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Spatial Relation of Stem Hydroids to Branch Hydroids in Four Pleurocarpous Mosses¹

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The anatomy of branch and main stem connections, with respect to the spatial relation of central strands, was studied in four species of pleurocarpous mosses: *Climacium americanum*, *Climacium dendroides*, *Rhytidiadelphus triquetrus*, and *Rhytidium rugosum*. In each of these species the central strand consisted entirely of hydroids. Fresh specimens obtained in Iowa and Wisconsin were fixed in CRAF III. To soften tough cell walls, samples were soaked in concentrated (50% aqueous) hydrofluoric acid for one week prior to dehydration in ethyl alcohol. Paraffin (61°C mp) was used as the embedding medium. In the several branch connections studied for each species there was no direct connection between stem and branch central strands.

INDEX DESCRIPTORS: branching, central strand, hydroids, pleurocarpous mosses.

The existence in moss gametophytes of a central strand that contains tissue resembling the conducting tissue of vascular plants has been known since 1782, when Hedwig (as cited in Héban, 1970) first published a drawing of a cross-section of *Mnium hornum*. By 1886, Haberlandt (as cited in Héban, 1977) had shown that in some species the "hydroids" (cells resembling tracheids) of the central strand actually conducted water. Most research has concentrated on the acrocarpous mosses (Héban, 1970, 1977). Members of this group generally bear sporophytes terminally on major branches, have an erect growth habit, and often possess a complex central strand. The most widely studied acrocarpous mosses have been the Polytrichaceae, due to the large size and complex nature of their central strand. Conversely, the pleurocarpous mosses generally bear their sporophytes on short lateral branches, have a prostrate growth habit, and have a reduced central strand or none at all. This group has a very large number of species but has received very little attention with regard to central strand anatomy and architecture.

Moss gametophytes commonly have branches, but little work has been done on either acrocarps or pleurocarps regarding the spatial relation of branch central strands to the central strand of the main stem. Based on available evidence, the branch central strand in acrocarpous mosses connects directly to the stem central strand (Frey, 1974a). This arrangement was first accurately described by Schoenau (1912) and has been best investigated in the Polytrichaceae. In addition to typical branches, members of the Polytrichaceae are also reported (Héban and Berthier, 1972) to produce branches from previously inhibited lateral buds after apical damage. However, in these branches the central strand does not connect to the central strand of the main stem. Other acrocarps (some members of Dicranaceae, Grimmiaceae, Bartramiaceae, Timmiaceae) are also known to possess a direct connection but differ in detail from the Polytrichaceae (Frey, 1974a).

Only one investigator (Frey, 1974a) has examined pleurocarps with regard to branch stem central strand connections. Based on his observations of seven pleurocarpous species he generalized that among pleurocarps there is a consistent lack of a direct connection between the central strand of branch and stem. Frey (1974b) has also investigated another putatively pleurocarpous moss that did have a direct connection. In this moss, *Hypnodendron dendroides*, an unusually large erect species, the connection was not formed by hydroids but by modified

cortical parenchyma cells. Frey, for several reasons, suggested that *Hypnodendron* should be regarded as having close affinities to the acrocarps. However, the occurrence of a modified direct connection in a large erect moss that produces its sporophytes in pleurocarpous fashion, as does *Hypnodendron* (Brotherus, 1924), suggests that other pleurocarps of similar growth habit would be particularly worthy of investigation. Four such species are examined in this study.

METHODS AND MATERIALS

Four species of pleurocarpous mosses were chosen for study: *Rhytidium rugosum* (Hedw.) Kindb., *Rhytidiadelphus triquetrus* (Hedw.) Warnst., *Climacium dendroides* (Hedw.) Web. & Mohr, and *Climacium americanum* Brid. Two species from the genus *Climacium* were chosen because *Climacium dendroides* was collected from a xeric site whereas *Climacium americanum* was collected from a very moist site. All of these species have an erect growth habit and reach a height of 5-10 cm. Samples of each species were collected from northeastern Iowa and adjacent southwest Wisconsin in late October, 1977. Specimens chosen for study were killed and fixed in CRAF III (Sass, 1958) within 36 hours after collection. After fixation, small sections of main stems, each including the basal portion of one branch, were selected for anatomical study.

