Burdon Sanderson's 1849 undergraduate essay on 'Vegetable Embryology'

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ABSTRACT

John Scott Burdon Sanderson was a leading nineteenth century biologist who became Regius Professor of Animal Physiology at Oxford University. This paper outlines his early botanical investigations focusing on the rediscovery of his prize-winning essay on *Vegetable Embryology* written for his botany courses while he was a medical student at Edinburgh University. This unpublished fifty-two page essay, written in 1849, is remarkable for an undergraduate. It provides an accurate review of the history of plant fertilization and argues that the plant embryo develops from a cell in the embryo sac, rather than from the tip of the entering pollen tube, as posited by Schleiden, the founder of the cell-theory. The essay also criticizes the cell theory for failing to explain the fundamental need for fertilization to ensure the continuation of life. The essay includes his own observations of the embryology of *Hippuris*, *Orchis*, and *Capsella* and other plants. Burdon Sanderson's early botanical studies on plant movement and was likely a stimulus for his later work on *Dionaea* (Venus' flytrap), now fully appreciated for its foundational demonstration of electric action potentials in plant signal transduction. His reluctance to use the word 'germ' in his later studies of infectious diseases may have stemmed from his common usage of that word in describing the cell originating the plant embryo.

[Entire text: 7,557; Abstract: 216 words]

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INTRODUCTION

Sir John Scott Burdon Sanderson (1828-1905) (Fig. 1a) was a major scientific figure in late nineteenth century Britain, but a person now largely forgotten in the popular sphere, but who carried out incisive experiments that drove forward our understanding of infectious diseases in the pre-Pasteur era (Worboys 2000). As Regius Professor of Animal Physiology at Oxford, he established medical research as an important enterprise, independent from but complementary to clinical and hospital settings (Romano 2002). Details of his life can be found in Sturdy (2004), in a biography (Burdon Sanderson, G. 1911) written by his wife, Ghetal Burdon Sanderson (1833-1909), and in several obituaries (Anon. et al. 1905; Galton 1907). However, in these biographies there are no detailed analyses of his early botanical contributions.

Burdon Sanderson had an intellectual breadth and experimental application that was exceptional for those times. He produced books on experimental physiology (Burdon Sanderson 1867, 1882) and made large inroads into our understanding of the germ theory of disease (Burdon Sanderson 1867, 1870). Charles Darwin (1809-1882) used his work on cattle plague (Burdon Sanderson 1866) as an analogy to illustrate his theory of pangenesis (Darwin 1875: 272, footnote 47). Later as Professor of Physiology at University College, London, Burdon Sanderson corresponded with Darwin on insectivorous plants, their movement and digestion (Darwin Correspondence Project[1]). When he is cited in the current literature (Hedrich & Kreuzer 2023), it is usually not for his work on animal physiology or infectious disease, but for the measurement of electrical signaling in the insectivorous plant *Dionaea muscipula*, Venus' fly trap (Burdon Sanderson 1873; Williams 1973[2]).

A brief note about Burdon Sanderson's family name may be helpful. It is unhyphenated and became necessary to enable Burdon Sanderson's father, Richard Burdon (1791-1865) to receive the hand of Elizabeth Sanderson (1797-1864), the only daughter of the then Mayor of London (Collinge 1986). As a young student at Edinburgh University, Burdon Sanderson dropped 'Burdon' and signed himself as John Scott Sanderson.[3] When a doctor in London, and

[1] https://www.darwinproject.ac.uk/letter/?docId=nameregs/nameregs_4177.xml&query=professor; accessed 26 Aug 2025.
[2] Contains a full bibliography of his studies on movement in Venus' flytrap.
[3] I use his unhyphenated last name throughout. Where the name is otherwise in the original publication (including references) this is indicated by square brackets.

living on the same street as another Sanderson, confusion in postal delivery led him to change his name back to Burdon Sanderson (Burdon Sanderson, G. 1911: 22). Through his sister Mary Elizabeth Burdon Sanderson's (1825-1925) marriage to Robert Haldane (1805-1877), the "John Scott Burdon Sanderson" combination of names have persisted into subsequent Haldane generations. Perhaps the best known, to biologists at least, is John Burdon Sanderson Haldane (1892-1964), often known simply as "J.B.S.", whose work on population genetics was central to understanding evolutionary mechanisms, and who achieved notoriety as an ardent social reformer, communist and apologist for Stalin (Clark 1984; Subramanian 2020). J. B. S. Haldane's father, John Scott Haldane (1860-1936), was also a pioneering scientist involved in detection of toxic and explosive gases in mines and sewers, and in researching gas composition for survival in submarines during World War One. John Scott Haldane's brother, Richard Burdon Haldane (1856-1928), became Secretary of State for War from 1905 to 1912, though was criticized for his attempts to negotiate a peace with Germany early in the First World War (Campbell 2020; McLauchlan 2022).

The biography of Burdon Sanderson by his wife, Ghetal (née Herschell, 1833-1909), recounts that botany was "a subject which had from his childhood interested him greatly" and that this early interest was stimulated by the botany courses he took from John Hutton Balfour (1808-1884) (Fig. 1b) while studying medicine at Edinburgh University (Burdon Sanderson, G. 1911: 22). In Scotland, the medical degree was undertaken by undergraduates,[4] and botany was a required part of the curriculum. While there is substantial information on Burdon Sanderson's later life, most of his early family correspondence was destroyed in a fire at a furniture depository in London in 1874 (Burdon Sanderson, G. 1911; p. 36).

In this paper, I discuss Burdon Sanderson's botanical work while he was studying medicine at Edinburgh University, focusing especially on a previously undiscovered prize-winning essay on "Vegetable Embryology". I present an analysis of the contribution of this essay to plant embryology in the context of Burdon Sanderson's interactions with Balfour, his teacher and the Regius Keeper (=Director) of the Royal Botanical Gardens Edinburgh (Morrow 2018). A transliteration of the essay is included in the Supplementary Online Materials. In the Perspectives

[4] This is still the case in the UK, whereas in the USA it is a post-graduate degree requiring 'pre-med' undergraduate courses for admission.

section, I then discuss the legacy of his early botanical work in the context of his other scientific contributions.

THE ESSAY

Provenance and authorship

The essay "Vegetable Embryology. The Origin and Development of the Embryo In Phanerogamous Plants" [5] is unsigned, but the flyleaf carries a written inscription "Prize Essay, July 1849, John Scott Sanderson. The author." [6] This inscription seems to be in John Hutton Balfour's handwriting as judged by Balfour's other handwritten notes and letters. The authenticity of Burdon Sanderson's authorship of the essay is confirmed by the date[7], the similarity of the handwriting to that in later letters[8], and by verbatim reproductions of the text in [Burdon] Sanderson (1849), and of the figures in Burdon Sanderson (1859).

The notebook has been bound in hard cloth covers in a now faded magenta and has no titles on the cover or spine.[9] The five plates are glued to thicker card paper as fold outs at the back. How the essay came to be bound and placed in the Balfour archives is unknown.

Summary of the text

I summarize the contents of the essay, using the headings and page numbering in the original (Supplementary Online Materials). Direct quotations from the text are in quotation marks[10] and author's cited in the essay are given date in the supplementary materials.

Vegetable Embryology (pp.1-8)

Burdon Sanderson states that while plant morphology is complex, it is underlain by an aggregate of similar cells, each one of which is capable under favorable circumstances of

[5] Currently available online via the Royal Botanic Garden Edinburgh Library catalog.
[6] A narrow strip at the top of the front-end page (ca. 1.5 cm) has been cut off, suggesting that someone didn't want to show something that had been written there. Also, the words "The author" appear to have been written as an addition, as it is distinctly fainter than the rest of the writing.
[7] In the summer school listing (Royal Botanical Archives, GB235/CL/05Class List1840-1853), his signature appears for Summer Session 1848 (May 2nd) as 'J S Sanderson', No. 77 out of 186 enrolled, and for 1849 (May 1st) as 'John Scott Sanderson', No. 3 out of 184 enrolled.
[8] Correspondence of John Hutton Balfour. Vol. XI. Rogers to Tetley. Royal Botanical Garden Archives.
[9] The binding is somewhat worn and scuffed, as if the bound version had been frequently used or consulted.
[10] I have not provided specific page references for each quotation because I include them only to give a sense of the style.

becoming the parent of a new plant. He adds that this "cell theory", initiated by Schleiden, is well accepted but generates its own contradictions. In particular, he finds it "difficult to see how the necessity for the concurrence of two distinct individual organisms for the origination of the embryo is to be explained" if a single cell is capable of producing a parent plant. He says that fecundation is "beyond the ordinary process of cell growth" and is a process defined by the term "sex" (in quotation marks in the original). He considers Schleiden wrong in considering sex in plants as being different from that process in animals. The embryo in plants, says Schleiden, originates from the pollen tube without reference to the female which simply provides a nidus for its development, and that all that is needed for a new generation is "the same formative tendency" as the parent plant. Burdon Sanderson finds this hard to reconcile this with Gaertner's demonstration of both male and female traits in interspecific hybrids, and with the presence of sexual organs within the lower plants. He concludes by saying that the "asexual theory is … unworthy of our adoption", and passes on to a historical review of this topic

Historical Notice (pp. 9- 24)

Burdon Sanderson begins by mentioning Grew, Millington, Morland, Ray, Camemarius and Linnaeus who "supported view that the sexual organs of plants were entirely analogous to those of animals", and contrasts this with Gleichen and Schleiden who had argued that "the male plant prepared the 'seminal germs' to which the female organ only afforded the means of development".

He then discusses t the function of the pollen. The early investigators such as Mirbel in 1808 thought the pollen produced a "delicate substance", the 'aura seminalis', that was transmitted to the ovule by conducting tissue. St. Hilaire considered that the 'aura' acted without the intervention of a vascular connection, till Brown in 1825 showed "tubes communicating between the stigma and ovule".This was confirmed by Amici in 1831: "the pollen grains, where they come into contact with the stigmatic surface, become each of them prolonged into an appendage the pollen tube, which passed down the cavity of the style into the ovary".

Turning to fertilization, Burdon Sanderson cites Brogniart's observation in 18xx that "the embryo is developed from a single cell or vesicle, either produced before or after impregnation" and Corda's 1834 work showing that "pollen tubes pass through the opening of the secundine [=integuments] to the apex of the nucleus [=embryo sac]". He states that the controversy about the role of the pollen tube appeared settled when Horkel in 1836, "on at least 50 families…traced

the pollen tube from the stigma to the ovary, and in numerous instances, to the micropyle", yet in 1837, Schleiden, Martins and Wydler still considered "the pollen grain as the 'germ of the new individual' to which the embryo-sac "serves the office of nourishment".

Burdon Sanderson then summarizes the accumulating evidence that the cells forming the embryo originate before the arrival of the pollen tube. Meyen in 1839 showed that "the first cell from which the embryo is to be developed, originates in the sac, without ever coming into direct connection with the termination of the tube". Mirbel and Spach also argued that "embryo vesicle is developed prior to impregnation, and that the contents of the pollen tube only act in determining the development of the embryo within it." By 1840, Meyen was asserting that "on the arrival of the pollen tube at the embryo-sac, a perfect cohesion took place between the one and the other." Hartig concurred, "fecundation is effected either without the emission of tube[s] altogether or with the emission of imperfect cues", and in 1842 Giraud noted that "the embryo-vesicle [egg cell] originated before the period of impregnation".

Throughout, Burdon Sanderson is highly critical of Schleiden and on more than one occasion he damns as much as he praises: "we have here another example of the not infrequent inaccuracy of that great observer"[11], and "it is difficult to conceive how so accurate an observer as Schleiden could be led into such important mistakes …. had he studied the facts of the development in their chronological order, he certainly would not have … supposed the embryo-vesicle to be the end of the pollen-tube."

As far as I can assess, Burdon Sanderson's historical survey was a thorough and accurate account of the controversies in the first half of the 1800's regarding fertilization in plants. It conforms remarkably well with subsequent historical accounts (Sachs (1890: pp. 431-436); Harvey-Gibson (1919: pp. 157-160); Johansen (1950: pp. 2-12); Ducker and Knox (1985). Of the twenty-nine authors mentioned by Burdon Sanderson, Johansen's (1950) account of the history of plant embryology included seventeen of them. Johansen also labelled the controversy more explicitly, as that between the "pollinists" who argued that the embryo was a product of the pollen tube, and the "preformists" who held that the embryo developed from inside the embryo sac. These contrasting views are clearly outlined in the essay; Burdon Sanderson, to use a modern phrase, was "well up on the literature".

Examples from Natural Orders and Species (pp. 24-49)

[11] Notes opposite p. 25 continuing on p. 26.

In this section, Burdon Sanderson proposes to describe "the facts ascertained as to the fecundation and the embryo-growth of a few examples of Natural Orders and Species." The section is divided by family, starting with non-flowering plants (Rhizocarpeae and Marsiliaceae). Burdon Sanderson confesses that these are not Phanerogams, but includes them because Schleiden did so too. He says he will divide the family descriptions into: I. Early condition of the ovule, II. Changes prior to impregnation, III Changes subsequent to impregnation, and IV. Development of the embryo. He largely succeeded in this with the Gramineae, the Orchidaceae and the Haloragaceae, but later sections on Onagraceae, Convolvulaceae, Santalaceae, Ericaceae, and Cruciferae were not systematically sub-sectioned.

This section might be expected to provide direct observational evidence on the "pollinist" vs. "preformist" views of the origin of the embryo, but it is hard to interpret the text and figures given the absence of any description of the methods, sources of the materials, or the timing of the various stages presented. It is also unclear from his descriptions which of the observations were made by Burdon Sanderson himself or if they were made by others. Many of the interpretations are pre-judged in favor of the preformist views, and there is no forgiveness considering that Schleiden's error were understandable ones given the techniques then available to him. Many of Burdon Sanderson's illustrations of the embryology of *Hippuris* and *Capsella* are impressive in their detail and accuracy; in *O. morio* he could even delineate the ovule and synergid cells in the embryo sac.

"Endeavouring to draw a conclusion" (pp. 48-51)

He finishes by a "tabular" (= classified and enumerated) view of the development of the embryo. The terminology in this section is confusing from a modern perspective but reaffirms that there is an embryo sac within which one of the cells develops into the embryo.[12] He ends with a quote from Horace: "*Ab ovo usque malum*", liberally translated by him to reflect the topic of his essay: "From the germ vesicle to the mature embryo".

