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Introduction

Georg Bojung “Scato” Lantzius-Beninga (1815-1871) published his Latin dissertation in 1844, entitled “*De evolutione sporidiorum in capsulis muscorum*”, on the formation and development of spores within the capsules of mosses. He went on to study the anatomy of moss capsules in more detail, with the aim of investigating the composition and origins of the different tissues as well as the various structures that constitute this organ. He published two principal works, both entitled “*Beiträge zur Kenntniss des inneren Baues der ausgewachsenen Mooskapsel, insbesondere des Peristomes*”, in 1847 and 1850. The former work presented a summary of his findings and the later work was a more complete treatise of his observations, accompanied by 11 lithographs. Strongly influenced by the earlier findings of HEDWIG (1782, 1798, 1801), and a number of plant anatomy and key bryological works of the time (see Table 1), Lantzius-Beninga microscopically examined capsules in species of *Aulacomnium* Schwägr., *Barbula* Hedw., *Bartramia* Hedw., *Ceratodon* Brid., *Dicranum* Hedw., *Fissidens* Hedw., *Funaria* Hedw., *Grimmia* Hedw., *Gymnostomum* Nees & Hornsch., *Hypnum* Hedw., *Orthotrichum* Hedw., *Phascum* Hedw., *Polytrichum* Hedw., *Sphagnum* L., *Splachnum* Hedw., *Tetraphis* Hedw., *Trichostomum* Bruch and *Weissia* Hedw., as recognised at that time (see Table 2 for a list of the species studied by Lantzius-Beninga), providing descriptions of his observations and comparisons between the different entities that he had studied. Lantzius-Beninga studied a total of 48 species from 38 genera, and illustrated 24 of them in his works. Unfortunately, LANTZIUS-BENINGA (1847, 1850) did not give any details on the methods that he employed to prepare and examine the capsules.

LANTZIUS-BENINGA (1847, 1850) principally based his observations on mature moss capsules and, in particular, on the internal structure of the capsule and the junction of the peristome teeth with the capsule wall in the peristomate mosses he studied. He proved for the first time that the peristome of arthroodontous mosses is made up of cell wall remnants and demonstrated that the three innermost cell-layers of the amphithecium gives rise to the peristome (see in SCHWARTZ, 1991). He also deduced that the single rank of teeth in the haplolepidous mosses that he studied (in *Dicranum*) corresponded to the inner rank of teeth in the mosses that he has observed with a double rank of teeth (*Hypnum*, *Orthotrichum*) (see in EDWARDS, 1984). Based on his detailed examinations and observations Lantzius-Beninga proposed that the capsule wall – peristome tooth junction region in mosses could hold important traits for use in species distinction: “*Bei allen guten Arten fand ich im Bau wesentliche Unterschiede von andern verwandten, ebenfalls sichern Arten, wogegen ich bei einigen schwankenden Species keine Abweichungen wahrnehmen konnte*” (LANTZIUS-BENINGA, 1850: 600), interpreted as: “In all good species I found, in the construction, essential differences to other related, clearly defined species, on the other hand in some varying species I could not recognize differences”.

Lantzius-Beninga’s works contain fundamental details on the structure and anatomical composition of moss capsules in the studied species as well as detailed illustrations of his associated observations. Despite the long history of the study of moss capsules and the use of sporophyte characteristics, particularly the peristomes, in their classification (see review of the

developmental studies in mosses of SCHWARTZ, 1991) Lantzius-Beninga's theory has yet to be widely tested within and across the mosses. Apart from some scattered mentions within the bryological literature (see SCHWARTZ, 1991 and MAIER & PRICE, 2005) and the application of his method of examining sections of capsules and peristomes by a few early bryologists (KIENITZ-GERLOFF, 1878a, 1878b; LIMPRICHT, 1888-1889), his findings have been largely forgotten within the body of bryological work. EDWARDS (1979, 1984) evoked the discoveries of Lantzius-Beninga, indicating his contribution to the understanding of the homologies of the structures in haplolepidous and diplolepidous mosses, later re-formulated by PHILIBERT (1902; see also the translated and abridged version of Philibert's series of peristome articles in TAYLOR, 1962). MAIER & PRICE (2005, based on MAIER, 1999) discuss the context of Lantzius-Beninga's work and highlight some examples of species specific characteristics of the capsule wall – peristome tooth junction region within *Grimmia*.

