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Comparing pollen development in the Commelinaceae with those of the Passifloraceae; a translation of Wilhelm Hofmeister's 1848b paper "Ueber die Entwicklung des pollens"

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Abstract

Although Wilhelm Hofmeister (1824–1877) did not have a formal education in science, he was perfectly capable of designing scientific strategies that ensured his work was significant and influential. His observations in a model plant (*Tradescantia virginica*) were convenient to obtain, but Hofmeister did not know if they were limited to one group of plants or more widely distributed. Hofmeister sought universal phenomena of life rather than entertaining but unique observations. In this paper Hofmeister's observations of membranes and nuclear phenomena were extended to distantly related flowering plants of the Passifloraceae.

In this and the previous paper, which described *Tradescantia*, details of histochemical methods were defined. Hofmeister was limited to use of compounds such as iodine, hydrochloric acid and ammonium carbonate, with no access to histochemical stains, which could provide significant contrast between tissues or cell contents. Even so, separation of the cell membrane from the cell wall was seen, showing their existence as two separate organelles. Separation of the nucleus from cytoplasm was achieved, revealing two more organelles. Most interestingly, Hofmeister was able to show that Nägeli's observation of chromosomes was a general phenomenon, widely significant for flowering plants.

Introduction

Schleiden confused cells of the suspensor with the embryo (Morton 1981) and assumed that plant embryos were an outgrowth of the pollen tube (Kaplan and Cooke 1996). While Hofmeister's reaction to Schleiden's theory of plant fertilization was negative (Witty 2015a), his reaction to Nägeli's was a positive one. Matthias Jakob Schleiden (1804–1881) and Carl Wilhelm von Nägeli (1817–1891) were long-standing colleagues and editors of the short-lived journal *Zeitschrift für Wissenschaftliche Botanik*, though this journal was almost entirely the work of Nägeli and may have amounted to self-publishing (Nägeli and Schleiden 1844–1846), a practice denigrated in the 20th and 21st centuries. However, this was a productive form of publication in the 19th century, which Hofmeister also practised, with the help of his father, to communicate his discovery of alternation of generations in plants (Hofmeister 1851). Nägeli's most important contributions relevant to this paper were his discovery of bodies, which he referred to as "transitory cytoblasts," and the nuclear spindle (reviewed in Scott 1891). The term transitory cytoblast [*transitorischer Cytoblasten*] was used by Hofmeister (1848, reviewed by Kasten 1983), and these cytoblasts were later identified as chromosomes. Hofmeister supposed that nuclear phenomena, such as those first seen by Nägeli, were important to botany and worked on this subject, contributing to the foundation of our present knowledge of the nucleus and chromosomes and adding a technical quality surpassing Nägeli. Their precise role in heredity was, however, not known to either scientist.

In addition to the report of transitory cytoblasts, Hofmeister may also have been very strongly influenced by Nägeli in his practical decisions, at least in his choice of *Trandescantia* as a scientific subject, a plant that was also used by Nägeli (Baker 1953; Sirks 1953).

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Both, in turn, may have been influenced by Brown (1866, first published in 1833), who published a tantalizing description of young *Tradescantia virginica* anthers (cited in Ducker and Knox 1985), which were transparent and also displayed significant features visible under the microscope, including the nucleus and nuclear membrane.

> The nucleus may even be supposed to exist in the pollen of this family … in *Tradescantia virginica* and several nearly related species, it is uncommonly distinct, not only in the epidermis and in the jointed hairs of the filaments, but in the tissue of stigma, in the cells of the ovulum even before impregnation, and in all the stages of formation of the grains of pollen, the evolution of which is so remarkable in those species of *Tradescantia* … In the very early stage of the flower-bud of *Tradescantia virginica*, while the antherae are yet colourless, their loculi are filled with minute lenticular grains, having a transparent flat limb … this disk is the nucleus of the cell, … These nuclei may be readily extracted from the containing grain by pressure, and after separation retain their original form (Brown 1866).

Brown also stated that some degree of pollen development could be followed in this species; although neither Nägeli or Hofmeister cited Brown, it may have been widely known that *Tradescantia virginica* was a very amenable model plant with which to work. However, in addition to studying features that may be limited to model plants, Hofmeister consciously sought universal phenomena of life, as shown in this passage from his 1848 publication:

> The fact that in many other genera from families that have little in common with the rest of the Commelinaceae, development of these nuclei does not differ materially from that in *Tradescantia*, *Campelia* and *Commelyna*, I will show in the sequel to this paper (Hofmeister 1848a, cited in Witty 2015a).

