The formation of plicae in capsules of mosses of the order Bryales, with a focus on the genus Grimmia Hedw.

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Objekttyp: **Article**

Zeitschrift: **Candollea : journal international de botanique systématique = international journal of systematic botany**

Band (Jahr): **59 (2004)**

Heft 1

PDF erstellt am: **04.07.2024**

Persistenter Link: https://doi.org/10.5169/seals-879317

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EVA MAIER

ABSTRACT

MAIER, E. (2004). The formation of plicae in capsules of mosses of the order Bryales, with a focus on the genus Grimmia Hedw. *Candollea* 59: 51-63. In English, English, French and German abstracts.

The structure of moss capsules and the formation of plicae in selected species of the genus *Grimmia* Hedw. and from further species of different moss families in the order *Bryales* are described. These descriptions are accompanied by drawings of transverse sections of capsules in immature and mature states. The study shows two different pathways of development of plicae in capsules: 1) plications that originate in the capsule wall tissue (eg. *Grimmia* subg. *Rhabdogrimmia* Limpr.); 2) plications that have their origin in the constitution of the exothecial cells. The differences and similarities between the two developmental patterns and the various capsule sections are commented upon here.

RÉSUMÉ

MAIER, E. (2004). La formation de plis dans les capsules de mousses de l'ordre des Bryales, plus particulièrement dans le genre Grimmia Hedw. *Candollea* 59: 51-63. En anglais, résumés en anglais, français et allemand.

La structure des capsules et le développement de plis au sein d'espèces sélectionnées dans le genre *Grimmia* Hedw. ainsi que dans d'autres espèces de différentes familles de mousses de l'ordre des *Bryales* sont décrits. Des dessins de coupes transversales de capsules à l'état immature et mature illustrent les descriptions. L'étude met en évidence deux concepts différents du développement des plis: 1) la formation des plis a son origine dans la structure du tissu capsulaire (p. ex. dans *Grimmia* subg. *Rhabdogrimmia* Limpr.); 2) la formation des plis a son origine dans la constitution cellulaire de l'exothecium. Les différences et similitudes sont commentées.

ZUSAMMENFASSUNG

MAIER, E. (2004). Die Faltenbildung in Kapseln von Laubmoosen der Ordnung Bryales, insbesondere der Gattung Grimmia Hedw. *Candollea* 59: 51-63. In Englisch, englische, französische und deutsche Zusammenfassungen.

Der Bau von Laubmooskapseln und die Entwicklung von Falten in ausgewählten Arten der Gattung *Grimmia* Hedw. und weiterer Arten aus verschiedenen Laubmoosfamilien der Ordnung *Bryales* werden beschrieben. Zeichnungen von Kapselquerschnitten im unreifen und im reifen Zustand veranschaulichen die Beschreibungen. Die Untersuchung belegt zwei verschiedene Möglichkeiten der Faltenbildung: 1) Die Faltenbildung entsteht im Kapselgewebe (z. B. *Grimmia* subg. *Rhabdogrimmia* Limpr.); 2) Die Faltenbildung hat ihren Ursprung in der Konstitution der Exotheziumzellen. Unterschiede und Ähnlichkeiten werden besprochen.

KEY-WORDS: BRYALES – *Grimmia* – *Grimmia* subg. *Rhabdogrimmia* – Species concept – Capsule structure – Development of plicae

CODEN: CNDLAR
ISSN: 0373-2967
59(1) 51 (2004)

Introduction

Species of the genus *Grimmia* Hedw. are defined by the primary diagnostic characters of haplolepidous peristomes with sixteen teeth separated down to the insertion (LIMPRICHT, 1885-1889: 694) and costae with ventral guide cells (LIMPRICHT, 1885-1889: 722). The sporophytes have either smooth-walled or plicate capsules. The species with smooth-walled capsules are members of the genus *Grimmia s. str.*, and those with plicate capsules belong to the subgenus *Rhabdogrimmia* Limpr. of the genus *Grimmia* (LIMPRICHT, 1885-1889: 759). Characters correlated with plicate capsules (section *Rhabdogrimmia*) are bent setae and mitrate calyptrae, although bent setae and mitrate calyptrae appear sporadically in the genus *Grimmia s. str.* in various combinations too. The name *Rhabdogrimmia* originated from the Greek *«rhabdos»,* stick or rod, a reference to the vertically striate capsule wall.

Plicate capsules also appear within other families of the *Bryales* as they are given in VITT (1984: 744), for example members of the *Ditrichaceae*, *Rhabdoweisiaceae*, *Orthotrichaceae*, and *Brachytheciaceae*. In haplolepidous and diplolepidous mosses both plicate and smooth capsules are produced. In spite of differences in capsule wall form, smooth or plicate, the architecture of a typical moss capsule follows the same fundamental plan (SCHIMPER, 1848; LIMPRICHT, 1885-1889: 44). CAVERS (1911: 27) states that «the Bryales, by far the largest group of Bryophyta, present extraordinary uniformity in the early development of the sporogonium».

The plicae of the capsules in the diverse families presented here (see **Table 1**. for taxonomic and species listing) seem to be more or less uniform. However, upon anatomical investigation the plicae perceptible in the species of the subgenus *Rhabdogrimmia* appeared to deviate from the more normal cell pattern. LIMPRICHT (1885-1889; 1890-1895) had already observed this difference in plicae as seen by his selection of different terms for the description of plicae in moss capsules. The terms «Längsrippen» or «Rippen», translated as «ribs» (by the present author), is reserved to describe the plications of the *Grimmia* subg. *Rhabdogrimmia* capsules. The capsules of members of other genera with plicate capsules are described as having «gestreifte» or «gefurchte Kapseln», translated as «striped» or «furrowed capsules» (by the present author).

The aim of the study is to aid in the understanding of the origins and development of the plicae in moss capsules. To achieve this, the architecture of capsules and the capsule wall region of selected species of the order *Bryales* are investigated.

