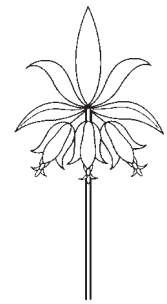
HUNTIA

A Journal of Botanical History



VOLUME 15 NUMBER 1
2014

Hunt Institute for Botanical Documentation
Carnegie Mellon University

Pittsburgh

The Hunt Institute for Botanical Documentation, a research division of Carnegie Mellon University, specializes in the history of botany and all aspects of plant science and serves the international scientific community through research and documentation. To this end, the Institute acquires and maintains authoritative collections of books, plant images, manuscripts, portraits and data files, and provides publications and other modes of information service. The Institute meets the reference needs of botanists, biologists, historians, conservationists, librarians, bibliographers and the public at large, especially those concerned with any aspect of the North American flora.

Huntia publishes articles on all aspects of the history of botany, including exploration, art, literature, biography, iconography and bibliography. The journal is published irregularly in one or more numbers per volume of approximately 200 pages by the Hunt Institute for Botanical Documentation. External contributions to *Huntia* are welcomed. Page charges have been eliminated. All manuscripts are subject to external peer review. Before submitting manuscripts for consideration, please review the "Guidelines for Contributors" on our Web site. Direct editorial correspondence to the Editor. Send books for announcement or review to the Book Reviews and Announcements Editor. Subscription rates per volume for 2014 (includes shipping): U.S. $65.00; international $75.00. Send orders for subscriptions and back issues to the Institute. All issues are available as PDFs on our Web site, with the current issue added when that volume is completed. Hunt Institute Associates may elect to receive *Huntia* as a benefit of membership; contact the Institute for more information.

Hunt Institute for Botanical Documentation
Carnegie Mellon University
5th Floor, Hunt Library
4909 Frew Street
Pittsburgh, PA 15213-3890
Telephone: 412-268-2434
Email: huntinst@andrew.cmu.edu
Web site: http://www.huntbotanical.org

Editor and layout	Scarlett T. Townsend
Book Reviews and Announcements Editor	Charlotte A. Tancin
Associate Editors	Donald W. Brown
	Lugene B. Bruno
	T. D. Jacobsen
	J. Dustin Williams
Photographer	Frank A. Reynolds

Printed and bound by R.R. Donnelley,
Hoechstetter Plant, Pittsburgh, Pennsylvania

© 2014 Hunt Institute for Botanical Documentation
All Rights Reserved

ISSN 0073-4071

Contents

HUNTIA 15(1) 2014

"Untersuchungen des Vorgangs bei der Befruchtung der Oenothereen"; a translation of Wilhelm Hofmeister's (1824–1877) 1847 paper on fertilization in the Onagraceae (evening primrose family)

Michael Witty

Abstract

Wilhelm Hofmeister (1824–1877) is best known for his work on the life cycles of land plants and his theory of alternation of generations, published in 1851. This may be in part because it was translated into English early and widely circulated, unlike Mendel's work, which was obscure for many years after its first publication. However, Hofmeister had very productive careers before and after his great work. He published extensively on plant cell biology and morphology in book form late in his career. Before 1851 he published several high-quality papers in botany journals on plant fertilization, including this work on the Onagraceae, which included microscopic observations of a standard so high they can stand beside modern drawings of the plant embryo sac, despite Hofmeister working without embedding, microtome sectioning or cover slips, after 143 years. Hofmeister observed the development of a four nucleus embryo sac, pollen tube entry and early embryogenesis. This is an even greater achievement when it is remembered that Hofmeister used hand-cut sections and comparatively simple microscopes and was entirely self taught. He never attended university as a student—only as a professor after his merit was recognized from his outstanding amateur work, including this paper.

Introduction

It is difficult to understand the mind of Wilhelm Friedrich Benedikt Hofmeister (24 May 1824 to 12 January 1877), not because of what he discovered but because the large amount of knowledge that we assume all botanists accept today had not been discovered or was not widely known when he was working. As reviewed in Kaplan and Cooke (1996), Hofmeister made all his discoveries and insights before Pringsheim's elucidation of plant fertilization (1858), Darwin's theory of evolution (1858), Mendel's work on genetic inheritance (1865) and Strasburger's work on meiosis (1888) and alternation of chromosome numbers (1894), as reviewed in Raven et al. (2005).

The best brief source for the life and works of Hofmeister is Kaplan and Cooke (1996), not least because these authors are botanists who have read Hofmeister's many works in German. I have used this paper as a guide to the life of Hofmeister, supplementing it when I can from earlier works. Hofmeister was a self-taught biologist whose highest level of formal education was a *Realschule,* which he completed by age 15. The *Realschule* system had a more technical emphasis than the *Gymnasium* system, which emphasized the classics and humanities. After this brief formal education Hofmeister worked as an apprentice in Hamburg then in his father's publishing business. Significantly, in addition to being the proprietor of a music store, publisher and book dealer (Larson 1930), Hofmeister's father was an enthusiastic home botanist, which was a popular and benign recreational activity of the 19th century when gentleman amateurs had a status similar to salaried professionals (Hagen 1994). Hofmeister followed his father's interest in plants, but, perhaps because Hofmeister was nearsighted, he concentrated on small specimens and microscopic studies, which are

