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Introduction

The genus *Grimmia* Hedw. nomenclaturally dates from HEDWIG (1801). He described five species under *Grimmia* and only one, *Grimmia plagiopodia* Hedw., the type of the genus, remains in it today. Hedwig defined the genus *Grimmia* as follows: *"Peristomium simplex,* dentibus sedecim latiusculis, reflexibus; *Flores masculi* axillares gemmacei, terminales capituliformis in eadem planta" (HEDWIG, 1801). The first comprehensive description of *Grimmia,* as currently understood, appeared later with the issue of *Bryologia Europaea* of BRUCH, SCHIMPER & GUEMBEL (1837-1855). The fascicule of 1845(1-8) contains a detailed description of the characters that defined it, peristome characters included.

LANTZIUS-BENINGA (1844, 1850) initiated extensive studies on the peristomes of mosses (MAIER, 1999; MAIER & PRICE, 2005) with the intention of elaborating species-specific diagnostic characters. A few years later, LORENTZ (1867-1868), attempted studies on costal anatomy for the first time with the aim of finding stable correlations between costal characters and species. The findings of Lantzius-Beninga and Lorentz were widely used by Limpricht in *Die Laubmoose Deutschlands, Oesterreichs und der Schweiz* (LIMPRICHT, 1885-1889) for the descriptions of the moss species he treated therein. The definition of the genus *Grimmia* is given by LIMPRICHT (1889: 694, 722) as follows: "Peristom einfach, die sechzehn Zähne allermeist bis zur Insertion gesondert, immer nach dem Typus der Aplolepideen gebaut… Rippe vollständig, an der Bauchseite oberwärts mit zwei basalen Deutern", translated as "peristome haplolepidous, the sixteen teeth mostly separated down to the insertion, built always following the type of the Haplolepideae… costa complete, on the ventral side in upper part with two basal guide cells".

The description of the genus *Grimmia* given by LIMPRICHT (1889: 722-786), lists general characters such as a central strand present, seta twisted to the left (anticlockwise), calyptra not plicate, and operculum detaching without the columella. Despite its division into subgenera, the unity, or concept, of the genus itself is maintained based on Limpricht's defining characters. The subgenera are as follows:

- *Gasterogrimmia* Schimp.: capsules smooth, bilaterally symmetrical, seta mostly curved, shorter than the capsule, stomata present, calyptra mitrate (*Grimmia crinita* excluded).
- *Grimmia s. str.*: capsules smooth, radially symmetrical, seta mostly straight, longer than the capsule, stomata present, calyptra mostly mitrate.
- *Guembelia* Hampe: capsules smooth, radially symmetrical, seta straight, longer than the capsule, stomata lacking (*Grimmia caespiticia* excluded), calyptra cucullate.
- *Rhabdogrimmia* Limpr.: capsule ribbed, radially symmetrical, seta bent, longer than the capsule, stomata present, calyptra mitrate (*Grimmia orbicularis* excluded).

Limpricht was the first bryologist to recognize that plicae formation follows different developmental pathways in the different genera of the Bryales. The investigation of plicae developmental processes is discussed in a separate article (MAIER, 2004). The concept of *'Rhabdogrimmia'* circa LIMPRICHT (1889), defined by the possession of ribbed capsules, is used in this work.

This present work, in accordance to the definition of Limpricht from 1889, defines the genus *Grimmia* as a unity of fifty-one species. This study is based on the examination of morphological and anatomical characters of both the gametophyte and the sporophyte. Character traits are illustrated using a series of drawings of the examined specimens and type specimens for each of the recognised species (Figures 1-51).

The nomenclature follows CORLEY & al. (1981) and CROSBY & al. (1999). Names published after 1999 are presented in the form given by their authors. The abbreviations for the names of authors follow BRUMMITT & POWELL (1992) and those for bryological nomenclatural literature follow CROSBY (1999).

Important note.– The author is aware of the work of OCHYRA & al. (2003) but the proposed nomenclatural changes are not adopted herein.

