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The Taxonomic Use of Leaf Characteristics in the Funariaceae.

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The Taxonomic Use of Leaf Characteristics in the Funariaceae

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TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

Introduction

The taxonomy of the Funariaceae has been characterized by considerable discussion and revision due to the interpretation of a quantity of genetical and cytological work, and an increased tendency to include gametophyte characters in classification; these factors have effected a gradual change in generic and specific definitions in this family.

Genera occurring in North America are *Funaria*, *Entosthodon*, *Physcomitrium*, *Pyramidula*, and *Aphanorhegma* (here including, *Physcomitrella*). There are consistent morphological differences between the capsules of these genera, by which genus separation is traditionally made. However, there is still basic disagreement on the generic concept in this family. Dixon (1896) combined *Entosthodon* with *Funaria*, as had Braithwaite (1888), noting that it was probably intermediate between *Funaria* and *Physcomitrium*. Brotherus (1924) also united *Entosthodon* and *Funaria* on the basis of an elevated capsule and entire calyptra, but Grout (1935) and later, Nyholm (1956) upheld the separation on peristome characteristics. Crum (1955), while recognizing the apparently close relationship of the two, believed that such easily distinguished groups should be separated for convenience.

A similar situation exists with the classification of the other genera. Brotherus (1924) separated Aphanorhegma and Physcomitrella on the basis of the operculum, but Grout (1935) united them because of the immersed capsules and the method of dehiscence. Andrews (1918, 1929) suggested that Aphanorhegma, Physcomitrella and Physcomitrium might better be regarded as one genus on the basis of hybridization, and even suggested (1942) that only one genus, Funaria, might be adopted for this family without doing damage to general generic concepts. However, most workers in this family still follow the general scheme of Brotherus' treatment (1924), which lists nine genera (world-wide), separated by sporophyte characters.

Treatments of the generic concept in this family have generally ignored the gametophytic generation, although there is ample evidence supporting its use. The use of gametophytic characteristics in taxa definitions is probably desirable, because much emphasis has been placed on typological and morphological variants, with the result that many of the presently defined taxa may actually be expressions of infraspecific variation. On the basis of polyploid races, this has been suggested within the genus Physcomitrium by Crum (1955), and in the genus Funaria by the work of Wettstein (1932). Polytypic variation may be prevalent in the Entosthodon-Funaria complex, as well as that of Aphanorhegma-

Physcomitrella-Physcomitrium.

The results of special techniques (experimental genetics, cytotaxonomy, etc.) suggest that in some genera the gametophyte may provide a more accurate indication of the degree of relationship among taxa than the sporophyte (Steere, 1947). In those families in which the members hybridize and have almost identical gametophytes, but in which the sporophytes exhibit significant variation, an actual close relationship of the taxa may be obscured by a reliance on diploid characters. Such reliance could result in widely separating forms which may merely be races or subgenera.

The validity of a sporophyte-based classification is further questioned by a consideration of asexual populations. Anderson (1963) suggests that the evolution of the mosses progresses towards the abandonment of sexuality; it is known that most mosses are facultatively asexual, and what observational work has been done suggests that a substantial percentage of mosses rarely, or never fruit (Gemmel, 1950). In the Funariaceae, it is readily apparent that, although the overwhelming percentage of collected specimens possess sporophytes, in the past only those specimens with sporophytes were collected, or collections were ignored, because of the lack of a useful gametophyte key. The high percentage of sporophyte-bearing packets in herbarium collections of Funariaceae does not preclude the existence of a large number of asexual clones, if one considers the collection methods. Of course, sporophyte keys are useless in this case.

Another factor which points to the desirability of a gametophyte key is the probability that selection is strongest in the mosses against the gametophyte. Any variation in sporophyte form probably is more sheltered than in the gametophyte, because of the dependent nature of the diploid generation and the sheltering effect of heterozygosity upon recessive genes. This and the increased compliment of genic material may result in a much wider range of variation than in the gametophyte. Such variation would not necessarily impose reproductively isolative barriers, nor would it define non-crossing populations, but <u>is</u> presently used for taxon definition. It might also be suggested that populations differing greatly in the diploid generation hold enough genic material in common (see Bryan, 1957), to allow frequent crossing, but with the retention of a parental sporophyte form in the resulting progeny. The close relationship of these populations would not be reflected in taxonomic treatments based upon variation in the sporophyte. Considering geographical distribution, ecology, cytology and hybridization in this family, the apparently close similarity of the gametophytes may reflect the actual condition: that the taxa are more closely related than previously thought, and frequently may simply be morphs within the same gene pool.

One of the problems in the Funariaceae is the fact that so much descriptive work and the resulting generic and specific definitions are based on the sporophyte, a structure which may be present only sporadically and, if present, may be of limited reliability in reflecting actual taxon differences.

In any event, there is indication of a need for supportive evidence from gametophyte studies for the problem of taxon definition.

The purpose of this paper is to make an examination of gametophyte leaves in the Funariaceae, and with results of this study, to attempt to answer some basic taxonomic questions:

1. What is the range of leaf variation?
2. Are taxonomically significant characters present in the leaf?
3. Is a purely vegetative key possible?
4. What is the correlation between a taxonomic classification based on the gametophyte and one based on the sporophyte?
5. Is a gametophyte-based classification consistent with the results of previous research?

Methods and Materials

A total of fifty herbarium packets of the Funariaceae were examined. These collections were obtained from the Walter Kiener Memorial Collection and from private material of Dr. Paul V. Prior and Dr. David Sutherland. For comparison with American plants, packets of European specimens were also obtained from the Herbarium of the British Bryological Society. Collection data is included in Table I.

