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ACTES COLLOQUE ASCONA

*USES, PRACTICES AND FUNCTIONS OF HISTORICAL HERBARIA*

# THE FOUNDING OF MODERN BRYOLOGY AND THE LEGACY OF JOHANNES HEDWIG: EIGHT GOOD PRACTICES FOR BRYOPHYTE TAXONOMY

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**Abstract**

The « Uses, practices and functions of historical herbaria » conference in Ascona, Switzerland in November 2023 provided an unprecedented opportunity for exchange and discussion on the roles, importance and scientific value of historical herbarium specimens. The scientific contributions of the cryptogamist and bryologist Johannes Hedwig (1730-1799), including his 250-year-old herbarium collection, which is housed in the Conservatory and Botanical Garden of Geneva, have had a long-lasting impact on modern bryophyte systematics. He was a pioneer in his time, using his critical thinking, specimens, observations, microscopes, experiments and interpretations of living and preserved material to explore and document diversity in cryptogams, especially mosses, and attempting to understand their life cycles, reproductive structures and dispersal mechanisms. A brief biography of J. Hedwig is presented, followed by a focus on the scientific significance of his published works and herbarium. Reflections on the type and scope of his contributions to the field of bryology led to the realisation that a set of eight good practices for bryophyte taxonomy can be derived from his approaches and way of thinking, namely the importance of field work; specimens and reference herbaria; microscopic observations; scientific illustration; detailed botanical descriptions; standardised terminology; critical analysis of traits, forms and functions; and questioning both the known and the unknown.

**Keywords:** historical herbarium, descriptions, illustrations, terminology, microscopes.

**Résumé**

La conférence « Usages, pratiques et fonctions des herbiers historiques » qui s'est tenue à Ascona, en Suisse, en novembre 2023, a offert une occasion sans précédent d'échanger et de discuter des rôles, de l'importance et de la valeur scientifique des spécimens d'herbiers historiques. Les contributions scientifiques du cryptogamiste et bryologue Johannes Hedwig (1730-1799), notamment sa collection d'herbiers vieille de 250 ans conservée au Conservatoire et Jardin botanique de Genève, ont eu un impact durable sur la systématique moderne des bryophytes. Il a été un pionnier en son temps, utilisant sa pensée critique, ses spécimens, ses observations, son microscope, ses expériences et ses interprétations du

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matériel vivant et préservé pour explorer et documenter la diversité des cryptogames, mais surtout des mousses, ainsi que pour tenter de comprendre leur cycle de vie, leurs structures de reproduction et leurs mécanismes de dispersion. Une brève biographie de J. Hedwig est présentée, suivie d'une mise en lumière de l'importance scientifique de ses publications et de son herbier. Des réflexions sur le type et la portée de ses contributions au domaine de la bryologie ont permis de réaliser qu'un ensemble de huit bonnes pratiques pour la taxonomie des bryophytes peut être dérivé de ses approches et de sa façon de penser, à savoir l'importance du travail sur le terrain, des spécimens et d'un herbier de référence, des observations microscopiques, de l'illustration scientifique, des descriptions botaniques détaillées, de la terminologie standardisée, de l'analyse critique des traits, des formes et des fonctions, et de la remise en question à la fois de ce qui est connu et de ce qui est inconnu.

**Mots-clés**: herbier historique, descriptions, illustrations, terminologie, microscopes.

## Zusammenfassung

Die Konferenz « Uses, practices and functions of historical herbaria » im November 2023 in Ascona (Schweiz) bot eine noch nie dagewesene Gelegenheit zum Austausch und zur Diskussion über die Rolle, die Bedeutung und den wissenschaftlichen Wert historischer Herbariumsexemplare. Die wissenschaftlichen Beiträge des Kryptogamisten und Bryologen Johannes Hedwig (1730-1799), einschließlich seiner 250 Jahre alten Herbarsammlung, die im Konservatorium und Botanischen Garten von Genf aufbewahrt wird, hatten einen nachhaltigen Einfluss auf die moderne Bryophyten-Systematik. Er war zu seiner Zeit ein Pionier, der sein kritisches Denken, seine Proben, seine Beobachtungen, sein Mikroskop, seine Experimente und seine Interpretationen von lebendem und konserviertem Material einsetzte, um die Vielfalt der Kryptogamen, insbesondere der Moose, zu erforschen und zu dokumentieren und zu versuchen, ihren Lebenszyklus, ihre Fortpflanzungsstrukturen und ihre Ausbreitungsmechanismen zu verstehen. Nach einer kurzen Biografie von J. Hedwig wird die wissenschaftliche Bedeutung seiner veröffentlichten Werke und seines Herbariums hervorgehoben. Überlegungen zu Art und Umfang seiner Beiträge zur Bryologie führten zu der Erkenntnis, dass sich aus seinen Ansätzen und seiner Denkweise eine Reihe von acht bewährten Praktiken für die Taxonomie der Moose ableiten lassen, nämlich die Bedeutung von Feldarbeit, Belegexemplaren und einem Referenzherbarium, mikroskopische Beobachtungen, wissenschaftliche Illustration, detaillierte botanische Beschreibungen, standardisierte Terminologie, kritische Analyse von Merkmalen, Formen und Funktionen sowie die Hinterfragung sowohl des Bekannten als auch des Unbekannten.