Materials and methods

Materials

The species selected for the study were those known to produce plicate capsules. They were chosen from four of the seven «phylogenetically significant lineages presented in a synthetically derived cladogram» given by VITT (1984: 716). These lineages are the *Orthotrichineae*, the *Hypnineae*, the *Encalyptineae* with the *Pottiineae*, and the *Dicranineae* including the *Seligerineae* and the *Grimmiineae*. The species are arranged following the classification of suborders in the order *Bryales (Arthrodontae)* given in VITT (1984: 744) with the exception of *Amphidium mougeotii* (Bruch & Schimp.) Schimp. (see **Table 1**). VITT (1984: 753) placed the species in the *Rhabdoweisiaceae*. In LIMPRICHT (1890-1895: 3) however, in the opus cited by VITT (1984), *A. mougeotii* was placed in the *Orthotrichaceae*, an opinion adopted here. The most recent presentation of the systematic position of *Amphidium* is treated in LA FARGE & al. (2000: 270).

Table 1. Presentation of species used in the investigation, according to VITT (1984).

Suborder	Family	Genus and species
Orthotrichineae	*Orthotrichaceae*	*Amphidium mougeotii* (Bruch & Schimp.) Schimp. *Orthotrichum anomalum* Hedw. *Orthotrichum stramineum* Brid.
Hypnineae	*Brachytheciaceae*	*Eurhynchium striatum* (Hedw.) Schimp.
Encalyptineae	*Encalyptaceae*	*Encalypta rhaptocarpa* Schwägr.
Pottiineae	*Pottiaceae*	*Tortula subulata* Hedw.
Dicranineae	*Dicranaceae*	*Cynodontium strumiferum* (Hedw.) Lindb. *Oreas martiana* (Hoppe & Hornsch.) Brid.
	Leucobryaceae	*Leucobryum glaucum* (Hedw.) Ångstr.
	Rhabdoweisiaceae	*Rhabdoweisia fugax* (Hedw.) Bruch & Schimp.
	Ditrichaceae	*Ceratodon purpureus* (Hedw.) Brid.
Seligeriineae	*Seligeriaceae*	*Brachydontium trichodes* (F. Weber) Milde
Grimmiineae	*Grimmiaceae*	*Grimmia* Hedw. *s. str.* *Grimmia elongata* Kaulf. *Grimmia laevigata* (Brid.) Brid. *Grimmia ovalis* (Hedw.) Lindb.
		Grimmia subg. *Rhabdogrimmia* Limpr. *Grimmia consobrina* Müll. Hal. *Grimmia dissimulata* E. Maier *Grimmia elatior* Bals.-Criv. & De Not. *Grimmia meridionalis* (Müll. Hal.) E. Maier *Grimmia pulvinata* (Hedw.) Sm.

The nomenclature follows CORLEY & al. (1981).
NOTE: the author is informed of the work of OCHYRA & al. (2003).

Methods

The developmental pattern of a moss capsule from the green stage to the spore dispersing stage are based on SCHIMPER's (1848) meticulous anatomical and morphological studies of capsule ontogeny. The transformation that happens in a moss capsule as it matures can be traced up to the states of necrosis and maturation, as indicated by the change in capsule colour from deep green to a faded yellow-green that appears first in the annulus region. In the necrosis phase the tissues constituting structures in the capsule are rapidly destroyed by the desiccation of the columella, the rupture of the archesporium, and the collapse of the endothecium. It is just before the necrosis stage that the capsule is in its green stage (KREULEN, 1972a: 65) and pure green in colour. This green stage should be selected for the study of the capsule architecture, an observation confirmed by KREULEN (1972a: 65). The colour of the capsule, as a whole, changes with the proceeding maturation process and can be used as a guide to the state of maturation of the capsule.

The green capsule is humidified with a minimum of water to adhere it to the slide. The most instructive and comparable transverse sections are achieved from below the middle of the capsule. The immature capsule is cut free hand with a sharp razor-blade directly on the slide. The sections are carefully heated on the slide in some drops of KOH 1.5%. The heated preparations are then covered with a glass cover slip and a drop of water is added.

After necrosis and the desiccation of the capsule structures comes the mature phase. In this phase the capsule becomes yellow-brown, spores mature and eventually are released from the capsule upon and after de-operculation. The capsule wall structure in mature capsules is best investigated in the transverse sections of capsules just before their de-operculation.

The mature capsule is gently heated in KOH 1.5%. From the softened capsule the operculum, the remaining collapsed capsule tissues, and the spores are carefully removed. The transverse capsule sections are executed directly on the slide using a sharp razor-blade. The preparations are then covered with a glass cover slip and a drop of water is added.

The drawings for the present study were performed from material in wet state taken from herbarium specimens in Herb. Lübenau and G.

Descriptions

Glossary

A transverse section through a capsule in the green stage at the spore-bearing region (MAGILL, 1990) in the lower third of a specimen of G. *pulvinata* illustrates the cell layers that constitute a moss capsule **(Fig. 1.1)**. In magnified sections of the same transverse section **(Fig. 1.2, 1.3)** the letters indicate the designations of the cell layers:

A, amphithecium (the sterile cell layers), comprising:

a1, exothecium;

a2, capsule wall tissue;

a3, air space;

a4, outer spore sac;

E, endothecium (the fertile cell layers), giving raise to:

e1, archesporium;

e2, inner spore sac;

e3, columella.

The terms «exothecium» and «endothecium» were first used by KIENITZ-GERLOFF (1878: 40) and the term «columella» was first described as «columnula» by HEDWIG (1798) (WAGENITZ, 1996).

The big, rounded cells with fine walls protruding from the cell wall tissue into the air space **(Fig. 1.2, 1.3)** are arranged in distinct lines or alignments. LIMPRICHT (1885-1889: 518, 723) used the term «assimilierende Längsleisten,» translated as «assimilating protrusions» or «tabs» (by the present author) for the description of these structures. They arise at the base of the peristome teeth and run down to the capsule base, thus connecting the capsule wall to the outer spore sac. They are arranged in sixteen groups of a different number of cells. In some species, such as in *Orthotrichum anomalum* **(Fig. 4.1, 4.2)** the tabs are made up of two cells, but in others, such as in Brachythecium rutabulum (Hedw.) Bruch & Schimp., the tabs are composed of four cells (KREULEN 1972b: 157). The arrangement of the cell layers composing a moss capsule given here is based on LIMPRICHT (1885-1889: 44), and on a schematic representation in KREULEN (1972b: 158, Fig. 6).

