Further Studies on the Apogamy and Hybridization of the Hieracia

(Experimental and Cytological Studies on the Hieracia, by C. H. OSTENFELD and O. ROSENBERG, Part III)

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(with Plate 4).

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Introduction.

In 1906 I published a paper on some experimental investigations on the apogamy and hybridization of the Hieracia (OSTENFELD 1906, 1907). It was the beginning of rather extensive studies on the reproduction of this interesting genus, which studies I am still pursuing and of which I shall here publish some results. I do not mean to say, however, that the investigations are near their end, far from it, and I can very well repeat what I wrote in 1906 (l. c., p. 247), "that at present we are only at the very beginning of our knowledge of these phenomena". In the meantime, however, I have discovered facts which, in my opinion, are rather interesting and which I think worthy of publication. They touch upon both problems, apogamy and hybridization.

As to the apogamy, a species has been found whose "races" differ in this respect, and we have here, in all probability, the apogamy *in statu nascendi.* And with regard to the hybridization it has become apparent that the first hybrid generation (F_1) affords such a complexity of combinations of the characters[1]), while the later hybrid generations (F_2, F_3, etc.) breed true, that — for the one subgenus — an understanding of the famous polymorphy of the genus is suggested.

A good deal of the following remarks may perhaps seem fragmentary; this is due, at least in part, to the fact that several experiments have failed, and that transplanting and the like have checked the investigation. Moreover, I have been away from the Gardens part of the summer every year, and the summer of 1909 was so unusually rainy and cold as to greatly influence the thriving of the delicate species.

My friend, Dr. O. ROSENBERG of Stockholm has, as before, taken his share in the experiments in that he has had collected materials for cytological use of all my experimental plants. I only need to point to his well-known cytological investigations on the Hieracia (ROSENBERG 1906, 1907), in order to show the benefit I have had from his excellent collaboration.

I.

Apogamy.

(Castration Experiments.)

In 1906 I summed up the results of my experiments on the apogamy of the Hieracia in the following way (l. c., p. 235): — „In

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[1]) H. WINKLER (1909, p. 342) has advanced the theory: „Es scheint demnach, als sei es ein wesentlicher Unterschied des Pfropfbastardierungsprozesses von dem sexuellen Bastardierungsprozeß und für ihn besonders charakteristisch, daß er nicht wie dieser eine im wesentlichen homogene, sondern eine vielgestaltige Generation F_1 liefert", and STRASBURGER (1909 b, p. 519) seems to agree with him herein and expresses himself still more explicitly, saying: „Pfropfbastarde, denen zudem die besondere Eigenschaft zukommen soll, daß sie nicht homogen wie sexuelle Bastarde, sondern vielgestaltig sind", and further: „Derartiges [verschiedene Kombinationen der Merkmale] ist für sexuelle Bastarde nicht bekannt." Both authors must have forgotten that heterogeneity in F_1 has been found in several cases in sexual hybrids, e. g. in *Rubus* and, already discovered by MENDEL, in *Hieracium*. It is therefore not a special property of the supposed grafting hybrids.

the genus *Hieracium* we have apogamic and non-apogamic species together with transitions between both kinds. The three subgenera are in this respect not quite alike; the subgenus *Stenotheca* representing the most primitive stage with typical fertilization; the subgenus *Pilosella* being intermediate as it comprehends both apogamic and typically fertilizing species, nevertheless mostly apogamic; and the subgenus *Archieracium* representing the most developed stage with nearly all species apogamic, only excepting the *H. umbellatum* group." — This main result is still valid, but several details have been found, enlarging our knowledge of the phenomena.

1. Subgenus Stenotheca.

For the subgenus *Stenotheca* I have nothing really new to add; my plantings of the species of this subgenus have not been successful. These North American species seem to require a longer and warmer summer than we have in Denmark.

In the spring of 1908 I succeeded in getting seeds of *H. Gronovii* L., *H. longipilum* Torr. and *H. scabrum* Michx.; they were sown immediately at the end of April, but did not reach flowering that year. After wintering in pots in a frost-less place they were planted out in 1909, but is was not till towards the end of September that a few specimens of *H. Gronovii* came to flowering, and then it was too late to try castration. No fruit, further, was developed in any of the plants left to themselves.