LANTZIUS-BENINGA (1844, 1850) appears to have had ready access to the historical and current bryological literature of his time. He consulted the works of his predecessors (for example, HEDWIG, 1798, 1801; BROWN, 1811, 1819) and contemporaries (especially *Bryologia europaea*, BRUCH & al., 1836-1847), comparing his findings with these published works (see Table 1). His ability to interpret the structures that he saw and to compare them to previous observations demonstrates the depth of his studies. However, LANTZIUS-BENINGA (1850) was not always complementary about the authors of *Bryologia europaea* or of their illustrations and interpretations of structures in moss capsules given therein. His rather critical approach to the research of his contemporaries may have been one of the reasons why his works were not widely appreciated at the time.

Herein the two works of LANTZIUS-BENINGA (1847, 1850), and a later biography on him (BIELEFELD, 1897), all published in German, have been transliterated and the original lithographs have been reproduced (see Table 3 for a list of the species that he illustrated in his works). The rich information held within LANTZIUS-BENINGA (1847, 1850) on the construction and development of the capsules in the mosses he studied can be interpreted using his text and illustrations. Rather than undertaking a strict translation of his works in a more modern style, the spirit and charm of the original German text has been maintained. BIELEFELD's (1897) biography of Lantzius-Beninga gives some insights into his privileged background and his professional career as well as his behaviour, character and philosophy.

Note: The images are reproduced in the original format.

Acknowledgments

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Table 1. List of botanical and bryological works cited in LANTZIUS-BENINGA's works, entitled *Beiträge zur Kenntniss des innern Baues der ausgewaschenen Mooskapsel, insbesondere des Peristomes*, of 1847 and 1850.

- BROWN, R. (1811). Some observations on the parts of fructification in mosses; with characters and descriptions of two new genera of that order. Some observations on the parts of fructification in mosses; with characters and descriptions of two new genera of that order. *Transactions of the Linnean Society of London* 10: 312-324.
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- BRUCH, P., W. P. SCHIMPER & T. GÜMBEL (1836-1847). *Bryologia europaea, seu genera muscorum Europaeorum monographice illustrata* I-XI. E. Schweizerbart, Stuttgart.
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- HEDWIG, J. (1801). *Species muscorum frondosorum*. Lipsiae [Leipzig]: sumtu Joannis Ambrosii Barthii.
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- LANTZIUS-BENINGA, S. (1844). *De evolutione sporidiorum in capsulis muscorum*. Huth, Göttingen, Germany.
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- SCHLEIDEN, M. J. (1846). *Grundzüge der Wissenschaftlichen Botanik nebst einer Methodologischen Einleitung als Anleitung zum Studium der Pflanze. Part 2. Morphologie, Organologie*. Verlag von Wilhelm Engelmann, Leipzig.
- WILSON, W. (1841). Notes and notices in reference to British Muscology. *Journal of Botany* 3: 374-386.

Table 2. Modern names for the species studied by LANTZIUS-BENINGA (1847, 1850). Authors names have been added to the names that were used in the original texts. The modern equivalent of the names are given, using TROPICOS (2014) as a reference, in bold. After each name, reference is made to its first use by citation of the year and page in the publication.

- **Anacalypta rubella* Huebener = ***Erythrobarbula rubella*** Boros (1847: 19; 1850: 570)
- Aulacomnium palustre*** (Hedw.) Schwägr. (1850: 574), as “*Aulacomnion*” but later as “*Aulacomnium*”
- Barbula fallax* Hedw. = ***Didymodon fallax*** (Hedw.) R. H. Zander (1847: 19; 1850: 572)
- Barbula muralis* (Hedw.) Crome = ***Tortula muralis*** Hedw. (1850: 573)
- Barbula reflexa* (Brid.) Brid. = ***Didymodon ferrugineus*** (Besch.) M. O. Hill (1847: 21)
- Barbula tortuosa* (Hedw.) F. Weber & D. Mohr = ***Tortella tortuosa*** (Hedw.) Limpr. (1847: 21; 1850: 571)
- Bartramia fontana* (Hedw.) Turner = ***Philonotis fontana*** (Hedw.) Brid. (1850: 584)
- Bryum capillare* Hedw. = ***Rosulabryum capillare*** (Hedw.) J. R. Spence (1850: 581)
- Bryum crudum* (Hedw.) Turner = ***Poblia cruda*** (Hedw.) Lindb. (1850: 581)
- Bryum cuspidatum* (Hedw.) Crome = ***Plagiomnium cuspidatum*** (Hedw.) T. J. Kop. (1850: 581)
- Bryum turbinatum*** (Hedw.) Turner (1850: 581)
- Catharinea undulata* (Hedw.) F. Weber & D. Mohr = ***Atrichum undulatum*** (Hedw.) P. Beauv. (1850: 586)
- Ceratodon purpureus*** (Hedw.) Brid. (1850: 574)
- Dicranum glaucum* Hedw. = ***Leucobryum glaucum*** (Hedw.) Ångstr. (1850: 576)
- Dicranum rufescens* (With.) Turner = ***Dicranella rufescens*** (With.) Schimp. (1850: 576)
- Dicranum schreberianum* Hedw. (1850: 576) = ***Dicranella schreberiana*** (Hedw.) H. A. Crum & L. E. Anderson
- Dicranum scoparium*** Hedw. (1850: 575)
- Dicranum varium* Hedw. = ***Dicranella varia*** (Hedw.) Schimp. (1850: 576)
- Fissidens adiantoides*** Hedw. (1850: 576), as “*adiantoides*”
- Funaria hygrometrica*** Hedw. (1850: 568)
- Grimmia apocarpa* Hedw. (1850: 575) = ***Schistidium apocarpum*** (Hedw.) Bruch & Schimp.
- Gymnostomum pyriforme* Hedw. = ***Physcomitrium pyriforme*** (Hedw.) Hampe (1850: 568)
- Gymnostomum tenue* Hedw. = ***Gyroweisia tenuis*** (Hedw.) Schimp. (1850: 569)
- Hypnum commutatum* Hedw. = ***Palustriella commutata*** (Hedw.) Ochyra (1850: 585)
- Hypnum cuspidatum* Hedw. = ***Calliergonella cuspidata*** (Hedw.) Loeske (1850: 585)
- Hypnum stramineum* Brid. = ***Straminergon stramineum*** (Brid.) Hedenäs (1850: 585)