The capsule architecture of species of the genus Grimmia

The most striking feature of the exothecium of a member of the subgenus *Rhabdogrimmia* is the lack of any visible sign of plications in surface view. No vertical striae, formed by either differentiated exothecium cell walls or by change of colour in capsule wall, are perceptible. Only in very young, shiny capsules with few layers of capsule wall cells, such as in *G. pulvinata*, fine stripes can be observed in surface view. These begin at the annulus region and reach down to the capsule base. These stripes are produced by the tabs which are correlated with the peristome teeth. Already at the green stage in the capsule of *G. pulvinata* plications can be seen in transverse section **(Fig. 1.1)**. In this early state the spores in the archesporium are scarcely perceptible, and the

innermost cell layer of the capsule wall tissue is filled with grains of chlorophyll. Later on in the development the endothecium collapses, the immature spores fill the capsule, and the plications become more pronounced **(Fig. 2.1)**. Later still in the development the capsule and the spores reach their mature state and the plicae are very pronounced, initiated by the shrinking of the thin-walled cells of the innermost layers of the capsule wall tissue. The plicae, in contrast to the tabs, are not correlated with the teeth. In the final stage, the tissue involved is nearly decomposed **(Fig. 2.2)**. The outer walls of the exothecium cells have not changed, they are of uniform thickness. Some examples, all taken from mature capsules, support these statements: *G. consobrina* **(Fig. 2.3)**, *G. dissimulata* **(Fig. 2.4)**, *G. elatior* **(Fig. 2.5)**, and *G. meridionalis* **(Fig. 2.6)**.

The capsules of the species of *Grimmia s. str.* are formed and develop as above, with the exception that they do not develop plicae. **Figure 3.1** shows a transverse section of a capsule of *G. laevigata* in green stage. At this early stage just a slight undulation of the exothecium may be observed. With progressive maturation the exothecium becomes smooth. The cell walls are of uniform thickness **(Fig. 3.2)** which is a character shared with the *Grimmia* subg. *Rhabdogrimmia* species. To support these observations the transverse sections of capsules in mature state of two other members of the genus *Grimmia s. str.*, e.g. *G. elongata* **(Fig. 3.3)**, and *G. ovalis* **(Fig. 3.4)**, are drawn here and may be compared with *Grimmia* subg. *Rhabdogrimmia* species cited in the above paragraph.

The capsule architecture of species of the genera other than Grimmia

Orthotrichum anomalum **(Fig. 4.1)** has been chosen to demonstrate the formation of plicae different from that in the subgenus *Rhabdogrimmia*. The drawing is made from a transverse section of a capsule in the green stage showing the same general architecture as in *G. laevigata* **(Fig. 3.1)** or *Tortula subulata* **(Fig. 5.1)**. A strong difference can be seen in the arrangement of the exothecium cells which are in groups of cells with strongly thickened outer cell walls alternating with groups of much thinner walled cells **(Fig. 4.2)**. These outer cell walls are formed by the deposition of wall thickening material, that is mostly coloured. In the genus *Orthotrichum* in general eight or sixteen coloured stripes are present (LIMPRICHT, 1890). A transverse section **(Fig. 4.3)** from a mature *O. anomalum* capsule shows the thickenings of the exothecium cells in a more pronounced form. In the genus *Orthotrichum* they are in clear correlation with the teeth. As in *Orthotrichum* species, in the other species from the selected families used in this study, the stripes are arranged in eight or sixteen rows and are orange or brownish tinged. It gives an insight to the pattern of formation of the bulging stripes and the depressed furrows, appearing as plicae in dry capsules.

The following eight species have plicate capsules. The plicae are formed in the same manner as in *O. anomalum* **(Fig. 4.1-3)**. The transverse sections are taken from mature capsules: *Encalypta rhaptocarpa* **(Fig. 4.4)**; *Cynodontium strumiferum* **(Fig. 4.5)**; *Oreas martiana* **(Fig. 4.6)**; *Leucobryum glaucum* **(Fig. 4.7)**; *Amphidium mougeotii* **(Fig. 4.8)**; *Rhabdoweisia fugax* **(Fig. 4.9)**; *Ceratodon purpureus* **(Fig. 4.10)**; *Brachydontium trichodes* **(Fig. 4.11)**. The drawings show the strengthened outer walls of the exothecium cells, and in addition, illustrate specific differences between the species.

Concluding statements

The statements that moss capsules are constructed following a general plan made by LIMPRICHT (1885-1889: 44) and CAVERS (1911: 27) can be emphasized by drawings of transverse sections of capsules in green stage. Similar capsule architecture can be seen in *G. pulvinata* **(Fig. 1.1)** with a plicate capsule, and *G. laevigata* **(Fig. 3.1)** with a smooth capsule from the *Grimmiaceae*, and *Tortula subulata* **(Fig. 5.1)** from the *Pottiaceae*, all haplolepidous series of mosses. *Eurhynchium striatum* **(Fig. 5.2)** from the *Brachytheciaceae* with smooth capsules, and *Orthotrichum stramineum* **(Fig. 5.3)** from the *Orthotrichaceae* with plicate capsules are from the diplolepidous series of mosses. The general architecture of the capsule is apparently not influenced by the plicate or smooth capsule form or the haplolepidous or diplolepidous peristome type within the *Bryales*.