Math and Science Department, Florida SouthWestern State College, 8099 College Parkway H-224, Fort Myers, FL 33919 U.S.A.
Email: mwitty@fsu.edu

easier when your own personal focal length is very small for it allows examining objects very closely. He also developed an interest in examining the internal structures of plants and favored using a blade to hand section live plant material, rather than fixing tissues and using a microtome as many contemporaries did (Strasburger 1895), even succeeding in the dissection of pollen tubes and embryo sacs from flowers without damaging their structures (Hofmeister 1847). He was influenced by reading the botany text of Schleiden (1842) and inspired to study the life histories of plants (Goebel 1905). Schleiden (1842) omitted illustrations, and the illustrations in Schleiden and Vogel (1839) were so obviously stylized that they seemed to represent a theoretical expectation rather than empirical reality. Hofmeister may have attempted to find clarity by making his own observations and drawings and then concluded that they had merit and that they could represent a contribution to the understanding of botany, if published.

Very early in his career Hofmeister was able to use his considerable practical skill making hand-cut sections for microscopy to reveal embryology of plants (Hofmeister 1847) and to combine this with his innovative theoretical concept of alternation of generations (Hofmeister 1851). His conclusion of fertilization of a female gamete by a male gamete derived from the pollen tube was in contradiction to the view of Schleiden (1842), which was that the embryo was an outgrowth of the pollen tube (Kaplan and Cooke 1996). The quality of images on which the view of Hofmeister was based was much superior to similar subjects from Schleiden and Vogel (1939) and showed the importance of empirical skill in botany. Once the pollen sac was identified with a separate plant organism, i.e., the female gametophyte, later workers were able to understand the contribution of pollen and ovules to plant embryology, and several patterns with a common theme were identified in the 19th and early 20th centuries, as reviewed in Maheshwari (1948), Baroux et al. (2002) and Brukhin (2005).

Even though he began as an amateur, Hofmeister immediately began to work to a high scholarly standard, publishing works in respected journals at an early age (for example Hofmeister 1847 was published when he was 23). His early work concerned the development of plant embryos from pre-existing egg cells rather than simply from the pollen tube as asserted by Schleiden (1842). His amateur work culminated in publication of *Vergleichende Untersuchungen der Keimung, Entfaltung und Fruchtbildung höherer Kryptogamen* (Hofmeister 1851; Currey 1862), describing significant similarities between cryptogams and seed plants — groups previously thought to be very distantly related. Hofmeister predicted that sperm cells, a feature of cryptogams, would later be found in gymnosperms — a prediction later fulfilled in the case of cycads (Ikeno 1896) and *Ginkgo* (Hirase 1896). This work was done between 4 AM and 6 AM in summer mornings (Goebel 1905) and at other odd hours while raising a large family (Larson 1930), and then the written results were published by his father. This book was largely concerned with the presentation of observation and *concluded* with the revolutionary theory of alternation of generations, i.e., that all land plants are homologous and have a common life cycle. This ensured his recognition as a leading experimental and theoretical botanist. It was the beginning of a significant career that led to posts as professor of botany at Heidelberg and Tübingen (Goebel 1905), a "transfer of Hofmeister from the bookshop to the lecture room." As Professor Karl Ritter von Goebel (1855–1932), Hofmeister's student from 1873 to 1876, said:

> After the first lecture the benches in the auditorium were nearly empty, and of 80

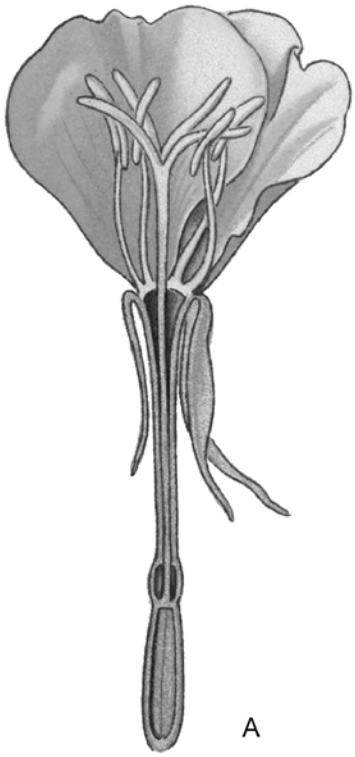
> to 100 attendants in Tübingen … hardly a dozen remained. These however had a rich opportunity for study, for it was a pleasure to listen to a man who could draw upon the fullness of his knowledge, who from first to last trod his own path, and who did not allow himself to be dependent upon the representations of the text books … In his "microscopical practicum" we could not but admire his mastery in making preparations which was nothing less than marvelous. It will be recalled that at that time there were in use neither microtomes nor hardening or staining agents, and only occasionally were alcoholic materials used. But Hofmeister was able, by holding an ovule so small as to be scarcely visible to the naked eye between the thumb and forefinger, so to cut it that the embryo-sac could be clearly shown. In this, his marked shortsightedness was of use to him, while it did not hinder him in the least in out-of-doors work in finding research materials of small plants such as liverworts. He had a fine instinct for plant habitats, and would throw himself flat on the ground in a place where he expected to find some desired plant, as e.g., an *Anthoceros*, and he would usually soon find it (Goebel 1905).