The Figures

The five hand drawn plates drew a gasp when I first saw them, being impressive in their detail, albeit faint and without the clarity of copper-plate engravings. They appear to be drawn directly in pencil (Fig. 2; see Supplementary Online Material for all plates). The order of the

[12] Curiously, he adds that there may be two such suspensors, one at the apex and the other at the base of the embryo sac, but this may be confusion of the endosperm with the suspensor.

plates and of the figures within them does not follow the text; for example, the first figure referenced is Plate III, Fig II[13]. Moreover, the figures have no legends, making cross referencing the text and the figures difficult. In the transliteration in the Supplementary Online Materials I have inserted brief legends to the figures.

Because the methods are not described, there is ambiguity about whether the figures are of original specimens or copied from other sources. To address this, I looked for prior published work on the species that were illustrated. Plate I of embryo development in *Orchis morio*, *Monotropa hypopitys* and *Begonia cucullata* is clearly taken from Muller (1848: Plate 1). On examination of Burdon Sanderson's plate through a microscope at 6X with side-lighting, I found pinpricks corresponding to cell-wall junctures, consistent with them having been copied. Plate IV, Figures III-XIV, of fertilization and development in *Oenothera* is almost identical to that in Hofmeister (1848: Plate 4) and subsequent Figures XV to XVIII showing pollen tubes on the embryo sac of *Mesembryanthemum glomeratum* are very similar to (Meyen 1838: Plate 8). Unlike Plate I, no marks or other indentations were found on Plate IV even though many of the figures are close to the putative originals; they therefore may have been traced.

In contrast, the Plates II, III, and V, illustrating embryo development in *Hippuris*, *Orchis*, and *Capsella* were likely to have been drawn by Burdon Sanderson himself. This is confirmed because he reproduced the figures of *Hippuris vulgaris* in Burdon Sanderson (1850a,b) and in Burdon Sanderson (1859) he used engravings taken from his plates, adding (in the legend to Fig. 198) that they were original.[14] and even included the magnification.[15] The figures of *O. mascula* were very similar but not identical when compared to equivalent stages drawn by others (Meyen 1838; Henfry 1852) showing that his own drawings were accurate.[16]

It is likely that Burdon Sanderson, then a second-year undergraduate, was unaware of any norms (if such existed) related to copying other people's figures. For example, immediately before referring to Plate I, he does say it is "to the later researches of Hugo Mohl and Karl

[13] In general, at this time Plates were labelled in Latin numerals, and figures using normal Arabic numerals.
[14] *Hippuris vulgaris, Capsella bursa-pastoris* and *Orchis mascula* occur commonly in and around Edinburgh. (Botanical Society of Britain and Ireland: https://bsbi.org/maps/, accessed 2025 Aug 10th). The species he likely copied are rare or absent from Scotland.
[15] In the same article, some of the description of *Orchis* development is taken from Henfry (1852) yet fully acknowledged (Burdon Sanderson 1859: Fig. 199).
[16] I have been unable to identify any source for first Figures (I and II) in Plate IV; they may be schematic representations of Schleiden's hypothesis drawn by Burdon Sanderson himself.

Muller, that we are indebted for the comparatively complete series of facts" but does not acknowledge that the figures were taken from their work. In the text relating to Plate IV that was copied from Hofmeister, he writes "That observer has …beautifully represented his results" but again there is no direct acknowledgement.

PUBLICATION AND CITATION OF THE ESSAY

Parts of the essay, on embryo formation in *Hippuris*, were published soon after the essay was written (Burdon Sanderson, 1850a, b).[17] They incorporate verbatim much of the text in the essay. The *Hippuris* paper (Sanderson (1850a, b) is referenced in Balfour's second textbook, *Classbook of Botany* (1859b; p. 589) which includes two figures from the essay.[18] The *Hippuris* work is also listed in the bibliography of Fournier (1863) but not mentioned in a later paper on embryogeny in *Hippuris* (Souèges 1922).

A direct reference to the essay appeared in the *Annals and Magazine of Natural History* (Cobbold 1852a) but carried a curious introduction: "Dr. Cobbold laid before the Edinburgh Physiological Society a brief account of some investigations into the embryology of *Orchis, Gesneria*, and other Phanerogamia. These observations, together with a preliminary account of the labors and opinions of Schleiden, Amici [etc.]…formed the subject of an essay written in the summer of 1849. Dr. Sanderson, who at the same time investigated this subject, has since published in the Annals of Natural History". Why Burdon Sanderson's results were presented by Cobbold rather than by himself remains unknown.[19] Thomas Spencer Cobbold (1828-1886) (Bettany and Osbourne 2004) was a fellow undergraduate with Burdon Sanderson, and became an expert on parasitology, writing several books on this subject. He and Burdon Sanderson both graduated in 1851 with 3-stars for "those who have obtained Prizes for their Dissertations" (Anonymous. 1851). Cobbold and Burdon Sanderson were active in the Edinburgh Physiological Society and frequently contributed to *The Monthly Journal of the Medical Society*. Cobbold's

[17] These papers are identical in content but in different journals (one the Society Proceedings, and the other in a report of the papers at that meeting).
[18] Because of a dispute with the publishers, his first text Manual of Botany (Balfour 1849), remined unchanged for many editions (Morrow 2018).
[19] The attribution at the end, "*Proc. Edinb. Phys. Soc.*", confirms that it was a paper originally presented at the Edinburgh Physiological Society, but the original report (Cobbold 1852b) is identical, and sheds no light on the actual authorship or if he was co-involved in this study with Burdon Sanderson.

article contains a clear, accurate twelve-point summary of Burdon Sanderson's essay which is more complete and thorough than in the original. Whether this summary was actually produced by Cobbold is unclear, and it is not known why Cobbold gave the oral presentation rather than Burdon Sanderson.

Burdon Sanderson (1859) while employed as a junior doctor at St. Mary's Hospital, London, subsequently produced an extensive forty-five page entry on 'Vegetable Reproduction' in Todd's *Cyclopaedia of Anatomy and Physiology* . This article, with seventy five figures, covered algae, fungi, lichens, as well as mosses, ferns, gymnosperms and flowering plants. Surprisingly, the section on flowering plants was barely five pages (pp. 248-252), and largely an account of the results for *Hippuris vulgaris* and *Orchis morio* as presented in his essay. The appendix (pp. 256-257) discussed the difficulty of drawing parallels between the plant and animal kingdoms in their fertilization and embryo development.

The encyclopedia entry was a vast 'professional improvement' on his undergraduate essay: it was fully referenced, the figures were attributed to sources and included magnifications. Viewed from a present perspective (knowledge of double fertilization, alternation of generations and the laws of genetics), the text seems somewhat haphazard, but Burdon Sanderson again recognized that some aspect of fertilization was necessary for "rejuvenescence" and formation of the next generation (Burdon Sanderson 1959: p. 211, 254) but did not pursue the issue. Nevertheless, the article is a detailed review of what was known about plant reproduction in the mid-1800's. For example, he bemoaned that sexual reproduction in mosses had been only indirectly inferred by mixing thalli with separate sexes, and that conjugation in the archegonium had only been observed twice.

In terms of evaluating the contribution of Burdon Sanderson's essay and subsequent publications to ideas in plant fertilization and embryology in the mid-19th century, my strong impression is that his essay rode the wave of an increasingly accepted "preformist view". The alternative "pollinist" view that the embryo came from the pollen grain, was already crumbling. For example, Unger (1849, p. 336) argued that in *Hippuris* there was a recognizable cell that which develops into the embryo "without direct external influence" (p. 336) [20] as also observed by Burdon Sanderson. Unlike Burdon Sanderson, Unger, not wishing to criticize Schleiden

[20] "ohne unmittelbaren Einfluss von Aussen."

"leaves it to the reader to judge if the facts he presents can be reconciled with that [Schleiden's] theory" (p. 330) [21].

I was curious to discover whether Burdon Sanderson's analysis of the historical background in his essay was perhaps a direct product of Balfour's lectures. We do not have Balfour's original lecture notes for that time, but in 1849, the same year of the essay, Balfour published his *Manual of Botany* (Balfour 1849). In its 641 pages, many botanists are mentioned, but there are only 19 footnotes with explicit references. The most extensive footnote is in the section on 'Theories of Embryology' (pp. 241-247, paragraph 515) and it has nine citations. Six are the same as in the essay, but three others are not mentioned[22]. The text and the details of the abbreviations used for the citations are, however, quite different; I could find no evidence of 'direct copying' from Balfour's book.

BURDON SANDERSON'S OTHER BOTANICAL STUDIES

Burdon Sanderson is first mentioned in the records of the December 1848 meeting of the Edinburgh Botanical Society (Murchison 1849). In the remarks following this presentation, Burdon Sanderson is recorded (in 3 lines on p.63) as informing Murchison that his reported symmetry of cells at the base of epidermal hairs had also been observed by Raspail. (1840; Plate V, Figs. 1, 5, of hairs on cucumber shoots). I found it remarkable that Burdon Sanderson could recall such a small botanical detail from an extensive text written in French, more so because Raspail was considered a somewhat renegade scientist (Weiner 1968).

Burdon Sanderson's first direct written contribution was a short paper on the cause of the rapid downward movement of the style of *Goldfussia* (=*Strobilanthes*) after being touched ([Burdon] Sanderson 1849). In this paper, read at a meeting of the Edinburgh Botanical Society on 12th April 1849 and chaired by Balfour, he criticized the conclusions of a French scientist (Morren 1839) on the cause of the stylar movement. Morren thought the stylar movement was stimulated by granules within the tubular cells of the style. Burdon Sanderson had observed cross

[21] "..überlasse ich es dem Leser, zu beurtheilen, ob die von mir hier mitgetheilten Thatsachen sich mit jener Theorie vereinbaren lassen."
[22] Balfour's includes Griffith (1845) in the footnote, and while Burdon Sanderson also mentions Griffith in the text, there is no accompanying citation.

walls in these tubular cells, and argued that these would have prevented the movement of the granules.[23]

The subject of rapid plant movement must have intrigued Burdon Sanderson. He became a member of the Royal Medical Society of Edinburgh, a rather select student society which expected inductees to present and defend a paper on a subject of their choice. When he was elected to the society in November 1848, he chose "Vegetable Irritability" as the subject of his talk (Burdon Sanderson, G. 1911: p. 25). Much of the inspiration for this was likely to have been Balfour who frequently lectured on plant movement and irritability[24] using *Goldfussia* as an example. *Goldfussia* is also mentioned in his *Manual of Botany* (Balfour 1849: p. 33). Among Balfour's other examples of plant movement was Venus' fly trap (*Dionaea muscipula*), which in lecture was exemplified by a large twelve-page fold-out poster prepared by his wife (Morrow 2018: pp. 459, 485).

Burdon Sanderson developed a close relationship with Balfour. Not only did he go on Balfour's celebrated Saturday field trips with the botany class, often by train and sometimes by steamboat, but in July 1849, he was asked to join Balfour's small select group of botanists for a five-day excursion to Ben Lawers in the Highlands.[25] They also continued correspondence after Burdon Sanderson graduated from Medical School. In November 1854 he thanked Balfour for a copy of his book ("which will be a useful form of text book"), sent preparation of "pro-embryos" of the polypody fern (*Polypodium vulgare*) and enclosed instructions (and a clearly drawn diagram) of his method for growing fern gametophytes.[26] In 1858 they corresponded about a visitor to London,[27] and Burdon Sanderson asked Balfour for recommendations about what plants to grow on the grounds of St. Mary's Hospital in London. He passed on "kind remembrances to Mrs. Balfour".[28] His contact with the family continued, as in 1877, Burdon Sanderson then a Professor in Oxford, wrote a testimonial on behalf of Balfour's son Isaac Bayley Balfour (1853-1922) for a professorship at the University of Aberdeen (Anon. 1877, p.

[23] There is a contradiction here, as Morren also records cross-walls, but simply as not being frequent. Regardless, it is difficult to distinguish cause and effect with such observations.
[24] J. H. Balfour. Undated. *Syllabus of a course of Lectures in Botany*. In J. H. Balfour. Bound Reprints. Papers 2. Paper # 21. 16 pp. RBGE archives
[25] Balfour, J. H. Botanical Excursions 1846-1878. No publisher or date. Title page is headed "History of the Royal Botanic Garden, Edinburgh," "Botanical Excursions made by Professor John Hutton Balfour, in the years from 1846 to 1878 inclusively".
[26] Correspondence of John Hutton Balfour. Vol. XI. Rogers to Tetley." RBGE Archives. (Letter #14)
[27] No name appears in this letter (missing some pages).
[28] Correspondence of John Hutton Balfour. Vol. XI. Rogers to Tetley." RBGE Archives. (Letter #15)

19).[29] Isaac Bayley Balfour eventually become Keeper at the Royal Botanic Gardens Edinburgh from 1888 to 1922.

Burdon Sanderson continued his interest in botany after his medical studies. He read a paper before the Botanical Society of Edinburgh in 1954 (Burdon Sanderson 1854) that disputed the rather strange suggestion of Grisebach (1844) that small projections on the developing leaves of *Rhamnus cathartica* (common buckthorn) were the equivalent of antheridia in mosses or ferns. Burdon Sanderson argued they were simply cellular projections in the stipules (accessory leaves). It is now unclear whether they had been looking at the same thing, especially as *Rhamnus* is also the primary host of *Puccinia coronata* (crown rust) and Grisebach may have observed the pycnidial stages of the rust. In this paper, Plate III is identified as being drawn by Burdon Sanderson himself, confirming his proficiency at drawing.[30]

PERSPECTIVE

Many questions remain about the essay. We do not know if essays were a required part of the course nor what the 'prize' was for the winner. We don't know why and by whom the essay was bound into book form, nor any sense of the discussions that passed between Balfour and Burdon Sanderson on plant reproduction. Even though Balfour taught botany to Edinburgh medical students for over thirty years between 1845 and 1879, I have been unable to find other essays written as a part of his courses and none are mentioned in an extensive biography of his contributions to teaching (Morrow 2018). The essay may simply have been a project that was undertaken by Burdon Sanderson, and not part of the curriculum. The fact that it was eventually bound in hard covers does suggests a special story.

While it is difficult to argue that Burdon Sanderson's essay was groundbreaking or far ahead of its time, it is still remarkable as an undergraduate project, especially for a degree in medicine. The essay states a problem clearly, carries out a thorough review of the prior literature, and records original microscopic observations on presumably living specimens. As a grumpy teacher, I could only fault it for lack of a section on methods, and for not clearly distinguishing

[29] Royal Botanical Garden Edinburgh Archives has the request for and the reply to this letter in Isaac Bayley Balfour's copy letter-book, on page "S").
[30] "Dr. Sanderson" with abbreviation for "delineavit" (he drew it).

his own observations from those already published. I cannot judge the norms for undergraduate essays at that time, but they would likely have been looser and less well defined than today. My own undergrad tutorial essays referred to various scientists and authors, but they rarely had direct citations, nor were these encouraged. I would undoubtedly give his essay an A+ (or a first-class grade), and it is no surprise that it was judged prizeworthy.

