Liverworts and Hornworts of the Virginia Piedmont

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INTRODUCTION

Years of pleasurable work with the liverwort flora of the Virginia Piedmont have led me to write an illustrated guide to the regional species of these too often ignored plants. My intention has been, in this manner, to make the citizens of this pygmy plant world understandable and accessible to naturalists who may have been discouraged from their study by the lack of a means of identification. Because of its focus on a small geographic region, it has been possible to utilize simple diagnostic characters which may not be applicable to the various taxa in their broader context. Heretofore the liverwort flora of this region has been treated only superficially or neglected entirely, perhaps because of a misconception that agricultural over-development or hot dry summers have militated against local diversification of these plants which require sustained conditions of humidity and moisture for survival.

Liverworts and hornworts are well-represented in Virginia with approximately 150 species dispersed through all of the topographic regions. The Piedmont flora is actually substantial, with about 60 species in 40 genera, and additional species will surely be found with future field work (e.g., several southern species known from North Carolina (Hicks, 1992) but still unrecorded from Virginia).

The earliest instate collections were made in the mountains of southwestern Virginia by William S. Sullivant and Asa Gray and the results of their forays were reported in "Mosses of the Alleghenies" (Sullivant, 1846). In the latter part of the 19th century Anna Vail and John K. Small collected liverworts, identified by Alexander Evans of Yale University, in the vicinity of Marion (Small & Vail, 1893).

Thomas Kearney, a vascular plant taxonomist, conducted a botanical survey of the Dismal Swamp in 1901, incidentally picking up six species of liverworts (Patterson, 1949). During the 1930s, M. L. Fernald made a number of collecting trips to southeastern Virginia, accompanied by Bayard Long of the Academy of Natural Sciences of Philadelphia. Mr. Long collected many bryophytes, including 34 hepatics of which *Anthoceros adscendens* was found for the first time north of South Carolina (Patterson, 1951).

Hepatics were collected around the Mountain Lake Biological Station during the decades of 1940-1970. Aaron J. Sharp of the University of Tennessee was the first of many bryologists to conduct field courses on these plants at the station. His collections for the summer season of 1940 alone included 80 different species, 61 of them leafy, 19 thallose (Sharp 1944). At different intervals, Paul M. Patterson, Rudolf M. Schuster, David A. Breil, and Susan Studlar also taught courses at Mountain Lake and added substantially to our knowledge of the Hepaticae of southwestern Virginia. While formal regional lists of these collections have not been published, some have been documented in generic revisions and in notes on distribution and ecology.

During the summer of 1944, Irma Schnooberger and Frances Wynne (1944) collected bryophytes including 31 hepatics in the Blue Ridge Mountains of the Shenandoah National Park. The majority of their finds were widely distributed boreal species.

H. H. Iltis (1950) reported a number of hepatics for the vicinity of Fredericksburg, Virginia, including the first state records for southern species of leafy Hepaticae. This paper is also significant in recording the first comprehensive collection of bryophytes from the Piedmont section of Virginia.

During the mid 1950s, Rudolf Schuster and Paul Patterson foraged for liverworts in the Dismal Swamp and in the mountains of southwestern Virginia. Jointly they reported (Schuster & Patterson, 1957) 16 taxa new to the Virginia Coastal Plain and a similar number for the mountains. All but five of the liverwort species were leafy.

Since coming to Longwood College in 1968, I have collected bryophytes throughout the state with primary emphasis on the plants of the central and southern Piedmont. The accumulated material forms the basis of the following treatment.

THE VIRGINIA PIEDMONT

The Piedmont Topographic Province extends in a NE -SW direction throughout the length of Virginia and is about 96 km wide at the northern end, broadening to about 192 km wide along the North Carolina border. The eastern edge of the Piedmont is formed by the Fall Line, a series of rapids occurring in rivers (James, Rappahannock, Potomac, Appomattox and Roanoke) draining to the east. The western boundary of the Piedmont is marked by the base of the Blue Ridge Mountain escarpment, about 300 m elevation. The Piedmont is underlain by ancient crystalline rocks mainly covered by residual soils which are somewhat acidic (pH 5.0 -6.0). The area is hilly, with elevational differences not usually exceeding 15 m. Occasional resistant ridges or monadnocks occur as solitary outliers of the Blue Ridge Mountains. Precipitation averages about 45 inches (114 cm) per year occurring throughout the year except during the drought season during late summer, usually August.

Braun (1950) described the outer Piedmont as occurring in the pine-oak region of the Eastern Deciduous Forest. Mature upland deciduous forests are composed of populations of oaks (white, red, post, Spanish, chestnut, scarlet), hickories (sweet pignut, pignut, shagbark, mockernut), and mixtures of other hardwood species (red maple, sweetgum, tulip poplar, ironwood, beech, black gum, dogwood, sourwood), often with old successional pines scattered throughout. North slope forests are dominated by American beech with white oak, red or Florida maples, tulip poplars and ironwood. Successional community stages range from old fields to conifer forests (loblolly, Virginia scrub, red cedar), and some hardwood types (including sweetgum and tulip poplar). Wetland communities include small streams (with hazel alder, sycamore), rocky river shorelines, floodplain forests (with river birch, sycamore, willow oak, American elm, box elder) and grassland marshes. Most reservoirs, lakes and ponds were created in the last hundred years but strongly influence the vegetation of this region. Microhabitats of soil hummocks, rock ledge, rocky ravines, logs, stumps, tree trunks and roots are especially important to the liverworts with the greatest diversity always being found in the more moist shaded areas.

THE SURVEY AREA

The Virginia Piedmont has been virtually unsurveyed for the presence of bryophytes prior to this study. The central and southern part of the Virginia Piedmont from Louisa county in the northern part to the North Carolina border was utilized. A buffer zone of about one Piedmont county to the east and west was maintained in order to diminish the direct influence of plants from the mountains and the coastal plain. The counties included in this study are Amelia, Appomattox, Buckingham, Campbell, Charlotte, Cumberland, Fluvanna, Goochland, Halifax, Lunenburg, Louisa, Mecklenburg, Nottoway, Pittsylvania, Powhatan, and Prince Edward (see Figure 88, p. 28).

BRYOPHYTE CHARACTERISTICS

Bryophytes consist of hornworts, liverworts, and mosses, all of which are small (normally less than two inches long) and have a similar life cycle. Hornworts (anthocerotes) generally occur on the soil and are flat, dark green thalloid plants producing narrowly cylindric sporophytes. Liverworts have two growth forms: thalloid (flat, scale-like, ribbon-shaped, sometimes branched) and leafy: with stem and leaves, occurring in all habitats but most commonly on tree trunks and roots. Leafy liverworts may be confused with mosses but differ from mosses in leaf and sporophyte structure. Leafy liverworts have leaves in two or three distinct rows, each leaf possessing two or more lobes that lack midribs. Moss leaves occur in more than three rows and have singly pointed unlobed leaves with midribs. The sporophytes of liverworts are short-lived and produce black cylindric or ovate sporangia (capsules) which split into four valves to release the spores. Mosses usually develop persistent green to brown sporophytes with sporangia that are ovate, cylindric, spherical, or oblong and allow the escape of spores through the release of a terminal cap.

KEY TO THE SUBDIVISIONS

- Plants thallose, each cell with a single large chloroplast bearing a central pyrenoid; sporophytes linear Anthocerotae
- 1b. Plants thallose or leafy, each cell with several small chloroplasts, pyrenoids absent; sporophytes producing stalked spherical or ovoid capsules Hepaticae

Anthocerotae (Hornworts)

Key to Genera

- Sporophytes erect, narrowly cylindric, several times 1a. longer than enclosing collar of tissue at base (Fig. 1) Anthoceros Sporophytes barely emerging from the thallus collar 1b. (Fig. 2) Notothylas Hepaticae (Liverworts) Key to Genera 1a. Plants thallose, thallus simple, lobed or branched 2 1b. Plants thallose 2a. Thallus surface almost obscured by ovoid sheaths surrounding sex organs or sporophytes (Figs 23, 24) 2b. Midrib distinct, cordlike, remainder of thallus thin (Figs 3a. 3b. Midrib indistinct, often covered with rhizoids or scales.

