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Pollination Effects on Orchid Flowers and the First Suggestion by Professor Hans Fitting (1877–1970) that Plants Produce Hormones

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Kull, Arditti and Wong (eds.), *Orchid Biology: Reviews and Perspectives*, *X*,

Introduction

A tropical orchid, *Vanilla* (Fig. 2-1D) was first brought to Europe in 1510 by the Spanish as a perfume (Lawler, 1984). Clusius (Fig. 2-1A) published what may be the first notice about it in his *Theatrum Botanicum* (Fig. 2-1A). The first plant may have reached England in 1739 (Lawler, 1984). *Bletia verecunda* (now a synonym of *Bletia purpurea*, Fig. 2-1F) was the first tropical orchid cultivated in England (Lawler, 1984). A plant received by Peter Colinson (Fig. 2-1B) from the Bahamas in 1731 was cultivated by Admiral Sir Charles Wager (Fig. 2-1G). Even before that a North American "Ladyes Slipper" (Fig. 2-1C) was reported to have been brought from North America and drawn by Sydney Parkinson (Parkinson, 1640; Lawler, 1984). A number of other orchids were brought to Europe between the 1640s and 1800. Still, tropical orchids remained a mystery and a source of fascination even as late as the 1860s when Darwin became interested in orchid pollination while vacationing at Torquay on the Devon coast with his daughter Henrietta. Once he became interested in orchids, Darwin was not satisfied with his own observations on British orchids. He read widely and corresponded extensively with a remarkable German botanist in Brazil, Fritz Müller (Fig. 2-2).

Fritz Müller

It is not uncommon for scientists to be progressive and free thinkers, disagree with established ideas, clash with autocratic regimes and run afoul of dogma. Galileo's (1564–1642) clash with the Church is probably the best known such conflict. In the Soviet Union those who disagreed with Trofim Lysenko (1898–1976), a charlatan who managed to pervert genetics under the banner of Marxism, ended in the Gulag and suffered or perished (Medvedev, 1971). The French revolution beheaded Antoine Lavosier (1743–1794) and the cultural revolution sent many "bourgeois" scientists to learn from the peasants. And, in the Germany of the 1852 it was not wise to disagree with Otto von Bismark (1815–1898), the Iron Chancellor.

Johann Friedrich Theodor 'Fritz' Müller (1821 or 1822, Thuringia, Germany-1897, Blumenau, Brazil; Fig. 2-2) began to question religion and became an atheist in 1846. He refused to take the medical oath in Germany at the time because it included the words "so help me God." Müller was also a supporter of the Prussian revolution in 1848 and held views which were too liberal for the regime. Therefore he had to leave the country (W. F. H. B, 1897). He left in 1852, settled in Brazil and reported on his numerous observations in journals and in an extensive correspondence with several scientists in Germany and Charles Darwin.

Müller became an early convert to the theory of evolution and in 1864 wrote his book *Für Darwin* (Fig. 2-2A) in which he used Brazilian crustaceans to support Darwin's views. He also corresponded extensively with Charles Darwin (Fig. 2-2C)

Fig. 2-1. The first orchids in Europe and persons associated with them. **A.** Charles l'Écluse, Carolus Clusius or Clusius (1526–1609) who published the first botanical notice of *Vanilla* and the cover of his *Theatrum Botanicum*. **B.** Peter Colinson (1694–1768). **C.** *Cypripedium acaule*, one possible "sort of our Ladyes Slipper" (Parkinson, 1640) from North America. **D.** *Vanilla* flower. **E.** Sydney Parkinson (*c*.1745–1771). **F.** *Bletia verecunda* flower. **G.** Sir Charles Wager [(1666–1743); (A, B, D, E and G, J. Arditti's collection; B, Wikipedia; C, courtesy Charles Cleland; D, J. Arditti; F, T. W. Yam).

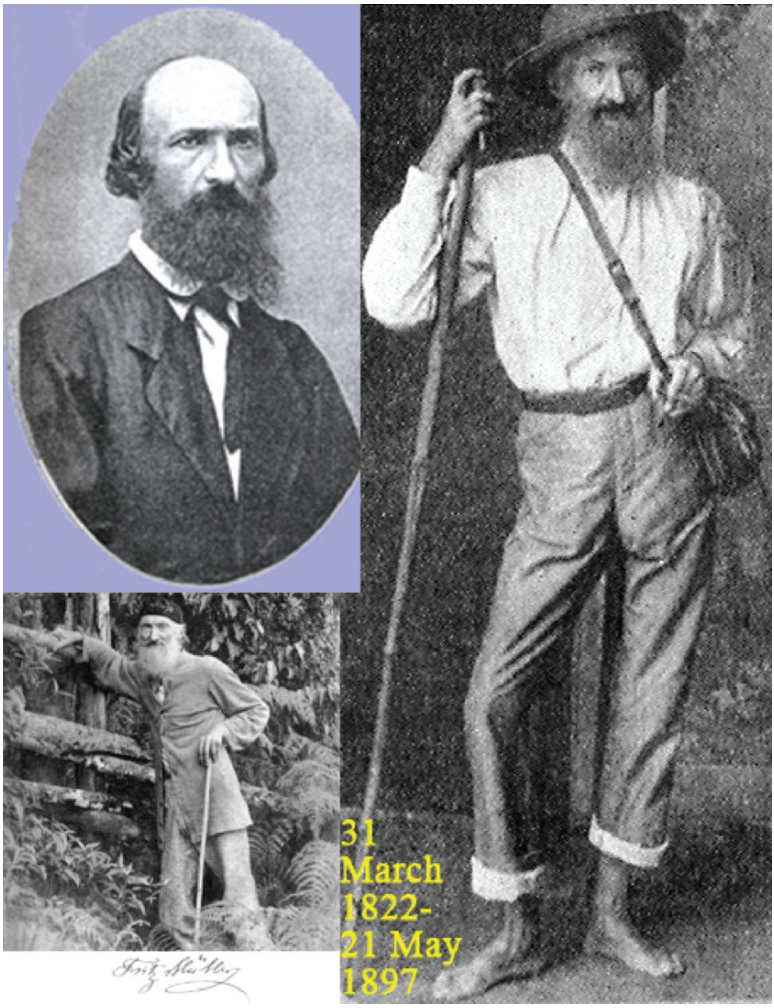

Fig. 2-2. Johann Friedrich Theodor 'Fritz' Müller (1821–1897) in Brazil during different stages of his life (Moeller, 1920, Wikipedia).

about orchids. Some of his letters and reports dealt with the effects of orchid pollen (Fig. 2-3B, 2-3D–2-3I) on flowers (Müller, 1868, 1886; Darwin, 1904; for a review see Avadhani et al., 1994) which Darwin described in *The Variation of Animals and Plants Under Domestication*, volume 2 as being "injurious and poisonous." Darwin seems to have accepted Müller's views and this lead to their wider acceptance. Müller's writings about orchids are very interesting and deserve a separate treatment. They will not be discussed in this chapter.

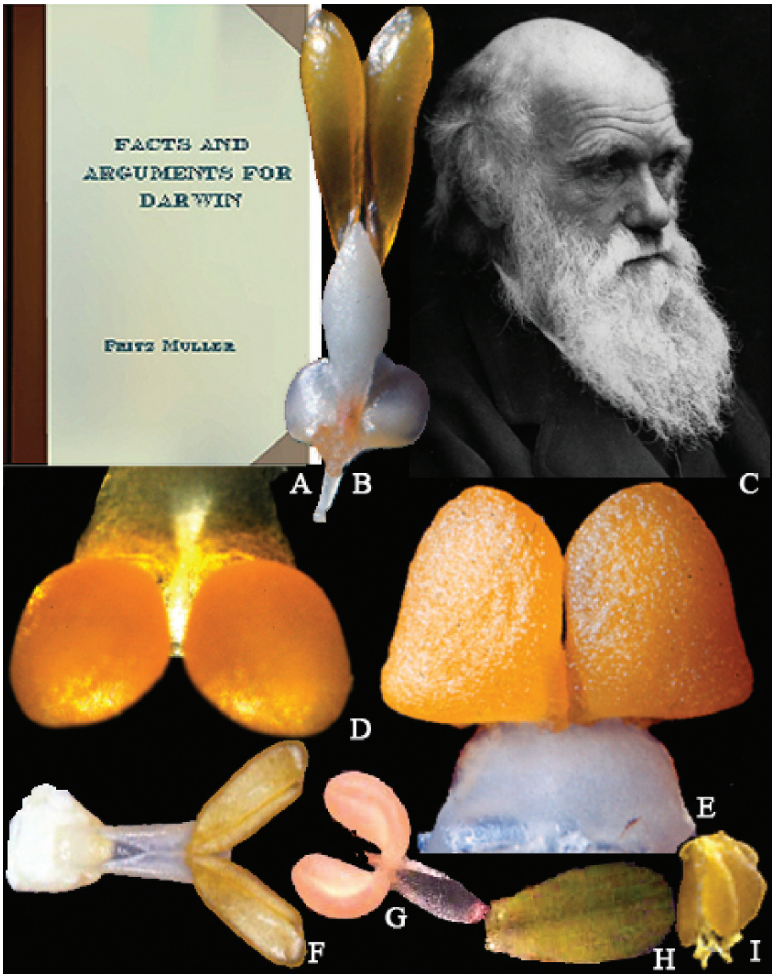

Fig. 2-3. "For Darwin," Darwin and orchid pollinia. **A.** Cover of an English translation of Fritz Müller's book *Für Darwin*. **B.** *Stanhopea* pollinarium. **C.** Charles Darwin. **D.** *Phalaenopsis* pollinia. **E.** *Cymbidium* pollinarium. **F.** *Catasetum* pollinarium. **G.** *Oncidium* pollinarium. **H.** *Masdevallia glandulosa* pollinia. **I.** *Cattleya* pollinia. (A, facsimile of Muller's 1869 *Facts and Arguments for Darwin*; B, D–F, I, J. Arditti; C, J. Arditti's collection; G, H, courtesy Lotte and Thomas).

Hans Fitting

The "theory that [was] very common in the older German literature on pollination biology, namely that the pollinia of many exotic orchids act like a poison during cross-pollination" attracted the attention of Hans Fitting (Fig. 2-4) in 1907 who also read a letter by Müller to Darwin dated 1 January 1867 which "elaborates on

the toxicity of the orchid pollinia" [the statements in quotes are from a letter dated 10 November 1969 by the late Hans Fitting to Joseph Arditti (J.A.) translated by Hubert Kurzweil (H.K.); Appendix 1].[1] He obtained a travel grant and visited the Bogor Botanical Gardens in Indonesia to study the phenomenon.[2]

Johannes Theodor Gustav Ernst 'Hans' Fitting (Fig. 2-4) was born on 23 April 1877 in Halle a. d. Salle, Germany, the son of Herman Fitting a Professor of Law and his wife Clara (maiden name Merkel). At the age of nine young Hans declared that he will become a "*Blumenprofessor*" (Professor of Flowers). After attending gymnasium (1886–1895) and university in Halle (1895–1896) he served in the military (1896–1897). In January of 1900 Fitting became a doctoral student under H. Graf zu Solms-Laubach (1842–1915) and was granted a degree summa cum laude (Halbsguth, 1962, 1974). Due to lung disease Fitting had to take time off work and spend the first half of 1901 in the mountains.

After recovering Fitting worked with Wilhelm Pfeffer (1845–1920) in Leipzig[3] for a year (fall 1901–1902). He accepted a position under Professor Herman Vöchting (1847–1917) in Tübingen in October 1902 and remained there until the fall of 1907 when a *Deutschen Reichs* tropical stipend made it possible for him to travel until June 1908 and visit Sri Lanka (then Ceylon) and Java (specifically the Bogor Botanical Gardens). At Bogor Fitting carried out numerous experiments often as early as 06:00 and sometimes even earlier. Fitting seems to have enjoyed his stay in Bogor because he inquired about the gardens with interest and concern sixty years later in one of the letters[1] to J. A.

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[1] In advanced age and suffering from heart problems when he wrote three letters to JA in longhand. They are dated 2 November 1969, 10 November 1969 and 10 December 1969. The letters include many details and citations and are very clear. Prof. Fitting clearly enjoyed being remembered and reminisced about work he did 61 years in the past with obvious pleasure.

Professor Kenneth V. Thimann recalled meeting Fitting at the 1935 Botanical Congress in Amsterdam and wrote that "he was in good form and gave a talk, not about pollination…he must have been 60 years old at the time, but was very lively" (letter by Prof. Kenneth V. Thimann to J. A. dated 27, January 1971).

The late professor Frits W. Went, the discoverer of auxin, wrote about Fitting that he "was…an indefatigable digger of facts which he published in incredible detail…but somehow, he always missed the boat." In "his work on the transmission of the phototropic stimulus…he failed to notice that most of his results were due to leakage across a wound gap…I was not impressed with his scientific reasoning…Every botanist had assumed that the stomata of desert plants would be closed, but Fitting…found that they were wide-open. His explanation was…'of course they should be open, otherwise the leaves could not photosynthesize. He did not even mention the opposite argument that they should be closed to conserve water" (letter dated 19 June 1974 by Prof. F. W. Went to J. A.).

Mrs. Sigrid Fitting provided photographs and details about Professor Fitting after his death.

All letters and photographs are part of the reprints collection J. A. donated to the Singapore Botanic Gardens.

[2] The names of orchids employed by Fitting in his experiments which are used in this chapter are those he included in his papers. Currently accepted names are listed in Appendix 2.

[3] There is an indirect connection to orchids in Fitting's association with Pfeffer. Prof. Lewis Knudson's used Pfeffer's solution in the research which lead to his first solution (Knudson B) for the asymbiotic germination of orchid seeds.

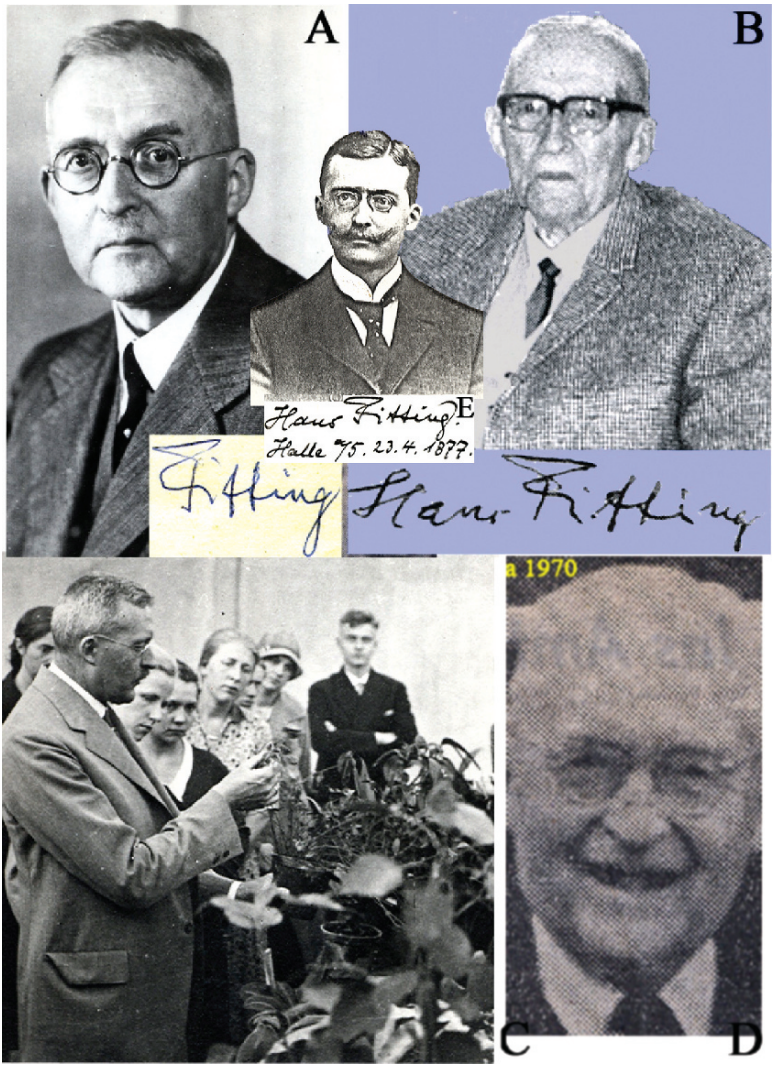

Fig. 2-4. Hans Fitting during various stages of his life. **A.** In mid life. **B.** In 1969. **C.** Teaching in the greenhouse, University of Bonn. **D.** In 1970 shortly before his death. **E**. Photograph from about the time he went to Bogor. Signature is from later with 1877 indicating year of birth.

On returning from Indonesia Fitting was appointed Associate (Extraordinarius) Professor at the University of Strasbourg.[4] He assumed the position in the summer of 1908 and carried out additional research on orchids there. In March–April 1910

[4]We thank Dr. Wolfgang Zierau, Institute of Solid State Theory, Westfälische Wilhelms Universität, Muenster, Germany for explaining the mysteries of German university titles.

Fitting left Strasburg for a 2.5 months study tour of Algerian Sahara. After that he accepted a position as Associate (Extraordinarius) Professor at the University of Halle and remained there until the fall of 1911. He left Halle to become Full Professor at the Colonial Institute in Hamburg and Director of the State Botanical Garden in the same city. While in Halle Fitting must have spent time in pursuits other than botany because he married Sigrid Meyer, the daughter of a University of Halle official in the summer of 1911. They had two daughters and three sons. All sons served in the military during World War II. The youngest, Rudolf, a lieutenant in an anti tank armored unit was killed between 15 and 16 of October 1943 in Volturno, Southern Italy.[5]

In 1912 Fitting was appointed to succeed Eduard Strasburger (1844–1912)[6] as Full Professor (Ordinarius) at the University of Bonn. This was one of the most prestigious botanical professorships in Germany and Fitting further increased its prestige. He remained at the University of Bonn for the rest of his life, became one of the best known plant physiologists in Germany at that time, retired on 1 October 1946 and was Professor Emeritus for the rest of his life.

World War II was not kind to Fitting and his wife. As already mentioned they lost one son in Italy. In addition, their house was destroyed during an air raid. The botanical institute was also damaged by a bomb. After the war, the University was reopened in the fall of 1945 with Fitting as Dekan (academic head) of the Mathematics and Natural History Faculty. His lack of the support for the Nazi regime and the saving of his Jewish colleague V. Simon served him in good stead during the postwar years (Halbsguth, 1974).

Fitting rebuilt his house in 1952 and remained in relatively good health until 1962. He had a heart attack then (his age was 85), but survived it. He died on 6 July 1970 at 93. When one of us (J. A.) initiated research on post pollination phenomena of orchid flowers in the late 1960s it did not seem reasonable to assume that Professor Fitting was still alive. As a result J. A. failed to visit Prof. Fitting on his trip to Germany in 1968. When the late Professor Erich L. Nuernbergk informed J. A. that Fitting was alive, Miss Brigitta H. Flick, J. A.'s technician at the time visited and photographed him in 1969 (Fig. 2-4B).

[5] Professor Erich Nuernbergk, an opponent of the Nazi regime in Germany, told one of us (J.A.) that Fitting also opposed the Nazis and helped Jewish colleagues (one of them being V. Simon) escape to safety. Fitting described himself as not being politically active, but a member of the Deutschen Volkspartei (according to Dr. Zierau this party which existed during the Weimar Republic in Germany was conservative and pro monarchy, but not pro Nazi).

[6] Eduard Strasburger was the first botanist to fix tissues and stain them and to describe meiosis and mitosis between 1877 and 1885. He coined the terms phototaxis, cytoplasm, nucleoplasm, prophase, metaphase, anaphase, plasmodesmata, haploid and diploid.

Fitting's Research on Pollination and Developmental Physiology of Orchid Flowers

The "Tropen (or Buitenzorg) Stipendium des Deutschen Reiches" (Halbsguth, 1962, 1974) made it possible for Fitting to engage in research at the Bogor (then Buitezorg) Botanical Gardens in Indonesia from September or November 1907 until June 1908 (Halbsguth, 1962, 1974). While in Bogor the 30 years old Fitting (Fig. 2-4E) carried out a total of 79 numbered experiments (some simple and consisting of one part and others multi part and elaborate), and many more that were mentioned but had no numbers (Fitting, 1909a, b). He described his experiments in great detail. At present his descriptions would be considered to be excessive, excruciatingly ponderous and tedious. Many of the details he provided are simply unnecessary. On the other hand the details about how he worked provide an insight into the mind of an influential plant physiologist and explain why Fitting became so well known during his life-time. In addition to being a resourceful and clever investigator Fitting was also a very hard worker. To carry that many experiments in the relatively short time he had, Fitting often started to work at 06:00 and worked 10–12 h a day 7 days a week.

Pollination and Other Applications to Stigmas

Despite being familiar with both Müller's and Darwin's writings Fitting established his own baselines (Table 2-1). He carried out his experiment with several orchid species (Figs. 2-5–2-9) probably for two reasons. One reason may have been his intent to determine whether the effects of pollen were universal or at least widespread in the Orchidaceae or limited to a few species. The second reason was practical: Even at the Bogor Botanical Gardens there was often a shortage of flowers of a single species (Fitting, 1909a, b). For this reason he also had to use a single flower for some experiments (i.e., there were no replications).

He pollinated flowers (self, cross, geitonogamous and xenogamous) and observed that in most cases pollination caused swelling of the ovary and gynostemium not long after the application of pollen to the stigma and shortened the life span of the flowers. Exceptions were flowers of: (1) *Liparis latifolia* (Fig. 2-8E) which did not wilt after six days (Table 2-1), (2) *Cymbidium sanguinolentum* (now *Cymbidium chloranthum)* which did not exhibit pronounced wilting, and (3) *Phalaenopsis violacea* (Fig. 2-8C) which yellowed, closed (Table 2-1) and underwent major changes (Fig. 2-6F) and, as shown by recent research (Tran et al., 1995), producing chlorophyll and probably becoming photosynthetic.

Fitting emasculated flowers of *Rhynchostylis retusa* (Table 2-1) and reported that changes were slower to occur than after pollination. This is in line with our current knowledge about the induction of post pollination phenomena and floral senescence in orchid flowers (Avadhani et al., 1994). He also made cuts in the gynostemium (Fig. 2-7H) and reported that the flower did not wilt even after 2 weeks

Table 2-1. Hans Fitting's experiments with orchid pollination at the Bogor Botanical gardens in 1908 (Fitting, 1909a).

Experiment number	Orchid[a]	Description	Results	Fitting's conclusions	Current explanation
1 (4–10 Jan 1908)	*Rhynchostylis retusa* (Fig. 2-7)	Placed sand in stigmas (11 flowers) Six flowers pollinated (geitonogamous pollination) Unpollinated flowers	7 flowers wilted in 9 h and all 11 wilted in 44 h All 6 flowers wilted in 96 h. Ovaries and gynostemia swollen Flowers fresh until February	Sand caused wilting but not swelling at 44 h. Ovaries and gynostemia not swollen Pollination caused both wilting and swelling. Emasculation did not shorten the life span of flowers	Sand wounded stigmas causing shortened flower life. Ethylene evolution which induced senescence Emasculation should have done the same. Pollen effects are normal
2 (12–16 Jan 1908)	*Rhynchostylis retusa* (Fig. 2-7)	Ten flowers pollinated both geitonogamously and xenogamnously and self pollinated Sand placed in stigmas of 21 intact flowers Sand placed in stigmas of 16 emasculated flowers Flowers emasculated	All 10 flowers started to wilt after 24 h; wilting increases after 48 and 72 h No change after 24 h, 3 flowers wilted after 48 h and all 21 wilted after 72 h No change after 24 h, 7 flowers wilted after 48 h and all 16 wilted after 72 h No change until start of February	Sand shortened flower life span, and caused wilting, but not swelling of ovaries and gynostemia Pollination, but not emasculation caused all of these. Shortening of life spans does not require or depend on swelling of gynostemia and ovaries	Sand wounded stigmas causing ethylene evolution which induced wilting and senescence. Emasculation should have done the same Pollination effects are normal. Shortening of life span and swelling are not interdependent
3 (8–25 Jan 1908) (10–21 Jan 1908)	*Rhynchostylis retusa* (Fig. 2-7)	Cut made in gynostemium below stigma, above the perianth point of origin Gynostemium squeezed or crushed with forceps at level of or below stigma of 7 flowers	All 5 flowers unchanged and still fresh after 13 and 15 days 2 flowers, one after 5 days, the other after 9 days start to wilt and damaged areas turn black	Wounding the gynostemium does not shorten the life span of flowers The sand does not shorten the life span of flowers by damaging the gynostemium	If wounding the gynostemium induced ethylene evolution it should have shortened flower life span. Sand wounded the stigmas thereby inducing ethylene evolution which shortened the life span of flowers

(continued)

(20–25 Jan 1908)		Gynostemium treated as above, but mostly crushed in 6 flowers	1 flower started to wilt after 2 days, damaged areas blackened in all flowers		
(31 Jan–12 Feb)		Cuts below stigmas made in gynostemia of 12 flowers	All flowers unchanged after 12 days		
5–20 Feb 1908)		Gynostemia removed	Flowers remained fresh until end of experiment		
4A (17–28 Jan 1908)	*Rhynchostylis retusa* (Fig. 2-7)	River sand placed in stigmas of 12 flowers	9 flowers started to to wilt after 5 days. All flowers wilted after 12 days	Sand does not have a mechanical effect which shortens the life of flowers	Either sea sand has no sharp edges and is not injurious or boiling it in acid eliminated sharp edges and rendered sea sand non injurious
		Acid washed sea sand placed in 12 stigmas	All 12 flowers not wilted after 12 days	Acid washing removed iron, aluminum, magnesium, manganese and cobalt from sea sand	
4B (20–29 Jan 1908)		River sand placed in stigma of 6 flowers Acid washed sea sand placed in 6 stigmas	All 6 flowers started to wilt after 2 days 1 flower started to wilt after 2 days, 5 not wilted after 10 days		
4 (22 Jan noon–24 Jan 7 a. M. 1908)		Pollinated (18 flowers)	All 18 flowers wilted after 43 h		
No number or date	Not listed	10% KNO_3 in water, aqueous solution of amylase, sea sand wetted with 1% iron chloride	None of these had any effect on the life span of flowers	None	Not necessary
5–16	The purpose of these experiments was to determine whether the observations with *Rhynchostylis retusa* were unique and specific to this one orchid. Unless indicated otherwise or is obvious from the experimental procedure the flowers used in the following experiments were not emasculated and the life span of the control blossoms was longer than that of the experimental ones				

(continued)

Table 2-1. (continued).

