MORPHOLOGICAL STUDY OF THE GENUS GRIMMIA HEDW.  
(GRIMMIACEAE, BRYOPSIDA)

ANNE STREIFF

ABSTRACT. This work investigates the phylogenetic relationships among species of Grimmia Hedw. using cladistic analyses based on morphological and anatomical characters. The genus Grimmia is taxonomically difficult, because of morphological homogeneity of both gametophyte and sporophyte, principally due to growth conditions. The forty Grimmia species used in this study represent the majority of those found in Europe and Asia. Ten taxa belonging to the Grimmiaceae and Grimmiales were included as outgroups. Fifty-two morphological and anatomical traits (33 gametophytic and 19 sporophytic) were identified. Based on these data, a maximum parsimony (mp) method was applied to construct a phylogeny of Grimmia. Eight hundred and nineteen mp-trees were found and although they had relatively low statistical support on the internal branches, the tree topology was stable. Based on the RC re-weighted consensus tree, Grimmia as currently defined was found to be paraphyletic. Three subclades corresponding to the subgenera Rhabdogrimmia Limpr., Litoneuron I. Hagen and Gasterogrimmia Schimp. were observed in the trees, while the remainder of the Grimmia species formed an unresolved group indistinct from the other Grimmiaceae.

KEY WORDS: Grimmia, Grimmiales, morphological and anatomical characters, phylogeny

INTRODUCTION

The genus Grimmia Hedw. belongs to the monophyletic group of mosses called the Haplolepidae, or alternatively the Dicranidae (Hedderson et al., 2004). Grimmia is the most speciose member of the Grimmiaceae (Bryopsida, Grimmiales). More than 800 names for Grimmia have been proposed in literature, and 71 species are currently recognized (Muñoz & Pando, 2000). Grimmia species are found on every continent (Muñoz & Pando, 2000) mostly in temperate areas, or on mountains in the tropics. The majority of Grimmia species are saxicolous, xerothermophilous and acidophilous (Loeske, 1913) and these plants support extreme conditions in both temperature and dryness. In the Swiss Alps, the altitude record for plants is for Grimmia sessitana De Not., which was found at 4550 m in the Mont Rose Massif (Maier & Geissler, 1998).

The genus Grimmia is characterized by small (a few millimeters) or medium (several centimeters) size stems; a dark brown-green to blackish color; a growth form of small tufts or cushions (sometimes in dense mats); erect to ascending stems with appressed to erect leaves; lanceolate leaves that are tapering to the apex (spatulate in G. crinita Brid.); hair-points generally present; leaves in cross-section keeled or canaliculate; leaf laminae and margins uni- to multistratose; nerves developed from leaf base to apex, with at least two ventral guide-cells throughout; setae longer than or as long as the urn, straight or curved; urn symmetrical, rarely asymmetrical, ovate to cylindrical, generally with stomata at base;

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peristomes composed of a single ring of 16 teeth, teeth divided to insertion, entire or irregularly perforate; opercula rostrate or conical; and cucullate or mitrate calyptrae (Crum & Anderson, 1981; Maier & Geissler, 1995; Muñoz, 1998; Nyholm, 1998).

Different classifications of the genus Grimmia have been proposed since the description of it by Hedwig in 1801. Over 90 subgenera or subsections have been described in literature using both gametophytic and sporophytic characters. The most commonly used subdivisions are outlined here. Bridel (1819) in ‘Muscologia Reuentorium Supplementum’ listed 17 species as belonging to Grimmia and defined the genus by pyramidal and reflected peristome teeth, and mitrate calyptrae (Bridel, 1819). Bridel, in the same publication, described the genus Schistidium Brid. for 6 species based on the following characters: ‘stoma nudum,’ calyptra mitrate to campanulate-conical, and fringed at base. Bruch, Schimper & Guembel (1845), in ‘Bryologia Europaea’ treated 26 Grimmia species, defined by lanceolate or linear-lanceolate leaves, hair-points, small cells in the upper part of leaf laminae, long and rectangular basal cells, short setae and immersed capsules, or longer setae and exserted capsules, smooth or furrowed capsules, and mitrate or cucullate calyptrae. They subdivided the genus into two tribes: Curvisetae Bruch & Schimp. (curved seta) with 14 species and Rectisetae Bruch & Schimp. (erect seta) with 11 species (Bruch et al., 1845). Hampe (1846) considered the ‘Grimmien’ species with cucullate calyptrae to constitute an independent genus, which he named Guembelia Hampe. Schimper (1876) in his ‘Synopsis Muscorum Europaeorum’ recognized 39 species of Grimmia, which he placed in four subgenera: Schistidium (Brid.) Schimp., Guembelia (Hampe) Schimp., a new subgenus Gasterogrimmia Schimp., and Grimmia (Hedw.) Schimp. Gasterogrimmia was defined by growth-form in cushions, its short leaves, monoicous sexuality, calyptrae with five lobes or cucullate, immersed or emergent capsules with short setae, ovate and bulbous urns, mamillose opercula, peristome lacking or a peristome with perforate teeth, and differentiated annuli (Schimper, 1876). Limpricht (1890) in ‘Die Laubmoos Deutschlands, Oesterreich und der Schweiz’ enumerated 36 species of Grimmia. He adopted three subgenera previously described by Schimper (Gasterogrimmia, Grimmia and Guembelia) and introduced a new subgenus, Rhabdogrimmia Limpr., for species with curved setae, furrowed capsules, mitrate calyptrae (except in Grimmia orbicularis Wilson), keeled leaves with at least one leaf margin recurved, and variably multistratose leaf laminae (Limpricht, 1890). Limpricht (1890) recognized Schistidium at the generic level.