The species of *Grimmia*, with or without plicate capsules, share the character of uniform exothecium cell walls with species with smooth capsules of other families in the order *Bryales*. A transverse section through a capsule of *G. pulvinata* **(Fig. 1.1, 1.2, 1.3)** in green stage, however, shows even in this early stage the plication of the capsule. The development of the capsule wall into the well-expressed plicae in the mature capsule is achieved by the shrivelling and shrinking of the fine-walled cells constituting the caspule wall tissue. Plicae seen in the capsules of *Grimmia* subg. *Rhabdogrimmia* have their origin in the constitution of the capsule wall tissue which is in contrast to the origin of the plicae formation in other genera seen in this study.

The species with plicate capsules selected from different families in the order *Bryales* develop the plicae following a common scheme. In the progress of capsule maturation the outer walls of the exothecium cells become mostly thicker and are frequently coloured. Groups of cells with thickened walls alternate with groups of cells with not or scarcely thickened walls. Upon desiccation the groups of exothecium cells with finer cell walls shrink, thus forming the depressed furrows. The groups of exothecium cells with their thicker cell walls form the bulges. The plications of these capsules have their origin in the constitution of the exothecium cells (LIMPRICHT 1885-1889: 48-49). In contrast to the other members of the *Bryales* investigated here the exothecial cells in *Grimmia* subg. *Rhabdogrimmia* are not involved in the process of formation of the plicae.

Conclusion

The study brings to light two different pathways of development of plicae in capsules of mosses of the order *Bryales*. In the majority of the moss capsules studied the plicae formation follows the same scheme: they have their origin in the constitution of the exothecial cells. In about one third of the species used here of the genus *Grimmia* the plicae formation deviates from this general scheme: the plications originate in the capsule wall tissue. LIMPRICHT (1885-1889) decided to maintain the unity of the genus *Grimmia* by creating the subgenus *Rhabdogrimmia* for this group of species. The reason may be the strong weight given to the primary diagnostic characters of *Grimmia* itself, namely the peristome construction and the costal architecture. Findings in this study, based on the techniques of investigation of capsule architecture, may offer new insights into certain systematic problems. The striking difference in the pathway of plicae development in *Grimmia* subg. *Rhabdogrimmia* may further support an isolated position of the *Grimmia* subg. *Rhabdogrimmia* species within the genus *Grimmia*, or alternatively a more distant relationship of the subgenus *Rhabdogrimmia* to the genus *Grimmia*. Further morphological and genetic investigations are needed to confirm the taxonomic status of the group of «*Rhabdogrimmia*» species, and to investigate the systematic weight of capsule wall development patterns.

Specimens examined and selected for the descriptions

Amphidium mougeotii Bruch & Schimp. **FRANCE. Auvergne**: «Sur les rochers humides de trachyte de la grande cascade dans les Monts-Dore», *Lambertye s. n.* (G).

Brachydontium trichodes (F. Weber) Milde. **GERMANY. Bavaria**: «Oberallgäu, Obermeiselstein, Bolgen, Riedbergpass, 1620 m, Bergwald, Sandstein», 27.VI.1995, *Maier 9812* (G).

Ceratodon purpureus (Hedw.) Brid. **FRANCE. Ain**: «Pentes rocheuses au dessus de Culoz, 300 m», 23.IV.1950, *Vautier 648* (G).

Cynodontium strumiferum (Hedw.) Lindb. **SWITZERLAND. Canton of Grisons**: «Zernez, Val Zavru, 2400 m, rocher de gneiss», VII.1921, *Meyland s. n.* (G).

Encalypta rhaptocarpa Schwägr. **AUSTRIA. Carinthia**: «Neben der Pasterze bei Heiligenblut», 25.VIII.1860, *Jack s. n.* (G).

Eurhynchium striatum (Hedw.) Schimp. **SWITZERLAND. Canton of Geneva**: «Collex-Bossy, 440 m, Laubwald, auf Erde nahe Versoix», 10.XII.2003, *Maier s. n.* (G).

Grimmia consobrina Müll.Hal. **CHILE. Valparaiso**: «Valparaiso, Alto del Puerto. On a block of stone on a rivulet», 18.VIII.1940, *Santesson M150* (G).

Grimmia dissimulata E. Maier. **GREECE. Crete**: «Chania, Phyrgana, Passhöhe ca. 600 m, an Felsen», 1964, *Düll 1a* (G).

Grimmia elatior Bals.-Criv. & De Not. **SWITZERLAND. Canton of Valais**: «Martigny-Combe, Ravoire, 1200 m, Wegrand, Felsblock, Silikatgestein», 23.III.1994, *Maier 8841* (G).

Grimmia elongata Kaulf. **AUSTRIA. Salzburg**: «Hagener Hütte, Bergweg Nassfeld, 2320 m, alpiner Rasen, Felsbänder, basenarmer Silikatschist», 27.VIII.1994, *Maier 9138* (G).

Grimmia laevigata (Brid.) Brid. **SWITZERLAND. Canton of Valais**: «Fully, Les Follatères, 630 m, Felsensteppe, Silikatsteinplatten», 7.XI.1992, *Maier 7667* (G).

Grimmia meridionalis (Müll. Hal.) E. Maier. **GREECE. Cyprus**: «Trimiklini, Troodos, 1320 m, Gestein, kalkfrei», 12.IV.1993, *Lübenau Z116* (herb. Lübenau).

Grimmia ovalis (Hedw.) Lindb. **SWITZERLAND. Canton of Valais**: «Martigny, La Bâtiaz, 520 m, Weinbergmauer Krone, Beton», 29.XI.1991, *Maier 6178* (G).

Grimmia pulvinata (Hedw.) Sm. **SWITZERLAND. Canton of Geneva**: «Stadt Genf, WTO, 380 m, Mauerkrone, trocken, schattenlos», 14.I.2003, *Maier 1* (G); «Stadt Genf, WTO, 380 m, Mauerkrone, trocken, schattenlos», 5.III.2003, *Maier 2* (G); «Bernex, Sézenove, 445 m, Vorgarten, Granitplatten, Fussweg», 12.V.2002, *Maier 3* (G).

Leucobryum glaucum (Hedw.) Ångstr. **GERMANY. Bavaria**: «München», XI.1849, *Arnold s. n.* (G).

