The genus *Orthodicranum* (Musci: Dicranaceae) in Maine

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Orthodicranum is a segregate taxon of *Dicranum* Hedw. It has often been recognized as a genus in European floristic treatments, but generally given only subgeneric or sectional status in North American and Japanese floristics works. Peterson (1979) revised the taxon for North America and considered it worthy of generic rank because of six differences with *Dicranum*: 1. capsules straight vs. curved; 2. capsules smooth to wrinkled vs. ribbed; 3. alar cell region unistratose vs. bistratose; 4. peristome teeth <60 µm wide vs. > 70 µm; 5. specialized asexual structures common vs. rare; 6. habitat of rocks and wood vs. soil or humus. Of these six differences, two (specialized habitat and specialized asexual structures) are probably correlated characters best treated as a single feature. The peristomal difference can be dismissed outright since in both structure and ornamentation the peristomes of *Orthodicranum* and *Dicranum* are identical. Likewise, the capsule surface distinction is of little importance since a continuum exists between the genera: *Orthodicranum* has smooth to weakly furrowed capsules, *Dicranum* has weakly to strongly furrowed capsules.

Whether *Dicranum* should be recognized in a broad sense with many subgeneric units or subdivided into segregate genera such as *Orthodicranum* is an academic question that plagues many large, complex genera. This is because while genera and subgeneric units must not be polyphyletic both are abstract constructions capable of implying the same phylogenetic relationships. The choice of any one system is subjective and can depend as much on the utility of the classification as on perceived and weighted structural differences. In a monographic sense generic recognition is often given to any non-polyphyletic group with at least three distinguishing features. *Orthodicranum* in a monographic sense should be recognized at the generic level on the basis of the above three differences with *Dicranum*. However, the criteria for generic recognition in a floristic sense are stricter in that the utility of the classification should be taken into account. It makes no sense to use a generic classification in a floristic work that requires detailed microscopic work to discover the genus at hand. In such cases a broad generic category which reflects phylogenetic relationships at the subgeneric level is pragmatic and sensible.

In the case of *Orthodicranum* it is especially difficult to decide on its level of recognition in a floristic sense. On the one hand, *Orthodicranum* and *Dicranum*

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are gametophytically very similar, but on the other hand they generally occupy distinctly different habitats which makes their recognition, in a practical way, possible. Habitat preferences in mosses can be unreliable, and indeed in *Orthodicranum* and *Dicranum* there are some species that blur the habitat distinctions between the two groups. Nevertheless, the habitat differences between these two groups are distinct enough that, in conjunction with the above noted structural differences, I am inclined to recognize *Orthodicranum* at the generic level. A single key treating all *Dicranum* and *Orthodicranum* species in Maine will be given in a future account of *Dicranum*.

Orthodicranum (C. Müll.) Loeske, Stud. Morph. Syst, Laubm. 85: 1910.

Dicranum sect. *Orthodicranum* C. Müll., Syn. Musc. Frond. 1: 371. 1848. Lectotype: *Dicranum flagellare* Hedw. (Peterson, 1979)

Dicranum sect. *Orthocarpa* Bruch & Schimp. in B.S.G., Bryol. Eur. 1: 115. 1847 (fasc. 37--40 Mon. 11).

Dicranum sect. *Montana* Hartm., Handb. Skand. Fl. (ed. 5): 390. 1849.

Dicranum [rank not indicated] *Orthodicranum* B.S.G., Bryol. Eur. 1: 6. 1851. (fasc. 46--47 Consp. 1: VIII). *Nom. nud.*

Dicranum subg. *Crassidicranum* Limpr., Laubm. Deutschl. 1: 370. 1886.

Dicranum sect. *Crassidicranum* (Limpr.) Nyh., Bot. Not. 1953: 297. 1953.

Dicranum subg. *Leiodicranum* Limpr., Laubm. Deutschl. 1: 367. 1886.

Dicranum sect. *Leiodicranum* (Limpr.) Amann, Fl. Mouss. Suisse 2: 58. 1919.

Dicranum sect. *Crassinervia* Roth, Eur. Laubm. 1: 237. 1904.

Scytalina Hagen, Kongel. Norske Vidensk. Selsk. Skr. 1914 (1): 129. 1915. *Nom. illeg. incl. gen. prior.*

Dicranum subg. *Crassidicranum* Limpr. *emend.* Takaki, J. Hattori Bot. Lab. 27: 76. 1964.