Care was taken to obtain leaves from only those plants which bore sporophytes, so that accurate identification and correlation between gametophyte and sporophyte characteristics would be possible. Leaves were selected from the plants at random, relaxed with dilute detergent and permanently mounted in Hoyle's Medium.

Each leaf was examined for six characters:

1. Leaf cell size--apex, median, basal, mid-marginal
2. Ratio of leaf length to width
3. Costa length
4. Margin configuration (plane, involute, serrate, entire)
5. Cell shape
6. Leaf shape

Characters 1-3 are quantitative and give the size of the leaf and cells; characters 4-6 are qualitative and describe general shape. These characters were essentially

Table I. Specimens Examined

Species	Collector-Location
Funaria americana	Holzinger, Winona, Minn.
Funaria attenuata	Crundwell, Loch Drsyut, Wales
Funaria calcarea	Broome, Millers Dale, Wales
Funaria calvescens	Griffin, Uvalde Co., Texas
Funaria Convulata	Morse, Soda Springs, Calif.
Funaria Convulata	Baker, San Mateo Co. Calif.
Funaria flavicans	Koch, Jefferson Par., La.
Funaria flavicans	Nelson, Centennial, Wyoming
Funaria flavicans	Stifles, Anna Maria, Florida
F. hygrometrica	Rapp, Sanford, Florida
F. hygrometrica	Sutherland, Seattle, Wash.
F. hygrometrica	Koch, St. Chas. Par., La.
F. hygrometrica	Koch, New Orleans, La.
F. hygrometrica	Cavanagh, Dickinson Co., Iowa
F. hygrometrica	Prior, Cottonwood Co., Minn.
F. hygrometrica	Shimek, Mason City, Iowa
F. hygrometrica	Cavanagh, Iowa Co., Iowa
F. hygrometrica	Prior, Luray, Virginia
F. mediterranea	Bartram, Pima Co., Arizona
F. microstoma	Webber, Lincoln, Nebraska
F. muehlenbergii	Perry, Llanymynech Hill, Wales
F. muehlenbergii	Cornwall, Tintagel, Wales
F. serrata	Sull. and Lesq. #157
Pyramidula tetragona	Prior, Cottonwood Co., Minn.

Table I. (Continued)

Species	Collector--Location
Discelium nudum	Holzinger, Bethlehem, Pa.
Entosthodon Bolanderi	Bartram, Pima Co., Ariz.
Entosthodon Templetoni	Truskmore Co., Sligo, Wales
Meesia uliginosa	Crum, Alberta, Canada
Amblydon dealbatus	-----, Nova Scotia
Nanomitrium synoicum	Conard, Poweshiek Co., Ia.
Entosthodon Drummondi	Mohr, Mobile, Alabama
E. attenuatus	Kiener, Great Britain
E. epipedostegia	Pringle, coll. in Mexico
Aphanorhegma serratum	Kiener, Saunders Co., Nb.
A. serratum	Holzinger, Exsiccati
A. serratum	Holzinger, Exsiccati
Physcomitrium hookeri	Prior, Milford, Ia.
Physcomitrium hookeri	Prior, Estherville, Ia.
P. turbinatum	Conard, Jones Co., Ia.
P. turbinatum	Conard, Jones Co., Ia.
P. pyriforme	Koch, Jefferson Par., La.
P. pyriforme	Koch, New Orleans, La.
Funaria calvescens	Nash, Eustis Lake, Fla.
Physcomitrium pyriforme	Ireland, Batesville, Kans.
Funaria flavicans	Kiener, Lincoln, Nb.
Physcomitrium immersum	Kiener, Lincoln, Nb.
Entosthodon Drummondi	Holzinger, Georgia
E. Drummondi	Kiener, Kisatchie, La.
E. Drummondi	Holzinger, Alabama
Funaria flavicans	Grout, Anna Maria, Fla.

chosen for ease of measurement. All measurements were made with an ocular micrometer. Leaf length:width ratio was determined by measurements of the longest and widest parts of the leaf. Other areas of measurement are described in Figure 1.

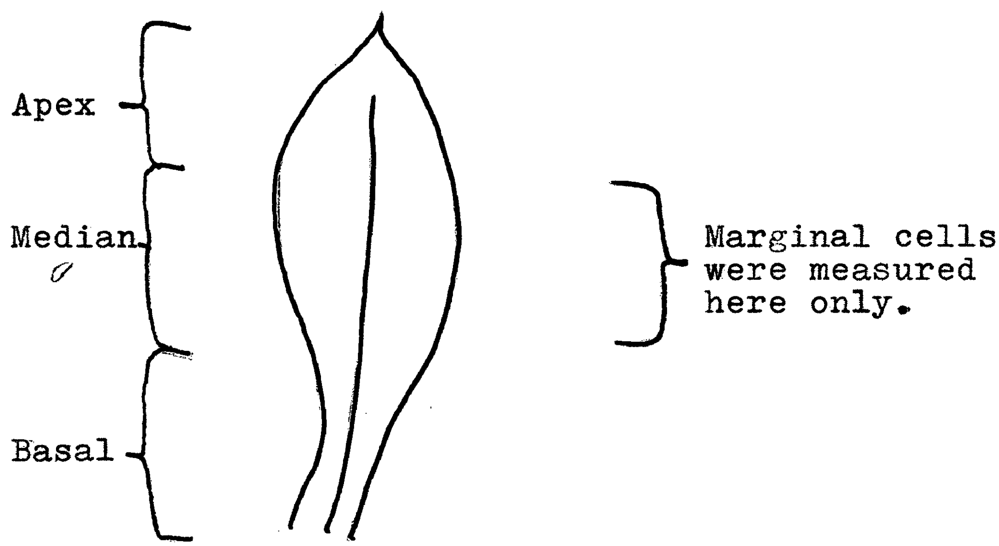


Figure 1. Areas of cell measurement. Each leaf is divided into three equal parts by length.