Hagen (1909) in ‘Forarbejder til en Norsk Lavmosflora’ treated 34 species of Grimmia that he divided into 7 subgenera: Streptocolea I.Hagen, Litoneuron I.Hagen, Rhabdogrimmia, Schistidium, Gastrogrimmia, Hydrogrimmia I.Hagen and Guembelia. Streptocolea was defined by leaves not arranged in a spiral, recurved leaf margins, dorsally prominent nerves with uniform cells, vaginulae in a spiral, and filiform columnellae not attached to the opercula (Hagen, 1909). Litoneuron was characterized by leaves arranged in a spiral, plane leaf margins, nerves non-prominent dorsally, ovate vaginulae, opercula not attached to columnellae and calyptrae covering completely the opercula (Hagen, 1909). Finally, Hydrogrimmia was defined by soft and loosely reticulated leaves, dorsally prominent nerves, shortly conical vaginulae, smooth capsules, ‘columella paene ad fundum capsulae retracta’ interpreted as columella attached to base of the capsule, and calyptrae covering opercula
Loeske (1913) in his monograph of the European Grimmiaceae ‘Die Laubmoose Europas. I. Grimmiaceae,’ divided the 24 species of Grimmia treated into 6 subgenera: Litoneuron, Guembelia, Ovatae Loeske, Rhabdogrimmia, Torquatae Loeske, and Pulvinatae Loeske. The subgenus Ovatae was characterized by well-developed dorsally prominent nerves, leaves with at least one leaf margin recurved, smooth capsules, conical opercula, and cucullate calyptrae. The two other subgenera, Torquatae and Pulvinatae were composed of species previously belonging to the subgenus Rhabdogrimmia sensu Limpricht. Torquatae were robust plants that had crisped leaves arranged in a spiral. They were both considered close to Rhabdogrimmia (Loeske, 1913). Loeske described Pulvinatae based on Grimmia pulvinata (Hedw.) Sm. and this subgenus contained two species (G. pulvinata and G. orbicularis). The author gave no other morphological characteristics, but remarked that the cell pattern and the hair-points in these two species looked different than those in the other Rhabdogrimmia members. Loeske (1913) recognized Hydrogrimmia and Schistidium as independent genera. Brotherus (1923) in ‘Die Laubmoose Fennoskandias’ and Brotherus (1924) in ‘die Natürlichen Pflanzenfamilien’ listed over 150 Grimmia species. In both books, the author recognized the same 7 subgenera: Streptocolea, Schistidium, Hydrogrimmia, Litoneuron, Guembelia, Rhabdogrimmia, and Gasterogrimmia.

Since Brotherus, no new major subgenera or sections have been described for Grimmia in the literature. Instead authors have rearranged and/or adopted the existing subgenera or sections and focused on taxonomy and species level problems. Various taxonomic revisions have been published for the genus Grimmia, often as regional treatments and including other genera from the Grimmiaceae: Grimmia, Coscinodon Spreng. and Schistidium from Japan (Deguchi, 1979), Grimmia and Schistidium from China (Cao & Vitt, 1986), Grimmia from Europe (Greven, 1995), Grimmia of the World (Greven, 2003), the subgenus Orthogrimmia Schimp. (Muñoz, 1998), Grimmia from South America (Muñoz, 1999), Grimmia from Central Europe (Maier & Geissler, 1995), from the Mediterranean area (Maier, 2002a), and the Himalaya’s (Maier, 2002b).

Cladistic and phylogenetic analyses

Churchill (1981) and Cao & Vitt (1986) have examined the relationships between some species of Grimmia based on morphological characters and using cladistic methods. These two works are presently the only cladistic studies that have been done for Grimmia. They include only a small number of species with few morphological characters. Churchill (1981) suggested that Grimmia was probably paraphyletic, and that complementary studies should be done to test this hypothesis. Cao & Vitt (1986) studied the classification of 22 Grimmia species in China and their placement in the different subgenera cited in literature. Since they considered only Grimmia species and no outgroups in their morphological data set, there was no possibility to test the paraphyly of the genus Grimmia, as suggested by Churchill (1981). On a molecular phylogenetic level, few studies have included more than one species of Grimmia, because most of these studies were focused on higher level relationships (for example La Farge et al.; 2000, Goffinet et al., 2001). The first study on the Grim miales has been recently published (Tsubota et al., 2003) using the cp DNA rbcL
marker to investigate the phylogeny of this group. This study, including 24 species of Grimmiales of which 13 from the Grimmiaaceae, supported the monophyly of the Grimmiaaceae, although the analyses lacked resolution at the genus level. Furthermore, the results suggested the paraphyly of the genus *Grimmia*. Finally, a recent study on the Haplolepidae using *rps4* sequences included 9 members of Grimmiaaceae and two other members of the Grimmiales. The results supported the monophyly of the family and suggested the paraphyly of the genus *Grimmia* (Hedderson et al., 2004).

