

Keys to *Grimmia* species in Europe

This is a translation of Eva Maier's keys to the European species of *Grimmia*, originally published in German in the journal *Herzogia* (Maier, 2009). The translation has been prepared by **Peter Erzberger** with reference to the English descriptions in Maier's recently published worldwide monograph of the genus (Maier, 2010).

This translation is published here with the consent of the author and the permission of the publisher and editor of Herzogia. Revised descriptions and illustrations (with captions also in English) of all the species, as well as methodological advice, can be found in Maier's paper in Herzogia and in her monograph. Additions made by the translator are included in square brackets.

The following species of *Grimmia* are recognized in Europe:

- | | |
|---|--|
| 1. <i>G. alpestris</i> | 18. <i>G. longirostris</i> |
| 2. <i>G. anodon</i> | 19. <i>G. meridionalis</i> |
| 3. <i>G. anomala</i> | 20. <i>G. montana</i> |
| 4. <i>G. atrata</i> | 21. <i>G. muehlenbeckii</i> |
| 5. <i>G. caespiticia</i> | 22. <i>G. nutans</i> |
| 6. <i>G. crinita</i> [incl. <i>G. capillata</i>] | 23. <i>G. orbicularis</i> [incl. <i>G. curviseta</i>] |
| 7. <i>G. decipiens</i> | 24. <i>G. ovalis</i> |
| 8. <i>G. dissimulata</i> | 25. <i>G. plagiopodia</i> |
| 9. <i>G. donniana</i> [incl. <i>G. arenaria</i> & <i>G. triformis</i>] | 26. <i>G. pulvinata</i> |
| 10. <i>G. elatior</i> | 27. <i>G. ramondii</i> |
| 11. <i>G. elongata</i> | 28. <i>G. sessitana</i> |
| 12. <i>G. funalis</i> | 29. <i>G. tergestina</i> [incl. <i>G. poecilostoma</i>] |
| 13. <i>G. fuscolutea</i> | 30. <i>G. torquata</i> |
| 14. <i>G. hartmanii</i> | 31. <i>G. trichophylla</i> |
| 15. <i>G. incurva</i> | 32. <i>G. unicolor</i> |
| 16. <i>G. laevigata</i> | [<i>G. teretinervis</i> is regarded as a species of <i>Schistidium</i> .] |
| 17. <i>G. lisae</i> | |





◁ *G. orbicularis* (23). Michael Lüth

Explanation of terms

A glossary of botanical terms used in these keys can be found on p. 31.

Leaf length is measured without the hair point.

The leaf is subdivided into the basal part, a transitional zone, and the laminal or upper part.

Guide cells are large empty cells in the nerve; in *Grimmia* they are usually exposed on the ventral surface of the nerve.

Joint thickenings are thickened (bulging) areas of the cuticle on the leaf surface above the junctions of the cell walls, and should not be confused with papillae, which occur over the cell lumen.

Key to plants with sporophytes

(Gametophyte characters should be assessed in moist conditions, and sporophytes in dry conditions. G. anomala and G. torquata are omitted from this key, since their sporophytes are unknown in Europe).

- 1 Capsule smooth 2
- 1* Capsule wrinkled or ribbed 22

- 2 Seta erect or inclined, much longer than the capsule. 3
- 2* Seta erect, curved or S-shaped, slightly longer than the capsule 17

- 3 Seta erect. 4
- 3* Seta inclined 16

- 4 Costa in transverse section at leaf base close to insertion with more than 8 ventral cells, most of them guide cells; costa indistinct in dorsal view from transitional zone to apex 5
- 4* Costa in transverse section at leaf base close to insertion with 8, 6 or 4 ventral cells, or with 4 ventral cells of which the outer 2 are transitional with the lamina cells, all of them guide cells; costa clearly distinct in dorsal view from transitional zone to apex 7

- 5 Leaf base short, ca 1/5 of leaf length, half clasping the stem, in the sheathing part cells close to margin transversely oval, transverse walls thicker than longitudinal walls; margin unistratose from base almost to apex; in laminal part of leaf guide cells recessed in a shallow furrow, with markedly incrassate ventral cell walls. Calyptra mitrate, lobed, operculum conical, beak straight, obtuse. *G. laevigata* (16)
- 5* Leaf base long, ca 1/3 of leaf length; other characters different. 6
- 6 Leaf apex broadly rounded, hair point always lacking; costa in transverse section consisting of uniform cells, hydroids always lacking. Calyptra mitrate, lobed, fugacious, operculum conical, beak short or long, straight *G. unicolor* (32)
- 6* Leaf apex narrowly rounded, with hair point of variable length; costa cells in transverse section differentiated, hydroids present. Calyptra cucullate, lobed, operculum conical, beak long, oblique. *G. ovalis* (24)
- 7 Costa in transverse section at leaf base near insertion with 8 guide cells; leaf apex obtuse, rarely cucullate, without hair point; costa strong, with median band of substereids; leaf margins at insertion and at leaf base sometimes with alar cells, in transverse section mostly bistratose on both sides of the leaf, or on one side only. Calyptra mitrate, operculum conical, obliquely rostrate. *G. atrata* (4)
- 7* Costa in transverse section at leaf base close to insertion with 6 or 4 guide cells, or with 4 guide cells of which the outer 2 are transitional with the lamina cells 8
- 8 Costa in transverse section at leaf base close to insertion with 6 guide cells 9
- 8* Costa in transverse section at leaf base close to insertion with 4 guide cells, or with 4 guide cells of which the outer 2 are transitional with the lamina cells 10
- 9 Stem without central strand, epidermis dark brown, formed by [at least] 2 layers of stereids with narrow lumina, sharply contrasting with the large, thin-walled inner cortical cells; at leaf base 2–3 rows of paracostal cells elongate-rectangular, other cells rectangular or isodiametric, all walls smooth; multicellular propagules developed at leaf apices, leaving the apex modified after their release. Calyptra mitrate, operculum conical, beak long, straight *G. hartmanii* (14)
- 9* Stem with narrow central strand, clearly contrasting with the surrounding cells; at leaf base several rows of elongate-rectangular paracostal cells with nodulose walls, transverse walls markedly thin, mostly oblique; propagules not developed. Calyptra mitrate, operculum conical, beak of variable shape and length *G. longirostris* (18)
- 10 Costa in transverse section at leaf base close to insertion with 4 guide cells 11
- 10* Costa in transverse section at leaf base close to insertion with 4 guide cells of which the outer 2 are transitional with the lamina cells 15
- 11 Lamina cells and dorsal cells of costa in transverse section with mamillose protuberant outer walls; leaf margin inflexed in upper part of leaf; costa in dorsal view narrow at leaf base,

