

Geologic History of Carbohydrates. IV. Bryophytes (Mosses, Hornworts,
Liverworts}

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Summary

The bryophytes include mosses (Class Bryophyta), hornworts (Class Anthocerotophyta) and liverworts (Class Hepatophyta), which are independent lines of polyphyletic origin. (Stewart and Rothwell, 1993) According to some authorities, they are all embryo-forming, non-vascular plants, in contrast to the Tracheophyta, which are embryo-forming vascular plants. Other workers disagree with this distinction, stating that bryophytes have conducting tissues similar to the trachea of vascular plants and suggest that primitive vascular plants may have been ancestral to the bryophytes in which vascular tissue has been lost or modified. The bryophytes, however, differ from Tracheophyta in having an alternation of heteromorphic phases in which sporophytes are dependent on dominant gametophytes. This contrasts to the Tracheophyta in which there are dominant sporophytes and reduced gametophytes (ibid. p. 77). Distinctions among the bryophytes lie in the position, shape and degree of branching of the gametophytes and sporophytes.

The oldest unequivocal bryophyte is the liverwort *Pellavicinites* (ibid., p. 79; Hueber, 1961) of the Upper Devonian, which is similar to the extant *Pellavicinia*. Other excellent examples of fossil liverworts occur in the Carboniferous (Walton, 1925) and in the Mesozoic and Cenozoic (Lundblad, 1961; Stewart and Rothwell, 1993)

The oldest record of true mosses is that from the Carboniferous (Stewart & Rothwell, 1993) in the genus *Musites*. Other records are from the Permian (Neuberg, 1969; Smoot and Taylor, 1986), Eocene (Janssens, Horton and Basinger, 1979). The Upper Devonian genus *Protosalvinia* lies intermediate between the algae and the bryophytes (Stewart and Rothwell, 1993, p. 83)

Carbohydrates of the bryophytes. In their study of the primary wall structure of the bryophytes, Popper and Fry (2003) found **xyloglucan** to be a universal PCW (primary cell wall) component of hornworts, mosses and leafy and thalloid liverworts, as well as of numerous vascular plants. The key to the detection of xyloglucan is that Driselase (an enzyme extracted from a basidiomycete fungus, *Irpex lacteus*), digestion of xyloglucan yields the disaccharide isoprimeverose, but not from any other polymer. Cellulase (enzyme) digestion of the charophycean green alga *Chara* yielded oligosaccharides of xylan, but not those of xyloglucan.

Geological occurrence. The earliest liverwort and earliest byyophyte are known from the Upper Devonian, when major evolutionary advances in land dwelling plants were occurring..

Among **uronic acids** glucuronic acid was found by Popper and Fry (2003) to occur in high amounts in charophytes, hornworts, liverworts and a basal moss. and in higher concentrations than any vascular plants tested. Galacturonic acid furthermore was found in higher concentration in charophycean algae and in all byrophytes than in any vascular plant. Mannuronic acid has been reported to be the major unronic acid in some liverworts, but Popper and Fry did not find this to be true.

Geologic occurrence. The earliest charophyte records are from the early Devonian, while the bryophytes appeared in the late Devonian. As in the xyloglucans the uronic acid components of bryophyte cell walls are inferred to have developed together with the evolutionary progress of the Devonian land plants.

3-O-methylrhamnose. This component was found by Popper and Fry in charophytes, bryophytes, and homosporous lycopodiaphytes.

Geologic occurrence. The lycopod land plants appeared in the Middle Devoinan. Thus the charopycean algae, bryophytes and lycopods seem to be genetically related in the constitution of theircell wall carbohydrates.

Mannans. Mannose residues represented by by mannans, glucomannans, glucogalactomannans and glucouronomannans were found by Popper and Fry (2003) in bryophytes, psilophytes, equisitophytes and in eusporangiate ferns to a greater degree than in green algae, leptosporangiate ferns, gymnosperms and angiosperms.

Geologic occurrence. The vascular plant psilophytes appeared in the Lower Devonian. The equisitophytes (horsetails) in the Upper Devonian; the eusproangiate ferns (thick-walled sporangia (pteridophytes)) in the Lower Devonian; the leptosporangiate ferns (thin-walled sporangia) not until the Pennsylvanian. The relationship of mannose residues of the bryophytes and earlier vascular plant categories seems to be close, but such relationship to more advanced vascular plants is less evident.

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