Materials

The material used for the descriptions in this study consisted of 2800 specimens, including 274 types and 1150 specimens from E. Specimens came from ALTA, AUT, B, BM, BISH, BOL, BP, BR, CANM, CHR, COLO, E, F, FH, G, GOET, GLAM, GZU, HAL, HBG, H-BR, H-SOL, ILL, JE, KOCH, KRAM, L, LE, M, MA, MAK, MEL, MICH, MO, MW, NICH, NMLU, NMW, NY, PC, PMAE, PRE, RO, S, STU, TNS, U, UBC, UPS, US, W, WTU, WU, Z and ZT, from the following private herbaria: J. Bertram, T. L. Blockeel, J. Chavoutier, R. Düll, O. Dürhammer, P. Erzberger, J. and V. Geibel, J. P. Gruber, R. Lübenau, M. Lüth, H. van Melick, R. B. Pierrot, E. Sauer, A. Schäfer-Verwimp, M. Siegel, R. Skrzypczak, and from the author's own herbarium collection, partly now in G.

The choice of material investigated reflected the aim of representing the distribution of each of the 51 species of *Grimmia* recognised. The selection of specimens, to achieve a good geographic representation for each species, was based on *Index Muscorum* (WIJK & al., 1962) and the work of MUÑOZ & PANDO (2000). The careful study of type specimens and comparison of general specimens with the types permitted the establishment and testing of species concepts, as well as of the new synonyms proposed.

Note.– The type citations follow MUÑOZ & PANDO (2000), although in some cases these are different from the labels or label annotations associated with the specimens themselves.

Methods

The first impression of a *Grimmia* species is given by its growth form. Young shoots, which are in many cases useful for identification purposes, are best viewed in the internal part of the cushion and from the underside. Wetting induces the typical movement of the leaves and this can be seen under the dissecting microscope by placing a plant onto a drop of water. Development of sexual organs may influence the expression of cell patterns in the leaf base, therefore plants in the vegetative state should be chosen to obtain comparable and reproduceable results in morphological and anatomical investigations. The material is prepared by gently heating some plants in a solution of 1% or at most 2% KOH. This is a simple method that is used to soften dry or old material, to reconstitute the natural structure of the cells and cell patterns, to confer transparency on the cells and to ensure the stability of the tissues, thus preventing the shrinking of cells caused by the fixing agents.

Leaves which are not too young, from the upper stem, are carefully removed one by one to prevent damage to the tissue at the leaf base. To remove dirt from plants a fine, soft water-colour brush, is helpful. Transverse sections of the stem and the leaves are cut free-hand with a razor blade directly on the surface of the microscope slide. Comparable transverse sections are obtained only when the razor blade is placed in a perpendicular position and at right angles to the leaf axis. To obtain an instructive series of transverse sections two leaves are sufficient, which is an important advantage when investigating type material. One leaf is cut from the apex down to mid-leaf, the other from the insertion up to mid-leaf. The remainders can be kept with the resulting sections.

Capsules are prepared in the same manner. Comparable results are obtained by using mature and preferably operculate capsules. The softened capsule is cut lengthwise into two equal halves. The spores are removed with a fine spatula, the spore sac is carefully extracted, and the preparation cleaned with a brush and water to remove any remaining debris and spores. Finally, the rounded capsule base is cut off to flatten the capsule. Observed at the capsule base are the stomata. The dorsal and the ventral sides of the peristome should also be observed. As the peristome is highly transparent attention must be paid to correct focusing so that the papillosity of both the dorsal and ventral sides of the teeth can be seen. The operculum is cut longitudinally to observe the cell pattern. To accomplish longitudinal sections of peristome teeth and the teeth insertion point in the capsule wall (which clearly show the specific characters) it is necessary to make the sections as thin as possible, executed along the axis of the capsule.

Glossary

Commonly used terms are taken from MAGILL (1990), cited here with their English cross-reference numbers, and from SMITH (1978).

Capsule epidermis: smooth or ribbed (LIMPRICHT, 1889: 759), (MAIER, 2004: 52).