Plants small to medium-sized, in mats on living or dead bark, decaying wood, and rocks, occasionally on humus or bare soil. Stems erect, sparsely branched, moderately tomentose. Leaves erect-spreading, erect-incurved, falcate-secund to crisped when dry, ovate-lanceolate to lanceolate, smooth or papillose at back, acute to long acuminate, margins entire, serrate or serrulate; costa excurrent or percurrent; upper cells quadrate to short rectangular, smooth-walled, basal cells elongate, short rectangular to subquadrate, smooth or porose, alar cells, thin-walled, inflated, reddish-brown, unistratose. Vegetative reproduction by fragile leaf apices, flagellate branches or microphyllous leaves. Dioicous. Monseteous. Capsules erect, cylindric, smooth, wrinkled or weakly furrowed, not strumose, stomates at base of capsule, annulus rudimentary, opercula conic-rostrate; peristome haplolepideous, teeth 16, divided in upper half, outer surface vertically striate. Spores 10--25 µm, smooth to lightly papillose or roughened. Calyptrae cucullate.

1. Leaf tips broken, leaves stiffly erect-incurved when dry .....*O. virde*
1. Leaf tips intact, leaves falcate-secund or crisped when dry 2
    2. Plants with stout, terete flagellate branches in upper leaf axils that bear erect, non-contorted leaves .....*O. flagellare*
    2. Flagellate branches absent or flagellate branches weak, bearing contorted, crispate, microphyllous leaves 3
3. Leaves bistratose above; costa occupying 1/3 or more of the leaf base ....*O. fulvum*
3. Leaves unistratose above; costa occupying less than 1/3 of the leaf base 4
    4. Dry leaves slightly crisped to falcate-secund, cells smooth or slightly papillose at back ..... *O. flagellare*
    4. Dry leaves strongly crisped, cells bulging to papillose at back .... *O. montanum*

1. *Orthodicranum flagellare* (Hedw.) Loeske, Stud. Morph. Syst, Laubm. 85: 1910.
    Dicranum flagellare Hedw., Sp. Musc. Frond. 130. 1801.
    Scytalina flagellaris (Hedw.) Hagen, Kongel. Norske Videnskab. Selsk. Skr. 1914 (1): 132. 1915.

Plants small to medium sized, dull or shiny, dark-green, green, or yellowish-green above, brownish below. Stems 3--50 mm long. Leaves crowded, falcate-secund or erect-patent to erect-spreading when wet, falcate-secund to crisped when dry, ovate-lanceolate to lanceolate, smooth or roughened above at back, 2--4 mm long, acute; margins erect below, subtubulose above, serrulate near apex; costa percurrent to short excurrent; upper cells irregularly subquadrate, thick-walled, not porose, 17--25 µm x 12 µm wide; basal cells rectangular-elongate, thick-walled, 32--62 µm x 5--10 µm; alar cells enlarged, thin-walled, bulging, forming distinct groups of reddish-brown rectangular cells. Clusters of branches with minute appressed leaves commonly present in the upper leaf axils. Setae 10--15 mm long, yellow becoming brown with age; capsules erect, cylindrical, weakly furrowed, 1.5--3 mm long; opercula 1.5--2 mm long. Spores lightly papillose, 12--18 µm. Calyptra 2.5--3 mm long.

On tree trunks, rotting stumps, logs, or boulders in woods and in crevices of rock outcrops in shaded or exposed situations, on rocks along ocean shoreline, and on humus and stream banks. In Maine known from Androscoggin (*Allen 2427* MO), Aroostook (*Allen 16304* MO), Cumberland (*Allen 6028* MO), Franklin (*Allen 15850* MO), Hancock (*Redfearn 37743* MO), Kennebec (*Allen 15743* MO), Lincoln (*Allen 9243* MO), Oxford (*Allen 16679* MO), Penobscot (*Allen 16524* MO), Piscataquis (*Richards & Cooper 87* MAINE), Sagadahoc (*Allen 14602*