With the numerous recent taxonomic studies, *Grimmia* species are in general well-defined. What remains unclear is the relationships among the species or species groups. This is reflected in the different classifications presented, and in the recognition and definition of the various subgenera. One reason for the difficulties in *Grimmia* subgeneric classification is the relative homogeneity of morphological traits. *Grimmia* species share the same kind of habitat, and similar growth conditions which may explain the homogeneity.

The relatively well-defined species of *Grimmia* give a good basis from which to develop a character data set (morphological and/or molecular) and explore some of the problems concerning the subgeneric classification. The development of the morphological data set will complement future molecular analyses. The main aims of this research are to use a cladistic analysis based on morphological and anatomical characters to 1) test phylogenetic relationships among *Grimmia* species, 2) test the different infrageneric classifications found in the literature, and 3) explore character state distribution and the level of morphological homoplasy in the genus *Grimmia*.

For this phylogenetic study, 33 gametophytic and 19 sporophytic characters have been used. The 50 studied specimens (40 species of *Grimmia* and 10 species from different genera in the Grimmiales) have been selected to represent a large spectrum of morphological variation and geographical distribution.

**Material and Methods**

I. **Material**

This study is based on 40 species of *Grimmia* and 10 outgroup taxa (Table 1). The selected taxa represent the majority of species growing in Central Europe, in the Mediterranean Area and in the Himalayas. These regions contain the largest number of species from *Grimmia* (Muñoz & Pando, 2000). Three works which contained descriptions of the *Grimmia* species used in this study have been done by Maier (Maier, 2002a; Maier, 2002b; Maier & Geissler, 1995) and used as a reference for this work.

In order to encompass intraspecific variability, three samples per species have been chosen from across a large geographic range, except where there was insufficient herbarium material available (Appendix 1). Species nomenclature follows Table 1 and all author names are cited here. In Table 1, the arrangement of the species used in this study in the different subgenera following three authors is presented (Limpricht, 1890; Brotherus, 1924; Nyholm, 1998). The specimens used in this work came from the bryophyte herbarium of Conservatoire et Jardin Botaniques de la ville de Genève (G) and from collections made in France, Corsica and Switzerland (hb. Streiff).

Ten species from the Grimmiales (Buck & Goffinet, 2000) have been chosen as out-
Table 1. Studied species and their position in the different sections proposed by Limpricht (1890), Brotherus (1924), and Nyholm (1998). Species with a * are not considered as Grimmia by the previous authors.

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<td>Rhabdogrimmia</td>
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<td>Streptocolea</td>
<td>Atratae</td>
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<td>Rhabdogrimmia</td>
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<td><strong>Grimmia handelii</strong> Broth.</td>
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<tr>
<td><strong>Grimmia hartmannii</strong> Schimp.</td>
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<td>*Dryptodon hartmanii</td>
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<td>Rhabdogrimmia</td>
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<td><strong>Grimmia laevigata</strong> (Bridd.) Brid.</td>
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<td>Rhabdogrimmia</td>
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<td><strong>Grimmia meridionalis</strong> (Mühl. Hal.) E. Maier</td>
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<td>Guembelia</td>
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<td>Gasterogrimmia</td>
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<tr>
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<td>Rhabdogrimmia</td>
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<td>*Dryptodon patens</td>
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<td><strong>Grimmia teretinervis</strong> Limpr.</td>
<td>*Schistidium teretinerve</td>
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<tr>
<td><strong>Grimmia tergestina</strong> Bruch &amp; Schimp.</td>
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<td>Litoneuron</td>
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<td><strong>Grimmia torquata</strong> Hook. &amp; Drummm.</td>
<td>Rhabdogrimmia</td>
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</table>
groups. Coscinodon cribrosus, *C. calyptratus*, Hydrogrimmia mollis, Schistidium apocarpum s.l., Racomitrium aciculare, and *R. crispatum* were sampled as representatives of Grimmiaaceae, and *Ptychomitrium polyphyllum, P. crispatum* (Ptychomitriaceae), *Campylostelium pitardii* (Ptychomitriaceae), and *Scouleria aquatica* (Scouleriaceae) as representatives of two families related to Grimmiaaceae. The outgroup species have been selected based on the classification system of Buck and Goffinet (2000).

2. **Character coding**

Morphological and anatomical characters were observed, and coded from each herbarium sample listed in Appendix 1. Characters referring to size or measure of size were not used extensively in the analysis since size may be correlated to phenotypic variability. A total of 52 characters (33 gametophytic and 19 sporophytic characters) were evaluated from the specimens. These characters and character states were described and are listed in the following paragraph. Character states were coded (0), (1) or (2). This order did not indicate plesiomorphic or apomorphic states (no polarization). All characters were coded as unordered and treated as discontinuous. Missing values were coded as “?” if the character is not present in the specimen and as “—” if the character doesn’t exist in the species (for example peristome teeth are always absent in *Grimmia anodon*). Information on characters was also obtained from the literature. Coded character states for each species are presented in Table 2.
Table 2. Matrix of characters for ingroup and outgroup species. Character states with more than one number indicate polymorphism. "?” is used in case of missing information on a character and “—” in case of an absent character. Taxa with a majority of sporophyte character states replaced by question marks are species where sporophyte is unknown in literature (Grimmia anomala, G. handelii, G. hartmanii, G. teretinervis and G. torquata).