* In LANTZIUS-BENINGA (1847 & 1850) the name of *Anacalypta rubella* Huebener (now *Erythrobarbula rubella* Boros) was treated as being close to *Weissia recurvirostris* (written as “*Weissia recurvirostra*”).

- Hypnum sylvaticum* Brid. = ***Plagiothecium sylvaticum*** (Brid.) Schimp. (1847: 22; 1850: 585)
- Orthotrichum anomalum*** Hedw. (1850: 593)
- Orthotrichum affine*** Brid. (1850: 579), as “*Orthotrichum affine (pumilum)*”
- Orthotrichum striatum*** Hedw. (1850: 580)
- Phascum cuspidatum*** Hedw. (1850: 566)
- Phascum patens* Hedw. = ***Physcomitrella patens*** (Hedw.) Bruch & Schimp. (1850: 567)
- Pohlia elongata*** Hedw. (1850: 581)
- Polytrichum commune*** Hedw. (1850: 566)
- Polytrichum nanum* Hedw. = ***Pogonatum nanum*** (Hedw.) P. Beauv. (1850: 586)
- Polytrichum piliferum*** Hedw. (1850: 586)
- Polytrichum urnigerum* Hedw. = ***Pogonatum urnigerum*** (Hedw.) P. Beauv. (1850: 586)
- Racomitrium ericoides*** (Brid.) Brid. (1850: 574), as “*Rhacomitrium*”
- Sphagnum acutifolium* Schrad. = ***Sphagnum capillifolium*** (Ehrh.) Hedw. (1850: 565)
- Sphagnum obtusifolium* Ehrh. = ***Sphagnum palustre*** L. (1850: 565)
- Splachnum ampullaceum*** Hedw. (1850: 577)
- Splachnum sphaericum*** Hedw. (1850: 577)
- Syntrichia subulata* (Hedw.) F. Weber & D. Mohr = ***Tortula subulata*** Hedw. (1850: 573)
- Tetraphis pellucida*** Hedw. (1850: 569)
- Trichostomum tortile* Schrad. (1850: 574) = ***Ditrichum pusillum*** (Hedw.) Hampe
- Weissia controversa*** Hedw. (1850: 571)
- Weissia fugax* Hedw. = ***Rhabdoweisia fugax*** (Hedw.) Bruch & Schimp. (1850: 571)
- Weissia recurvirostris* Hedw. = ***Bryoerythrophyllum recurvirostrum*** (Hedw.) P. C. Chen (1847: 21; 1850: 570)

Table 3. Index of species that were illustrated in LANTZIUS-BENINGA's works of 1847 and 1850. The modern equivalent of the names are given in Table 2.