My own interest in John Burdon Sanderson arose from researching his great-nephew and namesake J. B. S. Haldane, a leading population geneticist, instrumental in reconciling Mendelian genetics with Darwinian natural selection. In 1949 he published a seminal paper on *The evolution of infectious diseases* (Haldane 1949) which suggested that there may be genetic variation in resistance to infectious diseases in humans, drawing parallels with the observed genetic specificity of infection in many plant diseases. The origin of this paper has been much discussed (Lederberg 1999) and it seems Haldane's ideas came about through correspondence and meeting Italian medical researchers who were investigating inherited blood deficiencies and their relationship to the occurrence of malaria (Canali 2008). I was curious if his father's work on air quality in overcrowded dwellings had had any relationship to his interest in disease (I could find no direct evidence of this) and this led me to discover Haldane's great uncle, Burdon Sanderson, who had done original research on the nature of infectious disease, much of it between 1865 and 1870 (although he subsequently wrote many reviews[31]). It came as an additional surprise, mixed with incomprehension that, although on the verge of becoming "England's Pasteur" with his experiments on contagious diseases, Burdon Sanderson essentially abandoned infectious diseases and turned instead to insectivorous plants. This shift in research focus becomes much more understandable given his excitement as an undergraduate about the causes of "plant irritability".

My re-discovery of Burdon Sanderson's essay was nevertheless accidental. I was in Edinburgh for personal reasons and being aware that Burdon Sanderson's had received his medical degree there, I casually browsed the library catalog of the Royal Botanic Garden Edinburgh in hope of finding something interesting. It was therefore a delight to find the essay of a "J. S. Sanderson" (then mistakenly recorded as from 1869 rather than 1849).

[31]All published in the *British Medical Journal* as series of lectures: 1878, Lectures on the infective process of disease I-IV; 1882, The Lumleian Lectures on inflammation I-III; 1891 The Croonian Lectures on the progress of discovery relating to the origin and nature of infectious diseases I-IV.

At first there seems little connection between his work on plant embryology and his later studies on infectious disease. However, there possibly is a link in a somewhat unexpected but very consequential way. In his entry on plant reproduction in Todd's cyclopedia (Burdon Sanderson 1859), he explicitly emphasizes that he uses the term 'germ' or 'germ-cell' to indicate the cell from which the embryo originates; these words occur over sixty times in the article. While discussing terms he could use for an infectious agent, Burdon Sanderson (1870a) settled on 'microzyme'. This term joins the idea of a 'micro-organism' with the idea of a 'zymotic disease' (Farr 1842), a term then commonly used for contagious epidemic diseases (many thought they had a chemical origin and a 'catalytic' or 'enzyme-like' mode of action). The word 'microzyme' created immediate confusion, so much so that Burdon Sanderson had to write in a letter to the *Lancet* on 'the misuse' use of his term (Burdon Sanderson 1870). He argued that his term 'microzyme' for infectious agents was appropriate because "there is no reason to believe that they are or that they are not" identical to contagious particles. His research might have had much more impact had he gambled on the term 'germ' as Pasteur did several years later (Pasteur1878). It is ironic that in Burdon Sanderson's letter to the *Lancet*, he even uses the term 'germ' in his introduction to the topic. It is likely he was loath to use this for an infectious agent because of his ingrained sense that 'a germ' was the cell that starts the embryo. His essay therefore not only reinforces the over-riding impression of a brilliant student but also presages many of his later contributions to medical science, and to animal and plant physiology.

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ACKNOWLEDGEMENTS
I wish to thank Leonie Paterson and Lorna Mitchell for extensive help in the archives and library at the Royal Botanic Gardens Edinburgh (RGBE), and for locating papers and sources. Lynsey Wilson, staff photographer at RGBE, produced the high-resolution plates. The Ecology and Evolutionary Biology (EEBIO) discussion group at the University of Virginia provided useful input, and Emme Bruns and Michael Hood provided comments on the manuscript.

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[33] Royal Botanical Garden Edinburgh Archives, John Hutton Balfour archive.
[34] Identical to Sanderson 1850a.

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[37] Authored by "F. G.", presumably Francis Galton.
[38] 38 Stuck, 20 September 1844.
[39] Two volumes numbered sequentially.

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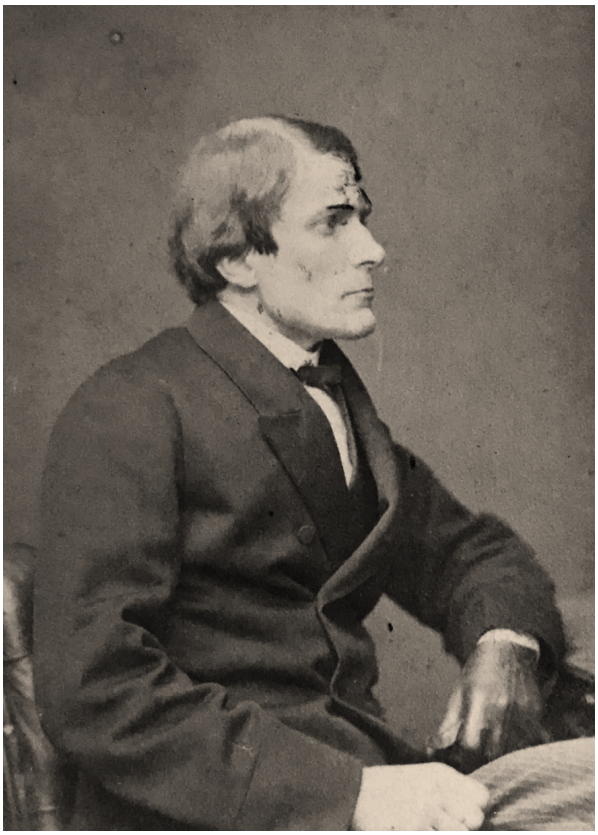
[40] The above is text only. For Plates (but incomplete text) see: https://www.biodiversitylibrary.org/page/33805715#page/188/mode/1up (accessed 2025/08/21)

LIST OF FIGURE CAPTIONS

Fig. 1. *Left*. Photograph of John Scott Burdon Sanderson (probably taken ca. 1870, during his time at University College London). Enlarged portion from the original photograph by "Crellin, 87 Regent Street W., London". The eyebrows and forehead appear to have been touched-up in the original. University College London Archives, Box MS ADD 179/120.
Right. Engraving showing John Hutton Balfour as Professor of Medicine and Botany at the University of Edinburgh, ca. 1845. Enlarged portion from the original engraving by "Schenk and Ghémar Lithographers, Edinburgh. Royal Botanic Gardens Edinburgh Archive Portrait Collections (from Morrow 2018).

Fig. 2. Burdon Sanderson's drawing of fertilization in *Orchis mascula*, taken at increased resolution by the author from Plate III of his undergraduate essay on *Vegetable Embryology*.

Fig. 1.



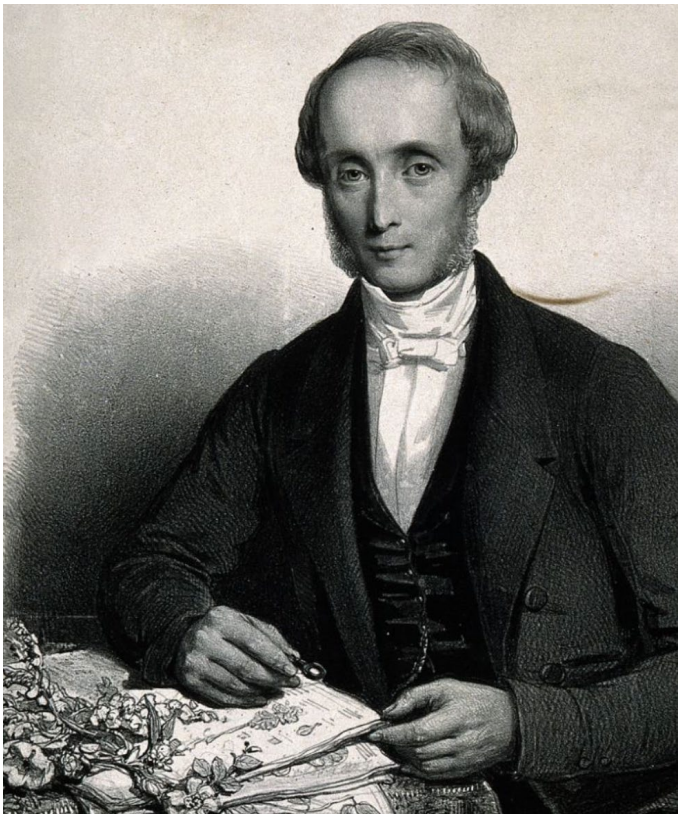
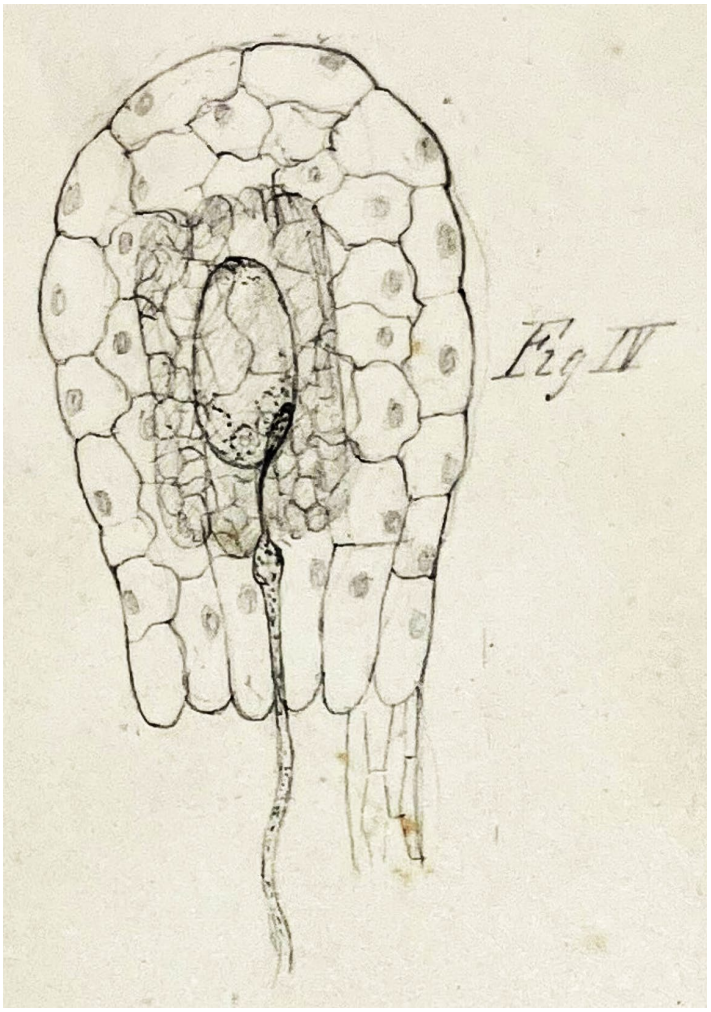


Fig. 2.



Burdon Sanderson's 1849 undergraduate essay on 'Vegetable Embryology'

Janis Antonovics

SUPPLEMENTARY MATERIAL

Transliteration of John Scott Burdon Sanderson's prize-winning essay on "Vegetable Embryology"

INTRODUCTORY NOTES

The essay is in a cloth bound notebook in the Archives at RBGE, Archive Catalog Number (Catalog No. GB_235 SJS). The essay is handwritten on lined notepaper. The text itself is on the right-hand leaves of the paper, while the opposite left-hand side has references and added notes. The text pages are numbered sequentially, and in the transliteration these original page numbers are in italics on the right-hand side.[1] The notes of the essay are placed at the end of the page to which they refer.

Because in the original the references are in abbreviated form, I have included the intended author and date in square brackets, and the full citation is in the Bibliography as an added section at the end.

I have tried to reproduce the text accurately in terms of spelling, punctuation and grammar, and though errors on my part cannot be excluded, I have aimed for a literal copy of the handwritten text and format. When text is underlined, it is underlined in the original. My own notes on the text are in square brackets.

The figures for the essay are in Plates I to V as foldouts at the end. They are referred to by their Roman numerals, and each Plate has multiple figures, also in Roman numerals, some of which are further sub-numbered in normal numerals. The order of the plates and their figures does not follow the order in which they are cited in the body of the essay.

I have added legends to the Plates to clarify the species being illustrated and the source of the material if it is not original: Plates I and IV are likely copied from earlier work, while the others are drawn by Burdon Sanderson (see Text).

[1] Page 21 is double labelled in the original, and so are termed 21a and 21b.

I wish to thank Leonie Paterson, the archivist at the RBGE library, and the staff for help with locating this essay and associated materials, and Lynsey Wilson for high-resolution photography of the Plates.

THE TRANSLITERATION

Inside flyleaf page

"Prize Essay. - July 1849 –
John Scott Sanderson. The author." (not in JSBS's handwriting)

Title Page

Vegetable Embryology

The
Origin and Development
of the
Embryo
in
Phanerogamous Plants

[initials " I B/D? " are added in different handwriting after the title - possibly Isaac Balfour]

Page 1

Vegetable Embryology

In tracing the modifications of vital phenomena from the lowest to the highest member of the vegetable and animal series respectively, it is impossible to avoid remarking the great absence of correspondence between form and function in the flower as contrasted with what we observe in the latter. For while in the animal world we find that (excepting those parts of it in which strong analogies may be drawn with the vegetable) a definite individual vital expression may be attached to any organ, corresponding to a form definite and differing from that of other organs, among plants it is precisely the reverse. For in them, as Schleiden observed, there is generally speaking, a "perfect" independence of the physiological and morphological import of individual organs.

This relation, which is among the most

Page 2

important that can be drawn between plants and animals, results from the fact that the vital phenomena of which the plant is the subject, are but repetitions of those of the individual cell, while the life of the most simple animal is of a compound nature, or in other words while one vegetable cell is capable of performing all the functions of the plant, we must have a plurality of cells, which are no doubt physiologically different, to constitute an animal.