My plants of the only European species of this group, *H. staticifolium* Vill., did not fruit in 1909, neither without nor after castration, so that I have nothing positive to say about this species either.

The plants of *H. venosum* L. and *H. Gronovii* L. used for my experiments in 1905 (OSTENFELD 1906) and their offspring died already in the winter 1906—1907; they did not seem to be able to endure our winter, and in the summer of 1906 they did not flower early enough to give ripe fruits. Thus I cannot say anything more about the reproduction in the subgenus *Stenotheca* than in my paper of 1906, viz., that both the two hitherto examined species require normal fertilization in order to produce seeds capable of germinating.

It will be of great importance to have some more species of this subgenus examined, and I think it a promising task to an American botanist to subject this matter to examination. He will also be able, more easily than I am, to procure rich material of seeds. It will be specially interesting, if he could get seeds of the peculiar Andine species.

2. *Subgenus Archieracium.*

The castration experiments with species of the subgenus *Archieracium* have been continued in 1906—1909, always with new species, in order to examine as many as possible of the immense number of species of this subgenus. In this way it was hoped to ascertain how common apogamy is in this subgenus and whether certain sections perhaps differed from the others.

I think it appropriate here briefly to explain my method of investigation, whose main point is the so-called "castration" invented by C. RAUNKIAER (1903):

The seeds of the species to be examined are always sown in small pots with baked soil to prevent contamination by other Hieracia; when they have germinated, they are transplanted to somewhat larger pots with good nutritive soil (the baked soil is not good for the growth of the seedlings), and when they have reached a sufficient size, generally 5 1) individuals are planted out in beds. If the sowing has taken place in spring, some species come to flowering in autumn, and the experiments may then be made, but a good and plentiful flowering and favourable conditions for experiments are generally not obtained before the next summer. When the flowering has begun, a number of heads of one individual, and preferably in the same shoot of the plant, are chosen for castration; they must not yet have opened, but must be so near flowering, that it can be expected in 2 or 3 days. The castration is made by cutting off, with a sharp razor, the upper half of the head. By this operation are removed: the upper part of the involucral bracts, the corolla to the tube, the anthers and the upper part of the styles with the stigmas, besides the uppermost part of the pappus rays. There remain: the lower part of the bracts, the ovary and the lower part of the pappus. It is thus not a castration in the proper sense of the word, but an operation which removes both the male element and the conducting parts of the female element.

The castrated head becomes covered on the wounded surface with a quickly coagulating latex, which, however, later, as a rule, drops

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1) In experiments to show the heterogeneity or homogeneity of crosses and the like, of course, all the material is used.

off or is removed. Notwithstanding this violence, the heads of the apogamic species develop themselves undisturbedly and the fruits ripen as usual, but the heads are, in the ripe state, when they have opened, easily distinguished from the intact heads by the short pappus, which renders them much smaller in size and less conspicuous.

By this "castrating" process we would imagine that every possibility of fertilization has been removed. The objections which might be raised, can all be refuted, and they fall to the ground before the cytological investigations of ROSENBERG (1906, 1907) in the apogamic species. The seeds of the castrated head are always sown in order to test their germinating power, and the plants raised are generally preserved till full development to compare them with their parents.

In the Hieracia — as in the other *Compositae* — not all the fruits in a head develop, so that they contain a seed capable of germinating. With a little practice one can rather easily distinguish with great probability the full fruits (that is, those which have seeds capable of germination) from the empty ones, merely from their outer appearance. The empty fruits are generally somewhat smaller and more slender and of a paler colour (pale-brown to dark-brown), whereas the full ones are bigger and plumper and, in most species, of a black or black-brown colour (in some species brown in different shades, in a few species pale-brown, almost straw-coloured). The percentage of empty fruits in a head varies greatly in the different species, in the different plants of the same species, and even in the same plant, according to the season and from year to year, but the heads which ripen about the same time in the same plant have no doubt about the same proportion of empty fruits and full ones.

Now it may be supposed that this proportion is altered by the castration. This seems probable considering that certain species of the subgenus *Pilosella*, which produce fruits apogamically, are also able to hybridize, which requires a fertilization of those ovules that develop into seeds from which hybrids come forth. The investigations of ROSENBERG have also shown that in these species a few normally developed embryo-sacs are found. In such cases the number of full fruits should be smaller in castrated heads than in heads which have had an opportunity for pollination from the visits of insects, so numerous in these plants (especially of bees, humble-bees and butterflies).