Capsule form: radially symmetrical (actinomorphic) (MAGILL, 1990: 18) or bilaterally symmetrical (zygomorphic) (MAGILL, 1990: 1154).

Cell wall thickenings seen in surface view:

- **sinuose** (MAGILL, 1990: 973) in transitional part of leaves, such as in *G. meridionalis* (Fig. 31.8), or *G. pygmaea* (Fig. 44.21);
- **nodulose** (MAGILL, 1990: 706) in the leaf base, such as in *G. decipiens* (Fig. 12.8) or *G. fuscolutea* (Fig. 18.17).

Cell wall thickenings seen in transverse sections of leaves:

- **bulging** exterior cell walls with uniform thickenings, such as in *G. alpestris* (Figs. 2.10-13);
- **mammillose** exterior cell walls with thickenings in the middle of the cells as in *G. caespiticia* (Fig. 9.13).

Costa channelled: form on ventral side, described as "hollowed out like a gutter and semi-circular in cross-section" (MAGILL, 1990: 201), determined as broadly channelled, or channelled, such as in *G. abyssinica* (Fig. 1.8), and *G. decipiens* (Figs. 12.13, 12.16).

Costa angulate: form of costa on dorsal side, seen in transverse section of leaf, such as in *G. hartmanii* (Fig. 20.14) or in *G. muehlenbeckii* (Fig. 33.12).

Costa prominent: form of costa on dorsal side, seen in transverse section of leaf; prominence is produced by contraction of the costa at the place of attachment of the two lamina halves, such as in *G. elatior* (Figs. 15.10, 15.19) or *G. nutans* (Figs. 36.8, 36.21).

Costa rounded: form of costa on dorsal side, expressed in breadth: thickness ratio, determined as broadly rounded ≈ 3-3,5:1 or rounded ≈ 1,5-2:1.

Diagnostic characters: are selected specific characters. The examination of a large number of specimens of a species brings to light the variability of characters initially thought to be specific because they were seen only in the species investigated. Such unstable characters are eliminated progressively by an ongoing selection process. The few remaining characters then may be considered to be specific (= diagnostic) and together enable the differentiation of one species from another.

Furrow: indentation formed by the two sides of the lamina inserted on the costa in the same direction before spreading, such as in *G. alpestris* (Fig. 2.11) or *G. sessitana* (Fig. 46.13).

Guide cells: large, vacuolated costal cells (MAGILL, 1990: 483) in the leaf costae. In *Grimmia* species the guide cells are ventrally arranged and their number is of taxonomic value ("Deuter", LORENTZ, 1867-1868: 374).

Hydroids: thin-walled costal cells arranged dorsally between the guide cells and stereids or substereids ("Begleiterzellen", LORENTZ, 1867-1868: 378). In younger leaves the walls are thin, in mature leaves cells are often star-shaped (vacuolate) with concave walls, appearing in bands or in groups.

Insertion of the leaf: the lowest row of cells at the leaf base, the inferior delimitation of a leaf, counterpart of "the place or line of attachement of a structure" (MAGILL, 1990: 572).

Insertion of the peristome: line of attachement of the peristome teeth to the capsule wall, to be observed on the inner side of the capsule orifice.

Joint thickenings: thickenings (DEGUCHI, 1979: 136), seen in transverse section of leaf, developed on both ends of vertical cell walls where the two cells come into contact, such as in *G. anomala* (Figs. 4.16, 4.17).

Lamina: part of leaf extending from above the leaf base to the apex, divided into the lower part of lamina, the upper part of lamina, and a short part in the leaf point designated as the apical part.

Leaf base: lowest part of leaf extending from insertion to the transitional part, generally the broadest part of leaf, mostly 1/3 to 1/4 of leaf length. Cell shape, especially of the elongate paracostal cells, is different from the cell shape above the transitional part.

Leaf keeled: description of spatial aspect, created by the position of lamina halves relative to the leaf axis, presented in a series of outlines of transverse leaf sections shown at low magnification, expressed in degrees, determined as broadly keeled >45°, keeled ≈ 45°, narrowly keeled <45°, spreading ≈ 90°.

