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Developmental evidence of acrocarpy in *Hedwigia ciliata* (Musci: Hedwigiaceae).

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Abstract. The growth habit of the Hedwigiaceae has been described variously as acrocarpous, pseudopleurocarpous, or pleurocarpous. Anatomical evidence presented here indicates that *Hedwigia ciliata* is acrocarpous. The archeogonia are terminal on the main shoot, and the branching pattern is sympodial. The main axis of each plant thus consists of a succession of subterminal innovations, rather than a single shoot of indeterminate growth. Since the plants are plagiotropic and are pleurocarpous in appearance, this growth pattern can be also called pseudo-pleurocarpous.

Resumen. El hábito de crecimiento presente en las Hedwigiaceae se ha descrito como acrocarpo, pseudopleurocarpo, o pleurocarpo. La evidencia anatómica presentada aquí indica que *Hedwigia ciliata* es acrocarpo. Los arquegonios son terminales en el tallo principal y el patrón de ramificación es simpódico. El eje principal de una planta consiste de una sucesión de inovaciones subterminales, en vez de un tallo principal de crecimiento indeterminado. Dado que las plantas son plagiotrópicas y son pleurocárpicas en apariencia, este hábito también puede denominarse pseudo-pleurocarpo.

Introduction

The majority of mosses are modular in their individual construction as well as in their colonial structure. The general appearance of the colony is commonly referred to as the 'life form' (Mägdefrau, 1982), whereas the general morphology of the individual is often referred to as the 'growth form' (Gimingham and Robinson, 1950; Horikawa and Ando, 1952; Mägdefrau, 1982; Meusel, 1935). In addition to growth form, the synonymous terms 'growth pattern', and 'growth habit' are also used in this paper.

Despite the morphological diversity exhibited by moss gametophores, there are two basic growth forms: acrocarpous and pleurocarpous (Schofield and Héban, 1984). These have commonly been

defined by the position of the perichaetia and by the branching pattern. Perichaetial position and branching pattern are usually deduced from the mature architecture of the mosses. In some mosses a more detailed study has been necessary to understand the growth habit. Correns (1898), Koponen (1982), Meusel (1935), and Stark (1985) have suggested additional morphological aspects that can be studied, for example phyllotaxy, arrangement of branch primordia, presence of pseudoparaphyllia, and final branch orientation, among others. However, as Schofield and Héban (1984) have stated, 'branching of moss gametophores has been little studied in its anatomical aspects'.

The growth habit has been considered of particular phylogenetic importance in some moss taxa. For example, several studies

have used morphological aspects of growth form as a basis for taxonomic decisions (cf. Koponen, 1972, 1979; Nishimura, 1985; Sastre-De Jesús, 1987; Tuomikoski and Koponen, 1979). Also, Buck and Vitt (1986) erected several groups of families (orders and suborders) based on a combination of peristomial features, the position of archegonia in relation to the main shoot, and the type of branching. Moreover, detailed study of the allegedly pleurocarpous growth pattern in *Mesotus* (Lindberg, 1873; Allen, 1987 a) was helpful in reassigning it to a systematic position among the acrocarpous families.

Understanding of the phylogenetic relationships of the Hedwigiaceae has been limited by uncertainty about the type of growth habit and the lack of a peristome. The purpose of this research was to study the growth form of *Hedwigia ciliata* (Hedw.) Ehrh. ex P. Beauv., based on developmental anatomy.

The family Hedwigiaceae has traditionally included six genera: *Hedwigia* P.-Beauv., *Hedwigidium* B. S. G., *Braunia* B. S. G., *Pseudobraunia* (Lesq. and James) Broth., *Rhacocarpus* Lindb., and *Bryowijkia* Noguchi (Barthlott and Schultze-Motel, 1981; Brotherus, 1925; Vitt, 1982). Current research (De Luna, 1989; in press) corroborates earlier suggestions to exclude *Rhacocarpus* (Buck and Vitt, 1986) and *Bryowijkia* (Vitt and Buck, 1984) from the Hedwigiaceae. Thus, the Hedwigiaceae is treated here as a family of four genera of predominantly saxicolous mosses, with rugose spores, globular protonemata, ecostate leaves, papillose, short leaf cells, and eperistomate capsules.