The Commelinaceae are monocots where some species produce anthers amenable to study. Similarly amenable flowers are produced by the distantly related Passifloraceae, i.e., *Passiflora*. This dicotyledonous genus was well known to botanists in the 19th century and was repeatedly mentioned in botany texts, including those published well before Hofmeister's pollen research (for example, Fritzsche 1832). Both *Passiflora caerulea* and *P. kermesina* have large anthers and are a very abundant and attractive source of pollen for microscopic studies (Figs. 4, 5). Similarly large amounts of pollen are available from species of the Pinaceae, as anyone that has seen ponds surrounded by pines turn yellow in spring can tell. Among them, species from these three families were useful for confirming that his observations were of a general nature, rather than limited to *Tradescantia* and closely related genera.

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P. cærulea, Linn. Passiflore bleue. — Plante excessivement vigoureuse, susceptible de couvrir de grandes surfaces d'une verdure abondante et agréable. Ses rameaux nombreux, très longs, herbacés et verts, sont pourvus de vrilles simples, opposées aux feuilles,

Fig. 30. — Passiflora cærulea (Passiflore bleue).

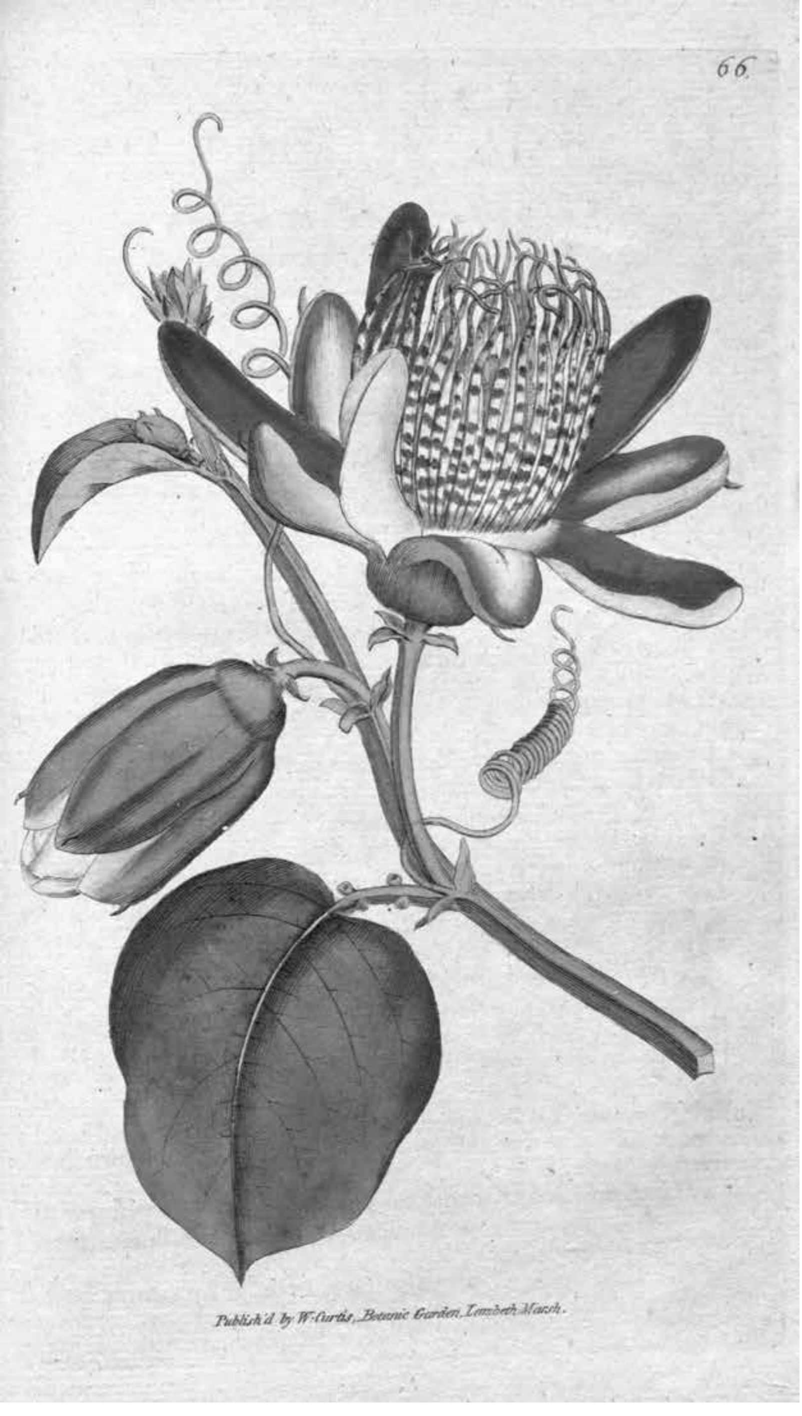

Figure 4. *Far left*, Gross anatomy of the dicot *Passiflora caerulea*, engraving by an unknown engraver after an original by an unknown artist for G. Boucher and S. Mottet, *Les Clématites, Chèvrefeuilles, Bignones, Glycines, Aristoloches et Passiflores* (Clematis, honeysuckle, jacarandas, wisteria, *Aristolochia* and *Passiflora*; Paris, O. Doin, 1898, fig. 30). Image courtesy Biodiversity Heritage Library (http://www.biodiversitylibrary.org) and the LuEsther T. Mertz Library at the New York Botanical Garden.

Figure 5. *Left*, Gross anatomy of *Passiflora alata*, hand-colored, copper-plate engraving by James Sowerby (1757–1822) or Sydenham T. Edwards (1768–1819) after an original by Sowerby or Edwards for William Curtis (1746–1799), *Botanical Magazine* (1788, vol. 2, pl. 66). Image courtesy Biodiversity Heritage Library (http://www.biodiversitylibrary.org) and the Peter H. Raven Library at Missouri Botanical Garden.

On the development of pollen

By W. Hofmeister

Hereto Pl. 6 [see Fig. 7 in Witty 2015c for plate]

(Continued from part 23 of the year)

Anthers one *Ligne* long from *Passiflora coerulea* [*sic*, *P. caerulea*] and *alata* flower-buds and ½ to ⅔ *Ligne* long buds of *P. kermesina* consist of a homogeneous tissue with cells of ¹⁄₅₀₀ *Ligne* average diameter, central nuclei, which are hard to discriminate and which usually contain just one relatively large nucleolus. In the intercellular spaces of slightly older anthers, excluding masses of cells from which vascular bundles, connective tissue and the contents