Experiment number	Orchid[a]	Description	Results	Fitting's conclusions	Current explanation
5 (12–18 Jan 1908)	*Liparis latifolia* (Fig. 2-8E)	Pollinated (2 flowers) River sand placed in stigma of 4 flowers	2 of 2 flowers not wilted after 6 days All 4 flowers not wilted after 6 days, but 2 abscised	The conclusions listed below in this column pertain to experiments 5–19	Current comments and explanations are opposite each conclusion below
6 (12–18 Jan 1908)	*Cymbidium sanguinolentum* (Fig. 2-8B)	Pollinated (2 flowers) River sand placed in stigma of 5 flowers	2 of 2 flowers do not exhibit pronounced wilting 5 of 5 flowers not exhibit pronounced wilting	1. River sand caused rapid closing and wilting only in flowers which are affected similarly by pollen	Interesting, but not very profound
7 (15–23 Jan 1908)	*Cymbidium finlaysonianum* (Fig. 2-8D)	Pollinated (single flower) River sand placed in stigmas of 3 flowers Diastase (amylase) in stigmas of 2 flowers	Flower slightly closed after 6 days, abscised after 7 days All 3 flowers slightly closed after 7–8 days and abscised Both flowers slightly closed after 5 days and abscised	2. River sand does not usually act more rapidly than pollen 3. River sand only shortens the lifespan of flowers 4. River sand does not bring about swelling of gynostemium and ovary	There is no reason why sand should act more rapidly Yes, it probably acts by inducing ethylene evolution Yes, because ethylene only brings about senescenc
8 (22 Jan–4 Feb 1908)	*Vanda tricolor* (Fig. 2-8H)	Pollinated (single flower) River sand placed in stigma A Acid washed sea sand placed in stigma A	Color changes of perianth started 2 days after pollination and proceeded slowly after that Flowers unchanged until 9th and 10th day	5. River sand had no effects on *Vanda tricolor* 6. Acid-washed sea sand and river sand usually have the same effect	Hard to explain why There is no reason why they should not
8a (13–24 Jan 1908)	*Oncidium incurvum* (Fig. 2-8G)	Pollinated (single flower) River sand placed in stigma	Flower wilted after ca 5 days Flowers wilted after ca. 6–7 days	7. Sand exerts its effects by wounding the stigma	Very astute observation for the time This is how sand probably acts

(continued)

9 (20–26 Jan 1908)	*Dendrobium antennatum* (Fig. 2-8A)	Pollinated (2 flowers) River sand places in stigmas of 2 flowers	All 4 flowers not wilted and nearly unchanged after 6 and 10 days	The conclusions lead Fitting to his next set of experiments which involved wounding of stigmas and gynostemia
10 (20–22 Jan 1908)	*Coelogyne pandurata* (Fig. 2-8F)	Pollinated (3 flowers) River sand placed in stigmas of 2 flowers Acid washed sea sand Placed in 4 stigmas	Treated flowers closed after 1 day. Untreated flowers remained open	On the whole Fitting's experiments and conclusions were very much ahead of their time
11 (17–23 Jan 1908)	*Coelogyne asperata* (Fig. 2-8I)	Pollinated (1 flower) River sand placed in stigmas of 2 flowers Acid washed sea sand Placed in 3 stigmas	Treated flowers closed after 1 day. Untreated flowers remained open 2–3 additional days	
12 (13–19 Jan 1908)	*Phalaenopsis esmeralda* (*P. regnieriana;* Fig. 2-8J)	Pollinated (2 flowers) River sand placed in stigmas of 2 flowers	All wilted after 3 days and were somewhat closed All wilted after 3–4 days and somewhat closed	The wounding experiments were numbered 17–40 by Fitting. They are summarized in Table 2-2
13A (18–22 Jan 1908)	*Phalaenopsis amabilis* (similar to Fig. 2-5, Fig. 2-13A)	Pollinated (2 flowers) River sand placed in stigmas of 2 flowers Acid washed sea sand placed in stigma of 1 flower	Both closed after 1½ days and wilted after that Both closed after 3 days and wilted after that Flower closed after 4 days and wilted after that	
13B (21–23 Jan 1908)		River sand placed in stigmas of 2 flowers	Both closed after 2 days and wilted after that	
13C (26–31 Jan 1908)		Pollinated (2 flowers) River sand places in stigmas of 2 flowers Acid washed sea sand placed in stigmas of 2 flowers	Both closed after 1½ days and wilted after that One flower closed after 3 days and wilted after that The second remained unchanged and closed next day Both remained unchanged	

(continued)

Table 2-1. (continued).

Experiment number	Orchid[a]	Description	Results	Fitting's conclusions	Current explanation
14A (18–23 Jan 1908)	*Phalaenopsis violacea* (Fig. 2-6F, 2-8C)	Pollinated (1 flower) River sand placed in stigma of 1 flower	Flower closed and yellowed after 2 days Flower closed and yellowed after 5 days		
14B (24–30 Jan 1908)		River sand placed in stigmas of 4 flowers	2 flowers closed and yellowed after 5 days; 2 did the same after 6 days		
15A (26 Jan–5 Feb 1908)	*Dendrobium superbum*	Pollinated (1 flower) River sand placed in stigmas of 2 flowers	Closed and wilted after 1 day Both flowers closed and wilted after 2 days		
15B (14–24 Feb 1908)		Pollinated (3 flowers) Rivers sand placed in stigmas of 3 flowers	All pollinated and sand-treated flowers closed and wilted after 1 day		
15C (16–22 Feb 1908)		River sand placed in stigmas of 2 flowers	1 flower closed and wilted after 2 days, the second closed and wilted after 3 days		
15D (16–20 Feb 1908)		Pollinated (2 flowers) River sand placed in stigmas of 2 flowers	All pollinated and sand-treated flowers closed and wilted after 1 day		
15E (24–29 Feb 1908)		River sand placed in stigmas of 2 flowers	Flower closed after 1 day, the other closed after 4 days		
16 (14–20 Feb 1908)	*Aerides odorata* (Fig. 2-9)	Pollinated (4 flowers) River sand placed in stigmas of 4 flowers	All pollinated and sand-treated flowers wilted after 4 days		

[a]The orchid names in this table are those used by Hans Fitting. Please see Appendix 2 for updated nomenclature.

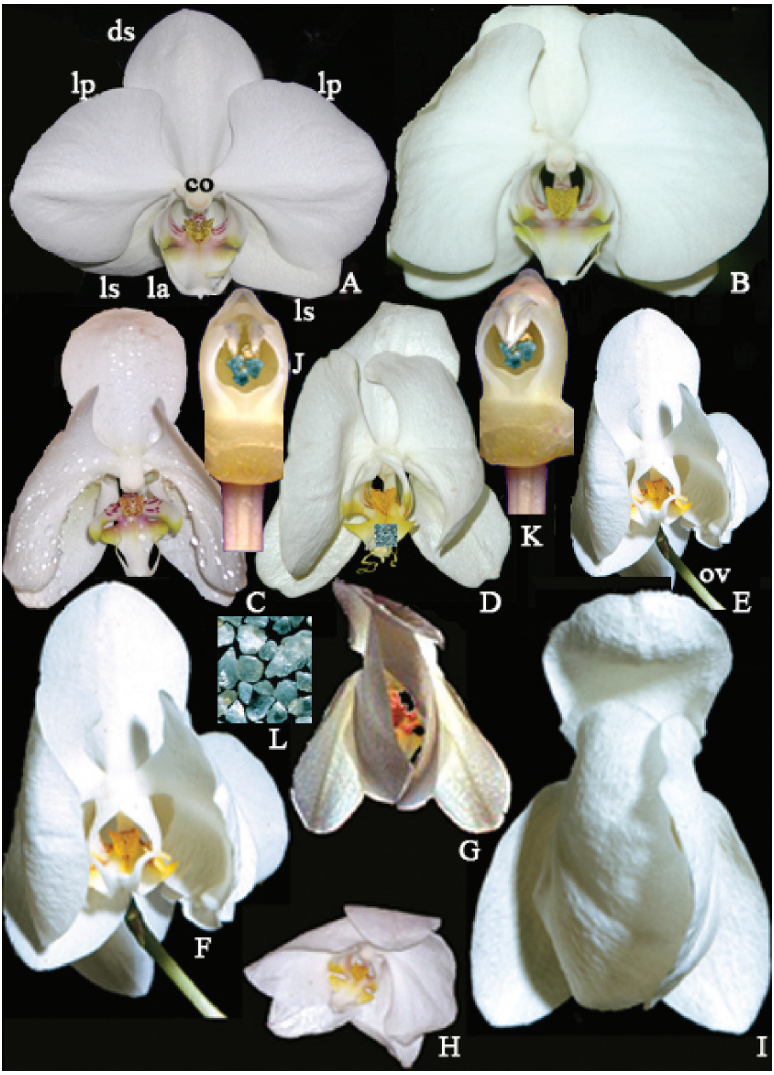

Fig. 2-5. Post-pollination hyponasty of lateral petals and floral aging in *Phalaenopsis amabilis*. **A.** Unpollinated flower. **B–I.** Post-pollination phenomena. **J.** Sand in stigma of emasculated gynostemia. **K.** Sand in stigma of an intact gynostemium. **L.** Sand. (J and K are computer-generated simulations). Explanation of symbols: co, column (gynostemium), ds, dorsal sepal; la, labellum (median petal); lp, lateral petal; ls, lateral sepal; ov, ovary (source: J. Arditti; some of the pictures were taken in Changi Airport, Singapore where one of the terminals was decorated with hundreds of *Phalaenopsis* plants).

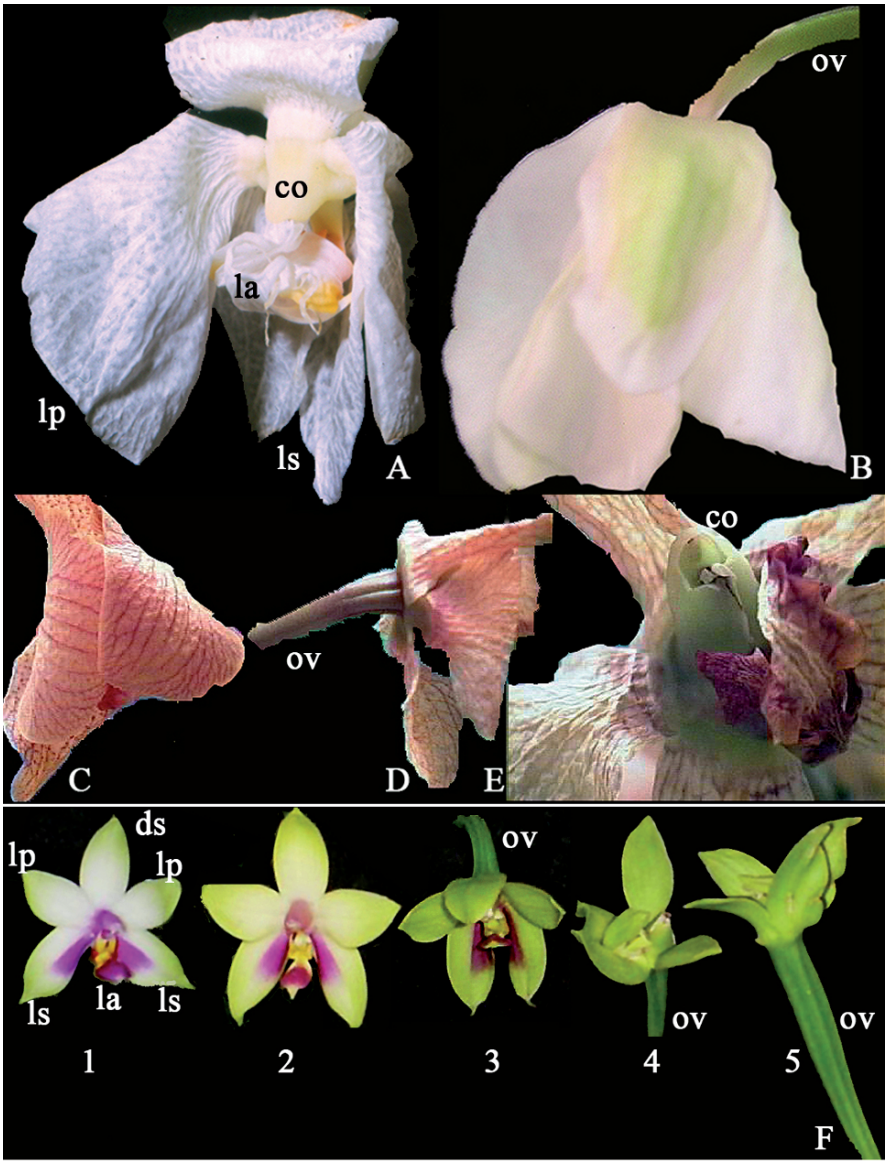

Fig. 2-6. Post-pollination phenomena in *Phalaenopsis* flowers. **A-E.** Senescence of perianth. **D.** Swelling of ovary. **E.** Greening and swelling of gynostemium. **F.** *Phalaenopsis violacea*. 1 unpollinated flower; 2–5 changes following pollination. Explanation of symbols: co, column (gynostemium), ds, dorsal sepal; la, labellum (median petal); lp, lateral petal; ls, lateral sepal; ov, ovary (Photographs and montage by J. Arditti).

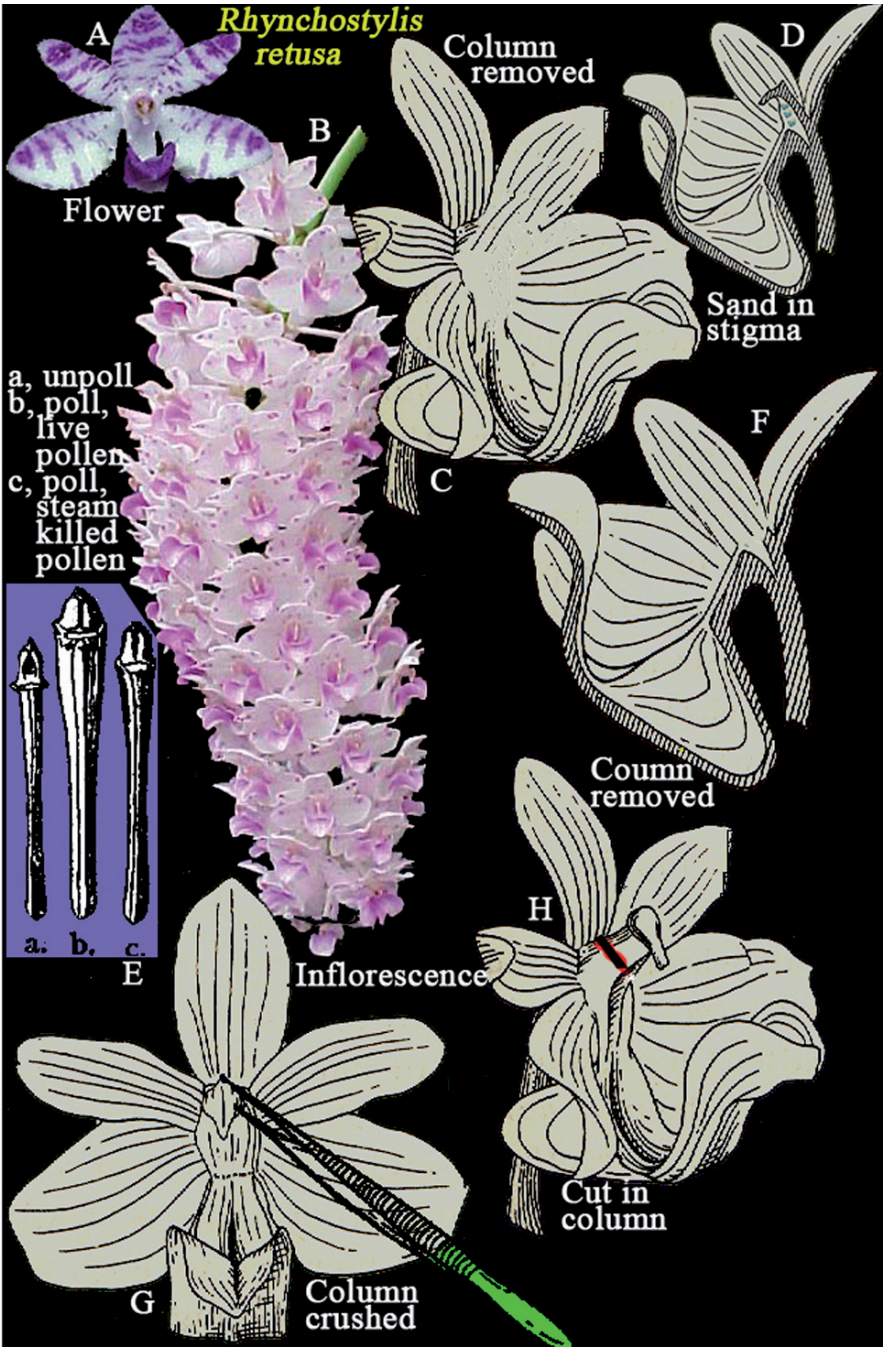

Fig. 2-7. *Rhynchostylis retusa*, a species used by Hans Fitting in his experiments. Explanations are on the figure itself (A, B, T. W. Yam, C–E, Fitting's papers).

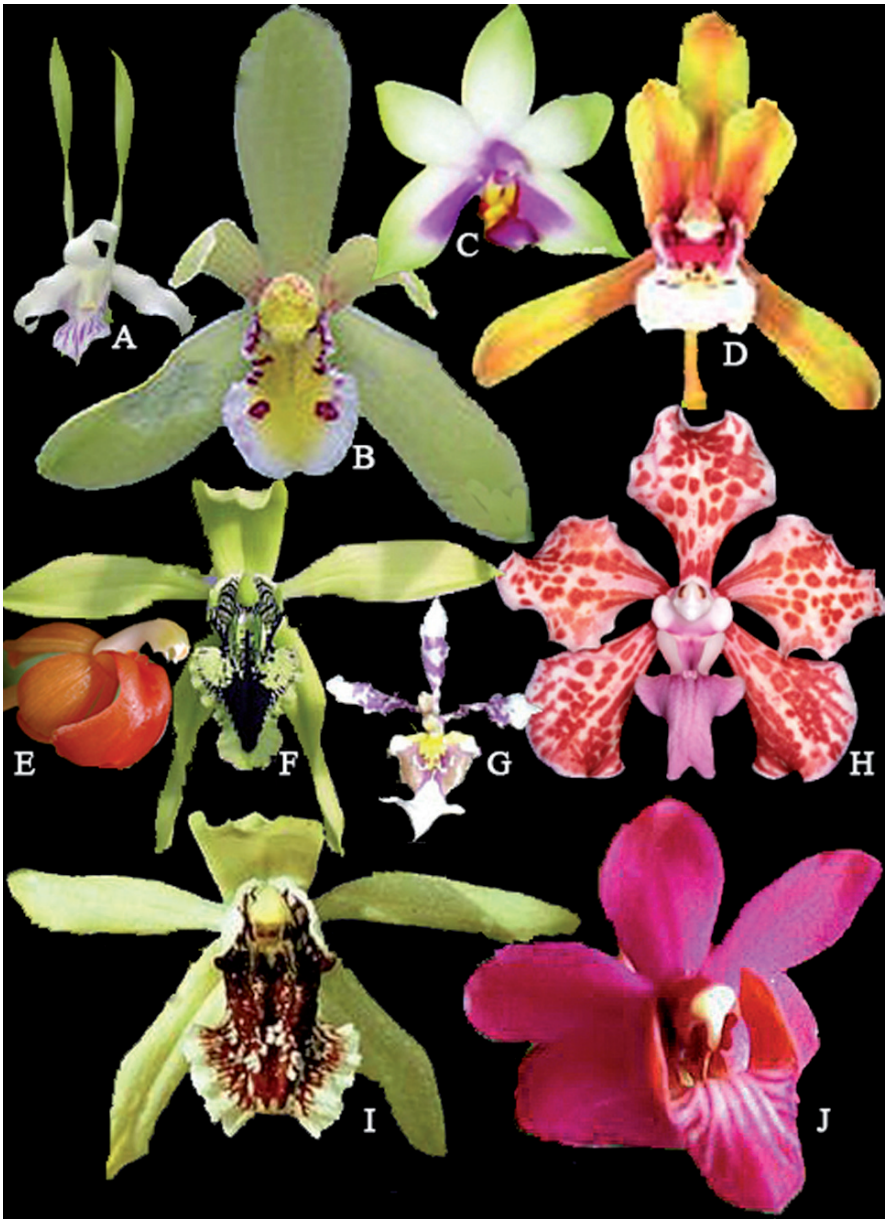

Fig. 2-8. Orchids used by Hans Fitting in his experiments. **A.** *Dendrobum antennatum*. **B.** *Cymbidium sanguinolentum*. **C.** *Phalaenopsis violacea*. **D.** *Cymbidium finlaysonianum*. **E.** *Liparis latifolia*. **F.** *Coelogyne pandurata*. **G.** *Oncidium incurvum*. **H.** *Vanda tricolor*. **I.** *Coelogyne asperata*. **J.** *Phalaenopsis esmeralda*. (A–C, F–J, T. W. Yam and J. Arditti; D, E, courtesy Eric Hunt).

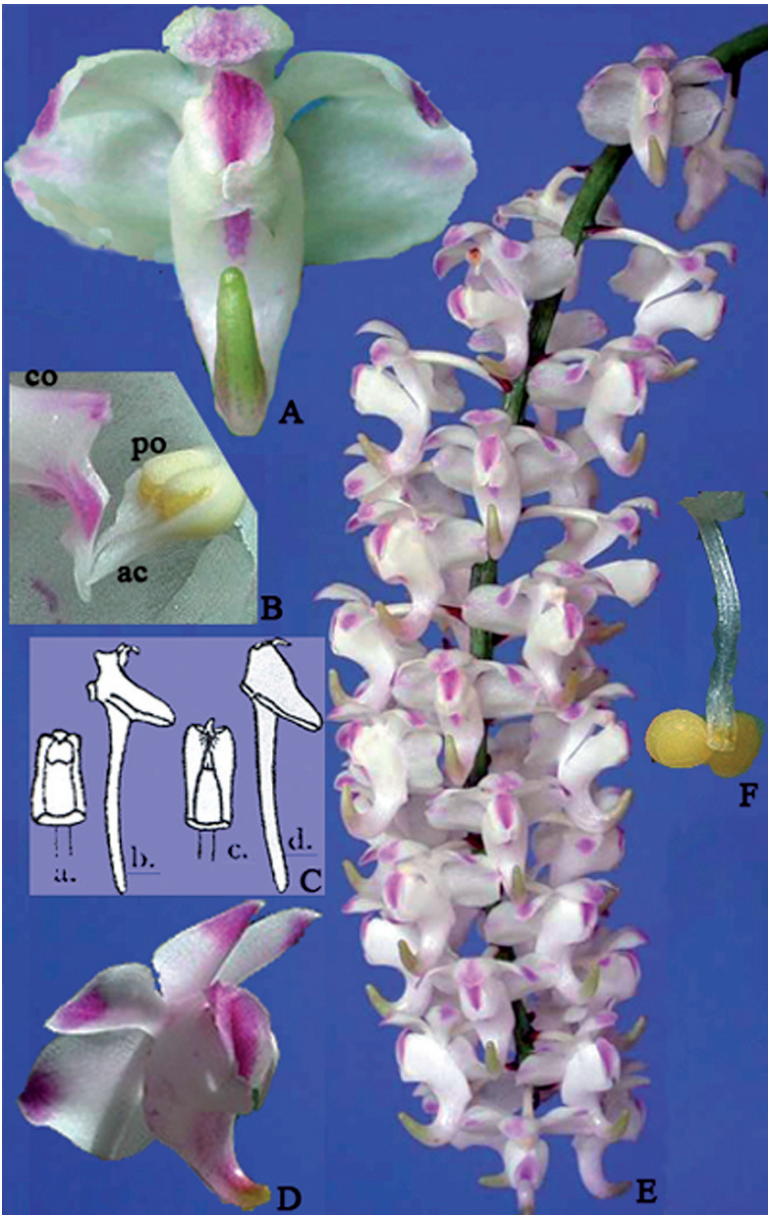

Fig. 2-9. *Aerides odorata* and *Aerides falcatum*. **A.** Front view of flower of *Aerides odorata*. **B.** Front of column of *Aerides odorata* showing detached pollinia inside anther cap. **C.** Column and ovary of *Aerides odorata*: a, front view of untreated gynostemium; b, side view of untreated ovary with labellum; c, front view of swollen gynostemium following application of pollen extract to stigma; d, side view of ovary with labellum following application of pollen extract to stigma. **D.** Side view of flower of *Aerides odorata*. **E.** Inflorescence of *Aerides odorata*. **F.** Pollinarium of *Aerides falcatum* (A, D, E, T. W. Yam and J. Arditti; B, F, courtesy Heinz Schneider; C, Fitting, 1909).

(Table 2-1). This is surprising since the cuts can be expected to evolve wound ethylene which would cause senescence. Removal of the gynostemium (Fig. 2-7C, F) also did not cause floral senescence (Table 2-1). It is possible that in both cases (Fig. 2-7C, F, H) the cuts were not severe enough to induce copious ethylene evolution. That this may be the case is suggested by the fact that crushing the gynostemium (Fig. 2-7G) did bring about senescence (Table 2-1).

For reasons which he did not explain, Fitting applied aqueous solutions of potassium nitrate (10% KNO_3) and amylase to stigmas of *Rhynchostylis retusa*. Both were without effect (Table 2-1). However when he applied an aqueous solution of "diastase [amylase]" to stigmas of two flowers of *Cymbdium finlaysonianum* both closed slightly after 5 days and abscised. Fitting did not explain the reasons for the different responses of the two species and they remain unclear. On the face of it there are no reasons why potassium nitrate should induce floral senescence and post pollination phenomena. The starch-hydrolyzing enzymes may have induced the slight stigmatic closure by breaking down starch reserves to glucose which raised the sugar levels inside cells. This in turn probably brought about water influx which caused the swelling that lead to stigmatic closure.

In a letter (to J. A.) about Hans Fitting, Prof. Frits W. Went[1] (Fig. 2-25C) wrote that "he was too much steeped in the 'stimulus' [the German word *Reizung* is a rough equivalent] concept." Fitting must have been concerned with *Reizung* even while in Bogor because he placed sand in stigmas of *Aerides odorata, Coelogyne asperata, Coelogyne pandurata, Cymbidium finlaysonianum, Cymbidium sanguinolentum* (now *Cymbidium chloranthum*)*, Dendrobium antennatum, Dendrobium superbum* (now *Dendrobium anosmum*)*, Liparis latifolia, Oncidium incurvum, Phalaenopsis amabilis* (Fig. 2-5D, 2-5J–L)*, Phalaenopsis esmeralda* (now *Phalaenopsis pulcherrima*)*, Phalaenopsis violacea, Rhynchostylis retusa* (Fig. 2-7) and *Vanda tricolor* (Table 2-1). He probably used what he described as "sand" without any additional details and also river sand to determine whether a purely physical stimulus would have any effects. The sand caused wilting in some flowers, but had no effects on *Cymbidium sanguinolentum* and *Liparis latifolia* which also did not wilt after pollination (Table 2-1). River sand caused wilting in *Rhynchostylis retusa*, but not if it was acid washed (Table 2-1). However, both washed and unwashed river sand caused wilting in both *Coelogyne* species and *Phalaenopsis amabilis*.

These findings suggest that *Cymbidium sanguinolentum* and *Liparis latifolia* flowers may be incapable of ethylene production, but this speculative suggestion requires experimental confirmation. The different effects of acid washed and unwashed sand on *Rhynchostylis retusa* on the one hand and on both *Coelogyne* species and *Phalaenopsis amabilis* on the other are more difficult to explain. If the acid somehow rounded off edges in the sand and blunted them thereby causing the sand not to injure the stigma and not to bring about ethylene production the effects should have been the same on both species. The same would be true if the acid removed injurious substances or heavy metals which could cause ethylene evolution. Differential sensitivity of the species seems to be the only remaining explanation.

Wounding

The possibility that sand exerted its effects by wounding the stigma lead to a series of experiments in which Fitting wounded gynostemia and stigmas in several places and in different ways (Fitting, 1909a, b). He also removed portions of gynostemia (Fig. 2-10: Table 2-2).

Wounding or damaging the stigma in any way brought about wilting of the perianth, senescence and shortened the life span of flowers (Fitting could not have known that the wounds induced ethylene production). The exceptions were:

- Wounds in the lower or middle part of the stigma (Table 2-2). This suggests that not all parts of the stigma can produce ethylene or produce enough of the gas to bring about senescence. The rostellum is known to be capable of producing large amounts of ethylene (for a review see Avadhani et al., 1994). Fitting's findings show that the upper parts of the stigma which are close to the rostellum have a similar capability.
- Wounded stigmas of *Aerides odorata* flowers (Fig. 2-9) which is surprising because pollination does bring about senescence of these blossoms (Table 2-2).
- Flowers of *Armodorum sulingi* (Fig. 2-11B), *Dendrobium macrophyllum* (Fig. 2-11A, 2-11D), *Renanthera maingayi* (now a synonym of *Arachnis* ×*maingayi*, Fig. 2-11C) and *Trichoglottis geminata* (Fig. 2-11E) all of which are fleshy. These flower also remained fresh and did not change following pollination. Not enough information is available at present regarding post pollination phenomena in fleshy orchid flowers to allow speculations regarding Fitting's findings with these species.

The effects of wounding are easy to explain at present: Wounding brought about the production of ethylene which induced senescence and other post-pollination phenomena (for a review see Avadhani et al., 1994). In those early days of plant physiology Fitting could not have known, let alone suggest the involvement of ethylene despite the fact that its effects on pea seedlings were already known (Neljubov, 1901). At a time when even solid substance, but soluble plant hormones were yet to be discovered the existence of a gaseous hormone would have been impossible to imagine. However, the facts are that Fitting observed both auxin and ethylene effects.