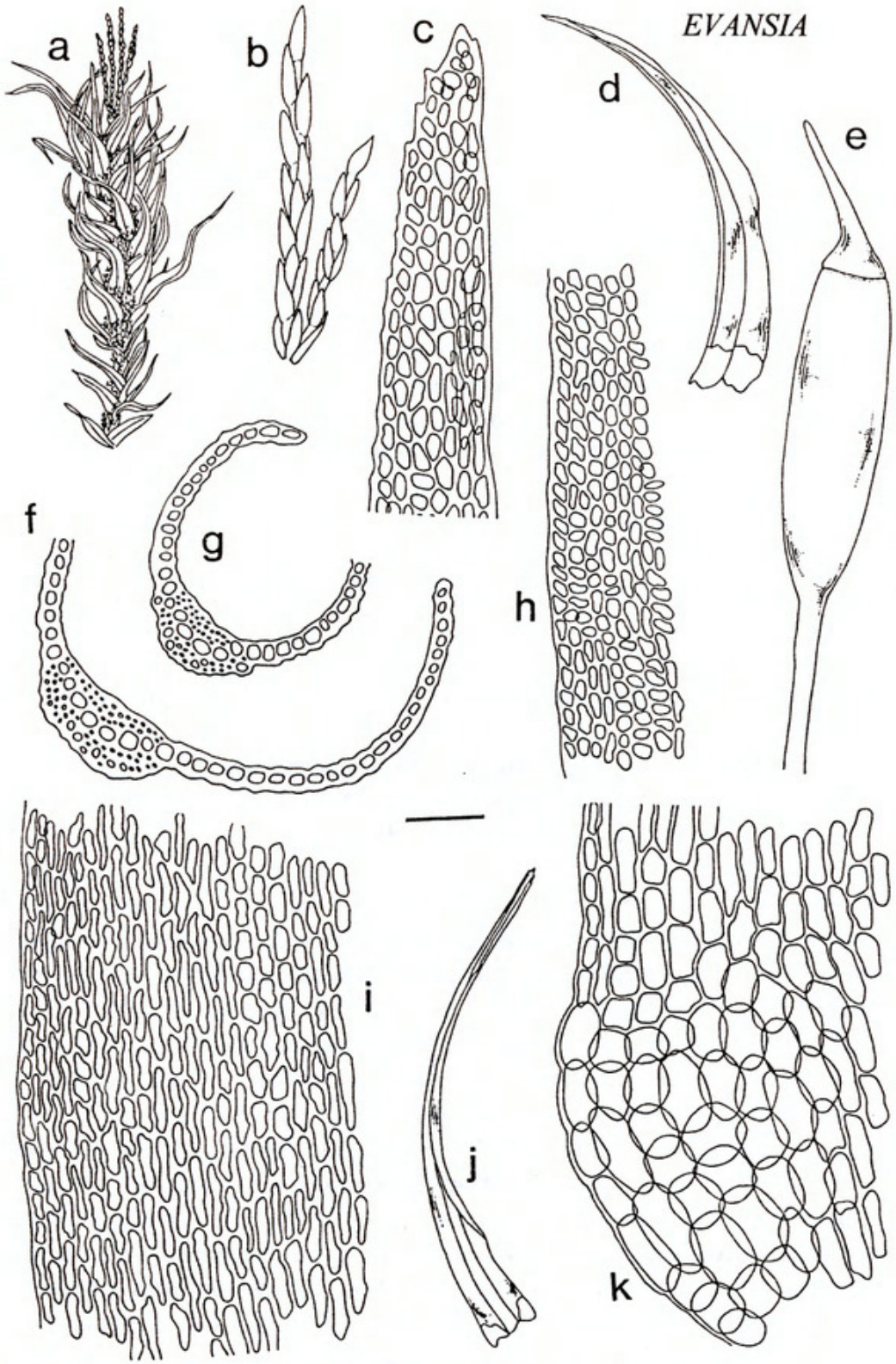

Figure 1. *Orthodicranum flagellare*. a. Habit. b. Flagellate branches. c. Leaf apex. d. & j. Leaves. e. Capsule and operculum. f. & g. Leaf cross-sections. h. Median leaf cells at margin. I. Basal leaf cells at margin. k. Alar cells. Scales in mm: bar = 0.05 (c,f,g,h,i,k); bar = 0.64 (d,j); bar = 0.77 (b); bar = 1.37 mm (a); bar = 0.74 mm (e). Figures c,f,g,h,i,k from *Allen 14602*, figures d,j from *Allen 2427*, figure b from *Redfearn 37743,* figure a from *Allen 2439*, figure e from *Allen 9407d,* (all MO).

MO), Somerset (*Allen 9401* MO), Washington (*Pedano 319* MO), and York (*Redfearn 37824* MO) Counties. Reported from Waldo (Parlin 1924, 1939) County.

Orthodicranum flagellare is a moderate sized species with shiny, concave, usually erect-patent leaves, subquadrate, non-porose upper leaf cells, and elongate basal cells. A distinctive feature of *O. flagellare* is its apical clusters of microphyllous branchlets that are nearly always present. It is a very common species in Maine where it occurs in a broad range of habits, e.g., tree bark, rotting logs, humus, soil or bare rock. It can be found along trails, in moist forests, dry rock faces, and even on the rocky coast line within reach of salt water. Not surprising, it is widely distributed throughout the northern hemisphere and also found in the Caribbean, Central and South America, Asia and India. *Orthodicranum flagellare* often grows mixed with *O. fulvum* or *O. montanum*. *Orthodicranum fulvum* is a somewhat larger plant with dark-green leaves, an exceptionally wide costa, and short basal leaf cells. *Orthodicranum montanum* is usually a smaller more slender and delicate plant with strongly crispate leaves and upper leaf cells bulging- papillose at back. *Dicranum fuscescens* differs from *O. flagellare* in having leaf margins partially or entirely bistratose.

2. *Orthodicranum fulvum* (Hook.) Roth *in* Cas. Gil, Fl. Ibér. Brióf., Musg. 176. 1932.

    Dicranum fulvum Hook., Musci Exot. 2: 149. 1819.

    Campylopus fulvus (Hook.) Kindb., Bih. Kongl. Svenska Vetensk.-Akad. Handl. 7(9): 88. 1883.