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<th>Ingroup species</th>
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<th>Number of character</th>
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<th>Grimmia pilifera</th>
<th>Grimmia plagiopodia</th>
<th>Grimmia pulvinata</th>
<th>Grimmia ramondii</th>
<th>Grimmia sessitana</th>
<th>Grimmia sessitana</th>
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<th>Grimmia tergestina</th>
<th>Grimmia torquata</th>
<th>Grimmia trichophylla</th>
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**Table 2. (Continued)**

<table>
<thead>
<tr>
<th>Outgroup species</th>
<th>Campylostelium pitardi</th>
<th>Coscinodon calypratus</th>
<th>Coscinodon cribrosus</th>
<th>Hydrogrimmia mollis</th>
<th>Ptychomitrium crispatum</th>
<th>Ptychomitrium polyphyllum</th>
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</tr>
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</table>
3. List of morphological characters

Gametophytic characters

1. Growth-form is a cushion (as in *Grimmia orbicularis*) (0), a loose mat (as in *G. eliator*) (1) or a compact mat (as in *G. muehlenbeckii*) (2).
2. The plant is dioicus (0) or autoicus (1).
3. Young stems are absent (0) or present (1) in the plant. Young stems are visible when the cushion is turned over and examined from its base (as in *G. jitmatis*). These stems are different from mature stems and look like small strings. Leaves are very small and appressed to the stem.
4. In mature plants, leaves are developed regularly along the stem (0) or leaves are well developed in the upper part of the stem only and form an apical tuft (1).
5. In the upper part of the stem, dry leaves are appressed (0) or spreading (1).
6. In the upper part of the stem, dry and wet leaves are not enrolled and are spreading (0) or are enrolled in dry state and spreading in wet state (1).
7. Hair-points are absent (0) or present (1) at least in apical leaves. For a lot of *Grimmia*, the presence of hair points is variable in a species. Absence of hair point is rare and found only in *G. ramondii*, *G. unicolor* and *G. atrata*.
8. Hair-point cell lumens are not visible (0) or are visible (1) at the hair-point insertion.
9. Gemmae in apical leaf are absent (0) or present (1). Gemmae grow on the leaf apex (*G. harrmanii* or *G. anomala*) or on the leaf base (*G. torquata*). They are spherical and composed of a few cells.
10. Central-strand in the stem just under the apex, is present (0) or absent (1). Central-strand absence in some genera and species of the Bryidae is frequent and considered to be the result of a regression (Schofield, 1985).
11. Stem epidermis just under apex is composed of at least a layer of cells with thickened walls (on a centripetal axis in the stem, lumen width < sum of wall width on each size of the lumen) (0), or epidermis is composed of cells with non-thickened walls (on a centripetal axis in the stem, lumen width > sum of wall width on each size of the lumen) (1).
12. Mature leaves are tapering to apex (0), have a leaf shoulder (1) or are spatulate (as in *G. crinita*) (2).
13. Leaf basal cells are uniform (0) or cells from the upper part of the leaf descend along the margins to the leaf base (1).
14. Leaf basal cells are isodiametric (0), rectangular (1) or elongate (at least 5 times longer than
15. Basal cells in ranks are longitudinal (0) or latitudinal (as in G. laevigata) (1) in orientation.
16. Basal cell-walls are smooth (0), nodulose (1) or sinuose (as in Racemitiurn) (2).
17. Laminal cells between the basal and the upper cells (transition zone) are isodiametric (0) or rectangular (1).
18. Laminal cells between the basal and the upper cells (transition zone) have smooth walls (0) or sinuose walls (1).
19. Marginal cells at the leaves are not differentiated (as in G. alpestris) (0) or are differentiated from base to mid-leaf (as in G. lisae) (1).
20. In transverse section at mid-leaf, lamina is unistratose (0), multistratose (1) or variably uni- or multistratose (2).
21. In transverse section at mid-leaf, the margin is unistratose (0) or bi- or multistratose (1).
22. In transverse section at mid-leaf, leaf is canalicate (0), keeled (1) or in a W-shape (as in G. alpestris) (2).
23. In transverse section at mid-leaf, nerve ventral surface is rounded (0) or furrowed (1).
24. In transverse section at mid-leaf, margins are plane (0), margins are recurved on both side (1) or margins are recurved on one side (2).
25. In transverse section at mid-leaf, the cells are smooth (0) or with mamillae (or papillae) (1).
26. In transverse section at mid-leaf, cell walls have no “joint thickening” (0) or have a “joint thickening” (1). Definition of “joint thickening” is from Deguchi (1979): thickenings which develop strictly in both extremities from the vertical walls in leaf transverse section, otherwise in the joints where the vertical walls are in contact with free wall of lamina cells.
27. In transverse section at mid-leaf, nerve is rounded (0) or angular (1).
28. In transverse section from mid-leaf, nerve is well-developed to the apex (0) or nerve is poorly developed from mid-leaf (1). In G. khasiana or G. laevigata for example, the nerve is visible when looking at the leaf, but when the leaf is sectioned the nerve is not clearly differentiated in the upper part of the leaf.
29. In transverse section at mid-leaf, guide-cells are in a median position (0) or in a ventral position (1).
30. In transverse section at mid-leaf, guide-cells are in one rank (0) or in two ranks (as in G. elatior) (1).
31. In transverse section at mid-leaf, there are more than 4 guide-cells (0), 4 guide-cells (1) or 2 guide-cells (2).
32. In transverse section, at leaf insertion, there are more than 6 guide-cells (0), 6 guide-cells (1) or 4 guide-cells (2).
33. In transverse section of the leaf, hydroids are absent in the nerve (0), are present only at leaf base (1) or are present from the base up to the middle of the leaf (2).