Results

Representative species of each genus in the Funariaceae were examined for generic and specific characters. Results, in the form of qualitative descriptions and quantitative measurements, are presented by genus.

1. APHANORHEGMA Sullivant (1848).

Leaves oblong-lanceolate to obovate, acute to acuminate, serrate above by projecting cells; costa variable in length, ending at mid-leaf to subpercurrent; margins plane, unbordered or indistinctly bordered with elongated cells; cells of the lamina parenchymatous, thin-walled, elongate-rectangular at the base, rhombo-rectangular centrally, becoming shorter and hexagonal in the apex; plants very small, 1-5 mm tall, light green, found on wet soil, marshy land, or damp banks of ponds and streams.

Table II. Measurements of
<u>Aphanorhegma</u> <u>serratum</u> (Hook. & Wils.) Sull.

Character	Average (microns)		Range (microns)
Leaf:			
length..........	1.65 mm	.....	1.14-2.43 mm
width...........	.52 mm	.....	.43-.73 mm
Length/width ratio...	3.2	.....	2.3-4.1
Cell length:			
apex............	44	.....	26-69
median..........	54	.....	33-82
margin..........	97	.....	65-166
basal...........	90	.....	55-163
Cell width:			
apex............	20	.....	16-26
median..........	19	.....	13-26
margin..........	18	.....	13-23
basal...........	29	.....	16-39

Table III. Leaf Characters of Aphanorhegma spp.

	Costa	Margin	Leaf Shape
A. serratum	percurrent, not forked	upper 1/2 serrate by projecting cells	obovate-lanceolate
A. patens[1]	to 3/4 leaf, not forked	upper 1/2 serrate by blunt cells	narrow-lanceolate
A. californica[2]	to ± 1/2 leaf, often forked	upper 1/3 serrate by blunt cells	oblong-lanceolate

[1] Synonym: Physcomitrella patens (Hedw.) Bruch. & Schimp.

[2] Aphanorhegma californica (Crum & Anderson) Christiansen nov. comb. See description of Physcomitrella californica in Bryologist 58:4 (1955).

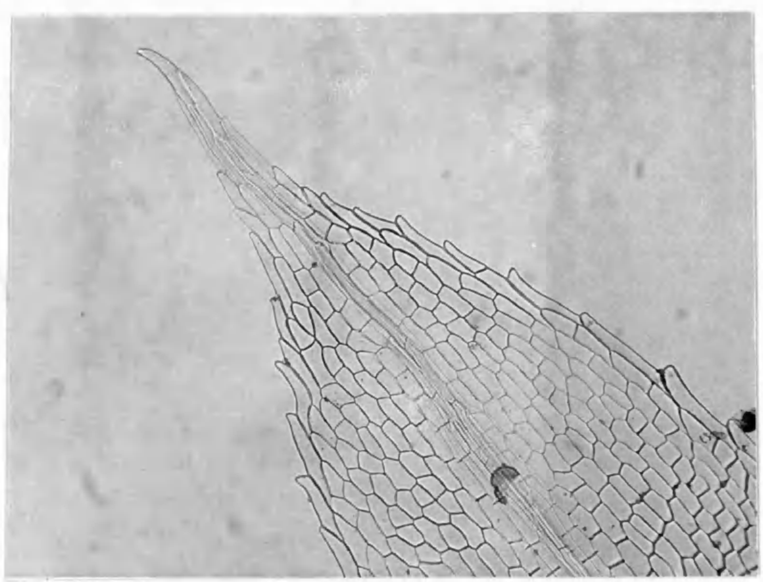


Figure 2. A. serratum, showing costa length and projecting cells of the margin.

It was found that the measurements for cell length and leaf length in Aphanorhegma serratum varied over a wide range. However, it can be seen (Table II.) that much longer cells are found in the margin and basal areas than in the median or apex. Cell width varied much less than did length, and appears to be a more reliable taxonomic character. Apex, median and marginal cells are approximately the same width and basal cells are only slightly wider. Leaf length/width ratio also seems to be rather consistent; most of the leaves from a single plant are 3:1.

I chose A. serratum as the representative species, because it is the only species that bryologists universally accept for this genus. However, there are two very similar species which are often confused with Aphanorhegma, but which have been placed in a separate genus, Physcomitrella, on the basis of an irregularly dehiscing capsule and thin-walled exothecial cells, neither of which is found in A. serratum.

Grout (1935) united Physcomitrella with Aphanorhegma; supporting Grout's revision, Bryan (1957) reported the close similarity in cytology and chromosome number of the two taxa. For the present, I see no useful purpose in separating these species and will consider them as Aphanorhegma.

2. PYRAMIDULA Bridel (1819).

Leaves variable in length, the upper 1-1.5 mm long, the lower half as long or less, ovate, ending in a slender acumination, entire; costa percurrent to excurrent; margins plane, the marginal cells slightly shorter and wider than median cells; cells of the lamina parenchymatous, thin-walled, quadrate to rectangular at the base, becoming hexagonal or elongated at the apex; plants very small, 1-2 mm tall, pale green, on soil, rare in North America.