    Paraleucobryum fulvum (Hook.) Loesk. *in* Podp., Consp. Musc. Eur. 153. 1954.

Plants medium to robust, dull or shiny, dark-green above, yellow to brown or blackish below. Stems 1--4 cm long. Leaves crowded, falcate-secund or erect spreading when wet, irregularly crisped to falcate-secund when dry, lanceolate, strongly roughened above at back, 5--7 mm long, acuminate; margins erect below, subtubulose above, serrulate near apex; costa short- excurrent, very broad and filling 1/3 or more the leaf base and nearly the entire upper leaf, in cross-section with a gradual transition from costa to lamina; upper cells short rectangular to irregularly subquadrate, thick-walled, not porose, 7.5--12.5 µm x 7.5--10 µm; basal cells short-rectangular to subquadrate, thick-walled, not porose, 7.5--30 µm x 12.5 µm; alar cells enlarged, thin-walled, bulging, forming distinct groups of reddish-brown rectangular cells. Setae 10--25 mm long, yellow to brown; capsules erect, cylindrical, 2--3 mm long, annulus non-revoluble; opercula 1--2 mm long. Spores 15--20 µm, lightly roughened. Calyptra 4 mm long.

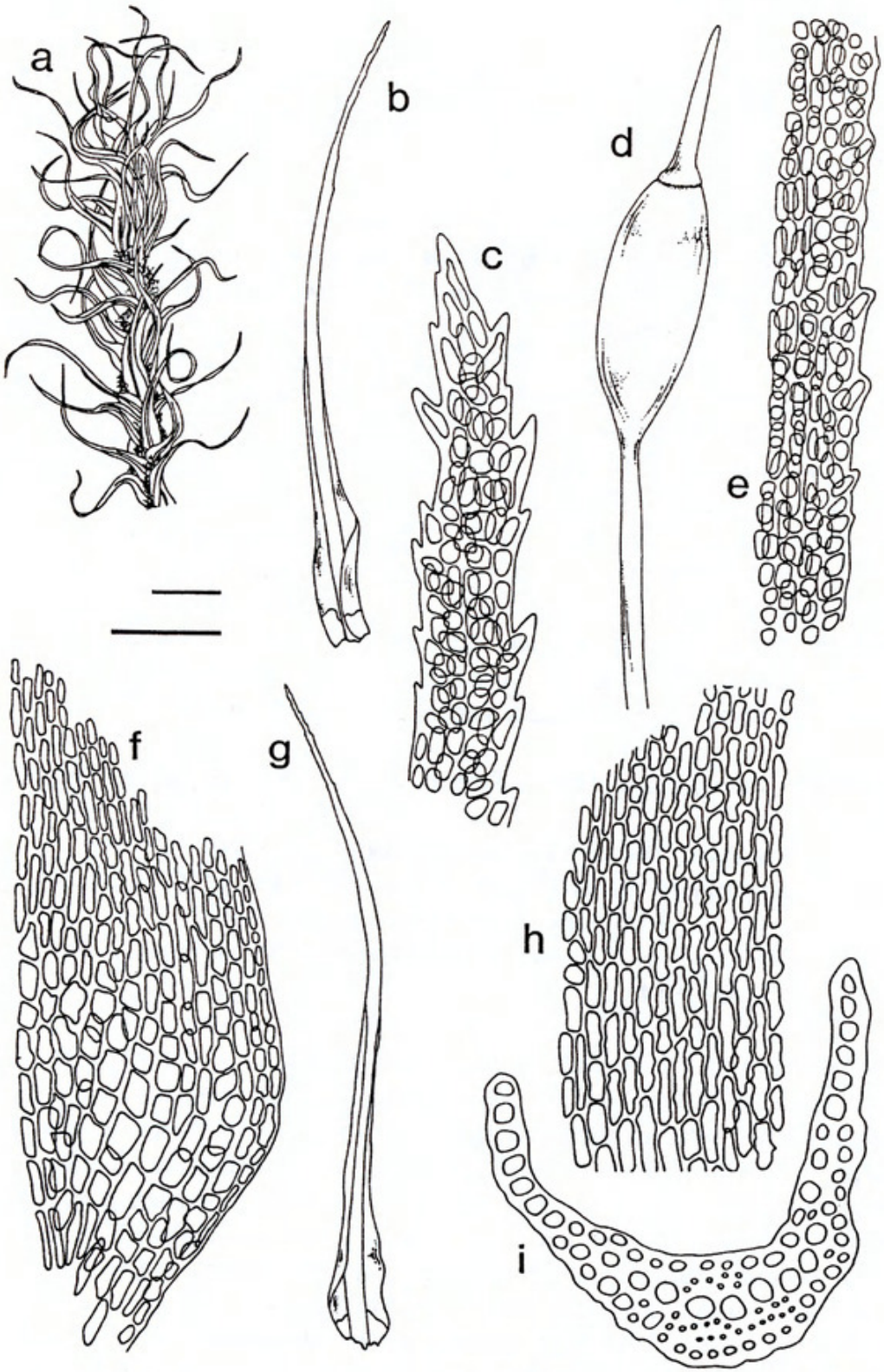

Figure 2 *Orthodicranum fulvum*. a. Habit. b. & g. Leaves. c. Leaf apex. d. Capsule and operculum. e. Median leaf cells at margin. f. Alar cells. h. Basal leaf cells at margin. I. Leaf in cross-section. Upper bar = 0.05 (h); lower bar = 0.1 (f); lower bar = 0.05 (c,e,i); lower bar = 1.1 mm (b,d,g); lower bar = 4.25 mm (a). All figures from *Allen 19964* (MO).

In dense mats or cushions on rocks and boulders in woods and along streams, on bare surfaces or in cracks of vertical rock faces. In Maine known from Androscoggin (*Allen 14731* MO), Cumberland (*Lowe* MAINE), Franklin (*Allen 15837* MO), Hancock (*Allen 2071* MO), Kennebec (*Allen 15709* MO), Knox (*Allen 14636* MO), Lincoln (*Allen 9235* MO), Oxford (*Allen 10079* MO), Penobscot (*Allen 16531* MO), Piscataquis (*Allen 16565* MO), Sagadahoc (*Allen 16629* MO), Somerset (*Allen 9374* MO), Waldo (*Allen 10377* MO), Washington (*Holmes 104* MO), and York (*Redfearn 31134* MO) Counties.

Orthodicranum fulvum is found on bare rocks and boulders or over humus on rocks in mesic, forest conditions. It also occurs on bare, very dry but shaded, cliff faces and rock outcrops. It is a dark green moss with a brown to blackish color at base and usually crispate leaves, but its leaves can also be falcate-secund both wet and dry. The best diagnostic feature of *O. fulvum* is its extraordinarily broad costa which occupies up to 1/3 the leaf base and nearly the entire upper leaf. In cross-section the costa gradually tapers into the lamina making it difficult to determine where the costa ends and the lamina begins. This odd feature is also seen in some species of *Campylopus*. Other distinctive features of the species include its short, non-porose basal leaf cells and mostly bistratose upper lamina.