Because his work on the alternation of plant generations was translated into English (Currey 1862), it is his best-known work in botany and is cited 107 times (Google 2010a). Hofmeister also made significant contributions to plant embryology (this paper), cell biology and gross anatomy (Kaplan and Cooke 1996), and plant physiology (Larson 1930). These remain largely untranslated and poorly known (cf. Hofmeister 1848, a French translation of Hofmeister 1847). This is why Hofmeister 1847 is cited only ten times (Google 2010b), showing that translation of German texts to English is important for their dissemination.

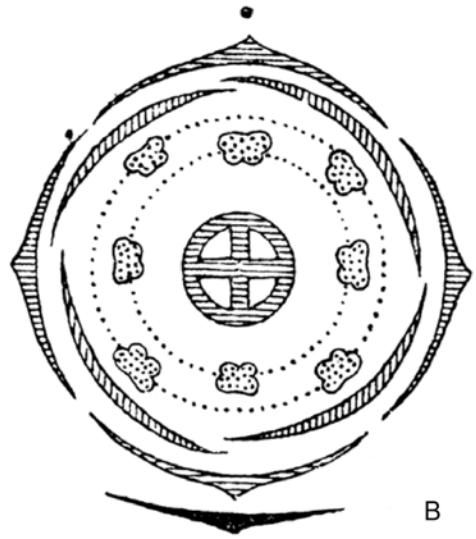
Hofmeister also made a great contribution to science in the quality of his students, many of whom were listed in Larson (1930) and some of whom are still well known today. One such was Theodor Wilhelm Engelmann (1843–1909), famous for his perennially published textbook experiment on the action spectrum of *Spirogyra* photosynthesis, determined by observing the movement of aerotactic bacteria towards effective light wavelengths, divided into a spectrum (Engelmann 1882, 1883). Pierre-Marie-Alexis Millardet (1838–1902) also studied under Hofmeister before his work in plant pathology, developing copper salt fungicides and the use of American root stocks to resist *Phylloxera* damage to the French grape crop (Galloway 1914).

The practical difficulty of observing flowering plant fertilization and what makes it different to any other fertilization process is that it happens inside tissues cemented together by pectin, not free in the environment (Li and Ma 2002) or even in a contained liquid microcosm, such as the human uterus. While animal gametes are produced in a simple process of meiosis, plants undergo meiosis then further cell division before gametes are produced. The male gametophyte is composed of two sperm cells contained by a tube cell, each with its own nucleus. The female gametophyte consists of an embryo sac with up to eight nuclei including the egg produced deep within the ovule and ovary (Southworth 1996). Hofmeister observed the development of the embryo sac and its interaction with the pollen tube in Onagraceae (evening primrose family). While there are several patterns of embryo sac development in flowering plants of which the eight nuclear *Polygonum* type is most common (70% of species, Reiser and Fischer 1993; Fig. 1C), the Onagraceae develop a four nuclear embryo sac (Brukhin et al. 2005; Maheshwari 1948; Fig. 1D), and this is what Hofmeister described in this paper.

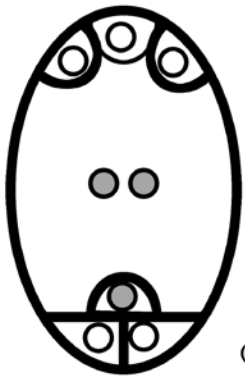
It is difficult to deduce exactly which species of Onagraceae Hofmeister used, in terms of today's taxonomy, and a precise definition must be the subject of detailed historical research and publication of a separate paper. That the taxonomy of the Onagraceae is still debated (Ford and Gottlieb 2007) complicates this problem. However, by searching databases



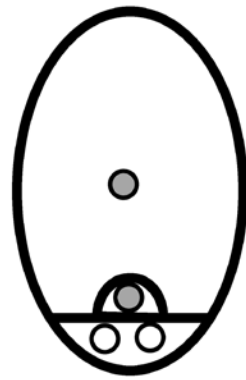
A



B



C



D

(USDA 2010) using the species or genus name cited by Hofmeister and noting synonyms, the following possible identities can be made: *Boisduvalia concinna* (*Epilobium* sp.), *Godetia quadrivulnera* (*Clarkia davyi* or *Clarkia purpurea*), *Godetia rubicunda* (*Clarkia* sp.), *Oenothera longiflora* (*Oenothera* sp., *Calylophus* sp. or *Camissonia* sp.), *Oenothera sellowii* (*Oenothera* sp., *Calylophus* sp. or *Camissonia* sp.). A good indication of the species with which Hofmeister was working comes from 19th-century texts, such as Strasburger 1894 and Thomé 1885, which contained useful images of *Oenothera* sp. (Fig. 1A–B). This is important for interpreting Hofmeister's work because a variety of female gametophyte forms have been seen in flowering plants (reviewed in Baroux et al. 2002 and Brukhin et al. 2005) where many contain an egg apparatus of two synergid cells in addition to the egg cell, three antipodal cells and two polar nuclei. This eight nuclear type includes the model plant *Arabidopsis thaliana*. The Onagraceae differ from this pattern because they lack antipodal cells and have only one polar nucleus (Jalouzot 1975; Baroux et al. 2002). This may be due to the loss of the chalazal module of antipodal cells (Friedman and Williams 2004). Hofmeister's work corresponds to this modern view, for example figure 2, drawing 12, which shows the three-celled egg apparatus but no antipodal cells, and drawing 10, which shows the migration of a single polar nucleus. His work is a great and enduring record of early observation that has remained relevant for over a century and a half.