Table IV. Measurements of
Pyramidula tetragona (Brid.) Bridel

Character	Average (microns)	Range (microns)
[1]Leaf:		
length	711	657-757
width	347	314-371
Length/width ratio	2.1	2.0-2.1
Cell length:		
apex	22	13-39
median	17	13-23
margin	16	9-23
basal	23	13-43
Cell width:		
apex	18	13-23
median	19	13-23
margin	23	19-26
basal	22	16-29

[1]Leaf measurements are of lower leaves.

This genus includes only one species, *Pyramidula tetragona*. It is usually separated from the other members of the family by the large four-sided calyptra and the short seta. Lesquereux and James (1884) used these characters to distinguish *Pyramidula*, as Brotherus (1924) later did in his world-wide treatment of the Funariaceae. The generic key of Brotherus was undoubtedly used as the basis for the separation of North American genera by Grout (1935), whose work, in turn, was the foundation of Conard's key (1944).

It is true that the calyptra is distinctive and consistent. It is a good taxonomic character and has been used effectively to separate this genus. However, it is unusual that these bryologists should fail to mention that *P. tetragona* has the most distinctive and easily recognized leaf cells of the family. The small size of the leaves (0.5-1.5 mm long) and the almost regularly quadrate small median cells clearly distinguish this species. Another interesting, but less consistent character is the lower marginal cell length:width ratio of 1:2.

Figure 3. Pyramidula tetragona

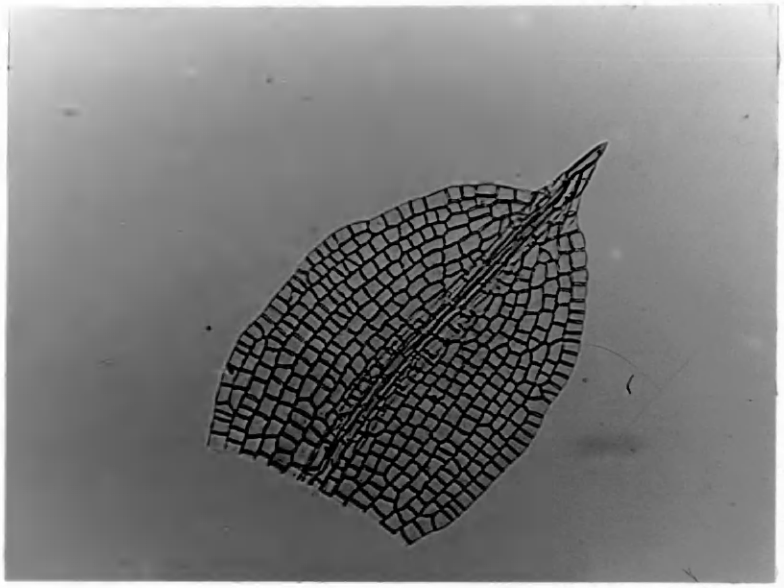
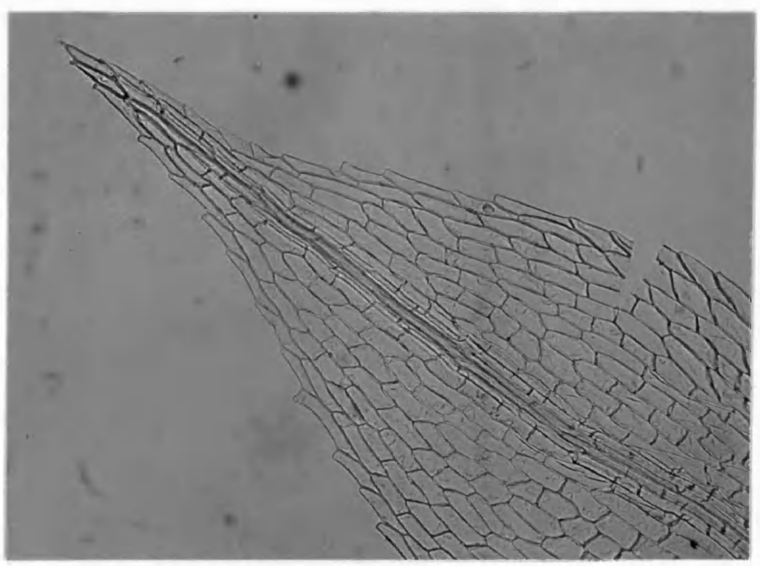


Figure 4. Physcomitrium pyriforme



3. PHYSCOMITRIUM (Brid.) Fürnrohr (1829).

Leaves variable in shape, ovate to oblong-lanceolate, acute to acuminate, entire to distinctly serrate; costa vanishing to excurrent; margins plane or (rarely) reflexed, bordered with one or more rows of elongated cells; cells of the lamina parenchymatous, thin-walled, oblong-rectangular to swollen at the base of the leaf, becoming shorter above; plants small, stems to 4 mm tall, found on soil.

Table V. Measurements of
Physcomitrium pyriforme (L.) Bridel.

Character	Average (microns)	Range (microns)
Leaf:		
length..........	3.20 mm	.... 2.35-3.75mm
width...........	0.98 mm	.... 0.714-1.17mm
Length/width ratio...	3.3	.... 2.7-3.8
Cell length:		
apex............	55	 39-82
median..........	60	 32-98
margin..........	152	 120-196
basal...........	137	 71-173
Cell width:		
apex............	21	 16-29
median..........	30	 22-49
margin..........	17	 13-26
basal...........	39	 26-52

Table VI. Measurements of
Physcomitrium *Hookeri* Hampe.