Orthodicranum viride is structurally similar to *O. fulvum* in having a dark green color, broad costa, and short basal leaf cells. The two species are often placed in their own subgenus (*Crassidicranum*) or section (*Crassinervia*). *Orthodicranum viride*, however, is found primarily on bark rather than rock, has leaves stiffly erect to erect-incurved, and fragile leaf apices that are entire above. *Orthodicranum flagellare* and *O. fulvum* occupy similar habitats, have much the same aspect, and can be more or less the same size. *Orthodicranum flagellare* differs from *O. fulvum* in its narrower costa, unistratose lamina, long, often porose basal leaf cells, and the common presence of apical clusters of terete, flagellate branches with erect, non-contorted leaves. *Dicranum fuscescens* is also similar in aspect to *O. fulvum*, but it differs in its narrower costa, and its lamina that is bistratose only on the leaf margins. In the field *O. fulvum* can be very difficult to distinguish from *Paraleucobryum longifolium*. This is because both species have very broad costae and erect symmetric capsules. *Paraleucobryum longifolium* has slender, falcate-secund leaves that are very different from the crispate leaves of *O. fulvum*. However, the leaves of *O. fulvum* are sometime falcate-secund when dry. *Paraleucobryum longifolium* differs radically from *O. fulvum* in its costa cross-section which like *Leucobryum* has a layer of chlorocysts between two layers of hyalocysts. In the field *P. longifolium* can be distinguished from falcate-secund expressions of *O. fulvum* by its narrower leaves with gray-green to slate color rather than dark-green to fulvous.

3. *Orthodicranum montanum* (Hedw.) Loeske, Stud. Morph. Syst, Laubm. 85: 1910.

Dicranum montanum Hedw., Sp. Musc. Frond. 143. 1801.

Scytalina montana (Hedw.) Hagen, Kongel. Norske Vidensk. Selsk. Skr. 1914 (1): 129. 1915.

Plants small to medium sized, dull or shiny, dark-green, green, or yellowish-green above, brownish below. Stems 4--20 mm long. Leaves crowded, erect to patent-spreading when wet, curled and crispate when dry, ovate-lanceolate to lanceolate, roughened above at back, 2--4 mm long, acute; margins erect below, concave above, serrulate near apex; costa percurrent to short excurrent; upper cells irregularly subquadrate, thick-walled, not porose, 3--8 µm x 2--4 µm; basal cells rectangular-elongate, thick-walled, smooth or porose, 8--23 µm x 4 µm; alar cells usually enlarged, thin-walled, bulging, forming distinct groups of reddish-brown rectangular cells, at times poorly developed. Plants often with clusters of weak branches with minute, crispate microphyllous leaves in the leaf axils. Setae 8--10 mm long, yellow becoming brown with age; capsules erect, cylindrical, smooth to lightly furrowed, 1.5--2 mm long; opercula 1--1.5 mm long. Spores 12--17 µm, smooth to lightly papillose. Calyptra 2 mm long.