The growth habit in the Hedwigiaceae has been variously interpreted as acrocarpous (Hedwig, 1801; Bruch et al, 1846), pseudo-pleurocarpous (Frey, 1970; Meusel, 1935), cladocarpous (Frey, 1970), or pleurocarpous (Brotherus, 1925; Buck and

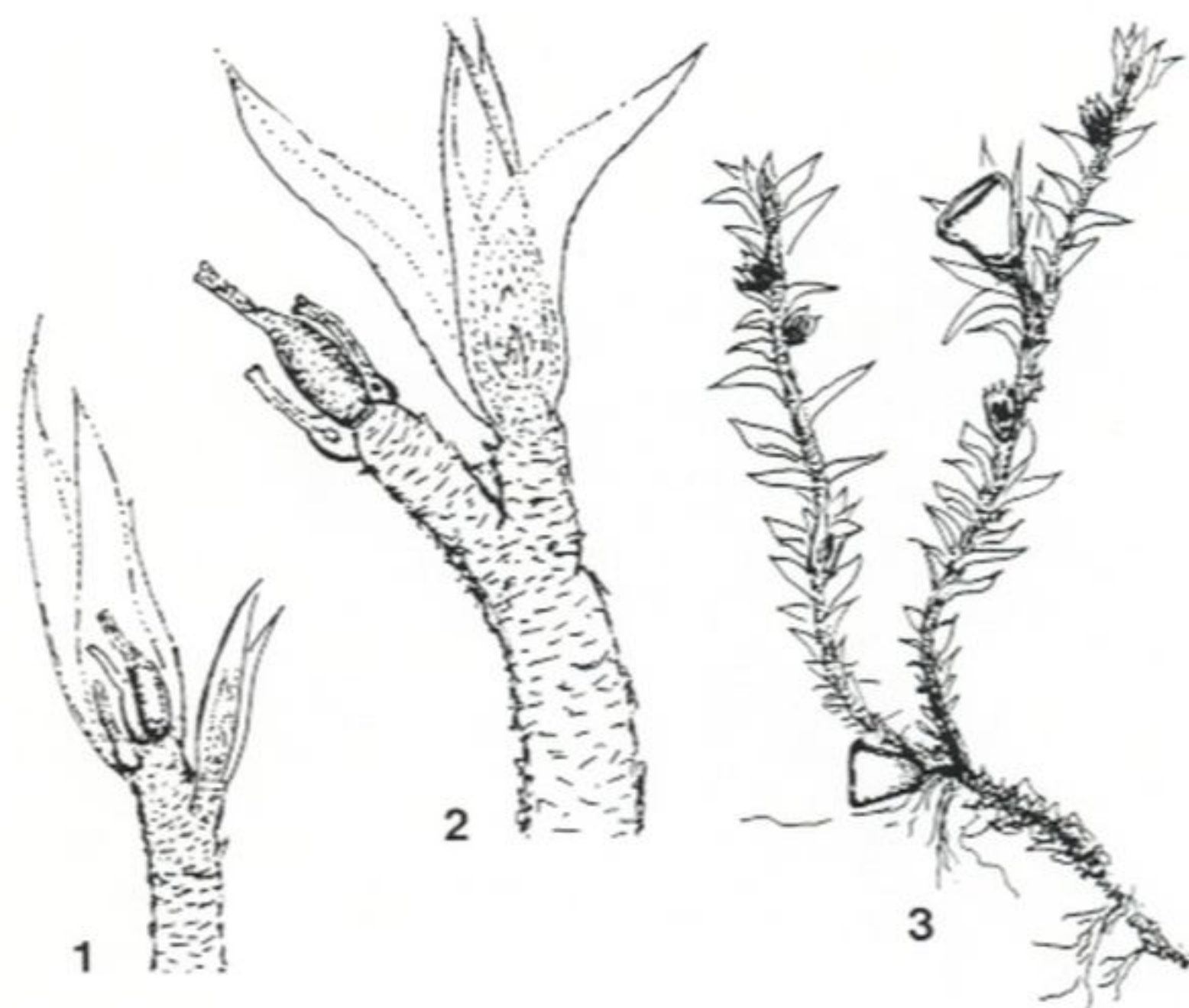
Vitt, 1986; Frey, 1970; Vitt, 1982). A number of authors described *Hedwigia ciliata* as having archegonia terminal on main or lateral branches, and they implicitly interpreted it as pleurocarpous (Catcheside, 1980; Crum and Anderson, 1981; Ireland, 1982; Jones, 1933; Nyholm, 1960; Sainsbury, 1955; Sim, 1926; Smith, 1978). However, Scott and Stone (1976) explicitly described the growth pattern in *H. ciliata* as sympodial, 'the stems ending in capsule production and being replaced by one or two side branches from just below.'