In translating Hofmeister, I also wanted to preserve his style, which is similar to 19th-century botany journals and newspapers in general. These publications were much less precise and polished than journals of the 21st century and have quite an elaborate system of parallel footnotes and references, undoubtedly related to the cumbersome and difficult process of typesetting by hand. It is as if Hofmeister published a draft and then responded to criticism by adding corrections to the draft, which was too expensive to rewrite after the type was set. For example, I have preserved Hofmeister's unusual use of em dashes, which he often employed at the end of a sentence, although they may seem random or extraneous to a modern editor or reader.

Figure 1. *Left*, *A*: *Oenothera biennis* gross anatomy (Thomé 1885); *B*: *Oenothera* sp. floral diagram (Strasburger et al. 1894). The flowers are actinomorphic, Ca4 Co4 A4+4 G(4), and with a stigma that divides into four. The ovary is inferior and lies beneath a hypanthium that is typical of hawkmoth pollinated flowers (Grant 1983); *C*: Eight nuclear female gametophyte, redrawn from (Baroux et al. 2002); *D*: Four nuclear female gametophyte, redrawn from (Baroux et al. 2002).

Investigations into the process of fertilization in the Onagraceae.

W. Hofmeister.

Hereto Pl. 8 [see Fig. 2 for all figures cited in the translation below]

Pigmented petal cells of *Oenothera* and some *Godetia* begin to develop 3 days prior to anther dehiscence. At the same time the embryo sac contains numerous 1/3500 to 1/5000''' [*Ligne* or Line, a nonstandard unit of length, 1/12 inches] size granules in viscous fluid but no fixed structures. The upper end of the embryo sac is bulbous; at approximately half the longitudinal diameter of the ovule it narrows (in the case of *Godetia* more than ⅔ of its diameter) and extends to the chalaza as a narrow cylindrical tube (Fig. 1) — in *Oenothera* and *Boisduvalia* the reduction of the embryo sac lumen is smaller. Initially it is surrounded by a layer of small almost laminar cells, which are filled with granules of protoplasm and starch. A strand of small cubic cells with the same content goes from its upper end (Fig. 3) to the tip of the nucellus (Fig. 2).

Soon after petals show the first hint of color development a vast amount of material produced in the upper (micropyle) end of the embryo is seen. In the granular mass are several (two to four) free-floating nuclei, some with distinct nucleoli and some without (Fig. 3). — Around one of these nuclei a pear-shaped cell is formed whose conical end touches the membrane of the embryo sac and whose other end floats freely in the cell cavity (Fig. 4). At the same time, close to the narrow end of the embryo sac, a nucleus with a distinct membrane and large nucleolus appears. The contents of this nucleolus are often frothy and refractive, indicating a semi-liquid substance (Fig. 5). The pear-shaped cell is the true egg of the plant; the foundation of the future embryo, the first of its cells to be distinguished. It is the structure that Meyen[1] called the *germinal vesicle* (*Keimbläschen*) in *Mesembrianthemum glomeratum* and *Helianthemum canariense*, and Amici[2] called the *embryonic vesicle* (*vescichetta embrionale*) in *Orchis Morio*. — Beside this a second cell forms, similar in all respects (Figs. 5a, b, 6, 7, 8), which results in two daughter cells (Fig. 9) divided in two (Figs. 10, 11). The latter process is more common in *Godetia* and *Boisduvalia* and rarer in *Oenothera*. These two or three elements of the embryo apparatus are probably of equal value, and all able to be fertilized. However, I examined a very large number of fertilized *Oenothera* ovules and never saw more than one embryo in the embryo sac; embryo cells that are not fertilized die during the development of the fertilized embryo. It seems that in this family the embryo sac can be fed no more liquid food than is requisite for the nutrition of embryo cells. — In some cases two of the embryo cells dissolved, before fertilization (Figs. 12, 13). As the dying nucleus is resorbed its cellulose membrane disappears, there is a strong contraction of the primordial sleeve and the conversion of its contents to a lumpy greenish yellow mass, with a liquid transparent core. Finally, the remainder of the dying embryo cells are transformed into tawny lumps with no definite shape.

After *Oenothera's* corolla withers, and while *Godetia* and *Boisduvalia* are still fresh, pollen tubes appear as whitish strands in the ovary near the placenta. The pollen tube penetrates

between the cells at the tip of the embryo sac. The tip of the nucellus has strands of cells that separate from each other and partly liquefy as the pollen tube pushes through them (Fig. 13), and when the pollen tube reaches the embryo sac its diameter has doubled or tripled and its membrane has considerably thickened (Fig. 14). The contents of cells enclosing the nucellus are by far more concentrated than that located outside the ovule. They contain a very large number of small starch and protein granules.[3]

When the pollen tube reaches the micropyle end of the embryo sac the membrane invaginates slightly. The very delicate wall of the *Oenothera* embryo sac is usually pushed further back than the firm wall of *Boisduvalia* and *Godetia* (cf. Figs. 15–24 and captions). The embryo sac resists pressure from the end of the pollen tube, especially in the latter two, sometimes so strongly that the pollen tube is forced to spread over the bowl-shaped bulbous end of the embryo sac (Figs. 15, 22).