By examining a sufficient number of castrated and non-castrated heads of the same plant one should now be able to decide the question. This means, in other words, to answer the question, whether the plant concerned has wholly lost the power of developing fertilized seeds or some flowers of each head require fertilization in order to produce seeds, while others develop seeds apogamically. I think that this way of solving the problem is better than that of the microscopical examination. Then, if only a small number of the flowers require fertilization, it is very difficult by means of microscopical investigation to find the rare stages in the development of the embryo-sac, which show the phases of chromosome-reduction and which consequently prove the necessity of fertilization¹).

A difficult thing to find out is, how great a numerical material is required to get trustworthy results from these investigations, and here I am sorry to say that my material is hardly sufficiently extensive. My tables (I—III) show just that the greater the numbers are, the better the percentages agree.

In 1906 I could enumerate 14 species of *Archieracium* in which I had found apogamy. As the tables (I and II) show, the number of forms has now increased to **60.** The seeds of most of these I have had from various Botanical Gardens from their seed catalogues. The names under which these seeds were received have in many cases been wrong, and to get better determinations I applied to our best hieraciologist, Dr. H. DAHLSTEDT of Stockholm and asked him to determine my experiment-plants. I take here the opportunity of expressing my sincerest thanks to him for his obliging answer to my request. His determinations have led to the number of examined forms being considerably diminished; it comprehends only about 33 species, taken in a very wide sense.

The species examined belong to very different groups of the subgenus, and considering that among all the experiment plants only one species, viz. *H. virga aurea* Coss. — setting aside the forms of *H. umbellatum* L. and the nearly allied *H. lactaris* Bert. — has not been found to be apogamic, I think I am justified in saying that almost all the numerous species of the subgenus Archieracium are apogamic. There is no reason to go through the list of the single species, it must be sufficient to refer to the

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1) I think it hardly correct, therefore, when S. MURBECK (1904, p. 294) concludes that, because in three *Hieracium* species examined he never found pollen tubes in the style nor in the micropyle, "die drei betreffenden Arten sehr wahrscheinlich stets parthenogenetisch sind". The result is, in all probability, right, but the conclusion is not allowable.

Table I, where they have been put down alphabetically. The species belong to both sections: *Aurella* and *Accipitrina* into which A. PETER (1894) in ENGLER & PRANTL, Natürliche Pflanzenfamilien, divides *Archieracium*, and almost all the 23 groups, into which the two sections have been divided, are represented. Of course, it would be desirable to get more of the aberrant species examined than I have succeeded in getting into cultivation, but the seed catalogues do not present many more than I have got hold of, and otherwise it is difficult to get seeds. I may especially point out the desirability of studying the South European forms (mostly group *Italica* PETER) and the group *Pseudostenotheca* where differences might perhaps be found.

Of the species enumerated in the table, I may direct attention to *H. alpinum* L., var. *Halleri* Vill.; it has the peculiarity that the heads never open; the yellow tips of the corollas are seen peeping out of the bracts, but they do not reach farther. In spite of this, the plant has plenty of fruits with seeds capable of germinating. On the whole several forms of *H. alpinum* seem to have this peculiarity, in good harmony with the apogamy.

Further it is worth noticing that *H. canadense* Michx. which is classed among the group *Umbellata*, is apogamic, in contrast to its allies, *H. umbellatum* and *H. lactaris*. Furthermore, it is a native of North America, so that not all North American species require fertilization, as do the species of *Stenotheca*. — With regard to our northern *Archieracia* I think I can say that I have examined species of all groups and found that all are apogamic with exception of *H. umbellatum*.

If we turn to the question, if something can be said numerically whether the species are absolutely apogamic or not, I think that the numbers given in Table I permit the following conclusion: by far most of the examined species are absolutely apogamic. The percentage of full fruits is not disturbed by the castration in any degree worth mentioning, and the deviations go now to the one, now to the other side.