**Stichwörter:** Historisches Herbarium, Beschreibungen, Abbildungen, Terminologie, Mikroskope.

## INTRODUCTION

The cultural, patrimonial and scientific significance of natural history collections, including herbaria, is well documented (Bebber *et al.*, 2010; Carine *et al.*, 2018; Davies, 2023; Flannery, 2023; Funk, 2018; Johnson *et al.*, 2023; Suarez & Tsutsui, 2004). Collections of plant specimens that have been deposited in the herbaria of recognised botanical institutions for safekeeping, centralisation and assured access provide a window into past and present biodiversity. Collectively, herbaria play a crucial role in the documentation, description and understanding of plant species. In a traditional context, the over 400 million plant specimens held in global botanical collections, also termed a meta-herbarium (Davies, 2023), form the foundation for taxonomic endeavours as they provide material that is used for comparative purposes, establishing taxa concepts, describing and circumscribing species, underpinning nomenclature, and classifying taxa in an evolutionary context. Herbaria are also a source of data for research that goes above and beyond the traditional taxonomy-based approaches to specimen use, providing opportunities to utilise plant specimens in many different ways, such as herbariomics and phenological, distribution or herbivory studies, and long-term datasets for change analyses and conservation purposes, among others (Card *et al.*, 2021; Davies, 2023; Lister, 2011; Meinecke *et al.*, 2019; Soltis, 2017).

Within the body of plant specimens housed within any given institution, there may be sets of specimens of a particular origin or related to a particular voyage, collector, taxonomist or scientific publication that are of special scientific and historical interest. These are often termed «historical collections». They are frequently accorded curatorial priority for preservation purposes and may also be stored separately from general holdings. Historical collections may contain a disproportionally large number of types that form essential nomenclatural reference points in the taxonomic process or material that is critical in understanding the original concepts of taxa within the context of the time. Historical collections vary in their format, volume and state of preservation, as well as the procedures that were used for drying, mounting, labelling, presenting and storing the material, which can be far from the standards and best practices that are implemented today. Additionally, the information available on the specimen sheets or packets or accompanying them, such as the labels, notes or associated field journals, differ in the amount, quality and accuracy of the information provided.

Scientists working with historical material are thus confronted with plants that were collected, dried, mounted, labelled, documented and stored in ways that differ, often widely, from the practices of today. Working with older collections often requires the skills of a historical detective to establish where, when and from whom the collection originated, retrace how the collection arrived at its current location, establish which scientists were associated with it over its lifetime, and if there is archival material in existence on the collection and/or its creator as well as on any of its subsequent owner(s). This type of historical detective work continues at the level of the specimens, often on a specimen-by-specimen basis, as it is necessary to decipher who may have written labels or annotated the original labels by hand, what the label information signifies, from when and where the specimen(s) originated, and who collected the organism(s) or part thereof, if all specimens in the same preparation originate from one gathering and/or represent a single taxon and what the label and annotations or citations may signify, if present, on the original sheets.

The richness of taxonomic, geographic, biological and ecological information contained within botanical collections is being mobilised across the globe through specimen digitisation efforts, often on a massive scale

(De Smedt, 2024; Hedrick *et al.*, 2020; Page *et al.*, 2015). The implementation of agreed standards for the generation, accessibility, sharing and interconnection of biodiversity data from specimens, according to FAIR data principles (Wilkinson *et al.*, 2016), and the aggregation of biodiversity knowledge by global initiatives provides unprecedented open digital access to botanical data for scientific research on an ever increasing scale (Nelson & Ellis, 2019; Page *et al.*, 2015; Soltis, 2017; Walker *et al.*, 2022). Digital access to historical specimens as well as any associated documents or publications associated with them, if they have been scanned, provides unprecedented opportunities for researchers to view material that is important for interpreting the historical and taxonomic context of specimens. The use and interpretation of historical specimens adds an important time dimension to the description, circumscription and understanding of species, especially as they may show how species were interpreted when described, allowing us to see how circumscriptions or concepts may have changed over time.

An example of the importance of historical specimens is demonstrated by the moss collection of Johannes Hedwig (1730-1799) that was compiled by him between around 1765 and 1798. Acknowledged as one of the founders of modern bryology, Hedwig was a pioneer of his time, using his specimens, observations, microscopes, experiments, critical thinking and interpretations of living and preserved material to explore and document diversity in mosses as well as attempt to understand their life cycles, reproductive structures and dispersal mechanisms. From a bryological perspective, Hedwig promoted the use of the microscope to better define and understand mosses and their specific traits. He described 82 species that were new to science and greatly increased the number of moss genera in use at the time, from 6 in Dillenius (1741) and 8 in Linnaeus (1753) to 35 in his seminal work (Hedwig 1801), effectively beginning the process of scientific recognition of the taxonomic diversity of this group of plants using their microscopic and macroscopic traits.

## JOHANNES HEDWIG (1730-1799)

Several biographies of Johannes Hedwig have been published (see Wagenitz, 2000), the most significant of which are Schwägrichen (1801), Deleuze (1803) and Römer (1909), with those of Florschütz (1960), Frahm (2000) and Heltmann (1980), providing syntheses of earlier works.