On boulders or rocks, vertical rock faces, tree trunks (*Abies*, *Acer*, *Betula*, *Quercus*), decorticated and rotting logs or tree stumps, also on bare soil or humus. In Maine known from Androscoggin (*Allen 14692* MO), Aroostook (*Allen 16313* MO), Cumberland *(Allen 2443* MO), Franklin (*Allen 10277* MO), Hancock *(Magill 11783* MO), Kennebec (*Allen 10130* MO), Knox (*Allen & Allen 6071* MO), Lincoln (*Allen 19960* MO), Oxford (*Allen 16697* MO), Penobscot (*Allen 16545* MO), Piscataquis (*Allen 16577* MO), Sagadahoc (*Allen 16618* MO), Somerset (*Allen 9436* MO), Waldo (*Allen 10315* MO), Washington (*Pedano 607* MO), and York (*Allen 13052* MO) Counties.

Orthodicranum montanum is a small species with a dark-green color and strongly crispate leaves. It is a common species especially abundant on bark at the base of trees, but is also found on boulders and rock faces or even bare soil. It generally reaches its largest size on saxicolous substrates. It is often confused with *Orthodicranum flagellare*, and the two species frequently grow mixed. *Orthodicranum flagellare* is a larger plant than *O. montanum*, with firmer, less crispate leaves that are smooth to weakly papillose at back, and it has stout, terete brood branches in the upper leaf axils. *Orthodicranum montanum* has weak, fragile brood branches bearing minute and strongly crispate, microphyllous leaves. Its small size, strongly crispate leaves, and leaf cells that are often stoutly mammillose dorsally can cause confusion with the Pottiaceae or *Amphidium*. It