Character	Average (microns)		Range (microns)
Leaf:			
length..........	2.26 mm	.....	1.95-2.50 mm
width...........	1.15 mm	.....	0.88-1.35 mm
Length/width ratio...	1.97	.....	1.79-2.26
Cell length:			
apex............	59	.....	32-72
median..........	57	.....	42-75
margin..........	81	.....	55-147
basal...........	87	.....	52-163
Cell width:			
apex............	25	.....	19-33
median..........	26	.....	19-33
margin..........	22	.....	19-26
basal...........	32	.....	22-39

Table VII. Measurements of
Physcomitrium *immersum* Sullivant.

Character	Average (microns)		Range (microns)
Leaf:			
length..........	1.84 mm	.....	1.70-2.00 mm
width...........	0.76 mm	.....	0.71-0.83 mm
Length/width ratio...	2.41	.....	2.26-2.54
Cell length:			
apex............	56	.....	26-72
median..........	72	.....	42-104
margin..........	147	.....	97-196
basal...........	104	.....	58-130

Table VII. Measurements of
Physcomitrium immersum Sullivant. (Continued)

Character	Average (microns)		Range (microns)
Cell width:			
apex..........	23	.....	16-30
median........	23	.....	16-30
margin........	15	.....	13-20
basal.........	32	.....	22-46

Table VIII. Leaf Characters of Physcomitrium spp.

Species	Costa	Margin
P. pyriforme	percurrent to excurrent	upper 1/2 serrate, plane
P. megalocarpum	percurrent	upper lvs. entire, lower lvs. serrulate, reflexed
P. californicum	sub-percurrent	entire, plane
*P. delicatulum	vanishing at base of acumen	serrulate, plane
P. pygmaeum	sub-percurrent	serrulate
*P. washingtoniense	vanishing at base of acumen	upper 1/2 serrulate, erect
P. Hookeri	percurrent	entire, plane
P. immersum	sub-percurrent	upper 1/2 serrate

*New species described in Bryologist, 58:1-10. (1955) by Crum and Anderson.

Table VIII. Leaf Characters of <u>Physcomitrium</u> (Continued).

Species	Leaf Shape	Cell Shape
P. pyriforme	oblong-lanceolate obovate	oblong lamina cells, inflated alar area, narrow margins
P. megalocarpum	lanceolate-spatulate	oblong lamina cells, inflated alar area, narrow margins
P. californicum	broadly acute	cells rectangular, no alar region
P. delicatulum	lower leaves ovate, upper spatulate	oblong lamina cells, no alar region
P. pygmaeum	ovate-lanceolate, acute	marginal area of 5-7 rows of narrow cells
P. washingtoniense	oblong-ovate, filiform acumen	oblong lamina cells, long clear cell at tip
P. Hookeri	broadly ovate, shortly acuminate	oblong lamina cells, basal cells wider but not inflated
P. immersum	ovate-lanceolate, acuminate	oblong lamina cells, basal cells larger, narrow margins

4. FUNARIA Hedwig (1801).

Leaves broadly ovate to lanceolate, acute, acuminate, or ending in a long filiform tip, entire, crenulate, or sharply serrate above by projecting cells; costa variable in length, ending well below the apex to long excurrent; margins plane or involute, unbordered or bordered with narrow elongated cells; cells of the lamina parenchymatous, thin-walled, elongate-rectangular at the base, becoming shorter and narrower above; plants extremely variable, found widely distributed, many times on disturbed soil.

Table IX. Measurements of
Funaria hygrometrica (L.) Hedwig.

Character	Average (microns)		Range (microns)
Leaf:			
length..........	2.67 mm	.....	2.21-3.63 mm
width...........	.94 mm	.....	.75-1.14 mm
Length/width ratio...	2.9	.....	2.3-4.7
Cell length:			
apex............	70	.....	52-92
median..........	65	.....	35-85
margin..........	88	.....	48-120
basal...........	115	.....	78-157
Cell width:			
apex............	26	.....	19-35
median..........	41	.....	29-52
margin..........	24	.....	16-32
basal...........	38	.....	29-62

Table X. Measurements of
<u>Funaria americana</u> Lindb.

Character	Average (microns)		Range (microns)
Leaf:			
length..........	2.31 mm	.....	1.82-2.67 mm
width...........	.94 mm	.....	.67-1.11 mm
Length/width ratio...	2.5	.....	2.0-3.0
Cell length:			
apex............	67	.....	42-85
median..........	64	.....	42-85
margin..........	71	.....	52-88
basal...........	75	.....	52-95
Cell width:			
apex............	28	.....	16-39
median..........	31	.....	23-39
margin..........	30	.....	20-42
basal...........	32	.....	26-39

Table XI. Measurements of
<u>Funaria Muhlenbergii</u> Turn.

Character	Average (microns)		Range (microns)
Leaf:			
length..........	2.75 mm	.....	2.07-3.29 mm
width...........	1.14 mm	.....	.85-1.37 mm
Length/width ratio...	2.4	.....	2.2-2.7
Cell length:			
apex............	69	.....	52-98
median..........	68	.....	49-114
margin..........	93	.....	65-117
basal...........	120	.....	75-173

Table XI. Measurements of
Funaria Muhlenbergii Turn. (Continued)

Character	Average (microns)		Range (microns)
Cell width:			
apex..........	29	.....	26-33
median........	31	.....	23-39
margin........	20	.....	16-23
basal.........	43	.....	36-52

Table XII. Measurements of
Funaria serrata Bridel.