Johannes Hedwig (1730-1799) was born on 10 December 1730 in Brașov (Kronstadt or Brassó) in Transylvania, in present-day Romania, to Agnetha and Jakob Hedwig, a family of shoemakers of modest means (see Györffy, 1930 for information on Hedwig's birth date and Flörschütz, 1960 on the profession of his father). After the death of his father, at the age of 17, Hedwig went to Vienna, Austria, and then to Bratislava in the current day Slovakia to pursue his education. Two years later, he left for Zittau in Saxony, Germany, to attend secondary school and prepare to enter university. In 1752, he attended the University of Leipzig, working in the library and botanical garden to finance his studies. He was awarded his bachelor's degree in 1756 and his doctoral degree in 1759 based on his thesis «De emesi in febribus acutis» or «On emesis in acute fevers». A university career at that time was out of his means, as he needed to obtain a formal qualification to become a university professor; thus, he moved to the German town of Chemnitz in 1760. He started a medical practice there, and about two years afterwards married his first wife, Susanne Sophia Teller, the daughter of a local minister, with whom he had 9 children, 3 of whom died in infancy and 2 in childhood. His medical practice enabled him to gain some financial independence as well as affording him time to botanise early in the morning and to study the plants he had collected in the evening. It is thought that he first became familiar with the flowering plants of his region before turning his attention to cryptogamic plants, especially mosses. His collection activities also led him to create a herbarium of note (see section *The nomenclatural significance of Hedwig's works and herbarium collection*).

Hedwig appears to have communicated with botanists of his time, including Johann Christian Daniel von Schreber (1739-1810), a student of Carl Linnaeus, who was writing a flora of the Leipzig region. Schreber is said to have sent him a microscope with a 50× magnification capacity and some books, although which ones remain unknown. With a microscope at his disposal, Hedwig began to examine vascular plants (he was one of the first scientists to document and interpret stomata [HEDWIG, 1784, Tab. III; 1793-1797]) and then cryptogams and their reproductive structures before turning his attention to mosses. As time went on, he was able to update his microscope to a compound one with a 170-290× magnification capacity, with some sources citing a Mr. J. G. Köhler, inspector of mathematical instruments at Dresden, as having given Hedwig this instrument (FRAHM, 2000). Aware of the critical importance of drawings in communicating his observations, around 1774, he taught himself to draw so he could properly illustrate the structures and morphological features of the different taxa he examined. His original illustrations were reproduced, most likely using copper plates, and hand coloured to accompany his published works. They are a great testament to both his observational and botanical illustration skills. Unfortunately, the whereabouts of Hedwig's original illustrations are unknown.

After losing his first wife in 1776, Hedwig married Klara Benedikta Sulzberger, originally from Leipzig, in 1778, with whom he had a further six children, five of whom died in infancy and one at the age of 16. This same year, he published his first scientific article on the sexual organs of mosses wherein he detailed antheridia for the first time (HEDWIG, 1778). In 1781, Hedwig and his family moved to Leipzig, and he published his two-part work *Fundamentum historiae naturalis muscorum frondosorum* (HEDWIG, 1782) that focused on anatomy (fig. 1) and reproduction, including fertilisation, in mosses, with a synoptic key (Part II, pages 83-84) to the genera of mosses he recognised that incorporated characteristics that he had observed over his 20 years of study. This work significantly raised his scientific standing at the time, even if some of his contemporaries were rather sceptical of his findings (for example, PALISOT DE BEAUVOIS, 1805).

In 1783, the Academy of Sciences of St. Petersburg, Russia, offered a prize for the best publication on reproduction in cryptogams. Hedwig prepared and submitted a work entitled *Theoria generationis et fructificationis plantarum cryptogamicarum*, synthesising his observation-based knowledge on reproduction in fungi, lichens, algae, liverworts, mosses, horsetails, lycopods and ferns. This work was presented by group and accompanied by 37 illustrative plates. It was published in the proceedings of the Academy in 1784, and he was awarded a sum of money and a gold medal for his efforts. With this recognition, his scientific reputation was established both inside and outside of Germany. He was appointed as a physician at the Leipzig military hospital, a position that he held for two years before being nominated as Professor of Botany and Director of the Botanical Garden at the University of Leipzig, with this appointment supported by the Prince of Saxony, Frederick Augustus (1750-1827), to overcome his lack of the necessary formal requirements to become a professor at that time. Hedwig went on to publish several more books, such as *Descriptio et adumbratio microscopico-analytica muscorum frondosorum* in four volumes, each with 40 plates (HEDWIG, 1785-1787, 1789, 1791-1792, 1793-1797) and