The numbers given under *H. pulmonarioides* Vill. present a fine example. Of this easily recognisable species I have had experiment plants from 4 different sources, and they formed fruits very well and did not show any dissimilarity in their outer appearance. Of these 4 sets one shows a slight tendency in favour of the castration (83 : 80 p. ct.); while the others go a little to the other side (97 : 99; 97 : 98; 69 : 76 p. ct.); these numbers refer to a great many fruits and are therefore more trustworthy than many of the other numbers.

Table I.

				A. Castrated Heads.				B. Not castrated Heads.				
No.	Archieracium I	Origin of the Plants	Year of the Experiments	Number of Heads.	Full Achenes	Empty Achenes	Percentage of full Achenes	Number of Heads.	Full Achenes	Empty Achenes	Percentage of full Achenes	Difference between A and B, Percentage
234	*alpinum, Halleri* Vill.	Zürich	1907	3	226	40	86	1	146	74	66	+ 20
224	*anglicum* Fr.	Dublin	1907		x >	y						
273	*balcanum* Uechtr.	Budapest	1906		329	25	93		94	8	92	+ 1
228	*bifidum* Fr. (?), an spec. nova?	Salzburg	1906		307	47	87		151	10	94	÷ 7
	boreale Fr.	Svendborg (spont.)	1909	5	302	32	90	5	291	16	95	÷ 5
377	*boreale* Fr., coll.	Stockholm	1909	8	248	399	38	5	193	190	50	÷ 12
257a	*boreale* Fr., coll.	Lille	1906		33	116	22					
327$_2$	,, ,, ,,	Offspring of 257^a	1908	9	181	332	35	4	62	156	28	+ 7
327$_2$	,, ,, ,,	,, ,, ,,	1909	5	104	253	29	5	145	245	37	÷ 8
269	*boreale* Fr., aff.	Dublin	1906		157	110	59		280	153	65	÷ 6
246	*boreale, chlorocephalum* Uechtr.	Klausenburg	1906		214	76	74		298	51	83	÷ 9
241	*Bornmülleri* Freyn	Göttingen	1907		195	249	44		221	308	42	+ 2
218	*bupleuroides, Tatrae* Griseb.	Klausenburg	1907	4	739	105	88	4	705	102	87	+ 1
250	*canadense* Michx.	Petersburg	1907		217	11	95		262	41	86	+ 9
251	*canadense* Michx.	Paris	1906		115	90	56		73	87	45	+ 11
276	*canadense* Michx., aff.	Northampton, Mass.	1906		162	127	56		182	145	56	0
236	*carpaticum* Griseb.	Budapest	1906		153	3	97		103	4	96	+ 1
217	*compositum* Lap.	Budapest	1907		x >	y						
227	*corruscans* Fr., subsp.	La Mortola	1907		472	228	67		401	239	63	+ 4
275	*Dewarii* Boswell	Dublin	1907		377	34	92		250	21	92	0
265	*hirsutum* Bernh., Fr.	Greifswald	1969		242	97	71		326	90	78	÷ 7