of the four anther compartments are formed, some air is eliminated; cross sections of such anthers under low magnification show four circular and horseshoe-shaped brighter bodies; the former are the tissue portions out of which the mother cells and the first enveloping tissue form, the latter is the one that forms vascular bundles and connective tissue. In the center of each of the four translucent cylindrical tissue strands, cells lie on all their sides; the cells of the outermost layer of the cylinder propagate quickly at a tangent fourfold and extend radially. The nuclei of those cells first expand, but they fall behind the growth of the cells more and more. At a certain stage the size of the mother cells dissolves the intimate connection between them, and they separate in the water of the slide. A significant thickening of the membrane is noticeable. The cell nucleus, grown large in rather light watery fluid, can be distinguished as a floating nuclear membrane and nucleolus, which occupies only a relatively small portion of cell space and is filled with fine-grained mucus.—On prolonged exposure of the mother cell to water and as a result of coagulation of the albuminous substances of the cell sap, irregular cavities filled with clear liquid form in the more solid granular clot, and the content of the nuclear liquid congeals into a shapeless lump.

Sometimes in freshly harvested buds of living plants and very often in slightly withered (not too much) ones, the cell membrane of the mother cell appears as a free spherical bubble, not touching the inner wall of the cell. Its surface is perfectly smooth, not at all wrinkled or shriveled. When these cells absorb water, they expand slowly and lie down on the inner wall of the cell at all points. The phenomenon just described, contraction of the cell membrane, is different when caused by the action of dilute acids, alcohol and similar reagents especially in that the contraction is not consistent but that with abundant water inflow, expansion could follow. Von Mohl observed analogous processes in a liverwort (Bot. Ztg. 12. Apr. 1844; [Mohl 1844]). With further development of the mother cell, liquid can enter, and more solid grains sometimes develop in the nucleus. The outline of the nucleoli are more delicate, and their contents are similar to the nucleus. Finally, they fade from observation, and within a short time the nuclear membrane follows. Had solid bodies been formed in the same, they are now free in the center of the mother cell; otherwise there is nothing further to be noted, all is a brighter patch. The less refractive the liquid, which accumulated in the former location of the nucleus, becomes, the more uniform mixing with the contents of the rest of the cell occurs, and the cell space now appears as a slimy turbid liquid filled with larger and smaller granules.