Therefore, however complicated a plant may appear from the complexity of its morphological development, it is yet but a repetition of the cell and consequently essentially and in its nature simple. It is indeed an aggregate individual consisting of cells, either in a living or active state or in a state of death, each one of which has been, or is capable of becoming under favourable circumstances, the parent of a new plant.

This simple method of viewing plant life, though it is in general to be considered as the only correct one, is not to be taken in the strict sense as of universal application.

Page 3

For it will be found that some of the consequences which follow from it are at variance with acknowledged and incontrovertible facts. It is the view which is in particular adopted by Schleiden and his followers, who derive from it some of the most important peculiarities of their doctrines in vegetable physiology. With respect to the subject of this paper especially – the origin of the embryo in higher plants – inferences which it is very difficult to reconcile, seem capable of being drawn. If, as Schleiden supposed each individual cell to be considered as self subsistent, possessed of a power of reproducing the organism and capable of forming a new plant, according to the same morphological laws as the original, it is difficult to see how the necessity for the concurrence of two distinct individual organisms for the origination of the embryo is to be explained. Whatever view we take of the mechanism of the act of fecundation, we must admit that there is some purpose in the bringing together of the parts which belong to different organs or individuals, beyond the ordinary processes of cell growth. And as we have a accu-

Facing page 3:
Principles of Botany Pp 524-527. [Schleiden 1849]

On the Development of the Organization in the Phanerogamous Plants Taylors Phil. Mag. 1838. [Schleiden 1938a]

On Phytogenesis [Schleiden 1938c]

Page 4

-mulated evidence to show that this conjunction of parts or, as it might be with equal correctness expressed, conjunction of cells is a constant condition necessary for the development of the embryo, it follows that a cell cannot be considered, as possessing the power inherent in itself of becoming self subsistent or of giving origin to a self subsistent new organism.

In this condition is implied neither more nor less than what is generally understood by the term "sex" whether applied to plant or animals. The presence of sex in the vegetable kingdom though a generally received doctrine is denied altogether by Schleiden. It is, says he, "a word without any foundation and only expressing foregone conclusions from Zoology to Botany.

It may be interesting to enquire, what, according to this view is the idea which can be entertained of the nature of the reproduction of the higher plants, and how the difficulties we have noticed are to be overcome.

The highest form of the reproductive process defined by Schleiden, as "the development of a reproductive cell to a new individual, under

Page 5

the circumstances of a material influence of the parent plant[”]. This takes place in all phanerogamous plants and the Rhizocarpeae. In this definition two conditions are given as necessary to embryo development – the first is the existence of a reproductive cell – the second the after influence of the parent plant. We must therefore first enquire in what this reproductive cell consists. It is defined to be a special cell "normally found in the development of the new plant."

In the Algae and other lower plants it becomes developed after separation. But in the Rhizocarpeae and higher plants, the cell is developed under the influence of the parent plant and

its specific formation tendency. It is therefore to be considered as capable of developing a new organism independently, but in the higher plants, in order to the completion of its development up to the more complicated forms, the second definition must be introduced, that is, it must be developed by connection with the parent whereby, as Schleiden says, "the specific formative tendency encloses the organism within narrow limits of law," and thus as the circumstances of the

Page 6

parent plant, under which the reproductive cell must develope [sic] become more complicated" a "similar morphological development" is communicated to it, whereby it is caused "as a new individual to represent the same formative tendencies as the parent plant."

What then are we to conclude in the function of what is usually considered as the female organ, namely that in connection with which, according to Schleiden the reproductive cell is developed? The only function wh. it can perform is to afford the necessary conditions for the growth of the embryo, all the elements of which exist in the reproductive cell before they are brought into connection, and which is therefore originated without any reference whatever to the female organ.

The principal argument against the asexual view of the reproduction of plants (without reference to the facts connected with the act of impregnation) is derived from what is observed in the production of hybrids. On this subject Schleiden in his principles says nothing. If, as we have seen, the male organ only is concerned in originating the embryo, we cannot account for the fact that when the male organs belong to one species, and the female to another

Page 7

female [sic; perhaps 'species' is intended]. It should seem indeed from the researches of Gaertner that the general tendency of the hybrids is to pass in this direction.

Another series of arguments against Schleiden views is to be obtained from the facts made out by Meyen and others with respect to the existence of organs in the lower plants, which will admit of the supposition that they are endowed with sexual properties, and indeed cannot be well explained otherwise. In the Mosses and Liverworts especially, it is difficult to assign any other meaning to the arrangement and structure of the located antheridia and pistillidia, and the same remark is applicable to the peculiar reproductive organs of Chara. The subject however is still involved in some obscurity, as we are as yet, unacquainted with the manner in which the contents of the one organ act on the other. In the Confervae, especially, it is difficult to explain the fact of the spores being produced in some species

Page 8

invariably without conjugation – from others indifferently either with or without. The progress of future enquiry may however, clear up this apparent inconsistency.

Having now, it is to be feared imperfectly, considered the general nature of the reproductive process in plants and endeavoured to shew that the asexual theory is liable to objections, which render it unworthy of our adoption, we pass on to the subject more immediately before us, namely the Origin and Development of the Phanerogamous Embryo. And, with a view to the more complete elucidation of our subject, we shall in the first place notice in succession and as briefly as possible, the more important observations which have been made and the opinions which have been held by various authors, who have directed their attention to this department of vegetable physiology.

Page 9

Historical Notice

Up to the commencement of the present century, the usual opinion of vegetable Physiologists, with respect to the fecundation of plants seems to have been, that the pollen grain descended entire, down the cavity of the style, into the cavity of the ovary, and these entered the foramen of the ovule. This view was originated by our countryman Samuel Morland, who made a series of observations on the subject, consequent on the anatomical discoveries of the illustrious Grew. With respect, however, to the actual origin of the embryo the most contradictory opinions were held by authors. Grew & Millington and Morland at the beginning of the century, and, at a later period Ray and Camerarius & especially Linnaeus supported the opinion that the sexual organs of plants were entirely analogous to those of animals – while others, the principal of whom was Gleichen, asserted that the male plant prepared the "seminal germs" to which the female organ only afforded the means of development. The only difference between this

Facing page 9:
For further Information see Meyen, Pflanzen Physiologie Pp. 273-283 [Meyen 1839]

Horkel, Historische Einleitung in die Lehre von den Pollenschläuchen [Horkel 1936]

St. Hilaire, Morph. Veg. p. 566[or 7?] [Saint-Hilaire 1841]

New observations on the parts & use of the flower in Plants. Phil. Trans. 1703 [Morland 1703]

Ausserlesene mikroscopische Entdeckungen Nürnberg 1781 [Gleichen 1781]

Page 10

view and that afterwards brought forward by Schleiden resulted from Gleichens ignorance of the function of the pollen tube, In 1808 Mirbel advanced the doctrine that fecundation was due to the escape of a very delicate and subtle substance to which the name "aura seminalis" was given, and which he believed to be transmitted to the ovule by means of the placenta & by what he called "conducting vessels." This opinion was adopted by all botanists for some years after this period, till St. Hilaire from observations on Cuphea and the Primulacea [sic], having shown that in these plants the conducting vessels of Mirbel had no existence brought forward the supposition, since revived in another form by Roesser [? my transliteration appears correct, but no one relevant found, could be Roemer is intended] and others, that, at least with respect to these plants – the "aura" acted on the ovule, simply by a kind of imbibition, without the intervention of vascular connection.

After this for some years, no further attention seems to have been paid to the subject, botanists being contented with the vague and indefinite views wh. have been already alluded to.

Facing page 10:
Note – The idea of an "aura seminalis" was first proposed in the previous century by Vaillant "Discours sur la Structure des Fleurs" – Leiden 1718. At that period however it does not seem to have attracted much attention. [Vaillant 1718]

Page 11

In 1825 however the illustrious Robert Brown inferred from a consideration of the position of the ovules in certain plants, in relation to the placenta, that the view of Mirbel, which was still held by many, was irreconcileable [sic] with facts. At the same time, he considered the imbibition theory just alluded to as unlikely, and therefore ventured the supposition that fecundation might

be effected by means of tubes, distinct from the placenta, and communicating between the stigma and the ovule.

From this period a new era commenced in the history of the subject. The suppositions of Brown were confirmed by the actual observations of Amici & Brongniart, and the sexual theory of Linnaeus was once more set upon a firmer basis than ever.

In 1831 Professor Amici of Padua made the important discovery that the pollen grains, where they come into contact with the stigmatic surface, become each of them prolonged into an appendage the pollen tube, which passed down the cavity of the style into the ovary. At the same period, Brown also himself observed

Facing page 11:
Note – Amici was not the first to note the existence of pollen tubes. They were described in Asclepias by Gleichen in 1781 who, however, was not aware of their development from the pollen grain. [Gleichen 1781]

Observations on the Organs and mode of Fecundation in Orchids & Asclepiadaceae 1831 [Brown 1831]

Page 12

observed the same phenomenon in the Orchidaceae and Asclepiadaceae, - he was however unable to trace any connection between that tube and the ovule. Amici in his observations on Cucumis was more successful-. He found that in that plant the tube entered the micropyle, and that by its means fecundation was effected. From the discovery of this most important fact in Cucumis, Amici assumed that this was the probable mode of fecundation in all plants, and in the succeeding year Robert Brown from a more careful examination of the Orchideae [sic] and Asclepiadaceae, found that such was actually the case in those families. He, however being able to trace the continuity of these tubes with those given off by the pollen grains though it more probable, that the tubes observed to enter the ovules, were to be considered as prolongations of the cylindrical cells of the conducting tissue developed under the influence of the pollen, rather than as themselves pollen tubes.

About the same period, Mr. Brongniart

Facing page 12:
Supplementary Observations on the fecundation of Orchideae & Asclepiadaceae London July 1833 [Brown 1833]

Annales des Sciences Naturelles 1832 [? no relevant citation located in this issue]

Page 13

in a memoir read before the French Academy communicated some important observations on various genera of Orchidaceae and Cactaceae, in which he also observed that the tubes were supposed to be merely continuations of the conducting tissue, entered the micropyle and afforded the means of fecundation to the ovule. Brongniart was the first to recognise the fact, afterwards found to be general in all plants, that the entry is developed from a single cell or vesicle, either produced before or after impregnation. In this organ he gave the name of “embryonal vesicle”, which has since been adopted by almost all authors. He considered it as originating from an involution or doubling in of the embryo sac.

In 1834, Corda published his observation on the act of impregnation of the Conifervae. He saw the pollen tubes pass through the opening of the secundine to the apex of the nucleus, into the opening of which, represented in his figures of large size, it also entered, and then became narrowed, and emitted its

Facing page 13:
Beiträge zur Lehre von der Befruchtung der Pflanzen. Nova Acta Tom XVII [Corda 1835]

Page 14

contents as a thick fluid. These contents were soon after observed to become organized, so as to form the embryo-sac, with which the pollen tube did not remain connected long after impregnation. These observations, which were accompanied with elaborate illustrations, have been since shewn to be perfectly inaccurate and are therefore only of historical interest.

About this period the Swedish naturalist Agardh revived the views of Gleichen and his followers, in another form. From a fancied resemblance in the pollen grain and its tube to the germination of some plants, he drew the inference that the pollen grains were to be considered as simply embryos germinating on the stigma.

In 1836, Horkel published a long series of observations, on at least 50 families, in which he traced the pollen tube from the stigma to the ovary, and in numerous instances, to the micropyle. And during the next year (1837), his nephew Schleiden published his celebrated paper on the Development of the Organism in Phanerogamous Plants, and brought forward

Facing page 14:
London & Edin. Philosophical Magazine Vol XII Pp 244-245 [Schleiden 1838b]

Page 15

as a result of his observations, that the pollen tube after passing through the foramen of the ovule, penetrated the intercellular spaces of the nucleus and reached the embryo-sac, which it indented, and formed a cylindrical bag to be afterwards developed into the Embryo. The most important result was founded on a long series of observations of plants of various natural families – particularly of the Coniferae, Lathraea squamaria & the Orchidaceae -, in the last of wh. according to Schleiden , the process is most "beautifully distinct." In this paper, among many new view[] in vegetable morphology, the author first brought forward, as the most important result of his embryological observations, the conclusion, wh. has already been noticed namely, that the pollen grain is to be considered as the "germ of the new individual" to which the embryo-sac "by conveying new organizable fluids, only serves the office of nourishment.

The results of Schleiden were soon after confirmed by two other observers Martius & Wydler of Berne, who though they differ in some

Facing page 15:
Wydler – Bibliothèque universelle de Genève Oct. 1838 [October issue is in Volume 17, starting p. 209; Anonymous 1838]

Page 16

minor points, agree in the most essential that is in asserting that the embryo is originated within the termination of the pollen tube. Martius think that, before the arrival of the pollen tube, at the apex of the nucleus, there is a cell ready prepared to receive it, Wydler, whose observations

extended to sixty different natural families, thought that the embryo-sac was open superiorly communicating by a narrow canal with the micropyle.

In 1839 Meyen, in his "Pflanzen Physiologie", brought forward a new series of observations on the process of conjugation in many of the same plants as had been described by Schleiden, as well as others. From these he was unable to contradict the alleged facts of that observer, and to demonstrate the fallacy of his new and singular generalizations. In the Orchidaceae, as well as in many other plants of various classes, he shewed that the pollen tube never indents the embryo-sac, but that the first cell from which the embryo is to be developed, originates in the sac, without ever coming into direct connection with the

Page 17

termination of the tube. For this first-cell, which is identical to the with the embryo vesicle of Brongniart, Meyen gave the name of germ vesicle. He believed it to be originated in the sac by the "material and dynamic influence of the pollen-tube", and that from it was eventually produced the embryo by a process of successive cell-formations, modified in various ways according to the circumstances of the developments.

The observations of Meyen on Fritillaria and Tulipa are somewhat unsatisfactory, and have been taken up by Schleiden in support of his views. He says that, in Fritillaria, "the end of the pollen tubes sometimes swells very considerably, after its entrance into the nucleus, and that then there are developed from it two or three sometimes very large cells, so as to form together a cord resembling the suspensor of Dicotyledonous Plants but differing in its further history". This discovery at first sight it certainly would appear to be corroboration of the doctrine of Schleiden, is not considered as such by Meyen. On the contrary,

Facing page 17:
Pflanzen Phys. p. 308 [Meyen 1839]
Op. cit. p. 312

Page 18

he remarks on the next page "We have, in the preceding detail, assumed ourselves that the entry is not developed from the end of the pollen tube. We have indeed so satisfactorily ascertained the structure of what we have called the germ-vesicle, and the changes it undergoes up to the development of the embryo, that no one can admit that the germ of the future Embryo is situate [sic] in the end of the pollen tube."