9а. 9Ь.	Plants with green gemmae cups on upper surface (Fig. 7)
10а. 10Ь.	Pores and net-pattern present on upper surface (some- times indistinct); scales on lower surfaces (Fig. 8) 11 Pores or pattern on surface of plant lacking; lower surface lacking scales
11a.	Thallus very large, 1 - 3 cm wide; a distinct net-like surface pattern developed around pores
11b.	Thallus smaller, less than 0.8 cm wide; surface pattern present but not distinct; plants often in rosettes 12
12a.	Thallus 5-8 mm wide; epidermal cells with thin walls and large trigones; capsules of elevated receptacles
12b.	lacking white, scale-like fringe
13a.	Lower surface densely covered with brownish rhizoids along center line; sporophytes developing from a flap or low cup-like structure near apex of thallus (Figs. 17,18)
13b.	Lower surface sparsely covered with rhizoids (or absent); sporophytes developing from lateral branches
14a. 14b.	Plants 3-10 mm wide, sparingly branched; yellowish green; always on wet rotten logs and stumps Aneura Plants less than 2 mm wide, abundantly branched; deep green; on wet rock, soil or moist rotten logsRiccardia
	Plants leafy, with stem and leaves
15a.	Leaves composed of hair-like filaments 1-2 cells wide, or leaf blades fringed with long hairs; underleaves similar
15b.	to leaves (Figs. 30, 32, 34, 36)
16a.	Plants delicate, less than 1 mm wide; leaves divided
16b.	at base; underleaves of 34 filamentous segments 17 Plants robust; leaves divided to middle or beyond into 25 lobes, the lobes soon divided into many hair-like segments



17a.	Plants pinnately branched; underleaves 2.3	3 lobed with 1
	or more lobes often very short	Kurzia
17b.	Plants irregularly branched; underleaves	of (3)4 well-
	developed, filamentous segments	Blepharostoma

18a.	Leaf	blades	6-10	cells	wide	at	base;	cells	with	large
	trigo	nes; pla	nts no	ormall	y redd	ish	brown	1	Ptil	idium

- 19b. Stems with conspicuous underleaves (Figs. 37, 53, 70, 83, 87)

 33

- 22b. Leaves broadly ovate to round, barely longer than wide; lobules ovate to rectangular, pointing at an oblique angle to the stem; gemmae ovoid, smoothScapania

23b.	Lot	oules or	vate o	r redu	iced t	o a very	narrow tol	d; rhizoids
	on	stem;	leaf	cells	and	lobule	papillose;	perianths
	infl	ated, p	lants	minu	te (Fi	g.72)		Cololejeunea

- perianths spherical, cylindrical, or flattened contracted or closed at the apex; stem hairs colorless, pink, or 25a. Leaves toothed along margins or leaf apex 24 lobed 25b. Leaves entire, round, rounded-rectangular, or ovate. 26a. Leaf margins toothed all around (sometimes entire 27a. Leaves 2-3 lobed, the lobes toothed on margins Lophozia 27b. Leaves 2 lobed, the lobes not toothed along margins 28a. Leaf lobes drawn into a fine hairpoints, each several single cells in length; the deeply concave leaf resembling a billowing sail (Fig. 57) Nowellia 28b. Leaf lobes acute to obtuse, never drawn into a
- 29a. Leaves attached transversely to stem; plants minute; cells with small oil bodies (Figs. 63, 65) Cephaloziella

hairpoint; leaves mostly flat to moderately concave ... 29

Figures 1-13. 1. Anthoceros laevis subsp. caroliniana. Thallus with erect sporophyte, X3. 2. Notothylas orbicularis. Thallus with emergent sporophytes (mature), X3 3-4. Asterella tenella. 3. Thallus with receptacle, male organs behind, X5. 4. Detail of female receptacle showing papery sheaths around sporophytes, X7. 5. Reboulia hemisphaerica. Thallus with elevated female receptacle bearing sporophytes beneath, male pad behind receptacle, X3. 6-7. Marchantia polymorpha. 6. Habit with female receptacle and gemma cup, X2. 7. Gemma cup, gemmae within, X4. 8. Conocephalum conicum. Dorsal surface of thallus, X3. 9-10. Fossombronia brasiliensis. 9. Ventral surface, X6. 10. Spore, X280. 11. Fossombronia wondraczekii. Spore, X280. 12. Metzgeria conjugata . Ventral surface of thallus, X10. 13. Metzgeria crassipilis. Ventral surface of thallus bearing gemmae and rhizoids on wings, X10.

BANISTERIA



- 30a. Stems producing long white leafless branches from the lower surface (a long leafy stem must be examined); leaves mostly orbicular (Figs. 84, 86) Odontoschisma

- 32a. Leaves rectangular on mature shoots; leaf cells with bulging trigones; perianths smoothly cylindric, abruptly constricted to a smooth beak (Fig. 47) Jungermannia
- 32b. Leaves circular, elliptical, or ovate; perianths cylindric, longitudinally creased (Figs. 40, 42, 48) Solenostoma

- 34a. Underleaves distinctly bilobed for 1/3 to 1/2 their length, lobule helmet-shaped (occasionally strap-shaped)
 35

36b.	Lobule rectangular, extending parallel to leaf margin and broadly attached to it; one (rarely 2) large oil-body(s) in each cell
37a.	Leaves 3-toothed at apex; underleaves multitoothed (Fig. 37)
37b.	Leaves entire or bilobed; underleaves bilobed
38a. 38b.	Leaves entire (sometimes barely indented at apex) 39 Leaves broadly bilobed (a few often entire) (Fig. 52) Lophocolea
39a.	Leaves rectangular but rounded at the corners, broadly rounded at the apex: pear or in water
39b.	Leaves ovate-pointed (often bidentate at apex); on soil (Fig. 38)

Annotated Species Accounts

1. Aneura Dum.

Plants thalloid, deep green, 3-10 mm wide, lacking a midrib although thickened in the center. Dioecious; male plants with many elongate antheridial branches arising laterally from thallus; female plants developing erect sporophytes within a fleshy, warty, translucent calyptra.

Aneura pinguis (L.) Dum. (Figs. 20-21) Pioneers on moist rotten logs and stumps, less commonly on tree roots and humus in swamps and shaded margins of ponds and streams. Buckingham, Prince Edward counties.

2. Anthoceros L.

Thalloid plants 0.5-3.0 cm broad, in green rosettes or clusters, the margins and upper surface smooth to ruffled, lacking a midrib or scales on lower surface; cells each with a single large chloroplast with a central pyrenoid. Monoecious (our species);

Figures 14-28. 14-17. Pallavicinia lyellii. 14. Female plant, X7. 15. Male plant, antheridia beneath flap, X7. 16. Sporophyte within perigynium on female plant, X7. 17. Pellia epiphylla. Monoecious thallus, sporophyte at tip with antheridial bumps behind it, X7. 18. Pellia neesiana. Female thallus with emerging sporophyte, X5. 19. Blasia pusilla. Thallus with 2 kinds of gemmae and embedded clumps of blue-green bacteria, X7. Thallus, X9. 20-21. Aneura pinguis. 20. Male plant, X4. 21. Female plant with sporophyte, X4. 22. Riccardia multifida. 23-24. Sphaerocarpus texanus. 23. Female thallus with dorsal, occluding perigynia (each later with a sporophyte), X7. 24. Male thallus, with small male organs, X7. 25-26. Riccia huebenariana subsp. sullivantii . 25. Dorsal view of thallus with embedded sporophytes, X7. 26. Lateral view of embedded sporophytes, X17. 27. Riccia sorocarpa. Thallus with embedded sporophytes, X5. 28. Riccia membranacea. Thallus, X6.



antheridia and archegonia developed in open cavities beneath the upper surface. Sporophyte resembling a single elongated horn, erect, long exserted beyond an enclosing collar from thallus tissue at base.

 1a.
 Spores yellow
 A. carolinianus

 1b.
 Spores black
 (A. punctatus)

1. Anthoceros carolinianus Michx. (Fig. 1) Also known as Anthoceros laevis subsp. carolinianus, dark green, thalloid plants occurring in rounded clumps on mineral soil along ditches, streambanks and in old cornfields; fruiting from late fall through spring. Plants small in this area. Amelia, Buckingham, Cumberland, Prince Edward counties

2. (Anthoceros punctatus L.) Also known as Aspiromitus punctatus, dark green thalloid plants, dichotomously lobed, occurring in disturbed habitats such as gardens, pathways and ditches, fruiting in winter and spring. Monoecious. Widely distributed through the influence of man's activities thus expected in gardens.