277	*hirsutum* Bernh., Fr.	Madrid	1906		734	27	96		456	21	9[illegible]	0
267	*intybaceum* Jacq.	Marburg	1906		97	9	92		15	1	94	÷ 2
267	,, ,,	,,	1907		252	14	95		132	12	92	+ 3
225	*iricum* Fr.	Dublin	1907		291	83	79		488	152	76	+ 3
229	*laevigatum* Willd.	Madrid	1906		152	101	58		128	22	85	÷ 27
238	*laevigatum* Willd.	Leipzig	1906		322	196	62		206	83	71	÷ 9
222	*longifolium* Schleich.	Lausanne	1907		280	189	60		413	241	63	÷ 3
244	*lycopsifolium* Froel.	Salzburg	1906		338	32	91		190	9	95	÷ 4
376	*porrifolium* L.	Stockholm	1909	7	621	17	97		427	11	97	0
264	*prasiophaeum* Arv.-Touv., subsp.	Triest	1906		255	42	86		447	37	92	÷ 6
247	*prasiophaeum* Arv.-Touv , subsp.	Madrid	1906		504	97	84		452	78	86	÷ 2
242	*prasiophaeum* Arv.-Touv., subsp.	Berlin	1907		486	30	94	6	302	51	85	+ 9
262	*prenanthoides* Vill., subsp.	Stockholm	1906		99	41	71		179	34	84	÷ 13
216	*pseudoillyricum* Zahn, forma	München	1907		67	1	98	4	174	7	96	+ 2
221	*pulmonarioides* Vill.	Nancy	1907	7	563	18	97	4	302	2	99	÷ 2
231	*pulmonarioides* Vill.	Lyon	1907	11	819	167	83	12	724	181	80	+ 3
237	*pulmonarioides* Vill.	Berlin	1907	6	522	19	97	6	470	11	98	÷ 1
271	*pulmonarioides* Vill.	Krakau	1907		428	189	69		626	193	76	÷ 7
	rigidum Fr., coll.	Svendborg (spont.)	1909	5	211	79	73	5	309	21	94	÷ 21
454	*sabaudum* L., subsp.	St. Louis	1909	5	180	97	65		259	23	92	÷ 27
	silvaticum L., coll.	Svendborg (spont.)	1909	10	439	49	90	5	199	14	93	÷ 3
	silvaticum L., aff.	Herculesbad (spont.)	1907		192	51	79					
235	*speciosum* Hornem.	Dublin	1906		167	72	70					
220	*speciosum* Hornem.	Breslau	1907	7	786	310	72		347	142	71	+ 1
13	*virosum* Pall.	Breslau	1906		107	43	71		227	92	71	0
263	*virosum* Pall.	Madrid	1906	1	12	23	34					
	viscosum Arv.-Touv.	Alpes marit. (spont.)	1906		x >	y						
	vulgatum (Fr.) Almq.	Svendborg (spont.)	1909	4	81	66	55	5	192	39	83	÷ 18
215	*vulgatum* Fr., coll.	Göttingen	1906		472	32	94					

Of course these countings are based on gatherings of castrated and non-castrated heads of the same individual (generally even from the same shoot) and taken at the same time. How necessary it is to make the comparison only between gatherings from the same year is shown by the following case: in 1908 the offspring of a form of *H. boreale* Fr. (from Lille) turned out in favour of apogamy (difference: 7 p. ct.), while in 1909 the same individual gave the reverse result (8 p. ct. in favour of fertilization).

The objection that such a sorting from the outer appearance into full and empty fruits is uncertain and ought to be replaced by germination experiments, will apply in the same degree both to the castrated and to the non-castrated fruits and may therefore be dismissed as unimportant for a purely comparative consideration[1]).

If we go through Table I, we still find some deviations so considerable that we cannot explain them as casual. The above mentioned form of *H. alpinum* seems to have had advantage from the castration (86 : 66), but I think we ought not to regard this case as convincing, as only the fruits in one non-castrated head have been counted, and in these species with few and large heads the largeness of the heads varies considerably.

The other more noteworthy deviations are, 1°: *H. sabaudum* L. where the castration no doubt has diminished the fruiting power (65 : 92); 2°, the case is similar with *H. laevigatum* Willd., of which there are countings of two different sets and of which one set has a great deviation (58 : 85), the other only a small one (62 : 71), both in favour of fertilization, 3°, and finally, a *H. vulgatum* Fr. and a *H. rigidum* Fr., both from Svendborg in Denmark, seem to show the same (55 : 83 and 73 : 94). As to these deviations, the differences in percentage between castrated and non-castrated fruits seem to indicate, that these species have not wholly lost the power of having fertilized fruits[2]). If we were to try to make hybrids within the *Archieracia*, we have here hints, which species we are to use.

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[1]) In order to get an idea how great the germinating power is in the fruits considered as full, I have made a simple germination experiment, laying "full" fruits on wet filter-paper under glass in an ordinary room. The result was in one case 83 p. ct. germinated seeds, in another 70 p. ct.

[2]) The supposition is only of a restrained value, as the investigations are few, and most of the deviations are from 1909 with its rainy summer. Thus it is possible that the frequent rains may have had more influence on the heads made open through castration than upon the intact heads, which are protected by their bracts.

Table II.