The germinal nucleus is separated from the end of the pollen tube at the moment of fertilization by the undamaged permanent membrane of the embryo sac and is often completely free in the bulbous enlargement of the micropyle-end of the embryo sac (Fig. 15), or the membrane touches a quite different position than that which binds the pollen tube (Fig. 18). Only by twofold endosmosis can the liquid in the germinal nucleus and in the pollen tube come into contact. Observation shows that the contents of the pollen tube are far more concentrated than that of the embryo sac and the germinal nucleus. The strong endosmotic flow allows the germinal vesicle in the pollen tube to cross through to the embryo sac. We think of fertilization as the stimulus to specific development of the germinal vesicle, as affected by the osmotic movement of influential fluid from the pollen tube into the embryo sac. Known physical laws may affect this process only slightly.

Until this stage the nucleus of the germinal vesicle has always been clearly visible, especially in *Godetia*. During fertilization this nucleus disappears, and with it the threads of protoplasm, which led from the outer walls of the egg apparatus to the nucleus of the embryo sac. The fertilized germinal vesicle assumes a pear shape (Fig. 18). The end of the pollen tube accumulates liquid (Figs. 16, 19). The result of this is an accumulation of cytoplasm in the nucleus (Fig. 17). Immediately afterwards, the lower hemispherical end of the germinal vesicle separates the upper, bulbous, larger half with a horizontal wall (Figs. 20, 21). This cell wall is suddenly visible; I never found cells of intermediate structure between cell wall formation and formation of a nucleus in the hemispherical end of the germinal vesicle. Everything suggests precipitation of cellulose on the entire surface of the cell at the lower end of germinal vesicle. It is the first cell of the embryo.

Shortly after its development the nucleus reduces its width and two nucleoli appear (Fig. 22). Soon afterward two small nuclei form, between which, two membranes form immediately (Figs. 23, 24, 25). At the same time the upper bulbous portion of the germinal vesicle begins cell propagation and transforms into the suspensor (Figs. 23, 25). At the same time free nuclei in the embryo sac form the endosperm (Fig. 25).

In each of the two cells, which now constitutes the embryo, two new cells soon form, vertically above each other (Figs. 26, 27, 28);—then in each of the four daughter cells, more cells form, horizontally side by side (Fig. 29). This process is repeated several times with the vertical orientation alternating. The embryo is thus transformed into a spherical cell body, the globular proembryo. After a series of such cell divisions, for example in *Godetia*, after the sixth, four of which are in the horizontal and two in the vertical orientation (Fig. 30), a multiplication of cells begins in the radial

direction. The cells begin to fill with opaque materials that make observations of further cell divisions impracticable.

Both cotyledons and the radicle develop from the globular proembryo. No cell of the suspensor participates in the formation of the latter portion.

At no stage of *Oenothera* embryo development are daughter cells found lying loose in the mother cells. Daughter cell walls are always contiguous. I am of the view that no other explanation of cell formation is possible except that the nucleus of the mother cell disintegrates into two daughter nuclei, each of the two daughters gathers one half of the cell contents and both secrete cellulose over their whole surface.

There are still traces of the pollen tube in mature *Godetia* seeds. Strangely, the pollen tube continues growing during germinal vesicle development and becomes a thick walled tube with various outgrowths, which protrude into the cavity formed when cells surrounding the embryo sac are absorbed. In this cavity, i.e., the cavity of the nucellus, the intact embryo sac lies completely free, embracing the embryo.

Up to the fourth generation of embryo cells, the pollen tube appears to be densely filled with a lumpy mass. It is always completely separate from the germinal vesicle and the developing embryo by the membrane of the embryo sac. In *Godetia quadrivulnera* and *rubicunda* the embryo sac and pollen tube have such a rough and tough membrane that it is difficult to separate them with a needle under a microscope. However, when separated, the ends that touched each other are completely unharmed (Figs. 15b, 20b); you may be strikingly convinced that Schleiden's theory of embryo development in the *Oenothera* family is totally inapplicable.

I do not know how to explain Schleiden and Vogel's (1839) drawings. I sometimes found the end of the pollen tube display a similar shape, but I never saw free cell nuclei, or the embryo sac invaginated so deeply by it, as drawn by these authors. The drawings of pollen tubes in Schleiden (1846) show a sudden decrease in the thickness of the pollen tube similar to my own observations of the relationship of the pollen tube to the embryo. Perhaps only a slight touch of the germinal vesicle with a needle was needed to make the matter clear.

Explanation of figures

1. *Godetia quadrivulnera*. Longitudinal section of unfertilized ovule, after the petals turned greenish yellow. The embryo sac contained only granular mucilage.
2. *Godetia rubicunda*. Tip of nucellus in longitudinal section, from an ovule the same age as previous.

3, 4. The same plant. Upper portion of the embryo sac and its surrounding tissue, a little later.

5a. *Godetia quadrivulnera*. Upper portion of the embryo sac and surrounding tissues. The primary and secondary cells are formed.

5b. The same embryo sac, dissected free from surrounding tissues.

6. *Godetia rubicunda*. Embryo sac, same stage of development.

7, 8. *Boisduvalia concinna*. Upper portion of the embryo sac, same stage of development.