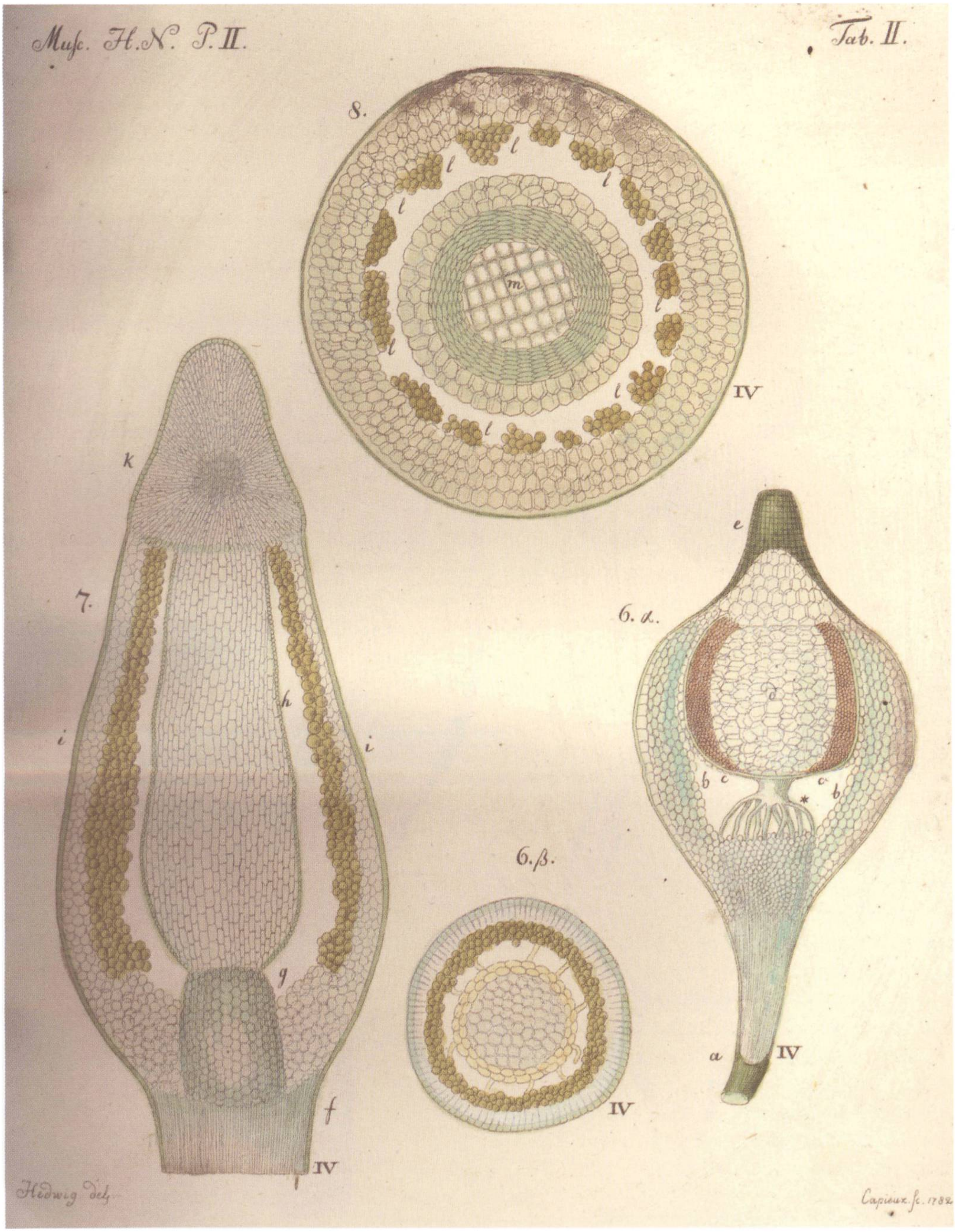


**Figure 1.** A plate (Part II, Tab. II) from Hedwig's *Fundamentum historiae naturalis muscorum frondosorum* of 1782 showing the details he observed in a longitudinal and transverse section of the capsule in *Leptobryum pyriforme* (Hedw.) Wilson (given as «Bryi *pyriformis*», fig. 6) and *Orthotrichum striatum* Hedw. (given as «Bryi *Striati* Linn.», fig. 7, 8).

scientific articles (see WISSEMANN, 2000), with his award-winning *Theoria generationis* reprinted in Leipzig in 1798 with revisions. He died on 18 February 1799 at the age of 69 after his health deteriorated due to the flu and possibly typhoid. He was survived by his second wife and four children from his first marriage, two girls and two boys, one of whom, Romanus Hedwig (1772-1806), followed in his fathers' footsteps becoming a physician and botanist, taking over his position at the University of Leipzig.

## THE SCIENTIFIC SIGNIFICANCE OF HEDWIG'S WORKS

A relatively late starter, Hedwig began to study cryptogams, including mosses, around the age of 35, publishing his first scientific contribution on them at the age of 48 and his last, while living, at the age of 68. Although his works (see WISSEMANN, 2000) are not as numerous as some of his contemporaries, they still represent a consequent body of publications. His thorough, detailed and well-illustrated scientific accounts of his observations have had a long-lasting impact in the field of bryology (see also FLORSCHÜTZ, 1960; GEISSLER, 2000; VITT, 2000) as well as on the recognition and understanding of the biology of cryptogams more broadly. At the time Hedwig was active, organisms that did not have overtly visible reproductive structures were frequently grouped together under the «Cryptogamae» of LINNAEUS (1753), such that lichens, bryophytes, some algae and lycopods were treated as being part of one class within the Linnaean system. Hedwig proposed the separation of lichens and bryophytes and further separated mosses from liverworts (HEDWIG, 1784).

