

Zeitschrift: Boissiera : mémoires de botanique systématique
Herausgeber: Conservatoire et Jardin Botaniques de la Ville de Genève
Band: 63 (2010)

Artikel: The genus Grimmia Hedw. (Grimmiaceae, Bryophyta) : a morphological-anatomical study
Autor: Maier, Eva
Kapitel: Reflections on taxonomic arrangements
DOI: <https://doi.org/10.5169/seals-1036227>

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Elevational distribution

Species growing at altitudes of between 2300 and 5700 m, are considered as high alpine taxa. Based on their elevations *G. abyssinica*, *G. bicolor*, *G. fuscolutea*, *G. handelii*, *G. macrotheca*, *G. nepalensis*, and *G. percarinata* can be considered as such.

The largest elevational range is found in *G. donniana* that grows from sea level to 5230 m. *Grimmia alpestris*, *G. anodon*, *G. consobrina*, *G. elatior*, *G. elongata*, *G. ovalis*, *G. sessitana*, *G. tergestina*, and *G. unicolor*, are found growing from the foothills to the high alpine zone, thus they inhabit a range of about 4500 m.

Grimmia sessitana, by its broad distribution across both hemispheres, its presence in Antarctica, and its vertical distribution range of 350 to 4750 m, may be regarded as the most widely distributed *Grimmia* species.

Grimmia asperitricha, *G. decipiens*, *G. dissimulata*, *G. humilis*, *G. kidderi*, *G. lisae*, *G. meridionalis*, *G. nutans*, *G. orbicularis*, *G. pilifera*, *G. plagiopodia*, *G. pulvinata*, and *G. trichophylla* probably do not extend above 2000 m.

Reflections on taxonomic arrangements

The diagnostic characters elaborated for each taxon treated in this study, namely the cell morphology in the leaf base, costal architecture and sporophyte morphology, unite fifty-one accepted species in *Grimmia*. The genus is defined by the primary diagnostic characters of haplolepidous peristomes [Aplolepideen] with sixteen teeth separated down to the insertion and costae with ventral guide cells, as previously defined by LIMPRICHT (1889: 694, 722).

The taxa form groups within *Grimmia* although these groups depend on the choice of the defining characters used. They do not have the status of a rank, reflecting instead natural groupings of the species based on morphological and anatomical characters.

Grimmia includes the taxa with:

- **smooth capsules on elongate straight setae** – *G. alpestris*, *G. anomala*, *G. asperitricha*, *G. atrata*, *G. bicolor*, *G. caespiticia*, *G. donniana*, *G. elongata*, *G. hartmanii*, *G. incurva*, *G. khasiana*, *G. laevigata*, *G. longirostris*, *G. montana*, *G. nivalis*, *G. ovalis*, *G. tortuosa* and *G. unicolor*;
- **smooth capsules on elongate inclined setae** – *G. elongata*, *G. macrotheca*, *G. mammosa*, *G. percarinata* and *G. sessitana*;
- **smooth capsules on short straight setae** – *G. kidderi*, *G. tergestina* and *G. pilifera*;
- **smooth capsules on short inclined seta** – *G. crinita*;
- **smooth capsules on short setae in S-form** – *G. anodon*, *G. plagiopodia* and *G. tergestina*.

Groups can be formed by the **two characters** of:

- **cells in leaf base that are elongate with smooth cell walls** – *G. donniana*, *G. elongata*, *G. incurva*, *G. ovalis*, *G. percarinata*, *G. sessitana* and *G. tortuosa*;
- **cells in leaf base that are elongate with nodulose cell walls** – *G. khasiana*, *G. kidderi*, *G. longirostris*, and *G. macrotheca*;
- **cells in leaf base that are short-rectangular with smooth cell walls** – *G. alpestris*, *G. anodon*, *G. anomala*, *G. asperitricha*, *G. atrata*, *G. bicolor*, *G. caespiticia*, *G. crinita*, *G. hartmanii*, *G. montana*, *G. nivalis*, *G. plagiopodia*, *G. tergestina* and *G. unicolor*.