Character	Average (microns)		Range (microns)
Leaf:			
length........	1.83 mm	.....	1.58-2.14 mm
width.........	.60 mm	.....	.57-.64 mm
Length/width ratio.	3.0	.....	2.5-3.3
Cell length:			
apex..........	49	.....	36-62
median........	72	.....	39-95
margin........	123	.....	98-156
basal.........	89	.....	62-127
Cell width:			
apex..........	28	.....	23-36
median........	34	.....	23-42
margin........	23	.....	16-33
basal.........	38	.....	33-49

Table XIII. Leaf Characters of *Funaria* spp.

Species	Costa	Margin
F. americana	strongly excurrent	entire, slightly narrower
F. californica	ending below apex	very entire, plane
F. flavicans	excurrent to percurrent, variable	entire, plane
F. hygrometrica[1]	percurrent to excurrent, variable	entire or crenulate
F. microstoma	percurrent	entire
F. Muhlenbergii[2]	ending well below the apex	variable, entire to serrate
F. serrata	ending below the apex	sharply serrate by projecting cells
F. Orcutti	long excurrent into hair-point	serrate above, hardly bordered

[1]Synonymy: *F. calvescens* Schwaegr.
F. convoluta Hampe

[2]Synonymy: *F. calcarea* Wahl.
F. mediterranea Lindb.

Table XIII. Leaf Characters of Funaria spp. (Continued)

Species	Leaf Shape	Cell Shape
F. americana	oblong-lanceolate, acuminate, 2-2.3mm	apex ending in a hair point .4 mm long, lamina cells oblong
F. californica	oblong-ovate, broadly acute, 1mm	apex rarely ends in single-cell apiculus, other cells oblong
F. flavicans	obovate slenderly acuminate	lamina cells oblong
F. hygrometrica	oblong-ovate acute to short acuminate, 2-4 mm	lamina cells oblong, basal cells longer
F. microstoma	slenderly acuminate to long apiculate	median cells oblong, basal cells elongate
F. Muhlenbergii	obovate-lanceolate, acuminate, 1.5-3 mm	apex ending in filiform point .2-.6 mm, cells rectangular
F. serrata	elliptic to lanceolate, broadly acute to short acuminate, 2-3 mm	oblong cells above, rectangular below
F. Orcutti	broadly ovate to obovate, ca. 2 mm	apex ending in a filiform point .6-1 mm, hyaline at tip

5. ENTOSTHODON Schwaegrichen (1823).

Leaves obovate, spatulate, to oblong-lanceolate, acute to acuminate, sometimes ending in a filiform point, entire below to serrate or entire-crenulate above; costa ending mostly well below the apex, rarely shortly excurrent; margins unbordered or bordered with thin, narrow cells or rarely with short, inflated cells; cells of the lamina parenchymatous, rectangular to oblong-hexagonal above, becoming larger at the base; plants widespread, but many species are found exclusively in the regions of the southwestern United States.

Table XIV. Measurements of *Entosthodon Bolanderi* Lesquereux.

Character	Average (microns)		Range (microns)
Leaf:			
length..........	1.61 mm	.....	1.38-1.96 mm
width...........	.62 mm	.....	.52-.67 mm
Length/width ratio...	2.6	.....	2.1-3.0
Cell length:			
apex............	49	.....	36-65
median..........	56	.....	33-68
margin..........	45	.....	33-52
basal...........	62	.....	42-85
Cell width:			
apex............	25	.....	20-36
median..........	30	.....	26-36
margin..........	29	.....	23-33
basal...........	36	.....	29-49

Table XV. Measurements of Entosthodon Drummondii Sull.

Character	Average (microns)		Range (microns)
Leaf:			
length........	1.81 mm	.....	1.69-1.92 mm
width.........	.61 mm	.....	.57-.64 mm
Length/width ratio.	3.0	.....	2.9-3.1
Cell length:			
apex..........	53	.....	33-75
median........	69	.....	46-98
margin........	112	.....	95-121
basal.........	82	.....	59-130
Cell width:			
apex..........	25	.....	16-33
median........	29	.....	23-39
margin........	28	.....	23-33
basal.........	35	.....	26-42

Table XVI. Leaf Characters of Entosthodon spp.

Species	Costa	Margin
E. attenuatus	ending well below the apex	entire-crenate, bordered by 2 rows of narrow cells
E. Bartramii	ending well below the apex	serrate above, short inflated cells in the margin
E. Bolanderi	ending at 1/2 to 3/4 leaf length	entire-crenulate, marginal cells narrow, elongate

Table XVI. Leaf Characters of *Entosthodon* spp. (Continued).

Species	Costa	Margin
E. Drummondii	subpercurrent	entire-crenulate, marginal cells narrow, elongate
E. Leibergii	variable, ending below apex to shortly excurrent	entire-serrulate, marginal cells narrow, elongate
E. planoconvexus	ending below apex	serrate, marginal cells elongate at acumen
E. rubiginosus	variable, vanishing to excurrent	entire, unbordered
E. rubrisetus	ending below apex, brownish-green	bluntly serrate, unbordered
E. tucsoni	ending below apex	entire-sinuose, unbordered
**E. kochii*	ending below apex	entire, unbordered

*New species described in Bryologist, 58:12-13 (1955) by Crum and Anderson.