Though there appears to be some obscurity with respect to the observation on Fritillary, we may observe, as a general fact connected with researches of this kind, that is only by studying and following out the modification of development, that any accurate results can be assigned to an individual observation, however satisfactory in itself.

During the same year Mirbel and Spach in their research on the Graminaceae, brought forward some what similar views. They however differed from Meyen, in believing that the embryo vesicle is developed previously to impregnation, and

Facing page 18:
Compts Rendus March 1839 [Jussieu 1839]

Page 19

that the contents of the pollen tube only act in determining the development of the embryo within it. These researches will however be more fully noticed when we treat of the development of the embryo in the Grapes.

In 1840, Meyen published as a supplement to the embryological part of his former work, another series of observations, confirmatory of the views there advocated. His researches were directed to various species of Mesembryanthemum. In these, especially in M. pomeridianum, he observed the process of impregnation very minutely. he found that, on the arrival of the pollen tube at the embryo-sac, a perfect cohesion took place between the one and the other, similar to the conjugation of Confervae,and that consequently on this cohesion, which he considered as the act of impregnation, the germ vesicle originated, being formed out of the substance of the two cohering membranes. He did not suppose that there was any escape of the contents of the tube into the sac, but only the escape of a small quantity into the

Page 20

developing vesicle, soon after which he observed that the "free accumulation of this last with the tube cealed [sic] by a construction resulting from the formation of diagonal septa. This cohesion of the pollen tube was observed and figured by Meyen in his former work on Alsine media, and other plants, and we may suppose that, in the case of Fritillaria referred to above, a similar process may take place.

Here we may notice a view, which was brought forward the year before by Endlicher, & wh. seemed to be a modification of the doctrine of Schleiden , He compared the anther of higher plants to the ovarium of animals, and considered the male fertilizing organ to exist in the glands of the stigma, which consequently was not to be regarded merely as a conducting organ, but one whose peculiar secretion excites the pollen tube too that activity, which rendered it capable of penetrating into the tissue of the pistil, and arriving at the covering of the germ. These views, as being supported in assumptions purely

Facing page20:
Grundzüge einer neuen Theorie der Pflanzenzeugung [Endlicher 1838]

Page 21
First of 2 pages numbered 21

arbitrary have not attracted much of the attention of botanists, and consequently, the memoir is only of historical interest.

In the same light probably, we may correctly consider another work which appeared three or four years later. It contained speculations, which were based upon a foundation not much more substantial, but which, as they were associated with details of researches, conducted by an observer of such repute as Hartig – were, at the time considered of more importance. The object of this author seems to have been, rather to account for negative facts and observations, than to deduce conclusions from positive ones. Having observed, that in some plants the contact of the pollen tube has never been detected, & that in cases [in] which nothing is apparent in the surrounding circumstances, to account for such a fact, - and that in others there seems to be a provision in the embryo-suspensor (as in Euphrasia Pedicularis etc.) for the accomplishment of fecundation without the contact of the tube with the embryo sac, he argued from the consideration of these and many other facts of the like

Page 21
Second of 2 pages numbered 21

indefinite and unsatisfactory nature, that the usual opinions as to the functions of the pollen tubes are fallacious, and that fecundation is effected either without the emission of tube[s] altogether or with the emission of imperfect cues. These views are evidently contrary to ascertained facts, and are not maintained bf y any physiologist of the present day.

In 1842 Dr. Giraud read to the Linnean Society the details of some well conducted observations on Tropaeolum. In this plant he shewed satisfactorily, that the embryo-vesicle originated before the period of impregnation, and that it is perfectly distinct from the embryo sac both in its origin and development. He therefore concludes very correctly, that Tropaeolum is an exception to the doctrine of Schleiden .

The development of the embryo of this plant is peculiar. The embryo vesicle is see to increase in the usual manner, by successive cell developments, into a cylindrical body or suspensor, at the superior termination of which the embryo is formed. After this period the suspensor is seen to take on an extraordinary growth upwards.

Facing page 21:
Trans. Linnean Society Vol XIX [Giraud 1845]

Page 22

It elongates in this direction, till it passes out of the micropyle, piercing apex of the embryo sac, and entering the carpillary cavity outside of the ovule, where it forms a cellular cylindrical and elongated body, similar, according to Giraud to a spongiole.

In connection with this remarkable structure, the author draws some "physiological inferences", with wh. he concluded his paper, but which are founded on assumptions certainly not at all deducible form the actual facts. He advances the supposition that impregnation does not take place, till the suspensor is so far developed as to project considerably beyond the micropyle, and consequently the embryo had attained some size. This view wh. is certainly contrary to what we know of what takes place in other plants, is derived from an assumption wh. has no better foundation than an unsuccessful negative experiment, in wh. Giraud was unable to trace the pollen tube to the ovule at the proper period. This however has been since done by Schleiden and others, and the question is consequently set at rest

Page 23

Having now endeavoured, however unsuccessfully, to give as clear a view as possible of all the various opinions and observations, which may be considered as of any importance, we next proceed to attend to our subject in another & more interesting point of view.

In order to investigate thoroughly the nature of a development like that with which we are at present occupied, it is evidently most desirable, that we should take into account all the modifications presented by it in all classes of plants. This, however, we are unable to do, as in many families the anatomical peculiarities preclude any certain or satisfactory examination. But as we are possessed by the admirable researches of Amici Meyen Mirbel Hoffmeister and others, of well ascertained developments in plants belonging to very various morphological types, we may be enabled from these to draw conclusions which, if not of universal application in every particular, may be safely considered as such in the main.

For this purpose we propose to devote the remainder of this paper to the discussion of the

Page 24

facts ascertained as to the fecundation and the embryo-growth of a few examples of Natural Orders and Species, in which we shall find, that, in all plants, there is a great similarity, in the general features of the process, and in the order in which the different steps are brought about.

The first class of plants which we shall notice is one which, properly speaking, is not included in our subject, as not belonging to the Phanerogamia. It possesses however analogies so

strong to them that it may probably be noticed with advantage, especially as it has been brought forward by Schleiden in confirmation of his views. The

Rhizocarpeae or Marsiliaceae

only differ from the Phanerogamia, according to this author in the fact that the pollen tube penetrated the ovule after the separation of that body from the parent.

The reproductive organs of these plants are of two kinds. The one consists of membraceous [sic] sacs containing spore like bodies (pollen grains Schl.), the other of large cells (embryo sacs Schl) each surrounded [by] a membrane, forming at one extremity a papilla

Facing page 24:
Principles of Botany P. 205 [Schleiden1849]

Page 25

(nucleus), which organ is sometimes covered by another envelope, opening opposite the papilla. At the period of fertilization, the pollen grain extends itself into a tube of various length, and at the same time cells are developed in the nucleus. Among these cells, the pollen tube penetrates and, according to Schleiden expands into a vesicular form from the development of cells within it, destined to become the embryo. Other authors on the contrary believe that the cell from wh. the embryo is formed is developed by the female organ in the nucleus and originates the embryo under the fecundating influence of the pollen. With regard to these interesting plants, there seems however, to be considerable obscurity, but few observers having directed their attention to them, so that as yet it is impossible to give any decided opinion as to the real nature of their reproduction.

For the purpose of facilitating the comparison of corresponding changes in the different plants which we shall notice we shall divide our description of each example into the corresponding heads, corres-

Facing page 25:
Note – Since writing this notice of the Rhizocarpeae, I have seen the researches of Carl Naegeli, originally published in Schleiden s "Zeitschrift fur Wissenschaftliche botanik" [Schleiden and Nägeli 1844] in answer to this observation of that botanist. In there the author shews, in a satisfactory manner, that the embryo-vesicle – from which the embryo is
continued on facing page of Page 26:
afterward developed -, is formed in the cavity of the papilla (bourselet embryonnaise) immediately above the apex of the so called embryo-sac – without ever coming in direct relation with the pollen tube which indeed never penetrated the papilla at all. Hence it is evident that Schleidens observations are incorrect, and that we have here another example of the not infrequent inaccuracy of that great observer – Sec Mech. des Sciences Nat. Feb 1848. [probably Mohl 1848; but in Sec. Botanique not Sec. Mech].

Page 26

ponding to successive stages of development
I In the first we shall notice the early condition of the ovule and the formation of the embryo sac.
II In the second – the changes wh. take place in the embryo sac or cavity previous to impregnation.

III In the third – the changes consequent on impregnation.
IV In the fourth – the development of the embryo

Gramineae

For our knowledge of the development of the ovule and embryo in this class of plants, we are principally if not entirely indebted to the elaborate researches of Mirbel and Spach already alluded to.

The act of impregnation has also been described by Schleiden, for the purpose of refuting whose results, the subject was originally taken up by the first mentioned observers.

I Early condition of the ovule – In Zea mais, which may be taken as a typical example, as it has found that, in all other species which have been examined, the process is entirely similar, the ovule at its earliest condition, consists of nucleus surrounded by the rudiments of the

Facing page 26, after previous continuation:
Note – In all the following details, the terms inferior and superior will be used with reference to the embryo, not the actual direction.

Comptes Rendus Tome VIII Pp 367 [Mirbel and Spach 1839a], 417[Mirbel and Spach 1839b].

Page 27

secundine and primine, the former of which is the longest. At this period, the axis of the nucleus is parallel with that of the ovary, to which it subsequently becomes inclined at an angle of about 90^0. In the interior of the nucleus, near its apex, there then appear a small ovoid cavity, containing a mucous matter perfectly transparent,

II Changes previous to impregnation – The mucilage contained in the embryo-cavity disappears, towards the apex, and at that point an ovoid diaphonous utricle is produced called by the authors, the primordial utricle. This is surrounded by a circle of smaller oval cellules which they are tempted to believe are aborted primordial utricles. Here the observations of Mirbel & of Schleiden differ. The latter says “that the formation of the cavity indicates the origin of the embryo sac, which immediately afterwards appears. Growing incessantly it encloses a considerable space in the nucleus, and becomes filled with a cellular membrane” He in fact asserts that the cavity becomes changed into a complete sac while afterwards grows to considerable size. The stages of these conversions, he has not traced, and as

Page 28

we cannot suppose such a process to take place otherwise than gradually, and as Schleidens assertion is inconsistent with the facts of the development, progressively detailed by Mirbel and Spach, we must give preference to the latter.

III Changes subsequent to impregnation

According to Schleiden the extremity of the pollen tube after arriving at the “embryo sac” “pushes before it the all of the sac which yields so as to form a caecum, in which it lodges its anterior extremity”. This extremity then “swells into a mass and produces in its cavity a cellular [hand drawn line in marginalia next to the lines of text indicated by {}] { tissue” which soon becomes “metamorphosed into the embryo.” As to the alleged inversion of the embryo-sac, as the latter has no existence it is unnecessary to say that it is impossible, and it is not a little} remarkable that in Schleidens figure no such involution is represented.

According to the more satisfactory observations of Mirbel and Spach, the embryo-vesicle which as was mentioned, originates before impregnation contains at that period a fluid opaque matter, called by the authors "globula[r] cellular cambium". After impregnation, the exact nature of wh. process

Page 29

in the Grasses, has not been made out, this cambium becomes formed into a mass of membranous tissue filling the cavity of the vesicle and suspensor, which last then sensibly elongates and enlarges.

To satisfy themselves of the most important fact in the development, namely the origin of the vesicle before impregnation Mirbel and Spach afterward carefully examined the ovule at a period considerably previous to the opening, either of the male or female flowers, when consequently neither the stigmata nor the anthers had attained their development. They found that at this early period, the embryo-cavity existed in the nucleus – that the embryo-vesicle was already formed, and that even the globula[r?] cellular cambium was observable within it.

It is difficult to conceive how so accurate an observer as Schleiden could be led into such important mistakes – If, however, instead of depending entirely on isolated observations, however well conducted, he had studied the facts of the development in their chronological order, he certainly would not have described the inversion of an embryo-sac which had no existence, or supposed the embryo-vesicle to be the end of the pollen-tube.

Page 30

IV Developement of the Embryo

The cells contained in the embryo vesicle assume the general form of the embryo wh. becomes elongated superiorly into a cellular lanceolate point, the cotyledon, while inferiorly the radicle is developed while still attached to the remains of the suspensor. On the upper side of the cotyledon, at the base, is developed the plumule, imbedded in a kind of hood in wh. the first rudiments of the stem leaves make their appearance.

Orchidaceae

Of all the classes of plants which have been made the subject of embryological research, the Orchidaceae certainly present the greatest advantages, and have yielded the most important results. From the small dimensions of the ovule as well as from the transparency of its coverings, so little dissection is required that all the principal facts of the development may be made out with comparative ease.

It was from these plants that the first accurate knowledge was obtained of the general nature of the fecundating process by Robert Brown, Brongniart and Amici, and it is to the last observer

Facing page 30:
Amici – Annales des Sciences Naturelles April 1847 [Amici 1847]

Page 31

as well as to the later researches of Hugo Mohl and Karl Muller, that we are indebted for the comparatively complete series of facts, which we possess with respect to their development.

I Early Condition of the Ovule

At the period of the expansion of the Perianth, the nucleus of the ovule is attached to the end of the umbilical cord at a right angle (Pl III fig 2 [=II]). It consists of a central column of cells surrounded by a layer of others, which are of much smaller dimensions. The superior cell of

the column, especially, (Fig. II, 1 [this should be Pl. III, Fig. III]) is about double the size of the cells of the outer layer. This cell encloses a very visible nucleus. At this period the bundles of pollen tubes have entered the style. They are easily distinguished from the cells of the conducting tissue, with which they were confused by Brown, by their being no more than one third of the diameter.

Three or four days after, the flower is withered and the ovary considerably enlarged. The pollen-tubes have entered the apex of its cavity, where they divide

Facing page 31:
Mohl – Botanische Zeitung N^{o}. 27 July 1847 [Mohl 1847, no illustrations]
Muller – Annales des Sciences naturelles Jan^{y}. 1848 [Muller 1848]

Page 32

into three or rather six bundles, which pass about half way down the placentas. The ovule now presents the appearance represented in Fig. III, being more curved towards the base of the funiculus. The primine had enveloped the nucleus, while the secundine is hardly at all developed. The embryo sac is much enlarged and, according to Mohl, the cells which form the external layer of the nucleus are flattened so as to constitute a thin envelope round the embryonal-sac.