Killed Pollinia and Pollen Extract

Even if the wounding experiments were an aspect or an extension of Fitting's interest in "stimulus" or "*Reizung*" his interests were wider and very advanced for his time. He decided to determine the effects of dead pollinia killed by submerging them in chloroform or boiling water and subjecting them to steam (Figs. 2-13–2-15; Table 2-3; Fitting, 1909a, b).

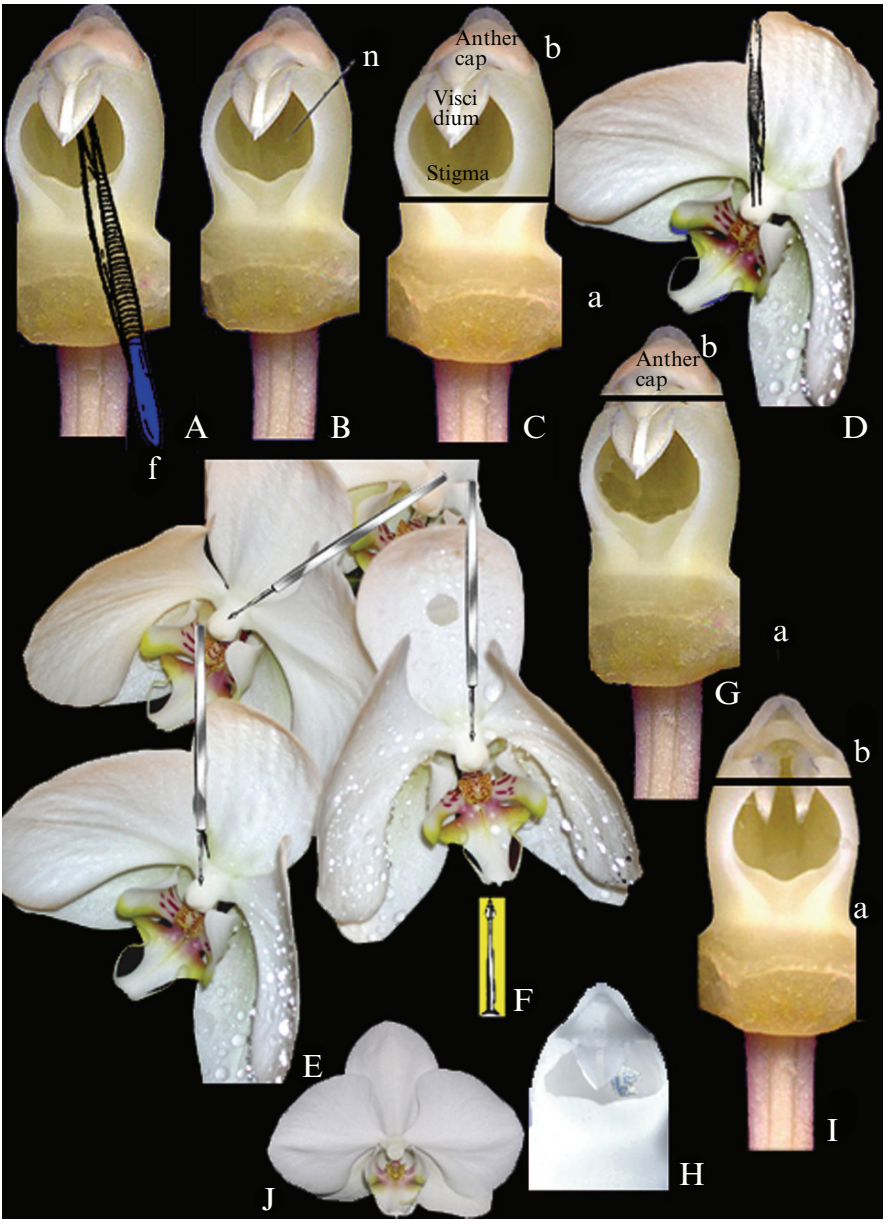

Fig. 2-10. Experimental treatments of *Phalaenopsis amabilis* gynostemia. **A.** Wounding or scratching stigma with forceps. **B.** Scratching or wounding stigma with needle. **C.** Removing all of gynostemium above the stigma (b) and leaving only the base (a) in place. **D.** Crushing gynostemium with forceps. **E.** Peeling epidermis from dorsal surface of gynostemium with "Starnadel." **F.** "Starnadel." **G.** Removing tip (b) from intact gynostemium above stigma leaving the rest (a) in place. **H.** Wad of paper or cotton in stigma. **I.** Removing tip (b) from gynostemium without anther cap and pollinia above stigma leaving the rest (a) in place. **J.** Gynostemium removed. Explanation of symbols: a, base or lower portion; b, top or tip; f, forceps; n, needle (J. Arditti and computer generated using a digital photograph).

Table 2-2. Hans Fitting's experiments involving the wounding of gynostemia and stigmas at the Bogor Botanical Gardens in 1908 (Fitting, 1909a)[a].

Experiment number	Orchid	Description	Results	Fitting's conclusions	Current explanation
17 (21 Jan–11 Feb 1908)	*Phalaenopsis amabilis* (Fig. 2-10A, 2-10B, 2-10; 2-13A)	Stigma of recently opened flower wounded with flamed forceps	Flower started to close after 24 hours, closed and started to wilt after 48 hours	Wounding of the stigma, not cutting or wounding of the gynostemium shortens the life span of flowers like pollination	Fitting's conclusion is consistent with current knowledge. Wounding of the stigma quickly induces copious ethylene evolution which brings about rapid senescence. Cutting or wounding the gynostemium induces much lower levels of ethylene evolution more slowly if at all
		Stigma of just opened flower wounded with flamed forceps	Flower started to close after 24 hours, closed and started to wilt after 48 hours		
		Stigma of newly opened flower wounded with needle	Flower closed after 24 hours		
		Flower pollinated	Flower closed after 24 hours		
		Top of gynostemium cut below stigma on 29 Jan	Flowers remained fresh until 1 March, then closed rapidly		
18A (dates not listed)	*Phalaenopsis amabilis* (Fig. 2-10A, 2-13A)	Stigmas of 3 flowers wounded by numerous scratches made with sterilized forceps	Flowers closed after 1-1½ days	Flowers close 1–1½ days after larger and 3 days after a smaller puncture wound with a needle	This is consistent with present day knowledge. Larger wounds induce more extensive ethylene evolution which bring about more rapid senescence and closing of flowers
18B (dates not listed)	*Phalaenopsis amabilis* (Fig. 2-10A, 2-13A)	Stigmas of 2 flowers wounded by 5 longitudinal scratches made with sterilized forceps	Flowers closed after 1-1½ days		
18C (dates not listed)	*Phalaenopsis amabilis* (Fig. 2-10A, 2-13A)	Stigma of 1 flower wounded by 4 longitudinal scratches made with sterilized forceps	Flowers closed after 1-1½ days		

(continued)

Table 2-2. (continued).

Experiment number	Orchid	Description	Results	Fitting's conclusions	Current explanation
18D (dates not listed)	*Phalaenopsis amabilis* (Fig. 2-10A, 2-13A	Stigmas of 2 flowers wounded by 3 longitudinal scratches made with sterilized forceps	1 flower closed after 1½ day, the other remains fresh		
18E (dates not listed)	*Phalaenopsis amabilis* (Fig. 2-10A, 2-13A)	Stigma of 1 flower wounded by 2 longitudinal scratches made with sterilized forceps	Flower closed after 1½ day		
18F (dates not listed)	*Phalaenopsis amabilis* (Fig. 2-10A, 2-13A)	Stigma of 1 flower wounded by longitudinal scratch made with sterilized forceps	Flower closed after 1 day		
18G (dates not listed)	*Phalaenopsis amabilis* (Fig. 2-10B, 2-13A)	Stigma of 1 flower punctured once with a needle	Flower remained fresh for 8 days		
		Multiple scratches made with a needle in stigma of 1 flower	Flower closed after 3 days		
19 (dates not listed)	*Phalaenopsis amabilis* Fig. 2-10C, 2-13A)	Gynostemia of 8 flowers cut just below the stigma	3 flowers remained fresh for a month, 1 for 19 days, 3 for 9 days and 1 for 8 days		
20A (dates as listed in 3rd and 4th columns)	*Phalaenopsis amabilis* (Fig. 2-10E, 2-10F, 2-13A)	7 scratches, 2–3 mm long and not very deep made at stigma levels on dorsal and lateral sides of gynostemium of 1 flower on 1 Feb 1908. A "Starnadel" was used	Flower remained fresh until 5 Feb 1908 when stigma was wounded lightly with a needle. Wound had no effect and flower was still fresh on 8 Feb 1908 when it was wounded more severely Flower wilted on 9 Feb 1908	Flower remained fresh when wounds on the gynostemium were not deep, extensive or severe	An explanation based on current knowledge would be that these wounds did not induce ethylene production which was not sufficient to bring about floral senescence

(continued)

20B (dates as listed in 3rd and 4th columns)	*Phalaenopsis amabilis* (Fig. 2-10E, 2-10F, 2-13A)	4 scratches, 2–3 mm long and not very deep made at stigma levels on dorsal and lateral sides of gynostemium of 1 flower on 31 Jan 1908. Starnadel used	Flower remained fresh until 7 Feb 1908 when stigma was wounded severely with a needle. The flower closed after 2 days
20C (dates as listed in 3rd and 4th columns)	*Phalaenopsis amabilis* (Fig. 2-10E, 2-10F, 2-13A)	4 scratches, 2–3 mm long and not very deep made at stigma levels on dorsal and lateral sides of gynostemium of 1 flower on 31 Jan 1908. Forceps used	Flower remained fresh until 8 Feb 1908 when stigma was wounded severely with a forceps. The flower closed after 2 days
20D (dates as listed in 3rd and 4th columns)	*Phalaenopsis amabilis* (Fig. 2-10E, 2-10F, 2-13A)	1 scratch, 2–3 mm long and not very deep made at stigma levels on dorsal side of gynostemium and 2 on its side (1 flower) on 31 Jan 1908. Needle used	Flower remained fresh until 7 Feb 1908 when stigma was wounded severely with a needle. The flower closed after 3 days
20E (dates as listed in 3rd and 4th columns)	*Phalaenopsis amabilis* (Fig. 2-10D, 2-13A)	Dorsal side of gynostemium crushed with forceps behind the anther on 4 Feb. Forceps used	Flower still fresh on 8 Feb when the upper part of the stigma was wounded severily with a needle. The flower closed after 1 day. All flowers were still fresh on 19 Feb when the upper parts of the stigmas of 2 flowers were scratched. These flowers closed after 1½ days
20F (dates as listed in 3rd and 4th columns)	*Phalaenopsis amabilis* (Fig. 2-10E, 2-10F, 2-13A)	The epidermis on the dorsal and lateral sides of the gynostemium above the stigma was peeled in 3 flowers on 9 Feb. "Starnadel" used	

(continued)

Table 2-2. (continued).

Experiment number	Orchid	Description	Results	Fitting's conclusions	Current explanation
21A (dates not listed)	*Phalaenopsis amabilis* (Fig. 2-10E, 2-10F, 2-13A)	Deep wounds were made on the dorsal surface and sides of the gynostemium of 1 flower with a "Starnadel"	Flower closed after 1½ days. Wound reached, but did not damage a vascular bundle	Deep wounds in the gynostemium have the same effects on flower longevity as wounding the stigma. Hence it seems that mechanical effects of wounding of the gynostemium are the same as sea sand in the stigma. The sand probably damages specific cells in the stigma	An explanation based on current knowledge is that the wounding and the sand damage to the stigma induce ethylene production levels which are sufficient to bring about closing of the flower
21B (dates not listed)		One deep wound was made near the stigma and two were deep enough to almost reach vascular bundles. Cuts were made with a "Starnadel" in 1 flower	Flower closed after 1–1½ days		
21C (dates not listed)	(Fig. 2-10G, 2-10I, 2-13A)	The tip of the of the gynostemium above the stigma was excised with a transverse cut which did not damage the stigma	Flower closed after 1½ days		
22A (dates not listed)	*Phalaenopsis amabilis* (Fig. 2-10H, 2-13A)	A cotton wad was inserted gently and carefully into the stigma of one flower The stigma was rubbed with the cotton wad 7 days after the initial insertion	Flower was still fresh 1½ days after the insertion The flower closed 1½ days after the rubbing	Superficial wounding of the dorsal surface and sides of the gynostemium did not shorten the life span of flowers. The same is true	An explanation based on current knowledge is that wounding and/or damage to parts of the gynostemium other than to the stigmatic surface do not

(continued)

22B (dates not listed)	Stigma of 1 flower was rubbed with a cotton wad	The flower closed 1½ days after the rubbing	for cuts at the base of the stigma. Only damage to	induce ethylene production which was high enough to bring about closing of
22C (dates not listed)	Stigma of 1 flower was rubbed with a cotton wad	The flower closed 2 days after the rubbing	the stigma (even if minor) and	flowers. Deep or severe wounds do induce high enough levels of ethylene
	A cotton wad was inserted gently and carefully into the stigma of one flower	Flower remained fresh	the wiping of stigmatic papillae and secretions	production to shorten the life
	Uppermost part of stigma was wounded 7 days after insertion of the cotton	Flower closed 1½ days after the wounding	reduce the life span flowers. However deep or sever wounds on the dorsal side of the	
22D (dates not listed)	Stigmas of 2 flowers were rubbed with cotton wads	1 flower closed 1½ days after the rubbing; the other remained fresh, but closed 1½ days after uppermost part of stigma was wounded	gynostemium which come close to the stigmatic surface of vascular bundles do shorten the life span of flowers.	
22E (dates not listed)	Upper part of stigma was wiped with cotton wad (1 flower)	Flower closed after 1½ days	span of flowers and bring about floral closure	
	Lower part of stigma was wiped with a cotton wad (1 flower)	Flower closed after 1½ days		
	Fitting examined the closed flowers from this series of experiments and found that rubbing and wiping of stigmas removed stigmatic papillae and secretions but did not cause wounding other than at most damaging a single cell layer			

(continued)

Table 2-2. (continued).

Experiment number	Orchid	Description	Results	Fitting's conclusions	Current explanation
23 (dates not listed)	*Phalaenopsis amabilis* (Fig. 2-10E, 2-10F, 2-13A)	Uppermost parts of stigmas, below rostella were wounded in 15 flowers	12 flowers closed after 1½ days. Stigmas of the 3 flowers which remained open were wounded in the same spots. These flowers closed after 1½ days	Wounding of the upper part of the stigmatic surface brings about closing of the flowers. When only other parts of the stigma are wounded flowers do not close	This observation suggests that the site of ethylene production is in the upper part of the stigma near the rostellum. This seems logical since ethylene production requires energy and the rostellum contains numerous mitochondria
24 (dates not listed)	*Phalaenopsis amabilis* (Fig. 2-10E, 2-10F, 2-13A)	The lowermost part of the stigma just above the stylar canal and the cells of the stylar canal were wounded with a needle (9 flowers)	1 flower closed after 1½ days, 8 remained fresh after 5 days when the upper part of the stigma was wounded. Of these flowers 4 closed after 1½ days and 2 after 3 days, but 2 remained fresh after 4 days when they were wounded again. They closed after 3 additional days	Flowers also close if both the upper and another part are wounded	
		The middle part of the stigmatic surface was wounded in 2 flowers	Both were open after 4 days, but closed 1½ days after the upper parts of their stigmas were wounded		
25A (dates not listed)	*Phalaenopsis violacea* (Fig. 2-6F)	The stigmatic surfaces of 6 flowers were wounded	The flowers closed after 1–2 days	There are 6 conclusions:	These observations and conclusions can be explained in terms of ethylene evolution. If the wounding was severe enough to induce
25B (dates not listed)		Stigma of 1 flower was wounded minimally with a needle	The flower closed after 1½ days	1. With the possible exception of *Aerides odorata* wounding of the stigma	

(continued)

25C (dates not listed)		Stigma of 1 flower was wounded at insertion point of stylar canal	Flower is still fresh after 5 days, but close 2½ days after upper part of stigma is wounded	shortens the life span of flowers in all species in which river sand has the same effects	ethylene evolution and if the affected area was capable of producing this gaseous hormone shortening of the life span of flowers was to be expected
25D (dates not listed)	(Fig. 2-10C is representative)	Gynostemia of 3 flowers cut below stigma	Flowers remained fresh for 6 Days, then closed	2. If pollination did not bring about changes in the perianth, river sand and and wounding of the stigma had no effects either	
25E (dates not listed)	(Fig. 2-10D is representative)	Dorsal surface and sides of the gynostemia of 2 flowers were crushed severely with forceps	Flowers closed after 2 days		
25F (dates not listed)		Several shallow scratches made with needle on dorsal surface and sides of gynostemium (1 flower)	Flowers remained fresh for an extended period	3. In two species (*Vanda tricolor* and *Calanthe veratrifolia*) pollination brings about changes in the perianth, but wounding of the stigma does not (experiments 33 and 35)	
25G (dates not listed)		Epidermis peeled from dorsal surface and sides of gynostemium (1 flower)	Flower closed after 1½ days		
25H (dates not listed)		Epidermis peeled from dorsal surface and sides of gynostemium (1 flower)	Flower remained fresh for an extended period		
26 (dates not listed)	*Phalaenopsis esmeralda* Rch. *f.* (Fig. 2-8J)	Stigmatic surface wounded (2 flowers) Pollinated (1 flower)	All 3 flowers wilted after 2–3 days	4. Wounding of the stigma had different effects on two *Vanda* species (experiments 32 and 33)	
27A (dates not listed)	*Phalaenopsis cornu-cervi* Bl. et Rchb. *f.*	Stigmatic surfaces of 9 flowers were wounded	All flowers wilted after 2–4 days	5. In all species in which wounding had any effects, wounding of the stigma was more effective than	

(continued)

Table 2-2. (continued).

27B (dates not listed)	(Fig. 2-12A, 2-12B)	Gynostemia of 3 flowers cut under the stigma	Flowers remained fresh for 6 days and wilted on the 7th day	wounding of other parts. In two experiments wounding the dorsal surface of the gynostemium at stigma height was also effective (experiments 25G and 29E)
		Pollinated (1 flower)	Flower started to wilt after 2–3 days	
28 (5–7 Feb 1908)	*Rhynchostylis retusa* (Fig. 2-10B is representative)	Stigmas of 12 flowers wounded with needle	7 Feb: 6 flowers wilted and 6 are starting to wilt	
28 (31 Jan–6 Feb 1908)	(paper lists 31 Feb as date)	Stigmas of 12 flowers wounded with needle	4 Feb: 8 flowers wilted 5 Feb:10 flowers wilted 6 Feb: all 12 flowers wilted	6. Both river sand and wounding the perianth, did not cause swelling of the ovary and/or gynostemium
28 (5–8 Feb 1908)		Stigmas of 9 flowers wounded with needle	8 Feb: all 9 flowers wilted	
28 (8–10 Feb 1908)	(Fig. 2-10B)	Upper parts of stigmas of 12 flowers wounded with needle	10 Feb: all 12 flowers wilted	
29A (dates not listed)	*Dendrobium superbum*	Stigmas of 7 flowers wounded with needle	All 7 flowers closed after 1–2 days	
29B (dates not listed)	(Fig. 2-12G)	Uppermost part of stigma of 1 flower wounded	Flower closed after 3 days	
29C (dates not listed)		Lowermost parts of stigmas of 2 flower wounded	Flowers remained fresh for 6 days	
29D (dates not listed)		Gynostemia of 4 flowers removed	Flower closed after 4 days	
29E (dates not listed)		Epidermis peeled from dorsal surfaces and sides of gynostemia of 5 flowers	1 flower closed after 1 day. The other 4 were still open after 6 days	
30 (start 6 Feb 1908)	*Oncidium flexuosum* (Fig. 2-12F)	2 flowers pollinated Stigmas of 5 flowers wounded Gynostemia of 5 flowers removed	Both wilted after 3 days All 5 flowers wilted after 3 days Flowers still fresh after 5 days	
31 (8–10 Feb 1908)	*Dendrobium wardianum* (Fig. 2-12D)	Stigma of 1 flower wounded on 8 Feb	10 Feb: Flower closed	

(continued)

32 (8–10 Feb 1908)	*Vanda insignis* (Fig. 2-12C)	1 flower pollinated. The stigma of 1 flower wounded with needle	10 Feb: Both flowers start to discolor and wilt
33 (start on 6 Feb 1908)	*Vanda tricolor*	Stigmas of 6 flowers wounded	Flowers were still fresh after 6 days
34 (4–10 Feb 1908)	*Aerides odorata* (Fig. 2-9)	4 Feb: 3 flowers pollinated 4 Feb: Stigmas of 3 flowers wounded 6 Feb: 2 flowers pollinated Stigmas of 2 flowers wounded	8 Feb: Slow wilting 8 Feb: Flowers unchanged 10 Feb: Flowers start to wilt 10 Feb: Flowers unchanged
35 (6–12 Feb 1908)	*Calanthe veratrifolia* (Fig. 2-12E)	3 flowers pollinated Stigmas of 4 flowers wounded	8 Feb: Flowers start to wilt 12 Feb: All flowers wilted
36 (4–12 Feb 1908)	*Dendrobium antennatum* (Fig. 2-8A)	2 flowers pollinated Stigmas of 2 flowers wounded	12 Feb: All 4 flowers still unchanged (i.e., still fresh)
37 (9–19 Feb 1908)	*Trichoglottis geminata* (Fig. 2-11E)	9 Feb: 2 flowers pollinated and stigmas of 2 flowers wounded 14 Feb: Stigmas of 2 flowers wounded	14 Feb: All 4 flowers did not change substantially (i. e., still fresh) 19 Feb: Flowers did not change (i.e., still fresh).
38 (27 Feb 3 Mar 1908)	*Dendrobium macrophyllum* (Fig. 2-11A, 2-11D)	3 flowers pollinated and stigmas of 2 flowers wounded	3 Mar: All flowers unchanged (i.e.,still fresh)
39 (26 Feb–2 Mar 1908)	*Arachnanthe sulingi* (Fig. 2-11B)	3 flowers pollinated and stigmas of 4 flowers wounded	2 Mar: All flowers unchanged (i.e., still fresh)
40 (16–27 Apr 1908)	*Renanthera maingayi* (Fig. 2-11C)	2 flowers pollinated and stigmas of 2 flowers wounded	27 Mar: All flowers unchanged (i.e., still fresh)

[a] The orchid names in this table are those used by Hans Fitting. Please see appendix 2 for updated nomenclature.

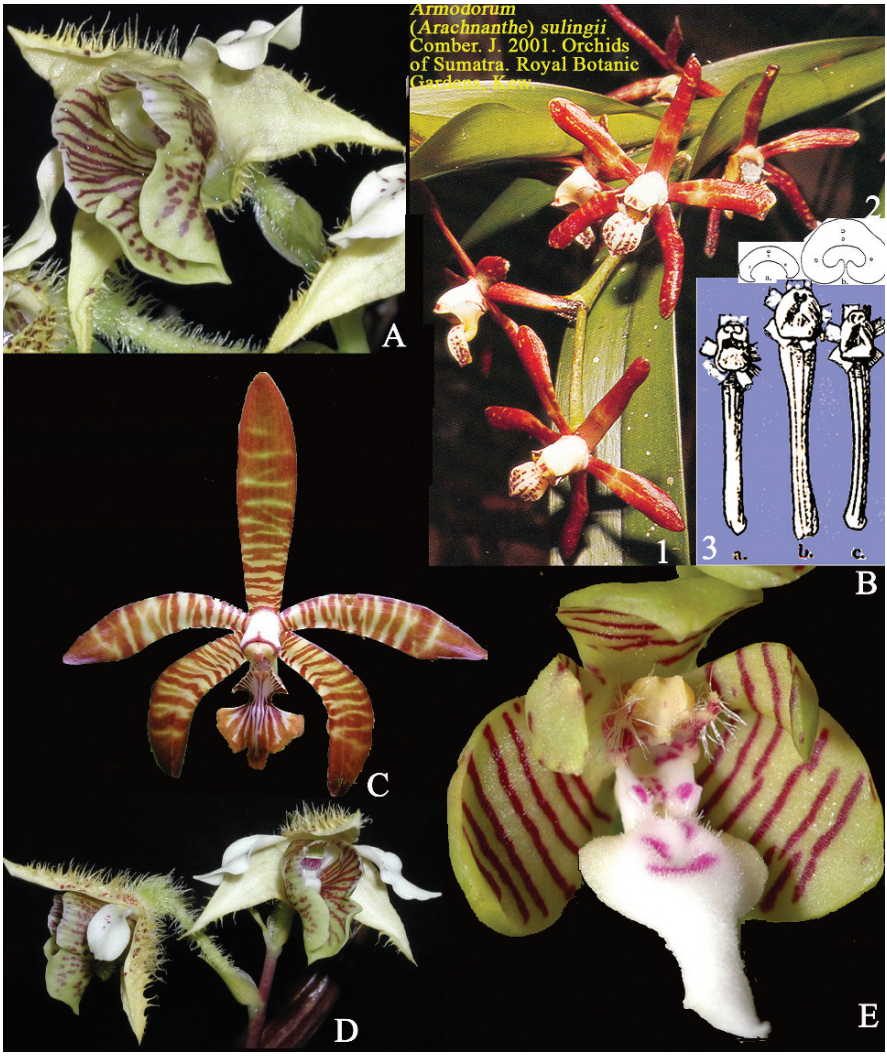

Fig. 2-11. Orchids used by Hans Fitting in wounding experiments. **A.** *Dendrobium macrophyllum*, **B.** *Armodorum* (*Arachnanthe*) *sulingii*. **1.** Plant in bloom. **2.** Cross-section through gynostemium and stigma: left, before pollination; right, a few days after pollination. **3.** Front view of gynostemium: a, before pollination; b, seven days after pollination with living pollen; c, seven days after pollination with steam-killed pollen. **C.** *Arachnanthe clarkei*. **D.** *Dendrobium macrophyllum*. **E.** *Trichoglottis geminata* (Fitting, 1909; C, T. W. Yam and J. Arditti; E, courtesy Eric Hunt).

Flowers pollinated with pollinia which were submerged in chloroform for 30 min exhibited phenomena which were the same as those which are brought about by live pollen. Onset of such phenomena was also equally rapid (Table 2-3). The phenomena were reduced in intensity following pollination with pollen which was soaked in chloroform for 1 h (Table 2-3).

Fig. 2-12. Species Hans Fitting used in wounding experiments. **A.** Intact flower of *Phalaenopsis cornu-cervi*. **B.** Flower of *Phalaenopsis cornu-cervi* without gynostemium. **C.** *Vanda insignis*. **D.** *Dendrobium wardianum*. **E.** *Calanthe veratrifolia*. **F.** *Oncidium flexuosum*. **G.** *Dendrobium superbum* inflorescence. **H.** Flower of *Dendrobium superbum* without gynostemium (A, J. Arditti and T. W. Yam; B, the flower in A altered with Photoshop; C, T. W. Yam; D, J. Arditti; G, H, Orchid Album published in 1882).