The extreme hardness of the cell walls made sectioning very difficult. This problem was somewhat alleviated by softening the samples in concentrated (50% aqueous) hydrofluoric acid for one week. Even after this treatment it was usually necessary to make cross-sections through branch connections rather than longitudinal sections since the latter tended to shatter during sectioning.

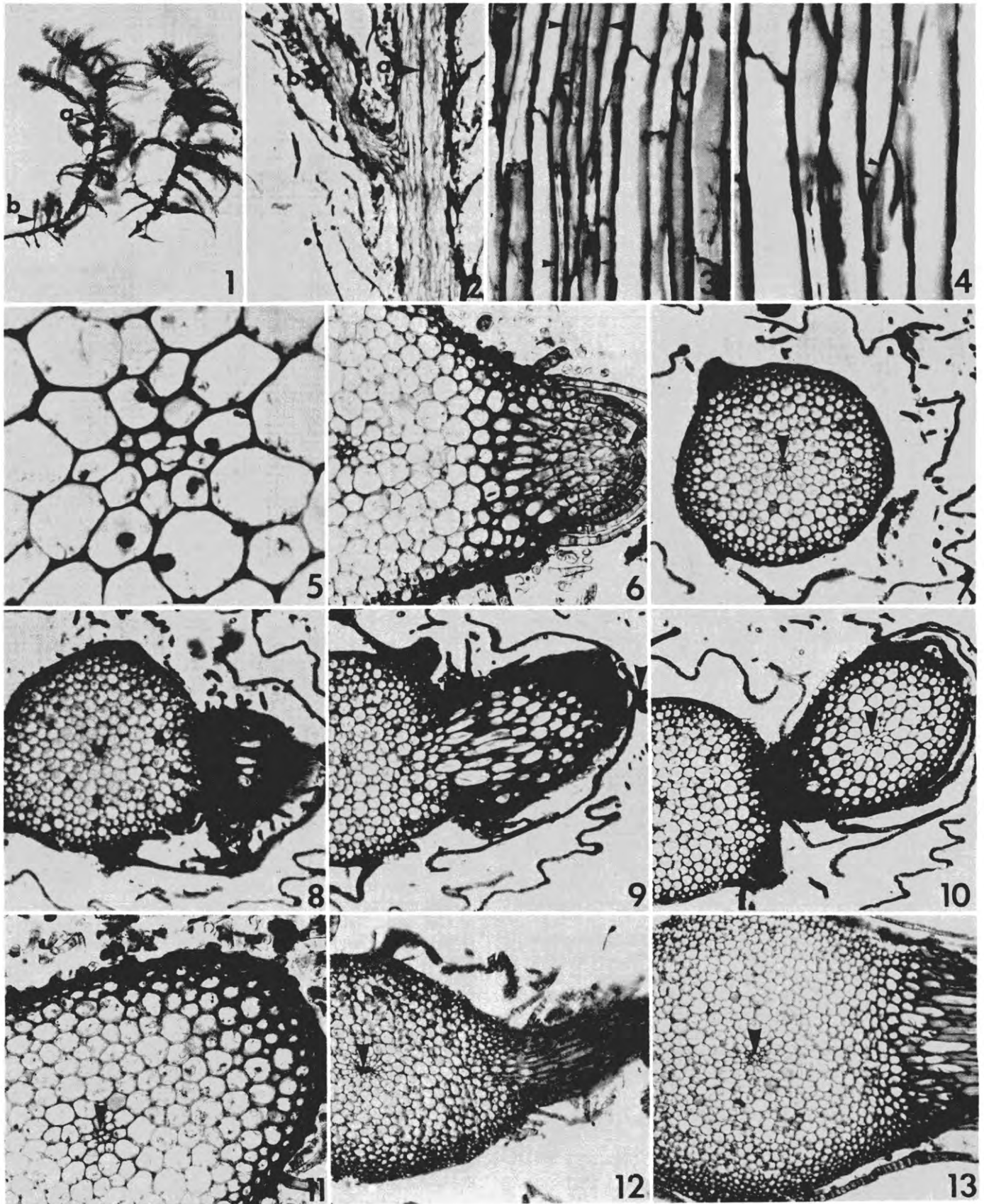
Following softening, the samples were dehydrated in a graded ethyl alcohol series, embedded in 61°C mp paraffin, and sectioned at 10µm thickness. The resulting sections were stained in safranin and counterstained in chlorazol black E. Photographs of representative sections were made with a Leitz Ortholux photomicroscope.

