

75 Years ago *Arabidopsis* was first suggested as a Model Plant – But how did *Arabidopsis* Col-0 become the standard Natural Accession?

A short history of *Arabidopsis thaliana* (L.) Heynh. Columbia-0

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The Origin of *Arabidopsis thaliana* Research (1905 – 1943)

Modern work with *Arabidopsis thaliana* goes back to the German botanist Friedrich Laibach who, while working as a Ph.D. student in the laboratory of Eduard Strasburger in Bonn, analyzed the number of chromosomes in different plants that he had collected around Bonn and his hometown Limburg^{1,2}. The first *Arabidopsis* plants to be experimented on were collected by Laibach in 1905, and belonged to the natural accession Limburg (Laibach introduced a system of naming the natural accessions after the places he collected them from)². Laibach found that they carried 5 pairs of chromosomes, one of the smallest numbers known at the time (he published his results in 1907, even though *Arabidopsis* was only included in the written thesis, but not specifically mentioned in the paper)¹⁻³. Unfortunately, the natural habitat of the Limburg population was destroyed shortly after to make way for the new “Autobahn” (highway), connecting the cities of Frankfurt and Köln². At the time, *Arabidopsis* was ‘only known to florists and taxonomists, who had nothing better to do than constantly change its name and systematic positioning’, as Laibach put it in 1965². However, he became interested in the little weed, and between 1930 and 1950 collected seeds from over 150 different natural accessions (or races, as he called them) of *Arabidopsis* from anywhere he or his colleagues travelled to^{2,4}. Laibach kept all of these individual seed lines meticulously organized and maintained in his Department at Frankfurt University, and his collection eventually formed the foundation of the *Arabidopsis* Information Service (AIS) seed bank in the 1960s, which itself served as the basis for the modern Columbus (ABRC), Nottingham (NASC) and Tsukuba (RIKEN) stock centres decades later^{2,5,6}.

29 *Arabidopsis thaliana* First Proposed as a Plant Model (1943 – 1957)

30 Laibachs' interest and preliminary studies of *Arabidopsis* eventually resulted in a now famous
31 publication titled 'Arabidopsis Thaliana (L.) Heynh. als Objekt für genetische und
32 entwicklungsphysiologische Untersuchungen' ('Arabidopsis Thaliana (L.) Heynh. as an object
33 for genetic, developmental and physiological analyses'), in which Laibach points out the benefits
34 of working with *Arabidopsis* (easy to grow, small genome, short lifecycle, high seed yield, can be
35 crossed and mutated...)³. Based on these observations he proposed to adopt *Arabidopsis* as a
36 model organism for plant science, pointing out how comparable it is in its suitability to the 'prime
37 example' of other models, *Drosophila melanogaster*³. This proposal however, was largely

38 ignored by the scientific community at the time, who needed almost another 40 years to finally
39 see the light and adopt *Arabidopsis* as a plant model system⁷. One academic who shared
40 Laibach's enthusiasm for *Arabidopsis* was György P. Rédei from Hungary, who in 1955 had just
41 finished his Ph.D. thesis, working on tomato and wheat⁸. After reading Laibach's article, Rédei
42 recognized the potential of *Arabidopsis* for genetic studies, and with the help of his supervisor,
43 Prof. Györffy, he asked Laibach for some *Arabidopsis* seeds to start his own work on this new
44 model⁸. The seeds he obtained were the four natural accessions Graz, Limburg, Estland and
45 Landsberg⁹. Rédei took these four lines with him, when he left Europe to start his own laboratory
46 at the University of Missouri in Columbia, Mo⁹. For the next 20 years Rédei remained the only
47 researcher working on *Arabidopsis* in the United States; or, as his former colleague Prof. Doug
48 Randall put it, “*George was 20 to 30 years ahead of his time*”¹⁰. This situation, however, made it
49 incredibly hard for Rédei to receive funding⁹. In fact, one of his funding applications to the
50 National Science Foundation was now famously rejected on the basis that ‘*the genetics panel*
51 *does not believe that it is worthwhile to develop Arabidopsis as a new model organism for*
52 *genetic studies because only prokaryotes can contribute significantly to new knowledge*’⁹. But
53 Rédei refused to give up on *Arabidopsis* and from the four seed lines he had received from
54 Laibach, chose Landsberg as his model for future work. This choice was due to that Estland
55 phenotypically did not match its description and Graz was late flowering, while Landsberg
56 matched the description and seemed vigorous and healthy (it is not clear on which grounds
57 Limburg was dropped)⁹.