Leaf form *in situ* (spatial aspect): the natural tridimensional form of a leaf in a wet state as it appears inserted on the stem, presented in a series of outlines of transverse leaf sections shown at low magnification.

Ochrea: upper part of vaginula (MAGILL, 1990: 721).

Seta, in dry state: seen in surface view the cells appear twisted from below left to above right, a general feature in the genus *Grimmia.* Extremely short setae are not twisted. Exceptions are noted in the chapter Taxonomic treatment.

Seta, in wet state: the bending of the seta is expressed by the terms arcuate, curved or inclined. Arcuate setae are bent over until the capsule touches the cushion (SAYRE, 1952: 256), curved setae are slightly bent and the capsule horizontally or obliquely turned, inclined setae are slightly deviated from the vertical position, such as in *G. elongata* (Fig. 16.3) or *G. sessitana* (Fig. 46.3).

Seta epidermal cells: the arrangement is a specific character observed in surface view. In general, the cells are turning from below left to above right.

Seta length: is measured without the vaginula.

Shoots: young shoots are slender elongate stems with reduced leaves. The catenulate young shoots, specific to *G. funalis* (Fig. 17.18) are an example of this.

Stereids: thick-walled cells, found in groups or bands in the costa (MAGILL, 1990: 1012).

Stratosity: cell layers in leaf base and lamina, described as unistratose, bistratose, tristratose, quadristratose, multistratose.

Striate: marked with ridges or fine lines (MAGILL, 1990: 1025).

Trabeculae: cross-bars formed from residual horizontal cell walls on the dorsal side of the peristome teeth, determined as broad as in *G. consobrina* (Fig. 10.14) and *G. funalis* (Fig. 17.14), as small as in *G. anomala* (Fig. 4.12), as thin as in *G. ramondii* (Fig. 45.13) and as wavy as in *G. dissimulata* (Fig. 13.14).

Transitional part of leaf: zone between the leaf base and leaf lamina, generally located in the broadest part of a leaf, where the elongate cells of leaf base with smooth or nodulose walls change to shorter cells of laminal part with mostly sinuose walls. At the same place, seen in dorsal view, the elongate costal cells change to short cells.

Generic description

Grimmia Hedw., Sp. Musc. Frond.: 75. 1801.

Type: *Grimmia plagiopodia* Hedw., Sp. Musc. Frond.: 78, tab. XV, fig. 6-13. 1801.

Gametophyte. Monoicous and dioicous, acrocarpous. ***Female plants:*** perichaetial leaves 6-9, the outer ones similar to the comal leaves, the inner ones shorter or longer, straight, concave, the tissue of the cells thin, the costae small; ***male plants:*** mixed with female plants or growing in separate cushions, perigonia bud-like, perigonial leaves 6, the 3 outer ones similar to the stem leaves, the inner ones ovate, concave, muticous, costa thin, antheridia mostly with paraphyses. ***Growth form:*** plants in dense or lax cushions, spreading, ascending to erect. ***Leaves:*** patent, recurved or incurved, lanceolate or elongate-lanceolate, concave or keeled, margins recurved or inflexed, apices muticous or with hair-points, costae percurrent or excurrent.

Sporophyte. ***Seta:*** straight or arcuate, short to elongate. ***Capsule:*** ellipsoid or cylindrical, smooth or ribbed, annulus persistant or disintegrating. ***Calyptra:*** mitrate or cucullate. ***Operculum:*** convex and mammillate or conical and rostrate. ***Peristome:*** haplolepidous, sometimes lacking, teeth lanceolate, entire or split into two or three divisions, trabeculate on outer side, covered with papillae on inner and outer sides, inserted near capsule rim, rarely deeply below, columella attatched to capsule base. ***Spores:*** small, smooth or papillose.

Distribution: in the Northern and Southern hemispheres.

Habitat and substrate: from sea-level to high alpine regions, on siliceous and calcareous rocks, and their deposits from weathering.