RESULTS AND DISCUSSION

All four species possess a central strand typical of pleurocarpous mosses; i.e., they contain only a few cells as seen in cross-section, all of which are evidently hydroids. The central strand cells are hydroids according to the criteria of Héban (1977): long narrow cells (cells between arrowheads in fig. 3), dead at maturity (note lack of protoplasmic contents in the 7 central strand cells in fig. 5), and with steeply inclined end walls which are often thin as a result of partial enzymatic hydrolysis (see hydroid end wall indicated by double arrowhead in fig. 4). Central strands of 1-20 cells were observed in this study (figs. 5-13).

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Notably, the cross-sectional size of the central strand in *Hypnodendron dendroides* is much larger than this.

Each of these species appeared to have two distinct kinds of branches, minor branches that were not further branched and major branches that produced additional branches and rivaled the main stem in size. This pattern is most distinct in *R. triquetrus* (fig. 1) and least distinct in *R. rugosum*. There was variation among individuals; however, both branch types were generally identifiable and few intermediate forms were found. Both types of branches were subtended by a leaf (fig. 9, arrowhead).

It seemed possible that the two branch types could differ in origin and anatomy as did the two types of branches in the Polytrichaceae. Consequently, both types were examined. As predicted by Frey (1974a), no direct central strand connection was ever observed between main stem and minor branches (figs. 7-10). The branch central strand did not penetrate the cortex of the main stem and no obviously modified cortical cells were found in the branch connection region. According to Hébert (1977), the lack of connection is a result of temporary inhibition of branch buds in pleurocarpous mosses. In one species (*R. triquetrus*) the minor branches were found to lack a central strand entirely, rendering the question of connection superfluous. The major branches proved very difficult to section even after softening in hydrofluoric acid but it was evident that they showed the same pattern as the minor branches.

Both branch types are evidently produced in typical pleurocarpous fashion, from temporarily inhibited lateral buds. Evidence of inhibition can be seen in figures 2 and 6. The thick-walled, approximately isodiametric cells at the base of the bud in fig. 6 (still visible at a later stage in development at the base of the branch in fig. 2) indicate a period of time during which these basal "connection zone cells" differentiated to their mature state while most of the bud remained inhibited and meristematic. The thick-walled connection zone cells presumably preclude eventual connection of stem and branch central strands, and indeed, branch hydroids were never observed to penetrate more deeply than the connection zone. Figure 14 is a summary of branching in these mosses.

This study adds four species to the short list of pleurocarpous mosses that have been investigated with respect to the spatial relationship of the branch central strand to the stem central strand. All species investigated