3. Asterella Beauv.

Plants thalloid, elongate, 2-3.5 mm broad, simple or forked, margins thin, wavy, often purple but green if growing in shade; the upper epidermal cells lacking trigones, the surface indistinctly net-patterned; the lower surface with rhizoids and two rows of crescent-shaped scales. Monoecious; antheridia clustered on upper surface immediately behind the elevated umbrella-like receptacle bearing archegonia and, eventually, papery sheathed sporophytes.

Asterella tenella (L.) Beauv. (Figs. 3, 4) Occurring on wet sandy soil in fields, roadside ditches, boulder crevices, rocks along streams; often with *Riccia* and *Anthoceros* species. Buckingham, Cumberland, Fluvanna, Prince Edward counties.

4. Bazzania S. Gray

Large, dull green leafy liverwort, 3-4 mm wide, forking at the tips and producing white, minutely leafy shoots in axils of the

underleaves. Leaves densely overlapping, trapezoidal, the apices terminated by 3 (4) shallowly triangular lobes; lobules absent. Underleaves distant to adjacent, large, wider than stem, the margins multitoothed. Not seen with reproductive structures.

Bazzania trilobata (L.) S. Gray. (Fig. 37) Occurring in moist shaded habitats over vertical granitic or gneissic rock, shaded banks on peaty soil; along rivers or hemlock bluffs. Campbell, Fluvanna, Halifax, Prince Edward counties.

5. Blasia L.

Plants thalloid, pale green, lobed, occurring in mats and forking more or less repeatedly to form rosettes; the thallus center thickened, often with a faint whitish line; rounded lobes with dark blotches at base; lower surface with pinkish scales; upper surface producing two kinds of multicellular gemmae: (1) clusters of star-shaped gemmae and (2) smooth elliptical gemmae within long-necked, flask-shaped structures. Reported dioecious but not seen with sexual structures.

Blasia pusilla L. (Fig. 19) Thalli occurring on moist eroding loamy slopes. Prince Edward County.

6. Blepharostoma (Dum. emend Lindb.) Dum.

Plants delicate, filamentous, 0.7-0.8 mm wide, in pale green mats or strands among other bryophytes. Leaves inserted transversely on stems, divided into four filamentous lobes nearly to base; underleaves similar to leaves, 3- or 4-lobed. Monoecious. Antheridia in axils of leaves along stem; perianth cylindrical, contracted towards the ciliate mouth, terminating a stem or branch.

Blepharostoma trichophyllum (L.) Dum. (Figs. 29,30) With other bryophytes or in thin mats on moist shaded rocks; logs, tree bases. Campbell, Fluvanna, Prince Edward counties.

7. Calypogeja Raddi

Pale green to green medium sized leafy hepatics, occurring singly or loosely intertwined in thin mats; shoots simple or

Figures 29-43. 29-30. Blepharostoma trichophyllum. 29. Shoot, dorsal surface, X12. 30. Leaf, X64. 31-32. Ptilidium pulcherrimum. 31. Shoot, dorsal surface, X15. 32. Leaf, X35. 33-34. Kurzia sylvatica. 33. Shoot, ventral surface, X98. 34. Leaf, X202. 35-36. Trichocolea tomentella. 35. Plant, ventral surface, X10. 36. Leaf, X36. 36. Bazzania trilobata. Shoot, ventral surface, X13. 38-39. Calypogeja fissa. 38. Shoot, ventral surface, X16. 39. Leaf tips, X99. 40-41. Solenostoma gracillimum. 40. Male plant, antheridia in axils of upper leaves, X23. 40. Leaf marginal cells, X93. 42-43. Solenostoma hyalinum. 42. Shoot, X23. 43. Leaf marginal cells, X99. sparsely branched, branches ventral. Leaves ovate, broadly pointed, the apex bilobed or bidentate, less commonly entire. Lobules absent; underleaves conspicuous, entire and slightly notched or bilobed, frequently with a lateral tooth on each outer margin; rhizoids abundant from base of underleaves; unicellular gemmae sometimes produced on outer margins of leaves and at apex of erect branches. Plants monoecious, the male branch short, ventral, with 4-6 pairs of overlapping bracts. The female inflorescence on a short ventral branch, developing a sporophyte within an ovoid fleshy perigynium rather than a leafy perianth as in other leafy hepatics.

1a. Leaves entire, blunt or narrowly rounded at tips; underleaves rounded, less than 1.3 times as wide as long, with lobes not strongly spreading, their lateral margins evenly rounded, only occasionally toothed; plants robust, 2.5 to 4 mm wide *C. muelleriana*1b. Leaves frequently bidentate or sharply pointed at apex; underleaves broad, 1.5 to 2.0 times as wide as long, with spreading lobes which have a single tooth; plants smaller, 1.5 to 2.5 mm wide *C. fissa*

1. Cabpogeja fissa (L.) Raddi subsp. neogaea Schust. (Figs. 38, 39) On roadside banks or moist clayey soil of ditches or shaded roadside embankments. Buckingham, Campbell, Cumberland, Fluvanna, Prince Edward, Spotsylvania counties.

2. Cabpogeja muelleriana (Schiffn.) K. Mull. On thin soil or humus in ravines, over shaded rocks, humus on steep slopes, peaty soil. Lunenburg County.

8. Cephalozia (Dum.) Dum.

Small leafy plants (0.3 - 0.8 mm wide), in thin mats or mixed with other bryophytes; stems with a translucent outer cell layer; sparingly branched, the lower stem surface with rhizoids throughout; leaves ovate to round, deeply bilobed, distant to slightly overlapping; lobules and underleaves absent. Asexual reproduction by clumps of gemmae formed at tips of erect branches. Monoecious (our species). Male inflorescence on short branches, with 2-14 pairs of closely overlapping leafy bracts; perianths on short branches, ovate, obtusely 3-keeled, the apex constricted, toothed.

 Leaf lobes three to five cells wide at base; cells at base of leaf 40 - 60 μ longC. connivens

1b.	Leaf lobes five to nine cells wide at base; cells at base o	f
	leaf 15-35 μ long	2

1. Cephalozia catenulata (Hub.) Lindb. (Figs. 60, 61) In moist woods or swamps on moist rotten logs. Often associated with Nowellia curvifolia and Odontoschisma denudatum. Buckingham, Campbell, Fluvanna, Prince Edward counties.

2. *Cephalozia connivens* (Dicks.) Lindb. (Fig. 62) On shaded moist silty soil along paths, sometimes on moist rotten logs, often with other bryophytes. Campbell County.

3. Cephalozia lunulifolia (Dum.) Dum. (Figs. 58, 59) Occurring in woods on humus, peaty or sandy soil, sometimes on rotten logs. Fluvanna, Prince Edward counties.

9. Cephaloziella (Spruce) Steph.

Minute plants resembling *Cephalozia*, but without an outer stem layer of large cells; leaves bilobed with cells containing minute oil-bodies; underleaves absent or minute and narrowly triangular. Perianths and associated bracts large compared to the normal leaves.

- Plants sterile, i.e., sexual structures usually absent; underleaves of robust shoots present, often large; leaf cells thick-walled, some with spines C. byssacea
- 2a. Leaf lobes ovate-triangular, 6-9 cells wide at base of mature sterile shoots; leaf cells thin-walled C. hampeana
- 2b. Leaf lobes 4-6 cells wide on sterile shoots; leaf cells mostly thick-walled C. *rubella*

1. Cephaloziella byssacea (Roth.) Warnst. (Figs. 63, 64) Dioecious but usually sterile; plants green to brown; on wet seepage on granitic boulders or often mixed with other bryophytes such as *Scapania nemorosa*, *Dicranum*, or *Polytrichum*. Campbell, Nottoway counties.

2. Cephaloziella hampeana (Nees) Schiffn. - Monoecious; green to brownish plants growing over humus or logs, usually in swamps or other wet areas. Prince Edward County.

3. Cephaloziella rubella (Nees) Warnst. (Figs. 65, 66) Monoecious; green to reddish-tinged hepatics growing on peaty or sterile soil or rock, often with Solenostoma or protonema of the moss Pogonatum. Prince Edward County.

10. Chiloscyphus Corda

Green to pale-green leafy liverworts, the shoots 2.3 mm wide, irregularly branched; leaves squarish, rounded on the corners; underleaves as wide as the stems, the lobes elongate and triangular with often a thread-like tooth on either side. Monoecious. Antheridia occur in axils of leaves in small cuplike pockets next to the stem on the dorsal surface. The perianth occurs on a short ventral branch that is obscurely lobed and toothed.