- enlarged in laminal part towards apex; hair point short, nearly smooth, cell lumina often visible; secondary costae often developed in lower half of leaf. Calyptra cucullate, small, fugacious, operculum conical, obtuse *G. caespiticia* (5)
- 11* Lamina cells and dorsal cells of costa in transverse section with smooth outer walls; other characters different 12
- 12 Leaf margin recurved on one side 13
- 12* Leaf margin plane or inflexed in laminal part of leaf 14
- 13 Paracostal cells at leaf base elongate-rectangular, with nodulose walls, transverse walls markedly thin, often oblique; cells near margin quadrate or rectangular, walls smooth, incrassate, sometimes hyaline to widest part of leaf; cells in transitional zone shortly rectangular, walls nodulose or smooth; costa in transverse section in lower laminal part of leaf unevenly rounded, somewhat angulate, rounded in upper part. Calyptra mitrate, operculum conical, beak of variable shape and length *G. longirostris* (18)
- 13* Paracostal cells at leaf base elongate-rectangular, walls mostly smooth, transverse walls not oblique; near margin 3–4 rows of narrowly rectangular, hyaline, thin-walled cells gradually vanishing, the outermost row ascending to above widest part of leaf where the cells become short-rectangular to quadrate; lamina cells rectangular or elongate-rectangular, walls strikingly or only weakly sinuose; costa in transverse section strongly prominent dorsally in laminal part of leaf and occasionally weakly mamillate. Calyptra cucullate-mitrate, beak conical, obtuse *G. elongata* (11)
- 14 Leaf margins from base to apex becoming gradually more incurved; lamina bistratose, rarely unistratose beside costa; paracostal basal cells rectangular, near margin shortly rectangular or quadrate, all walls smooth, transverse walls incrassate, at margin some rows hyaline, above shoulder some marginal cells transversely oval in a longitudinal row. Calyptra cucullate, operculum conical, beak straight or oblique, obtuse, at capsule mouth several rows of transversely rectangular cells, the outer 2 rows suggesting an annulus *G. montana* (20)
- 14* Leaf margins not incurved at laminal part of leaf; lamina unistratose, locally bistratose, some marginal rows bi- to tristratose; basal cells elongate-rectangular, all walls equally thin and smooth, some hyaline cell rows reaching up to widest part of leaf. Calyptra mitrate, lobed, operculum conical, with obtuse, short tip, at capsule mouth 2 rows of round cells with thick walls and very narrow lumina *G. donniana* (9)
- 15 Lamina in transverse section bistratose to locally tristratose, cells to apex isodiametric with bulging exterior walls; cells at leaf base shortly rectangular or nearly quadrate, with smooth walls, at margin transverse walls incrassate; costa in transverse section markedly prominent in laminal part, somewhat angulate, recessed in a furrow. Calyptra cucullate, operculum conical, beak short, obtuse *G. alpestris* (1)
- 15* Lamina in transverse section unistratose or locally bistratose, at laminal part of leaf some marginal cell rows bi- to tristratose, leaf apex consisting of uniform cells, exterior walls

in upper part of lamina markedly stronger than interior walls; cells at leaf base elongate-rectangular, with smooth walls, rarely slightly nodulose, at margin 2 rows of rectangular, hyaline cells, vanishing at widest part of leaf; costa in transverse section prominent in laminal part, rounded, not recessed in a furrow. Calyptra conical-mitrate, lobed, operculum conical, obtuse *G. incurva* (15)

(from 3*) *Capsules smooth; seta much longer than capsule, inclined*

16 Basal cells of all stem leaves elongate-rectangular, walls smooth, rarely slightly nodulose, 2 marginal rows of hyaline cells, vanishing at widest part of leaf; in transverse section lamina unistratose or partly bistratose, at laminal part of leaf some marginal rows bi- to tristratose, leaf apex consisting of uniform cells, exterior walls in upper part of lamina markedly stronger than interior walls. At capsule mouth several rows of rounded cells; calyptra conical-mitrate, lobed, operculum conical, obtuse *G. incurva* (15)

16* Basal cells of upper stem leaves elongate-rectangular from costa to margin, walls thin, smooth, transverse walls incrassate at margin; basal cells of lower stem leaves elongate-rectangular near costa, towards margin becoming shortly rectangular or quadrate, walls smooth, transverse walls incrassate; all leaves with 1 marginal row of hyaline cells, vanishing at widest part of leaf; in transverse section lamina completely unistratose or partly bistratose, or completely bistratose in upper part, cells at leaf apex differentiated. At capsule mouth 1 row of transversely rectangular cells; calyptra cucullate, operculum conical, obtuse *G. sessitana* (28)

(from 2*) *Capsules smooth; seta erect, curved or S-shaped, slightly longer than the capsule*

17 Seta erect, slightly longer than the capsule; leaves from broad-ovate base lingulate with rounded apex or lanceolate with acute apex; hair point slightly denticulate, rarely strongly denticulate; basal paracostal cells elongate-rectangular, walls slightly nodulose or smooth, cells at margin short-rectangular; costa in dorsal view indistinct in upper part of leaf, in transverse section near the apex the 2 guide cells hardly differing from lamina cells overlying costa on ventral side. Calyptra mitrate, operculum conical, beak long, straight *G. tergestina* (29)

17* Seta curved or S-shaped, slightly longer than the capsule 18

18 Seta curved, slightly longer than the capsule 19

18* Seta S-shaped, slightly longer than the capsule 20

19 Basal cells elongate-rectangular from costa to margin, all walls equally thin and smooth, some hyaline cell rows ascending to widest part of leaf, lamina cells there short-rectangular, with sinuose walls; costa in transverse section broadly rounded dorsally at leaf base, rounded and smooth at laminal part, with hydroids from insertion to upper laminal part. Calyptra mitrate, lobed, operculum conical, with obtuse, short tip *G. donniana* (9)

19* Paracostal cells at leaf base elongate-rectangular, walls mostly smooth, near margin 3–4 rows of narrowly rectangular, hyaline, thin-walled cells, gradually vanishing, the outermost



△ *G. anodon* (2). Michael Lüth



△ *G. montana* (20). Michael Lüth

row ascending to above widest part of leaf where the cells become short-rectangular to quadrate; lamina cells there rectangular or elongate-rectangular, walls strikingly or only weakly sinuose; costa in transverse section rounded dorsally at leaf base, strongly prominent dorsally in laminal part of leaf, occasionally weakly mamillate, hydroids present from base to mid-leaf, costal cells uniform in upper part of leaf. Calyptra mitrate, beak conical, obtuse