Table XVI. Leaf Characters of *Entosthodon* spp. (Continued)

Species	Leaf Shape	Cells
E. attenuatus	obovate-oblong, shortly acuminate-apiculate, 2-3 mm	upper oblong, lower rectangular
E. Bartramii	oblong-obovate acute to shortly acuminate, 1.5 mm	upper oblong, lower rectangular
E. Bolanderi	obovate-oblong slenderly acuminate, 2 mm	acumen ending by single long cell
E. Drummondii	oblong-obovate, broadly acute	upper oblong-hexagonal, lower rectangular
E. Leibergii	oblong-lanceolate, acute to apiculate, 2-3 mm	inflated basal auricles
E. planoconvexus	oblong-ovate piliform, 2.5 mm	upper hexagonal-rhomboid, lower rectangular
E. rubiginosus	broadly ovate, short subulate point, 2 mm	upper rhomboid-hexagonal, lower rectangular
E. rubrisetus	oblong-spatulate, short yellow hair point, 2-3 mm	upper hexagonal-rhomboid, lower rectangular
E. tucsoni	oblong-ovate, shortly acuminate, 2-2.75 mm	upper hexagonal-rhomboid, lower rectangular
**E. kochii*	oblong-obovate, broadly acute to apiculate, 1 mm	upper oblong-hexagonal, lower rectangular

*New species described in Bryologist, 58:12-13 (1955) by Crum and Anderson.

From the results of the leaf and cell measurements and from compilation of species descriptions of those taxa not examined, an artificial leaf key to the species has been developed. I have attempted to use qualitative characters whenever possible. The following key is the first one for this family which uses leaf characters exclusively. It includes all the presently accepted species for the continental United States, except Alaska. All subspecific designations and previously established synonyms are ignored. However, the key does include several species which are infrequently collected. Only two certain collections of Entosthodon Leibergii are known, and Physcomitrium pygmaeum has not been collected for many years; however, confident determination of sterile material may result in increased reportings of those species thought to be rare.

This tentative key must be used with the realization that most characters may be extremely variable. The characters in the dichotomies are an average, which should indicate the use of more than one leaf (preferably three or more) for identification.

Leaf Key to the Funariaceae of the United States

1a. Costa reaching the apex, or longer..................2

1b. Costa ending well below the apex..................21

2a. Upper leaves serrate above the middle................3

2b. Upper leaves entire above the middle.................9

3a. Apex ending in a long filiform tip, .5-1 mm long......
........*Funaria Orcutti*..

3b. Apex not as above.....................................4

4a. Margins reflexed, with 2 rows of narrow cells.........
.....*Physcomitrium megalocarpum*.

4b. Margins not as above..................................5

5a. Leaves acute; plants rare (not to be expected).......6

5b. Leaves acuminate......................................7

6a. Leaves oblong-lanceolate, with 1-2 rows of narrow marginal cells..................*Entosthodon Leibergii*

6b. Leaves ovate-lanceolate, with 5-7 rows of narrow marginal cells.................*Physcomitrium pygmaeum*

7a. Leaves 1-2.5 mm long; plants small 1-8 mm tall.......8

7b. Leaves 3-5 mm long; plants mostly larger 3-25 mm tall.
......*Physcomitrium pyriforme*

8a. Leaves lanceolate, .4-.7 mm wide, the length/width ratio 2.5-4:1...................*Aphanorhegma serratum*

8b. Leaves broader, .7-.8 mm wide, the length/width ratio 2-2.5:1..................*Physcomitrium immersum*

9a. Apex ending in an elongate filiform tip.............10

9b. Apex acuminate, acute or apiculate.................12

10a. Basal cells not elongate.............*Funaria americana*

10b. Basal cells elongate.................................11

11a. Leaves not auriculate at the base..*Funaria flavicans*

11b. Leaves auriculate at the base...*Funaria hygrometrica*

12a. Leaves .5-1.5 mm long; median cells quadrate, 20 x 20μ ....*Pyramidula tetragona*

12b. Leaves not as above...............................13

13a. Leaves broadly ovate; 2 mm long, shortly acuminate or subulate.......................................14

13b. Leaves larger, oblong, lanceolate or obovate......15

14a. Costa subpercurrent in upper leaves; leaves shortly acuminate......................*Physcomitrium Hookeri*

14b. Costa excurrent in upper leaves; shortly subulate... .....*Entosthodon rubiginosus*

15a. Alar cells definitely inflated at basal angles....16

15b. Alar cells not differentiated, or if so, then not inflated at basal angles..........................18

16a. Leaves 2-3 mm long; plants rare... ....*Entosthodon Leibergii*

16b. Leaves 3-5 mm long; plants common.................17

17a. Margins of 2 rows of yellowish cells... .....*Physcomitrium megalocarpum*

17b. Margins not yellowish...........*Funaria hygrometrica*

18a. Leaves broadly acute..............................19

18b. Leaves acuminate..................................20

19a. Median cells rectangular..*Physcomitrium californicum*

19b. Median cells oblong-hexagonal..*Entosthodon Drummondii*

20a. Leaves shortly acuminate........Funaria hygrometrica

20b. Leaves long acuminate or long apiculate; costa ending in apex; plants rare.......Funaria microstoma

21a. Upper leaves serrate above the middle.............22

21b. Upper leaves entire above the middle..............33

22a. Leaves ending in a long hair-point................23

22b. Leaves not ending as above; leaves may be apiculate 26

23a. Costa brownish-green, short; hair-point yellow, clear.........................Entosthodon rubrisetus

23b. Costa not as above................................24

24a. Acumen ending in clear cells, terminated by a single long clear cell.Physcomitrium washingtoniense.......