These hepatics possess characters similar to those found in the genus *Lophocolea*, a taxon which has been transferred to *Chiloscyphus* by Engle and Schuster (1984).

Chiloscyphus pallescens (Ehrh.) Dum. (Fig. 53) Flat patches on moist shaded soil, on rock along streams, or in other wet areas. Amelia, Buckingham, Prince Edward counties.

11. Cololejeunea (Spruce) Schiffn.

A minute, yellow green species with freely branched, zigzagging stems ; leaves triangular to ovate, the cells with conical papillae on the outer leaf surfaces; lobules well developed, ovate, papillose, with a conspicuous tooth on free margins; underleaves absent; rhizoids developing sparsely along the lower surface of the stem. Monoecious; antheridia occurring at bases of bracts along the stem; large, 5-keeled perianths occur at tips of branches, resembling gas-filled balloons with a terminal beak .

Cololejeunea biddlecomiae (Aust.) Evans. (Fig. 72) In small patches on tree bark, roots, and rock in shaded moist habitats. Buckingham, Fluvanna, Mecklenburg, Prince Edward counties.

12. Conocephalum Wiggers

The largest thallose species, 23 inches long, and short

branched, occurring in deep green patches; abundant white rhizoids and 2 rows of large scales develop on the lower surface; upper surface with a conspicuous net-like pattern, each unit containing a single open pore leading to a green chamber beneath; gemmae cups and gemmae not produced. Dioecious. Male plants with a slightly elevated "pad" at the tip of the thallus in the spring. Female plants produce an elevated, umbrella-like, receptacle bearing archegonia (later, sporophytes) beneath. This plant is known as the "fragrant liverwort" because of its sweet, spicy odor.

Conocephalum conicum (L.) Underwood. (Fig. 8) Occurring over rocks, wet sandy soil, and logs, usually along streams. Buckingham, Cumberland, Fluvanna, Mecklenburg, Prince Edward, Spotsylvania counties.

13. Diplophyllum Dumort.

Small leafy plants occurring in green to reddish brown patches, seldom branched; leaves close, complicate-bilobed, the larger blade pointed outwardly, the smaller blade (lobule) pointed toward the stem tip, both lobes finely toothed; angular green gemmae often densely produced at stem apices. Monoecious; male bracts in a series along the stem, similar to leaves. Perianths on short to long branches, ovate, creased lengthwise, and contracted to a tooth-fringed mouth.

Diplophyllum apiculatum (L.) Underwood. (Fig. 51) Common on peaty banks, soil and rocks, especially along road cuts in forests or in partial shade, often occurring with *Scapania*, and "pigeon wheat moss," *Diphyscium*. Appomattox, Buckingham, Campbell, Fluvanna, Mecklenburg, Prince Edward counties.

14. Fossombronia Raddi

A thallose liverwort with deeply lobed wings resembling irregularly shaped leaves, the "leaves" producing spaced marginal hairs; stem rhizoids purple; lobules and underleaves lacking. Antheridia and archegonia on upper stem surface near the tips of stems or branches. False bell-shaped perianths develop at the base of the sporophyte revealing the spherical black capsule. Most distinctions between species are based on spore ornamentation. The plants are seasonal, often appearing with "pygmy mosses" on moist clayey soil.

Fossombronia brasiliensis Steph. (Fig. 9,10) Monoecious; occurring singly or in greenish patches on moist, clayey, compact soil in old fields, along streams or in swamps, often with *Riccia* species or *Sphaerocarpos*. Cumberland, Prince Edward counties. Fossombronia wondraczekii (Corda) Dum. may be present. It differs mainly in spore ornamentation, the spores having essentially parallel ridges (Fig. 11).

15. Frullania Raddi

Plants leafy, dark green, reddish, or brownish, highly branched, in thin mats closely attached to substrate; leaves entire, overlapping, producing a helmet-shaped lobule next to the stem from the underside of the leaf; occasionally some lobules flattened into a creased, strap-shaped "tongue" paralleling the stem; underleaves large and bilobed. Male branches with closely overlapping bracts in pairs; female perianths large, lantern-shaped and beaked at apex. Asexual reproduction, when present, occurs from dropped leaves which are able to develop into new plants.

- 1a. Leaves with a distinct oblique line of colored cells

 (ocelli); plants usually reddish brown *Examarisci* subsp. *asagrayana*1b. Leaves lacking ocelli; plants green to brownish red 2

- 3a. Underleaves 2.5 4 times as wide as the stem; leaves strongly curving away from stem when moist; plants frequently brownish red F. ericoides

- 4b. Underleaves slightly longer than wide with margins entire or a single tooth on either side; lobules not compressed at mouth; leaves often developing gemmae or falling away from stem *F. eboracensis* subsp. *virginica*

1. Frullania brittoniae Evans. (Figs. 73, 74) Dioecious; in patches on the bark of trunks and branches of trees in hardwood forests. Halifax County.

2. *Frullania eboracensis* Gott. subsp. *virginica* Schust. (Figs. 77-79) Dioecious, usually with perianths; occurring on bark of hardwood trees in oak forests but also along wooded streams and occasionally on red cedar trunks. Buckingham, Charlotte, Fluvanna, Mecklenburg, Prince Edward counties.

3. Frullania ericoides (Nees) Nees (Figs. 80, 81) Dioecious; found in a variety of somewhat open areas, on bark of hardwoods, red cedars, downed logs. (Frullania squarrosa) Appomattox, Buckingham, Cumberland, Halifax, Prince Edward counties.

4. Frullania inflata Gott. (Figs. 75, 76) Monoecious; in or near wet areas on trees, granite boulders and moist rotten logs in swamps, beech-maple slopes. Buckingham, Cumberland, Nottoway, Prince Edward counties.

5. Frullania tamarisci (L.) Dum. subsp. asagrayana (Mont.) Hatt. (Fig. 83) Dioecious; found on shaded boulders and rock faces; sometimes on tree trunks in humid shaded forests. Appomattox, Buckingham, Campbell, Cumberland, Prince Edward counties.

16. Jamesoniella (Spruce) Schiffn.

Plants leafy, large, greenish to reddish-brown (in sun), growing in patches, 2 - 3.5 mm broad, sparingly branched with erect growing tips erect; rhizoids numerous along stems; leaves entire, squarish, rounded at corners, somewhat overlapping; cell walls thin with small trigones; lobules lacking. Underleaves lacking or very small and narrowly triangular. Dioecious. Male plants producing short male branches with several pairs of bracts. Female plants producing cylindrical perianths, compressed near tips and producing cilia, perianths surrounded by ragged bracts at base. No asexual reproduction.

Jamesoniella autumnalis (DC) Steph. (Figs. 44-46) On shaded granite boulders and decaying logs, rarely on humus and rich soil near wooded streams. Amelia, Nottoway counties.

17. Jubula (Steph.) Evans

Plants dark green, leafy, medium sized, 1-2 mm broad, branching irregularly pinnately in prostrate mats; leaves overlapping, complicate-bilobed, the blade rounded and abruptly sharp-pointed at apex; lobule helmet-shaped, resembling those of *Frullania*, but much smaller; stylus absent; underleaves 2-3 times the width of stems, bilobed for 1/2 their length; rhizoids few from underleaf bases. Monoecious. Male branches with 4-5 sac-like bracts, overlapping; perianths lantern-shaped, large, constricted at apex to a small beak.

Jubula pennsylvanica (Steph.) Evans (Fig. 82) On wet rocks in and along streams. Appomattox, Campbell, Fluvanna counties.

18. Jungermannia L.

Plants leafy, medium-large, in flat green patches, 2-2.5 mm wide, the stems sparingly branched bearing pale brownish (with age) rhizoids to apex; leaves entire, somewhat overlapping, mostly rectangular and often notched slightly at apex; cells with bulging trigones; lobules and underleaves absent. Monoecious. Antheridia in the swollen bases of bracts immediately below the terminal perianth; perianth large, tubular, abruptly contracted at apex into a small beak in a flat or shallow depression. Asexual reproduction rare, by gemmae at tips of erect, small-leaved shoots; gemmae 2-celled, thin-walled.

Jungermannia leiantha Grolle. (Fig. 47) Also known as Jungermannia lanceolata; on soil or moist rocks in wet areas along streams, ditches, or in mixed oak forests; sometimes found with Jamesoniella autumnalis. Buckingham, Prince Edward counties.