It is very difficult to come to clarity about the way secondary nuclei appear within the mother cell. In the compartments of the same anther are found mother cells, which contain primary, those without a nucleus, those with two, three, four, five and nine secondary nuclei. Since, in all probability, all these states are found side by side, it may be assumed that the process of development is extremely rapid. The individual phenomena can hardly fail to arrange themselves according to analogy with unquestionable developmental processes of other phanerogams. In *Tradescantia*, there is no doubt that after the dissolution of the primary nuclei two secondary nuclei appear as spherical drops of clear fluid. Only very rarely have I been able to observe similar phenomena in *Passiflora*. I occasionally found two globular bright patches in the granular mucus of the cell content. The fact that this state is found so rarely seems to be sufficiently explained by the fact that, except in particularly favorable cases, it would be almost impossible to detect small drops of poorly light-refracting liquid in such a dull, grainy slimy liquid as the contents of *Passiflora* mother cells; only in nuclei located under a layer of cell sap are the outline of such delicate structures likely to be distinguished. — Mother cells with no observable nucleus, placed under fresh water, have uniformly turbid fluid contents. In the case of prolonged intake of water, solid granules accumulate preferentially at the center of the cell. You may see in some cases a peripheral sphere of light outlining a delicate nucleus with no solid content, or one to three very small nucleoli, rarely two such nuclei. —

In most cases the secondary nuclei show one or two nucleoli as soon as they become clearly visible; there are rarely those with three or more, even rarer are those with no granules. Of nuclei that are densely covered by opaque cell sap, usually nothing is seen more clearly than the nucleolus; such nucleoli do not appear different than when they are swimming freely in cell sap; the diameter of the nucleus is rarely much greater than that of the light mist that arises due to the interference of light beams around the granule. In such cases, when I broke the mother cell by gentle pressure, I never missed a nucleus with a watery core. In the example of formation of secondary nuclei of pollen mother cells of *Passiflora*, I can find no confirmation of the view that the nucleolus arises earlier than its nucleus, — a view that by close examination of the first appearance of free nuclei in the embryo sac of several plants is contradicted, as I shall show in another place. —

If there are only two secondary nuclei in the mother cell, they are large in size because of their currently large nucleoli and usually elliptical and often globular. — If three secondary nuclei, there are usually two rather large and one small. — Where four or five to nine secondary nuclei occur, they are usually about the same size. —

I believe the difference in the vital process of the secondary nuclei of the pollen mother cells of *Passiflora* [Passifloraceae] and those of Commelinaceen [Commelinaceae], Liliaceae and Abietineae [Pinaceae] can be as follows: in the former a nucleolus is produced very soon, and mostly just this; — in the latter however, equally sized multiple nucleoli occur only some time after the formation of nuclei. The fact that is more important for further development is that one of the nucleoli by far outweighs the others, consistent in all the families mentioned here.

When given the observations of *Passiflora* in various states, side by side, a new striking illustration of the situation forms: that after the disappearance of the central nucleus of the pollen mother cell, first two secondary nuclei form then; after their absorption there is formation of four (and more) nuclei, which are later enclosed by special mother cells — this is not contradicted at any point by the most important comparisons (*Tradescantia*, *Lilium*, *Pinus*).