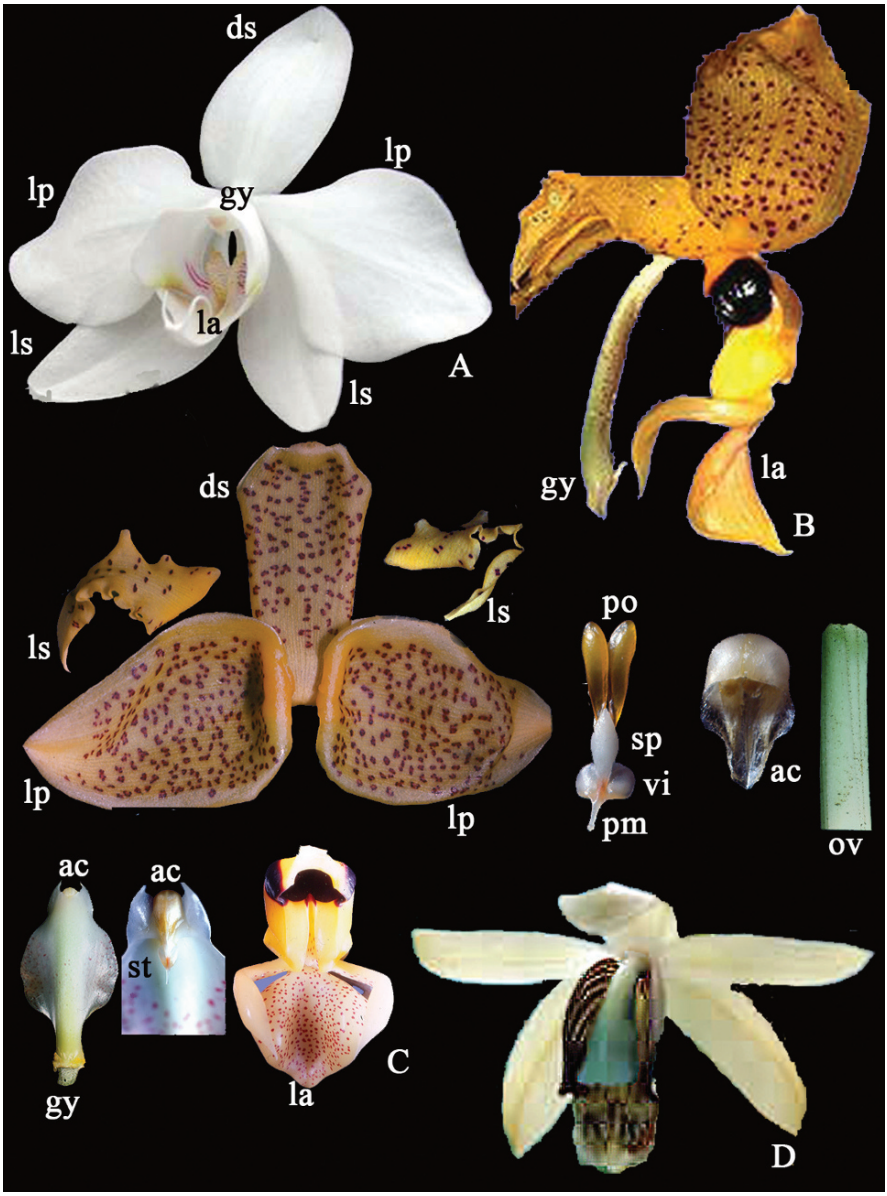

Fig. 2-13. Orchids used by Hans Fitting in experiments with live and dead pollinia and pollen extracts. **A.** *Phalaenpsis amabilis*. **B.** *Stanhopea*. **C.** Parts of *Stanhopea* flower. **D.** *Coelogyne swaniana*. Explanation of symbols: ac, anther cap; ds, dorsal sepal; gy, gynostemium; la, labellum; lp, lateral petal; ls, lateral sepal; ov, ovary; pm, pollinarium; po, pollinia; sp, stipe; st, stigma; vi, viscidium (A, the late Dr. Djunaidi Gandawijaja; B, C, D, J. Arditti and T. W. Yam).

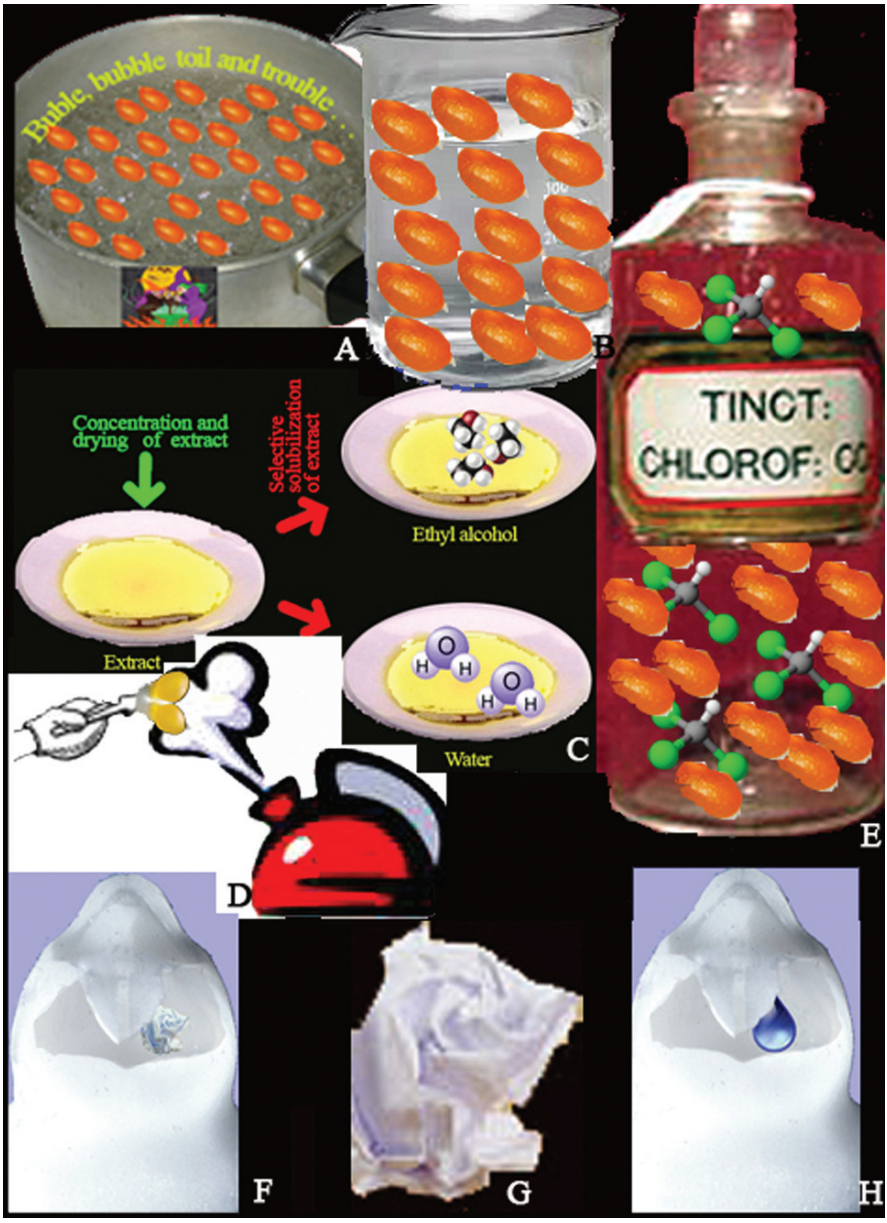

Fig. 2-14. Killing and extracting pollen. **A.** Pollen being killed and extracted with boiling water. **B.** Pollinia being extracted with cold water. **C.** Drying and extracting pollen extract. **D.** Steam-killing pollinia. **E.** Pollinia immersed in chloroform, **F.** Filter paper wad in stigma. **G.** Filter paper wad. **H.** Drop in stigma (A–H, prepared with a graphic program using separate images; C, The round plate-like objects are actually watch glasses which is what Fitting actually used; E, The chloroform bottle is old enough to be similar to the one Fitting may have had at his disposal; F, H, J. Arditti).

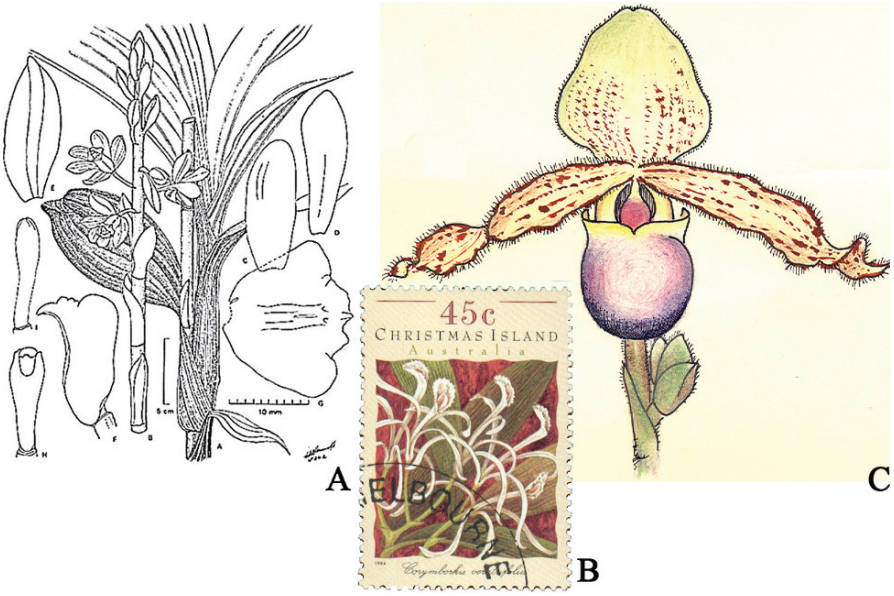

Fig. 2-15. Orchid used by Hans Fitting in experiments with inter- and intra specific pollination as well as with live and dead pollinia **A.** *Phaius amboinensis*. **B.** *Corymborkis veratrifolia*. **C.** *Paphiopedilum glaucophyllum* (compiled by J. Arditti).

Fitting's choice of killing agent was fortunate because IAA and the ethylene precursor, 1-aminocyclopropane-1-carboxylic acid (ACC) are not soluble or nearly insoluble in chloroform (Fig. 2-14E). This near insolubility may explain the different effects of pollinia which were soaked in chloroform for 30 or 60 min. Fitting gave no reasons for choosing chloroform, but since auxin was not known at the time it is clear that he did not make his choice on the basis of solvent/solubility characteristics. Had he chosen ethyl alcohol (which is usually more easily available and therefore would seem to be a more obvious choice) Fitting's result would have been different because auxin is ethanol soluble. Soaking the pollinia in ethanol would have extracted the auxin and ACC and rendered the pollen ineffective. This would have changed Fitting's findings and perhaps altered the course of his experiments.

Steam-killed pollinia (Fig. 2-14D) were as effective as live pollen (Table 2-3). However pollen killed by keeping it in boiling water (Fig. 2-14A; Table 2-3) did not bring about post-pollination phenomena. The reason for this is the solubility of auxin in hot water. This solubility is limited, but the exposure time was probably long enough to dissolve sufficient auxin from the pollen to render it ineffective. After these experiments Fitting concentrated and dried the extracts in watch glasses (Fig. 2-14C), extracted and/or redissolved them in several solvents and applied the resulting solutions to stigmas as drops (Fig. 2-14H) or in wads of filter paper (Fig. 2-14F, G; Table 2-3). A number of the extracts induced post pollination phenomena (Table 2-3). Cold water extracts (Fig. 2-14B) had a similar effect (Table 2-4).

Table 2-3. Hans Fitting's experiments with live and dead pollinia and pollen extracts at the Bogor Botanical Gardens in 1908 (Fitting, 1909a)[a].

Experiment number	Orchid	Description	Results	Fitting's conclusions	Current explanation
42A (13 Feb, 11:00 14 Feb, 11:00 1908)	*Phalaenopsis amabilis* (Fig. 2-13A)	2 pollinia submerged in chloroform for ½ h, air dried ¼ h and placed in stigma on 13 Feb 11:00	14 Feb, 06:00: Stigma closed, flower open; 11:00 flower closed. 18 Feb: Gynostemium strongly swollen down to its base, ovary starts to wilt without swelling. 19 Feb: Ovary wilted further, pollen grains collapsed, not germinated	1. The pollen does not have to germinate on the stigma to cause swelling of the gynostemium and wilting of the flower 2. Dead pollen does not function like live one 3. Dead pollen can cause the gynostemium to swell and the flower wilt, but it does not bring about swelling of the ovary 4. Swelling of the gynostemium and swelling of the ovary are not linked	Current knowledge is: (1) swelling of the gynostemium and the ovary are auxin effects, (2) wilting of the flower is caused by ethylene, (3) orchid pollinia contain IAA, and (4) there are good reasons to believe that orchid pollen contains ACC. IAA and ACC are insoluble in chloroform. Hence, it is not surprising that pollinia which were soaked in chloroform can bring about phenomena which are caused by auxin and ethylene. Swelling of the overy requires continuous supply of auxin which cannot be provided by dead pollinia
42B (13 Feb Feb, 12:00–14 Feb, 10:00 1908)		2 pollinia submerged in chloroform for ½ h, air dried ¼ h and placed in stigma of flower (cut and placed in water in a laboratory) at 12:00 on 13 Feb	13 Feb, 18:00: Start of inward movement of stigma edges. 14 Feb 06:00: Stigma completely swollen (i.e., closed; 08:00: Flower half closed; 10:00: Pollen grains collapsed, not germinated. Pollen grains collapsed and contents rough. Untreated pollen is well rounded and transparent		
42C (13 Feb 11:00)		1 pollinium placed in chloroform for ½ h, air dried for ¼ h and suspended in water			
43A (14 Feb 11:00–19 Feb 1908)	*Phalaenopsis amabilis* (Fig. 2-13A)	Flower pollinated with pollen subjected to 3 min of 98–99°C steam	15 Feb 06:00: Flower starts to close, stigma not closed; 11:00: Flower and stigma closed. 19 Feb: Ovary not swollen, but wilted. Flower abscised after a few days	1. Steam-killed pollen could cause wilting and stigmatic closure 2. The active principle in the pollen is heat stable	Fitting's conclusions are consistent with what is known about IAA and ACC at present

(continued)

Table 2-3. (continued).

Experiment number	Orchid	Description	Results	Fitting's conclusions	Current explanation
43B (14 Feb 11:00–19 Feb 1908)		Flower pollinated with pollen subjected to 3 min of 98–99°C steam	15 Feb 06:00: Flower half closed, stigma closed 19 Feb: Ovary not swollen, but wilted. Flower abscised after a few days		
43B (16 Feb 17:00–23 Feb 1908)		Flower pollinated with pollen subjected to 25 min of 98–99°C steam, allowed to stand for 3 h and subjected to an additional 3 min of steam	17 Feb 06:00: Flower open stigma half closed; 12:00: 12:00: Ovary swollen (i.e., closed), flower starts to close. 18 Feb 06:00: Flower wilted. 23 Feb: Ovary not swollen, but wilted Examination of the pollen in experiments showed that the pollen grains were collapsed and that pollen tubes did not develop		
44 (start on 17 Feb at 12:00)	*Phalaenopsis amabilis* (Fig. 2-13A)	2 flowers that were open for 2 days were pollinated with pollen subjected to 98-99° steam, 4 h to a moist environment and placed for 3 min in boiling water. This experiment was repeated twice	Flowers remained fresh	Steam does not kill the pollen which is unlikely, or the boiling water either extracts or destroys the active principle	ACC is water soluble. IAA is very sparingly soluble in water it at all, but both must have come out of the steam-killed pollen into the boiling water
45 (18 Feb 08:00–19 Feb 12:00 1908	*Phalaenopsis amabilis* (Fig. 2-13A)	Five pairs of pollinia were extracted by placing them in 2 ml of boiling distilled water for 3 min. After that the pollinia were removed from the water which was reduced in volume through evaporation to 2–3 drops. The experiments were carried out with 3 flowers who were open for several days			

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45A Start18 Feb 08:00 1908		Wad of filter paper wetted with distilled water was placed in stigma	19 Feb 12:00: Flower still open	1. The active principle can be extracted from pollen with hot water	ACC is water soluble. IAA is sparingly soluble or insoluble in water
45B Start 18 Feb 08:00 1908		Wad of filter paper wetted with pollen extract was placed in stigma	19 Feb 06:00: Stigma swollen (i.e. closed). Flower starts to close; 12:00: Flower closed	2. The extracted pollen lost its ability to affect the gynostemium and perianth	Fitting probably extracted both with boiling water and did not have a single compound in his extract
45C Start 18 Feb 08:00 1908		Drop of pollen extract was placed on stigma with "Starnadel"	19 Feb 06:00: Stigma swollen (i.e., closed). Flower starts to close; 12:00: Flower closed	3. Since it is water soluble the active principle is chemical in nature	
46A1 (18 Feb 10:00 1908)	*Cymbidium finlaysonianum* (Fig. 2-8D)	2 flowers pollinated xenogamously with living pollen	19 Feb 07:00: Gynostemium very swollen near stigma. 20 Feb 07:00: More swollen; 21 Feb 07:00: The same. 23 Feb morning: Flowers abscised	Fitting concluded that killed and living pollen had the same effect on swelling of the gynostemium and wilting of the flower. This is not the case. Boiled pollen is dead, but it did not induce swelling	IAA is not soluble in chloroform. This means that pollen soaked in chloroform still contained auxin which caused swelling and should have initiated ethylene evolution and senescence of the perianth. It is hard to explain why it did not do that
46A2 (start 18 Feb 10:00 1908)	*Cymbidium finlaysonianum* (Fig. 2-8D)	2 flowers pollinated with pollen which was submerged in chloroform for 1 hour	19 Feb 07:00: Gynostemium swollen near stigma, but less than the one pollinated with live pollen. 20 Feb 07:00: more swollen; 11:00: 5 fresh looking flowers abscised. 21 Feb 06:00: Last flower abscised		

(continued)

Table 2-3. (continued).

Experiment number	Orchid	Description	Results	Fitting's conclusions	Current explanation
46B (start 20 Feb 11:00 1908)		2 flowers pollinated xenogamously with living pollen	21 Feb 08:00: Gynostemium very swollen near stigma. 21 and 22 Feb: Swelling intensified. 24 Feb: Both flowers abscised		
47A (Start 20 Feb 11:00–end 24 Feb 1908)	*Stanhopea* sp. (Fig. 2-13B)	1 flower open for 2 days pollinated with pollen which was kept in chloroform for 1 h	21 Feb 06:00: Gynostemium somewhat swollen near stigma. 22 Feb: The same. 23 Feb 07:00: Flower started to wilt		IAA was not extracted with chloroform. It was extracted by boiling water, ACC was not extracted with chloroform
47B (Start 20 Feb 11:00–end 24 Feb 1908)		1 flower open for 2 days pollinated with pollen extracted for ½ h with boiling water	21 Feb 06:00, 22 Feb 06:00: No change in the gynostemium. 23 Feb 07:00: Flower started to wilt 24 Feb: Stigma closed and gynostemium swollen in A; Stigma open, gynostemium not swollen in B		
48A (Start 30 Jun 19:00 1908)	*Stanhopea insignis*	1 flower pollinated geitonogamously	2 Jul: Stigma swollen (i.e., closed), flower closed. 4 Jul: Gynostemium closed		IAA was not extracted from pollinia with chloroform
48B (Start 30 Jun 19:00 1908)		1 flower pollinated with pollen which was submerged in chloroform for 1 h	2 Jul: Stigma swollen (i.e., closed), flower closed. 4 Jul: Gynostemium swollen		
48C (Start 30 Jun 1908)		1 flower unpollinated	2 Jul: Gynostemium not swollen, flower closed		

(continued)

49A (21 Feb–23 Feb 1908)	*Coelogyne swaniana* Rolfe (Fig. 2-13D)	21 Feb 11:00: 3 flowers pollinated with normal pollinia	23, 24 Feb 07:00: All 3 flowers unchanged gynostemium tips widened	IAA was not extracted from pollinia with chloroform
49B		21 Feb: 3 flowers pollinated with pollen which was soaked in chloroform for 1 h	23, 24 Feb 07:00: All 3 flow- unchanged, gynostemium tips widened	
50A (25 Feb–13:00–27 Feb 07:00 1908)	*Dendrobium superbum* (Fig. 2-12G)	25 Feb 13:00: 2 flowers which were open for a few days were pollinated with pollen that was killed by subjecting it to steam for ¼ h	26 Feb 07:00: Gynostemium swollen, both flowers closed 29 Feb 07:00: Gynostemium swollen even more, flowers wilted	Nothing was extracted from steam-killed pollen
50B		25 Feb 13:00: 1 flower pollinated normally	27 Feb 07:00: Gynostemium swollen, flowers closed and wilted	
51A (21 Feb 10:00–29 Feb 1908)	*Arachnanthe sulingi* Benth. (Fig. 2-11B)	A. 1 flower pollinated with living pollen B. 4 flowers pollinated with pollen soaked in chloroform for 1 h C. 3 flowers pollinated with pollen subjected to steam for ¼ h	22 Feb 07:00: Gynostemia of all three flowers strongly swollen 25 Feb 07:00: Swelling of gynostemia intensified 27 Feb 07:00: No change 28 Feb 07:00: All C flowers and 2 B flowers abscised 29 Feb: 2 B flowers abscised All A flowers remained on the plant with swollen ovaries and wilted perianth	

(continued)

Table 2-3. (continued).

Experiment number	Orchid	Description	Results	Fitting's conclusions	Current explanation
52A (experiments started on 18 Feb 12:15	*Rhynchostylis retusa* (Fig. 2-7A)	4 flowers pollinated with pollen which was soaked in chloroform for ½ h	19 Feb 07:00: Gynostemium swollen. 20 Feb 06:00: swelling intensified, flowers start to wilt		Chloroform and steam did not extract IAA and/or ACC from the pollen, boiling water did
52B		4 flowers pollinated with pollen subjected to steam from 09:00 to 09:15 and 12:00 to 12:15	19 Feb 07:00: Gynostemium swollen. 20 Feb 06:00: flowers start to wilt		Since IAA is only sparingly soluble in water it is possible that Fitting did not extract or at least did not always extract all of it from the pollen
52C		2 flowers pollinated with pollen placed in boiling water for 3 min	20 Feb 07:00: Flower completely unchanged (i.e., fresh)		The IAA-like or ethylene-like effects he observed in some of his experiments could be due to residual IAA or other substances which remained in the pollen after it was killed and extracted with boiling or hot water
53A	*Aerides odorata* (Fig. 2-9A, 2-9D, 2-9E)	16 Feb 12:45: 5 flowers pollinated with pollen which was soaked in chloroform for ½ h	17 Feb 09:00: Gynostemium starting to swell. 18 Feb 11:00: Gynostemium very very swollen		
53B		17 Feb 12:45: 4 flowers pollinated with pollen subjected to steam from 09:00 to 09:15 and 12:00 to 12:03 (this is likely a typographical error, the time was probably 12:30)	18 Feb 09:00: Gynostemium swollen. 19 Feb: swelling even more pronounced		

(continued)

53C	21 Feb 11:00: 4 flowers pollinated with pollen soaked in chloroform for 1 h	22 Feb 07:00: All gynostemia swollen 23 Feb 07:00: Swelling of gynostemia more pronounced, flowers starting to wilt. 24 Feb: Same as on 23rd Feb. 25 Feb 07:00: Swelling of gynostemia of normally pollinated flowers is more pronounced than in the others
53D	21 Feb 11:00: 3 flowers pollinated with pollen subjected to steam for ¼ h	
53E	21 Feb 11:00: 1 flower pollinated normally	
53F	16 Feb 13:00: 4 flowers pollinated with pollen placed in boiling water	17 Feb 09:00: Gynostemia not swollen. 18 Feb 07:00: Same. 19 Feb for 3 min 07:00: Gynostemia swollen to a very limited extent. 20 Feb 07:00: Same
53G	7 pollinia were boiled in water (volume not given) for 3 min the extract (which was probably concentrated) was filtered and applied to stigmas of 4 flowers with the tip of a "Starnadel" at 09:30 on 18 Feb	18 Feb 18:00: Gynostemia start to swell 19 Feb 08:00: Swelling is intensified 20 Feb 08:00: Swelling is intensified further
53H1	18 Feb 11:00: dry filter wads placed in stigmas of 3 flowers	
53H2	18 Feb 11:00: filter paper wads wetted with distilled water placed in stigmas of 3 flowers	21 Feb: Flowers fresh

(continued)

Table 2-3. (continued).

Experiment number	Orchid	Description	Results	Fitting's conclusions	Current explanation
53H		18 Feb 11:00: filter paper wads wetted with pollen extract placed in stigmas of 3 flowers	19 Feb 08:00: Gynostemium swollen. 20 Feb: Gynostemium swelling intensified		
53I		18 Feb 11:00: 4 flowers pollinated with pollen extracted twice with boiling water	20 Feb 06:00: Flowers fresh 21 Feb 07:00: Gynostemium swollen slightly. 22 Feb: Same		
54	*Phalaenopsis cornu-cervi* (Fig. 2-12A)	24 Feb 16:30: 2 flowers open for a day pollinated with pollen subjected to steam for ¼ h	25 Feb 07:00: Stigmas swollen, flowers fresh. 29 Feb 07:00: Flowers half closed, wilting. 2 Mar 07:00: Flowers abscised, perianth not green		
55A	*Phalaenopsis violacea* (Fig. 2-6F1)	18 Feb 10:00: 3 flowers pollinated with pollen which was soaked in chloroform for 1 h	18 Feb 18:00: Stigmas closed, flowers open. 19 Feb 06:00: Gynostemium swollen, flower half closed, start of senescence. 20 Feb 06:00: Closing of flowers and yellowing progressing. 22 Feb 06:00: Same. 24 Feb 18:00: Flowers abscised, perianth not green		

(continued)

55B	19 Feb 11:00: flower which was open for a day pollinated with pollen which was subjected to steam for ¼ h	19 Feb 18:00: Stigma half closed, flower unchanged. 20 Feb 06:00: Gynostemium swollen, flower half closed, start of yellowing. 21 Feb 06:00: Flower completely closed. 24 Feb 18:00: Flower abscised, perianth not green
55C	20 Feb 11:00: Flower open for 1 day pollinated with pollen which was extracted twice with boiling water	21 Feb 06:00: Flower unchanged. 22 Feb 06:00: Stigma not closed, flower starts to close and turn yellow. 23 Feb 06:00: Flower wilted 24 Feb 16:00: Flower abscised
55D	25 Feb 13:00: Flower open for 1 day pollinated with pollen which was extracted twice with boiling water	26 Feb 06:00: Stigma open, flower starts to close. 27 Feb 06:00: Flower half closed, yellowing, stigma open. 28 Feb 06:00: Same. 1 Mar 06:00. Flower abscised
55E	27 Feb 11:00: Flower open pollen which was extracted first for 3 min with boiling water, then placed in new water and heated for 1 h in a water bath	28 Feb–29 Feb 06:00: Flower unchanged. 1 Mar 06:00: for 1 day pollinated with Start of floral closing and yellowing; 18:00: Flower closed, stigma open. The flower abscised after a few days without greening

[a] The orchid names in this table are those used by Hans Fitting. Please see Appendix 2 for updated nomenclature.

Table 2-4. Hans Fitting's experiments at the Bogor Botanical Gardens in 1908 on the extraction with cold water of an active principle from pollinia (Fitting, 1909a)[a].

Experiment number	Pollen source	Orchids pollinated and description of experiment	Results	Fitting's conclusions	Current explanation
60 (no dates listed)	*Aerides odorata* (Fig. 2-9A)	Pollinia, 20 pairs were extracted by soaking them in cold water for 2 h The extract was reduced to a small volume by placing it in a water bath for 5 min, Cotton wads saturated with the extract were placed in stigmas of *Aerides odorata, Cymbidium finlaysonianum,* and *Phalaenopsis amabilis*	Wads saturated with extract caused swelling of the gynostemia. Distilled water did not	The active principle can be extracted from pollinia by cold water in a relatively short time This active principle may be located not deep inside the pollen grains but at, near or on their surface or between them	Auxin is only sparingly soluble in cold water. Therefore these findings are puzzling. See text
61 (no dates listed)	*Phalaenopsis amabilis* (Fig. 2-13A)	Pollinia, 20 pairs were extracted by soaking them in 2 ml of cold water for 2 h. The extract was Reduced to a small volume By placing it in a water bath, Extract placed in stigmas of *Phalaenopsis violacea, Aerides odorata, Cymbidium finlaysonianum,* and *Phalaenopsis amabilis*	The extract caused swelling of the gynostemia		

[a] The orchid names in this table are those used by Hans Fitting. Please see Appendix 2 for updated nomenclature.

These extraction and redissolving experiments (Fitting, 1909a) showed (Table 2-5) that the active principle could be extracted by water and ethanol.

The extraction experiments suggested to Fitting that the effects of pollen are due to a chemical and this lead him to test a number of substances (Table 2-6; Fitting, 1909a). Fitting did not give any reasons for selecting the substances he tested. The selection of substances (Table 2-6) makes no sense at present and may not have been logical even in 1907. Therefore it is possible that he simply used whatever was easily available to him in Bogor at the time. Of the substances he used only 5% sucrose had an effect (Table 2-6) on a single flower of *Phalaenopsis amabilis*. This effect is hard to explain and one is tempted to invoke a dictum which may not have been unfamiliar to Fitting: *Ein Versuch, kein Versuch* (one experiment, no experiment). One possible explanation is that the sucrose acted as an osmoticum which caused an influx of water into the stigma and gynostemium.