58 The Columbia and Landsberg *erecta* lines Emerge (1957 – 1965)

59 In 1957 Rédei used his Landsberg seeds in a mutagenesis experiment, where he irradiated the
60 seeds with X-rays and then screened for mutants with interesting phenotypes (meanwhile, in
61 Australia, John Langridge was doing the same for Estland seeds he had received from
62 Laibach)^{9,11–13}. Gene mutagenesis by X-ray irradiation had been described in the 1920s for
63 *Drosophila* and *Antirrhinum*, and one of Laibach's students, Erna Reinholtz, went on to establish
64 this technique for *Arabidopsis* seeds^{4,14,15}. One of the first mutants Rédei recovered was the
65 *erecta* mutant, which, with its stunted growth, appeared to be quite sturdy, and he thought it
66 might come in handy for further experimentation^{9,16}. He published the Landsberg *erecta* mutant
67 in a paper dealing with heterosis, despite not being sure if the importance of his observation
68 warranted a full publication¹⁶. His paper therefore opens with the paragraph ‘*The author feels*
69 *somewhat hesitant to add to the large volume of the literature on the subject but its practical*
70 *importance and theoretical interest prompt the decision in favor of this brief account*’¹⁶.
71 However, in his mutagenesis screen Rédei also realized that the original Landsberg population
72 was actually not a homogenous line, but appeared to be a mix of different lines^{9,11}. Therefore, he
73 chose a single plant from the batch that he had not irradiated, to establish a new, clean line for all
74 further studies^{9,11}. Following Laibach's example of naming the different natural accessions after
75 the location where he found them, he named his new line Columbia^{9,11}. So interestingly,
76 Columbia is an American plant by name, but a central European plant by genetic heritage –
77 something that can be demonstrated experimentally, when analysing its genetic polymorphisms¹⁷.

78 In 1959, another plant biologist, Willem Feenstra from the University of Groningen in the
79 Netherlands, visited Rédei in Columbia and took the Landsberg *erecta* line with him for his own
80 research, establishing this line as a standard in Europe, while Rédei concentrated his work on his
81 own Columbia line^{9,11,18}.

82 ***Arabidopsis thaliana* gets its Breakthrough (1965 – 1996)**

83 In the following two decades, interest in *Arabidopsis* research slowly increased. By the mid-
84 1960s, the AIS (<https://www.arabidopsis.org/ais/newaisvols.jsp>) was established as a yearly
85 newsletter to connect the small *Arabidopsis* research community, and in 1965 the first
86 International Arabidopsis Symposium in Göttingen, Germany, already attracted a full 25
87 participants^{19,20}. The AIS would eventually evolve into the now invaluable The Arabidopsis
88 Information Resource (TAIR) database²¹. As a result of this increased interest, György Rédei
89 decided to take up Laibach's suggestion from 1943, and published the second article calling for
90 the acceptance of *Arabidopsis* as a plant model in 1975, simply titled 'Arabidopsis as a genetic
91 tool' (where he pointed out the same benefits Laibach had already pointed out 30 years earlier)²².
92 Following this publication and a couple of highly influential papers from people like Maarten
93 Koornneef (who worked with Will Feenstra), or Chris R. Somerville and Elliott M. Meyerowitz
94 (converts from the model organisms *Escherichia coli* and *Drosophila melanogaster*,
95 respectively), *Arabidopsis* finally got its break in the early 1980s^{7,23–25}. With *Arabidopsis* now
96 finally established, the third article discussing its role as a model (published in 1985 and pointing
97 out the same benefits that Rédei and Laibach had pointed out 10 and 40 years earlier) was now
98 published in the prestigious *Science* journal⁷.