..... *G. elongata* (11)

- 20 Leaves from broad-ovate base lingulate with rounded apex or lanceolate with acute apex, hair point slightly denticulate, rarely strongly denticulate; basal paracostal cells elongate-rectangular, walls slightly nodulose or smooth, at margin short-rectangular; costa in dorsal view indistinct in upper part of leaf, in transverse section the 2 guide cells hardly differing from lamina cells on ventral side of costa. Calyptra mitrate, operculum conical, beak long, straight. *G. tergestina* (29)

20* Characters different 21

- 21 Leaves from short wide base obovate, concave, spoon-like, in transverse section broadly keeled in laminal part of leaf, lamina unistratose or at leaf apex partly bistratose, rarely with a marginal bistratose cell row; cells uniformly isodiametric; basal cells short-rectangular or quadrate from costa to margin, walls smooth. Calyptra mitrate, operculum conical, mamillate. Peristome well developed. *G. plagiopodia* (25)

- 21* Leaves ovate or broad-lanceolate from elongate base, in transverse section keeled in laminal part of leaf, lamina unistratose or locally bistratose, 1 or 2 marginal rows bistratose; cells in upper part of leaf narrow and twice as high as wide [(viewed in section)]; basal paracostal cells elongate-rectangular, rectangular or quadrate towards the margin, walls smooth. Calyptra mitrate, lobed, fugacious, operculum convex, with short tip. Peristome not developed *G. anodon* (2)

(from 1*) *Capsule wrinkled or ribbed*

- 22 Capsule wrinkled after dehiscence, seta curved, short; leaves spatulate, markedly narrowed at insertion, widest above mid-leaf, apex rounded, hyaline to variable extent, basal cells from

- costa to margin elongate-rectangular, walls smooth; in transverse section leaf at insertion and in leaf base concave, in laminal part keeled, margin unistratose throughout, plane or slightly recurved in upper part of lamina; costa passing through hyaline apical part of leaf and excurrent in a faintly denticulate hair point. Calyptra cucullate, operculum conical, beak short, obtuse *G. crinita* (6)
- 22* Capsule ribbed, seta curved; other characters different 23
- 23 Costa in transverse section at leaf base near insertion with a variable number of 6–8 ventral cells, only 2–4 of them guide cells, dorsally with an additional 2–3 cells with wide lumina; the other costal cells nearly uniform, neither stereids nor hydroids present; lamina bistratose in upper part, mostly with scattered hemispherical papillae, rarely smooth. Calyptra mitrate, lobed, conical, operculum conical, beak long, straight *G. elatior* (10)
- 23* Costa in transverse section at leaf base near insertion with 8 or fewer ventral cells, all of which are guide cells; other characters different 24
- 24 Costa in transverse section at insertion with 8 guide cells 25
- 24* Costa in transverse section at insertion with 6 or fewer guide cells 27
- 25 Costa in transverse section on dorsal side strongly winged in upper part of leaf, costal cells

▽ *G. muehlenbeckii* (21). Michael Lüth

▽ *G. crinita* (6). Michael Lüth



- in winged part uniform, hydroids lacking throughout; ventral walls of costal cells markedly thickened; margin on one side revolute from insertion to upper half of laminal part, recurved on the opposite side; leaf apex sharply dentate, hair point lacking. Calyptra mitrate, operculum conical, beak long, oblique. *G. ramondii* (27)
- 25* Costa in transverse section not winged. 26
- 26 Costa in transverse section on dorsal side rounded throughout; basal paracostal cells rectangular or elongate-rectangular, walls smooth or slightly nodulose, basal marginal cells isodiametric or short-rectangular, walls smooth; margin on one side revolute from base to mid-leaf. Propagules developed on the dorsal side of leaf base. Calyptra mitrate, operculum conical, beak long *G. lisae* (17)
- 26* Costa in transverse section on dorsal side at leaf base broadly rounded, reniform in upper part of leaf, slightly angulate or uneven; basal paracostal cells markedly elongate, walls incrassate, nodulose or thin, smooth, towards margin several rows of short-rectangular or quadrate cells with incrassate walls forming a sharply contrasting band; margin revolute on one side from insertion to mid-leaf, recurved on the opposite side; propagules lacking. Calyptra mitrate, operculum with long, straight beak *G. decipiens* (7)
- 27 Costa in transverse section at insertion with 6 guide cells 28
- 27* Costa in transverse section at insertion with less than 6 guide cells. 30
- 28 Costa in transverse section in upper part of leaf mostly winged or angulate dorsally, rarely rounded; leaves lanceolate from a broadly ovate base, slightly narrowed at insertion, asymmetric, the lower third of the narrow side of the leaf markedly rounded in outline, the broad side nearly straight; margin recurved on the larger, rather straight side from insertion to above mid-leaf, margin of the rounded side plane, only slightly recurved in mid-leaf, plane in upper part; basal paracostal cells elongate-rectangular, walls nodulose, near margin short-rectangular or quadrate, walls smooth, at margin several rows of hyaline cells. Propagules developed on dorsal and ventral sides of leaf base. Calyptra conical-mitrate, lobed, operculum conical, beak long, straight. *G. muehlenbeckii* (21)
- 28* Costa in transverse section dorsally rounded throughout, other characters different 29
- 29 Costa in transverse section on dorsal side rounded throughout; basal paracostal cells rectangular or elongate-rectangular, walls smooth or slightly nodulose, basal marginal cells isodiametric or short-rectangular, walls smooth; margin on one side recurved from base to mid-leaf. Propagules developed on the dorsal side of leaf base. Calyptra mitrate, operculum conical, beak long *G. lisae* (17)
- 29* Costa in transverse section on dorsal side at leaf base broadly rounded, reniform in upper part of leaf, slightly angulate or uneven; basal paracostal cells markedly elongate, walls incrassate, nodulose or thin, smooth, towards margin several rows of short-rectangular or quadrate cells with incrassate walls forming a sharply contrasting band; margin revolute on one side from