The account, however, given by Amici differs. He says that this cellular layer opens by the separation of the cells which compose it, and that by this process, the embryo-sac is left, at its upper part, entirely bare. To reconcile this discrepancy and [crossed out] ascertain on which side of the truth lay, (as I was unable to procure suitable specimens of Orchis morio, the plant on which the observation of Mohl and Amici were made), I observed carefully the appearances presented by Or. mascula at the corresponding stage. I succeeded in confirming the description given by Amici, as shown in Pl. III Fig 3 [=III] & 7 [=VII]. In Fig. 3 [=III], the embryo sac is seen to be half-enclosed by the advancing primine, while the outer cells of the nucleus are separating from each other, and leaving the sac

Page 33

completely bare. The same is seen in various conditions in Fig. 7 [=Pl. III VII]. About a week after this period, or nearly a fortnight after the withering of the flower, - the external form of the ovule has changed considerably, and it assumes the appearance represented in Pl I Fig 1 [= I] (O. morio) & in Pl III Fig. 4 [=IV] (O. mascula). The secundine is seen to have become developed, so as to enclose the embryo sac, - and the primine, composed of larger diaphanous cells extends considerably beyond the secundine. After this no further change takes place in the external appearance.

II Changes in the embryo-sac previous to impregnation

Some time before impregnation the embryo sac is observed to contain a granular matter or Protoplasma, wh. however is not diffused over the whole, but collected at the extremities especially at the superior. This, according to Mohl, separated into three parts, at the period when the embryo sac is fully developed. From them as nuclei, three cells are developed placed side by side. (Pl. III Fig IX. 2, 6 [6? perhaps &c, 5th is last sub-figure]). That such a process does take place at some time cannot be doubted, - the question is – Does it take

Page 34

place before impregnation. Amici thinks that a single embryonal vesicle is developed from the protoplasm – containing at the period of impregnation a granular fluid superiorly and a limpid liquid at its apex or inferiorly, where it is near the pollen tube. Muller on the other hand believes that the embryo vesicle is not formed till after impregnation – his observations do not seem to be

very carefully conducted. From my own observations on O. mascula, I should be inclined to conclude that one or two embryo-vesicles exist previously to impregnation, consisting each of a simple membrane with a nucleus – that is of a cell in its simplest form – which immediately afterwards (Pl III Fig. IX. 2 Fig VI 4) developes into a cell such as that described by Amici. These vesicles may be observed in the embryo sac, even before it becomes covered with the primine and secundine, shewn in the nuclei [Pl. III] Fig III & VII, whence it is evident that the view of Muller is untenable – It also shows that the doctrine of Schleiden does not hold good in the Orchidaceae any more than in the Gramineae, as the structure out of which the embryo is developed – originates before the contact of the pollen-tube with the sac.

Page 35

III The act of impregnation and the changes which follow it.

The pollen tube enters through the opening of the primine, and its course is easily traced through that covering. Its passage through the secundine is not too easily seen – It seems to contract (Pl I Fig 1 [=I] Pl III Fig 4 [=IV]) its diameter very considerably. This however, is thought by Amici to be an optical illusion, depending on the refraction caused by the roundness of the cells of the secundine.- It becomes again distinct, when it emerges at the apex of the embryo sac and passes laterally upon its surface for a certain distance. This may be seen with a distinctness which places the fact beyond dispute, when the ovule is so situated as to present a profile view of the curve. The end of the pollen tube remains in its position for some time and projects more or less into the embryo sac. The fluid in its extremity has as Mohl remarks, no resemblance to blastoma destined to be transformed into tissues, but constitutes a "granulous [?] mass of a greenish yellow colour."

Shortly after impregnation one of the cells formed at the apex of the sac enlarges – (rarely two of them). The protoplasma accumulates at its superior extremity,

Page 36

and a transverse septum is formed. Others – follow so that the original vesicle is transformed into an ovoid body composed of three or four cells arranged one above the other, each of which contains a nucleus. At the same time cells are formed in the collection of protoplasma at the opposite end of the sac, which grow until they are eventually displaced by the embryo.

After this the ovoid body above mentioned is developed inferiorly into a confervoid filament (suspensor), which at last passes out of the micropyle. Along side of this is often seen the remains of the pollen-tube, thus illustrating the absurdity of Schleidens representation (Pl IV Fig 2 [=II; from the context, Fig. I and II may have been intended together]), in which he

figured this development as produced in the end of the tube.

The graneous looking yellow coloured mass, the remains of the end of the pollen tube, becomes eventually absorbed, but remains – for a very considerable time – presenting a form generally more or less angular. This is shewn in O. mascula, in Pl III Fig IV, VI.

From these circumstances as well as from what was before noticed of the existence of the embryo-vesicle before

Page 37

impregnation, the conclusion cannot be avoided that in the Orchideae, which Schleiden considered as particularly confirmatory of his views, the alleged facts of that observer are inaccurate &, consequently, his deductions valueless.

Halorageaceae

The Halorageaceae as far as I am aware, have not hitherto been carefully examined by any observer, with a view to ascertaining the origin and development of the embryo. M. Barneoud, in a paper "On the Organogeny of Trapa nutans["], has described the development of the ovule in that plant, up to the period of impregnation, but has not detected changes wh. take place in its interior. Besides Trapa is considered by many authors, as belonging to the neighbouring order Onagraceae, and it is difficult to say to which it bears the strongest affinity.

Hippuris vulgaris

The ovary of Hippuris is one celled, containing a single pendulous ovule - attached, mai[n]ly at its apex by a fleshy funiculus.

Early condition of ovule

I have not had an opportunity of examining

Facing page 37:

Annales des Sciences Naturelles May 1848 [Barneoud 848]

Page 38

the ovule of Hippuris at the very early stage. In that of Trapa wh. exactly resembles it, Barneoud found that the primine and secundine were developed from a ring at the base of the previously formed nucleus, which they gradually covered, and that, at the same time, the ovule became anatropous, as we have already seen in the Orchideae.

After these changes have taken place, at a period not long before impregnation, the ovule presents the appearance shown in Pl II Fig 1 [=I]. The nucleus *a* lies loosely in the cavity formed by the envelopes, which completely surround it, attached by rather a narrow neck to the chalaza at *b*. – The envelope is indistinguishable into primine and secundine, and extends considerably beyond the apex. It consists of small hexagonal cells arranged in series, each containing a nucleus. On one side, the raphe consisting of a bundle of imperfect spirals is seen passing from the hilum h to the chalaza.

The nucleus, [Pl. II] Fig. 2. [=II], the structure of which cannot be seen, on account of the opacity of the envelope, without dissecting it out, consists of a cavity – the entry-cavity – extending from its apex to about two thirds of its length, which is surroun-

Page 39

ded by a single layer of very transparent nucleated cells. At the apex of this cavity is observed an elongated club shaped cell, considerably larger than any of the rest (the embryo vesicle, Amici) which, in the early state, contains a transparent – slightly granular fluid – Towards the period of impregnation, the granular protoplasm increases in quantity, and accumulates towards the upper extremities of the embryo-vesicle, just as is described by Amici as taking place in the vesicle of Orchis Morio. – This is shewn – more enlarged – in [Pl. II] Fig. III.

III. Changes taking place after impregnation

After impregnation the granular protoplasm becomes transformed into a spherical cell [Pl. II] Fig. V, which soon after enlarges assuming an oval form. A septum is then observable at the lower part crossing it horizontally, by which it is divided into two cells – Of these the inferior becomes developed downwards – by successive merismatic [sic] division, so as to form a confervoid filament – the suspensor, which is seen in various stages in [Pl. II] Fig.VI, VII, VIII. The upper assumes at the same time a spheroidal form, and is distinguishable from the rest by being completely filled with granules, exactly as occurs

Page 40

in Orchis (see Pl. I Fig. VI). Soon after it divides by a longitudinal septum (Pl II Fig VII), and subsequently by a transverse ([Pl. II] Fig VIII). These are followed by successive divisions, and the embryo with its suspensor is formed, assuming the appearance represented in Plate III Fig I, where a much lower magnifying power is used than in the preceding.

While these changes are taking place, the embryo vesicle, which in the early state is adherent to the elongated cells, which form the lower part of the wall of the nucleus-cavity, becomes correspondingly elongated and enlarged. It is never however completely filled with the embryo or its suspensor, or at least not till a very late period. It becomes narrowed at its apex, either by the absorption of its contents by the developing embryo, or by the pressure of the contiguous cells.

From the preceding details it will be seen that Hippuris presents an exception even stronger than Orchis to the views of Schleiden as from its magnitude and the distinctness with which it can be seen before impregnation – the supposition cannot be entertained for one moment that the embryo-vesicle is the anterior extremity of the pollen tube.

Page 41

Onagrariaceae [sic=Onagraceae]

The observations of Hoffmeister [sic=Hofmeister], on this class of plants tend to the same conclusions, as those which we have already detailed. That observer has elaborately traced the whole development in several species, and beautifully represented his results.

In Oenothera, about three days previous to the opening of the flower, the embryo sac contains a viscous fluid, in which a very few transparent granules float. A little after the petals have begun to become coloured, there is a considerable agglomeration of the globules to the inferior extremity, - several nuclei and nucleoli float in the fluid and one or two of them develop into as many pyriform cells, Pl IV Fig 4 [=IV] , 5 [missing, likely VI is intended) generally in contact by their smaller extremity with the membrane of the upper part of the embryo-sac. These cells, (embryo vesicles), contain a mucous fluid, which refracts light strongly. One only becomes fully developed, while the others, even before the period of impregnation, shew signs of abortion ([Pl IV.] Fig. 7 [=VII]).

After the flowers have withered, the pollen tubes are seen entering the foramen of the of ovule. On arriving at the nucleus, it displaces the dense mass of cells which form the apex of that

Facing page 41:

Annales des Sciences Naturelles Feb^{y}. 1848 [Hofmeister 1848]

Page 42

body. It is then observed to swell out at its extremity to a considerable extent, and to contain numerous starchy and caseous granules.

In the embryo-sac with which the tube is now in contact, the embryo-vesicle is observed, in general, not in contact with the membrane but floating free towards its lower extremity ([Pl. IV] Fig. 8, 9.). After impregnation the embryo-vesicle divides by a horizontal septum into two cells. The superior, exactly as in Hippuris, is granular, divides into four and becomes the embryo - The inferior becomes divided into the suspensor. ([Pl. IV.] Fig. 10-14 [=X-XIV])

Convolvulaceae

To this order we may very briefly allude, as it is one which has been asserted by Schleiden to be confirmatory of his views.

Observations are wanting on the origin of the embryo vesicle in these plants, but we may safely conclude that the embryo is not developed within the pollen tube, as it has been observed

by Duchartre, that, for a short time after the origin of the embryo, the end of the pollen tube remains visible along side of it.

Facing page 42:

Annales des Sciences Naturelles May 1848 [Duchartre 1848]

Page 43

Santalaceae

Under this head we must very briefly notice the observations of Griffith on the Embryology of these plants as they are considered by Schleiden as confirmatory of his views.

The ovule of Santalum consists, according to this observer, of a naked nucleus, from which a much enlarged embryo-sac projects. - This sac is much elongated in the direction of the axis of the ovule, and possessed a very peculiar extension backwards beyond the back of the ovule to the placenta. At the period of impregnation, the apex of the sac contains a dense-opaque granular matter, and the whole is divided by transverse septa into numerous cells. The apex is split into four or five connivent lobes, by very visible fissures. On arriving at the sac the pollen tube enters between these lobes, and expands into a bulb in which afterwards the embryo is developed.

On this description we can, of course, make no comment. It may however be remarked that from the opacity of the granular contents of the sac, which according to Griffith resembled in appearance, a solution of gamboge, Santalum must be considered

Page 44

notwithstanding the isolation of the sac, and the apparent simplicity of its parts, a very unfavourable example for embryological investigation. We may suppose that if any future competent observer have the opportunity of examining this plant, it will be found that the facts are irreconcilable with those ascertained in other examples.

This is rendered the more probable, from the consideration that in Viscum, a plant very closely allied to Santalum, which has been described by Meyen, Decaisne and others, as well as by Griffith similar results have not been obtained. In this plant the ovule consists of a simple naked nucleus, without either primine or secundine. In this nucleus two or sometimes three embryo sacs are developed. In each of them, as has been shown by Meyen, an embryo vesicle originated, without any communication from the pollen tube, after which it becomes enclosed in a granular mass, analogous probably to the grainous body described by Griffith in Santalum. At the same time the whole embryo sac becomes divided as in Santalum into cells by transverse septa.

After the process of cell formation is completed and the cells have become filled with their granular

Page 45

and opaque contents, when the embryo-sac has arrived at its full development, the embryo vesicle begins sensibly to enlarge – and the embryo is developed from it. – This is probably the period of fecundation, the act of which has not been observed by Meyen, who thinks that it takes place at an earlier period.

Ericaceae

Monotropa hypopitys – In this plant and probably all the Monotropea [sic] we have the next favorable examples possible for the study of embryo development, but unfortunately they are not very accessible. In Pl I Fig. 7 [=VII] is shewn the ovule at the point of impregnation. The coverings are so transparent as to show the embryo-sac a [not labelled, but labelled in the

original plate of Muller 1848], with the greatest distinctness, with the pollen tube applied at its inferior extremity. In the interior of the sac is seen a large cell, the embryo-vesicle. b [labelled in the original plate of Muller 1848], which according to Müller is developed after the contact of the tube. It is however improbable if not impossible that so large a cell should be developed under such circumstances, in so short a time and, therefore, he appears to have made an observation at a

Page 46

period previous to impregnation, we may suppose that if such observations had been made, an opposite conclusion would have been arrived at, as we actually found to be the case in Orchis Morio, in which Müller makes a similar assumption.

The changes wh. the embryo-vesicle undergoes after impregnation are shewn in [Pl. I] Fig. VIII, X, XI. Three very transparent cells are developed in it, which. soon after multiply by division – so as to form a fusiform body consisting of a series of cells closely superimposed upon each other. The cells in the centre of this body become granular and enlarge laterally, and contribute the embryo, while those at the extremities elongate, so as to form a suspensor at each end, a form of development probably peculiar to the Monotropea. After this the cells forming the suspensor become obliterated, and the embryo is left as in [Pl. I] fig. IX. The persistent pollen tube is seen adherent to its base.

A similar series of observations was made by Muller on a plant belonging to another order – Begonia cucullata – with similar results. In Plate I Fig 12 & 13 [= XII & XIII] the ovule is shewn at the period of fecundation. [Pl. I.] Fig. 12 [=XII] represents the whole ovule[,]

Page 47

Fig. 13 [=XIII] the secundine isolated. This species will repay further observation, as the observation of Muller with respect to the development of the embryo-vesicle after impregnation, cannot be so easily explained as in the former instances.