Inter-Specific and Inter-Generic Pollination

Fitting's carried out all of his initial work by pollinating flowers with pollen of the same species. After that he studied the effects of pollinia of one orchid species on the stigmas of another and found that intra and inter taxon pollination had the same effects (Table 2-7). This is not surprising at present, but must have been a new and interesting finding at the time. Fitting's finding that some extracts of vegetative organs and a floral segment brought about post pollination phenomena (Table 2-8; Fitting, 1909a) must have been puzzling. At present these effects can be explained by the presence in the extracts of: (1) auxin and/or its precursors, and/or (2) ethylene precursors and/or substances which can induce its production.

Effects of Pollen of Non-Orchidaceous Plants

Having established that orchid pollinia have the same effects regardless of whether flowers are pollinated with: (1) their own pollen (i.e., self pollinated), (2) pollen from another flower of the same species, (3) pollen from flowers of other orchid species, (4) pollen from other orchid genera. Fitting took the next logical step. He determined whether pollen from several non-Orchidaceous plants (Fig. 2-16; Table 2-8) had the same effects as orchid pollinia. What he found was that the non-Orchidaceous pollen caused orchid flowers to wilt and senescence (all effects of ethylene), but did not bring about swelling of the gynostemium and stigmatic closure (both are auxin effects). What this means is that non-Orchidaceous pollen can induce ethylene evolution but does not contain any or enough IAA to bring about auxin effects. This is not surprising in view of the fact that orchid pollinia contain very high auxin levels (for a review see Avadhani et al., 1994), perhaps higher than in any other pollen.

Table 2-5. Hans Fitting's experiments at the Bogor Botanical Gardens in 1908 on the chemical nature of the active principle in pollinia (Fitting, 1909a)[a].

Experiment number	Description of experiment and its results	Fitting's conclusions	Current explanation
62 (no dates listed)	*Aerides odorata* pollinia, 20 pairs, mixed with acid-washed sea sand and glycerin were ground with a glass rod. More glycerin wad added, the solids were separated by filtration and suspended in 99.5% ethanol for 24 h. A flocculent gelatinous precipitate formed and was separated by filtration, washed with ethanol and air dried. Part of the precipitate was dissolved in water, absorbed into cotton wads and assayed. The rest was dissolved in water, filtered, precipitated with absolute ethanol and applied to flowers of *Phalaenopsis violacea, Aerides odorata* and *Cymbidium finlaysonianum*. The precipitate had no effect	The active principle is not an enzyme	Fitting discarded the glycerin used to grind the pollinia and the ethanol employed to produce and wash the precipitate. IAA is soluble in ethanol. Thus he probably dissolved IAA in the ethanol and discarded it along with other alcohol soluble substances. Glycerin soluble substances were also discarded. He probably also dicarded ACC
63 (no dates listed)	*Aerides odorata* pollinia, 22 pairs, were extracted by placing them in water for 2 h. The solution was filtered and reduced in volume on a water bath. The yellowish, glasslike, transparent precipitate which formed was active like pollen. A Lassaigne assay failed to detect the presence of nitrogen	The active principle is most probably "stickstoffrei" (i.e., nitrogen-free)	Both IAA and ACC contain nitrogen. Lassaigne's assay was probably not sensitive enough
64 (no dates listed)	*Aerides odorata* pollinia, 51 pairs, and 22 pairs of *Phalaenopsis amabilis* pollinia were extracted by placing them in cold water for 4 h. The solution was filtered and reduced in volume on a water bath. A Lassaigne assay showed that only traces of nitrogen were present	The active principle is most probably "stickstoffrei" (i.e., nitrogen-free)	Both IAA and ACC contain nitrogen Lassaigne's assay not sensitive enough That is why it failed to detect nitrogen when the sample consisted of 22 pairs of pollinia and detected only traces when 73 pairs were assayed

(continued)

65 (dates as listed in next column)	*Phalaenopsis amabilis* pollinia, 38 pairs were extracted by placing them in cold water for 5 h. The extract, filtered twice and reduced to a small volume on a water bath, was very active on *Aerides* flowers. Addition of absolute ethanol (AE) produced a flocculent white precipitate which was washed with AE. The filtrate was reduced to a small volume, AE was added again to form a precipitate. This was repeated until no additional precipitate was formed. The filtrate was dried in a watch glass and formed a glassy, transparent golden yellow precipitate. This was washed with AE, dissolved in water and dried to form a glassy, transparent, colorless precipitate. The extracts were assayed with *Aerides odorata* and *Phalaenopsis amabilis*. "The results were most interesting!" A. Assays with *Aerides odorata* 27 Feb 07:00: Cotton wads saturated with the fraction precipitated by AE placed in stigmas of 4 flowers 1 Mar: Flowers unchanged, still fresh. Gynostemium not swollen 27 Feb 07:00: Cotton wads saturated with the fraction not precipitated by AE placed in stigmas of 4 flowers 27 Feb 18:00: Gynostemium starts to swell 28 Feb 07:00: Gynostemium very swollen. 28 Feb: Same as 27th B. Assays with *Phalaenopsis amabilis* 26 Feb 06:00: Cotton wads saturated with the fraction precipitated by AE placed in stigmas of 2 flowers 27 Feb 06:00: Flowers unchanged 27 Feb 18:00: Gynostemium unchanged, flowers half closed 29 Feb 18:00: Flowers wilted, gynostemium not swollen 26 Feb 18:00: Cotton wad saturated with the fraction not precipitated by AE placed in stigma of one flower 27 Feb 11:00: Stigma half swollen 27 Feb 18:00: Stigma completely swollen 28 Feb: Flower completely closed, gynostemium swollen	1. The cold water extract contains two active principles 2. One of the active principles can be precipitated with AE, the other cannot 3. The principle which cannot be precipitated with AE is the one which causes swelling of the gynostemium and shortens the life span of flowers 4. The fraction which can be precipitated with AE does not cause swelling of the gynostemium, but it does shorten the life span of flowers	The cold water extract may have contained more than two principles IAA is soluble in ethanol. It causes swelling of the gynostemium and initiates ethylene evolution which shortens the life span of flowers The fraction which can be precipitated with AE probably brings about ethylene evolution Fitting was concerned with precipitates and some AE and water-soluble fractions, but he did not seem to consider the possibility that his precipitates and soluble fractions may have contained more than one substance He also discarded some fractions as for example the glycerin used to homogenize pollinia

(continued)

Table 2-5. (continued).

Experiment number	Description of experiment and its results		Fitting's conclusions	Current explanation
66 (dates as listed in next column)	*Phalaenopsis amabilis* pollinia, 27 pairs were extracted with cold water, the extract was fractionated as in experiment 65 and the dried concentrate was dissolved in two drops of water			
	A. 13 Apr 07:00: One flower treated with the fraction precipitated by AE	14 Apr 07:00: Flower half closed, gynostemium unchanged 15 Apr. 07:00: Flower completely closed, gynostemium unchanged		
	15 Apr 07:00: Two flowers treated with the fraction precipitated by AE	16 Apr 07:00: one flower closed and the other still open		
	B. 15 Apr 07:00: One flower was treated with the fraction not precipitated by AE	16 Apr 07:00: Gynostemium swollen, flower closed 16 Apr 18:00: Both flowers closed, gynostemium unchanged		
	14 Apr 07:00. Two flowers treated as above	15 Apr 07:00: Gynostemium swollen, flower half closed		
	(The experiments are listed here in the same order as in Fitting's paper.)			
67 (dates as listed in next column)	*Aerides odorata* pollinia, 18 pairs, were extracted with cold water for 4 h, the extract was dried over a water bath and the residue was extracted several times with AE. The alcohol solution was dried over a water bath and produced glassy transparent residue. The AE soluble and AE insolble fractions were assayed on *Aerides* flowers		The active principle is less soluble in AE than in water (but changed his mind later) The active principle is not an enzyme	IAA is very soluble in ethanol and sparingly soluble in water

(continued)

	28 Feb 13:00: Cotton wads saturated with the AE soluble fraction which was redissolved in water were placed in stigmas of 4 flowers	29 Feb 06:00: Gynostemium swollen 1 Mar 07:00: The same		
	28 Feb 13:00: Cotton wads saturated with the AE insoluble fraction which was redissolved in water were placed in stigmas of 4 flowers	29 Feb 06:00: Gynostemium swollen 1 Mar 07:00: The same		
Several unnumbered experiments and observations	• *Phalaenopsis amabilis* pollinia which were soaked in AE for 4 hours retained their activity (but see below)		The active principle is not very soluble in AE	IAA is very soluble in ethanol
	• Extracts obtained by extracting *Vanda tricolor* and *Zygopetalum makayi* with AE for 24 hours were active.		The active principle is soluble in ethanol	IAA is ethanol soluble
	• A 24 h chloroform:ethanol (99:1) extract had some activity			IAA is not chloroform soluble,
	• Cold water extracts of *Phalaenopsis* and *Aerides* pollinia are weakly acidic			As the name indole acetic acid indicates, IAA is an acid
	• When pollinia extract was heated in a crucible it turned brown-black and smelled like burned carbohydrates			Extract may have contained sugar(s)
	• After the extract was heated to glowing the remnant was a very small traces of white ash			Not surprising
	• The brown-black residue after heating and the white ash are inactive			IAA and ACC were destroyed by the heating
	• Fehling's solution was not reduced by the extract even after it was hydrolyzed for an extended period with 1% or stronger hydrochloric acid			The extract did not contain reducing sugars, or not enough to be detected with this test
	• Filtered extract is a clear solution			
	• The extract did not contain droplets and solid particles			An aqueous extract would not contain particles
	• The dried extract residue dissolves easily in water			Not surprising since the original extraction was with water
	• There are no lipid droplets in the extract			To be expected, the original extract was aqueous. Lipids are not water soluble.

(continued)

Table 2-5. (continued).

Experiment number	Description of experiment and its results	Fitting's conclusions	Current explanation
	• Both the AE soluble and insoluble fractions of the *Phalaenopsis* extract produced a copious flocculent precipitate when treated with lead acetate (PbAc). The AE soluble and very active fraction of dried extract of *Aerides* pollinia did not form such precipitate on treatment with PbAc. The AE insoluble and water soluble fraction of the extract did form a precipitate when PbAc was added. This precipitate became shiny and crystalline in areas where the watch-glass was rubbed with a glass rod. As a heavy metal lead probably precipitated proteins	The active principle cannot be precipitated with PbAc. Cold water extracts of pollinia contain more than one substance. Fitting gave no reasons for his PbAc assay	IAA and ACC cannot be precipitated with PbAc. Pollinia do contain more than one substance The active principle is not an (1) inorganic salt (2) organic compound, (3) a common hydrolysable carbohydrate, (4) a fat This conclusion excludes just about all compounds that could be extracted from pollinia

[a] The orchid names in this table are those used by Hans Fitting. Please see Appendix 2 for updated nomenclature.

Table 2-6. Hans Fitting's experiments at the Bogor Botanical Gardens in 1908 on the effects of various substances on orchid flowers (Fitting, 1909a)[a].

Substance applied to stigma	Orchid	Results
Citric acid, 0.5%	*Aerides odorata*, 2 flowers	No effects
Dextrin, 2%	*Aerides odorata*, 4 flowers	No effects
	Phalaenopsis amabilis, 2 flowers	No effects
Diastase (starch hydrolyzing enzyme)	*Cymbidium finlaysonianum*, 2 flowers	No effects
	Rhynchostylis retusa, 6 flowers	No effects
Ferric ($FeCl_3$, waters of hydration not indicated) or ferrous chloride ($FeCl_2$, waters of hydration not indicated), Fitting does not indicate which, 1%	*Rhynchostylis retusa*, 6 flowers	No effects
Malic acid, 0.5%	*Aerides odorata*, 2 flowers	No effects
Manitol, 5%	*Aerides odorata*, 4 flowers	No effects
	Cymbidium finlaysonianum, 2 flowers	No effects
Oxalic acid, 0.5%	*Aerides odorata*, 2 flowers	No effects
Potassium nitrate (KNO_3), 10%	*Rhynchostylis retusa*, 6 flowers	No effects
Sodium carbonate, 1%	*Aerides* (probably) *odorata*, 3 flowers	No effects
Succinic acid, 0.01%	*Aerides odorata*, 2 flowers	No effects
0.5%	*Aerides odorata*, 2 flowers	No effects
Sucrose, 0.1%	*Aerides* (probably) *odorata*, 3 flowers	No effects
	Cymbidium finlaysonianum, 3 flowers	No effects
0.5%	*Aerides* (probably) *odorata*, 3 flowers	No effects
	Cymbidium finlaysonianum, 3 flowers	No effects
5%	*Aerides odorata*, 3 flowers	No effects
	Arachnanthe sulingi, 4 flowers	No effects
	Phalaenopsis amabilis, 1 flower	Flower wilted after two days
	Rhynchostylis retusa, 4 flowers	No effects
Tartaric acid, 0.5%	*Aerides odorata*, 2 flowers	No effects

[a] The orchid names in this table are those used by Hans Fitting. Please see Appendix 2 for updated nomenclature.

Table 2-7. Hans Fitting's experiments on the effects of live and dead pollinia from one genus or species on other taxa at the Bogor Botanical Gardens in 1908 (Fitting, 1909a)[a].

Experiment number	Pollen source	Orchids pollinated and description of experiment	Results	Fitting's conclusions	Current explanation
56 (no dates listed)	*Phalaenopsis amabilis* (Fig. 2-13A)	Pollen soaked in chloroform or subjected to steam placed in stigmas of *Aerides odorata*, *Dendrobium superbum*, *Cymbidium finlaysonianum* Filter paper soaked in pollen extract placed in stigma of *Aerides odorata*	Pollen had same effects on the three species as on *Phalaenopsis amabilis* in previous experiments Extract had the same effects as dead pollen of *Phalaenopsis amabilis* or *Aerides odorata*	1. The effects of killed pollen are not species specific 2. Pollen which brings about swelling of its own gynostemium can have the same effect only on gynostemia whose own pollen can cause them to swell	Pollen brings about swelling of the gynostemium because it contains auxin and perhaps ethylene precursor(s) as well as possibly other hormones and/or induces production of ethylene and/or auxin and/or other substances by the stigma, rostellum and/or other parts of the column
57 (no dates listed)	*Aerides odorata* (Fig. 2-9)	Pollen soaked in chloroform or subjected to steam placed in stigmas of *Phalaenopsis amabilis, Cymbidium finlaysonianum, Dendrobium superbum, Rhynchostylis retusa, Phalaenopsis violacea* and *Arachnanthe sulingii*	Same as in experiment 56	3. Pollen which does not bring about the swelling of its own gynostemium can cause the gynostemia of other species to swell if their own pollinia can do so 4. The active principle in pollen is widespread	
		Filter paper soaked in pollen extract placed in stigma of *Phalaenopsis amabilis* and *Cymbidium finlaysonianum*	Same as in experiment 56		
		Dead *Aerides* pollen placed in stigmas of *Spathoglottis filuata*, *Corymbis disticha* and *Eulophia macrostachya*	Same effect as live pollen of treated species, but no notable swelling of gynostemia		

(continued)

58 (no dates listed)	*Calanthe veratrifolia* (Fig. 2-12E) *Spathoglottis filuata*, *Phajus amboinensis* (Fig. 2-15A) and *Corymbis disticha* (Fig. 2-15B)	Live and steam-killed pollen placed in the stigma of *Aerides odorata*	Same effect as live pollen of treated species
59 (no date listed)	*Paphiopedilum glaucophyllum* (Fig. 2-15C)	Steam-killed pollen placed in stigma of *Phalaenopsis amabilis*	Same effect as live pollen of treated species

[a] The orchid names in this table are those used by Hans Fitting. Please see Appendix 2 for updated nomenclature.

Table 2-8. Hans Fitting's experiments at the Bogor Botanical Gardens in 1908 on the effects on orchid flowers of pollen from plants other than orchids (Fitting, 1909a)[a].

Experiment number	Description of experiment and its results	Fitting's conclusions	Current explanation
68	Cotton wads containing extracts of: (a) leaves, (b) perianth segments, (c) fruits and (d) pollinia were applied to stigmas of two flowers of *Aerides odorata*. This experiment was repeated twice.	Only extract d caused swelling of the gynostemium	All parts of the plant contain IAA. Fitting's extracts a-c may not have contained enough auxin
69	Cotton wads containing an extract of gynostemia without pollinia were were placed in stigmas of *Phalaenopsis amabilis*. Two flowers were treated at 08:00 on 8 Apr: 10 Apr 07:00: Flowers closed; 11 Apr: Flowers wilted, gynostemium not swollen One flower was treated at 07:00 on 9 Apr: 10 Apr 18:00: Flowers closed; 11 Apr 18:00: Flowers wilted, gynostemium not swollen		
70	Pollen of *Eucharis grandiflora* (Amaryllidaceae), *Alpinia hookeriana*, *Canna* sp. (Cannaceae), and *Hedychium* sp., (last two, (Zyngiberaceae) had no effects when applied to stigmas of *Aerides*		The pollen did not contain enough IAA and could not induce ethylene production
71	A. *Hedychium* sp. pollen was placed in stigmas of *Phalaenopsis amabilis* 1 Mar 07:00: One flower treated: 2 Mar 07:00: Flower closed, stigma open; 3 Mar 18:00 Flower wilted, stigma open 2 Mar 06:00: One flower treated: 3 Mar 06:00: Flower unchanged. 18:00: Flower closed, stigma open; 4 and 5 Mar: Same 7 Apr 07:00: One flower treated: 9 Apr 07:00: Flower unchanged; 10 Apr 06:00: Flower closed; 11 Apr: Flower closed, stigma open	Since the pollen acted without germinating it is possible to assume that dead pollen will also be active	The pollen did not contain enough IAA, but could induce ethylene production

(continued)

	8 Apr 07:00: One flower treated	10 Apr 06:00: Flower closed 11 Apr: Flower closed, stigma open	
	B. *Hedychium* sp. pollen was placed in stigmas of *Phalaenopsis violacea*.		
	29 Feb 07:00: One flower treated	1 Mar 06:00: Flower starts to close 3 Mar 06:00: Flower closed, stigma open	
	7 Apr 07:00: One flower treated	10 Apr 06:00: Flower half closed and turning yellow	
	Pollen failed to germinate in both (A and B) sets of experiments, but shortened the life span of flowers of both species		
72	A. *Hedychium* sp. pollen which was subjected to steam for 5 min was placed in stigma of newly opened *Phalaenopsis amabilis* flower		
	7 Apr 07:00: Pollen applied	9 Apr 07:00: Flower unchanged 10 Apr 07:00: Flower starts to close 11 Apr 18:00: Flower wilted, stigma open	Pollen did not contain any or enough IAA to induce closing of the stigma, but it did bring about ethylene evolution
	B. *Hedychium* sp. pollen which was subjected to steam for 5 min was placed in stigma of newly opened *Phalaenopsis violacea* flower		
	7 Apr 07:00: Pollen applied	8 Apr 18:00: Flower started to turn yellow 10 Apr 06:00: Flower half closed and turned yellow 11 Apr 07:00: Flower completely closed, stigma open	
	The pollen shortened the life span of flowers of both species. Both the application of the pollen and the pollen itself did not wound the stigma		

(continued)

Table 2-8. (continued).

Experiment number	Description of experiment and its results		Fitting's conclusions	Current explanation
No number	Pollen of *Begonia geogensis* did not cause wilting of flowers of *Phalaenopsis* species			Pollen did not contain any or enough IAA to have an effect and did not induce ethylene evolution
73	*Impatiens rodrigesi* pollen was applied to stigmas of *Phalaenopsis violacea* flowers			
	7 Apr 07:00: Pollen applied	8 Apr 06:00: Flower starts to turn yellow 9 Apr 07:00: Flower is yellow, starts to close 10 Apr 07:00: Flower half closed 11 Apr: Flower fully closed, stigma open		Pollen did not contain any or enough IAA to induce closing of the stigma, but it did bring about ethylene evolution
	Pollen germinated partially. Experiment could not be repeated due to lack of flowers			
74	*Hibiscus rosa-sinensis* var. *genuinus* Hochr. pollen was applied to stigmas of *Phalaenopsis* flowers			
	A. 7 Apr 08:00: Pollen applied to stigmas of three flowers of *Phalaenopsis amabilis*	8 Apr 07:00: Tip of gynostemium and stigma swollen in one flower, all 3 flowers open 8 Apr 18:00: All 3 flowers closed 9 Apr 06:00: All 3 flowers closed Stigmas of 2 flowers open Pollen did not germinate	1. The pollen of *Hibiscus rosa-sinensis* shortened life span of flowers and caused stigmatic closure 2. Swelling of the gynostemium is less pronounced than after pollination with orchid pollen 3. The pollen did not germinate	This pollen contains a limited concentration of IAA and seems to induce low levels of ethylene evolution

(continued)

9 Apr 07:00: Pollen applied to stigma of one flower of *Phalaenopsis amabilis*	10 Apr 07:00: Flower open, stigma half closed 11 Apr 07:00: Flower half closed 12 Apr 07:00: Flower completely closed, stigma half closed
B. 7 Apr 08:00: Pollen applied to stigma of one flower of *Phalaenopsis violacea*	8 Apr 18:00: Stigma half closed, flower starts to close 9 Apr: Flower completely close. Pollen did not germinate
8 Apr 07:00: Pollen applied to stigma of one flower of *Phalaenopsis violacea*	8 Apr 18:00: Stigma almost completely closed 9 Apr 06:00: Stigma completely closed. Flower starting to turn yellow 10 Apr 07:00: Flower half closed 11 Apr 07:00: Flower fully closed
9 Apr 07:00: Pollen applied to stigmas of two flowers of *Phalaenopsis violacea*	10 Apr 07:00: One stigma half closed, the other slightly closed 11 Apr 07:00: Flowers yellowing, half closed. One stigma three quarter closed, the other half closed
9 Apr 07:00: Pollen applied to stigma of one flower of *Phalaenopsis violacea*	10 Apr 07:00: Flower unchanged 11 Apr 07:00: Flower yellowing half closed 12 Apr 07:00: Flower fully closed stigma open 13 Apr Same as above
15 Apr 07:00: Pollen applied to stigma of one flower of *Phalaenopsis violacea*	16 Apr 07:00: Flower unchanged 17 and 18 Apr 07:00: Stigma somewhat swollen. Stigma closed

(continued)

Table 2-8. (continued).

Experiment number	Description of experiment and its results		Fitting's conclusions	Current explanation
	C. 15 Apr 08:00: Pollen applied to stigma of one flower of *Phalaenopsis esmeralda*	16 and 17 Apr 07:00: Stigma half closed. Flower unchanged		
	13 Apr 08:00: Pollen applied to stigma of one flower of *Phalaenopsis esmeralda*	14 Apr 07:00: Stigma closed. Flower unchanged		
	The order in which these experiments are listed here is the same as in Fitting's original paper			
75	*Hibiscus rosa-sinensis* var. *genuinus* Hochr. pollen which was steamed for five minutes was applied to stigmas of *Phalaenopsis* flowers			
	A. 8 Apr 07:00: Pollen applied to stigmas of two flowers of *Phalaenopsis amabilis*	9 Apr 07:00: Flowers unchanged 10 and 11 Apr 07:00: Flowers closed. Stigmas closed 10 Apr 07:00: Flower open. Stigma half closed	Living and dead *Hibiscus* pollen have the same effect. *Hibiscus* pollen contains the same substance as orchid pollinia	
	B. 9 Apr 07:00: Pollen applied to stigmas of one flower of *Phalaenopsis violacea*	10 Apr 18:00: Flower yellowed. Stigma half closed 11 Apr 06:00: Both flower and stigma half closed		
No number	Sap of floral segments of *Hibiscus* applied to stigmas of flowers of *Phalaenopsis violacea* and *Phalaenopis esmeralda* had no effects			

[a] The orchid names in this table are those used by Hans Fitting. Please see Appendix 2 for updated nomenclature.

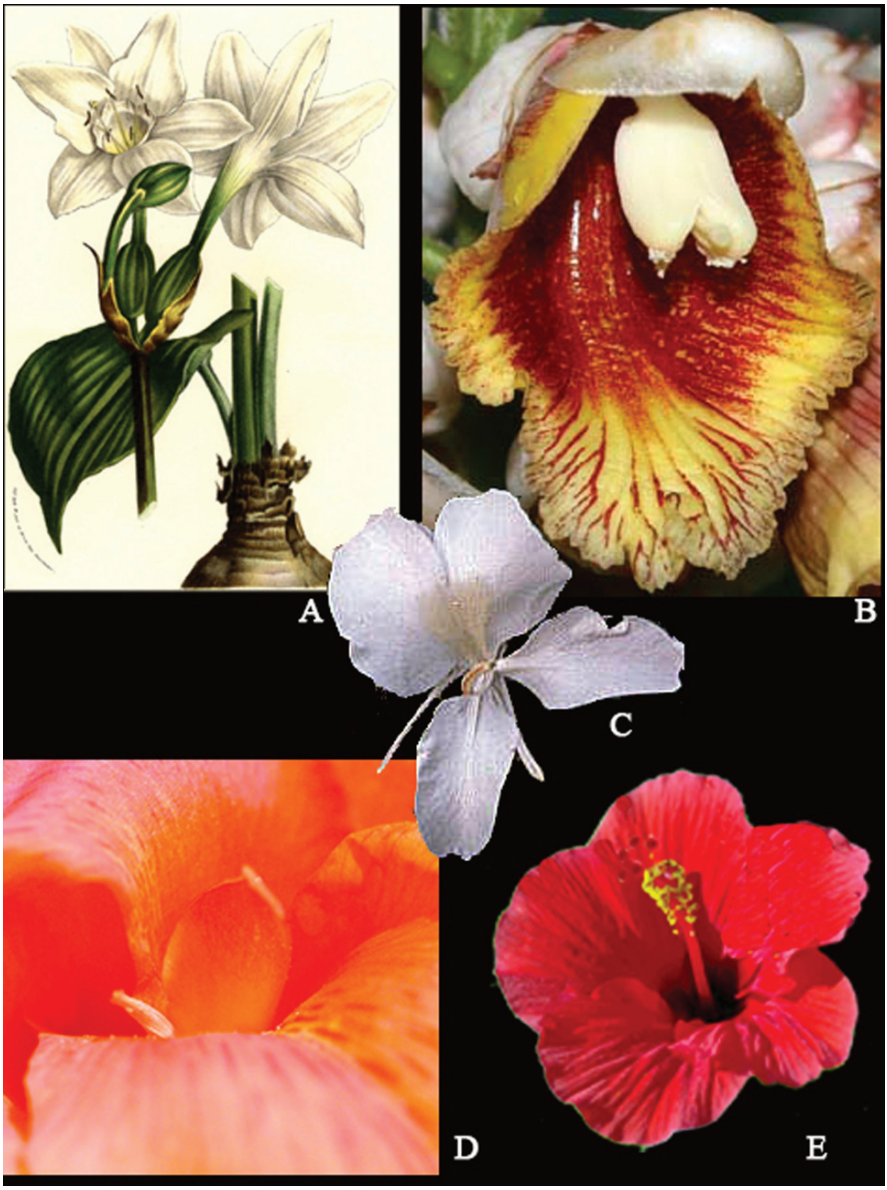

Fig. 2-16. Plants whose pollen was applied to orchids by Hans Fitting. **A.** *Eucharis grandiflora* Planch., Amarillidaceae. **B.** *Alpinia hookeriana*, Zingiberaceae. **C.** *Hedychium* sp., Zingiberaceae. **D.** *Canna* sp., Cannaceae showing anther. **E.** *Hibiscus rosa-sinensis*, Malvaceae (A, Lemaire, 1854; B, courtesy Aoki Shigenobu, Maebashi, Japan; C, E, J. Arditti; D, courtesy The Digital Flora of Texas).