Known as the «Father of Bryology», Hedwig revolutionised the way mosses were interpreted and understood by using his 50× linear magnification microscope to observe and document their macro- and microscopic features (see HEDWIG, 1787-1797). He examined different features of mosses in both stages of their life cycle, also focusing in some detail on the peristome (fig. 2). He was among the first to produce and publish numerous detailed illustrations of his observations of the features of cryptogamic plants, especially mosses, using a special technique to prepare material for microscopic examination using a hand lens (see also the illustration on page 269 from the 1798 version of *Theoria generationis*) and a method he had developed to draw the magnified structures from his microscope using the preparation slides he had made. He was also the first to extensively use microscopic characteristics to group and distinguish taxa, as evidenced in his descriptions, terminology and illustrations as well as in the generic keys he published in his works.

His treatments of the moss species he recognised, especially in *Descriptio et adumbratio microscopico-analytica muscorum frondosorum* (HEDWIG, 1785-1787, 1789, 1791-1792, 1793-1797), are very detailed for the time. In the latter work, his species treatments are composed of three sections: the species page, the plate and the description, in either order. The species pages were headed by the Roman numerals for the plate with the binomial name of the species, a short Latin diagnosis, citations of literature sources for the species and the figure legend. The descriptions are 1-3 pages in length and organised under sub-headings, depending on the taxon, that became standardised over the first volume as: «*Radices*», «*Truncus*», «*Folia*», «*Flos*», «*Vaginula*», «*Calyptra*», «*Pedunculus*», «*Theca*», «*Operculum*», «*Annulus*», «*Peristomia*» and «*Semina*». Following from the description, indications on the locality («*Locus*»), but not always, biology, features or comments on the species were given. Implementing standardisation in the format of the descriptions of the moss species he recognised facilitated comparisons between taxa and their subsequent