9. *Godetia quadrivulnera*. Upper portion of the embryo sac. The second embryo cell has divided to form the two tertiary cells. The primary cell is seen shimmering from below.

10, 11. *Godetia rubicunda*. Embryo sac and its upper half. Three germinal cells are present. At this stage of development, the petals are already red and the anthers ready to dehisce when touched.

12. The same plant. Embryo sac. Two of the germinal cells are dying (from the same cells as 10.).

13. *Godetia quadrivulnera*. Upper half of the nucleus [*sic*]. The pollen tube has traveled the greater part of its way to the embryo sac. Two of the germinal cells are dead, the third is still sharp in outline.
14. *Oenothera longiflora*. Ovule in longitudinal section, showing progress of the pollen tube to the embryo sac.

14b. Upper portion of the embryo sac enlarged. A living and a dying germinal cell.

15. *Godetia quadrivulnera* during fertilization. A living and a dying germinal cell. The nucleus of the former is gone, as is the flow of sap to the core of the embryo sac.

15b. The pollen tube of the previous preparation, pulled out.

15c. The same, rotated 90°.

16. *Godetia quadrivulnera*, after fertilization. One of the two dead germinal cells in the last stages of dissolution.
17. *Boisduvalia concinna*. Upper part of the nucleus [*sic*], immediately after fertilization.
18. *Oenothera Sellowii*, during fertilization.
19. The same, a little later.
20. *Godetia quadrivulnera*. One cell of the embryo is formed.

20b. The embryo sac (upper half) dissected free, perfectly intact and without any connection to the pollen tube.

21. *Oenothera longiflora*
22. *Boisduvalia concinna*
23. *Oenothera Sellowii*
24. *Godetia quadrivulnera*
25. *Boisduvalia concinna*
26, 27. *Godetia quadrivulnera*
28. *Oenothera longiflora*

} after fertilization, see the text.

} the remains of unfertilized cells are seen throughout.

29. *Godetia quadrivulnera*. The globular proembryo, which already consists of 16 cells, the pollen tube and unfertilized germinal cells are clearly seen.
30. *Godetia quadrivulnera*. Strange growth of the pollen tube during embryo development. See the text.

Leipzig, 23 August 1847.

Footnotes of Hofmeister 1847

(1) Physiology, volume III. p. 308. Meyen believed that this cell is created only after fertilization. The name is not a happy choice because it gives rise to misunderstandings. However, I will use Meyen's term, in the absence of a better one [Meyen, F. J. F. 1839. Neues System der Pflanzen Physiologie. Berlin.].

(2) In his memoir on the fertilization of orchids [Amici, J.-B. 1847. Sur la fécondation des Orchidées. Ann. Sci. Nat., Bot., sér. 3. 7: 193–205.].

(3) The protein compound of the pollen tube, which contains little brown globules after iodine staining, may be plant casein. The solid granules (albumin would be liquid) are not dissolved by dilute phosphoric acid, as would happen with plant fibrin.

Acknowledgments

Fang Xie of the Guggenheim library, Monmouth University, was very helpful in preparation of this paper. Hofmeister's German is clear and concise, though I did benefit from the French translation of this paper to interpret a very limited number of passages (Hofmeister 1848).

References

Artschwager, E. and E. M. Smiley. 1921. Dictionary of Botanical Equivalents. Baltimore: Williams and Wilkins.

Baroux, C., C. Spillane and U. Grossniklaus. 2002. Evolutionary origins of the endosperm in flowering plants. Genome Biol. 3(9): 1–5.

Brukhin, V., M. D. Curtis and U. Grossniklaus. 2005. The angiosperm female gametophyte. Curr. Sci. 89(11): 1844–1852.

Campbell, D. H. 1902. Recent investigations upon the embryo sac of angiosperms. Amer. Naturalist 36(430): 777–786.

Engelmann, T. W. 1882. Über Sauerstoffausscheidung von Pflanzenzellen im Mikrospectrum. Bot. Zeitung (Berlin) 40: 419–426.

Engelmann, T. W. 1883. Ein Beitrag zur vergleichenden Physiologie des Licht- und Farbensinnes. Archiv für die gesammte Physiologie des Menschen und der Thiere 30(1): 95–124.

Erbar, C. 2003. Pollen tube transmitting tissue: Place of competition of male gametophytes. Int. J. Pl. Sci. 164(5): S265–S277.

Faure, J. E. 2001. Double fertilization in flowering plants: Discovery, study methods and mechanisms