Oreas martiana (Hoppe & Hornsch.) Brid. **AUSTRIA. Tyrol**: «Felsiger Boden der Messerlingwand ober dem Windisch-Matreier Tauernhaus», 5.VIII.1876, *Arnold 1328* (G).

Orthotrichum anomalum Hedw. **SWITZERLAND. Canton of Valais**: «Dorénaz, Rosel, 500 m, alter Steinschlag», 1.III.1992, Maier 6611 (G); «Fully, Les Follatères, Fels», 1.V.1990, *Maier 3260* (G).

Orthotrichum stramineum Brid. **SWITZERLAND. Canton of Ticino**: «Villa-Luganese, Denti della Vecchia, 1000 m, Mischwald, Waldrand, toter Laubbaum», 28.VI.1992, *Maier 7118* (G).

Rhabdoweisia fugax (Hedw.) Bruch & Schimp. **SWITZERLAND. Canton of Ticino**: «Borgnone, 800 m, Waldweg, Erdwall», 27.VI.1992, *Maier 7069* (G).

Tortula subulata Hedw. **SWITZERLAND. Canton of Valais**: «Fully, Les Follatères, 1060 m, Erde, Überhang durch Anriss», 20.III.1990, *Maier 3607* (G).

ACKNOWLEDGEMENTS

I am greatly indebted to Michelle Price for discussions of capsule characters, for her advice, and for checking the English text. Specimens used in this paper came from G and herb. Lübenau. My warmest thanks go to Patrick Perret for his ongoing support and assistance with literature problems, and for having opened the safe of the library to allow me to read the precious original of W. P. Schimper's work on *Recherches anatomiques et morphologiques sur les Mousses* from 1848. I am particularly grateful to Professor Rüdiger Mues for the cautious review. The resulting suggestions greatly improved the work.

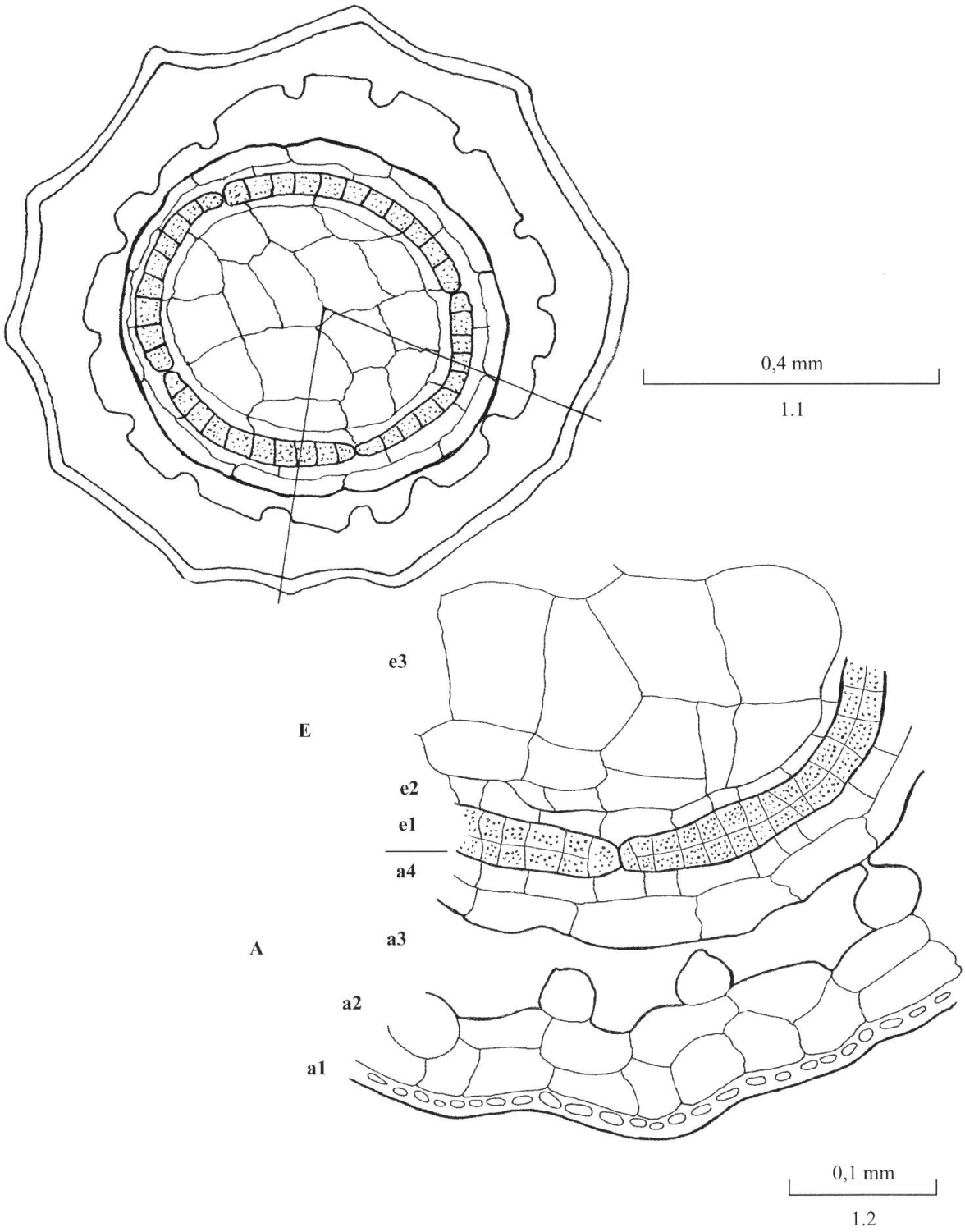
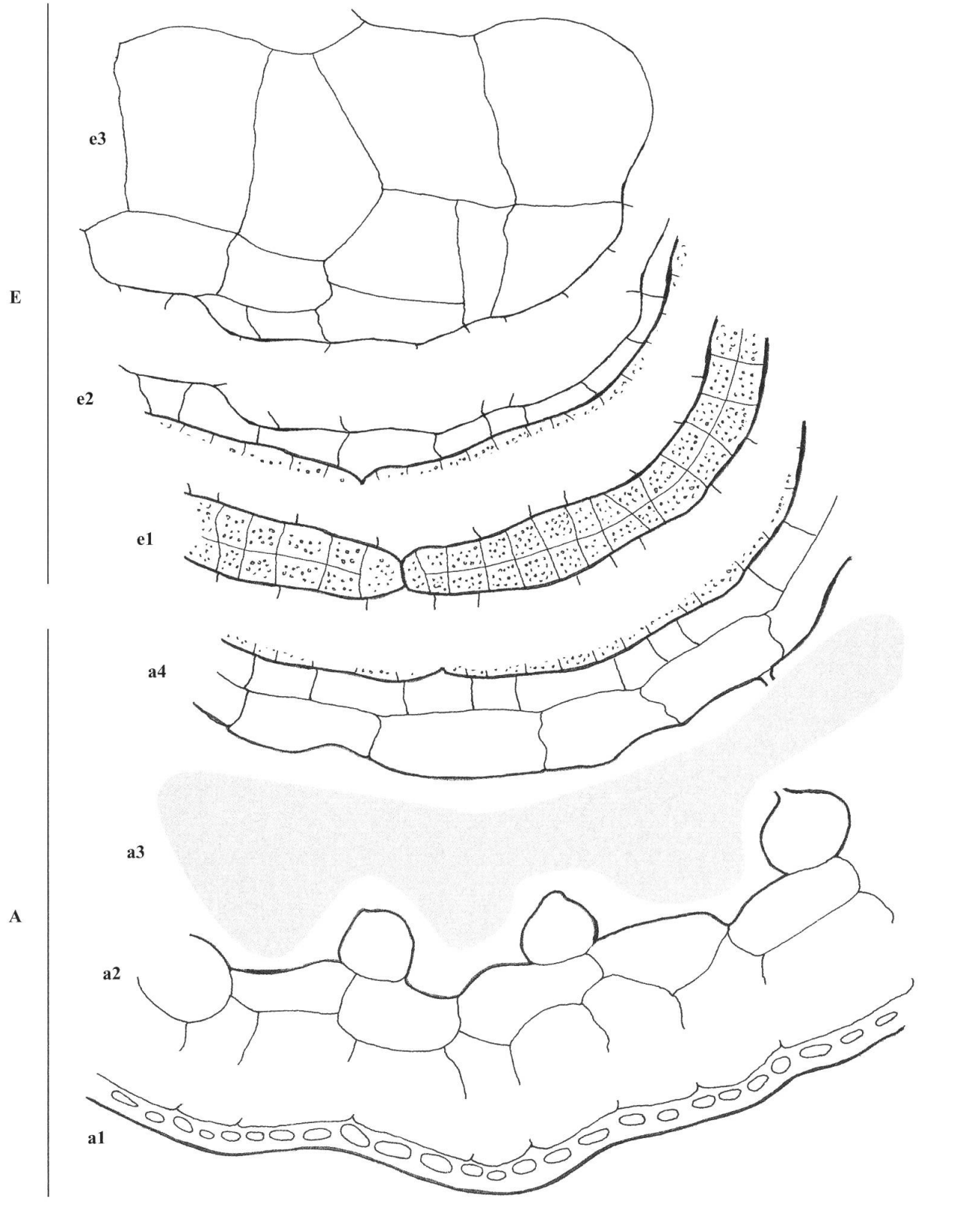