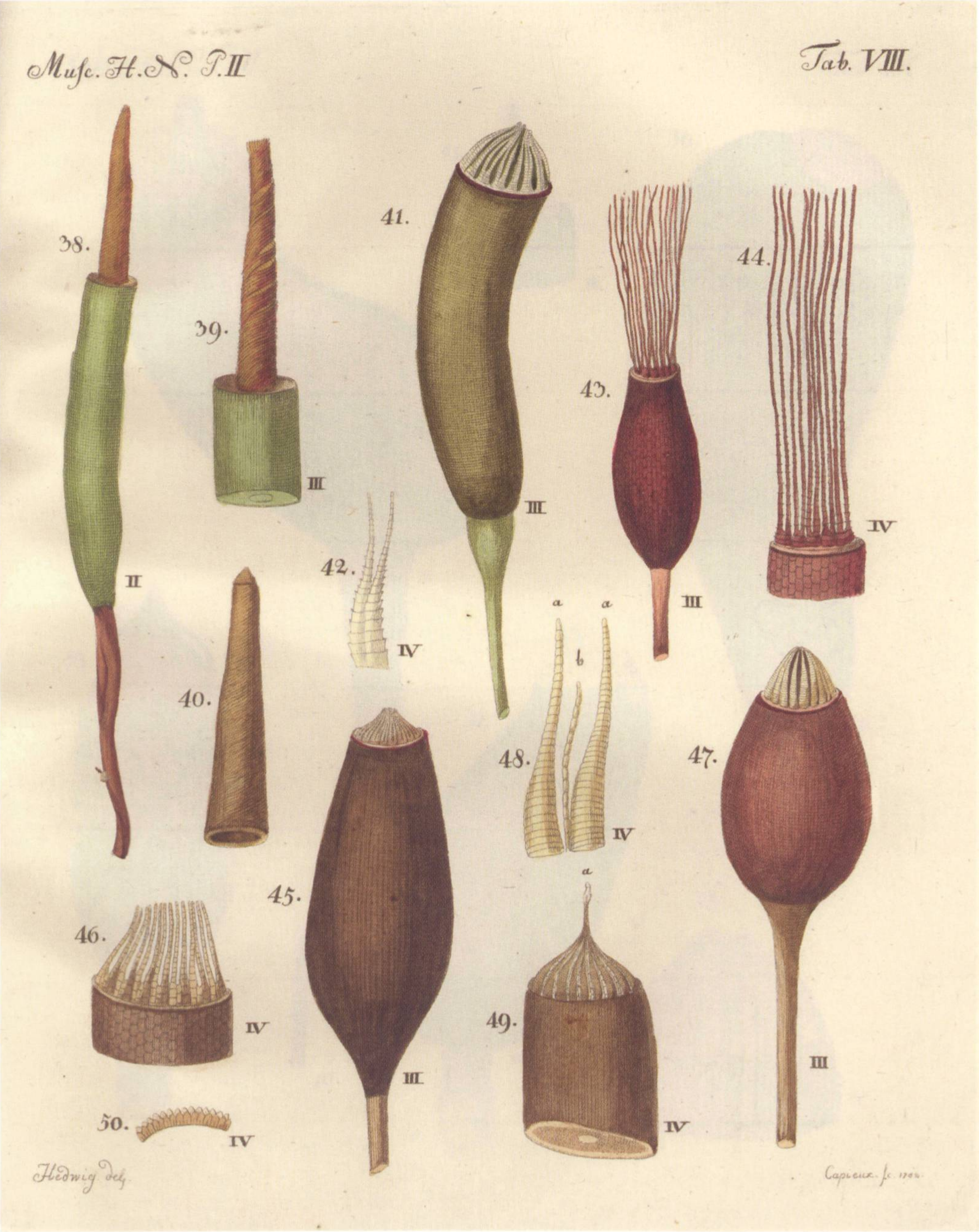


**Figure 2.** A second plate (Part II, Tab. VIII) from Hedwig's *Fundamentum historiae naturalis muscorum frondosorum* of 1782 showing a selection of different peristomes, an operculum, peristome teeth and an annulus, from five species of five modern families, as follows: *Tortula subulata* Hedw. (38-40), *Dicranum scoparium* Hedw. (41 & 42), *Racomitrium lanuginosum* (Hedw.) Brid. (43 & 44), *Leucodon sciuroides* (Hedw.) Schwägr. (45 & 46) and *Neckera crispa* Hedw. (47 & 48).

identification using the sets of traits given and supported by his illustrations.

His illustrations of mosses in *Fundamentum historiae naturalis muscorum frondosorum* (HEDWIG, 1782), *Theoria generationis et fructificationis plantarum cryptogamicarum* (HEDWIG, 1784), *Descriptio et adumbratio microscopico-analytica muscorum frondosorum* (HEDWIG, 1785-1787, 1789, 1791-1792, 1793-1797) and *Species muscorum frondosorum* (HEDWIG, 1801) amounted to 244 plates from a total of 284, with the remainder featuring hepatics, lichens, fungi, algae, horsetails and ferns. When illustrating moss species, for the most part, he included depictions of the plants in their original and magnified size (fig. 3, tab. IX, f. 55 & 56), frequently with sporophytes present, and magnified depictions of the leaves, capsules, peristomes, gametangia (often also the archegonia and antheridia *in situ*, see fig. 3, tab. IX, f. 60-64) and spores as well as, depending on the taxon, a close up of the leaf cells, leaves *in situ* on the stems, tomentum, the annulus, operculum or a close-up of the peristome teeth. Unlike the illustrations of mosses from his predecessor DILLENIUS (1741), Hedwig's images allow for the discernment and identification of species, with characteristics shown that remain recognisable and usable today.

Detailing different morphological and anatomical structures in mosses, as observed under the microscope, he proposed a terminology and definitions that he developed through his works, including a section «*Terminorum botanicorum as muscos applicato*» (HEDWIG, 1801: 1-16) where he detailed the parts of the plants he used in his descriptions (*radix, truncus, petiolus, pedunculus, folium, perigonium, genitalia feminea, vaginula, calyptra, sporangium, columella, sporangidium, apophysis sporangis, annulus, operculum*), elucidating the traits he had observed for each one across the taxa he treated, thus providing a standardised approach to descriptions that allowed for comparisons of similarities/differences between taxa. His collective works introduced a substantial number of concepts and terms into the bryological lexicon that we still use today. He used features observed under the microscope, namely the presence/absence of an operculum, the presence/absence of a peristome, peristomes with one or two rows of teeth, and the form of the antheridia, which he termed a «male flower», to propose an identification key for the moss genera he recognised (a fold-out insert added between pages 16 and 17). Although his key was not a true classification *per se,* it structured the arrangement of genera into a systematic order and provided diagnostic characteristics to distinguish them (see HEDWIG, 1801).

Above and beyond these taxonomic contributions, Hedwig revolutionised the bryological thinking of his era by interpreting mosses, their reproductive structures and their life cycles in a new light, explaining that mosses were not simply miniaturised vascular plants or organisms that did not reproduce sexually (VON HALLER, 1768; NECKER, 1774). His discovery of antheridia and their function as well as his theory that the capsule and spores, which he named «*sporangium*» and «*sporae*», were equivalent to a fruit with seeds in flowering plants, rather than an anther with pollen, as previously believed (LINNAEUS, 1753). This finding set the stage for rethinking the understanding of moss biology at that time. His theory was further supported when he germinated moss spores and noted that the young plants arose from the protonema, demonstrating that the spore was the unit of dispersal that gave rise to the next generation in mosses.

FRAHM (2000) indicated that Hedwig had an advantage by starting off as an invested amateur who was not attached to an institution or any particular school of thinking; thus, he was able to conduct his work free from any influences and to publish his observations without causing any immediate scientific offence. He also hypothesised that Hedwig did not adhere