- insertion to mid-leaf, recurved on the opposite side; propagules lacking. Calyptra mitrate, operculum with long, straight beak *G. decipiens* (7)
- 30 Costa in transverse section at insertion with 4 guide cells 31
- 30* Costa in transverse section at insertion with 4 guide cells of which the outer 2 are transitional with the lamina cells 37
- 31 Basal cells with smooth walls throughout 32
- 31* Paracostal basal cells with nodulose walls, marginal basal cells with smooth walls 34
- 32 Costa in transverse section at insertion and at leaf base with 4 guide cells and with an additional 1–3 cells on the dorsal side smaller than the guide cells but larger than surrounding costal cells; margin recurved on one side from insertion to mid-leaf. Propagules developed on dorsal and ventral sides of leaf base. Calyptra mitrate, lobed, operculum obliquely rostrate, rarely straight *G. trichophylla* (31)
- 32* Characters different 33
- 33 Lamina markedly striate in surface view; costa in dorsal view strikingly stout, narrowing at leaf apex, in transverse section dorsally rounded, prominent, exterior cell walls bulging; leaf margins plane in basal and transitional parts; lamina unistratose with several bistratose patches [appearing as ridges in surface view], some marginal rows [at least] bistratose, exterior walls bulging. Calyptra cucullate, lobed, operculum conical, beak long, oblique *G. nutans* (22)
- 33* Lamina not striate in surface view; costa in dorsal view not strikingly stout, in transverse section rounded, but not prominent, exterior cell walls not bulging; margin on one side recurved from insertion or leaf base, on the opposite side recurved from above transitional zone to mid-leaf; lamina unistratose, rarely with bistratose patches, some marginal cell rows bi- or tristratose, exterior walls not bulging. Calyptra mitrate, operculum conical, beak of variable length, straight or oblique *G. pulvinata* (26)
- 34 Cells at leaf base with strikingly nodulose walls; costa in transverse section from transitional zone to leaf apex with 2 narrow, elliptical guide cells arranged obliquely to the plane of the lamina [and forming an angle]; stem leaves arranged in tiers. Propagules developed on dorsal side of leaf base. Calyptra mitrate, lobed, operculum conical, beak long, straight *G. meridionalis* (19)
- 34* Characters different 35
- 35 Costa in transverse section in upper part of leaf mostly winged or angulate dorsally, rarely rounded; leaves lanceolate from a broadly ovate base, slightly narrowed at insertion, asymmetric, the lower third of the narrow side of the leaf markedly rounded in outline, the broad side nearly straight; a weak fold present near the costa on one side at leaf base; margin recurved on the larger, rather straight side from insertion to above mid-leaf, margin of the narrower, rounded side plane, only slightly recurved in mid-leaf, plane in upper part.

- Propagules developed on dorsal and ventral sides of leaf base. Calyptra conical-mitrate, lobed, operculum conical, beak long, straight *G. muehlenbeckii* (21)
- 35* Characters different 36
- 36 Leaves lanceolate from ovate base, tapering to acuminate apex, hair point slightly denticulate, rarely lacking; margin recurved on one side of leaf from insertion or leaf base to mid-leaf, sometimes slightly recurved on the opposite side; costa in transverse section dorsally flat at insertion and at leaf base, rounded in laminal part of leaf, with a group of large hydroids at insertion and at leaf base, extending as a band from transitional to apical part of leaf, rarely transformed to substereids; exterior walls of dorsal costal cells smooth, markedly incrassate. Propagules developed on dorsal side of leaf base. Calyptra mitrate, operculum conical, beak long, straight. *G. dissimulata* (8)
- 36* Leaves elliptical, widest at mid-leaf, apex obtuse, hair point of variable length, nearly smooth; margin recurved on both sides from below to above mid-leaf, rarely only on one side; costa in transverse section dorsally rounded, with a group of hydroids at insertion and at leaf base, vanishing below apical part; dorsal costal cells at leaf base mamillate, smooth in laminal part of leaf, not incrassate. Propagules unknown. Calyptra cucullate, operculum convex, with short, obtuse tip *G. orbicularis* (23)
- (from 30*) *Capsules ribbed; costa in transverse section at insertion with 4 guide cells of which the outer 2 are transitional with the lamina cells*
- 37 Cushions dense, with young shoots catenulate [originating from old stems]. Stem with narrow central strand of thin-walled cells, contrasting sharply with the incrassate, orange-tinged cortical cells. Leaves lanceolate from ovate, often orange-tinged base, [asymmetric,] one side rounded in outline, opposite side straight, margin of the straight side recurved from leaf base to widest part of leaf; basal paracostal cells elongate-rectangular, walls incrassate, nodulose, rarely nearly smooth, at margin 2 rows of rectangular hyaline cells with smooth walls, in transitional part lamina cells rectangular, incrassate, sinuose, in upper part isodiametric; costa in transverse section rounded at leaf base, prominent in laminal part, exterior walls of dorsal costal cells smooth. Calyptra mitrate, lobed, operculum conical, beak straight, obtuse *G. funalis* (12)
- 37* Cushions without catenulate young shoots. Stem with central strand, cortical cells not orange-tinged. Leaves not orange-tinged at base, lanceolate or broadly lanceolate, margin of the broader side recurved or revolute from leaf base to above transitional zone, weakly recurved on the opposite side; basal leaf cells elongate-rectangular from costa to margin, walls nodulose or smooth, with thin or thick walls, at margin 2 or 3 rows of shorter hyaline cells, vanishing above leaf base, in laminal part cells rectangular, walls strongly or weakly sinuose, arranged in strict, vertical rows parallel to costa, in apical part cells short-rectangular, walls sinuose; costa in transverse section rounded or triangular at leaf base, prominent in laminal part, exterior walls of dorsal costal cells occasionally mamillately bulging. Calyptra mitrate, lobed, operculum conical, beak of variable length, obtuse *G. fuscolutea* (13)



△ *G. elatior* (15). Michael Lüth

Key to plants without sporophytes

Plants should be examined in moist conditions.