(La double fécondation des plantes à fleurs: découverte, méthodes d'étude et mécanismes). Compt. Rend. Acad. Sci. Paris, Sér. 3, Sci. Vie 324(6): 551–558.
Floyd, S. K. and W. E. Friedman. 2000. Evolution of endosperm developmental patterns among basal flowering plants. Int. J. Pl. Sci. 161(S6): S57–S81.
Ford, V. S. and L. D. Gottlieb. 2007. Tribal relationships within Onagraceae inferred from PgiC sequences. Syst. Bot. 32(2): 348–356.
Friedman, W. E. and K. C. Ryerson. 2009. Reconstructing the ancestral female gametophyte of angiosperms: Insights from *Amborella* and other ancient lineages of flowering plants. Amer. J. Bot. 96(1): 129–143.
Friedman, W. E. and J. H. Williams. 2004. Developmental evolution of the sexual process in ancient flowering plant lineages. Pl. Cell 16: S119–S132.
Furness, C. A., P. J. Rudall and F. B. Sampson. 2002. Evolution of microsporogenesis in angiosperms. Int. J. Pl. Sci. 163(2): 235–260.
Galloway. 1914. Pierre-Marie-Alexis Millardet. Phytopathology 4(1): 1–4.
Goebel, K. 1905. Wilhelm Hofmeister. Pl. World 8(12): 291–298.
Google. 2010a. Google Scholar citations for Hofmeister 1851. http://scholar.google.com/ (accessed 2 May 2010).
Google. 2010b. Google Scholar citations for Hofmeister 1847. http://scholar.google.com/ (accessed 2 May 2010).
Grant, V. 1983. The systematic and geographical distribution of hawkmoth flowers in the temperate North American flora. Bot. Gaz. 144(3): 439–449.
Haberlandt, G. 1877. Wilhelm Hofmeister. Oesterr. Bot. Z. 27(4): 113–117.
Hagen, J. B. 1994. Amateurs, professionals, and the growth of American botany. Reviews in American History 22(1): 133–137.
Higashiyama, T. 2002. The synergid cell: Attractor and acceptor of the pollen tube for double fertilization. J. Pl. Res. 115(2): 0149–0160.
Higashiyama, T., H. Kuroiwa and T. Kuroiwa. 2003. Pollen-tube guidance: Beacons from the female gametophyte. Curr. Opin. Pl. Biol. 6(1): 36–41.
Hirase, S. 1896. On the spermatozoid of *Ginkgo biloba* (in Japanese). Bot. Mag. (Tokyo) 10: 325–328.
Hofmeister, W. F. B. 1847. Untersuchungen des Vorgangs bei der Befruchtung der Oenothereen. Bot. Zeitung (Berlin) 5(45): 785–792, pl. 8.
Hofmeister, W. F. B. 1848. Sur la Manière selon laquelle s'opère la fécondation chez les oenothèrees. Ann. Sci. Nat., Bot., sér. 3. 9: 65–72, pl. 4.
Hofmeister, W. F. B. 1851. Vergleichende Untersuchungen der Keimung, Entfaltung und Fruchtbildung höherer Kryptogamen (Moose, Farne, Equisetaceen, Rhizokarpeen and Lykopodiaceen), und der Samenbildung der Coniferen. Leipzig: F. Hofmeister.
Hofmeister, W. F. B. 1862. On the Germination, Development and Fructification of the Higher Cryptogamia and on the Fructification of the Coniferae, transl. F. Currey. London: Ray Society.
Ikeno, S. 1896. Spermatozoid of *Cycas revoluta* (in Japanese). Bot. Mag. (Tokyo) 10: 367–377.
Jalouzot, M. F. 1975. Aspects ultrastructuraux du sac embryonaire d'Oenothera lamarckiana. Compt. Rend. Hebd. Séances Acad. Sci., sér. D. 281: 1305–1308.
Kaplan, D. R. and T. J. Cooke. 1996. The genius of Wilhelm Hofmeister: The origin of causal-analytical research in plant development. Amer. J. Bot. 83(12): 1647–1660.
Kawashima, T. and R. B. Goldberg. 2010. The suspensor: Not just suspending the embryo. Trends Pl. Sci. 15(1): 23–30.
Kordyum, E. L. 2007. Double fertilization in flowering plants: 1898–2008. Cytol. & Genet. 42(3): 147–158.
Larson, A. H. 1930. Wilhelm Hofmeister. Pl. Physiol. (Lancaster) 5(4): 613–616, pl. 9.
Li, W. and H. Ma. 2002. Gametophyte development. Curr. Biol. 12(21): R718–R721.
Lloyd, F. E. 1935. Karl Ritter von Goebel. Pl. Physiol. (Lancaster) 10(2): 203–208.
Maheshwari, P. 1948. The angiosperm embryo sac. Bot. Rev. (Lancaster) 14(1): 1–56.
Otto, S. P. and A. C. Gerstein. 2008. The evolution of haploidy and diploidy. Curr. Biol. 18(24): R1121–R1124.
Raven, P. H., R. F. Evert and S. E. Eichhorn. 2005. Biology of Plants. New York: W.H. Freeman.
Reiser, L. and R. L. Fischer. 1993. The ovule and the embryo sac. Pl. Cell 5: 1291–1301.
Schleiden, M. J. 1842. Grundzüge der wissenschaftlichen botanik. Leipzig: W. Engelmann.
Schleiden, M. J. 1846. Die Botanik als inductive Wissenschaft behandelt. Leipzig: W. Engelmann. Pp. 583–584, pl. 4, fig 8.
Schleiden, M. J. and T. Vogel. 1839. Beitraige zur Entwickelunigsgeschichte der Blüthentheile bei den Leguminosen. Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 19(1): 59–84, tab. 7, fig. 7.8.
Southworth, D. 1996. Gametes and fertilization in flowering plants. Curr. Topics Developm. Biol. 34: 259–279.

Strasburger, E., H. Fitting, L. Jost, G. Karsten, F. Noll, H. Schenck, A. F. W. Schimper. 1894. Lehrbuch der Botanik für Hochschulen, ed. 12. Jena: Gustav Fisher. P. 512.