19. Kurzia Martens

Small filamentous plants often resembling large algae, green to brown, 0.5 mm wide and pinnately branched; leaves divided to base into 34 filaments; underleaves like leaves but slightly smaller. Dioecious. Antheridia in the axils of bracts on short lateral branches. Perianths on a short ventral branch, large, cylindrical, tapering to a short ciliate mouth.

Kurzia sylvatica (Evans) Grolle. (Figs 33, 34) In patches in shaded sites over peaty soil or in ravines; often with species of *Cabypogeja*, *Cephalozia*, or *Odontoschisma prostratum*. Buckingham, Campbell, Fluvanna, Lunenburg, Prince Edward counties.

20. Leucolejeunea Evans

Medium sized leafy hepatics in yellow green patches, sparingly branched, the shoots ca. 1 mm wide; leaves complicatebilobed, blades ovate, entire, slightly overlapping, each cell with a single large "grape-cluster" oil-body; lobules large, oblong with a folded keel about 1/3 the leaf length; underleaves distant and round, about twice as wide as the stem, bearing rhizoids at the base near attachment. Monoecious. Male branches short, lateral, with tightly over-lapping bracts; perianths on short lateral branches, ovate with five weak keels abruptly contracted to a tubular beaked mouth.

Leucolejeunea chypeata (Schwein.) Evans. (Fig. 88) In patches on granite boulders and base of trees (oak or hemlock) in shaded sites. Buckingham, Campbell, Charlotte, Fluvanna, Nottoway, Prince Edward counties.

21. Lophocolea (Dum.) Dum.

Pale green leafy plants in prostrate mats, occasionally branched. Leaves mostly bilobed, slightly overlapping; leaf cells thin-walled containing a few granular oil-bodies; lobules lacking; underleaves thin and transparent, bilobed, usually wider than the stem, often with a lateral tooth; rhizoids restricted to underleaf bases. Antheridia at base of bracts along the stem (if plants dioecious) or in sac-like bracts beneath the perianths. Perianths tubular, sharply 3-keeled, toothed at their tips. There is the possibility that *L bidenta* (L) Dum. will occur here (Schuster 1980, vol. 4) on moist soil. It is dioecious and the leaf lobes end in three to seven cells in a row.

Engel & Schuster (1984) merged this genus with Chiloscyphus because of several intermediate species found in the southern hemisphere. It is more convenient to maintain Lophocolea as a discrete genus, which is the option I have adopted here.

Lophocolea heterophylla (Schrad.) Dum. (Fig. 52) Also known as Chiloscyphus profundus; monoecious, usually with perianths; on moist rotten logs often as a pioneer or with other mosses, occasionally on rock or soil at the base of trees. This liverwort may produce either entire leaves that may be slightly notched at the apex, or deeply bilobed leaves. Small, juvenile plants are invariably bilobed with rectangular leaves. Appomattox, Buckingham, Charlotte, Cumberland, Fluvanna, Nottoway, Prince Edward counties.

22. Lophozia (Dum.) Dum.

Plants small, compact, green to brownish, relatively unbranched, bearing numerous rhizoids, the branch tips erect. Leaves concave, rounded but mostly bilobed, closely overlapping, with very thick walled cells; underleaves and lobules lacking. Asexual reproduction by means of reddishbrown gemmae attached to the leaf margins and often eroding them. Monoecious; antheridia in toothed bracts beneath the perianths; perianths cylindrical, emergent, bearing numerous folds in the upper portions with short teeth near the opening.

Lophozia bicrenata (Schmid.) Dum. (Figs. 55, 56) In small patches on moist soil on banks and road cuts; very rare, locally. Buckingham County.

Plants thallose, bright green, large, to 1 cm wide, several centimeters long, forking to form short branches, occurring in patches; upper surface with pores throughout, each within a faint net-like unit, producing conspicuous cups bearing greenish egg-like gemmae within; lower surface blanketed with colorless hairs and six rows of scales, not always obvious. Dioecious. Male thalli with terminal umbrella-like receptacles containing embedded antheridia. Female thalli with similar receptacles bearing short sporophytes dangling beneath nine or ten radiating limbs.

Marchantia polymorpha L. (Figs. 6, 7) moist, partially shaded soil especially on burned over ground (from forest clearing), wet ditches or other disturbed areas. Appomattox, Nottoway counties.

This is the classic example of a liverwort used to illustrate all liverworts in college textbooks.

24. Metzgeria Raddi

Plants small, thalloid, translucent-green, strap-shaped, the margins with numerous marginal hairs, the midrib linear, distinct, with thin see-through thallus wings and often, disk-like multicellular gemmae arising from the margins or the upper or lower surfaces; branching irregular, often by terminal forking. Monoecious or dioecious. Sexual branches from the lower surface of the plants, highly reduced as rounded or flattened sacks containing sex organs. *Metzgeria* species normally occur in mats on rocks or tree trunks as pioneers.

- 1b. Gemmae, if present, attached to the margins of the thallus; marginal hairs in pairs M. conjugata

1. Metzgeria conjugata Lindb. (Fig. 12) Monoecious and usually fertile; on vertical sides of moist shaded boulders in woods. Appomattox, Charlotte counties.

2. Metzgeria crassipilis (Lindb.) Evans. (Fig. 13) Dioecious, usually sterile; on sides of moist to dry boulders in hardwoods, often with *Leucolejeunea clypeata*. Buckingham, Prince Edward counties.

25. Notothylas Sull.

Deep-green to yellowish-green thalloid plants occurring in small circular patches, the margins irregularly lobed; cells each with a single chloroplast. Monoecious, sex organs embedded in the upper surface of the thallus. Sporophytes distinctive, short, cone-shaped and flattened against the surface, each surrounded by a collar of thallus tissue.

Notothylas orbicularis (Schwein.) Sull. (Fig. 2) On moist shaded, compact soil along rivers, swamps, mud puddles, ditches, often with *Riccia* and *Anthoceros*; fall and springtime. Prince Edward County.

26. Nowellia Mitt.

A small, delicate, green to brownish leafy liverwort occurring in intertwined mats, shoots 0.4-0.8 mm wide with occasional branches; leaves distinctive, each resembling a billowing Viking sail, ovate and deeply bilobed with lobes drawn out into long hair points. Dioecious but occasionally monoecious. Antheridial bracts in terminal spikes on branches; perianths large, ovate, mostly three-angled in cross-section, the mouth fringed with short cilia, on short branches.

Nowellia curvifolia (Dicks.) Mitt. (Fig. 57) Almost exclusively on moist barkless logs in forests, often with Cephalozia catenulata and Lophocolea heterophylla. Appomattox, Fluvanna, Lunenburg, Prince Edward counties.

27. Odontoschisma (Dum.) Dum.

Plants leafy, medium-sized, green to reddish, branching occasionally from lower stem surface with white leafless shoots; leaves round to elliptic, occasionally notched at apex and overlapping; leaf cells thick-walled with large trigones; oil-bodies large, segmented, 2-5 per cell; lobules lacking; under-leaves absent or very small and variable but distinct on ascending branches. Dioecious but often sterile. Perianths large, ovate, obtusely 3-keeled with slightly compressed ciliate mouths.

1. Odontoschisma denudatum (Nees) Dum. (Figs. 86, 87) On moist rotten logs in shady forests, rarely on humus over base of trees. Campbell, Fluvanna, Lunenburg, Prince Edward counties. 2. Odontoschisma prostratum (Sw.) Trev. (Figs. 84, 85) On moist peaty soil or humus on embankments in shady forests, often with *Calypogeja fissa* or mosses. Buckingham, Fluvanna, Lunenburg, Prince Edward counties.

28. Pallavicinia S. Gray

Thin, green, ribbon-like thallose plants, 2 - 3.5 mm wide, sparingly branched with a central, conspicuous, thickened midrib contrasting conspicuously with the much thinner, broad thallus wings; rhizoids developing from the lower surface of midrib. Dioecious. Reproductive organs on upper surface. Antheridia developing on either side of midrib partially covered by toothed scales. Female plants with a large, erect, centrally located perigynium above the midrib; perigynium ovate with a slightly constricted ciliate mouth, surrounded at the base by a fringed collar.

Pallavicinia bellii (Hook.) Carruth. (Figs. 14-17) On humus, in wet areas, along streams, sometimes moist decaying logs, over rootstocks of ferns. Amelia, Nottoway, Prince Edward, Fluvanna, Spotsylvania counties.