99 **Col-0 takes over as the Standard Accession (1996 – today)**

100 During the next decade, *Arabidopsis* research was mostly done using the Landsberg *erecta*
101 accession, even though Columbia also regularly appeared, especially in US laboratories or from
102 groups that had obtained seeds directly from Rédei. However, this was about to change when, in
103 1996, Columbia was chosen as the natural accession for the sequencing and annotation of the
104 complete *Arabidopsis* genome²⁶. Despite Landsberg *erecta* being more commonly used at the
105 time, this choice was the obvious one in this case, because the Landsberg *erecta* line had
106 previously been subjected to X-ray irradiation, and therefore carried several unnatural mutations,
107 while Columbia had been maintained as a clean homozygous line^{11,26}. Shortly after the genome
108 was eventually published in the year 2000, Columbia was also chosen as the natural accession for
109 a genome-wide mutagenesis project at the SALK institute in San Diego, resulting in the SALK
110 collection of T-DNA insertion lines – still the biggest resource of ready-to-order *Arabidopsis*
111 mutants²⁷. Following these two massive projects, it was clear that Columbia was firmly
112 established as the number one natural accession for *Arabidopsis* research, while the use of
113 Landsberg *erecta* has been declining ever since. And this all just because the Landsberg batch
114 that György Rédei received from Friedrich Laibach in 1955 was not a homogenous line.

115 **Addendum> What about the '(L.)' and the 'Heynh.' behind *Arabidopsis thaliana*, and the '0' behind Col?**

117 The '(L.)' and 'Heynh.', which are often found after *Arabidopsis thaliana*, are so-called
118 'authorities' - the official author abbreviation of the person who gave the plant its name²⁸.
119 Though *Arabidopsis thaliana* was first described by Johannes Thal, who gave it the name
120 *Pilosella siliquosa minor*, it was Carl Linnaeus who named it *Arabis thaliana* (*thaliana* in honour
121 of Johannes Thal)^{29,30}. Therefore, the '(L.)' behind genus and species is the author abbreviation
122 for Carl Linnaeus^{29,30}. Botanist Gustav Heynhold then merged similar plants into one new genus,
123 *Arabidopsis*, signifying *Arabis-like*, and added his own author abbreviation, 'Heynh.', behind the
124 one from Linnaeus (Heynholds book '*Flora von Sachsen*' is generally cited here, though I could
125 only find *Arabidopsis* in his book '*Nomenclator botanicus hortensis*')^{29,31,32}. The '0' behind the
126 Col name, on the other hand, signifies the source of an individual seed line³³. Over the years,
127 different laboratories that received Col seeds from György Rédei have propagated and
128 maintained their own inbred lines of the original batch. When all these lines were later donated to
129 the seed centres, a numbering system was developed to be able to distinguish these individual
130 lines³³. In this system, George Rédeis' Columbia line in the ABRC stock centre would be named
131 Col-1/CS3176, or Col-1 in short³³. The name is made up of [wild type]-[originator]/[maintainer
132 stock-#], with the wild type being 'Col', the originator George Rédei, who was designated the
133 number 1, and the maintainer, the ABRC stock centre, carrying it under the stock number 3176³³.
134 The line donated by Shauna Somerville to the ABRC, a direct descendent of Rédeis' Col-1, is
135 Col-2/CS907, or in short, Col-2³³. Confusingly, the Col-0 line (Col-0/CS1092) is actually a
136 descendent of Rédeis' Col-1 line³³. It received the lower originator number 0 because it was
137 already maintained and propagated in the original AIS-seed bank by Albert Kranz, and is
138 therefore an 'older' stock⁵.

139 **More 'History of *Arabidopsis*' Resources:**

140 - Friedrich Laibach - 60 Jahre *Arabidopsis*-Forschung, 1905-1965²
141 - György P. Rédei - *Arabidopsis thaliana* (L.) Heynh. A review of the genetics and biology²⁹
142 - Elliot M. Meyerowitz - *Arabidopsis thaliana*³⁴
143 - György P. Rédei - A heuristic glance at the past of *Arabidopsis* genetics⁹
144 - Elizabeth Pennisi - *Arabidopsis* Comes of Age³⁵
145 - Elliot M. Meyerowitz - Prehistory and history of *Arabidopsis* research³⁶
146 - Chris R. Somerville, Maarten Koornneef - A fortunate choice¹⁹
147 - Nicholas J. Provart et al. - 50 years of *Arabidopsis* research³⁷

148

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