- 1 Costa in transverse section at leaf base close to insertion with a variable number of 8 or more than 8 ventral cells, most of them guide cells 2
- 1* Costa in transverse section at leaf base close to insertion with a definite number of 8 or less than 8 ventral cells, all of them guide cells 5
- 2 Costa in dorsal view distinct from leaf base to apex; costa in transverse section at leaf base near insertion enlarged usually on both sides by additional layers of cells that form a transition with lamina cells, and with 2–3 additional cells dorsal to the guide cells and larger than the surrounding costal cells, the other costal cells nearly uniform, neither stereids nor hydroids present; lamina bistratose in upper part, [mostly] with scattered hemispherical papillae, rarely smooth *G. elatior* (15)
- 2* Costa in dorsal view indistinct in laminal part of leaf 3
- 3 Leaf base short, ca 1/5 of leaf length, half clasping the stem, in the sheathing part cells close to margin transversely oval, transverse walls thicker than longitudinal walls; margin unistratose from base almost to apex; in laminal part of leaf guide cells recessed in a shallow furrow, with markedly incrassate ventral cell walls *G. laevigata* (16)
- 3* Leaf base long, ca 1/3 of leaf length; other characters different. 4
- 4 Leaf apex broadly rounded, never with hair point; costa in transverse section consisting of uniform cells, never with hydroids. *G. unicolor* (32)
- 4* Leaf apex narrowly rounded, with hair point of variable length; costa cells in transverse section differentiated, hydroids present *G. ovalis* (24)

(from 1*) *Costa in transverse section at leaf base close to insertion with a definite number of 8 or less than 8 ventral cells, all of them guide cells*

- 5 Costa in transverse section at leaf base close to insertion with 8 guide cells 6
- 5* Costa in transverse section at leaf base close to insertion with 6 or less than 6 guide cells . . . 12

- 6 Leaves with inflexed margins in laminal part. 7
- 6* Leaves keeled in laminal part. 9

- 7 Leaves from broad-ovate base lingulate with rounded apex or lanceolate with acute apex, hair point slightly denticulate, rarely strongly denticulate; basal paracostal cells elongate-rectangular, walls slightly nodulose or smooth, cells at margin short-rectangular; costa in dorsal view indistinct in upper part of leaf, in transverse section near the apex the 2 guide cells hardly differing from lamina cells overlying costa on ventral side *G. tergestina* (29)
- 7* Characters different 8

- 8 Leaf apex broadly rounded, never with hair point; costa in transverse section consisting of uniform cells, never with hydroids. *G. unicolor* (32)
- 8* Leaf apex narrowly rounded, with hair point of variable length; costa cells in transverse section differentiated, hydroids present *G. ovalis* (24)

- 9 Leaf apex without hair point 10
- 9* Leaf apex with hair point 11

- 10 Leaves from ovate base lanceolate-lingulate with obtuse or cucullate apex; leaf margins at insertion and at leaf base sometimes with alar cells, in transverse section bistratose on both sides of leaf or on one side only; costa dorsally rounded in middle part of leaf, vanishing in the apex *G. atrata* (4)
- 10* Leaves from narrow base elongate-lanceolate, tapering to sharp, dentate apex, apical cells mostly chlorophyllose, rarely hyaline; margins in transverse section at insertion and at leaf base unistratose; costa in transverse section irregularly angulate above lower laminal part, winged in upper third of leaf, percurrent. *G. ramondii* (27)

- 11 Basal paracostal cells rectangular or elongate-rectangular, walls smooth or slightly nodulose, basal marginal cells isodiametric or short-rectangular, walls smooth; costa in transverse section dorsally rounded in laminal part of leaf, exterior walls with joint thickenings or smooth; propagules developed on dorsal side of leaf base *G. lisae* (17)
- 11* Basal paracostal cells markedly elongate, walls incrassate, nodulose or thin, nearly smooth, towards margin several rows of cells forming a sharply contrasting band of short-rectangular or quadrate cells with incrassate, smooth walls suggestive of alar cells; costa in transverse section on dorsal side at leaf base rounded, approximately reniform in upper part of leaf, rounded near apex, exterior walls of lamina cells lacking joint thickenings; propagules unknown *G. decipiens* (7)

- (from 5*) *Costa in transverse section at leaf base close to insertion with 6 or less than 6 guide cells*
- 12 *Costa in transverse section at leaf base close to insertion with 6 guide cells* 13
- 12* *Costa in transverse section at insertion with 4 guide cells, or with 4 guide cells of which the outer 2 are transitional with the lamina cells.* 20
- 13 *Leaves with inflexed margins in laminal part.* 14
- 13* *Leaves keeled in laminal part.* 15
- 14 *Leaves from broad-ovate base lingulate with rounded apex or lanceolate with acute apex, hair point slightly denticulate, rarely strongly denticulate; basal paracostal cells elongate-rectangular, walls slightly nodulose or smooth, at margin short-rectangular; costa in dorsal view indistinct in upper part of leaf, in transverse section near the apex the 2 guide cells hardly differing from lamina cells that overlie the costa on the ventral surface* *G. tergestina (29)*
- 14* *Leaves from ovate or elongate-ovate sheathing base narrowed to lanceolate lamina, thus forming rounded shoulder; leaf apex rounded, hair point denticulate; basal paracostal cells elongate-rectangular, walls nodulose, at margin rectangular or quadrate; costa in dorsal view indistinct in upper part of leaf, in transverse section the 2 guide cells clearly distinct from the lamina cells, the costa not overlain by lamina cells on ventral surface* *G. ovalis (24)*
- 15 *Costa in transverse section not rounded on dorsal side [or unevenly so]* 16
- 15* *Costa in transverse section [evenly] rounded on dorsal side* 19
- 16 *Costa in transverse section angulate or winged on dorsal side* 17
- 16* *Costa in transverse section unevenly [(irregularly)] rounded on dorsal side* 18
- 17 *Stem with central strand, central strand rarely lacking; costa in dorsal view uniformly broad above leaf base; leaves lanceolate from broad-ovate basal part, the lower third of the narrower side markedly rounded in outline, the wider side nearly straight, thus giving the leaf an asymmetrical appearance; margin on the rounded side plane to mid-leaf, there slightly recurved, on the straight side recurved from insertion to mid-leaf; propagules developed on the dorsal and ventral side of leaf base* *G. muehlenbeckii (21)*
- 17* *Stem always without central strand; costa in dorsal view stout from insertion to upper half of laminal part, becoming thinner in leaf apex; leaves lanceolate from elongate-ovate base, at insertion slightly narrowed, symmetrical in appearance; margin on one side recurved from insertion to mid-leaf; multicellular propagules developed at leaf apices, leaving the apex modified after their release.* *G. hartmanii (14)*
- 18 *Basal paracostal cells markedly elongate, walls incrassate, nodulose or thin, nearly smooth, towards margin several rows of cells forming a sharply contrasting band of short-rectangular or quadrate cells with incrassate, smooth walls suggestive of alar cells; costa in dorsal view stout, uniformly wide from insertion to upper third of laminal part, becoming thinner in leaf apex, but distinct, percurrent; costa in transverse section on dorsal side at leaf base broadly*