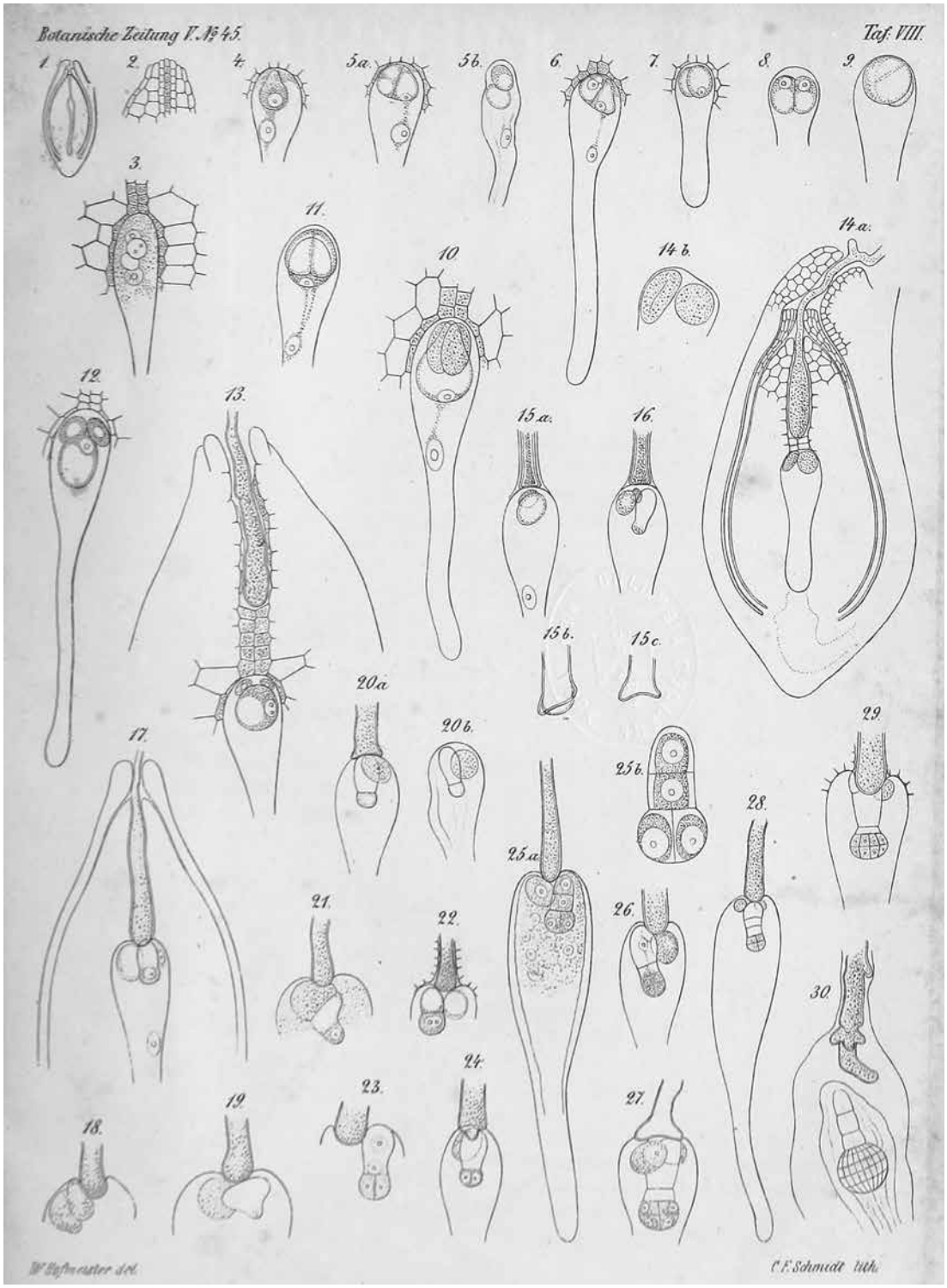
Strasburger, E. 1895. The development of botany in Germany during the nineteenth century. Bot. Gaz. 20(5): 193–204.

Thomé, O. W. 1885. Flora von Deutschland, Österreich und der Schweiz. Gera. Vol. 1. P. 439.

USDA. 2010. United States Department of Agriculture, Natural Resources Conservation Service PLANTS Database. http://plants.usda.gov/index.html.

Webb, M. C. and B. E. S. Gunning. 1990. Embryo sac development in *Arabidopsis thaliana*. Sexual Pl. Reprod. 3(4): 244–256.

Figure 2. *Page 58*, Hofmeister's illustrations of fertilization in the Onagraceae (evening primrose family). Image courtesy Biodiversity Heritage Library (http://www.biodiversitylibrary.org) and the LuEsther T. Mertz Library at the New York Botanical Garden.


Botanische Zeitung V. № 45.
Taf. VIII.
1.
2.
4.
5a.
5b.
6.
7.
8.
9.
3.
11.
10.
14b.
14a.
12.
13.
15a.
16.
15b.
15c.
20a.
20b.
17.
25b.
29.
28.
25a.
21.
22.
26.
30.
24.
23.
27.
19.
18.
W. Hofmeister del.
C.F. Schmidt lith.