29. Pellia Raddi

Green thallose plants 4 - 8 mm wide, branched irregularly or forked, rarely simple; thallus margins wavy, apices distinctly notched; brownish rhizoids developing along the thickened center of thallus on lower surface; no distinct midrib or scales. Antheridia in wart-like projections on the upper thallus surface; archegonia and sporophytes in cup- or flap-like enclosures near the apical notch. Sporophytes produced in the spring.

- 1a. Plants monoecious, antheridia developing within low conical warts behind the apical female flap, which lacks a forward wall (visible with a hand lens) *P. epiphylla*

1. Pellia epiphylla (Dicks.) Dum. (Fig. 17) Monoecious; on damp, often sandy or consolidated sand along margins of streams, frequently associated with *Conocephalum conicum*, Atrichum, and *P. neesiana*. Buckingham, Cumberland, Fluvanna, Nottoway, Prince Edward, Spotsylvania counties.

2. Pellia neesiana (Gott.) Limpr. (Fig. 18) Dioecious; on moist compact soil along rivers and streams, often in solitary

patches. Buckingham, Campbell, Fluvanna, Lunenburg, Prince Edward counties.

30. Plagiochila (Dum.) Dum.

A coarse, dark green leafy hepatic, 26 mm wide, sparingly branched; leaves ovate rounded, distant to moderately overlapping, margins normally toothed but occasionally entire; lobules absent; underleaves minute and inconspicuous. Dioecious. Male and female plants occur in separate patches but it is uncommon to find either in a reproductive condition.

Plagiochila asplenioides subsp. *porelloides* (Torrey ex. Nees) Schust. (Fig. 54) On moist rocks or roots at waters edge, frequently loaded with sand; occasionally, plants submerged during flooding. Buckingham, Campbell, Cumberland, Prince Edward counties.

31. Porella L.

Robust, green leafy plants, 1.8 - 4.0 mm wide, attached at base to substrate, pinnately branched, the branches often ascending; leaves elliptic to broadly ovate, curled around the stem when dry, spreading when moist, the margins curled; lobules tongue shaped, attached to posterior margin of leaf and paralleling the stem; underleaves tongue-shaped, large, entire, rounded at apex. Dioecious and frequently fertile. Male plants with androecia in short lateral branches, buttonlike. Female plant with inflorescences terminating short branches, the perianths ovate, flattened, the apex constricted but not forming a beak.

- 1a. Underleaves narrow, flat, not wider than stem; lobules narrow, strap-shaped, not wider than stem P. pinnata
- 1b. Underleaves much broader than stem, concave, the margins recurved; lobules ovate, large, concave, much wider than stem *P. platyphylla*

1. *Porella pinnata* L. (Fig. 70) In loose patches attached to roots, tree bases and rocks along streams at water level, occasionally trailing in streams often submerged. Buck-ingham, Prince Edward counties.

2. Porella platyphylla (L.) Pfeiff. (Fig. 71) Species includes *P. platyphylloidea*; in loose patches with ascending branches; on boulders or bark of hardwoods in mixed-oak or hardwood swamp forests. Amelia, Buckingham, Prince Edward, Spotsylvania counties.



















32. Ptilidium Nees

Plants leafy, medium sized, 1-2 mm broad, in reddish-brown mats, pinnately branched; leaves densely overlapping, divided into two or three (to five) principal lobes, fringed with hairs that are 4-5 cells in length; underleaves large, bilobed, fringed, similar to leaves; lobules absent. Dioecious. Male plants with terminal spikes on leading stems or branches, of 4 - 5 pairs densely overlapping, ciliate bracts; sporophytes rare; perianths cylindrical, longitudinally folded at apex, constricted, the mouth ciliate; inconspicuous and terminal on main stems.

Ptilidium pulcherrimum (G. Web.) Hampe. (Figs. 31, 32) In reddish-brown interwoven mats on soil along streams that are shaded, sometimes on logs or rocks. Fluvanna, Spotsylvania counties.

33. Radula Dum.

Plants leafy, medium sized to large (0.8-2.5 mm broad). irregularly pinnately branched, the branches often with smaller leaves, in yellowish to olive-green patches; leaves rounded, entire margined, adjacent to overlapping, complicate-bilobed, the smaller portion forming a squarish or kiteshaped lobule attached for 2/3 its length to both leaf and stem; rhizoids often attached to center of lobule; leaf cells normally with a single large slightly granular oil body; underleaves absent. Androecia formed of several (2-5) pairs of tightly overlapping bracts, each containing a single antheridium: perianths elongate, compressed at tips although rounded at base, squared off at mouth, and formed at tips of stems and branches. Asexual reproduction by formation of flat multicellular disk-like gemmae on margins of leaf or, by dropping entire leaves (which regenerate new plants) while the lobules remain attached to the stem.

- 1b. Plants robust, 1.2-2.5 mm wide; leaves not or only slightly sickle-shaped, not dropping off; asexual reproduction by disk like gemmae on margins *R. complanata*

1. *Radula complanata* (L.) Dum. (Figs. 67, 68) Monoecious and usually fertile, the antheridia occur in bracts beneath the perianth; on bark of trees and on rock, Lunenburg, Prince Edward counties

2. *Radula obconica* Sull. (Fig. 69) Monoecious. On boulders in shaded woods, sometimes on tree trunks in yellowish patches. Buckingham, Charlotte, Lunenburg counties.

34. Reboulia Raddi

Light green thalloid plants, 5-8 mm wide, with a narrow purple margin, thallus forking and forming rosettes or patches; the upper surface developing inconspicuous pores and almost no net-like pattern, the epidermal cells with conspicuous trigones; lower surface purplish, with two rows of purple to maroon scales. Monoecious. Antheridia in a small, slightly elevated curved pad just behind the stalk of the much elevated umbrella-like female receptacle; sporophytes develop beneath the lobed female receptacle not surrounded by papery sheaths.

Reboulia hemisphaerica (L.) Raddi (Fig. 5) In tightly attached patches on soil and over rocks, occasionally on open soil in fields. Campbell, Buckingham, Prince Edward counties.

35. Riccardia S. Gray

Small, narrowly and somewhat pinnately branched, deep green thalloid plants lacking a midrib; cells with 1-3 large oilbodies when collected fresh; occurring in permanently wet sites; asexual reproduction by 2- celled gemmae. Monoecious or dioecious. Male branches usually linear with two rows of sunken but conspicuous antheridia. Female branches short but distinct, surrounded at tip by short finger-like scales; sporophyte erect, surrounded by a fleshy, warty calyptra of translucent cells. I have collected three species of this plant in the Coastal Plain and mountains and strongly suspect that they are in the Piedmont, thus they are included (in parentheses).

Figures 44-57. 44-46. Jamesoniella autumnalis. 44. Shoot, x20. 45. Perianth, x12. 46. Leaf cells with oil-bodies, x115. 47. Jungermannia leiantha. Shoot with perianth and male bracts below, x12. 48-49. Solenostoma crenuliforme. 48. Shoot, dorsal view, x14. 49. Leaf cells with trigones, x130. 50. Scapania nemorea. Shoot, dorsal view, complicate-bilobed leaves; gemmae at apices, x23. 51. Diplophyllum apiculatum. Shoot, dorsal view, x3. 52. Lophocolea heterophylla. Shoot, ventral view, x26. 53. Chiloscyphus pallescens. Shoot, ventral view, x7. 54. Plagiochila asplenioides, subsp. porelloides. Plant, ventral view, x2. 55-56. Lophozia bicrenata. Shoot with gemmae, x27. 56. Leaves, x23. 57. Nowellia curvifolia. Shoot, x24.

1a.	Thallus regularly 2-3 pinnately branched, the terminal branches narrow, $1/4$ to $1/2$ mm wide, with a thin clear border 2-4 cells wide (1 cell thick) <i>R</i> multified
1b.	Thallus once pinnately branched, palmately or, irregularly branched; branches unbordered or border less than 2 cells wide
2a.	Thallus pinnately branched, the terminal branches over 1/2 mm broad, usually on wet rocks or wet stream banks
2b.	Thallus irregularly to palmately branched; on moist rotten wood or organic soil
3a.	Branching irregular; thallus branches 0.3 - 1.0 mm wide, the branches broadened at tips (<i>R. latifrons</i>)
3b.	Branching usually palmate to semi-pinnately branched, the branches narrowed at tips, 0.2-0.4 mm wide
1. (1	Riccardia chamedryfolia (With.) Grolle.) Monoecious; male

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1. (*Ruccardia chamedryfolia* (With.) Grolle.) Monoecious; male and female branches occurring in pairs, small. On soil, humus and wet rocks.