The developmental basis for the growth habit has never been fully described in *H. ciliata* or in any other species belonging to this family. It was expected that anatomical study of the perichaetial position and branching points of *Hedwigia ciliata* would provide a better characterization of the growth habit of the family.

Recent studies of growth form in plants have stressed the developmental significance of an architectural analysis (Hallé et al, 1978). According to Donoghue (1981), 'the study of growth patterns is the search for regularities in the construction of plants and the analyses of how such regularities are related to plant form.' Although conceived to describe the architecture of trees, some of the concepts reviewed by Donoghue (1981), Hallé et al (1978), Tomlinson (1978) and White (1984) can be applied to an analysis of moss architecture. Such a dynamic approach to morphology helps to identify the structural components and specific developmental processes that account for the growth form of mosses.

Methods

Populations of *Hedwigia ciliata* were collected on acid rocks in a deciduous forest in the Piedmont of North Carolina (De Luna 1751, 1752, DUKE). These populations were kept moist in a large covered tray and placed in a window-sill



Figs. 1-3. Acrocarpy in *Hedwigia ciliata*. 1.- Tip of main shoot with terminal archegonia and a subterminal innovation. 2.- Archegonia and distal part of the main shoot laterally displaced by growth of a subterminal innovation. 3.- A complete plant illustrating a main axis consisting of a chain of innovations.