Effects of the Location of Pollen Insertion

Fitting placed the pollen in stigmas in his initial experiments (Tables 2-1–2-8). In another series of experiments (Fig. 2-17; Table 2-9) he placed living and dead quarter pollinia sections inside gynostemia. Both the living and dead sections induced swelling of gynostemia and ovaries, stigmatic closure and wilting of the flowers regardless of where they were placed. Induction of these post-pollination phenomena is an indication that auxin and ACC diffused from the pollen section and that there was ethylene evolution. The latter could have been caused by auxin from the pollinia, the wounding of the gynostemium which must have been caused by the insertion of the sections, or ACC which diffused from the pollen.

The rostellum is a major site of ethylene evolution in pollinated orchid flowers (see Avadhani et al., 1994 for a review). Therefore it is not surprising that a pollinium section placed below it caused post-pollination phenomena.

A pollinium section placed in a stigma following removal of the stigmatic fluid also brought about post-pollination phenomena which are induced by auxin or ethylene. The latter is not surprising since removal of the fluid may have injured the stigma and caused ethylene evolution. Auxin-induced phenomena are more difficult to explain because movement of the hormone from the pollen section to the stigma requires a fluid. One possible explanation is that the stigma produced new fluid following the removal. Another possibility is that moisture from stigmatic cells facilitated diffusion of auxin from the pollen. It is also possible that Fitting did not remove all the fluid from the stigma.

These experiments were followed by studies of the nature of the active principle and lead Fitting to suggest that the active substance in orchid pollinia was a hormone (Table 2-5) which came to be known as *Pollenhormon* (Fitting, 1909a, b, c, 1910, 1911, 1912, 1921, 1936).

Fitting's experiments required a very large number of flowers. Even in Bogor he could not find enough flowers of any one orchid and used many species (Tables 2-1–2-4). He liked to work with *Phalaenopsis* (Figs. 2-5, 2-6, 2-10) and *Cymbidium* (Fig. 2-8) because the flowers are large and the phenomena are easy to observe. On his return to Germany he repeated some of the experiments with another large-flowered orchid with easily observable post-pollination phenomena, *Cattleya* (Fitting, 1910). After his experiments with *Cattleya* (Figs. 2-15, 2-18, 2-19) Fitting seems to have lost interest in orchids and pursued other avenues of research. He never worked with orchids again although he did mention them in several papers (Fitting, 1911, 1912, 1921, 1936).

One reason why Fitting abandoned orchids suggested by Professor Frits Warmolt Went (1903–1990) is that "he was too much steeped in the 'stimulus' concept" (letter dated June 19, 1974 to J. A.). Because of that Went concluded that Fitting's "work on orchid pollination, which could easily have led to an explosion on plant hormone work, did not have any lasting effect." In a way Went

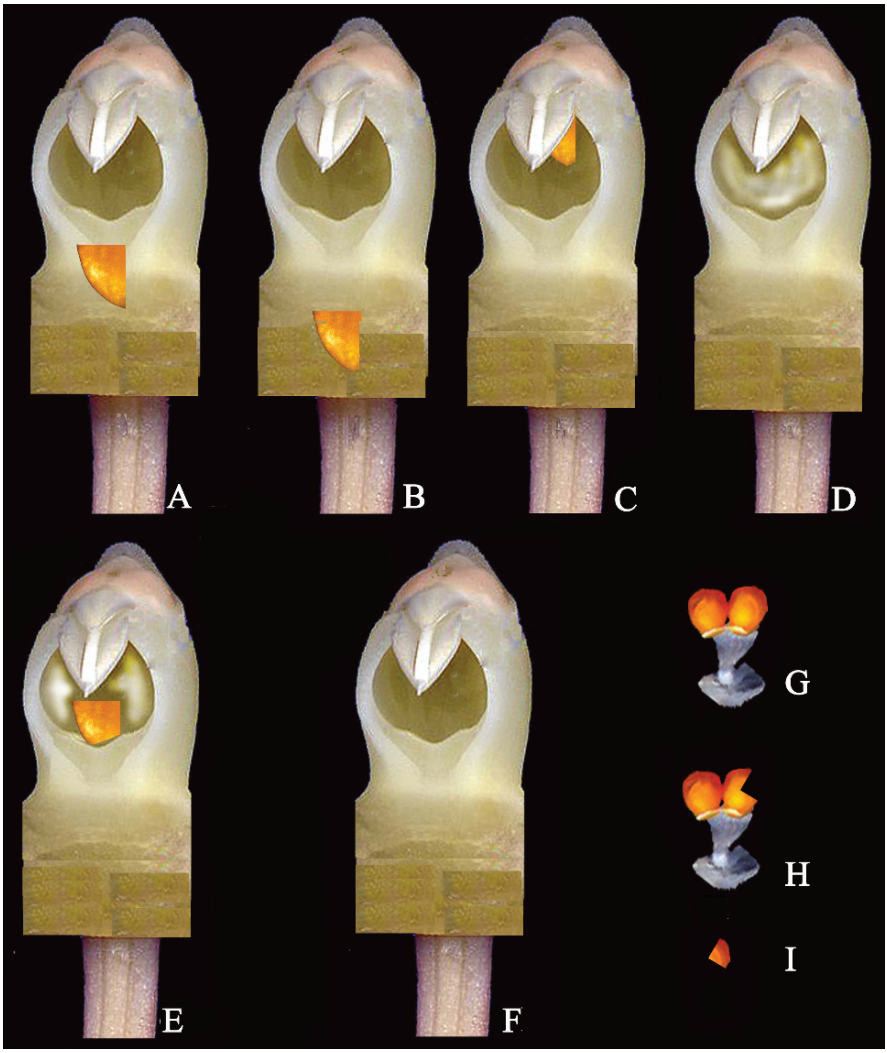

Fig. 2-17. Approximations of where Fitting placed pollinia quarters in gynostemia. The pollinia quarters were placed on the outside of the gynostemia in this illustration so that they and their approximate locations can be seen. Fitting placed them inside where they would not be visible except in sections. **A.** One quarter of living pollinium inserted deep into stylar canal without disturbing the stigma. **B.** One quarter of steam-killed pollinium inserted deep into stylar canal down to the region of the attachment of perianth segments. **C.** One quarter of steam-killed pollinium inserted just below the rostellum (only the lower portion of the quarter pollinium is showing). **D.** Stigmatic fluid removed from stigma. **E.** One quarter of steam-killed pollinium placed in stigma following removal of the stigmatic fluid. **F.** Intact unpollinated gynostemium. **G.** Intact pollinarium. **H.** Pollinarium with one quarter of a pollinium removed. **I.** One quarter of a pollinium (Computer generated from existing images by J. Arditti).

Table 2-9. Hans Fitting's experiments at the Bogor Botanical Gardens in 1908 on the effects on orchid flowers of inserting pollen in the gynostemium in locations other than the stigma (Fitting, 1909a)[a].

Experiment number	Description of experiment and its results		Fitting's conclusions	Current explanation
76	One quarter of a living pollinium was inserted deep into the stylar canal without disturbing the stigma			
	13 Feb 11:00: Pollinia inserted in gynostemia of four flowers	14 Feb 06:00: Stigmas start to close 14 Feb 11:00: Stigmas closed Perianth starts to close 14 Feb 14:00 (original paper lists this erroneously as 06:00, or it could be 15 Feb 06:00): Gynostemium swollen, flowers closed 16 Feb 11:00: Ovaries start to swell and turn green	1. Pollen, dead or alive need not be placed in the stigma to be active. It can be active even if placed in the stylar canal 2. Pollen can be active even if placed in the tip of the stigma 3. The influence which emanates from the stigma and affects the perianth is the same as the one which results from wounding	IAA in the inserted pollinia was effective in/from the insertion site and was also transported to a site where it initiated ethylene evolution Both pollination and wounding induce ethylene evolution
77	One quarter of a pollinium killed by steaming inserted deep into the stylar canal of *Phalaenopsis amabilis* down to the region of the attachment of the perianth segments without disturbing the stigma		4. The influence is produced even by pollen placed in stigmas after the removal of the stigmatic fluid	IAA diffused from pollen into the stigma even in the absence of stigmatic fluid
	A. 18 Feb 10:00: Pollinium inserted in gynostemium of one flower	19 Feb 07:00: Gynostemium tip and stigmatic area swollen. Flower half closed 19 Feb 12:00: Flower fully closed 21 and 22 Feb 06:00: Flower wilted. Ovary not swollen	5. Dead pollen can cause swelling of the ovary when placed deep in stylar canal close to the ovary	IAA from the pollen diffuses down into the ovary and causes the swelling

(continued)

	B. 28 Feb 08:00: Pollinium inserted in gynostemium of one flower	28 Feb 18:00: Flower starts to close 23 Feb: Flower abscised 29 Feb 06:00: Flower fully closed. Stigma starts to close 1 Mar 07:00: Flower wilted. Stigma almost fully closed 3 Mar 07:00: Ovary not swollen and wilted
	C. 28 Feb 08:00: Pollinium inserted in gynostemium of one flower	29 Feb 06:00-1 Mar 07:00: Same as in B above
78	A. 27 Feb 11:00: One quarter of a steam-killed pollinium inserted just below the rostella in stigmas of two *Phalaenopsis* flowers	28 Feb 07:00: Stigma half closed. Flower starts to close 28 Feb 18:00. Stigma and flower fully closed 3 Mar 06:00: Flower abscised
	B. 24 Feb: The stigmatic fluid was removed from the lowermost parts of the stigmas of two (probably *Phalaenopsis*) flowers	27 Feb 11:00: Flowers still fresh
	27 Feb 11:00: One quarter of a steam-killed pollinium was placed in the stigma	28 Feb 07:00: Flower and stigma start to close 28 Feb 18:00 (original paper states erroneously 06:00): Flower and stigma fully closed 3 Mar: Flower abscised

[a] The orchid names in this table are those used by Hans Fitting. Please see Appendix 2 for updated nomenclature.

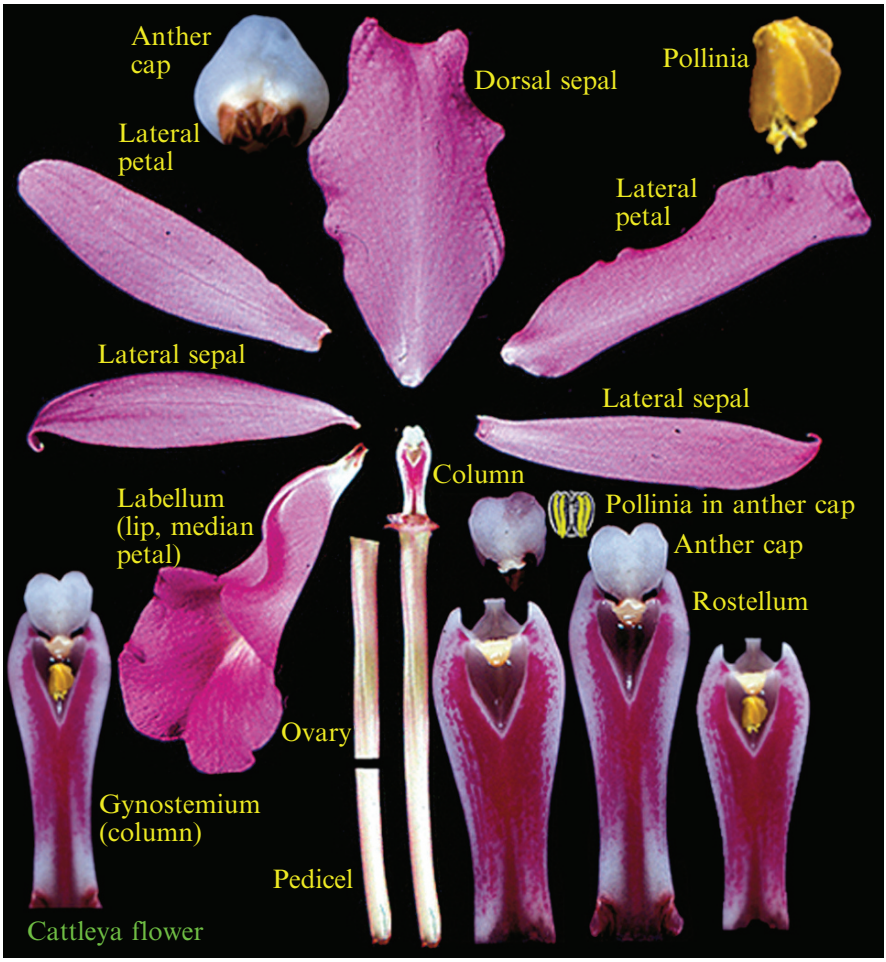

Fig. 2-18. *Cattleya* flower and its parts (Photographs and montage by J. Arditti).

was right because: (1) save for one paper from Japan (Morita, 1918), (2) a short period of work (eight papers) in Germany by Friedrich Laibach (1885–1967; Fig. 2-25) and his associates (1930–1934, see below), (3) research on ovulation (Heslop-Harrison, 1957; Magli, 1958; Dolcher, 1961a, b, 1967) which was only tangentially related to his research, and (4) several references in the first book on plant hormones (Went and Thimann, 1937), Fitting's work on orchids lay almost forgotten until one of us (J. A.) became interested in post-pollination phenomena of orchids (for a review see Avadhani et al., 1994).

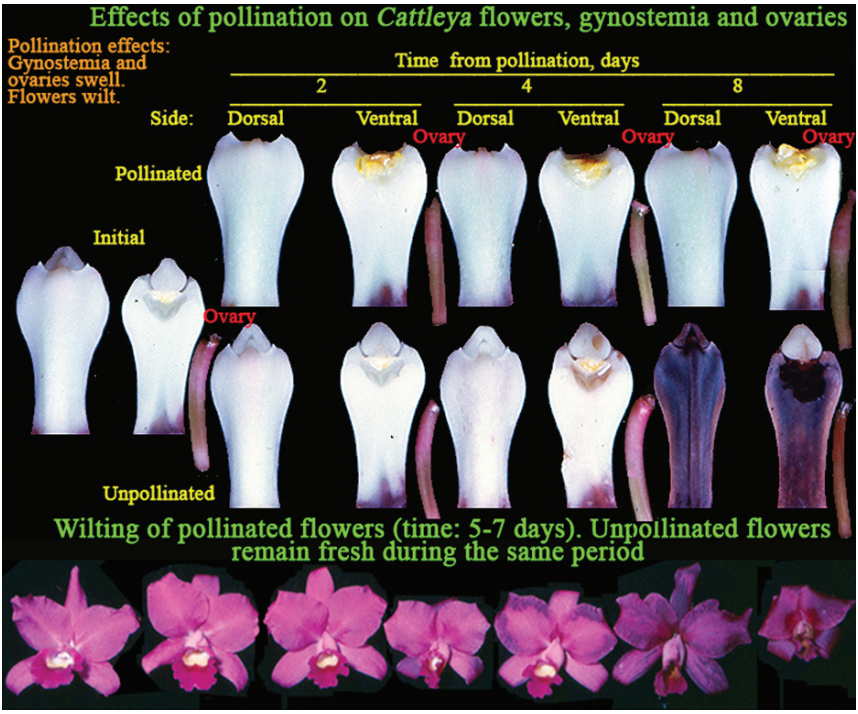

Fig. 2-19. Post-pollination phenomena in *Cattleya* (*Guarianthe*) flowers as Hans Fitting probably observed them. (source: the photographs were taken as part of research on post-pollination phenomena in orchid flowers in J. Arditti's laboratory; for a review see Avadhani et al., 1994).

In a conversation with one of us (J. A.) Went indicated that he did not make a connection between Fitting's research and his own work with *Avena* coleoptiles which led to the discovery of auxin. This is easy to understand because there is no obvious connection between the bending of coleoptiles and swelling of gynostemia and wilting of flowers. The connection was established only after auxin was discovered and its effects were studied extensively.

Ovary Swelling and Greening of Perianth

Post-pollination phenomena in orchid flowers are expressed in the: (1) perianth (sepals and petals) which move, senesce, and change color and structure and/or function, (2) gynostemium which swells, (3) stigma which closes, and (4) ovary which swells while the ovules develop internally. Fitting observed and describes all of these

and attempted to determine if one can be induced without the other, especially 1–3 (Tables 2-1–2-9). However, he was also interested in the swelling of the ovary (4 above) and the effects of pollen on it. To study this effect he pollinated flowers with living and dead pollen (Table 2-10) and concluded that pollinia can cause swelling of ovaries in some flowers, but not in others and that pollen tubes may be required for an ovary to swell. These conclusions were not entirely accurate (for a review see Avadhani et al., 1994).

Confirming Experiments

Fitting's experiments with *Cattleya, Odontoglossum* and *Zygopetalum* and European orchid flowers (Figs. 2-20, 2-21) on his return from Bogor involved pollination with their own and each other's living and dead pollen. The results of these experiments confirmed his findings in Bogor. *Zygopetalum mackayi* flowers exhibited phenomena similar to those of *Phalaenopsis violacea* in that perianth segments turned green and persisted on the fruit (Fig. 2-12, 2-13). It is reasonable to assume that the green segments carry out photosynthesis. Other studies carried out by Fitting in Strasbourg were designed to characterize the active principle in orchid pollen. They were physiological and chemical in nature, ahead of their time and modern (Table 2-11).

Classification of Phenomena

After concluding his experiments in Strasburg, Fitting separated the pollination induced phenomena into four categories and listed the factors which bring about or affect them (Table 2-12, 2-13). This classification is still valid at present, but it has been augmented by research since then (for a review see Avadhani et al., 1994).

Hormone

Fitting apparently read widely and seems have been familiar with literature on subjects other than plants because he knew of a suggestion by the British physiologist Ernest Starling (1866–1927) that substances he called hormones affect development in animals (Table 2-14). He concluded correctly that "the active substances in pollinia are hormones" (Fitting, 1910; Table 2-14). *Pollenhormon*, became a name associated with the hormone in orchid pollen. More recent research showed that Fitting was only partially right because orchid pollen contains (Fig. 2-24D) more than one hormone. It does contain a high concentration

Table 2-10. Hans Fitting's experiments at the Bogor Botanical Gardens in 1908 on swelling of orchid ovaries and greening of the perianth (Fitting, 1909a)[a].

Experiment number or observation	Description of observation of experiment and its results		Fitting's conclusions	Current explanation
Swelling of the ovary	Pollinia dead or alive do not generally cause noticeable swelling of ovaries in: *Coelogyne swaniana, Cymbidium finlaysonianum*, *Phalaenopsis amabilis, Phalaenopsis cornu-cervi*, *Phalaenopsis violacea* and *Stanhopea* sp. The only exception occurred in experiment 76: Ovaries of *Phalaenopsis amabilis* started to swell		Pollinia can cause swelling of ovaries in some flowers, but not in others. A pollen tube may be required for ovary swelling in the latter	Live pollinia which produce or cause the production of IAA may be required for ovary swelling in some orchids
Swelling of the ovary	*Arachnanthe sulingi* was pollinated with dead pollinia (a, ovary of unpollinated flower; b, ovary of flower pollinated with dead pollinia)	Ovary (b) was swollen 7 days after pollen was placed in stigma		
Swelling of the ovary	*Rhynchostylis retusa* was pollinated with dead pollinia (a, ovary of unpollinated flower; b, ovary of flower pollinated with dead pollinia)	Ovary (b) was swollen 8 days after pollen was placed in stigma		
Swelling of the ovary	*Aerides odorata* was pollinated with dead pollinia (a, ovary of unpollinated flower; b, ovary of flower pollinated with dead pollinia)	Ovary (b) was swollen 6 days after pollen was placed in stigma		
Swelling of the ovary	One flower of *Arachnanthe sulingi* was pollinated with it own dead pollinia (a). Another flower was pollinated with dead pollinia of *Aerides odorata* (b)	Ovary of *Arachnanthe sulingi* pollinated with dead pollinia of *Aerides odorata* (b) became more swollen than the ovary of a flower pollinated with its own pollen (a)		

(continued)

Table 2-10. (continued).

Experiment number or observation	Description of observation of experiment and its results		Fitting's conclusions	Current explanation
Swelling of the ovary	One flower of *Rhynchostylis retusa* was pollinated with it own dead pollinia (a). Another flower was pollinated with dead pollinia of *Aerides odorata* (b)	Ovary of *Rhynchostylis retusa* pollinated with dead pollinia of *Aerides odorata* (b) became more swollen than the ovary of a flower pollinated with its own pollen (a)		
76	A plug made of cotton was inserted into the stylar canals of two *Phalaenopsis amabilis* flowers and pushed in deeply to form an obstacle for the growth of pollen tubes. The flowers were pollinated after that		Pollen tubes must reach ovaries to cause swelling	That or at least auxin must do so
	13 Feb 11:00: Flowers pollinated with living pollinia	14 Feb 11:00: Flowers half closed. Stigmas swollen 16 Feb 11:00: Flowers wilted. Ovaries not swollen 19 Feb 06:00: Ovaries wilted and neither green nor swollen. Pollen tubes reached but did not grow past the cotton plugs		
Greening of perianth	Dead pollinia or pollen extract did not bring about the greening of the perianth in *Phalaenopsis violacea* and *Phalaenopsis cornu cervi*. The flowers closed, turned yellow, wilted and abscised. In *Phalaenopsis violacea* the flower closes and perianth segments turn and seem to be wilting before they start to turn green 5–6 days after pollination			
Pollination effects	Pollen of *Cattleya labiata* had the same effects on *Phalaenopsis violacea* and *Phalaenopsis cornu-cervi* as their own dead pollen. Ovary did not become swollen and perianth did not turn green			

[a] The orchid names in this table are those used by Hans Fitting. Please see Appendix 2 for updated nomenclature.

Fig. 2-20. European orchids used by Hans Fitting in his experiments in Strasbourg. **A.** *Gymnadenia conopea*. **B.** *Orchis latifolia*. **C.** *Platanthera bifolia* **D.** *Orchis fusca*. **E.** *Orchis morio* (sources: A–C, Schulze, 1894; D, Corrrevon, 1899).

Fig. 2-21. Tropical and European orchids used by Hans Fitting for his experiments in Strasburg. **A.** *Orchis maculata*. **B.** *Odontoglossum crispum*. **C.** *Cattleya trianei*. **D.** *Zygopetalum mackayi* [sources: A, Schulze, 1894; B, a collection of lithographs from the 1800s owned by J. Arditti; C, D, plates 5504 (1865) and 2748 (1827) respectively from the Curtis Botanical Magazine].

Table 2-11. Treatments and/or factors which bring about and/or affect post pollination phenomena in orchids (Fitting, 1909a)[a].

Phenomena	Factors which affect it and/or induce phenomena
I. Premature aging of flower (i.e., reduced life span)	Sand in the stigma; saliva in the stigma of *Rhynchostylis*; dead pollen from the species being treated or another species; alcohol soluble and alcohol insoluble fractions of aqueous pollen extract; dead pollen extracted with water several times in *Phalaenopsis violacea*; dead or living pollen of *Hedychium* (Zingiberaceae), *Hibiscus* (Malvaceae) and *Impatiens* (Balsaminaceae) in Phalaenopsis Gynostemium extract, 5% sucrose and wounding of the gynostemium and/or stigma in *Phalaenopsis amabilis*
II. Stigmatic closure and swelling of the gynostemium	Living or dead orchid pollinia from the species being tested or other orchids selected at random; alcohol soluble fraction of water extract of pollinia; living or dead pollinia of *Hibiscus* (Malvaceae)
III. Swelling of the ovary	Dead pollinia or pollen extract cannot cause swelling of the ovary in *Cymbidium finlaysonianum. Coelogyne swaniana, Phalaenopsis amabilis, Phalaenopsis cornu-cervi, Phalaenopsis violacea* and brought about only limited swelling in *Aerides odorata*, *Arachnanthe sulingi* and *Rhynchostylis retusa*. Only when inserted very deep in the stylar canal and close to the ovary did dead pollen cause some swelling
IV. Greening of the perianth	This occurs only in some species and is caused by living pollen

[a] The orchid names in this table are those used by Hans Fitting. Please see Appendix 2 for updated nomenclature.

of auxin (Fig. 2-24B), but it also contains ACC (Fig. 2-24C). There is also evidence that orchid pollen contains gibberellins and cytokinins (for a review see Avadhani et al., 1994).

Kôichi Morita and Japanese Orchids

If Fitting's research on orchid pollination generated any interest it was not enough to spur research by others for a number of years. However, eight years after his last research paper on orchid pollinia (Fitting, 1910) a Japanese investigator, Kôichi Morita (we could find no information about him) published a paper describing research which repeated and extended Fitting's experiments with *Cymbidium virens* Lindl and other Japanese orchids (Morita, 1918; Fig. 2-22, 2-23, Tables 2-15, 2-16). He reported that pollination extended the life span of *Cymbidium virens* (this name was introduced by Reichenbach and referred erroneously to *C. virescens* Lindl.,

Table 2-12. Observations on flowering, pollination and post-pollination phenomena in orchids (Fitting, 1909b)[a].

Orchid or process	Observation or terminology
Active principle in pollen	Soluble in hot water [IAA is sparingly soluble in water, more so in hot than in cold]. It is found on the surface of the pollen [actually IAA is inside the pollen grains]. There are two substances in the cold water extract. One, alcohol insoluble, brings about swelling of the gynostemium and shortens the life span of flowers. The other, alcohol soluble, causes wilting of *Phalaenopsis amabilis* flower, but not swelling of the gynostemium [IAA and ACC are alcohol soluble]. Both retain their activity after prolonged boiling. Characteristics of the alcohol insoluble fraction are: (1) occurs inside the anther, (2) organic compound, (3) easily soluble in hot or cold water [ACC is, IAA is not], (4) not easily soluble in alcohol [both IAA and ACC are alcohol soluble], (5) cannot be precipitated from aqueous solution with alcohol, (6) is heat resistant, (7) does not reduce Fehling's solution even after being heated with hydrochloric acid, (8) does not precipitate with lead acetate and according to other assays does not contain nitrogen, (9) not an enzyme, (10) could not be replaced by citric acid, dextrin, diastase, malic acid, oxalic acid, succinic acid, 5% sucrose or tartaric acid. The same active principle is also present in pollen of non orchidaceous plants
Aerides odorata	Pollination shortens life span. Volcanic windblown sand placed in the stigma causes rapid closing and wilting of the flower. For effects of dead pollinia see "Pollen" entry in this table
	Gynostemium became swollen when larvae ate a hole in the stigma
Arachnanthe sulingi	For effects of dead pollinia see "Pollen" entry in this table
Calanthe	Ovary swells when parasitized by larvae of a gall causing insect (Fitting quotes Forbes, 1885 on this)
Coelogyne swaniana	For effects of dead pollinia see "Pollen" entry in this table
Stanhopea sp.	For effects of dead pollinia see "Pollen" entry in this table
Cymbidium finlaysonianum	For effects of dead pollinia see "Pollen" entry in this table
Dendrobium crumenatum	Flowers last for a day
Dendrobium superbum	Flowers last 14 days. Pollination shortens life span. Volcanic windblown sand placed in the stigma causes rapid closing and wilting of the flower (wounding effect?)
Floral segments and stigma	"There is a correlative link of unknown nature between the 'Wundreiz' (wound stimulus) and the other floral segments which brings about some of the changes." Swelling and closing of the stigma is the result of direct contact. [These are Fitting's conclusions. Actually IAA is transported from the stigma into the gynostenium perhaps even into the ovary. In addition IAA probably diffuses from pollen tubes.]
Floral senescence following pollination	Pollination induced floral senescence and other processes is "Autonome Postflorationvorgange" (induced post anthesis processes). Note: Later Fitting called these "Aitionom" processes

(continued)

Floral senescence without pollination	Natural flower senescence and other processes is "Induzierte Postflorationvorgange" (autonomic post anthesis processes)
Gynostemium	Removal of gynostemium above the base of the stigma has no effect of the life span of flowers Removal of gynostemium tissue on ventral side above the stigma has no effect of the life span of flowers Deep wounding which reached vascular or stigmatic tissue did reduce the life span of flowers
Larvae, insect	See *Aerides odorata* in this table
Liparis latifolia	Ovary swells when parasitized by larvae of a gall causing insect (Fitting quotes Treub, 1883 on this)
Oncidium incurvum	Pollination shortens life span. Volcanic windblown sand placed in the stigma causes rapid closing and wilting of the flower
Orchis mascula	Ovary swells after the flower is pollinated with *Cypripedium parviflorum* pollen (Fitting quotes Hildebrand, 1865 and Strassburger, 1866 on this)
Orchis morio	Ovary swells after the flower is pollinated with *Frtillaria* pollen (Fitting quotes Hildebrand, 1865 and Strassburger, 1866 on this)
Ovary	Swells even when flower is pollinated with pollen which cannot fertilize ovules
Ovary	Wilts and abscises with the blossom if the flower is not pollinated
Ovules	Not present in the ovary at the time of pollination (Fitting quotes Hildebrand, 1863a, 1863b, 1868 on this
Perianth and stigma	See "Floral segments and stigma" in this table
Perianth segments	Greening occurs only after ovaries start to swell. Cannot be brought about by dead pollen
Phalaenopsis amabilis	Flowers last for a month. Pollination shortens life span. Volcanic windblown sand placed in the stigma causes rapid closing and wilting of the flower. Removal of gynostemium above the base of the stigma has no effect of the life span of flower. For effects of dead pollinia see "Pollen" entry in this table
Phalaenopsis cornu-cervi	Flowers last for a month. Pollination shortens life span. For effects of dead pollinia see "Pollen" entry in this table
Phalaenopsis esmeralda	Pollination shortens life span. Volcanic windblown sand placed in the stigma causes rapid closing and wilting of the flower
Phalaenopsis violacea	Flowers closes 1–2 days after pollination, turns yellow and starts to wilt. Then the ovary starts to swell and turns green. At this point wilting of yellowed perianth stops and starts to turn green. Volcanic windblown sand placed in the stigma causes rapid closing and wilting of the flower. For effects of dead pollinia see "Pollen" entry in this table

(continued)

Table 2-12. (continued).