2. (*Riccardia latifrons* (Lindb.) Lindb.) Monoecious; male and female branches close but not in pairs; normally occurring on moist rotten logs in swamps.

3. *Riccardia multifida* (L.) S. Gray. (Fig. 22) Monoecious; a highly variable species with at least two subspecies sometimes recognized; occurring on sandy to gravelly moist soil and rocks. Prince Edward County.

4. (*Riccardia palmata* (Hedw.) Carruth.) Dioecious; male plants with elongate branches (longer than in other species); on moist shaded rotten logs and, rarely, on humus.

36. Riccia L.

Thalloid plants dichotomously branched, in complete or partial rosettes on soil. Thallus with a lengthwise groove on upper surface or merely formed at apex; air chambers beneath surface narrow and erect or broad and open, chambers opening by inconspicuous pores to the surface; the lower part of the thallus with colorless rhizoids; scales on our species rudimentary or lacking. Monoecious or dioecious. Sex organs sunken in the thallus. Sporophytes dark, rounded capsules, embedded in the thallus and sometimes protruding from the lower surface. Spores are important taxonomic species indicators; they are released with the gradual disintegration of the thallus. Plants tend to be seasonal, appearing locally in late fall, winter and into spring.

1a.	Branches linear, repeatedly forking; plants aquatic
1h	Branches short and broad (0.4.0.7 mm wide) forking
	once or twice; terrestrial 2
2a.	Thallus with broad visible internal air-chambers
	through surface; upper surface sometimes sponge like
	with age
2b.	Thallus with narrow vertical air chambers between
1 	green tissue walls; spores with a pattern of net-like ridges
3a.	Thallus 24 mm broad; spores with acute prickles
	R. membranacea
3b.	Thallus branches narrower, 0.8 - 1.4 mm wide, rarely
	purplish on margins; spores with a net like pattern
4 a.	Thallus margins, at least towards apex, with distinct
•	short, stout hairs; branches 1.5 - 2.5 mm wide, the tips
	each with a broad groove on upper surface
	R. beyrichiana
4b.	Thallus margins lacking hairs; segments 0.8-1.5 mm
	wide, the tips with a narrow, deep groove R. sorocarpa

1. *Riccia beyrichiana* Hampe. Monoecious; plants in partial rosettes, thalli with a distinct groove at tip. On moist soil along ditches and in old fields. Buckingham County.

2. (Riccia fluitans L.) - Monoecious but usually sterile while aquatic. Suspended in masses just beneath the surface of ponds and pools, occasionally stranded. Expected here.

3. Riccia huebenariana subsp. sullivantii (Aust.) Schust. (Figs. 25, 26) Also known as *R. sullivantii*; monoecious; thalli notched at apices, sporangia bulge on lower surface; in rows of cultivated fields, soil of grassy ditches, or with sedges along pond shores. Buckingham, Prince Edward counties.

4. *Riccia membranacea* Gott. & Lindenb. (Fig. 28) Monoecious; broad, flat thalli, lacking an upper groove; sporangia bulge below; on moist compact soils along river floodplains or streams. Prince Edward County.

5. *Riccia sorocarpa* Aust. (Fig. 27) Monoecious; thalli form small thick rosettes; sporangia bulge on upper surface and are numerous; on soil in old fields; soil embankments along shaded, moist roadsides. Nottoway, Prince Edward counties.

37. Ricciocarpus Corda

Thalli green, wedge shaped, thick, 2 - 7 mm wide, often with deep purple margins; forking once or twice; upper surface firm, the groove deep and sharp throughout thallus; lower surface producing toothed, sword-shaped scales; aquatic plants with numerous purple, elongate scales; terrestrial forms with pinkish shorter scales. Monoecious. Sex organs sunken into upper groove. Sporangia embedded in upper surface and rupturing with decay of thallus.

(*Ricciocarpus natans* (L.) Corda) Floating on the surface of quiet pools and ponds, sometimes stranded on the shore. These are ephemeral and are expected here.

38. Scapania (Dum.) Dum.

Green to reddish-brown leafy hepatics occurring in mats on moist sandy soil. Plants sparsely branched, large, 1.5-5.5 mm broad; leaves entire to toothed all around, often developing 1-2 celled gemmae on leaf margins; leaves touching to overlapping, complicate-bilobed, the upper lobe (lobule) smaller than the lower, the lobule extending across the stem, hiding the stem. Dioecious. The leafy male bracts along the branches (intercalary); perianth terminal on stems, flattened and squared off at the mouth.

1. Scapania nemorea (L.) Grolle. (Fig. 50) Also known as S. *nemorosa*; on moist sandy soil over rocks, on wet soil along streams, often intermixed with other bryophytes. Appomattox, Buckingham, Fluvanna, Mecklenburg, Nottoway, Prince Edward counties.

2. Scapania undulata (L.) Dum. On moist sandy soil or rock along streams, often mixed with other bryophytes such as *Trichocolea tomentella* and *Thuidium delicatulum*. Mecklenburg, Lunenburg counties.

39. Solenostoma Mitt.

Plants leafy, in green to reddish tinged patches, rarely branched. Leaves round to elliptic, attached to stem obliquely to almost transversely, clasping at base; lacking lobules and underleaves; rhizoids covering the lower surface of the stem. Monoecious or dioecious. Androecia with male bracts occurring along stem with age, not on separate branches. Perianths developing at tips of stems, somewhat exserted beyond enclosing bracts, tubular but sharply constricted thus forming distinct folds near the mouth and narrowed to a small opening at the tip.

(Plants are not always determinable without reproductive material. If entire leaved species occur on sandy soil over rocks in and along streams, they are probably members of this genus if other sterile characteristics are observed.)

- 2a. Marginal cells 1 1.5 times as large as inner leaf cells, trigones of leaf cells distinct, often bulging; rhizoids red

1. Solenostoma crenuliforme (Aust.) Steph. (Figs. 48, 49) Dioecious; along streams on shaded rocks; often with *Scapania nemorea*. Higher elevations of Piedmont. Buckingham, Campbell, Prince Edward Counties.

2. Solenostoma fossombronioides (Aust.) Schust. Monoecious, concave male bracts develop below perianth; also in higher Piedmont areas over rocks thinly covered by soil along rocky streams.

3. Solenostoma gracillimum (Sm.) Schust. (Figs. 40, 41) Dioecious; a pioneer on disturbed soils of roadside banks and eroded paths in woods. Buckingham, Lunenburg counties.



4. Solenostoma hyalinum (Hook.) Mitt. (Figs. 42, 43) Dioecious; along streams that cut through rock outcrops on soilcovered rocks, usually toward higher elevations of the Piedmont. Campbell County.

40. Sphaerocarpos (Mich.) Boehm.

Strongly dimorphic thalloid plants occurring as rosettes on soil. Dioecious. Female thalli are clear green and bear clusters of erect, bottle-like ovoid perigynia constricted slightly toward the round apical opening, each developing a single sporophyte within and causing the perigynium to swell at base when mature. Male plants about 1/10th the size of female plants, reddish to purple, bearing clusters of flask-shaped involucres with narrowed neck, each containing an antheridium. The male involucres do not obscure the thallus surface as do the perigynia of the female plants. The spores remain together in dark brown tetrads at maturity.

Sphaerocarpos texanus Aust. (Figs. 23, 24) In furrows of one to three year old fallow fields, less often on soil along stream embankments subject to seasonal flooding. Amelia, Prince Edward counties

41. Trichocolea Dum.

Plants robust, in whitish green ciliate mats, three-pinnately branched, making shoots 14 cm wide. Leaves transversely attached, erect, the tips recurved, divided into four or five filamentous lobes almost to base, the lobes branched, multiciliate, near the base of leaf becoming two to three cells broad. Lobules absent. Underleaves similar but smaller than leaves, divided into four filamentous lobes nearly to base, the lobes branching, ciliate. Dioecious, but not seen with perianths in this area.

Trichocolea tomentella (Ehrh.)Dum. (Figs. 35, 36) On humus along banks of shaded, cool streams in woods with diffuse light. Cumberland, Fluvanna, Mecklenburg, Prince Edward, Spotsylvania counties.