Groups can be formed based on **more than two characters as follows**:

- **cells in leaf base short-rectangular with smooth cell walls and costa recessed in furrow and enlarged in apical part** – *G. alpestris*, *G. asperitricha*, *G. caespiticia* and *G. nivalis*; the affinity between *G. alpestris*, *G. caespiticia* and *G. nivalis* is supported by the morphology of male plants, which grow in separate cushions: the male plants are much smaller than the female plants, the perigonia, seen from the cushion in surface view, appear as markedly swollen, multifoliate buds and their comal leaves bend together thus covering the androecium. In addition, the cells of the setae of *G. alpestris*, *G. asperitricha*, *G. caespiticia* and *G. nivalis* turn to the right (male plants of *G. asperitricha* were not seen);
- **cells in leaf base short-rectangular with smooth cell walls and mitrate calyptrae, setae in S-form with quadrate cells arranged parallel to the axis** – *G. anodon* and *G. plagiopodia*;
- **cells in leaf base short-rectangular with smooth walls and propagule development at leaf apices, rim of capsules with two to four rows of small, rounded, hyaline cells** – *G. anomala* and *G. hartmanii*;
- **cells in leaf base elongate with smooth walls and margins on one side recurved, annulus cells rounded with narrow lumina, mitrate calyptrae, seta cells turning to the right** – *G. elongata* and *G. incurva*;
- **cells in leaf base elongate with smooth walls and margins plane** – *G. donniana* and *G. tortuosa*; these two taxa appear to be closely related and, as a group, related to *G. elongata* and *G. incurva*;
- **guide cells at insertion eight or more than eight, leaves concave, at broadest part of leaf with a shoulder, laminæ at least biserrate and costæ indistinct in laminal part** – *G. khasiana*, *G. laevigata*, *G. mammosa*, *G. ovalis*, *G. tergestina* and *G. unicolor*. The members of this group correspond to the definition of the subgenus *Litoneurum* (HAGEN, 1909: 10);
- **if the character seta cells arrangement** is taken into consideration then *Litoneurum* appears to be divided into two groups of three members each: the seta cells of *G. khasiana*, *G. ovalis*, and *G. unicolor* turn from below left to above right; the seta cells of *G. laevigata* and *G. mammosa* are arranged parallel to the axis in the lower part and turn to the right in the upper part, the cells of the very short seta of *G. tergestina* are arranged parallel to the leaf axis throughout;

- if the character **peristome insertion** is taken in consideration then *Litoneurum* may be divided in two groups of four and two members respectively: *G. khasiana*, *G. laevigata* and *G. mamosa* with peristome teeth that are inserted just below the capsule rim, in *G. tergestina* the teeth are inserted at the rim, whereas in *G. ovalis* and *G. unicolor* the teeth are inserted deeply below the rim;
- if the character **peristome very deeply inserted below orifice** is taken into consideration then *G. ovalis* and *G. unicolor* are closely related to each other and, by the possession of this character, distinct from the other species cited above.

Rhabdogrimmia includes the taxa with:

- **ribbed capsules on arcuate setae** – *G. abyssinica*, *G. austrofunalis*, *G. consobrina*, *G. decipiens*, *G. dissimulata*, *G. elatior*, *G. funalis*, *G. fuscolutea*, *G. humilis*, *G. lisae*, *G. meridionalis*, *G. muehlenbeckii*, *G. nutans*, *G. orbicularis*, *G. pulla*, *G. pulvinata*, *G. pygmaea*, *G. ramondii*, *G. torquata* and *G. trichophylla*; *Grimmia fuscolutea* occasionally has smooth capsules, the species, however, is maintained in *Rhabdogrimmia*.

Groups can be formed by **two characters** as follows:

- **cells in leaf base that are elongate with smooth cell walls** – *G. abyssinica*, *G. fuscolutea*, and *G. trichophylla*;
- **cells in leaf base that are elongate with nodulose walls** – *G. austrofunalis*, *G. consobrina*, *G. decipiens*, *G. elatior*, *G. funalis*, *G. lisae*, *G. meridionalis*, *G. muehlenbeckii*, *G. orbicularis*, *G. pygmaea*, *G. ramondii* and *G. torquata*;
- **cells in leaf base that are short with smooth walls** – *G. humilis*, *G. nutans*, *G. pulla* and *G. pulvinata*.