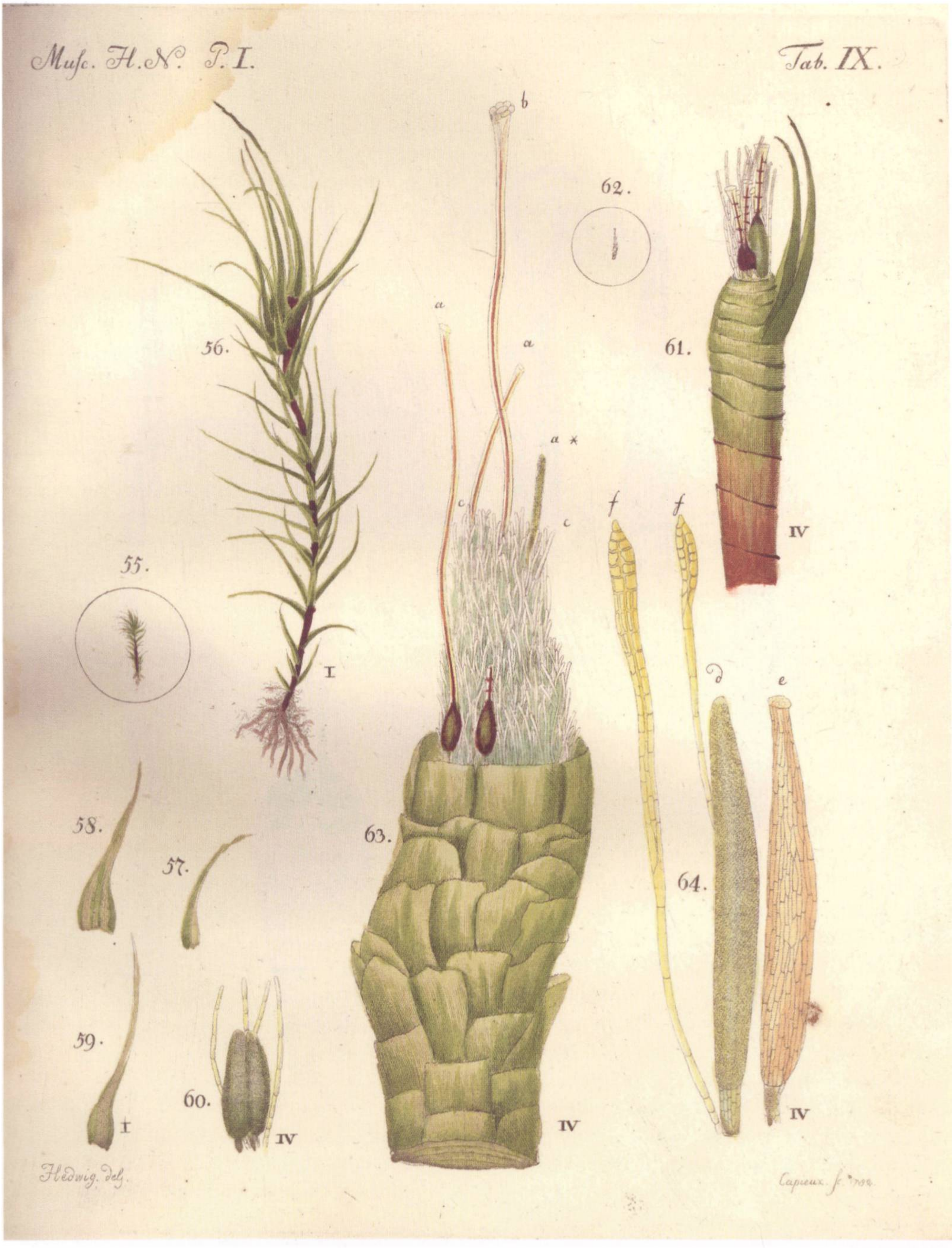


**Figure 3.** Illustration of the true-sized and magnified plants (55 & 56), magnified leaves (57-59) and gametangia (archegonia, 61-63 and antheridia, 60, 64) in *Dicranella heteromalla* (Hedw.) Schimp. from Hedwig's *Fundamentum historiae naturalis muscorum frondosorum* of 1782.

as closely as would be expected to the rule of «it cannot be what may not be» as ordained through a belief in the Bible or in the content of the works of Aristotle or Linnaeus (see FRAHM, 2000: 8). Thus, he freely questioned his observations and hypothesised based on his findings, without trying to fit either inside a pre-ordained system or school of understanding.

## THE NOMENCLATURAL SIGNIFICANCE OF HEDWIG'S WORKS AND HERBARIUM COLLECTION

Hedwig kept a herbarium collection of around 1200 sheets (C. BONNER in FLORSCHÜTZ, 1960) that he used as a reference for his studies and publications. His herbarium sheets, covers and storage materials were made using good quality materials and his specimens were carefully prepared and mounted (see PRICE, 2005). The herbarium sheets were kept inside blue covers that were grouped together within larger cardboard folders by genus and stored alphabetically in specially made protective storage boxes. He wrote an account on the preparation, use and storage of a herbarium for young botanists (HEDWIG, 1797), demonstrating his understanding of the importance of creating a practical tool for his taxonomic endeavours. His specimens were pressed and attached with glue to 17- × 21-cm herbarium sheets that were, for the most part, labelled in his hand with the citations of the sources of the species, for example, HEDWIG (1785-1797), *Muscologia recentiorum* of BRIDEL (1798), *Historia muscorum* of DILLENIUS (1741) and *Species plantarum* of LINNAEUS (1753, 1762). For some specimens, a locality and sometimes also a collector are given if the specimen was communicated to him by a fellow botanist, for example, Gotthilf Heinrich Ernst Muhlenberg (1753-1815) from Pennsylvania, USA, or Olof Swartz (1760-1818) from Sweden (see PRICE, 2005).