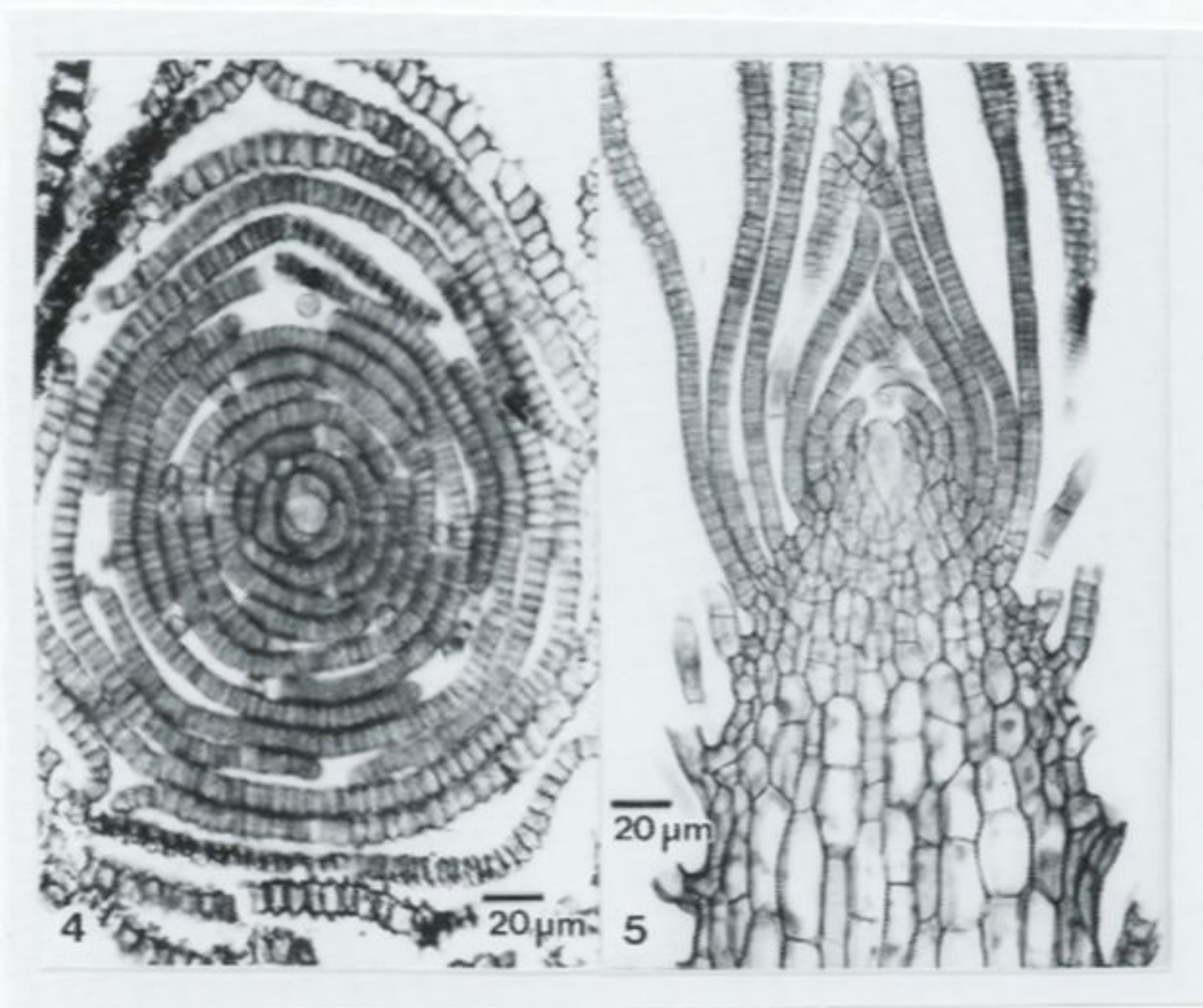
Results

The growth habit of *Hedwigia ciliata* is illustrated in Figs. 1-3. Most shoot apices either had archegonia and one bud (Fig. 1), or archegonia and a branch innovation (Fig. 2). Also, plants often had two or three capsules of different developmental stages. Capsules were always terminal on what appeared to be short lateral branches (Fig. 3). A detailed description of the plants based on anatomical observations is presented below. This description begins with the shoot apex, then continues with the formation of branch initials, the differentiation of archegonia, and the growth of innovations.

A shoot develops as a result of the activity of an apical cell. The apical cell is tetrahedral and has three cutting sides. In cross section, the cell derivatives are wedge-shaped (Fig. 4). The

pattern of division of the apical cell is a helicoidal $3/8$ pattern throughout shoot development. Leaves develop from the upper cell of the outer segment in each merophyte (Fig. 5). As the shoot develops, a heteroblastic leaf series is produced in which the first leaves retain juvenile features while later leaves develop characteristic adult features.

Few lateral buds are differentiated during shoot development. Secondary apical cells develop from the lower cell of the outer segment of a merophyte. Not all merophytes differentiate secondary apical cells. A lateral bud consists of an apical cell surrounded by cell derivatives and a few leaf initials. Some buds develop into very short perigonal branches (Fig. 6) while the apical cell of the main shoot is still active. Other buds remain dormant. In any case, buds, branch primordia, and mature branches have no pseudoparaphyllia.