△ *G. ovalis* (24). Michael Lüth



△ *G. lisae* (17). Sam Bosanquet

- rounded, reniform in upper part of leaf, slightly angulate or uneven, [irregular in outline], rounded at apex *G. decipiens* (7)
- 18* Basal paracostal cells elongate-rectangular, with nodulose walls, transverse walls markedly thin, often oblique, cells near margin quadrate or rectangular, walls smooth, incrassate, sometimes hyaline to widest part of leaf, not suggestive of angular cells; costa in dorsal view nearly uniformly wide, slightly narrower at insertion, indistinct in upper part of leaf, percurrent; costa in transverse section rounded dorsally at insertion and leaf base, in lower laminal part of leaf broadly rounded, mostly uneven, [irregular in outline], rounded in upper part *G. longirostris* (18)
- 19 Basal paracostal cells elongate-rectangular, walls mostly smooth, rarely slightly nodulose, towards margin shorter, 1 or 2 rows of marginal cells rectangular, hyaline, vanishing in transitional zone; costa in transverse section at insertion and at leaf base with 4 guide cells and with an additional 1–3 cells on the dorsal side smaller than the guide cells but larger than surrounding costal cells; exterior walls of lamina cells lacking joint thickenings; propagules developed on dorsal and ventral sides of leaf base *G. trichophylla* (31)
- 19* Basal paracostal cells rectangular or elongate-rectangular, walls smooth or slightly nodulose, basal marginal cells isodiametric or short-rectangular, walls smooth; costa in transverse section at insertion and at leaf base without additional cells on dorsal side of guide cells; exterior walls of lamina cells with joint thickenings or smooth; propagules developed on dorsal side of leaf base *G. lisae* (17)
- (from 12*) *Costa in transverse section at insertion with 4 guide cells, or with 4 guide cells of which the outer 2 are transitional with the lamina cells*
- 20 Costa in transverse section at insertion with 4 guide cells 21
- 20* Costa in transverse section at insertion with 4 guide cells of which the outer 2 are transitional with the lamina cells 34
- 21 Lamina in transverse section mamilliose or papillose 22
- 21* Lamina in transverse section smooth. 23

- 22 Lamina in transverse section bi- to tristrate, exterior cell walls bulging on ventral and dorsal sides; lamina in surface view not longitudinally striate, costa recessed in a furrow in upper part of leaf; in some leaves secondary costae developed on one or both sides; propagules unknown. *G. caespiticia* (5)
- 22* Lamina in transverse section unistrate with bistrate patches, exterior cell walls papillose and with joint thickenings on ventral and dorsal sides; lamina in surface view longitudinally striate, costa not recessed in a furrow; secondary costae absent; propagules developed at leaf apices, leaving the apex modified after their release *G. anomala* (3)
- 23 Costa in transverse section from transitional zone to leaf apex with 2 narrow, elliptical guide cells arranged obliquely with respect to the plane of the lamina [and forming an angle]; basal cells elongate-rectangular, with incrassate, nodulose walls, at margin rectangular in 3–4 rows, hyaline, with smooth walls, progressively vanishing at widest part of leaf; in transitional zone cells rectangular with strongly sinuose walls, marginal cells isodiametric in several rows; margin recurved on one side from insertion to upper part of leaf, on the opposite side from mid-leaf to upper part of leaf, at leaf apex both sides plane; propagules developed on dorsal side of leaf base. *G. meridionalis* (19)
- 23* Characters different 24
- 24 Basal cells short-rectangular or rectangular at least beside costa 25
- 24* Basal cells elongate-rectangular from costa to margin or at least beside costa. 27
- 25 Leaf margins from base to apex becoming gradually more incurved; lamina bistrate, rarely unistrate beside costa, lamina cells short-rectangular, [often] higher than wide [(viewed in section)], exterior cell walls smooth, margin at leaf base unistrate, in laminal part bistrate, towards apex even 3- to 4-stratose; costa in transverse section prominent on dorsal side in laminal part, narrowly channelled on ventral side *G. montana* (20)
- 25* Characters different 26
- 26 Costa in transverse section dorsally flat at insertion and at leaf base, with a broad group of hydroids, extending as a band from transitional to apical part of leaf, exterior walls of dorsal costal cells markedly incrassate; costa in dorsal view of nearly equal width from base to leaf apex; basal cells except paracostal cells broad short-rectangular, walls incrassate, sinuose, rarely smooth; lamina in transverse section unistrate, rarely with bistrate patches, occasionally exterior walls with joint thickenings; propagules developed on dorsal side of costa at leaf base *G. dissimulata* (8)
- 26* Costa in transverse section dorsally rounded at insertion and at leaf base, with a median group of hydroids, disappearing below apex; exterior cell walls of dorsal costa cells bulging; costa in dorsal view strikingly stout, narrowing at leaf apex; basal cells short-rectangular, with smooth walls; lamina in transverse section bistrate with unistrate patches in upper part, joint thickenings absent; propagules unknown. *G. nutans* (22)

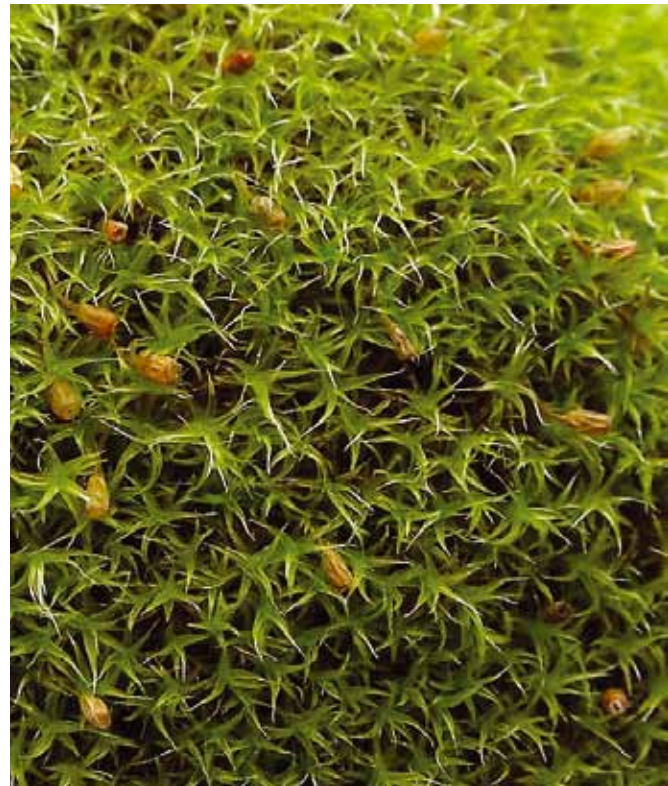
- 27 Basal cells elongate-rectangular near costa, [usually short towards margin]. 28
- 27* Basal cells elongate-rectangular from costa to margin 32