<i>Anacalypta rubella</i> Huebener (1847: Tab. 1, Figs. 1, 2; 1850: Tab. LVII, Figs. 6, 7)	25, 53
<i>Aulacomnium palustre</i> (Hedw.) Schwägr. (1850: Tab. LXII, Fig. 23)	63
<i>Barbula fallax</i> Hedw. (1850: Tab. LVIII, Fig. 9).....	55
<i>Barbula reflexa</i> (Brid.) Brid. (1847: Tab. 1, Fig. 4).....	25
<i>Barbula tortuosa</i> (Hedw.) F. Weber & D. Mohr (1847: Tab. 1, Fig. 3; 1850: Tab. LVIII, Fig. 8)	25, 55
<i>Bartramia fontana</i> (Hedw.) Turner (1850: Tab. LXIII, Fig. 28).....	65
<i>Ceratodon purpureus</i> (Hedw.) Brid. (1850: Tab. LXVI, Figs. 40, 41.)	71
<i>Dicranum rufescens</i> (With.) Turner (1850: Tab. LX, Fig. 16).....	59
<i>Dicranum schreberianum</i> Hedw. (1850: Tab. LX, Fig. 15)	59
<i>Dicranum scoparium</i> Hedw. (1850: Tab. LVIII, Figs. 10-13; Tab. LIX, Fig. 14)	55, 57
<i>Fissidens adianthoides</i> Hedw. (1850: Tab. LX, Fig. 17)	59
<i>Funaria hygrometrica</i> Hedw. (1850: Tab. LXII, Fig. 24, Tab. LXIII, Figs. 25-27)	63, 65
<i>Gymnostomum pyriforme</i> Hedw. (1850: Tab. LVII, Fig. 3).....	53
<i>Hypnum sylvaticum</i> Brid. (1847: Tab. 1, Fig. 5, 6; 1850: Tab. LXIII, Figs. 29, 30)	25, 65
<i>Orthotrichum affine</i> Brid. (1850: Tab. LXII, Figs. 21, 22)	63
<i>Phascum cuspidatum</i> Hedw. (1850: Tab. LVI, Fig. 2).....	51
<i>Polytrichum commune</i> Hedw. (1850: Tab. LXIV, Fig. 32, 38; Tab. LXV, Figs. 34-36; Tab. LXVI, Figs. 33, 37).....	67, 69, 71
<i>Polytrichum piliferum</i> Hedw. (1850: Tab. LXIV, Fig. 31).....	67
<i>Polytrichum unigerum</i> Hedw. (1850: Tab. LXVI, Fig. 39).....	71
<i>Sphagnum acutifolium</i> Schrad. (1850: Tab. LVI, Fig. 1)	51
<i>Splachnum sphaericum</i> Hedw. (1850: Tab. LXI, Fig. 18-20)	61
<i>Syntrichia subulata</i> (Hedw.) F. Weber & D. Mohr (1850: Tab. LVIII, Fig. 9*, 9**)	55
<i>Tetraphis pellucida</i> Hedw. (1850: Tab. LVII, Figs. 4, 5)	53
<i>Weissia recurvirostris</i> Hedw. (1847: Tab. 1, Fig. 1; 1850: Tab. LVII, Figs. 6, 7)	25, 53

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[original page 17]

Contributions to the knowledge of the inner structure of the mature moss capsule, especially of the peristome

S. Lantzius-Beninga,

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Table I.

The results of a series of examinations of the structure of the mature, not yet disintegrated moss capsule, especially in relation to the structure of the peristome which I had the occasion to execute this summer are presented here as a provisional excerpt; I hope to be able to present a more detailed description soon.

On the construction of the capsule in general I found not much remarkable. Hedwig at first distinguished the columella, and the inner and the outer capsule membrane; between the inner capsule membrane and the columella should be located the spores.

In my dissertation in the year 1844 (*De evolutione sporidiorum in capsulis muscorum*. Göttingae 1844. 4.) I said already, that I cannot take as natural such a separation and the designation of the inner parts of the moss capsule. At that time I made the suggestion that the inner capsule membrane and the two outer cell layers of the columella which, not only enclose the spore space and seem to be important for the support of the mother cells and for the forming of the spores, but also because the cells by their shape and content differ from all the other capsule cells, may be considered as a peculiar inner organ of the moss capsule. I have drawn the attention to the fact that in several species of *Polytrichum* this organ, along its entire length, [original page 18] is separated from the outer capsule membrane as well as of the columella and is connected with it only in the upper and lower parts of the capsule. At present, having examined many more moss capsules, I cannot but repeat this suggestion, in which I will use provisionally the name spore sac, however in a different sense to that of Bruch and Schimper. (The authors Bruch and Schimper inappropriately designate by the name spore sac Hedwig's membrana capsulae interior.)

All the mosses which I could examine agree essentially, so far, in that which concerns the construction of the lower and median parts of the capsule. More interesting is the upper part, beginning at the upper border of the spore sac, which after the operculum has detached, reveals the orifice of the capsule with the peristome.

Mosses without peristomes have in this part an absolutely uniform cell tissue showing nothing unusually remarkable. Worthy of mention is *Sphagnum* with the peculiarity that it has no separation of the spore sac from the outer capsule membrane and that the columella (at least from all the examinations I made) does not reach to the point of the operculum but is standing freely in the middle of the capsule like a pillar, being completely surrounded with spores at the sides and above.