Orchid or process	Observation or terminology
Pollen	Pollen causes its effects through a chemical agent. Dead pollen (killed by steaming or soaking in chloroform) can induce stigmatic closure and swelling of the gynostemium and even some, but not marked swelling and elongation of the ovary in *Aerides odorata*. *Arachnanthe sulingi* and, *Rhynchostylis retusa*. In *Cymbidium finlaysonianum*, *Coelogyne swaniana*, *Stanhopea* sp., *Phalaenopsis amabilis*, *Phalaenopsis cornu-cervi*, *Phalaenopsis violacea* and *Zygopetalum maka*yi stigmatic closure and swelling of the gynostemium are not accompanied by swelling and elongation of the ovary. To have an effect on ovaries pollen must germinate and produce tubes which enter the ovary. For details about the active principle see "Active principle in pollen" in this table
Pollen tubes	For pollen tubes to have an effect on the ovary they must enter it. For details about the active principle see "Active principle in pollen" in this table
Pollinia	Some pollinia are more active that others
Rhynchostylis retusa	Flowers last for a month. Pollination shortens life span. Volcanic windblown sand placed in the stigma causes rapid closing and wilting of the flower. Removal of gynostemium above the base of the stigma has no effect of the life span of flower. For effects of dead pollinia see "Pollen" entry in this table
Sand	When volcanic blown sand was placed in stigmas the life span of flowers was reduced
Several	Perianth turns green after pollination and remains on the fruit until it ripens
Several	Pollination shortens life span of flowers
Several	Stigma closes 1–2 days after pollination
Stigma and floral segments	See "Floral segments and stigma" in this table
Stigmatic fluid or secretion	Removal by wiping it away reduces the life span of flowers
Vanda tricolor	Pollination shortens life span. Volcanic windblown sand placed in the stigma does not cause closing and wilting of the flower
Water (hot) extract of pollen	Active
Wounding	Incisions, scratches or punctures of the stigma shorten the life span of flowers. Wounding of the gynostemium has a minor effect unless it is severe. Deep wounding which reached vascular or stigmatic tissue did reduce the life span of flowers. Wounding causes its effects through the formation of a "Wundreiz" (wound stimulus)
"Wundreiz"	Wound stimulus caused by wounding of the stigma which reduces the life span of flowers and causes other effects
Zygopetalum makayi	For effects of dead pollinia see "Pollen" entry in this table

[a] The orchid names in this table are those used by Hans Fitting. Please see Appendix 2 for updated nomenclature.

Table 2-13. Flowering, pollination and post-pollination phenomena in orchids (Fitting, 1910)[a].

Orchid or process	Observation, terminology and comments by Fitting or [the authors of this review]	
Active principle	Fitting carried out very elaborate (for the time) experiments on the characteristics of the active principle and reported that it is: (1) insoluble in chloroform [neither is IAA], (2) more easily soluble in water than in ethanol [the reverse is true for IAA, but Fitting may have isolated a mixture of IAA and other substances including ACC], (3) insoluble in ethyl and petroleum ether, (4) neither a reducing sugar not a polymer which produces reducing sugars on hydrolysis, (5) not a lipid, resin, wax, cholesterol, carbohydrate, glycoside, tannin, mucilage, enzyme, protein, an acid which is soluble in water, but not in alcohol, (6) not a salt, and (7) a nitrogen containing substance, (8) leached from pollinia suspended in water, but some activity remains in the pollen, (9) present, produced and releases by pollen tubes, (10) located on the surface of pollen grains inside the pollinia, (11) produced by pollen tubes	
Cattleya trianae	The active fraction of pollinia extract has the same characteristics as the active fractions of extracts Fitting obtained in Bogor in 1908	
Experiments with German native orchids to determine if pollen of temperate climate species has the same effects as that of those from the tropics		
Gymnadenia conopea	Four flowers wilted in 16 days if unpollinated and in 13 days if pollinated	These are experiments Fitting carried out in Strassburg after he returned from Indonesia
Orchis fusca	Four flowers wilted in 16 days if unpollinated and in 7 days if pollinated	
Orchis fusca	Four flowers wilted in 12 days if unpollinated and in 6 days if pollinated	
Orchis latifolia	Four flowers wilted in 14 days if unpollinated and in 7 days if pollinated	
Orchis latifolia	Four flowers wilted in 14 days if unpollinated and in 8 days if pollinated	
Orchis maculata	Four flowers wilted in 13 days if unpollinated and in 6 days if pollinated	
Orchis maculata	Four flowers wilted in 14–16 days if unpollinated and in 10 days if pollinated	
Orchis morio	Four flowers wilted in 13 days if unpollinated and in 6 days if pollinated	
Orchis morio	Four flowers wilted in 10 days if unpollinated and in 6 days if pollinated	
Platanthera bifolia	Four flowers wilted in 17 days if unpollinated and in 15 days if pollinated	
Injections of water or pollen extract into *Odontoglossum*	Both water- and extract-injected flowers wilted in 10–12 days and before untreated flowers. The extract did not cause swelling of the gynostemium. [The wilting is not surprising because it could have been due to wound ethylene. However, the lack of swelling is if the extract contained IAA.]	
Odontoglossum crispum	Gynostemium swells when pollinated with dead pollinia	

(continued)

Table 2-13. (continued).

Orchid or process	Observation, terminology and comments by Fitting or [the authors of this review]
Pollen	Both live and dead pollen shorten the life span of flowers, but living pollinia have a more rapid and more pronounced effect in some cases. Fitting concluded that the pollen contains a chemical principle
Pollinia	Pollinia of *Epipactis palustris, Orchis latifolia* and *Orchis mascula* brought about swelling of the gynostemium and shortening of the life span in flowers of *Oncidium sphacelatum* and *Oncidium sphegiferum*, but not *Orchis* species. Also pollinia of *Paphiopedilum callosum* brought about post-pollination phenomena in *Phalaenopsis amabilis* and pollinia *Paphiopedilum barbatum* had the same affect on *Oncidium sphacelatum*
Tropical and German native orchids	There are four main phenomena which are induced by pollination: (I) Closing and wilting of perianth, (II) Closing of stigma and swelling of gynostemium, (III) Swelling of ovary, and (IV) Greening of perianth segments [this is limited to a few species]. Pollination also reduces the life span on flowers. Gynostemium turns green in many species. The effects of pollination on German native orchids are not pronounced
Zygopetalum mackaii and other species	Pollination with live pollen increases the life span of perianth segments by causing them to change into leaf like photosynthetic structures which remain on the ovary until it ripens. Dead pollen and wounding of the stigma do not have this effect

[a]The orchid names in this table are those used by Hans Fitting. Please see Appendix 2 for updated nomenclature.

Table 2-14. Fitting's proposal that plants produce hormones (Fitting, 1910) with comments by the authors of this review between brackets.

Original German	English (free) translation
Starling[a] … [mentioned but not cited, but see below] hat für das Tier vorgeschlagen alle derartigen Stoffe, die im eigenen Stoffwechsel des Organismus erzeeugt, ohne Nahrugsstoffe zu sein als Reizstoffe die Enwicklung oder sonstige Lebenstätigkeit des Organismus beeinfluseen mit dem Namen Hormone (von ó□μάω ich reize, rege an) zu bezeichnen. Ich möchte vorschlagen, diesen Terminus auch für die Pfanzen zu verwenden … In diesem Sinne also wären wohl die Reizstoffe der ungekeimten Pollinien echte Hormone	Starling[a] [see below] suggested for animals substances which are not nutrients and function as stimuli for development or other life functions. He named them hormones (from ó□μάω to stimulate, to activate). I would like to suggest the same term for plants … In this sense the stimulating [i.e., active] substances in the pollinia are true hormones. [This is the first use of "hormone" relative to plants]

[a] Ernest Starling (1866, London-1927, on a ship near Kingston, Jamaica), An English physiologist is credited with coining the term hormone (from the Greek horman which means to set in motion) in The Croonian Lectures on the chemical correlation of the functions of the body which were delivered at the Royal College of Physicians and subsequently published in the Lancet (2: 339–341, 1905). Actually the term was suggested to him by the Cambridge Physiologist, William B. Hardy (1864–1934) during a visit to his laboratory.

the correct name now is *C. goeringii* var *goeringii*) flowers (Table 2-17). This is interesting because if pollination extends the life span of flowers it is usually by causing the perianth to turn green and persist on the fruit. In this case Morita reported that the flowers wilted eventually. Morita also obtained additional information regarding the solubility of the active principle and the effects of a number of substances. (Table 2-15). His approach was innovative because it was quantitative since he measured the elongation of the gynostemium (Fig. 2-24A) whereas Fitting's reports were only descriptive in this respect.

Relating Pollenhormon to Auxin

Despite Fitting's and Morita's efforts the identity of the active principle (or principles) in pollen was not established. The reasons could be the: (1) lack of appropriate technology, (2) fact that Fitting and Morita were ahead of their time, (3) state of plant physiology which had yet to include the hormone concept, and (4) lack of continued interest (both Fitting Morita did not publish any additional papers on the subject). The discovery of auxin by Frits Warmolt Went (18 May 1903–15 May 1990) in 1926 (Went, 1926, 1990) changed all that by: (1) firmly establishing the hormone concept in plant physiology (Went and Thimann, 1937), (2) providing the means to assay and quantify auxin (Fig. 2-26A, 2-26B, 2-26D),

Fig. 2-22. Some of the orchids used by Kôichi Morita in his experiments. **A.** *Goodyera repens*. **B.** *Calanthe discolor*. **C, E.** *Spiranthes australis*. **D.** *Gymnadenia cucullata.* (sources: A, C, J. Arditti's collection; B, Botanical Register 26: plate 55, 1840; D, E, Correvon, 1899).

and (3) spurring further research (for a review of early research on auxin see Went and Thimann, 1937).

The identity of the active principle was established by Friedrich Laibach (1885–1967; Fig. 2-5D) and his associates (Laibach, 1930, 1932, 1933a, b; Laibach and Kornmann, 1933; Laibach and Maschmann, 1933; Mai, 1934; Maschmann and Laibach, 1993). They used Went's *Avena* coleoptile bioassay (Fig. 2-26, Tables

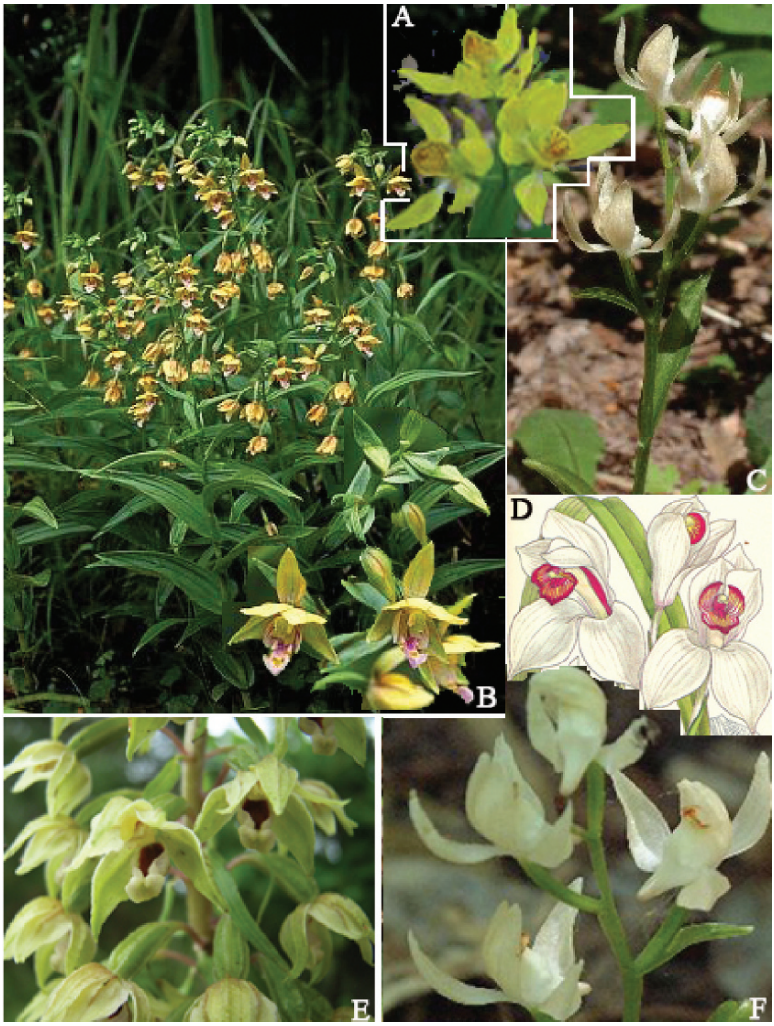

Fig. 2-23. Several of the orchids used by K. Morita for his experiments. **A.** *Epipactis falcata*. **B.** *Epipactis thunbergii*. **C, F.** *Epipactis erecta*. **D.** *Cymbidium virens*. **E.** *Epipactis papillosa* (A, C, E, F, J. Arditti's collection; D, plate 8151 from Curtis Botanical Magazine, vol. 135, 1907).

2-18, 2-19) and showed that Fitting's *Pollenhormon* had the same effects as auxin and its content in pollinia of different orchids is not the same (Fig. 2-26). They also demonstrated that its solubility in hot and cold water is different (Fig. 2-6). Actual determinations of auxin in orchid pollinia have shown that some orchids contain as much as 100 µg IAA g pollen^{-1} (R. Müller, 1953). This may be the highest or at least one of the highest concentrations of auxin in any plant tissue.

Table 2-15. Koichi Morita's experiments on the pollination of *Cymbidium virens* (Morita 1918)[a].

Experiment number	Description of experiment and its results	Morita's conclusions	Current explanation
Morita cites Fitting's papers (1909, 1910) and seems to have based his work on them. He determined the effects of pollination on the life span of *Cymbidium virens* flowers (Table 2-17) and other Japanese orchids (Table 2-19) thereby extending Fitting's work to temperate climate species.			
	Pollination extended the life span of *Cymbidium virens*, but what he observed may have been perianth greening as in some *Phalaenopsis* species. The gynostemium of this species did become swollen and elongated (Fig. 2-24A), the stigma closed and the ovary increased in size. It was 18 mm long and 2.5 mm in diameter before pollination and 38 mm long and 4 mm in diameter 7 days after pollination.		
1	24 Feb, 10:00: One flower of *Cymbidum virens* was pollinated with pollinia killed by soaking them in chloroform for ½ h 27 Feb, 10:00: Stigma started to close 28 Feb, 10:00; Stigma closed even more 1 Mar, 10:00: No change 16 Mar, 13:00: Flower starts to wilt	Dead pollen is as active as living pollinia The active substance is not deactivated by exposure to heat or chloroform	
2	25 Feb, 11:00: One flower of *Cymbidum virens* was pollinated with pollinia killed by steaming them for 10 min 27 Feb, 10:00: Stigma started to close 1 Mar: Stigma closed even more 16 Mar: Flower starts to wilt		
3	Six pairs of *Cymbidium virens* pollinia were extracted with warm water for 20 min and the extract was reduced to two drops on a water bath. Cotton wads saturated with extract were placed in stigmas 26 Feb, 10:00: Two flowers treated 1 Mar, 10:00: Stigma started to close 3 Mar, 10:00: Stigma closed even more Next days: No change		
4	Eight pairs of *Cymbidium virens* pollinia were extracted with cold water for 22 h and the extract was reduced to a small volume by placing it in a water bath for 7 min. Cotton wads saturated with extract were placed in stigmas 27 Feb, 10:00: Two flowers treated 3 Mar, 10:00: Stigma closed Next days: No change	The active principle can be extracted with both hot and cold water	

(continued)

5	Pollinia, 23 pairs were ground in a mortar with 5 ml water and allowed to stand for 22 h. After filtering the filtrate was reduced to 2 ml		
	6 Mar, 11:00: Two flowers treated	8 Mar, 11:00: Stigma starts to close 9 Mar, 13:00: Stigmatic closure is more pronounced Next days: No change	
6	Pollinia, 11 pairs were submerged in 3 mm of glycerine for 2 days. Both glycerin and the pollinia were used to treat flowers.		
	9 Mar: Glycerin was used to treat two flowers	No change	
	Pollinia were washed with distilled water and placed in the stigma of one flower	Pollinia had the usual effect	Glycerin could not extract the active substance
7	Pollinia, 10 pairs were placed in 5 ml ether for 24 h. The ether was reduced to two drops in volume. These drops were mixed with water and the mixture was used to treat flowers		The active substance can be extracted with ether and ethanol
	15 Mar, 13:00: Two flowers treated	16 Mar, 11:00: Stigmas start to close, but not as intensely as those treated with aqueous extract	
8	Pollinia, 10 pairs were extracted with 4 ml absolute ethanol for 14 days. The ethanol was reduced to a small volume which was used to treat flowers		
	7 Apr, 11:00: Two flowers treated	12 Apr, 10:00: One stigma closed, the other still open	
No number	Extract from experiment 5 was injected into the tip of the gynostemium		To be effective the active substance must be in the stigma

(continued)

Table 2-15. (continued).

Experiment number	Description of experiment and its results		Morita's conclusions	Current explanation
9	River sand boiled in hydrochloric acid for 5 min and washed several with distilled water was used to treat flowers			
	28 Feb, 11:00: Sand placed in stigma of one flower	3 Mar, 10:00: No change 7 Mar, 11:00: Flower starts to wilt 15 Mar: Flower wilted	1. Pollination has the following effects on flowers of *Cymbidium virens*: (a) shorten the life span of flowers, (b) cause stigmatic closure, (c) bring about swelling of the gynostemium, (d) induce swelling and elongation of the ovary	
10	Glass powder treated like the sand in experiment 9 was applied to stigmas 3 Mar, 11:00: Flowers treated	Next days: No change		
No number	Spores of saprophytic fungi placed in stigmas had no effects			
12, 13, 15, 16	Pollinia of *Dendrobium fimbriatum* var. *oculatum, Calanthe veitchii, Epipactis falcata* and *Calanthe discolor* were placed in stigmas of *Cymbidium virens* and caused stigmatic closure		2. Pollen killed with vapor or chloroform causes stigmatic closure, but does not reduce the life span of flowers	
14	Pollinia of *Paphiopedilum argus, Paphiopedilum boxallii* and *Paphiopedilum lathamianum* placed in stigmas of *Cymbidium virens* had no effects		3. Aqueous, ethanol and ether extracts of pollen cause stigmatic closure 4. Sand grains placed in the stigma and wounds in the gynostemium had no effects 5. Pollen of other orchids is effective	
No number	Pollen of *Thea japonica, Prunus mume, Narcissus jonquilla, Brassica campestris, Hyacinthus orientalis* and *Salix thunbergiana* placed in stigmas of *Cymbidium virens* had no effects		6. Some organic substances are effective	Morita confirmed Fitting's findings
No number	The following did not cause stigmatic closure: 5% NaCl; 1% K_2CO_3; 1% KNO_3; 0.025N, 0.05N and 0.1N acetic acid; 0.025N, 0.05N and 0.1N butyric acid; 2.5% and 5% glucose; 0.025 N formic acid; 2,5%, 5% and 10% fructose, 10% maltose and 1%, 2.5%, 3% and 5% sucrose. The following had an effect: 0.05N and 0.1N formic acid; 10% glucose; pure oleic, palmitic and stearic acids and 10% sucrose			

[a]The orchid names in this table are those used by Koichi Morita. Please see Appendix 2 for updated nomenclature.

Table 2-16. Koichi Morita's experiments on the effects of pollination on the life span of Japanese orchids (Morita 1918)[a].

	Life span (days)		
Species	Unpollinated	Pollinated	Remarks
Calanthe discolor	14	10	There was no swelling of gynostemia or closing of stigmas in any of these orchids. However the ovary enlarged
Cymbidium virens	14–25	30–40	
Epipactis erecta	8–10	7	
Epipactis falcata	8–12	8–12	
Epipactis papillosa	7	7	
Epipactis thunbergii	7–10	7–10	
Goodyera repens	8–10	7	
Gymnadenia cucullata	8–10	7	
Platanthera yatabei	7–10	7–10	
Spiranthes australis	10	5	

[a] The orchid names in this table are those used by Koichi Morita. Please see Appendix 2 for updated nomenclature.

Table 2-17. Effects of pollination on the life span of *Cymbidium virens* flowers (Morita, 1918)[a].

Unpollinated					Pollinated					
Full bloom (a)	Start to wilt (b)	Elapsed time, d (c: a to b)	Fully wilted (d)	Elapsed time, hr (e: b to d)	Full bloom (f)	Pollinated (g)	Start to wilt (h)	Elapsed time, d (i: g to h)	Fully wilted, d (j)	Elapsed time, d (k: h to j)
22 Mar	7 Apr, 10:00	16	10 Apr, 10:00	36	22 Mar	22 Mar, 10:00	21 Apr, 08:00	32	3 May, 08:00	12
22 Mar	15 Apr, 10:00	24	21 Apr, 10:00	144	22 Mar	22 Mar, 10:00	21 Apr, 08:00	32	1 May, 08:00	10
23 Mar	7 Apr, 10:00	6	13 Apr, 10:00	144	23 Mar	26 Mar, 11:00	26 Apr, 09:00	30	29 Apr, 11:00	3
23 Mar	10 Apr, 10:00	9	17 Apr, 16:00	176	29 Mar	31 Mar, 10:00	29 Apr, 11:00	29	1 May, 08:00	3
	Total elapsed time, a to d					Total elapsed time f to j				
	22 Mar-10 April: 17 days and 12 hours					22 Mar- 3 May: 42 days				
	22 Mar-21 April: 30 days					22 Mar- 1 May: 42 days				
	23 Mar-13 April: 12 days					23 Mar-26 Apr: 33 days				
	23 Mar-17 April: 16 days and 8 hours					29 Mar-29 Apr: 32 days				

[a]The orchid name in this table is the one used by Koichi Morita. Please see Appendix 2 for updated nomenclature.

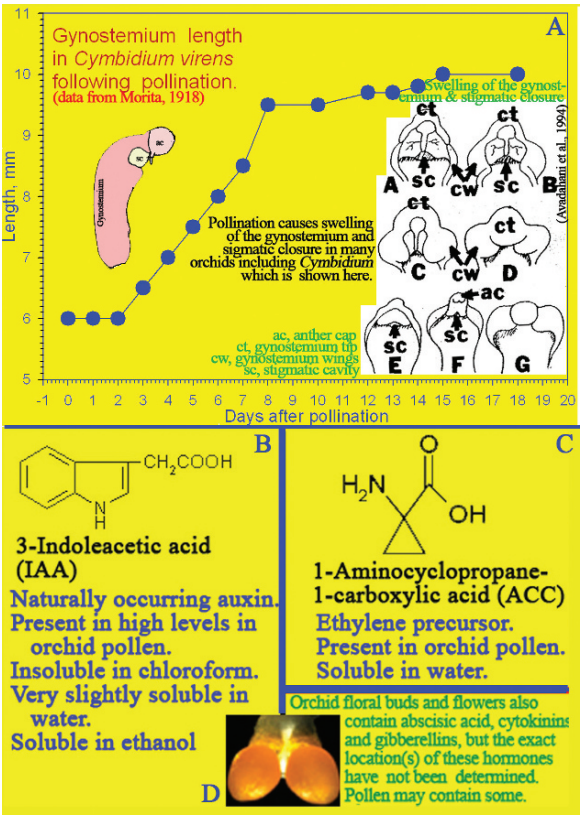

Fig. 2-24. Pollination effects on the gynostemium in *Cymbidium virens* following pollination and hormones which are present in orchid pollen. **A.** Elongation (graph) and swelling (line drawings) of the gynostemium of *Cymbidium virens*. **B.** Auxin, 3-Indoleacetic acid. **C.** 1-Aminocyclopropane-1-carboxylic acid (ACC), precursor of ethylene. **D.** *Phalaenopsis* pollinia, highly magnified (A, plot based on data from Morita, 1918 and drawings by Emma Web who was a technician in J. Arditti's laboratory at the time; B,C, computer generated; D, J. Arditti).

Fig. 2-25. Students of auxin. Friedrich Laibach (1885–1967) before or during (**A**) and after (**B**) World War II. **C.** Frits W. Went (A, courtesy the late Mrs. Sigrid Fitting; B, part of a group photograph taken at the First International Symposium on Arabidopsis Research, 21–24 April, Göttingen, Germany, courtesy Elliot M. Meyerowitz, California Institute of Technology; see also Meyerowitz, 2001; C, courtesy the late F. W. Went).

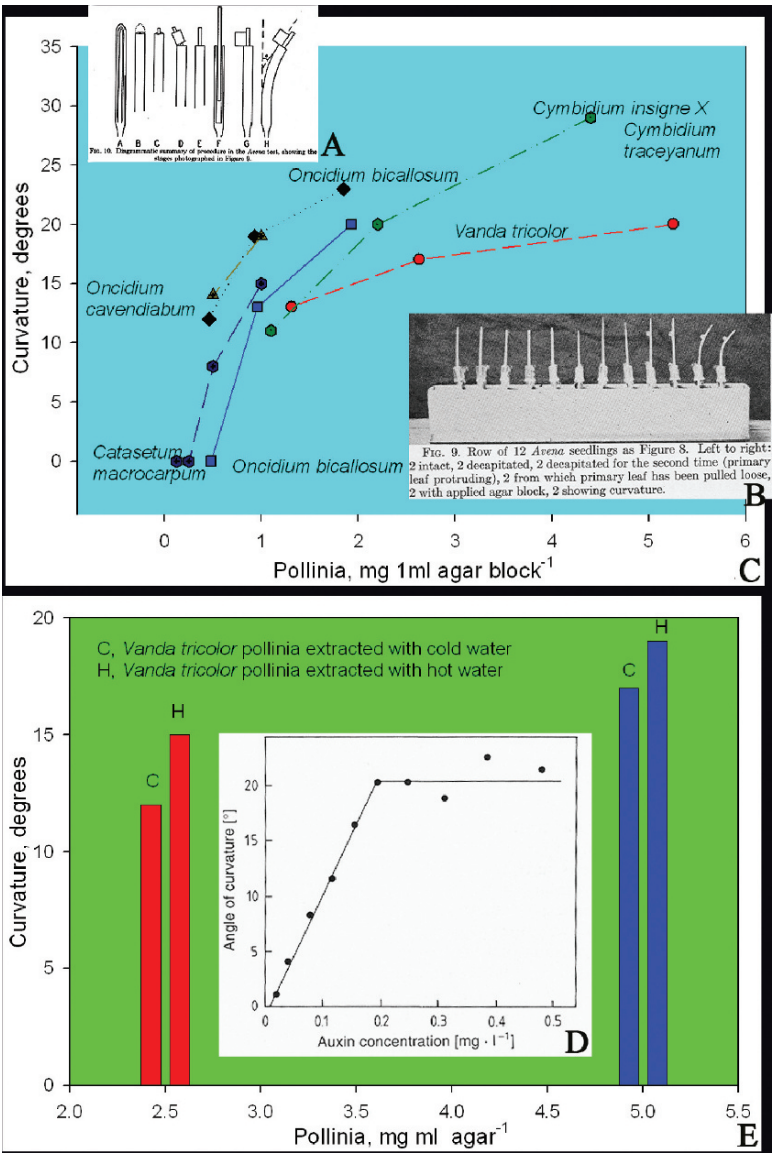

Fig. 9. Row of 12 *Avena* seedlings as Figure 8. Left to right: 2 intact, 2 decapitated, 2 decapitated for the second time (primary leaf protruding), 2 from which primary leaf has been pulled loose, 2 with applied agar block, 2 showing curvature.