- 28 Costa in transverse section in upper part of leaf winged or angulate dorsally, rarely rounded; leaves lanceolate from a broadly ovate base, slightly narrowed at insertion, asymmetric, the lower third of the narrow side of the leaf markedly rounded in outline, the broad side nearly straight; a weak fold present on one side of leaf base close to the costa; margin recurved on the larger, rather straight side from insertion to above mid-leaf, margin of the rounded side plane, only slightly recurved at mid-leaf, both margins plane in upper part; basal paracostal cells elongate-rectangular, walls nodulose, near margin short-rectangular or quadrate, walls smooth, at margin several rows of hyaline cells; propagules developed on dorsal and ventral sides of leaf base *G. muehlenbeckii* (21)
- 28* Costa in transverse section in upper part of leaf rounded dorsally, other characters different. 29

- 29 Leaves tapering from above leaf base to lanceolate laminal part 30
- 29* Leaves not tapering from above leaf base to lanceolate laminal part 31

▽ *G. anomala* (3). Michael Lüth

▽ *G. meridionalis* (19). Michael Lüth



- 30 Basal paracostal cells elongate-rectangular, walls mostly smooth, rarely slightly nodulose, transverse walls not oblique, all cell walls of equal thickness, cells towards margin shorter, 1 or 2 rows of marginal cells rectangular, hyaline, vanishing in transitional zone; costa in transverse section at insertion and at leaf base with 4 guide cells and with an additional 1–3 cells on the dorsal side smaller than the guide cells but larger than surrounding costal cells; propagules developed on dorsal and ventral sides of leaf base *G. trichophylla* (31)
- 30* Basal paracostal cells elongate-rectangular, with nodulose walls, transverse walls often oblique, markedly thin, cells near margin quadrate or rectangular, walls smooth, incrassate, sometimes hyaline to widest part of leaf; costa in transverse section at insertion and at leaf base lacking additional cells larger than surrounding costal cells and smaller than the guide cells; propagules unknown *G. longirostris* (18)
- 31 Leaves from short, ovate base lanceolate or broad-lanceolate, widest below mid-leaf, margin on one side recurved from insertion or leaf base, on the opposite side recurved from above transitional zone to mid-leaf; some marginal cell rows in transverse section bi- or sometimes tristratose; basal paracostal cells rectangular, walls smooth *G. pulvinata* (26)
- 31* Leaves elliptical, widest at mid-leaf; margin recurved on both sides from below to above mid-leaf, rarely only on one side; marginal cell rows in transverse section often unistratose at upper part of leaf, at most 1 bistratose cell row on one side near apex; basal paracostal cells elongate-rectangular, walls nodulose *G. orbicularis* (23)
- 32 Basal cells elongate-rectangular, all walls equally thin and smooth, marginal rows [of hyaline cells] progressively vanishing, the outmost row reaching the transitional zone, thus forming a boundary between the hyaline cells and the more incrassate, chlorophyllose lamina cells running in an oblique line from costa to margin; margin plane at leaf base on both sides; costa with hydroids from insertion to upper laminal part *G. donniana* (9)
- 32* Basal cells elongate-rectangular, other characters different 33
- 33 Basal cells with smooth walls; in upper stem leaves basal cells at margin elongate-rectangular, walls thin, transverse walls incrassate, in lower stem leaves basal cells at margin short-rectangular or quadrate, transverse walls incrassate, all leaves with one marginal row of hyaline cells, vanishing at widest part of leaf; in transverse section lamina unistratose with some bistratose patches, or sometimes partly or completely bistratose in upper part *G. sessitana* (28)
- 33* Basal cells of all stem leaves with slightly nodulose or smooth walls; near margin 3–4 rows of narrowly elongate-rectangular, hyaline, thin-walled cells, gradually vanishing, the outermost row ascending to above widest part of leaf with a few small quadrate incrassate cells; in transverse section lamina mostly unistratose, rarely with bistratose patches *G. elongata* (11)

(from 20*) *Costa in transverse section at insertion with 4 guide cells of which the outer 2 are transitional with the lamina cells*

- 34 Lamina bistratose or with tristratose patches, costa recessed in a furrow 35
- 34* Lamina unistratose or with bistratose patches, costa not recessed in a furrow 36

- 35 Exterior walls of lamina cells in transverse section mamillose protuberant on dorsal and ventral sides; in dorsal view margins of lamina and margins of plicae appearing weakly undulate, outline of costa strongly undulate; some leaves with secondary costae at leaf base on one or both sides of the costa. *G. caespiticia* (5)
- 35* Exterior walls of lamina cells in transverse section bulging [but not protuberant] on dorsal and ventral sides; in dorsal view margins of lamina and margins of plicae appearing smooth, outline of costa weakly undulate; all leaves lacking secondary costae *G. alpestris* (1)

- 36 Basal cells rectangular to quadrate from costa to margin 37
- 36* Basal paracostal cells elongate-rectangular 38

- 37 Leaves from short wide base obovate, concave, spoon-like, in transverse section widely keeled at laminal part of leaf; cells at apex isodiametric; costa in dorsal view narrow at leaf base, broadened in laminal part, enlarged at apex, excurrent through hyaline apex of leaf into a denticulate hair point, in mucous leaves not reaching apex. *G. plagiopodia* (25)
- 37* Leaves ovate to broad-lanceolate from elongate base, not spoon-like or concave, in transverse section keeled at laminal part of leaf; cells in upper part of leaf narrow and twice as high as wide [(viewed in section)]; costa in dorsal view narrow at leaf base, strikingly enlarged at apex, excurrent in all leaves, leaf apex not hyaline, hair point weakly denticulate *G. anodon* (2)

- 38 Costa in transverse section above widest part of leaf with 2 narrow elliptical guide cells arranged obliquely with respect to the plane of the lamina [and forming an angle] 39
- 38* Costa in transverse section above widest part of leaf with 2 round guide cells aligned with the plane of the lamina. 40