GLOSSARY

androecium - the collection of male reproductive organs, antheridia

antheridium - the male sex organ which produces sperm apex - the tip of a stem, thallus, leaf, branch, perianth archegonium - the female sex organ which resembles a bowling

pin and contains a single egg within the swollen base axil - the angle formed between the leaf and stem *bidentate* - two-toothed, used when discussing leaves *bilobed* - two-lobed, having 2 parts or lobes

bracts - modified leaves occurring beneath reproductive organs; on female branches, the first pair of leaves occurring below the perianth; on male branches, the modified leaves with antheridia in their axils

calyptra - a tissue enclosure around the capsule or sporangium *capsule* - the sporangium, an enclosure containing spores *ciliate* - having many hairs on the margins

complicate bilobed - a leaf folded back against itself tightly, one portion or lobe smaller than the other: the smaller lobe is

known as the lobule, the larger lobe is the leaf *dioecious -* having male or female structures on separate plants

dorsal - upper or outer surface; backside

elliptical - in the shape of a stretched elongated circle

epidermis - the outer layer of cells of stem or a thallus

esserted - extending beyond, as, an esserted perianth (extended beyond bracts at base)

fertile - having reproductive structures

filamentous - thread like

fruit - a sporophyte or capsule

gemma cup - a cup-like structure producing gemmae within

gemmae - single cells, cell masses, or modified buds, able to produce new plants asexually

gynoecium - the collection of female organs, the archegonia

hepatic - a leafy or thallose plant of the class Hepaticopsida in the division Bryophyta

involucre - a thin, enclosing sheath developed from the thallus and formed around sex organs or sporophytes

Figures 58-72. 58-59. Cephalozia lunulifolia. 58. Shoot, x24. 59. Leaf, x112. 60-61. Cephalozia catenulata. 60. Shoot with perianth, x68. 61. Leaf, x164. 62. Cephalozia connivens. Leaf, x61. 63-64. Cephaloziella byssacea. 63. Plant, x44. 64. Leaf, x184. 65-66. Cephaloziella rubella. 65. Plant, x38. 66. Leaf lobe, x222. 67-68. Radula complanata. 68. Sterile shoot with gemmae, ventral view, x27. 69. Fertile shoot with perianth and pairs of male bracts beneath. 69. Radula obconica. Sterile shoot missing leaves, ventral view, x19. 70. Porella pinnata. Shoot, ventral view, x7. 71. Porella platyphylla. Shoot, ventral view, x7. 72. Cololejeunea biddlecomiae. Shoot, ventral view with inflated lobules, x69.



keel - the V-shaped line formed by the folding of a leaf, or folds occurring in the perianth; in the sense of a ship's keel

lobe - a multicellular portion of a larger organ, clearly identifiable, as a leaf lobe or thallus lobe

lobule - the smaller lobe of a complicate-bilobed leaf

- *monoecious* the condition of both sexes, male and female, occurring on the same plant, sometimes together, sometimes on separate branches
- oilbody a glistening organelle common in cells of leafy liverworts and some thallose hepatics; there may be one or several and, for a particular species, the oilbody type may be simple or segmented (resembling a grape cluster), normally without coloration, but in some taxa brown or blue

ovate - egg-shaped

- *palmate -* a branching pattern, radiating out like fingers from the palm of the hand
- *papillose* bearing small projections from the surface of leaf cells or the margins of some thalloid hepatics
- perianth a leafy structure (of various shapes) that encloses the sex organs and, upon maturity, the sporophyte; evolutionarily developed from the fusion of two or more modified, usually larger leaves; occurring only in leafy hepatics
- perigynium a fleshy enclosing structure originating from the thallus; it grows up around the female sex organs and,
 when mature, the sporophyte; of various shapes; analogous to the perianth of leafy liverworts
- *pinnate* feather-like or plumose, referring to the branching appearance of a liverwort in which branches are formed regularly on either side of the stem and become progressively shorter behind the stem apex
- *pyrenoid* a small spherical starch-forming body attached to a chloroplast, found only in cells of hornworts
- receptacle a fleshy pad of thallus tissue bearing antheridia or archegonia, usually sunken and often elevated on stalks
- *rhizoid* single-celled hairs (in hepatics) that attach the plant to the substrate

rosette - formed into a circle like the petals of a rose

simple - non branched

sinuous - with a wavy outline; usually the margin of a leaf or thallus

- spike a male branch in leafy hepatics; composed of densely overlapping bracts
- sporophyte a spore producing plant that develops with the female archegonium and, when mature, produces a capsule (or sporangium) containing spores
- sterile not producing sex organs (antheridia or archegonia) or, a plant not producing perianths

thallose - the shape of a thallus: flat, ribbon-like

- trigone the juncture of walls of three or more cells forming a thickened area
- ventral the lower surface or "belly" of some plant or plant organ

wings - the thallus margins on either side of the central midrib

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Figures 73-87. 73-74. Frullania brittoniae. 73. Shoot, ventral view showing underleaves and lobules, x16. 74. Perianth, x11. 75-76. Frullania inflata. 75. Shoot with explanate lobules, ventral view. 76. Leaf cells, x154. 77-79. Frullania eboracensis. 77. Shoot, ventral view, x16. 78. Detail of leaf, inflated lobule, and underleaf; x33. 79. Stem partially denuded of leaves and lobules, x49. 80-81. Frullania ericoides. 80. Shoot, x16. 81. Leaf cells with intermediate wall thickenings, x201. 82. Jubula pennsylvanica. Shoot, ventral view. 83. Frullania tamarisci subsp. asagrayana. Shoot, ventral view, x38. 84-85. Odontoschisma prostratum. 84. Shoot, dorsal view, x9. 85. Leaf cells with oil-bodies, x360. 86-87. Odontoschisma denudatum. 86. Shoot, dorsal view, x9. Ascending shoot tip with

gemmae, X16. 87. Leucolejeunea clypeata. Shoot, ventral view, X34

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CHECKLIST OF VIRGINIA PIEDMONT LIVERWORTS

- Bazzania S. Gray (Lepidoziaceae) trilobata (L.) S. Gray

- Calypogeja Raddi (Calypogejaceae) fissa (L.) Raddi

- Cephalozia (Dum.) Dum. (Cephaloziaceae) catenulata (Hub.) Lindb. connivens (Dicks.) Lindb. lunulifolia (Dum.) Dum.
- Cephaloziella (Spruce) Steph. (Cephaloziellaceae) byssacea (Roth.) Warnst. hampeana (Nees) Schiffn. rubella (Nees) Warnst.
- Chiloscyphus Corda (Geocalycaceae) pallescens (Ehrh.) Dum.
- Cololejeunea (Spruce) Schiffn. (Lejeuneaceae) biddlecomiae (Aust.) Evans
- Conocephalum Wiggers (Conocephalaceae) conicum (L.) Underwood
- Fossombronia Raddi (Fossomnbroniaceae) brasiliensis Steph.
- Jamesoniella (Spruce) Schiffn. (Jungermanniaceae) autumnalis (DC) Steph.
- Jungermannia L......(Jungermanniaceae) leiantha Grolle
- Kurzia Martens..... (Lepidoziaceae) sylvatica (Evans) Grolle

- Leucolejeunea Evans (Lejeuneaceae) chypeata (Schwein.) Evans
- Lophocolea (Dum.) Dum. (Lophocoleaceae) heterophylla (Schrad.) Dum.
- Lophozia (Dum.) Dum. (Lophoziaceae) bicrenata (Schmid.) Dum.
- Marchantia L. (Marchantiaceae) polymorpha L.
- Metzgeria Raddi (Metzgeriaceae) conjugata Lindb. crassipilis (Lindb.) Evans
- Notothylas Sull. (Anthocerotaceae) orbicularis (Schwein.) Sull.
- Nowellia Mitt. (Cephaloziaceae) curvifolia (Dicks.) Mitt.
- Odontoschisma (Dum.) Dum. (Cephaloziaceae) denudatum (Nees) Dum. prostratum (Sw.) Trev.
- Pellia Raddi (Pelliaceae) epiphylla (Dicks.) Dum. neesiana (Gott.) Limpr.

- Ptilidium Nees (Ptilidiaceae) pulcherimum (G. Web.) Hampe

- Riccardia S. Gray (Aneuraceae) (chamedryfolia (With.) Grolle) (latifrons (Lindb.) Lindb.) multifida (L.) S. Gray (palmata (Hedw.) Carruth.)

- Sphaerocarpos (Mich.) Boehm. (Sphaerocarpaceae) texanus Aust.



Figure 88. Counties included in study area (shown by heavy black outline) showing location in Piedmont region of Virginia

