parts had commonly been regarded as sporophytes, and they are taken as such even today by many paleobotanists.

In 1977 we collected samples of the Rhynie Chert; on the surface of one sample we noticed two fractured bowl-shaped plant structures, which bore blackish, globular bodies. Such plant remains had not previously been described from the Rhynie Chert. They seemed to lie among axes, which we first referred to the Rhyniaceae on the basis of their recognizable features. Ensuing investigations of approximately longitudinal sections revealed that two of these axes were stalks of the bowl-shaped plant remains. The stalks are in organic connection with them and are up to 2 cm

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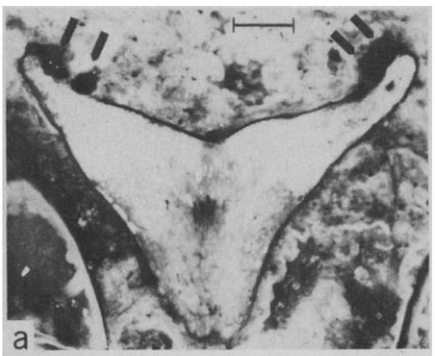

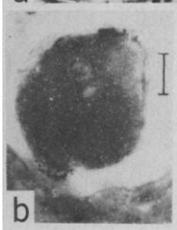

Fig. 1. (a) Approximately longitudinal section through a gametophyte passing through the bowl-shaped gametangiophore and the terminal part of the stem. On the rim of the gametangiophore, antheridia (arrows) can be seen. Scale bar, 1 mm. (b) Longitudinal section through an antheridium. The gametangiophore is below. The antheridium stalk and rows of fertile cells (within the central granular mass) can be seen. The stalk is separated from the gametangiophore by several layers of cells with dark contents. Scale bar, 100 μm.

long. They have diameters of about 3.2 mm without tapering. They are not seen intact in our material, partly because of the original fracture and partly as a result of cutting the chert; they must have been longer, perhaps much longer. We interpret these stalked plant remains as gametophytes and support this presumption by giving some details of the fertile organs.

The gametophytes seem to be independent plants without any apparent connection with sporophytes. We found in the sections more than 20 of the characteristic terminally borne, bowl-shaped parts (gametangiophores) of the gametophytes (Fig. 1a). The following description of the gametophytes is based on some main sections through the samples, which we investigated in reflected light. As far as we have seen, all the gametophytes have a more or less uniform and characteristic organization (see Fig. 2a). An apparently unbranched axis or stalk widens terminally into a bowl-shaped gametangiophore with a lobed rim. On its upper surface organs of two different types are borne, which are interpreted as antheridia and archegonia (see Fig. 2b).

About 70 presumed antheridia could be found in organic connection with the gametophytes. They all show a more or less uniform organization. They are short-stalked, globular bodies about 400 μm across (Fig. 1b). In sections of varying orientation a central granular mass is surrounded by a biserial, multicellular wall. In most of the antheridia (which were probably immature) this mass consists of distinct rows of cells with diameters of about 10 μm. Each cell shows a central, blackish grain about 7 μm in diameter. In apparently more mature antheridia no cell walls or cell rows are recognizable in the granular mass. Some of the antheridia, although of the same diameter, show fractured walls and are empty. In the basal parts of their stalks the antheridia are separated from the gametangiophore by several layers of small, blackish cells (Fig. 1b).

The second type of organ is more complicated in organization. Of this type we found seven specimens, which are in organic connection with the gametangiophores. In reflected light they can easily be recognized, and all seem to be of more or less uniform organization. From a central short-stalked complex some apparently hollow, tubelike bodies diverge. Careful focusing in reflected light showed the central complex to consist of numerous cells, which are very minute compared to those of the gametophyte tissues. The free, tubelike parts consist of larger cells. Comparisons with organs of similar organization suggest that these organs resemble the groups of archegonia seen in some Bryophyta. Indeed, we are inclined to interpret these organs as groups of archegonia. To our knowledge, no similar structures have previously been found.

In addition to the presumed gametangia, two anatomical features of the gametophytes are noteworthy. The central tissue of the stalk and of the basal parts of the gametangiophore is formed by elongated, brown cells. Their walls are slightly thickened compared to the surrounding parenchymatous tissue. Although no tracheophyte-like wall thickenings are noticeable, this tissue seems to have a vascular function. On the underside of one gametangiophore we found one stoma. This, in connection with the upright stalk, seems to be an indication of at least a partially terrestrial (subaerial) mode of life for these gametophytes.

Because the plants described here were hitherto unknown and similar fertile structures of fossil plants are unknown to us, we could not exclude the possibility that the presumed antheridia were sporangia. The uniform measurement of these organs (including the empty ones) of about 400 μm, the minute fertile cells (about 10 μm in diameter), and the fact that in spite of careful focusing tetrads or spores with a triradiate suture could not be observed seem to eliminate this possibility. These features lead us to interpret the organs as antheridia. If one follows this interpretation, the second type of organ should be interpreted as an archegonium. The whole plants can then only be regarded as gametophytes, as suggested here (*5*).

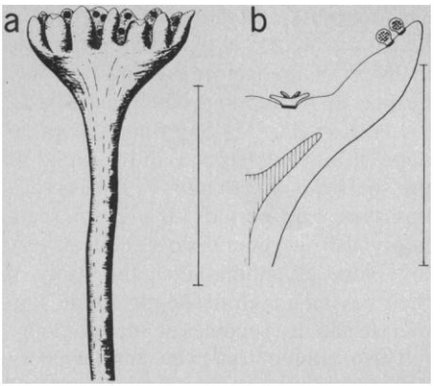

Fig. 2. (a) Reconstruction from the material studied. An upright stem widens terminally into a lobed gametangiophore. On its upper surface antheridia are borne (black dots). Scale bar, 10 mm. (b) Diagrammatic longitudinal section through a gametangiophore. Some antheridia and one archegonial group are cut. The central tissue (brown, thickened cells; see Fig. 1a) is indicated by striation. Scale bar, 5 mm.

The measurement and the organization of the gametophyte stalks suggest at first some relationship to the Rhyniaceae. However, the same arguments together with the anatomy of the gametangia make a more or less close relationship to the Bryophyta seem possible too. Perhaps the Rhyniaceae and the ancient Bryophyta may have been more closely related than has generally been supposed.

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6. We thank A. G. Lyon for assistance in collecting samples of the Rhynie Chert in 1977. H. Hass assisted in slide preparation and photography and made many constructive suggestions. This study was supported by the Deutsche Forschungsgemeinschaft, grant Re 200/10-Pflanzengewebe.

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