- 39 Cushions dense, with catenulate young shoots [originating from old stems]. Stem with narrow central strand of thin-walled cells, contrasting sharply with the incrassate, orange-tinged cortical cells. Leaves lanceolate from ovate, often orange-tinged base, [asymmetric,] one side rounded in outline, opposite side straight, margin of the straight side recurved from leaf base to widest part of leaf; basal paracostal cells elongate-rectangular, walls incrassate, nodulose, rarely nearly smooth, at margin 2 rows of rectangular hyaline cells with smooth walls, in transitional part lamina cells rectangular, incrassate, sinuose, in upper part isodiametric; exterior walls of dorsal costal cells smooth *G. funalis* (12)
- 39* Cushions without catenulate young shoots. Stem with central strand, cortical cells not incrassate, not orange-tinged. Leaves lanceolate or broadly lanceolate, not orange-tinged at base, margin of the wider side recurved or revolute from leaf base to above transitional

- zone, weakly recurved on the opposite side; basal leaf cells elongate-rectangular from costa to margin, walls nodulose or smooth, with thin or thick walls, at margin 2 or 3 rows of shorter hyaline cells, vanishing above leaf base, in laminal part cells rectangular, walls strongly or weakly sinuose, arranged in strict, vertical rows parallel to costa, in apical part cells short-rectangular, sinuose; exterior walls of dorsal costal cells occasionally mamillolesely bulging *G. fuscolutea* (13)
- 40 Plants in dry condition with leaves crispate, spirally twisted around stem; lower part of stem dark brown, stem tip mostly yellowish-green; leaves elongate-lanceolate from ovate base, weakly asymmetric, one side nearly straight, the opposite side rounded in outline, apex acute, mucicous or with short smooth hair point; multicellular, round, brown propagules developed on the dorsal side of costa above leaf base; basal cells elongate-rectangular, walls incrassate, mostly nodulose; lamina in transverse section unistratose, margins unistratose or at apex 1–2 rows bistratose, exterior walls of lamina cells bulging; costa in dorsal view forming an S-shaped curve from insertion to apex, percurrent; costa in transverse section rounded dorsally, often hyaline, dorsal costal cells bulging or mamilloles *G. torquata* (30)
- 40* Characters different 41
- 41 Leaves spatulate, markedly narrowed at insertion, widest above mid-leaf, apex rounded, hyaline to a variable extent, hair point lacking or of variable length, weakly denticulate; basal cells elongate-rectangular, at margin short-rectangular or quadrate with incrassate transverse walls, walls smooth; in transverse section margin and lamina unistratose, leaf at insertion and at leaf base concave, in laminal part keeled, margin plane or slightly recurved in upper part of leaf; costa in dorsal view weak in lower part of leaf, enlarged in upper part, passing through hyaline apical part of leaf into a hair point *G. crinita* (6)
- 41* Characters different 42
- 42 Basal cells elongate-rectangular, walls smooth, rarely slightly nodulose, 2 marginal rows of rectangular hyaline cells, vanishing at widest part of leaf; leaf in transverse section at insertion and at leaf base concave, keeled at laminal part; margin plane or near insertion recurved on one side; costa in dorsal view of nearly uniform width throughout, slightly weaker at leaf base, ceasing below apex, in transverse section consisting of uniform cells, exterior walls of costal cells markedly more incrassate than interior walls; in upper part of leaf dorsal costal cells longer than adjacent lamina cells *G. incurva* (15)
- 42* Basal cells elongate-rectangular, walls slightly nodulose, mostly smooth, near margin 3–4 rows of narrowly elongate-rectangular, hyaline, thin-walled cells, gradually vanishing, the outermost row ascending to above broadest part of leaf with a few small quadrate incrassate cells; leaf in transverse section at insertion and at leaf base on one side concave, on the other side plicate near the costa, lower laminal part keeled, upper part narrowly so; on the straighter side margin recurved from insertion to mid-leaf; costa in dorsal view weak at leaf base, stout in laminal part, reaching apex, in transverse section with differentiated cells at

apex, all cell walls of uniform thickness; in upper part of leaf dorsal costal cells of the same length as adjacent lamina cells *G. elongata* (11)

Acknowledgement

I would like to thank Tom Blockeel for his essential assistance with this translation.

Peter Erzberger

Belziger Straße 37, D-10823 Berlin, Germany
(e erzberger.peter@googlemail.com)

References

Maier, E. (2009). *Grimmia* in Europa: ein Bestimmungsschlüssel. *Herzogia* 22, 229–302.
Maier, E. (2010). The genus *Grimmia* Hedw. (Grimmiaceae, Bryophyta) – a morphological–anatomical study. *Boissiera* 63, 3–377.

Glossary

acuminate tapering to a long narrow point
angulate angled, or having angles or corners
annulus a ring of cells at the capsule mouth
bistratose 2 cells thick
catenulate chain-like
chlorophyllose containing chlorophyll
cortical referring to the outer layer of cells in a stem
costa nerve
crispate curved and twisted
cucullate hood-shaped, and (of calyptra) split down one side only (cf. *mitrate*)
dentate strongly toothed
denticulate finely toothed
dorsal lower surface of a leaf facing away from the stem (cf *ventral*)
fugacious readily falling away
hyaline colourless and transparent
hydroids specialized, elongate water-conducting cells in the nerve; with thin, delicate walls in section
incrassate thick-walled or thickened
insertion (of the leaf) the point where the base of the leaf is attached to the stem
isodiametric as long as wide
lamina leaf blade (upper part)
lanceolate lance-/spear-shaped
lingulate tongue-shaped
lumen cell cavity (pl. *lumina*)
mamillate convex with a short, blunt point
mamillose (of cells) bulging, with a protuberance of a uniformly thickened cell wall into which the cell lumen extends (cf *papillose*)

mitrate shaped like a bishop’s cap, conical, with an entire or regularly lobed base (cf *cucullate*)
muticous lacking a distinct point or hair at the apex
nodulose minutely knobbed
obovate egg-shaped, widest above the middle (cf *ovate*)
operculum capsule lid
ovate egg-shaped, widest below the middle (cf *obovate*)
papillose with local thickenings of the cell wall (cf *mammillose*)
paracostal cells cells of the leaf blade close to and alongside the nerve
percurrent extending to the apex, but not beyond
plicate folded lengthwise, forming pleats and furrows
quadrate square
reniform kidney-shaped
revolute (of a leaf) strongly rolled backwards and under at the edges
rostrate beaked
sinuose wavy
spathulate spatula-shaped
stereids cells (especially in the nerve) that provide rigidity; usually occur in groups, are thick-walled and have very narrow cavities when seen in section
striate finely ridged
substereids similar to *stereids*, but not quite so thick-walled and with larger cavities
tristratose 3 cells thick
unistratose 1 cell thick
ventral upper surface of a leaf, facing the stem when the leaf is erect (cf *dorsal*)