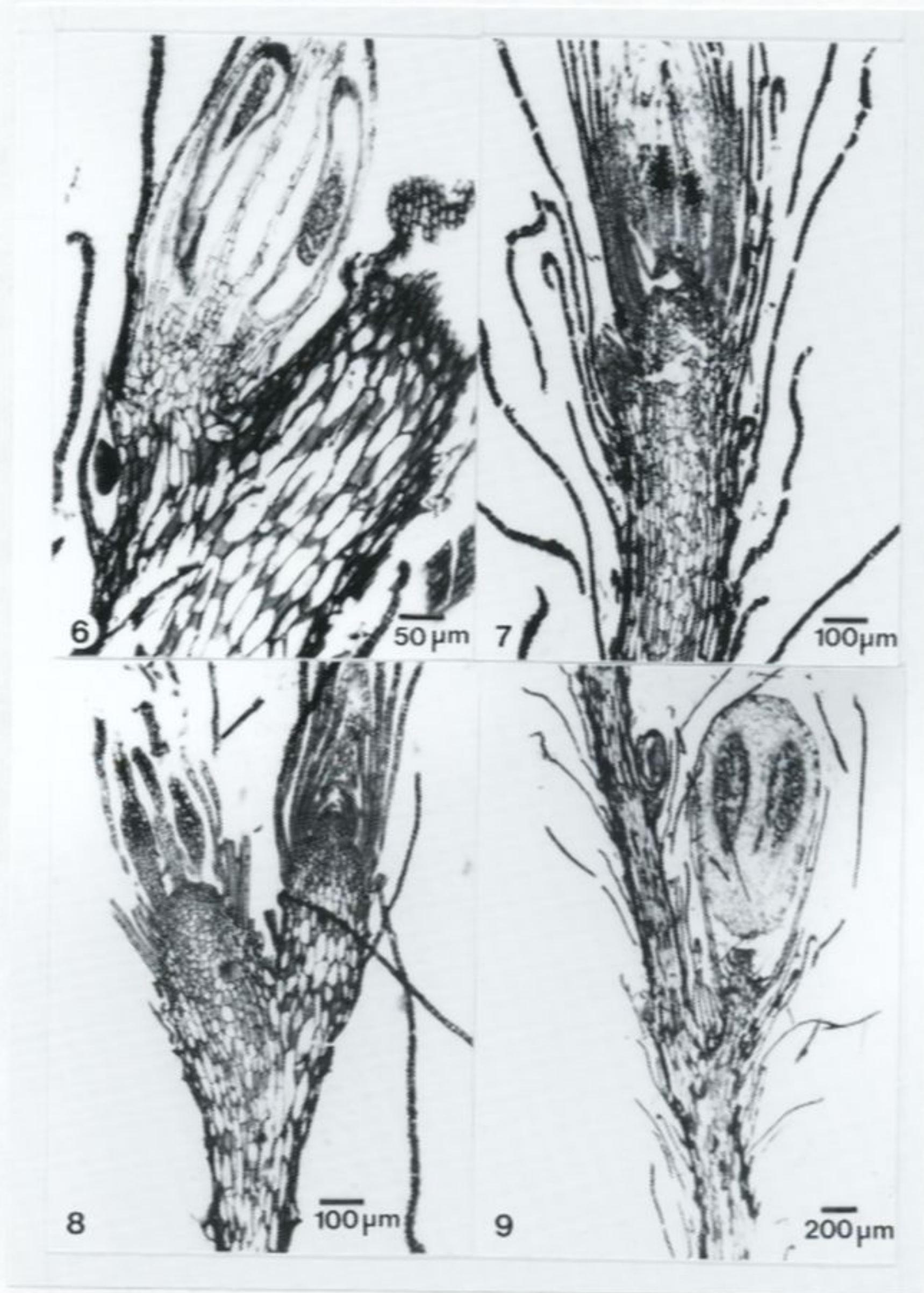
Figs. 4-5. Anatomy of the branching pattern in *Hedwigia ciliata*. 4.- Transverse section of the shoot apex showing the apical cell and an helicoidal segmentation pattern. 5.- Longitudinal section of the shoot apex illustrating the apical cell and merophytes.