From the time at which the firm connection of the mother cells ends and the appearance of special mother cells, it often happens that the mother cell, placed under water, swells so that its membrane bursts. This process sometimes takes place even if the cell membrane is free in the cell space. The rupture of the cell wall is thus at least partly due to the swelling of its own material, not exclusive due to swelling of the cell contents. This, by the way, is not an isolated phenomenon, and the spore mother cells of *Phascum* [Pottiaceae] show the same behavior. It seems to me probable that the primary cell membrane does not swell but only layers deposited on its inner surface thicken. As a result the cell space must necessarily narrow. Whether the cell membrane completely fills out, or whether the cell membrane lies freely in the cell space, surrounded by a water-clear liquid — which in all likelihood is water — the outcome will be the same: the liquid contents of the cell suffer a severe pressure, consequently they must turn to press the cell wall, which bursts. The fact that pressure of the contents of the cell wall from autonomous swelling of the former are a significant share means it becomes likely that even very delicate cells, those where thickening layers of the membrane are out of the question, may swell — vesicles of many phanerogam germinating embryos, for example, burst in water. — The membrane of young, extremely soft thin-walled mother cells of pollen on the other hand never tear. — If the tension of the cell membrane is significant, then the cell contents are expelled as a formless mush: but otherwise tears of the cell wall result in part of the cell membrane producing a spherical bubble. A lively flow results from the area enclosed by the cell into the protrubant bubble, which sometimes swells up to the size of the parent cell itself. I think this phenomenon is striking evidence that the cell membrane is a separate organ. — Greater pressure from inside the tear must of course hold the wall open quite wide; — I once observed that the small non-primary nucleus of the parent cell, in the shape of an elongated tube, slipped through the gap; — at the outer half of the cell membrane, it resumed its former, spherical shape.

The tear in the mother cell wall remains open only as long as pressure is applied to the inside of the cell wall. If a large portion of the cell contents have been expelled, the remainder exerts no more pressure on the inner wall of the cell, and by virtue of this the gap of the elastic cell membrane then closes, and the bulged portion of the cell membrane is pinched off and floats away as a closed bubble. — As long as water absorption continues, there can be protrusion of a new part of the cell membrane and, upon repeated relaxation of tension, be pinched off in its turn. This process sometimes repeats itself up to three times. Sometimes the cell membrane is broken in two or three points, and then part of the cell membrane bubbles forth at all these places. — It is often the case that mother cells contain a number of secondary nuclei, and a bubble in the projection of the cell membrane occurs. The pinch-off bubble looks very similar to a young free cell. Certainly there were signs of this kind, which led Schleiden to assume that you would find special mother cells firmly attached to the wall within mother cells. That the vesicular structures, which escape the tears of the mother cell wall, are undoubtedly not young special mother cells is seen from the fact that they occur even if the primary central nucleus of the mother cell is still present and there are no traces of secondary nuclei; furthermore, because of a vigorous flow, part of the cell membrane goes from the inside of the cell to the bubble outside the cell, an open relationship between the two takes place.—

Between every pair of secondary nuclei in mother cells, sheet-like accumulations of granules form. Amidst all the accumulating grains (as viewed from the narrow linear side) a delicate lighter line appears suddenly: the first trace of the resulting dividing wall between two special mother cells. Mother cells also show this phenomenon, and the cell membrane is free in the cell space. The assumption of Unger, "that the first sign of the delicate dividing walls is that the inner wall of the mother cells moves across " (über merismat, *Zellenbildung*, p. 4), is refuted by this observation. The formation of the special mother cell is achieved by *intra-utriculäre* cell formation, the entire contents of the cell divides into two or more portions, each of which is clothed with a membrane. Two equally developed and contiguous membranes fuse with each other to form the apparently homogeneous dividing wall between two special mother cells.—The above-mentioned lighter lines are the contact surfaces of two newly formed cell membranes formed from division of the mother cell membrane. It would be difficult to come to clarity concerning the chemical nature of these delicate membranes: even the prolonged effects of water covered its traces, let alone treatment with strong acting reagents.

Only after the lines of separation of the cell membrane of the special mother cells become apparent, prominent ridges occur on the inner wall of the mother cell, which extend exactly into the lines that separate the surfaces of the cell membranes. If mother cells in which the first trace of these strips appear are allowed to dry on the slide to the point that the apex of the cell is barely covered by liquid, it draws the complex of the cell membrane a little back from the cell wall, which now appears completely smooth;—but where the tender strips seemed to extend a shallow indentation is found in the surface of the cell membranes corresponding to the dividing line between the two cells.—The content of such mother cells, which have inner walls with very strongly projecting ridges, shrinks together strongly when treated with dilute acids; the cell membrane of the special mother cells have, separated on their contact surfaces, material that is not a membrane.

The number of special mother cells varies between 2, 3, 4, 5, 6 (5 and 6 are found most commonly in *P. caerulea*; with *P. alata* the number four is more usual). The total volume of each complex of special mother cells, though it may have 2, 3, 4, 5 or more cells, is pretty much the same.—Where only two special mother cells are formed, two special mother cells of the second degree occasionally occur in each of them; the formation of two nuclei and disintegration of the cell membrane precedes this. Just as often, however, only one pollen cell of enormous size is formed in each of the two special mother cells. The size of the special mother cells is in direct proportion to that of their nuclei: in a complex of three special mother cells where two are large, one very small, etc. is formed the remarkable difference between the size of the pollen grains.