Fig. 2-26. *Avena* coleoptile assays. **A**. Diagrammatic representation of the assay. **B.** An early assay at the California institute of Technology in Pasadena. Laibach probably used similar assays. **C.** Assay of auxin content in pollinia of several orchids. **D.** Standard curve for auxin levels. **E.** Comparison assays of hot and cold water extracts of *Vanda tricolor* pollinia (A, B, Went and Thimann, 1937 (this is a classic volume and the first book on the subject by the discoverer of auxin, the late Frits W. Went and one of the early workers in the area who became a very prominent and influential American plant physiologist, the late Kenneth V. Thimann; the illustrations were taken from a copy owned by J. Arditti which is autographed by both authors; C, E, graphs based on data by Laibach; E, modern version of a graph in Went and Thimann, 1937).

Table 2-18. Friedrich Laibach's (1885–1867) experiments on the nature of Fitting's *Pollenhormon* (Laibach, 1930, 1932, 1933a, 1933b; Laibach and Kornmann, 1933; Laibach and Masschmann, 1933; Mai, 1934; Maschmann and Laibach, 1933)[a].

Experiment number	Description of experiment and its results	Laibach's conclusions	Current explanation
Laibach used the term *Wuchsstoff* (growth substance) and defined as "Non nutritional substances, widely distributed in plants and animals which can promote the elongation of *Avena* coleoptiles (see also Table 2-14). He used F. W. Went's (1903–1990) *Avena* coleoptile method to assay for the presence and activity of growth substances (Laibach, 1932)			
1	Five pairs each of *Cattleya* sp. and *Coelogyne massangeana* were suspended in 0.5 ml of water for 15 min. After that both the water and the pollinia were mixed with 0.5 ml of 3% agar. When the agar solidified it was cut into small cubes, each containing a pollinium. These cubes were assayed with six coleoptiles, five of which which bent 25–40°. The cube was not attached well to the one which did bend	The substance which causes bending of *Avena* coleoptiles can be extracted easily from pollinia with water	Laibach seems to have ignored three possibilities: (1) not all of the active substance was extracted, (2) there may have been two substances, one which was extracted with the water and another which was not, and (3) there may have also been an inhibitor which was not extracted from the pollinia
2	Cubes remaining from experiment 1 were liquefied in a water bath, then the agar was allowed to solidify again, cut into cubes and assayed as before. All six coleoptiles bent 15–25°		
3	Five pairs of pollinia from *Cattleya* sp. were used to prepare agar cubes as in experiment 1 except that some contained pollinia and some did not. Six cubes with pollinia and an equal number without were assayed with *Avena* coleoptiles. Bending of pollinia was as follows: Cubes with pollinia: 15°, 10°, 18°, 28°, 26°, 5° [Ave: 17°]. Cubes without pollinia: 20°, 13°, 30°, 32°, 13°, 28° [Ave: 22.7°]		
4	Pollen of *Hibiscus syriacus* and *Hibiscus schizopetalus* was used to prepare agar cubes as in experiment 1. The extracts were assayed with five coleoptiles each with bending being 15–20° and 20–30° respectively	*Hibiscus* pollen contains growth substance	
5	Pollen of *Anoda cristata*, Malvacae was assayed and found to cause very limited bending	This species contains very little growth substance	

(continued)

6	Pollinia (75 mg) of several orchids (*Vanda tricolor*, *Coelogyne massangeana*, *Coelogyne speciosa*, and *Phalaenopsis amabilis*) were extracted as follows: (1) Suspended in 25 ml 70% ethanol under nitrogen at 70° C. (2) After filtration the pollinia were extracted in the same manner for a second time. (3) The alcohol was removed from the combined filtrates under nitrogen, 40° C and pressure of 15 mm mercury. (4) What remained was an aqueous extract which was acidified with 1.5 ml 2N acetic acid and extracted four times with 50 ml aliquots of peroxide free ether. (5) Following this the ether was shaken three times with 10 ml aliquots of 2.5% sodium carbonate. (6) The carbonate solution was acidified with acetic acid and shaken with four 50 ml aliquots of ether. (7) After 2 h drying with sodium sulfate the ether was evaporated under nitrogen and the residue was stored in a desiccator. (8) To assay the residue it was dissolved in 0.6 ml water and 0.5 ml of this solution was mixed with 0.5 ml of 3% agar. Half of this was cut into cubes and assayed with seven *Avena* coleoptiles. Bending was 15°, 20°, 10°, 8°, 0°, 25°, 10° [Ave: 12.6]		The growth factor has the same characteristics as the substance isolated by Kögl and Hagen Smit	Kögl and Hagen Smit isolated auxin (but there is more to this story)
7	*Anoda cristata* pollen (500 mg) was extracted as in experiment 6. Results of the assays were negative		Experiments 7–10 show pollen of orchids and Malvaceae contain a substance which can be extracted with hot water and which can induce swelling of the gynostemium and stigmatic closure. Substance(s) extracted from animal organs which cause bending of *Avena* coleoptiles can also bring about swelling of the gynostemium in tropical orchids	This experiment is not impressive for several reasons not the least of which is the lack of a cotton wad only control. In fact it is possible to ask if the experiment was necessary
8	*Vanda tricolor* 8 Sept 1932 10:00 One flower self pollinated	10 Sept 1932 10:00 Gynosteium swollen and yellow. Lip yellow, Stigma closed		
	Three flowers untreated	Unchanged		
	Cotton wads impregnated with extract of guinea pig liver placed in stigmas of three flowers	Slight color changes. Gynostemium slightly swollen, Stigma slightly closed		

(continued)

Table 2-18. (continued).

Experiment number	Description of experiment and its results		Laibach's conclusions	Current explanation
	Cotton wads wetted with tap water placed in stigma of one flower	Unchanged		
9	Agar blocks from experiment 6 were placed in stigmas of *Phalaenopsis amabilis* flowers			
	(a) 12 Sept 1932: Blocks placed in stigmas of two flowers	13 Sept 1932: Stigmas half closed 14 Sept 1932: Stigma fully closed. Gynostemium somewhat swollen and turning yellow. Perianth wilting		IAA was present in these blocks. No agar only controls
	(b) 12 Sept 1932: Cotton wad saturated with water soluble, ether insoluble fraction from experiment 6 placed in stigma of one flower	13 Sept 1932: Flower unchanged 14 Sept 1932: Flower started to wilt, gynostemium became yellowish, but did not swell, stigma open		This extract probably induced some ethylene evolution No controls
	(c) 12 Sept 1932: One flower was self-pollinated	Flower was wilting, gynostemium was turning yellow and was very swollen. Stigma was closing		
	(d) 14 Sept 1932: Cotton wads saturated with chicken liver were placed in stigmas of two flowers	16 Sept 1932: Stigma half closed		Why was this experiment carried out?

(continued)

10	(a) 12 Sept 1932 12:00: Cotton wads saturated with extracts as shown below were placed in stigmas of tree flowers	14 and 15 Sept 1932: Slight swelling of the gynostemia of all nine flowers		No dry cotton and solvent only controls
	Ether soluble pollen extract.			
	Water soluble fraction of ether soluble extract			
	Water soluble fraction of ether in soluble extract			
	(b) 13 Sept 1932: One flower self-pollinated	14 Sept 1932: Gynostemium very swollen		
	(c) 14 Sept 1932: Flowers were treated as listed below			
	Cotton wads impregnated with liver extract were placed in stigmas of two flowers	14 Sept 1932: Gynostemium slightly swollen		Were the liver extract experiments necessary?
	Agar block containing liver extract was placed in the stigma of one flower	20 Sept 1932: Gynostemium very very swollen	It is possible that *Pollenhormon* and *Wuchsstoff* (a word used at the time for auxin) are one and the same substance	Reasonable conclusion
	Cotton wad wetted with tap water was placed in the stigma of one flower	No change		No dry cotton wad control

[a]The orchid names in this table are those used by Laibach and his associates. Please see Appendix 2 for updated nomenclature.

Table 2-19. Friedrich Laibach's (1885–1867) and Ernst Maschmann's experiments on the nature of *Wuchsstoff* (growth substance) in orchid pollinia (Laibach and Maschmann, 1933a).

Experiment number	Descriptions of experiments and their results	Laibach's conclusions	Current explanation
This paper reports on large number of experiments some of which repeat previous work yet again. Therefore only some of the experiments will be summarized in this table			
Pollinia were extracted by macerating them in water and keeping the mixture at 70°C for 15–30 min. The solid material was separated from the liquid through centrifugation or filtration. Assays were carried out as described in Table 2-15 (Laibach, 1932)			
Several *Avena* assays	Extract was incorporated in agar block and assayed with Went's *Avena* coleoptile	Extracts caused bending (Fig. 2-24, 2-26)	*Wuchsstoff* content in orchid pollinia is higher than in any other plant assayed up to that time	This may be still true
Assays of pollinia and extracts	Dead pollinia and extracts were applied to stigmas of their own or different orchids	The results confirmed the presence of *Wuchsstoff* in pollinia	These repetitions of of experiments which were repeated several times before may not have been needed
Several extractions of *Wuchsstoff* from pollinia showed that the substance was soluble in water, ethanol, acetone and ether and was acidic in nature. Based on this and other findings the conclusion was that the substance has the same characteristic as auxin			Orchid pollinia do contain auxin, but Laibach may have extracted more than one substance
Irradiation with UV light (313–365 nm) had no effect on the extract			
Drying pollinia under illumination and the dark did not reduce the activity or their extract			
Avena coleoptile assays and experiments with *Phalaenopsis* flowers showed that the *Wuchsstoff* was also present in pollen tubes			
Laibach and Maschmann reached the following conclusions on the basis of their experiments:			This is to be expected
	1. All extracts which caused bending of *Avena* coleoptiles also induced swelling of gynostemia, and conversely extracts which did not cause bending had no effects on gynostemnia		
	2. The growth induced by the extracts was to increase in cell size, not cell division		An auxin effect
	3. Transport of the growth substance was mainly basipetal with very little of it moving upwards or sideways		Polar transport is a characteristic of Auxin
	4. The active principle is soluble in water, ethanol, acetone and ether. It is insoluble in aliphatic and aromatic organic solvents. The substance is acidic. It can be removed with ether from sodium bicarbonate solution and after acidification from the basic aqueous phase		IAA has similar characteristics
	5. Oxidation with hydrogen peroxide reduced or eliminated the activity of the substance		
	6. Prolonged heating at 100°C [and also autoclaving for 10 min at 130°] does not reduce or eliminate the activity of the substance		

Conclusions

There can be no question that the *Pollenhormon* is the auxin indoleacetic acid (IAA; Fig. 2-24B) or a mixture of hormones which included IAA. It is also possible that Fitting's extracts contained ACC (Fig. 2-24C). Had Fitting continued to work with orchids he may have discovered auxin. Some of the pollen effects he reported are known at present to be induced by ethylene. In 1901 the Russian plant physiologist Dimitry Neljubov (1879–1926) showed that ethylene affected the growth of pea seedlings (Neljubov, 1901), but it was too much of a stretch in 1909 to connect abnormal growth of pea seedlings and wilting of orchid flowers. Even had he made the connection there was no technology at the time that would have allowed Fitting to measure ethylene evolution by pollinated orchid flowers.

In summary, there can be no question that Fitting introduced the term "hormone" into plant science (Table 2-14). Fitting even had auxin in his extracts, but did not discover it because he stopped his orchid research too soon. Frits W. Went discovered auxin.

Dedication

I dedicate my efforts to the memory of Professor Grover C. Stephen, my first and best department chair at the University of California, Irvine, one of my few deans at UCI worthy of respect and most of all my life long friend – Joseph Arditti, Professor Emeritus.

Acknowledgments We thank Jean Miller and Kathryn Kjaer for assistance with literature searches and for obtaining papers for us through interlibrary loan and Dr. Gunther Gerlach for many valuable suggestions.

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Appendix 1

Letters from Prof. Hans Fitting to Prof. Joseph Arditti
Translated and annotated by Dr. Hubert Kurzweil
Comments are between brackets.
The letters are part of a reprint collection donated by Prof. Arditti to the Singapore Botanic Gardens.

Bonn, 2 Nov 1969

Dear Dr. Arditti,

Many thanks for the reprint of the extremely interesting paper '*Effects of Auxin*' by you and Mr. Robert L. Knauff, and your equally valuable friendly letter of 23rd Oct 1969. In both of these you acknowledged in an unusually friendly and appreciative way my own orchid work, which I have done many years ago. This was indeed very good for me, now that I am 93 years of age!

Unfortunately I cannot send you the reprints that you requested as already for a few years I have not got any left, and also because I had to give up my scientific work.

I wish you great success with the continuation of your research,

With my best wishes,

H. Fitting

I hope that you can read my letter; already for some time I am no longer allowed to use the typewriter!!

Bonn, 10th November 1969

Dear Dr. Arditti,

This is my reply to your very friendly letter of 12th Nov. 1969 [two days after he wrote this one?; one of these two dates must be wrong] in which you ask "what made you observe the orchid flowers"? While I was preparing my lectures on pollination biology (1903–1907) as a 'Privatdozent' at the University of Tübingen, I was very much interested in a theory that is very common in the older German literature on pollination biology, namely that the pollinia of many exotic orchids act like a poison during cross-pollination! At the time I was not able to find out who first proposed this theory! A long time after my trip to the tropics (namely in about 1920), I got to know volume II (1921, letters) of the new edition of Fritz Müller's "Work, letters and life" (newly published by Alfred Müller, 1915–1921, in three volumes). Müller lived in Brazil for a long time, wrote several important publications on pollination biology and is the founder of the "biogenetic rule" ["biogenetic law"]. I am sure you know about him (biogeography by E. Loens, *Berichte der Deutschen Botanischen Gesellschaft* 15, 1897). In volume II (which contains his letters) there is a very important letter,

written on 1st January 1867 and addressed to Charles Darwin!! It provides the solution to my above-mentioned mystery!! On pages 104–128 he elaborates on the toxicity of the orchid pollinia! In view of your own orchid work you should definitely read this important letter! According to my notes (unfortunately these are not very clear), Fr. Müller reported in 1886 something similar in male flowers of *Catasetum* [I don't know what he means with "(gleich mir, 1920)"; this could mean that Fitting observed the same in 1920]. This was also published it in *Verhandlungen des Botanischen Vereins der Provinz Brandenburg*, 1886, volume 28, page IV (I don't know if this is also written in his letters in 1921). But what is this apparent "poison" all about? This was the starting point for my orchid research in 1907 and 1908 in Buitenzorg! Unfortunately I did not mention this in my first orchid publication in 1909a, as I thought that the apparent toxicity of orchid pollinia was already well-known in Germany at the time! The result of my Buitenzorg work: Mueller's poison is obviously my pollen hormone!! [Pollenhormon]

In 1930 and the following years Laibach confirmed that β – Indolylessigsäure (IES [English IAA]) – that was discovered long time after 1907/08 – triggers the postfloral development of the orchids with all of its consequences, just like my pollen hormone also does! But to date there has not been exact chemical proof that my pollen hormone actually is the IAA!! As we have seen repeatedly in the meantime,β – Indolylessigsäure (IAA) causes so many different reactions that one should not be surprised that it also acts similar to my pollen hormone. The exact proof, that my pollen hormone is actually IAA would obviously be very difficult. Therefore I do not really support …….. 'convincion' [there is one word illegible; could be "Ihre" = your], that the pollen hormone and "Auxin" are the same. And besides: what actually is the so-called "Auxin" chemically? A few years ago a Dutch colleague, in a publication in *Acta Botanica Neerlandica* (unfortunately I forgot the volume and the page number!), inserted a big question mark after "Auxin"!

On a personal level I can assure you that I very much enjoyed my orchid work in 1907/08 in the magnificent Buitenzorg Botanical Garden (as you say, it has "inspired" me); and also, that the substantial German Buitenzorg-scholarship which was awarded to me in 1907 (= 6,000 German Mark!!) was put to good use for our beautiful *Scientia Amabilis*. So I returned to Europe in 1908 with the great feeling, that I had done something really worthwhile with this substantial scholarship, both important and valuable, namely that I had discovered the first plant hor….. [cut off, I suppose he means hormone].

I will be especially grateful to receive, as already promised, your article on "Fitting's pollen hormones", which I will certainly be very happy about and which I regard as a great honour.

I hope that you can read my bad but age-related hand-writing …….. [partly cut off; maybe he means "Writing"] is very difficult and gives me lots of pain! My heart is weak and requires constant medical supervision!!

With friendly regards,

…….

Postscriptum: Please do not take the following comment for immodest! It is rather important [in this sentence there is one word which I cannot read]!. My Danish colleague P. Boysen-Jensen said to me in Copenhagen in 1950, that my orchid publication (1909a) has inspired him to study the chemical conductivity of the phototropic impulse in Pfeffer's Institute in Leipzig and inspired by the same (see also the historical notes on p. 21–23 in P.B. Bell's book "Darwin's biological work etc."; Cambridge; 1959). And Boysen-Jensen's short, but deservedly so widely accepted work inspired Went to his great work on the Auxins, which you appreciate so much with reason.

10th December 1969

Dear Dr. Arditti,

Many thanks for your friendly letter of 1st December. I was motivated by this letter to read carefully through all of my orchid publications once again. Therefore I can now give you additions to my earlier letters! Making these additions was rather difficult as I have been suffering from heart problems for several years (but the diagnosis of my doctors is only 'age-related heart'). Therefore I am allowed only to go on short walks of 1/2–3/3 [maybe he means 3/4] hours. Unfortunately I can no longer visit the library at the university to look at old and current literature, as my home is situated in the southern part of Bonn, far away from the Institute of Botany and the library; and I had to sell my own very large library in 1952. Therefore, when replying to queries, I have to rely on my mostly superficial notes and on my aging memory.

But I would like to draw your attention to a few important questions!

Question I. How I got my results in Bogor is actually already contained on pages 1–2 of my paper in 1909a, if you read it carefully!!: namely through detailed description of the postfloral processes and their causes. At first I did not deal with the so-called "poison" of the great Fritz Müller which you can see from the fact that in all of my papers in 1909a, 1909b, 1910 I never mentioned Müller's "poison" and pointed out that this poison is apparently my pollen hormone. {I only mentioned Hans Winkler's paper of 1905 briefly (see Fitting, 1909a, p. 69) where he refers to the pollen "poison"}. Therefore the toxicity of the pollinia was only a very minor problem of my work, and it was quite a coincidence that I found the pollen hormone in the course of my developmental-physiological studies; but I have discovered it!!, simply through systematically and well thought-through experimenting.

Question II. From where and since when did botany in Germany know about the "toxicity" of pollinia? To answer this question you should read Fritz Müller's paper carefully (cited in my paper in 1909a; 1868, p. 629ff.), maybe he mentions the "poison". The thick book of Kerner von Marilaun (1895), that I have recently looked through carefully, does not make any mention of Fritz Müller's orchid work and his "poison"; did he not know about them??

Comment: Fritz Müller's paper in *Verhandlungen des Botanischen Vereins der Provinz Brandenburg*, 1886, volume 28, also seems to be mentioned in his work "Work, letters and life" on page 471 (my own rather superficial note says 8th May 1886, probably it refers to a letter of Fritz Müller??).

Question III. Who suggested that the pollen hormone and the much later discovered Indolylessigsäure (IAA) are probably the same? (I prefer the term IAA over the ambiguous term "Auxin" = growth hormone). This was of course Laibach and his students! At least they were able to show that IAA has got the same effect on orchid flowers as the pollen extract.

Question IV. But is that the proof, that my pollen hormone is actually the same as IAA? If I understood your paper of 1969 correctly, you showed that the postfloral processes consist of partial processes which are in their principle (partly chemically) actually quite different from IAA (I was not able to read any of the papers that you cited in 1969, and therefore do not know their contents). Therefore I repeat what I said already earlier, namely that we need exact chemical proof that the pollen hormone indeed contains IAA! Laibach has not done this! Of course I don't know if you would agree with me. Perhaps one should look through the papers of Laibach and his students again carefully; but I don't think that one would find something important.

[there is something missing,]

……..; I have not got them here – my reprint collection is at the Institute of Botany!!

I was most intrigued by your mention that you will go to Bogor soon! What will be the garden (and the primitive institute), now after the Dutch have left Java?? – I wish you all the best for this wonderful trip!!

At last some literature from my notes:

I. Dolcher, Tullio. 1961. Relazioni ormonali nello sviluppe dell'ovario delle Orchidee. *Nuovo giornal botan. ital*. 68(1–2): 213–215.

II. Dolcher, Tullio. 1961. Azione delle auxine in segmenti isolati dell' asse floral. *Nuovo giornal botan. ital*. 68(1–2): 216–219.

I have not read any of these two papers, and therefore do not know what their content is!

With best wishes,
Hans Fitting

Comments in brackets are by the translator.

Appendix 2

Plant Names Used in this Chapter

Plant names used in the chapter are listed in this appendix. Currently accepted names are listed in bold face. Names follow largely the World Checklist of Monocotyledons (The Board of Trustees of the Royal Botanic Gardens, Kew. Published on the Internet; http://www.kew.org/wcsp/monocots/ accessed 16 October 2006).

Orchids

Aerides falcata **Lindl. & Paxton**
Aerides odorata **Lour.**
Arachnanthe clarkei (Rchb. f.) Rolfe = ***Esmeralda clarkei*** **Rchb. f.**
Arachnanthe sulingi (Blume) Benth. = ***Armodorum sulingi*** **(Blume) Schltr.**
Armodorum sulingi **(Blume) Schltr.**
Bletia verecunda (Salisb.) R. Br. = ***B. purpurea*** **(Lam.) DC.**
Calanthe discolor **Lindl.**
Calanthe **×** ***veitchii*** **Hort.**
Calanthe veratrifolia (Willd.) R. Br. ex Ker Gawl. = ***C. triplicata*** **(Willemet) Ames**
Catasetum **sp.**
Cattleya labiata **Lindl.**
Cattleya trianae **Linden & Rchb. f.**
Coelogyne asperata **Lindl.**
Coelogyne massangeana **Rchb. f.**
Coelogyne pandurata **Lindl.**
Coelogyne speciosa **(Blume) Lindl.**
Coelogyne swaniana **Rolfe**
Corymbis disticha (Breda) Lindl. = ***Corymborkis veratrifolia*** **(Reinw.) Blume**
Corymborkis veratrifolia **(Reinw.) Blume**
Cymbidium finlaysonianum **Lindl.**
Cymbidium sanguinolentum Teijsm. & Binn. = ***C. chloranthum*** **Lindl.**
Cymbidium virens Rchb. f., sphalm. for *C. virescens* Lindl. = ***C. goeringii*** **(Rchb. f.) Rchb. f. var.** ***goeringii***
Cypripedium acaule **Aiton**
Dendrobium antennatum **Lindl.**
Dendrobium crumenatum **Sw.**
Dendrobium fimbriatum Hook. var. *oculatum* Hook. = ***D. fimbriatum*** **Hook.**
Dendrobium macrophyllum **A. Rich.**
Dendrobium superbum Rchb. f. = ***D. anosmum*** **Lindl.**

***Dendrobium wardianum* R. Warner**
Epipactis erecta (Thunb.) Sw. = ***Cephalanthera erecta* (Thunb.) Blume**
Epipactis falcata (Thunb.) Sw. = ***Cephalanthera falcata* (Thunb.) Blume**
***Epipactis palustris* (L.) Crantz**
***Epipactis papillosa* Franch. & Sav.**
***Epipactis thunbergii* A. Gray**
Eulophia macrostachya Lindl. = ***E. pulchra* (Thouars) Lindl.**
***Goodyera repens* (L.) R. Br.**
***Gymnadenia conopsea* (L.) R. Br.**
Gymnadenia cucullata (L.) Rich. = ***Neottianthe cucullata* (L.) Schltr.**
Liparis latifolia Lindl. = ***Stichorkis latifolia* (Lindl.) Pfitzer**
***Masdevallia glandulosa* Königer**
***Odontoglossum crispum* Lindl.**
***Oncidium flexuosum* Lodd.**
***Oncidium incurvum* Barker ex Lindl.**
***Oncidium sphacelatum* Lindl.**
Oncidium sphegiferum Lindl. = ***O. divaricatum* Lindl.**
Orchis fusca Jacq. = ***O. purpurea* Huds.**
Orchis latifolia L. = ***Dactylorhiza incarnata* (L.) Soó subsp. *incarnata***
Orchis maculata L. = ***Dactylorhiza maculata* (L.) Soó**
***Orchis mascula* (L.) L.**
***Orchis morio* L.**
***Paphiopedilum argus* (Rchb. f.) Stein**
***Paphiopedilum barbatum* (Lindl.) Pfitzer**
Paphiopedilum boxallii (Rchb. f.) Pfitzer = ***P. villosum* (Lindl.) Stein var. *boxallii* (Rchb. f.) Pfitzer**
***Paphiopedilum callosum* (Rchb. f.) Stein**
***Paphiopedilum glaucophyllum* J.J. Sm.**
Paphiopedilum lathamianum, name not traced
Phaius amboinensis Blume = ***P. terrestris* (L.) Ormerod**
***Phalaenopsis amabilis* (L.) Blume**
***Phalaenopsis cornu-cervi* (Breda) Blume & Rchb. f.**
Phalaenopsis esmeralda Rchb. f. = ***P. pulcherrima* (Lindl.) J.J. Sm.**
***Phalaenopsis regnieriana* Rchb. f.**
***Phalaenopsis violacea* H. Witte**
***Platanthera bifolia* (L.) Rich.**
Platanthera yatabei Maxim. [nom. nud.]
Renanthera × *maingayi* (Hook. f.) Ridl. = ***Arachnis* × *maingayi* (Hook. f.) Schltr.**
***Rhynchostylis retusa* (L.) Blume**
Spathoglottis filuata, name not traced
Spiranthes australis (R. Br.) Lindl. = ***S. sinensis* (Pers.) Ames**
***Stanhopea insignis* Frost**
***Trichoglottis geminata* (Teijsm. & Binn.) J.J. Sm.**
***Vanda insignis* Blume**

***Vanda tricolor* Lindl.**
***Vanilla* sp.**
Zygopetalum mackayi Hook. = ***Z. maculatum* (Kunth) Garay**

Other Plants

Alpinia hookeriana Valeton (Zingiberaceae) = ***A. latilabris* Ridl.**
***Anoda cristata* Schltdl. (Malvaceae)**
Begonia geogensis (Begoniaceae), name not traced
Brassica campestris L. (Brassicaceae) = ***B. rapa* L.**
***Canna* sp. (Cannaceae)**
***Eucharis* x *grandiflora Planch. & Linden* (Alliaceae)**
***Hedychium* sp. (Zingiberaceae)**
***Hibiscus rosa-sinensis* L.(Malvaceae)**
***Hibiscus schizopetalus* (Mast.) Hook. f. (Malvaceae)**
***Hibiscus syriacus* L. (Malvaceae)**
***Hyacinthus orientalis* L. (Asparagaceae)**
Impatiens rodgrigesi (Balsaminaceae), name not traced
***Narcissus jonquilla* L. (Alliaceae)**
***Prunus mume* Siebold. & Zucc. (Rosaceae)**
Salix thunbergiana (Salicaceae) = ***S. gracilistyla* Miq.**
Thea japonica (Theaceae) = ***Camellia japonica* L.**