Fig. 1.– Glossary: **1**, *Grimmia pulvinata*, capsule in green stage at spore-bearing region in lower third, transverse section; **2**, the same, magnified; **3**, the same, magnified with the cell layers separated for better understanding of the capsule architecture. **A**, amphithecium with: **a1**, exothecium; **a2**, capsule wall tissue; **a3**, air space; **a4**, outer spore sac. **E**, endothecium with: **e1**, archesporium; **e2**, inner spore sac; **e3**, columella.



[**1-3**, *Maier 1*]

1.3

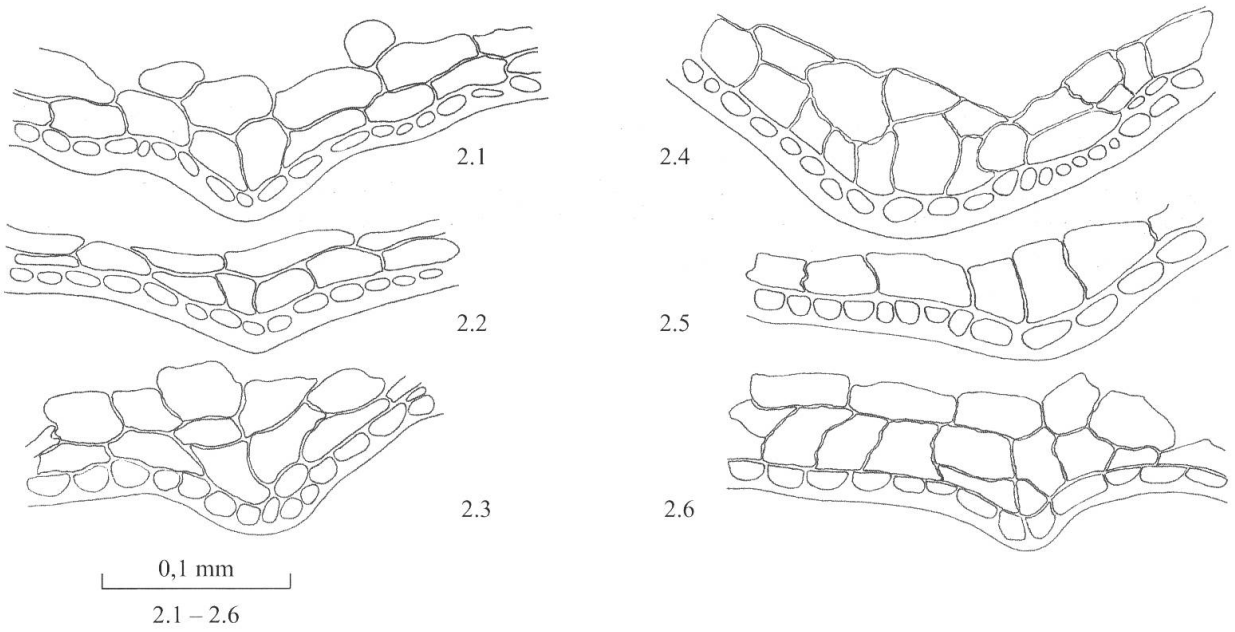


Fig. 2.– *Grimmia* subg. *Rhabdogrimmia* species: **1**, *G. pulvinata*, immature capsule, transverse section; **2**, *G. pulvinata*, mature capsule, transverse section; **3**, *G. consobrina*, mature capsule, transverse section; **4**, *G. dissimulata*, mature capsule, transverse section; **5**, *G. elatior*, mature capsule, transverse section; **6**, *G. meridionalis*, mature capsule, transverse section. [**1**, *Maier 2;* **2**, *Maier 3;* **3**, *Santesson M150;* **4**, *Düll 1a;* **5**, *Maier 8841;* **6**, *Lübenau Z116*]

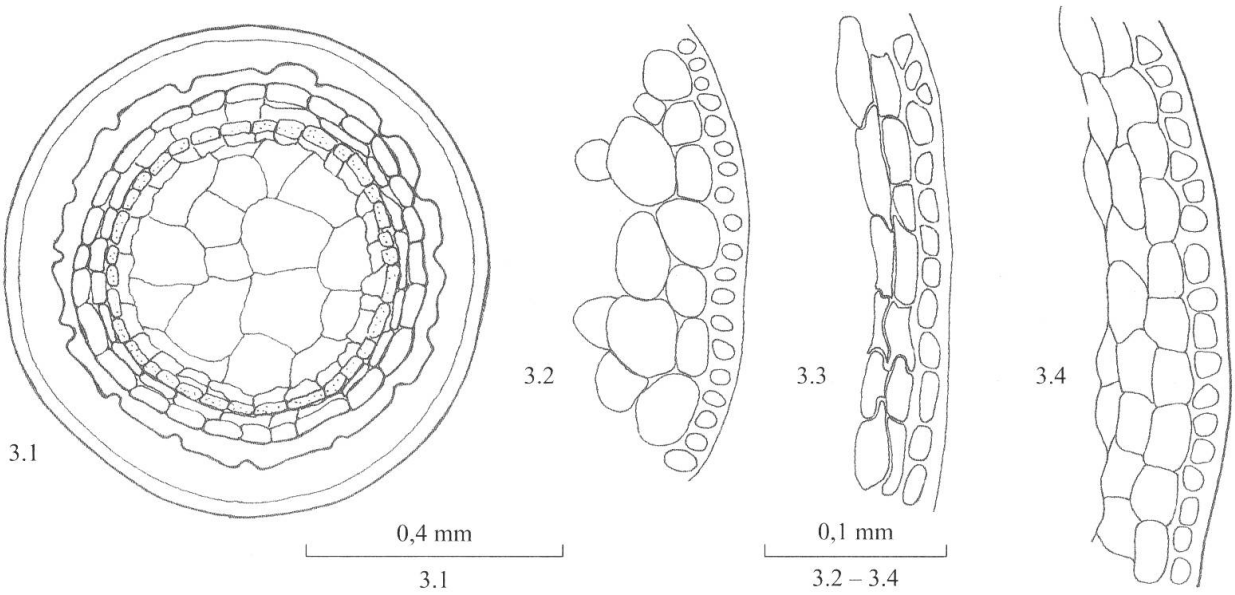


Fig. 3.– *Grimmia* species: **1**, *G. laevigata*, capsule in green stage, transverse section; **2**, *G. laevigata*, nearly mature capsule, transverse section; **3**, *G. elongata*, mature capsule, transverse section; **4**, *G. ovalis*, mature capsule, transverse section. [**1-2**, *Maier 7667;* **3**, *Maier 9138;* **4**, *Maier 6178*]