Groups can be formed by **more than two characters** as follows:

- **cells in leaf base elongate and costa form in an S-shape and leaf shape asymmetric** – *G. funalis* and *G. torquata*;
- **costa with two narrow-elliptical guide cells, obliquely arranged to the leaf axis and sinuose lamina cells in transitional part** – *G. funalis*, *G. fuscolutea*, *G. meridionalis* and *G. pygmaea*; the seta cells of *G. funalis* and *G. fuscolutea* are arranged parallel to the axis in lower part, turning to the right in upper part; in *G. meridionalis* and *G. pygmaea* the seta cells are arranged parallel to the axis throughout; in *G. meridionalis* and *G. pygmaea* the leaves are arranged around the stem in obvious tiers.

The characters **peristome inserted near the capsule rim and teeth anchored by cells with strongly thickened walls** group *G. nutans*, *G. pulvinata* and *G. pygmaea* which have ribbed capsules, and *G. plagiopodia* which has a smooth capsule.

Out of 48 species, 23 can be grouped by more than two characters (see sections “groups with more than two characters”): *G. anodon*, *G. plagiopodia*; *G. alpestris*, *G. asperitricha*, *G. caespiticia*, *G. nivalis*; *G. anomala*, *G. hartmanii*; *G. donniana*, *G. elongata*, *G. incurva*; *G. donniana*, *G. tortuosa*; *G. finalis*, *G. torquata*; *G. finalis*, *G. fuscolutea*, *G. meridionalis*, *G. pygmaea*; *G. khasiana*, *G. laevigata*, *G. mammosa*; *G. khasiana*, *G. laevigata*, *G. unicolor*; *G. khasiana*, *G. laevigata*, *G. mammosa*, *G. ovalis*, *G. tergestina*, *G. unicolor*; *G. ovalis*, *G. unicolor*.

Note.— *Grimmia handelii*, *G. maito* and *G. nepalensis* are excluded from the taxonomic arrangement because their sporophytes are unknown.

A connection to the genus *Racomitrium* may be seen in the peristome of *G. ramondii*. The peristome teeth are not completely separated down to the insertion but are connected by the two lowermost ventral cell plates. However, the cell pattern 2:3, following the peristomial formula for Haplolepidous moss peristomes, defined by EDWARDS (1979: 322), is not altered. The paradental triseriate tissue constituted of several rows of hyaline transversely arranged cells, seen on the outer side of the teeth of *G. ramondii* (**Fig. 45.14**) is a feature that may be compared with structures observed by BEDNAREK-OCHYRA (1995: 47, Fig. 17) in *Racomitrium lanuginosum* (Hedw.) Brid. and considered to be a preperistome. A similar structure can be seen in the longitudinal section of a tooth of *Racomitrium fasciculare* (Hedw.) Brid., illustrated in DEGUCHI (1979: 141, Fig. 6.11). Regarding these features, and taking into account the lack of a central strand in *G. ramondii*, a connection between *G. ramondii* and the genus *Racomitrium* Brid. should be considered.

Final statements

The genus *Grimmia*, based on Limprecht's defining characters, is considered here to be a well-defined entity. The characters ‘smooth capsule, straight seta’ and ‘ribbed capsule, arcuate seta’, divide the taxa into ‘*Grimmia*’ and ‘*Rhabdogrimmia*’. Within these groupings the taxa appear as entities with specific characters that distinguish one from the other. By the diagnostic characters they can be arranged in groups as given in the chapter ‘reflections on taxonomic arrangements’.

When comparing the results of this study that was based on morphological and anatomical characters with recent molecular phylogenetic studies of the genus *Grimmia* (STREIFF, 2006: 224-235) some findings are congruent: *G. anodon* and *G. plagiopodia*, *G. alpestris* and *G. caespiticia*, as well as *G. donniana* and *G. elongata*, appear to be closely related (STREIFF, 2006: 229, Fig. 1). The tree (STREIFF, 2006: 230, Fig. 2) obtained by the combination of chloroplast DNA sequences with morphological characters produces a clade that corresponds to the group *Litoneurum* I. Hagen, one that does not appear in the phylogenetic tree (Fig. 1) based on DNA characters alone. Discussing the results, STREIFF (2006: 231) stated that ‘the basal branch of the clade “*Rhabdogrimmia*” was not supported’. ‘The presence of gemmae was the only morphological synapomorphy of this clade’. However, some of the species