**Sporophytic characters**
34. Capsule is immersed (the seta is at most as long as the urn) (0), or exserted (the seta is coming out of the cushion and is longer than the urn).
35. When the plant is humid, the seta is straight (0) or curved (1).
36. When the plant is dry, the seta is not twisted (0) or is twisted in an anti-clockwise direction (1).
37. Perichaetial leaves are not differentiated from stem leaves (0) or are different from stem leaves: of a larger size and strongly enveloping the seta (1).
38. The mature capsule full of spores and with its operculum still attached is cylindrical (0) or ovate (1).
A. STREIFF: Morphological study of the genus *Grimmia* Hedw. (*Grimmiaceae, Bryopsida*)

39. The operculum is conical (0) or rostrate (1).
40. The calyptra is cucullate (0) or mitrate (1).
41. The calyptra is plicate (0) or smooth (1).
42. The capsule base is not differentiated (0) or is differentiated into a neck (1).
43. When the capsule is dry, it is smooth (0) or furrowed (1).
44. The capsule mouth, after spore release, is constricted (0), straight (1) or flared (2).
45. The columella is attached to the operculum (*Schistidium* and *Scouleria*) (0) or is free from operculum and remains in the capsule (1).
46. The annulus is absent (0) or is detached in pieces or spirally (1).
47. Stomata are absent (0) or present at capsule base (1).
48. The peristome is well-developed (0) or absent (1). *Grimmia anadon* does not have a peristome and is the only *Grimmia* with this trait. The following characters 49, 50 and 51 have therefore been coded as “—” for this species.
49. Peristome teeth are inserted at capsule mouth (0) or are inserted below the mouth (1).
50. Peristome teeth on the dorsal side are papillose to the base (0), papillose only in the upper part (1) or smooth (2).
51. Peristome teeth are fused at base (0) or are free to the point of insertion (1).
52. The spore sac is fixed to the middle of the capsule, and the empty space between the basal part of the capsule and the spore sac is small (0), or the spore sac is fixed only in the upper part of the capsule and a large “air space” is present at the capsule base (in *Coscinodon*, Limpricht, 1890) (1).

4. Methods

The character state matrix was done using McClade 3.08a (Maddison & Maddison, 1999). This matrix was imported in a “nexus” format into Paup 4.0b10 (Swofford, 2002). Taxa with multiple character states were considered to be polymorphic. Cladistic analyses were conducted with heuristic search options using 100 replicates of ‘random sequence addition’ and a maximum parsimony criterion. Each most parsimonious tree was saved and swapped with TBR (Tree Bisction and Reconnection) branch swapping. In a second analysis, the data was successively weighted as a function of the rescaled consistency index (RC), and the same search protocols were repeated. Finally, character states were positioned on the tree using McClade 3.08a.

RESULTS

Heuristic searches including all taxa: One character is parsimony uninformative (character 48: presence/absence of peristome) and 51 are parsimony informative. The unweighted analysis gives 819 maximum parsimonious trees (mp-trees) with a minimum length of 306 steps, a consistency index (CI) of 0.216 and a retention index (RI) of 0.577. The strict consensus tree (Fig. 1) is composed of two resolved subclades (1 and 2). Nine species of *Grimmia* and the two species of *Coscinodon* are unresolved and formed a grade at the base of the tree. *Scouleria aquatica*, *Campylostelium pitardii* and *Hydrogrimmia mollis* root the tree. *Ptychomitrium* species and other *Grimmiaceae* (except *Hydrogrimmia*) used as outgroups in this study are within the major clade (clade 1) with the *Grimmia* species.

The CI and RI stabilized after three rounds of re-weighting. The 13 resulting mp-trees
Fig. 1. Strict consensus from 819 trees (L=306, Cl=0.216, RI=0.577) from un-weighted analyses with 52 morphological characters and 50 taxa. Two subclades present: 1 and 2.
have a CI of 0.365 and a RI of 0.720. The strict consensus tree (Fig. 2) has two resolved subclades (1 and 2, Fig. 2) that are more structured than in the first analyses. The same species are present in an unresolved group within the tree and the same species root the tree. *Grimmia* is found to be paraphyletic with the species of *Racomitrium*, *Ptychomitrium*, *Schistidium* and *Coscinodon* present in the main clade amongst *Grimmia* species.

**Analyses excluding Scouleria, Hydrogrimmia and Campylostelium:** These genera were excluded from this analysis, because they are morphologically very different from *Grimmia* and may have influenced the tree topologies. *Scouleria*, considered a Grimmiales by some authors such as Buck & Goffinet (2000), appears to be phylogenetically distant from this order in recent molecular studies (Tsubota et al., 2003; Hederson et al., 2004). Four characters are parsimony uninformative. The un-weighted analysis gives 321 mp-trees with a minimum length of 277, a CI of 0.235 and a RI of 0.583. The strict consensus tree collapses most of the internal structure (not shown).