Cruciferae

This order, though, from the density of the tissues forming the envelopes of the ovule in all species which I have examined, it is unfavourable for studying the act of impregnation, yet it affords great advantages for obtaining the development of the embryo. In Capsella Bursa Pastoris and Draba verna the process had been observed by Meyen. In Capsella I have myself traced it and found it to resemble exactly that described above in Hippuris, and Oenothera. The embryo-vesicle is first observed (probably before impregnation) at the apex of the embryo-cavity in the form of a globular or oval cell. This afterwards divides into two by a horizontal septum. The superior of the two cells thus formed, contains a quantity of granular matter and become globular. It then divides in to four and subsequently each division, into two, till by successive cell multiplication the embryo is formed.

Page 48

In the mean time, the inferior cell become[s] divided massively by horizontal septa, so as to form the suspensor. This suspensor lengthens – very considerably – till it arrived at the micropyle – where the terminal cell becomes much enlarged, & so as to be three times the diameter of the embryo, at the same period. On the probable function of this remarkable cell, it is difficult to form any opinion – it probably subserves the purposes of nutrition. All these changes are seen in Plate V Fig 1-6 [=I-VI]. In endeavouring to draw a conclusion from the facts which have been noticed in the previous pages, it is impossible to avoid remarking the strong resemblance, which

exists between different classes of plants, with respect to the process of embryo-development, the steps which precede it and the conditions and circumstances under which it is brought about.

It may be laid down as an assertion of general application throughout organized nature that the development of new parts or individuals

Page 49

similar and analogous processes are always conducted in a similar manner and by similar means. This circumstance leads us to the conclusion that all these processes are contrived in accordance with some general principles or fixed laws or in other words in strict conformity to certain original types, capable of being modified in various manners, according to the accidental circumstances of the individual or of the class of organisms to which it belongs.

Taking it for granted that in all cases such a type exists, our business in studying any particular development consists simply in endeavouring to discover its nature, and, as before noticed, in order that we may form a certain induction – in so far, that is, as any induction can be drawn - it is necessary that we should be possessed of details of all the modifications of the type. In the instance of the subject before, as we are not possessed of these details, & we ought, therefore, not to bring forward any results with certainty, as has been done by some authors, as generally applicable. The difficulties which lay in our way in attempting

Page 50

even an approximation are very considerable, as we have, as it were without any data to discriminate between what is essential, and what is accidental, - between what is expressive of the type and what is peculiar to the individual.

According to the importance, in a morphological point of view of any development, we find that the strictness and universality of its conformity to a given type, correspondingly increases. we may therefore conclude that, when we are tracing a development, the most morphologically important that exists, viz. that of the embryo, we shall find the conformity marked, and, on that account be enabled , with some approximation to accuracy, to point out the general outlines of the type. Accordingly we have given below a tabular view of what appear to be the most essential features of the process we have been considering in Phanerogamous Plants, only promising that, as we said before, no results can be considered as certain in the present state of our knowledge. It is at the same time equally true that a doctrine, contradicted, in essential points, by a series of facts however limited, such as e.g. that of Schleiden – may be laid aside as inaccurate.

Page 51

Tabular view of the origin and development of the Phanerogamous Embryo

1. Development of a nucleated Cell (embryo vesicle) (Pl V. Fig 7 [=VII].) within a cavity containing a fluid blastema (embryo cavity). This cavity is probably in all cases, originally consists [=?] of the interior of a cell the water of which are absorbed…Embryo-cavity or are persistent…Embryo-sac
2. Division of embryo-vesicle under the influence of the contents of the pollen-tube, or rather, the formation of a new cell from a granular cytoblast, at the extremity opposite to the point of contact- (Embryo globule ([Pl. V.] Fig. 8 [=VIII]))
3. Development of new cells in the embryo-vesicles so as to form one or more confervoid filaments (suspensor) ([Pl. V.] Fig 9 [=IX]). One, developed towards the apex of the embryosac. Two – one towards the apex – the other towards the base, as in Monotropa.

II Development of embryo

1, Division of Embryo-globule into four, by the formation of four new cells within it ([Pl. V.] Fig. X)
2 Formation of the perfect embryo by successive cell-multiplications ([Pl. V.] Fig. XI)

"Ab ovo usque ad malum"
Horace
From the germ vesicle to the mature embryo [sic]

THE PLATES

Notes:

I have added brief legend to each plate to indicate the species being illustrated, and to provide information on whether the plates are copied from previous authors or probably original to Burdon Sanderson (see text).

Explanatory legend to Plate I below

Fig. I-VI *Orchis morio*.

Fig. I-VI are identical to those in Muller (1848: Plate 1 Figs. 1, 2, 3 and 5 (latter includes two figures, corresponding to Figs. IV and V above)), and likely have been traced. There are pin-pricks visible on the paper (when looked at with a 6x binocular scope with side illumination) on nearly all the component figures. There are no pin pricks evident on any other Plates; curiously pin-pricks are not evident in Plate IV which is also a copy (see legend to Plate IV).

Fig. VI, 1-4 are identical to those in Muller (1848: Plate 1 Figs. 6, 7, 9, 11).

Fig. VII-XIII *Monotropa hypopitys*.

These figures are identical to those in Muller (1848: Plate 1 Figs. 23, 25, 29, 27, 28).

Fig. XII and XIII *Begonia cucullata.*

Identical to those in Muller (1848: Plate 1 Figs. 38, 39).

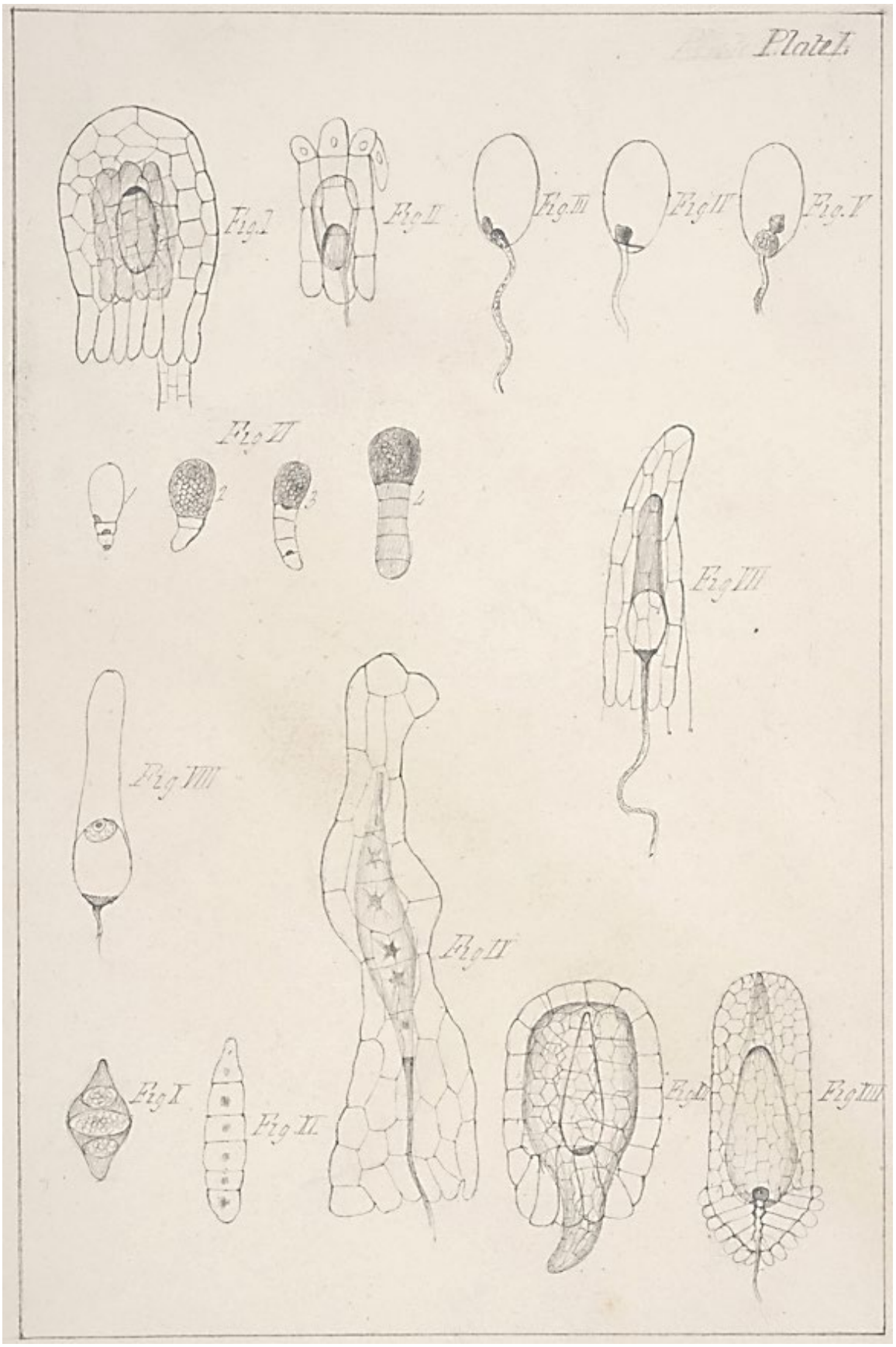


Plate I.
Fig. I
Fig. II
Fig. III
Fig. IV
Fig. V
Fig. VI
1
2
3
4
Fig. VII
Fig. VIII
Fig. IX
Fig. X
Fig. XI
Fig. XII
Fig. XIII

Explanatory legend to Plate II below

All the figures are of *Hippuris vulgaris*

Fig. I is similar but not identical to Barneoud (1848: Plate 15).
Fig. II
Fig. III Redrawn in Burdon Sanderson (1859: Fig. 191, p.249)
Fig. IV Redrawn in Burdon Sanderson (1859: Fig. 192, p.249)
Fig. V
Fig. VI
Fig. VII Redrawn in Burdon Sanderson (1859: Fig. 193, p.250)
Fig. VIII

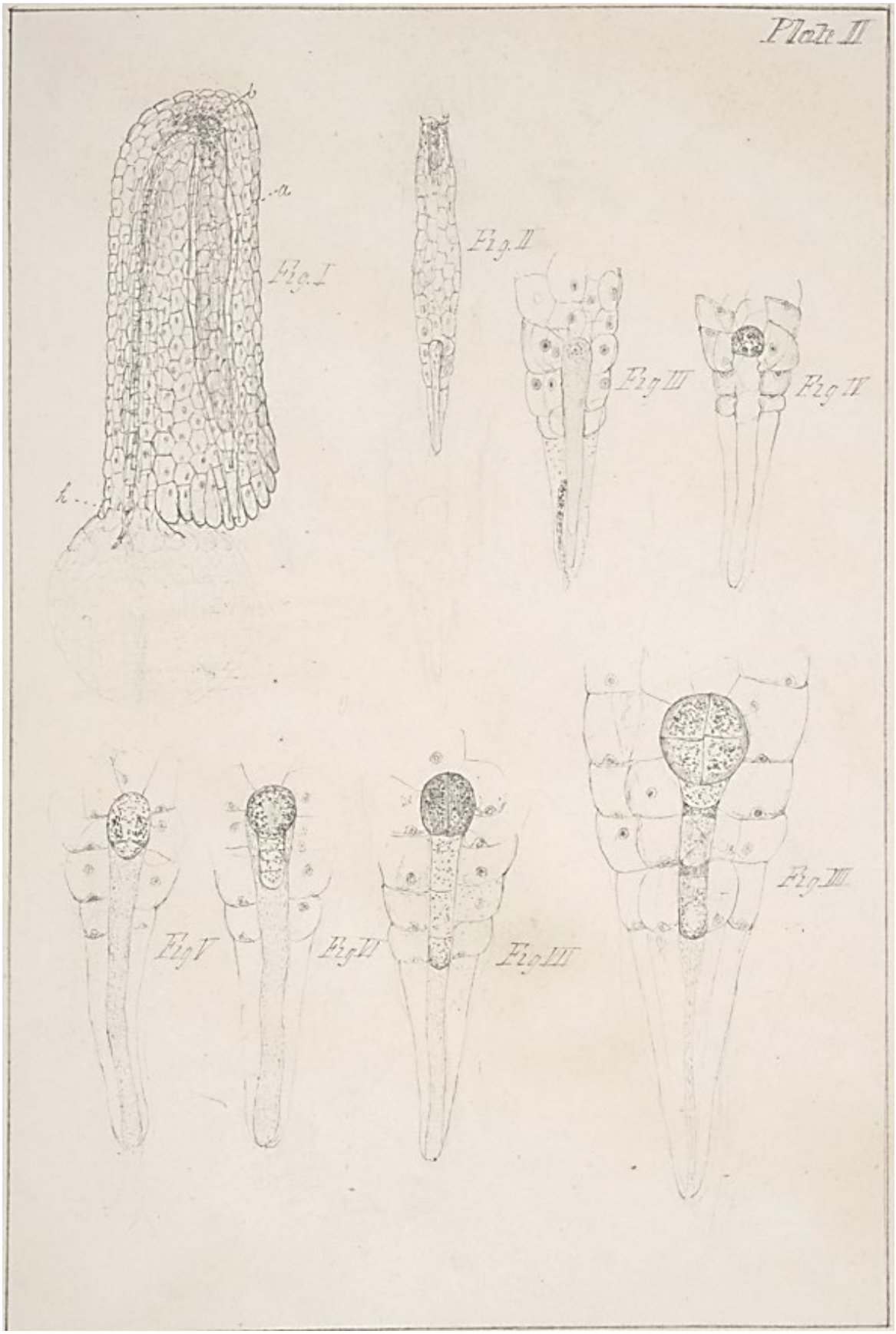


Plate II
a
b
Fig. I
Fig. II
Fig III
Fig IV
Fig V
Fig VI
Fig III
Fig III

Explanatory legend to Plate III below

Fig. I *Hippuris vulgaris*

Fig. II-IX *Orchis mascula*

Fig. II and III are similar, but not identical, to Meyen (1839: Tab. XIII).

Fig. III Redrawn in Burdon Sanderson (1859: Fig. 195, lower left).

Fig. IV Redrawn in Burdon Sanderson (1859: Fig. 197, lower right). Similar but not identical to Henfry 1852. Illustrated in Fig. 2 in the text.

Fig. V

Fig. VI 1-4

Fig. VII 1-5

Fig. VIII is not referenced in the text, but perhaps a lower magnification of Fig. IX 5.

Fig. IX 1-5.