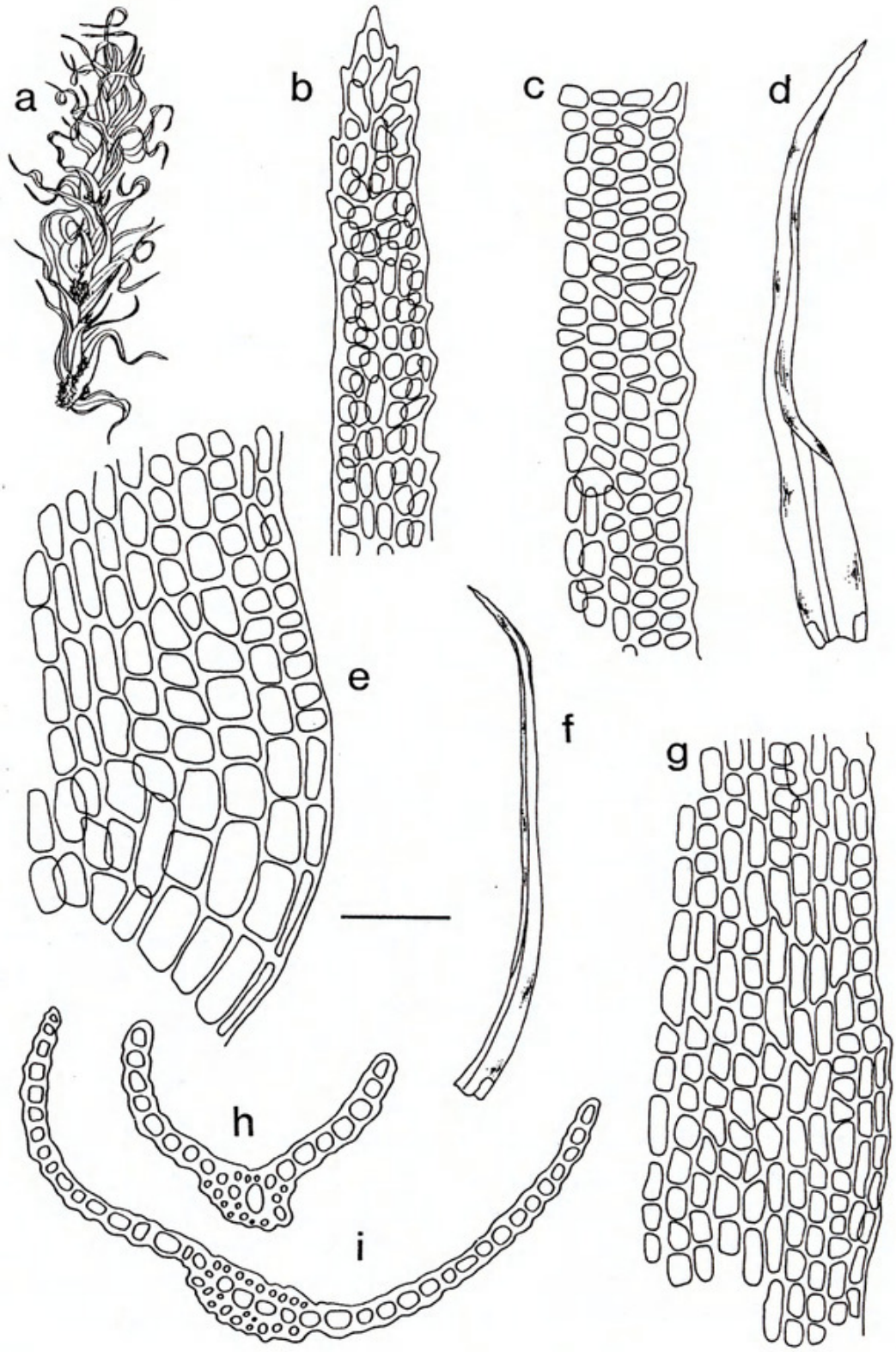

Figure 3. *Orthodicranum montanum*. a. Habit. b. Leaf apex. c. Median leaf cells at margin. d & f. Leaves. e. Alar cells. g. Basal leaf cells at margin. h & I. Leaf in cross-section. Scales in mm: bar = 0.05 (b,c,e,g,h,i); bar = 0.5 (d,f); bar = 2.1 (a). Figures a,i from *Allen 16627,* all others from *Allen 6071,* (both MO).

differs from those mosses in having usually well developed alar cells and a dicranaceous peristome. Its small size can also cause confusion with *Dicranella* which differs from *O. montanum* chiefly in having undifferentiated alar cells. Small plants of *O. montanum,* consisting mostly of minute, reduced leaves, can be especially difficult to recognize because their alar cells tend to be very weakly developed.

4. *Orthodicranum viride* (Sull. & Lesq.) Roth *in* Cas. Gil, Fl. Ibér. Bríóf., Musg. 176. 1932

Campylopus viridis Sull. & Lesq. *in* Sull., Musci Hep. U.S. 103. 1856.

Dicranum viride (Sull. & Lesq.) Lindb., Hedwigia 2: 70. 1863.

Paraleucobryum viride (Sull. & Lesq.) Podp., Consp. Musc. Eur. 153. 1954.

Plants medium sized, dull, dark-green to bright green, yellowish-green above, brownish below. Stems to 20 mm long. Leaves crowded, erect-spreading when wet, stiffly erect incurved to erect spreading, at times flexuose when dry, lanceolate, roughened-papillose above at back, 4--5 mm long, long-acuminate, ending in a linear, multistratose, deciduous point; margins erect below, subtubulose above, entire; costa long-excurrent; upper cells irregularly oblate, quadrate to short-rectangular, thick-walled, not porose, 7.5--25 µm x 10--12.5 µm wide, papillose or smooth; basal cells irregularly oblate, quadrate to short-rectangular, thick-walled, not porose, 7.5--22.5 µx 7.5--10 µm wide; alar cells enlarged, thin-walled, bulging, forming distinct groups of hyaline to reddish-brown, quadrate to rectangular cells. Sporophytes not seen from Maine. Setae 12--15 mm long, yellow becoming brown with age; capsules erect, cylindrical, smooth to weakly furrowed, 2--2.5 mm long; opercula 1.5 mm long. Spores smooth to lightly papillose, 12--18 µm. Calyptra not seen.

On tree trunks, bark of *Acer, Betula, Fagus*, and *Quercus*, rarely on boulders and rocks in woods. In Maine known from Androscoggin (*Allen 14693* MO), Aroostook (*Allen 16320* MO), Cumberland (*Allen 15919* MO), Franklin (*Allen 10270B*), Hancock (*Allen 16293* MO), Kennebec (*Allen 14787* MO), Lincoln (*Solomon 20125* MO), Oxford (*J.A. Allen* NY), Piscataquis (*Allen 16554A* MO), Somerset (*Allen 9310* MO), and Washington (*Pedano 545* MO) Counties.

In Maine *Orthodicranum viride* differs from all other *Orthodicranum* species in having stiffly erect-spreading to erect-incurved leaves with fragile, often broken, multistratose apices. Plants of *O. viride* from North Carolina are different from Maine plants in having a yellow-green rather than dark green color and more arching rather than stiffly erect-incurved leaves. The North Carolina plants have