The CI and RI stabilized after three rounds of re-weighting. The resulting 14 mp-trees are with CI of 0.453 and RI of 0.724. The strict consensus of reweighted trees (Fig. 3) rooted by the two species of *Ptychomitrium* shows a main clade (1) containing a majority of *Grimmia* taxa and a sister clade (2) including *Racomitrium aciculare*, *R. crispulum* and *Grimmia indica*. The main clade (1) is further divided in two well-defined clades (3 and 4) and a sister species *Schistidium apocarpum*. Clade 3 includes a series of un-resolved species and a relatively structured subclade. This subclade is differentiated into *Coscinodon* and two small subclades (G and L). Clade 4 is well-structured and composed of a subclade (R) and *Grimmia atrata* and *G. pilifera*. According to the studied morphological characters, the family of Grimmiaceae is monophyletic, and the genus *Grimmia* is paraphyletic, when the tree is rooted by *Ptychomitrium*.

**Character state distributions:** Character states have been positioned on the tree rooted by the two species of *Ptychomitrium* (Fig. 3). Character state distributions are discussed for the clades 3 and 4.

The first clade (clade 3, node I) is defined by the growth-form as a cushion (1) for the basal species. The clade 3, except *Grimmia longirostris*, is also defined by character state 11 (node II). The plants have a stem epidermis composed of at least one row of cells with non-thickened walls. Furthermore, the unresolved species and the two species of *Coscinodon* have a furrowed nerve (23). *Grimmia sessitana* and *G. alpestris* are joined to the terminal clade (node III) by their leaves well-developed in apex and forming an apical tuft on the stem (4). The terminal species that formed a well-differentiated clade are growing in compact mats (1, node IV). Canalicate leaves (22) and nerves not furrowed (23) distinguish the two last sister groups from the *Coscinodon* species and the unresolved species of the first clade (node V). The unistratose laminae (20) are common to the three species *G. anodon*, *G. crinita* and *G. plagiododia* (node VI). These three taxa also have an ovate capsule (38, not positioned on the tree Fig. 3, homoplasious in the tree except in this subclade where it is a synapomorphy and it units these three species). The three species form a distinct clade G, which includes members of *Gasterogrimmia*. Finally, the last clade (node VII) is defined by four character states, a multistratose lamina (20), a nerve weakly visible
Fig. 2. Strict consensus from 13 trees (CI=0.365 RI=0.720) from weighted analyses in function of RC with 52 morphological characters and 50 taxa. Two subclades present: 1 and 2.
Fig. 3. Strict consensus from 14 trees (CI=0.453 RI=0.724) from weighted analyses in function of RC of 52 morphological characters and 47 taxa (Ptychomitrium as outgroup). Important changes in character states are noted on the tree. In bracket: character state. Roman numerals: important nodes. 1–4: important clades. G: Gasterogrimmia, L: Litoneurron, R: Rhabdogrimmia.
in the leaf apex (28), 4 guide-cells in the middle of the leaf nerve (31), and more than 6 guide-cells at leaf insertion (32). The two first character states are synapomorphies present only in this clade. Grimmia khasiana, G. ovalis, G. laevigata, G. mammosa, G. tergestina and G. unicolor constitute this clade. This group of species (L), contains those belonging to the subgenus Litoneuron, and is the most supported subclade in this study.

In the second resolved clade (clade 4, node VIII), R contains species belonging to the subgenus Rhabdogrimmia, and is defined by sporophytic character states: curved seta (35) and furrowed capsule (43). Two sister groups are present in this clade. The first is defined by the presence of gemmae (9, node IX), a morphological trait present only in these taxa. These species are dioicous and three of them, Grimmia anomala, G. hartmanii and G. torquata, are not known with sporophytes and populations are composed most entirely of female plants. In the other species of this subclade, males are more frequent, and capsules are sometimes present. Grimmia decipiens and G. ramondii occupy a position between the two subclades present in the Rhabdogrimmia clade. They are morphologically close to the previous clade, but are monoicous and no vegetative reproduction is known in these two species. The second well-supported clade (node X) possesses another sporophytic character state in common: peristome teeth inserted at capsule mouth (49). The species constituting this clade have grow in cushions (1, node XI) except in G. elatior, which grows in loose mats. Grimmia fuscolutea, G. macrotheca, G. pulvinata and G. orbicularis form a small subclade (node XII) included in the Rhabdogrimmia clade and defined by two character states: the epidermis with non-thickened walls (11) as in node II, and unistratose laminae (20).

**Discussion**

The calculated consistency indices in this analysis are comparable to those found in similar morphological studies on vascular plants and bryophytes (Barker et al., 2003; Pederson, 2000; Pederson & Hedenás, 2001; Pederson & Hedenás, 2002; Virtanen, 2003). The different consistency indices obtained in this study support the hypothesis of a high level of homoplasy (Homoplasy Index = I - Cl), resulting from convergent evolution of morphological traits and multiple simplification events in moss evolution (Buck & Goffinet, 2000).

In this study, the different clades are defined by gametophytic characters only, with exception of the Rhabdogrimmia clade (Fig. 3, node IX) defined by a curved seta (35) and a furrowed capsule (43). Within this character matrix, the gametophytic characters are more informative than the sporophytic characters, the latter helping more to delimit the different species of Grimmia than to infer the relationships among them. Moreover, the sporophyte is extremely rare in 5 species of Grimmia (c.f. Table 2). In these cases, the information is not coded from the specimens available.