The archegonia in *H. ciliata* is terminal on the main shoot, as in all acrocarpous mosses (Figs. 1, 7). Six to ten archegonia develop from the apical cell and recently derived merophytes. Within the perichaetium, archegonia mature in basipetalous succession. Only one capsule develops to maturity within each perichaetium.

The branching pattern of *H. ciliata* is sympodial. As one or rarely two subterminal buds begin to grow, they displace laterally the tip of the previous shoot (Figs. 7-9). Capsules then appear to be terminal on 'short lateral branches'. However, longitudinal sections show that each of these 'lateral branches' is the distal portion of the original main shoot laterally displaced by the growth of a subterminal innovation (Fig. 9).

As the innovation develops, it produces the same heteroblastic series of leaves that is produced by the primary shoot. This heteroblastic leaf series can be used to interpret the architecture of mature plants. A plant can be recognized as consisting of a chain of innovations. The base of each innovation is marked by the presence of small juvenile leaves and a sudden change in the thickness of the branches. The innovation is slender at its point of attachment to the main shoot. The end of an innovation is marked by large mature leaves and a capsule.

The examination of herbarium specimens of other populations of *H. ciliata* for these criteria suggests that the same acrocarpous growth form is developed regardless of the geographical location, altitudinal distribution, size of the colonies, and degree of exposure of the habitat. Furthermore, observations of additional her-



Figs. 6-9. Anatomy of the branching pattern in *Hedwigia ciliata*. 6.- Longitudinal section of a perigonial branch and the point of attachment to the main shoot. 7.- Longitudinal section of the distal part of a main shoot with archegonia and a subterminal bud. 8.- Longitudinal section of a young branching point with a subterminal innovation. 9.- Longitudinal section of an old branching point; the apex of the older innovation has a capsule.

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Discussion

According to Schofield and Héban (1984), all acrocarpous mosses are characterized by terminal perichaetia on main shoots of determinate growth. Branching of the gametophytic shoot is thus sympodial in acrocarpous mosses (Flowers, 1973), with the exception of some annual mosses like *Bruchia* or *Pleuridium*, that do not branch at all. Branches of an acrocarpous mosses may be orthotropous, i.e., vertically oriented, or plagiotropous, i.e., horizontally oriented.

In contrast, pleurocarpous mosses are characterized by perichaetia positioned on

lateral branches. Frequently these branches are only small slender buds at the sides of the main shoot (Flowers, 1973). Generally, the growth of the main shoot is indeterminate and thus branching is monopodial (Buck and Vitt, 1986; Flowers, 1973; Schofield & Héban, 1984), although a few mosses apparently combine monopodial and sympodial branching. Most pleurocarpous mosses develop plagiotropic shoots; however, some of them also develop either erect or pendant branches.

The present description of archegonial and branch formation in *H. ciliata* fits the definition of acrocarpy in mosses. Furthermore, the organization of the shoot apex in *Hedwigia ciliata* is also similar to that described in other acrocarpous mosses (Berthier, 1972; Frey, 1970, 1974). The mature plants of *H. ciliata* are pleurocarpous only in appearance, since they are prostrate and bear capsules on what seem to be very short lateral branches. The results from this study show that the main axis of this moss is a chain of sympodial plagiotropic innovations rather than one shoot of indeterminate growth.

Each unit (i.e., innovation) of the main axis of *H. ciliata* constitutes a module (sensu White, 1984), since it consists of all the products of an apical cell. Thus, the architectural model (sensu Hallé et al, 1978; Tomlinson, 1978) includes repeated equivalent sympodial units which constitute the plagiotropic leader axis (i.e., a sympodium), as well as lateral adventitious branches, also plagiotropic, which develop at the base or medial parts of each sympodial unit.