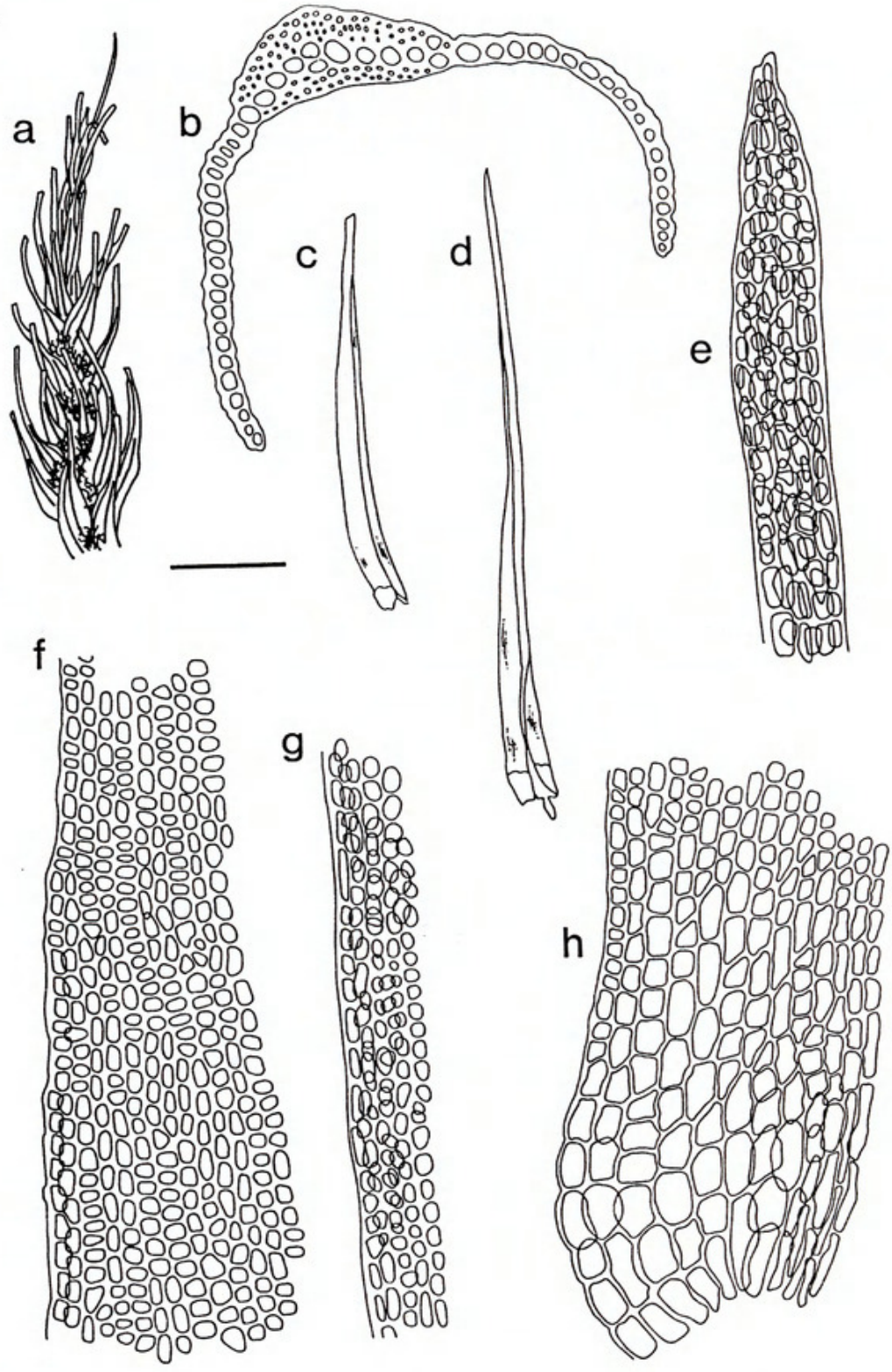

Figure 4. *Orthodicranum viride*. a. Habit. b. Leaf in cross-section. c. & d. Leaves. e. Leaf apex. f. Median leaf cells at margin. g. Upper leaf cells at margin. h. Alar cells. Scales in mm: bar = 0.04 (e); bar = 0.05 (b,f,g,); bar = 0.07 (h); bar = 0.5 (c,d); bar = 1.5 (a). Figures a,b,c,d,g from *Allen 16293,* figures e,f,h from *Allen 1330,* (both MO).

an aspect remarkably similar to some species of *Campylopus*, and the presence of a broad costa and short basal leaf cells adds to its similarity with that genus. A broad costa and short basal cells are features also found in *O. fulvum*, and both species have been placed in *Campylopus* and *Paraleucobryum*. The presence of erect rather than cygneous setae separates *O. viride* from *Campylopus*. *Paraleucobryum longifolium* differs in having falcate-secund leaves and a costal cross-section that has a layer of chlorocysts between two layers of hyalocysts. Sporophytes of *O. viride* are rarely seen in North American collections, the above sporophyte description was taken from a Canadian collection (*Ireland 14081* MO) gathered on Prince Edward Island.

Literature Cited.

Peterson, W. 1979. A revision of the genera *Dicranum* and *Orthodicranum* (Musci) in North America North of Mexico. xiv + 453 pp. Ph.D. Dissertation, University of Alberta, Canada.