**Circumscription of Grimmia and infrageneric classification**

When the cladogram is rooted with Scouleria aquatica, the family Grimmiaaceae appear to be paraphyletic. Hydrogrimmia mollis, considered a member of Grimmiaaceae (Nyholm, 1998), is in a basal position close to Campylostelium pitardii and distinct from the other Grimmiaaceae. Hydrogrimmia is the only Grimmiaaceae growing in wet places. This species differs from the other Grimmiaaceae by unistratose and transparent lamina, and
loose thin-walled cells (Loeske, 1913; Nyholm, 1998). Other Grimmiaceae exhibit morphological adaptations to dry habitats such as sinuose and thickened cell walls, hair-points on the leaves and a small size. Ptychomitrium (Ptychomitriaceae) species are found next to Racomitrium species in the clade containing Grimmiaceae members. When Ptychomitrium rooted the cladogram, Grimmiaceae are monophyletic. Grimmia indica is basal in the cladogram, closer to Racomitrium aciculare and _R. crispulum_ than to the other Grimmia species. Grimmia indica, specially in young capsules, has a strongly marked apophysis, a character state unique within the genus Grimmia (Maier, 2002b), although this character is present in other Grimmiaceae such as _Racomitrium aciculare_. At this point no conclusion on the taxonomic position of _G. indica_ and its relationships with the _Racomitrium_ species can be made and further investigations are needed. Grimmia incurva and _G. handelii_ are found outside the main clade which contains the remaining _Grimmia_ species, _Schistidium apocarpum_ and the two _Coscinodon_. In contrast to _Schistidium apocarpum_, _Coscinodon_ (clade 3, node IV) is not well-differentiated from _Grimmia_ based on the characters used here. Three subclades G, L and R appear in the cladogram (Fig. 3) and correspond to three subgenera described in the literature: Gasterogrimmia, Litoneuron and Rhabdogrimmia respectively. In this analysis G is defined by ovate capsules, a character used as a diagnostic feature for the _Gasterogrimmia_ (Schimper, 1876). The subclade L is partially defined by nerves weakly visible in the leaf apex, and in literature _Litoneuron_ is defined by the same character called ‘dorsally non-prominent nerves’ (Hagen, 1909). Finally, R is mostly defined by furrowed capsules corresponding to _Rhabdogrimmia_ in literature (Limprecht, 1890). The small clade present in R and composed of _G. pulvinata_, _G. orbicularis_, _G. macrotheca_ and _G. fuscolutea_ approach the Pulvinatae, as defined by Loeske (1913).

In both outgroup combinations, the genus _Grimmia_ appears to be paraphyletic as suggested by Churchill (1981), Tsubota et al. (2003) and Hederson et al. (2004).

Despite the low levels of statistical support in the cladogram, the topology of the trees is conserved throughout the different analyses. Because of the low support for tree topology in this study it is not possible to make taxonomic conclusions based on this data alone. This study will be used as a basis to compare the phylogenies inferred from morphological data with molecular phylogenetic analyses. Molecular data will bring additional sets of characters to study the relationships of Grimmiaceae members and within the genus _Grimmia_.

**Acknowledgements**

I thank the foundation Claraz and Bryolich for financial support for this study on _Grimmia_; the University of Lausanne and Conservatoire et Jardin Botaniques de la ville de Genève for financial and logistical support; to Michelle Price for her assistance and corrections to this manuscript; to Eva Maier for her help and guidance in _Grimmia_ identification; to Guillaume Besnard and Gwenael Jacob and one anonymous reviewer for their comments on this manuscript; to my thesis advisor Nicole Galland for her support and assistance.

**Literature Cited**

Barker, N. P., H. P. Linder, C. M. Morton & M. Lyle. 2003. The paraphyly of _Cortaderia_ (Dantho-


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APPENDIX

Index of studied specimens
Samples originate from Conservatoire et Jardin Botaniques de la ville de Genève herbarium (G), and the personal herbarium of Streiff.
* species with sample number lower than three.

Ingroup specimens
2. Grimmia anodon Bruch & Schimp., Switzerland. Valais: Fully, Branson, 11.03.1999, Maier s.n. (G); Egypt. Sinai: 1830 m, 16.03.1996, Lübbenau s.n. (G); Italy. Trentino: Lago di Ledro, 1580–1480 m, 25.06.2001, Maier s.n. (G).
4. Grimmia atrata Hoppe & Hornsch., Austria. Salzburg: Gastein, Nassfeld, 1940 m, 12.07.1994, Maier 9505 (G); India. Sikkim: West District Glacial Lake, 4650 m, 15.07.1992, Long 22611 (G); Norway. Forstigen: 1050 m, 7.7.1991, Lübbenau 6139 (G).
*5. Grimmia austrofimalis MuiI.Hal., Bolivia. La Paz: Inquisivi, 4200 m, 1.10.1997, Heinrichs 4133 (G); Bolivia. La Paz: Nor Yungas, 3690 m, 13.11.1999, Price 1343 (G).
*6. Grimmia caespiticia (Brid.) Jur., Switzerland. Bern: Guttanen, N-Ufer Grimselsee, 1940 m, 15.08.1987, Maier 2156 (G); Switzerland. Valais: Finhaut, Sur les Conches, 1940 m, 20.07.1994, Maier 9231 (G).
7. Grimmia crinita Brid., Syria. Rezata: 300 m, 6.06.1998, Lübenau SY20 (G); Switzerland. Vaud: Epesses, 380 m, 10.2.1997, Maier s.n. (Hb. Maier); Germany. Baden-Württemberg: Ravensburg, St-Christina, 7.5.1996, Maier s.n. (G).