This type of growth habit has been sometimes called pseudo-pleurocarpous (Buck and Vitt, 1986; Meusel, 1935). Anatomical evidence presented here corroborates earlier accounts (Hedwig, 1801; Meusel, 1935; Bruch et al, 1846; Scott and Stone, 1976) that described *H.*

ciliata as acrocarpous or pseudo-pleurocarpous. Meusel (1935) also described *Hedwigidium* as a pseudo-pleurocarpous moss. However, no anatomical data on *Hedwigidium* are available yet.

It has been suggested that the modular structure of mosses can be recognized in herbarium specimens through the examination of the heteroblastic leaf series that is produced each time a module develops (Mishler, 1986). The available anatomical data on module formation does not contradict observations of the heteroblastic leaf series in *H. ciliata*. Similarly, based solely on observations of herbarium specimens, it seems that the growth habit in *Hedwigidium*, *Braunia*, and *Pseudobraunia* is also pseudo-pleurocarpous.

A pseudo-pleurocarpous growth habit is uncommon, but present in a few groups of diverse relationships, notably species in the Grimmiaceae and Orthotrichaceae (Buck and Vitt, 1986), *Mesotus* (Dicranaceae, Allen, 1987 a), and Dicnemonaceae (Allen, 1987 b). Since pseudo-pleurocarpy has apparently originated independently in several groups, growth habit alone is of limited value in assessing the systematic position of the Hedwigiaceae.

The Hedwigiaceae has been classified in three different orders based on several features. For example, the growth form that resembles pleurocarpy is similar to that of mosses in the Grimmiales, Orthotrichales, and Isobryales. The leaf cells have sinuose walls and are similar to those in the Grimmiales. However, the multiple papillae are similar to those in the Orthotrichales, and some families in the Isobryales. Finally, the ecostate leaf is an additional feature shared with several families in the Isobryales.

Currently, most floristic works include the

Hedwigiaceae among the pleurocarpous families with diplolepidous peristomes, close to the Leucodontaceae, in the Isobryales. According to Vitt (1982), "affinities to the Leucodontaceae are evident in the capsules, basal cells, and leaf characters." However, the results from the present study indicate that the Hedwigiaceae may not belong in the Leucodontales or any other group of pleurocarpous mosses.

Smith (1978) classified the Hedwigiaceae in the Orthotrichales, another group with diplolepidous peristomes. A relationship to the Orthotrichineae (sensu Vitt, 1984), close to Orthotrichaceae, is suggested by the shape of leaf cells and papillae during shoot development, the type of calyptra development, as well as the acrocarpous growth habit.

The Hedwigiaceae has also been classified among the pseudo-pleurocarpous mosses with haplolepidous peristomes, i.e. near Grimmiaceae (Jones, 1933; Crum, 1976). However, a peristome is lacking in the Hedwigiaceae, so it is difficult to select the most plausible hypothesis of its ordinal relationships at present (Crum, 1976). Studies of developmental anatomy of the annular region of the capsule now in progress may provide a resolution to this problem.

Besides the potential use of growth pattern in evaluations of the systematic position of the Hedwigiaceae, it also may help to evaluate the circumscription of the family. The available information suggests that several characters, like spore ornamentation, protonemal development, shoot development, and leaf cell shape and papillae, are shared only by species in *Hedwigia*, *Hedwigidium*, *Braunia*, and *Pseudobraunia*. The basic pseudo-pleurocarpous pattern is also shared by these four genera. Thus, this information seems compatible with the preliminary interpretation that *Rhacocarpus* and

Bryowijkia should be excluded from the Hedwigiaceae, and that the Hedwigiaceae includes only the species currently included in *Hedwigia*, *Hedwigidium*, *Braunia* and *Pseudobraunia*. However, the circumscription of the family is a taxonomic problem still under study.

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