Complexes of 2 and 3 special mother cells are often found in buds that develop during the winter. In summer there are quite exclusively complexes of four, five or six special mother cells.—Is the occurrence of only two special mother cells a somewhat morbid state of inhibition caused by lack of light and heat?

Even after formation of the special mother cell, the mother cell wall tears easily in water. Then the delicate membrane of the nearest special mother cell extrudes a shallow elongated bubble from the tear. If the split is parallel to the plane of the stage, you will see the leaked part of the mother cell as a special mother cell appearing as a half-moon shaped sphere. — Treatment with dilute acids proves the bulging membrane of the special mother cell consists of cellulose.

The formation of the primary membrane of the pollen cell cannot be observed directly. The cell membrane of the special mother cell is sometimes located free in the cell space. When, after the wall of the mother cell bursts and the membrane separates, the young pollen cell is free. The (central) nucleus of the pollen cell is certainly identical to that of the special mother cell.

The first sight of the exine — the emergence of projecting reticular ridges on the outer surface of the pollen cell wall — takes place within the special mother cell; — however, the process itself, develops in the wake of the bouncing [*sic*] three covers of the pollen grain itself, only after the resorption of the mother and special mother cells.

The horizontally elongated tissue cells, which surround the strand of mother cells of each anther compartment, behave as follows during the formation of special mother — and pollen cells. The cell walls are very soft and gelatinous, so that the slightest pressure transforms it into a pulpy mass, releasing many free nuclei and small cells. When pollen cells appear, the primary cell membranes have completely disappeared; a suspension of free cells and cell nuclei surround the mass of mother cells. There are structures of this kind, which Unger (über merismat, *Zellbildung*, p. 6) designated "remaining mother cells halted at the first-stage of development"; an interpretation Nägeli (*Zeitschrift für Botanik*, issues 3 and 4, p. 310) has already refuted. — Many of the conditions occurring in embryo sacs of the Leguminosae and Liliaceae on which Schleiden founded his view of the formation of cells can be found side by side here; but also phenomena that contradict the theory of Schleiden. There occur: free nuclei of different sizes, with none, one or more nucleoli: — (nuclei with no granules, spherical bubbles with a thickish mucilage content that are on average the smallest); — cells — all spherical, with one to four nuclei; even cells with no nucleus, which differ only by their size from the loose granular nuclei. — It is often the case that the two nuclei contained in a cell enclose no nucleoli; — a fact that can not be combined with Schleiden's theory of the origin of cell nuclei, because obviously those nuclei are created anew. — I never found free nucleoli.

In many of the free cells are nuclei embedded in a mucus layer, which lines the inner wall (in which case they are always lenticular); — they are, according to Nägeli's terminology, parietal; — a relation in which, I believe, the interior location of the mucus depends only on the proportion of the spatial content of the cell to the mass. All this mucus fills the cell space, and the nucleus or the central nuclei are free; — it covers the walls as a thin layer (Hartig's Ptychoderaum), and the nucleus or nuclei are embedded in it, they are "constant walls."

It is remarkable that in many manifestations of the life of the mother cell and the surrounding layer a polar opposite prevails. — The seeds of the mother — and special mother cells of *Passiflora* as a rule contain only one very developed nucleolus; and the cell nuclei of the peripheral layer nearly always multiple, equally small, but often none. In the Tradescantieen [Commelinaceae] and Liliaceae the relationship is reversed; here the nuclei of most peripheral mucous cells show only one quite large nucleolus, while nucleoli in the nuclei of mother cells and special mother cells play a very minor role. — If *Passiflora caerulea* enjoys sufficient, light, heat and moisture, the development of the pollen mass so outweighs the mucus layer of cells it dwarfs them, otherwise it remains far behind. This is quite generally the case during the winter; this phenomenon was most conspicuous in one example, which vegetated in a cold house where the temperature only rose over + 5° R. [Réaumur scale, 6.25°C] in exceptional cases over two months. The 4½‴ *Ligne* long anthers of buds growing in the shade of a supporting beam looked like glass in yellow wax, and their compartments only included thousands of small free cells and cell granules, except for a few quite stunted complexes of special mother cells.

(Conclusions follow.)

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