Before his death in early February of 1799, Hedwig was working on his seminal book, *Species muscorum frondosorum*, which was published posthumously in 1801. Hedwig's widow invited one of his former students, Christian Friedrich Schwägrichen (1775-1853), to edit and complete the work for publication. Schwägrichen (1799) communicated that Hedwig had completely finished the manuscripts for 14 genera (see list in PRICE & ELLIS, 2011) and in part for *Barbula* Hedw., leaving the remainder of the genera and some previously un-described or otherwise troubling species to be completed, to varying degrees. Comments that Schwägrichen added to Hedwig's original text were indicated «[S]». Evidence of Schwägrichen's work with Hedwig's original material can be seen in his annotations of Hedwig's original labels when he added material alongside the original specimens on the Hedwig herbarium sheet (PRICE, 2005). The presence of different gatherings, and sometimes of different taxa, that were added at a later date implies that careful interpretation of the material and annotations on the herbarium sheets for the Hedwig moss names is needed to correctly identify the original material and ensure correct typification (see GEISSLER, 2000; PRICE, 2005).

Hedwig's careful observations of mosses, creation or application of terms and definitions for the macro- and microscopic structures he saw, detailed descriptions of the species he recognised, illustrations of the main features of the plants he observed, recognition of 35 moss genera, and his character-based identification keys provided what was one of the foremost systematic frameworks for this group of plants, as evidenced in *Descriptio et adumbratio microscopico-analytica muscorum frondosorum* (HEDWIG, 1785-1797) and cumulating in *Species muscorum frondosorum* (HEDWIG, 1801). This realisation led bryologists to propose that this latter work be designated as the starting point of nomenclature in mosses (expecting the Sphagnaceae). This proposal was accepted at the International Botanical Congress in Brussels, Belgium, in 1910, with the consequence that all moss names preceding its publication, now set as 1 January 1801, no longer had any nomenclatural standing (see FLORSCHÜTZ, 1960 and MARGADANT, 1968). *Species muscorum frondosorum* contains 372 descriptions of mosses, including 3 species of *Sphagnum* L. and 82 species and 2 varieties that were described by Hedwig as new to science. All 285 names (except for *Sphagnum*) enumerated in Hedwig's 1801 work, which were derived from earlier authors, were ascribed to him. His herbarium thus became an important source of potential original material for many of the early moss names (see GEISSLER, 2000 and PRICE, 2005), from which nomenclatural types could be designated. The cover illustration for this work contains references to Hedwig and his work, as a microscope can be seen, with the figures depicted appearing to be studying mosses (fig. 4).

## THE GOOD PRACTICES OF JOHANNES HEDWIG FOR BRYOPHYTE TAXONOMY

*Field work:* Observations of plants in their natural states and habitats is important in understanding their ecology, biology and features as observed under the microscope as well as to obtain material for a reference collection.

*Specimens and a reference herbarium:* Carefully collected, prepared and preserved specimens are an essential tool for morphological and anatomical study, for comparative purposes, and for providing material that can be used for species description, circumscription and illustration, with specimens serving as a «reference» for known species.

*Microscopic observations:* The examination and study of moss species under the microscope, especially of their anatomical and morphological structures, facilitates the interpretation of their construction, composition and functions, thus facilitating their detailed description and the elucidation of their relationships to other taxa.

*Scientific illustration:* Detailed drawings of plants, their different organs, and their diagnostic and morphological-anatomical features document the observations and facilitate their understanding, permitting reproducible comparisons within and between taxa as well as providing a tool for identification purposes.

*Botanical descriptions:* Comprehensive explanations of the observed plants and their different organs as well as their diagnostic and anatomical features, according to an organised and standardised schema, provide a tool for identification purposes as well as facilitating comparisons between taxa and the analysis of their different characteristics.

*Terminology:* The clear descriptive definition of morphological and anatomical structures is essential for promoting an understanding of the features observed and communicating on observations, with the application of consistent terms to define these features facilitating reproducibility, comparability and reuse.

*Critical analysis of traits, forms and functions*: The observation of plants in the field and under the microscope, combined with the exploration, documentation and analytical interpretation of their morphological and anatomical traits, increases the understanding of species, their biology, ecology and evolutionary relationships, especially when combined with innovative approaches or tools.

*Questioning the known and the unknown:* Integrative and innovative approaches to understanding species, their biology and their characteristics allow for novel findings and new interpretations of the body of knowledge. The constant reassessment of the state of knowledge based on new specimens, data or observations challenges our understanding and promotes discovery, sometimes also evoking paradigm shifts. The mode of thinking in Hedwig's time of «it cannot be what may not be» transforms into «it could be what may not be».

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SPECIES
MUSCORUM FRONDOSORUM
DESCRIPTAE ET TABULIS AENEIS LXXVII COLORATIS ILLUSTRATAE.

OPUS POSTHUMUM
EDITVM
A
FRIDERICO SCHWAEGRICHEN
MED. ET PHIL. D. SOC. BOT. RATISB. MEMB. HON. ET LINNEAN. LIPS. SOD.

LIPSIAE,
SUMTU JOANNIS AMBROSII BARTHII
MDCCCI.
PARISIIS, APUD AMAND KOENIG, QUAY DES AUGUSTINS NO. 18.

**Figure 4.** Cover page of Hedwig's posthumously published *Species muscorum frondosorum* of 1801. The illustration is a tribute to Hedwig in as much as a microscope is depicted and the figures appear to be studying mosses in some way or another.

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