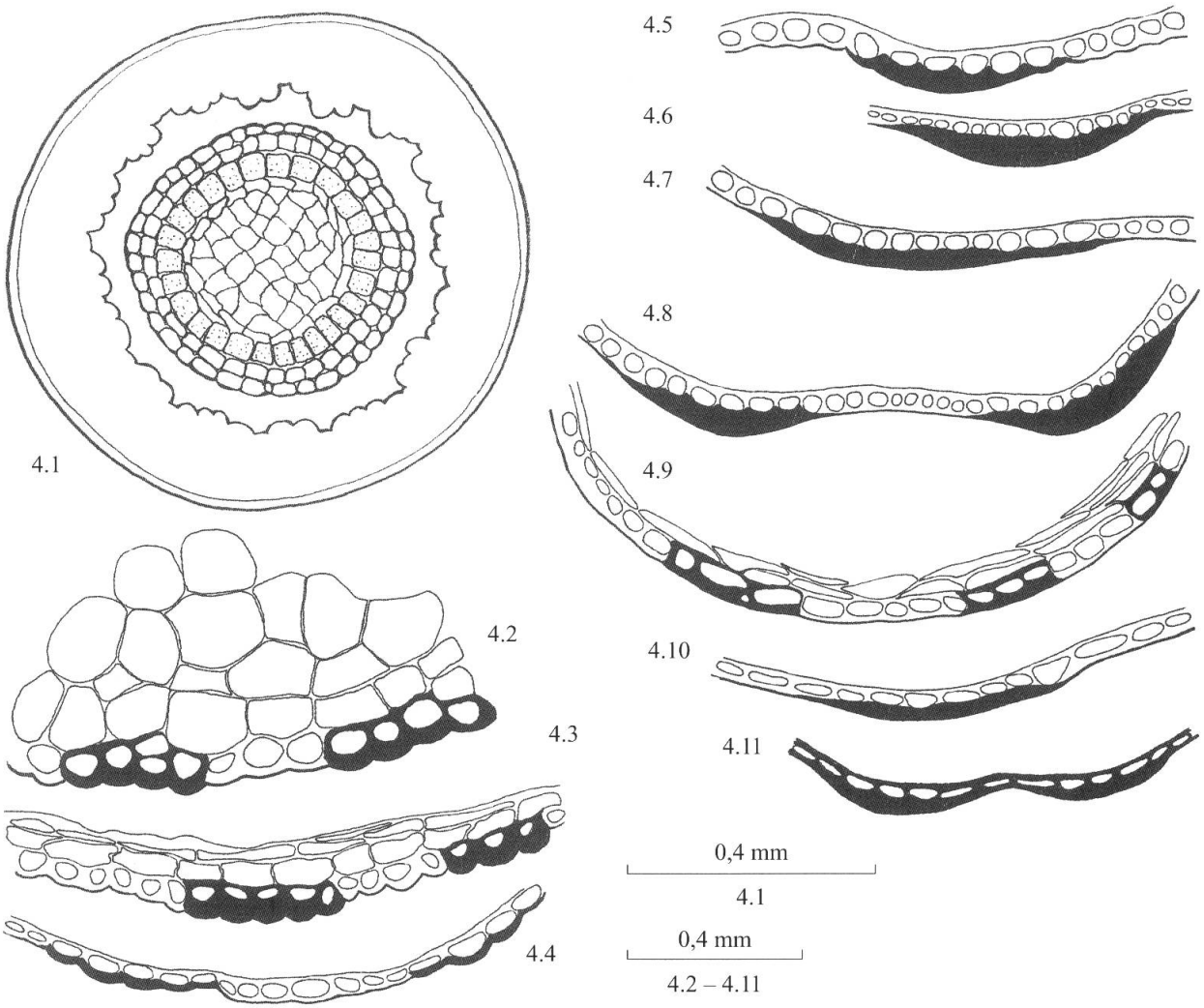


Fig. 4.– Other species in the *Bryales* with plicate capsules: **1**, *Orthotrichum anomalum*, capsule in green stage, transverse section; **2**, *O. anomalum*, capsule in green stage, transverse section; **3**, *O. anomalum*, mature capsule, transverse section; **4**, *Encalypta rhaptocarpa*, mature capsule, transverse section; **5**, *Cynodontium strumiferum*, mature capsule, transverse section; **6**, *Oreas martiana*, mature capsule, transverse section; **7**, *Leucobryum glaucum*, mature capsule, transverse section; **8**, *Amphidium mougeotii*, mature capsule, transverse section; **9**, *Rhabdoweisia fugax*, mature capsule, transverse section; **10**, *Ceratodon purpureus*, mature capsule, transverse section; **11**, *Brachydontium trichodes*, mature capsule, transverse section. [**1-2**, *Maier 6611*; **3**, *Maier 3260;* **4**, *Jack s. n.;* **5**, *Meylan s. n.;* **6**, *Arnold 1328;* **7**, *Arnold s. n.;* **8**, *Lambertye s. n.;* **9**, *Maier 7069;* **10**, *Vautier 648;* **11** *Maier 9812*]

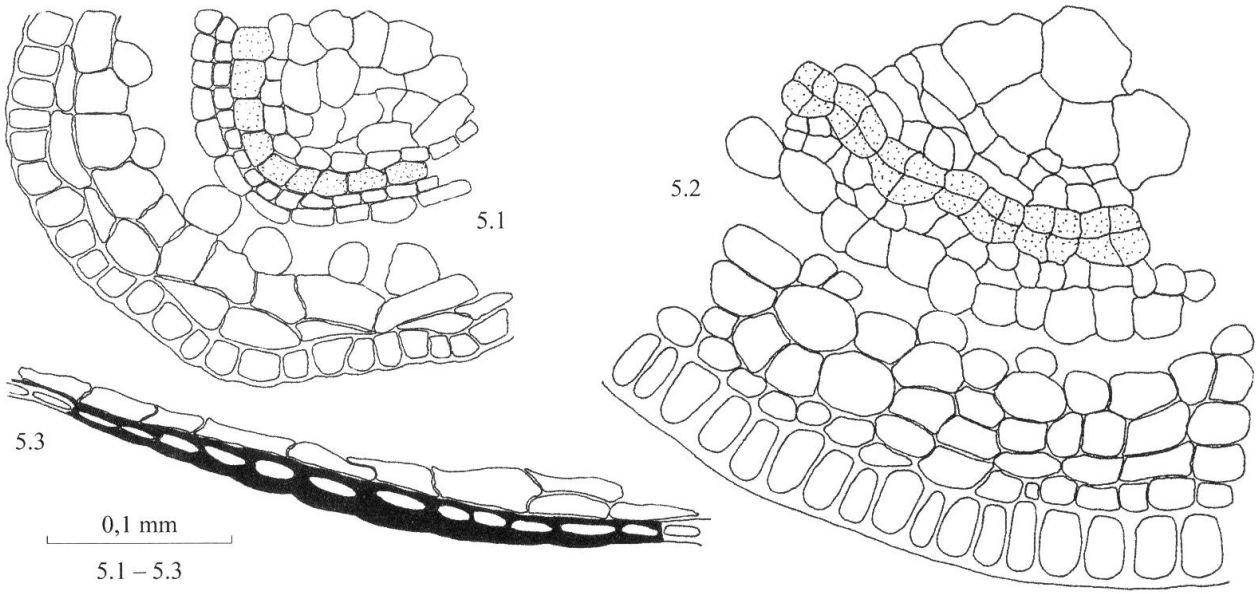


Fig. 5.– Species cited under statements: **1**, *Tortula subulata*, capsule in green stage, transverse section; **2**, *Eurhynchium striatum*, capsule in green stage, transverse section; **3**, *Orthotrichum stramineum*, mature capsule, transverse section. [**1**, *Maier 3607;* **2**, *Maier s. n.;* **3**, *Maier 7118*]

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