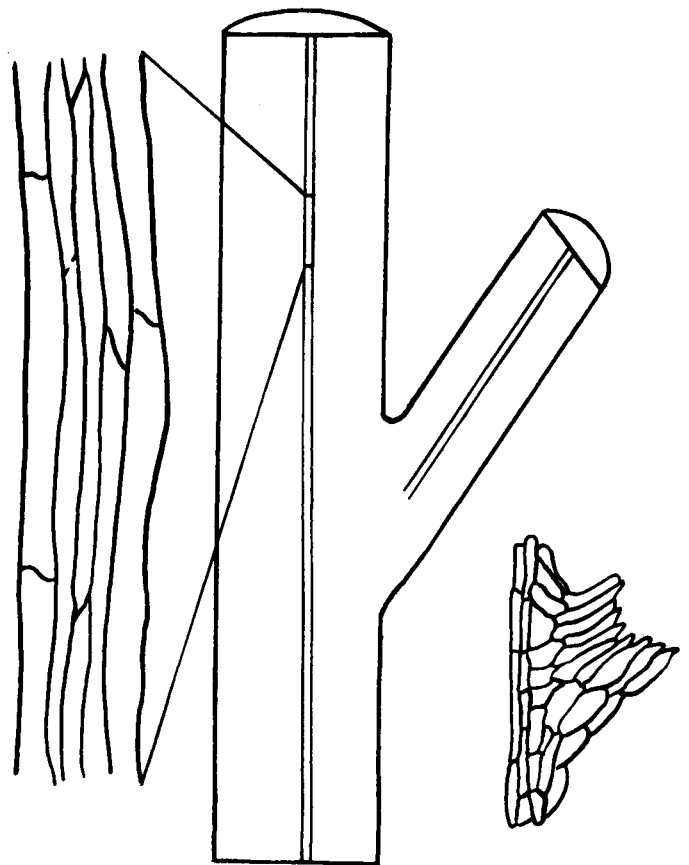


Fig. 14. Diagrammatic representation of branch connection showing approximate extent of branch central strand (center), cellular detail of central strand (left) and the approximately isodiametric connection zone cells at the base of the branch (right).

Fig. 1. Two specimens of *Rhytidiadelphus triquetrus* showing major branch (arrowhead a) and minor branch (arrowhead b). Approximately $\frac{1}{2}$ life size. Fig. 2. Longitudinal section of *Climacium dendroides* showing central strand of main stem (arrowhead a), central strand of branch (arrowhead b), and the connection zone cells at the base of the branch (double arrowhead). X49. Fig. 3. Longitudinal section of *Climacium dendroides*. Central strand is between arrowheads. Note long narrow appearance of hydroids as compared to cortex cells. Also note steeply inclined end walls of hydroids. X453. Fig. 4. Enlarged portion of fig. 3. Note hydrolysed end wall of hydroid delimited by double arrowhead. X893. Fig. 5. Central strand and cortex cells of *Climacium dendroides*. Note lack of protoplasmic contents in the 7 hydroids of the central strand. X1020. Fig. 6. Cross-section of *Climacium dendroides* stem showing branch bud. Arrowhead indicates apical cell of bud. Note presence of thick-walled connection zone cells at base of bud. X255. Fig. 7-10. Serial cross-sections of *Climacium americanum* stem through a branch origin; Fig. 7. Sectioned at point below branch. Asterisk indicates the side of the stem where the branch will emerge. Note absence of a branch trace composed of hydroids in this region. Arrowhead indicates central strand of main stem. X104. Fig. 8. Sectioned at base of branch. No branch hydroids in cortex of main stem. X104. Fig. 9. Sectioned at higher level, still without hydroids. Arrowhead indicates subtending leaf. X110. Fig. 10. Sectioned above branch connection. Some of lowermost hydroids (arrowhead) can now be seen in branch. X101. Fig. 11. Representative cross-section of *Climacium dendroides* showing central strand (arrowhead). X280. Fig. 12. Representative cross-section of *Rhytidium rugosum* showing central strand (arrowhead). X98. Fig. 13. Representative cross-section of *Rhytidiadelphus triquetrus* showing central strand (arrowhead). X99.

were found to conform to the generalization that in pleurocarpous mosses there is no direct connection between branch and stem central strands. This indicates that the growth habit of a pleurocarpous moss is probably not a good predictor of the relation between branch and stem central strands. Perhaps investigations that focus on pleurocarpous mosses possessing a large central strand would better determine whether any other pleurocarpous species have a direct connection. Interestingly, the normally occurring branches in pleurocarpous mosses appear to be similar to the abnormal type of branch found in the Polytrichaceae which results from activation of inhibited buds by apical damage.

The presence of cells (hydroids) that closely resemble the tracheids of vascular plants (Héban, 1977) raises the question of their evolutionary origin. Unfortunately, this study supports neither the theory that hydroids are independently derived and primitive water conducting cells, nor the theory that hydroids are water conducting cells derived by reduction from the water conducting cells of vascular plants. Further study is needed in at least two critical areas. Since only 12 pleurocarpous species have been studied, the question of the existence of a direct connection in other pleurocarps still remains. In addition, one can ask whether the hydroids of pleurocarpous mosses are functional as water conducting cells. Earlier work (Mägdefrau, 1935-6) has indicated that the hydroids of pleurocarpous mosses are non-functional, or at best very inefficient. Most water needs are reportedly supplied by external (capillary) conduction. The existence of mosses with demonstrably non-functional (vestigial) hydroids would best support the theory that mosses were derived by reduction from vascular plant ancestors.

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