*9. Grimmia dissimulata E.Maier, Greece. Rhodes: Profitis Ilias, 480 m, 1.4.1997, Lübenau s.n. (Hb. Lübenau); Switzerland. Vaud: Rivaz, 375 m, 6.3.1996, Maier 10489 (G).

10. Grimmia donnnana Sm., Switzerland. Grisons: between Lavin and Chamanna Linard, 1710 m, 4.7.2001, Streiff 117 (Hb. Streiff); Switzerland. Valais: Finhaut, Emosson, Sur les Conches, 1980 m, 30.06.1999, Maier s.n. (G); Germany. Baden-Württemberg: Bad Rippoldsau, 520 m, 25.06.1998, Maier 11438 (G).

11. Grimmia elatior Bals.-Crv. & De Not., Switzerland. Valais: Vernayaz, 500 m, 26.05.2001, Maier s.n. (G); Pakistan. Baltistan, Rupal Valley, 2980–3200 m, 8.7.1999, Peter 2098 (G); Russia. Central Caucasus: Distr. Linard, 1710 m, 1980 m, 20.06.1996, Maier G21 (G).


17. Grimmia incurva Schwägr., Switzerland. Grisons: Davos, Joriflielfurgge, 2700 m, 19.8.1998, Maier 11596 (G); Switzerland. Tessin: Quinto, Piora, 2250 m, 1993, Stober & Bergamini 8498 (G); Italia. Südtirol: Kurzzas, 2800–3200 m, 6.07.1984, Van Malieck s.n. (G).


19. Grimmia khasiana Mitt., USA. Arizona: Huachia Mountain, Sierra Vista, Scheelite Canyon, 1950 m, 28.4.1999, Lübenau s.n. (G); China. Yunnan: Diqing Prefecture, 3080 m, 8.06.1993, Long 24137 (G); Bhutan, Kunga Rabeng Dzong, 1900 m, 22.6.1972, Wärnli s.n. (G).


22. Grimmia longirostris Hook., Switzerland. Grisons: Lavin, Cushinia, ca. 1550 m, 3.07.2001, Streiff 105 (Hb. Streiff); Bolivia. Cochabamba: Tapacari, 19.11.1999, 4330 m, Price 1540 (G);


Ireland 15497 (G); Slovakia: Martinské hole: 1400 m, 7.1951, Pilous 1341 (G).

37. Grimmia tergestina Bruch & Schimp., Switzerland. Valais: Salvan, 790 m, 25.06.2000, Maier s.n. (G); Yemen. Sanaa: 2750 m, 25.10.1995, Liubenau s.n. (G); France. Roussillon: Pyrénées, Vallée de la Sègre, above Llo, 1400 m, 6.06.2001, Streiff 165 (Hb. Streiff).

38. Grimmia torquata Hook. & Drumm., Switzerland. Valais: Simplon, 1250 m, 28.8.1998, Maier 11669 (G); Finland. Lappland: Utsjoki, 90 m, 2.8.1984, Hegewald 10369 (G); Germany. Rhld-Pflaz.: Niederalen, 230 m, 18.3.1996, Maier 10300 (G).


40. Grimmia unicolor Hook., Switzerland. Valais: between Finhaut and Le Trétien, 1310 m, 22.04.1999, Streiff 23 (Hb. Streiff); Austria. East Tirol: Matrei, Tavernbach, 1700 m, 3.9.1998, Maier 11676 (G); France. Haute-Corse: Castifao, 1550 m, 19.9.1979, Geissler 7014 (G).

Outgroup specimens


44. Coscinodon cribleus (Hedw.) Spruce, Switzerland. Valais: between Finhaut and Le Trétien, 1310 m, 22.4.1998, Maier 11377 (G); Czech Republic: Bohnen Sumava mts, 1250 m, 12.6.1994, Kucera s.n. (G); Austria. Tirol: St. Anton/Arlberg, 718.8.1927, Koppe 10252 (G).

45. Hydrogrimmia mollis (Bruch & Schimp.) Loeske, Switzerland. Valais: Combe d’Orny, 2400 m, 29.07.1998, Streiff 18 (Hb. Streiff); Canada. Labrador: Torngat Mountains, MGR MA 454526, 800–1250 m, 19.08.1986, Hedderson 5015 (G); Bulgaria. Rila Mountain, 9.1967, Siegel s.n. (G).


*47. Psychomiterium polyphyllum (Sw.) Bruch & Schimp., Switzerland. Valais: Salvan, 710 m, 19.4.1997, Maier s.n. (G); France. Haute-Saône: Corravillers, 460 m, 6.10.1986, Frahm (G).

48. Racomitrium aciculare (Hedw.) Brid., Switzerland. Valais: Salvan, Les planards, 850 m, 26.05.2001, Streiff 146 (Hb. Streiff); France. Ardennes: Monthermé, 27.11.1982, Bruynseels s.n. (G); Poland. West Carpathians: Silesian Beskid, 22.9.1986, Jedrzejko & al. 267 (G).


50. Schistidium apocarpum s.l., Switzerland. Vaud: Vevey, 360 m, 19.3.1999, Streiff 46 (Hb. Streiff); Switzerland. Genève: Bernex, Sézenove, 445 m, 24.5.2001, Maier s.n. (G); Italy. Trentino: Lago di Trentino, 730 m, 24.4.2001, Maier s.n. (G).