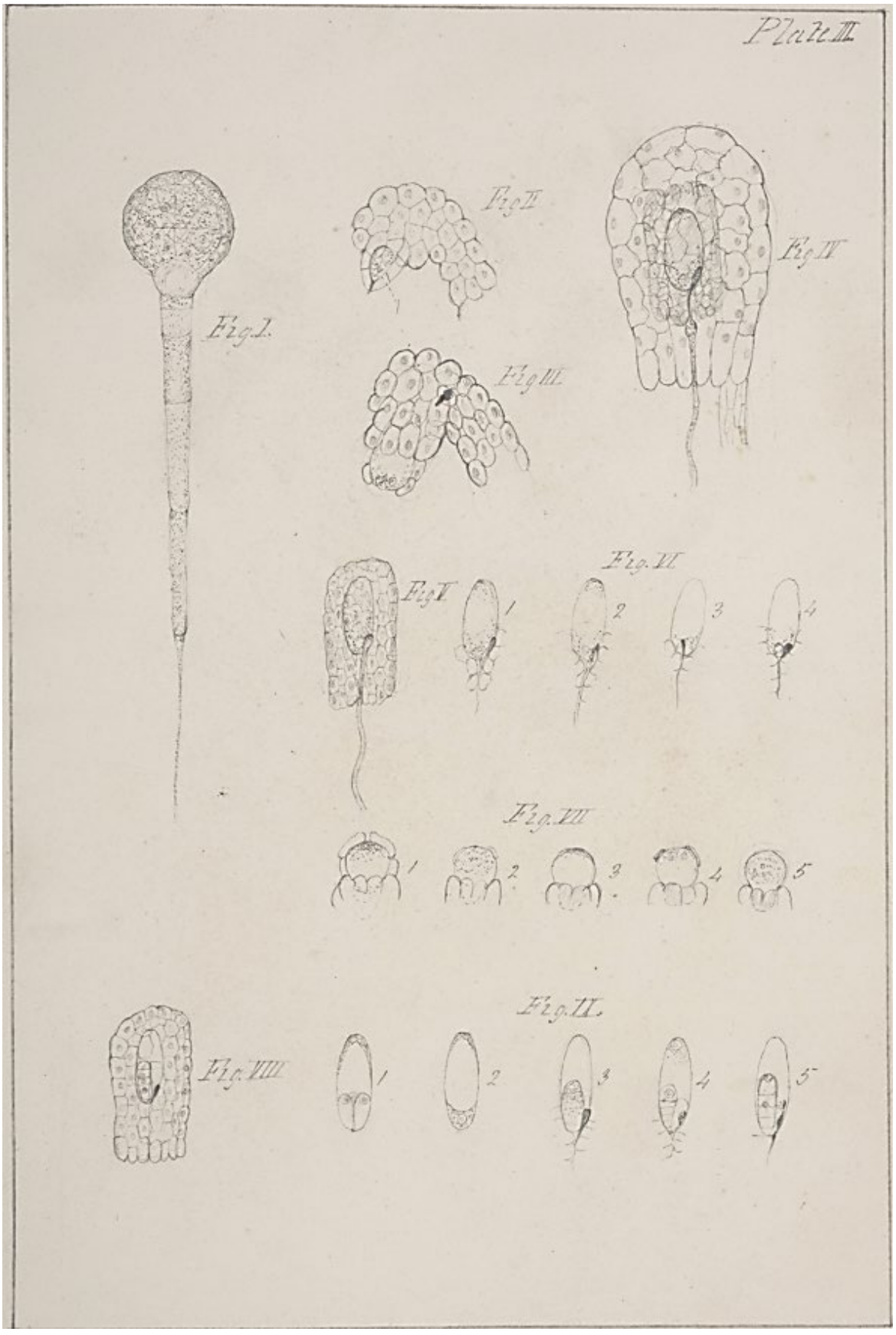


Plate III.
Fig. I.
Fig II
Fig III
Fig IV
Fig V
Fig. VI
1
2
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Fig. VII
1
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Fig. VIII
Fig. IX.
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5

Explanatory legend to Plate IV below

Fig. I-II Species undetermined.

Fig. I and II. Only Fig. II is referenced in the text (p. 36) as “illustrating Schleiden’s absurdity”, namely his hypothesis that the pollen tube produces the embryo. Fig. I is not referenced, but likely the intention was to cite both these figures together.

Fig. III-XIV The Onagraceae.

These all appear to be copied from Hofmeister (1848: Plate 4). Hofmeister’s corresponding figure numbers and the species are in parentheses: Fig. III (1, *Godetia quadrivuilnera*); IV (4, *G. rubicunda*); IV[V missing] (5b, *G. quadrivuilnera*); VI (7, *Boisduvalia concinna*); VII (10, *G. rubicunda*); VIII (15, *G. quadrivuilnera*); IX (16, *G. quadrivuilnera*); X (20, *G. quadrivuilnera*); XII (22, *B. concinna*); XIII (24, *G. quadrivuilnera*); XIV (25, *B. concinna*). The meaning of the letter or symbol ‘t’ added to the latter figure is unclear.

Fig. XV-XVIII *Mesembryanthemum glomeratum.*

These appear to be copied from Meyen (1839: Tab. 4), with the figure numbers in parentheses. XV (47); XVI (46); XVII (49); XVIII (48).
However, these figures are not referenced in the text of the essay.

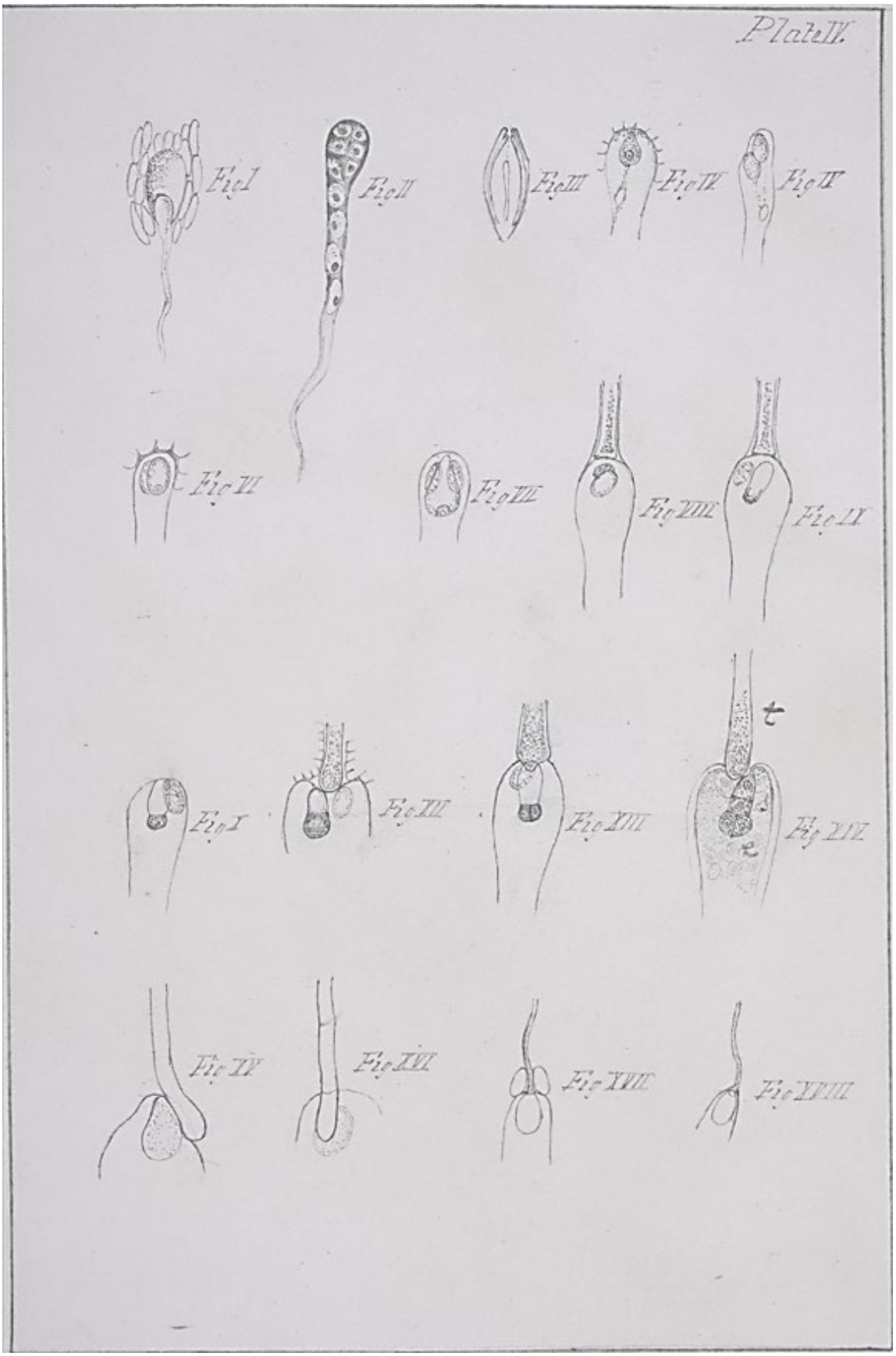
Plate IV.
Fig I
Fig II
Fig III
Fig IV
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Fig VI
Fig VII
Fig VIII
Fig IX
Fig X
Fig XI
Fig XII
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Fig XIII
Fig XIV
Fig XV
Fig XVI
Fig XVII
Fig XVIII

Explanatory legend to Plate V below

Fig. I-VI. *Capsella bursa-pastoris*
Similar but not identical to Meyen 1839.

Fig. VII- XII. Schematic summary, figures presumably drawn by Burdon-Sanderson.

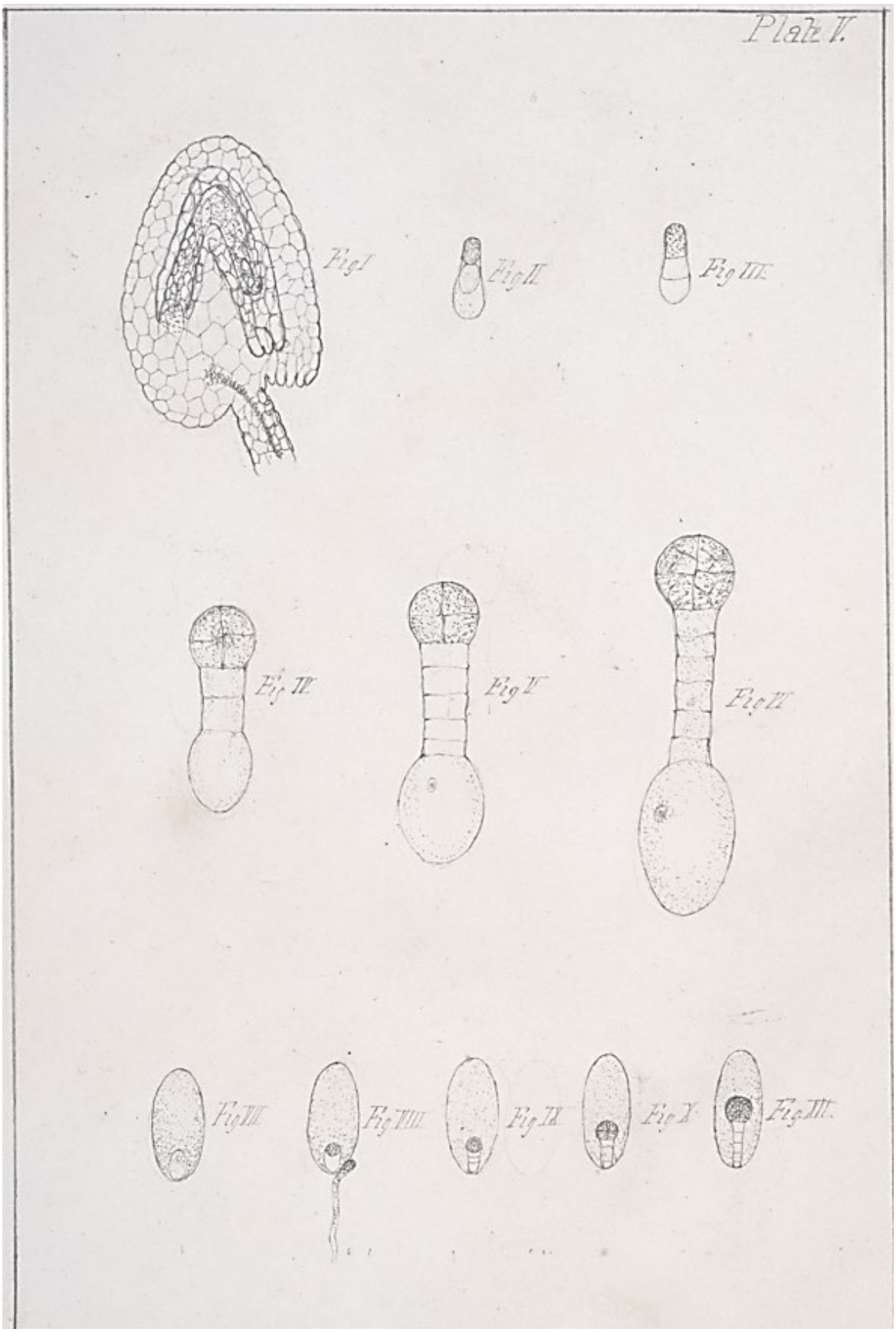
Plate V.
Fig I.
Fig II.
Fig III.
Fig IV.
Fig V.
Fig VI.
Fig VII.
Fig VIII.
Fig IX.
Fig X.
Fig XI.

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[2] Includes September and October issues, numbered continually. It is footnoted in on p.329 that Wydler's presentation will appear in the next issue of Bibl. Univ. but I have not located this volume.

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[4] It is likely that this author is Karl Müller (1817-1870), as the article is stated as translated from German into French by J. Riedel. Moreover, the foldout with the figures has "Karl Müller written in the bottom left-hand corner. He also uses his Latin name Carolo Mueller (Berol. = from Berlin) as editor of *Annales Botanices Systemicae* Vols IV-VII.

[5] From the pagination, it appears that JSBS read the English translation. The German original was published in 1842: *Grundzüge der Wissenschaftlichen Botanik nebst einer Methodologischen Einleitung als Anleitung zum Studium der Pflanze*. *Erster Theil: Methologische Einleitug. Vegetabilische Stofflehre. Dir Lehre von der Pflanzelle*. Leipzig: Engelmann. 1-289 pp. plus corrections. *Zweiter Theil: Morphologie, Organologie*. 1843. 1-564 pp.

[6] For notes and translation, see Bernasconi, P., and Taiz, L. 2002.