24b. Acumen not as above...............................25

25a. Apex ending in long tip, .2-.6 mm long; lower cells not differentiated from median..Funaria Muhlenbergii

25b. Apex tip shorter; lower cells elongated, differentiated from the median cells .....Entosthodon planoconvexus

26a. Margins of 1-2 rows of elongated, narrow cells, or margins unbordered..................................29

26b. Margins not as above..............................27

27a. Margins of 5-7 rows of long narrow cells; plants rare..........................Physcomitrium pygmaeum

27b. Margins not as above..............................28

28a. Margins of short, inflated cells .....Entosthodon Bartramii

28b. Margins of 2-3 rows of yellowish-thick walled cells ......<u>Physcomitrium delicatulum</u>

29a. Costa ending about 1/2 of the way up from the bottom of the leaf, often forked at tip .....<u>Aphanorhegma californica</u>

29b. Costa usually ending 3/4 or more of the way up from the bottom of the leaf, not forked at the tip.....30

30a. Leaves shortly acuminate, sinuose to almost entire above; margins not bordered......<u>Entosthodon tucsoni</u>

30b. Leaves acute to acuminate, distinctly serrate by projecting cells....................................31

31a. Costa ending just below the apex..................32

31b. Costa ending 3/4 of the way up from the bottom of the leaf.........................<u>Aphanorhegma patens</u>

32a. Margins bluntly serrulate-crenulate .....<u>Physcomitrium immersum</u>

32b. Margins serrate by projecting cells..<u>Funaria serrata</u>

33a. Apex ending in a filiform point...................34

33b. Apex not ending in a filiform point...............36

34a. Leaves slenderly acuminate, about 2 mm long; short acumen ending in a single long greenish tip-cell; costa reaching the apex in many leaves ...<u>Entosthodon Bolanderi</u>

34b. Leaves not as above in all characters.............35

35a. Apex ending in a long point, .2-.6 mm long; costa never excurrent.................<u>Funaria Muhlenbergii</u>

35b. Apex shortly subulate; costa excurrent in some upper leaves.................<u>Entosthodon rubiginosus</u>

36a. Leaves broadly acute..............................37

36b. Leaves shortly acuminate..........................40

37a. Margins unbordered, median cells hexagonal-oblong; leaves about 1 mm long, often shortly apiculate ...Entosthodon kochii

37b. Margins or leaves not as above....................38

38a. Median cells rectangular.Physcomitrium californicum

38b. Median cells oblong-hexagonal.....................39

39a. Leaves about 2 mm long.......Entosthodon Drummondii

39b. Leaves about 1 mm long..........Funaria californica

40a. Leaves bordered by 2 or more rows of narrow cells ......Entosthodon attenuatus

40b. Leaves not bordered, or only by 1 row of narrow cells..41

41a. Leaves broadly ovate, about 2 mm long ....Physcomitrium Hookeri

41b. Leaves oblong-lanceolate, mostly larger...........42

42a. Marginal cells elongate, narrow; alar cells inflated forming basal auricles; plants extremely rare, collected only in Idaho........Entosthodon Leibergii

42b. Marginal cells not differentiated; alar cells rectangular, not forming basal auricles; collected in Arizona.....................Entosthodon tucsonii

Discussion

The most consistent and distinctive taxonomic characters of the leaves in the Funariaceae are qualitative, especially apex shape and margin configuration. Costa length varies somewhat but is fairly consistent for most species. Cell and leaf length and width are not at all as significant as originally thought. Ranges of variation overlap to a great extent and are almost impossible to segregate. A notable exception is *Pyramidula tetragona*, which has such short median cells that it could not be mistaken for any other species. However, separation of the other taxa in this family by leaf or cell measurements is impractical.

A tentative leaf key has been proposed, although further study will undoubtedly necessitate much refinement. This key is artificial and cannot distinguish genera, although it is interesting that generic separation is possible with a sporophyte key. In view of the impossibility of generic segregation on the basis of the gametophyte and the reports of extensive intergeneric hybridization (Wettstein, 1932), I believe that there are indications of too many genera in this family.

The difficulty of separating some species by leaf characters indicates some problematic taxa. *Funaria hygrometrica* and *F. microstoma* are difficult to separate and the differences in leaf apices noted in the key may prove untenable; Brotherus (1924) believed F. microstoma does not occur in North America, so American bryologists may be simply listing a variant of F. hygrometrica as F. microstoma.

Two other species quite difficult to separate were Aphanorhegma serratum and Physcomitrium immersum. Although in two different genera, Grout (1935) stated that they were hardly to be distinguished on the basis of the gametophyte. However, Andrews (1918, 1929) believed that Aphanorhegma and Physcomitrium should be united; this is definitely supported by the close position of these two genera in the leaf key.

I suggest that only three genera are valid: Funaria, Physcomitrium and Pyramidula. Within these three complexes many species have been described which are simply morphological variants. The overabundance of species is a result of naming new taxa on the basis of a single collection, or when much too little is known about the normal range of variation.

Hopefully, the existence of a gametophyte key will result in a more accurate indication of the range of the species and the nature of generic relationships in this family by allowing determination of material not in fruiting season, or by the discovery of asexual clones.

Summary

1. The size of leaves or the size of leaf cells appear to be taxonomically insignificant in this family.

2. Qualitative characters of the leaf are found to be fairly consistent and distinct.

3. A tentative key to the Funariaceae has been proposed, based exclusively on leaf characters.

4. The proposed leaf key is artificial; this contrasts with sporophyte keys in which separation of genera is possible.

5. Those taxa which were difficult to segregate on the basis of leaf characters were the same taxa which have proved problematic in various respects to previous researchers.

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