No.	Archieracium II	Origin of the Plants	Year of the Experiments	A. Castrated Heads				B. Not Castrated Heads				Difference between A and B, Percentage
				Number of Heads	Full Achenes	Empty Achenes	Percentage of full Achenes	Number of Heads	Full Achenes	Empty Achenes	Percentage of full Achenes	
262	*virga aurea* Coss.	Roma	1906		0	∞	0		194	54	78	
262	,, ,, ,,	—	1909		0	∞	0		x	y		
383	*lactaris* Bert.	Lyon	1909	8	0	∞	0		152	227	40	
253	*umbellatum* L., s. l.	St. Petersburg	1906	8	0	∞	0		24	32	43	
253_1	,, ,,	—	1909		0	∞	0	5	152	372	29	
253_4	,, ,,	—	1909		0	∞	0		x <	y		
256	*umbellatum* L., s. l.	Madrid	1906	2	0	∞	0		117	86	58	
256_1	,, ,,	—	1909		0	∞	0	5	313	202	61	
257_2	*umbellatum* L., s. l.	Lille	1907	3	0	∞	0		127	61	68	
257_1	,, ,,	—	1909		0	∞	0		339	222	60	
257_2	,, ,,	—	1909		0	∞	0		x >	y		
258	*umbellatum* L., s. l.	Stockholm	1906		0	∞	0		x	y		
258_3	,, ,,	—	1907		0	∞	0	10	674	342	66	
258_3	,, ,,	—	1909		0	∞	0		291	156	65	
259	*umbellatum* L., s. l.	Kristiania	1906		0	∞	0		340	84	80	
281	*umbellatum* L., s. l.	Leiden	1906		0	∞	0		89	378	19	
281_5	,, ,,	—	1909	12	0	∞	0		39	95	29	
389	*umbellatum* L., s. l.	Zürich	1909		0	∞	0	8	646	113	85	
446	*umbellatum* L., s. l.	Lithauen (spont.)	1909		0	∞	0	5	275	183	60	
449	*umbellatum* L., s. l.	Danmark, Skaarup (spont.)	1909		0	∞	0	5	343	97	78	
	umbellatum L., s. l.	Svendborg (spont.)	1909		0	∞	0	5	219	217	50	
261	*umbellatum* L., s. l.	St. Petersburg	1906		274	75	79		214	22	91	÷ 12
261_{3+4}	,, ,,	—	1907	10	640	142	82	10	655	169	79	+ 3
261_2	,, ,,	—	1909	6	184	218	46	6	347	99	78	÷ 32
261_3	,, ,,	—	1909	5	196	156	56	5	316	51	86	÷ 30
261_4	,, ,,	—	1909	6	257	166	61	6	345	122	74	÷ 13
329_2	,, ,,	Offspring of 261 (1906)	1908	5	208	122	63	5	152	138	52	+ 11
329_2	,, ,,	—	1909	8	295	286	51	8	541	104	84	÷ 33

The two sets of *H. canadense* Michx. give a tendency in favour of castration (95 : 86 and 56 : 45), while the form named *H. canadense, aff.* gives no tendency (56 : 56). Here more investigations must be made before an opinion can be expressed.

As mentioned above, *H. virga aurea* Coss. is not apogamic; I have tried castration several times, but always got the same result, that the heads are quite sterile if castrated. When left to itself, it fruits rather well, and from these fruits come a very heterogeneous offspring, which indicates that crossing must have gone on. It flowers too late, however, in our latitude to be a good experiment plant. —

Among the *Archieracia* is still left the group *H. umbellatum*, which I have studied more thoroughly, as it seems to me to be particularly interesting. When, in 1905, it had become evident that four forms of this group required fertilization in order to fruit, or more correctly that they did not fruit after castration, I procured from the seed catalogues as many forms of this group as possible. I have in the years since then examined altogether twelve forms (sets), see Table II. From the castration experiments made in 1906 I got the result that two sets of *H. umbellatum* were apogamic, the other sets not. I had, however, to go to work with caution, for the seeds received from the Botanical Gardens were so untrustworthily determined that not even the five experiment plants selected from a sowing were similar. For example, in 1906 in the one experiment, with a *H. umbellatum* from Lille, I got seeds after castration, while the two plants of the same set that were examined in 1907 and 1909 gave a negative result. The offspring of the apogamic individual — that evidently has been among the three of the five original experimental plants which died in the winter 1906—1907 — gave also fruit after castration, just as the parent had done. This dissimilarity is easily explained when we learn that the apogamic individual belongs, not to *H. umbellatum*, but to *H. boreale*, the seeds of which must have been intermingled with those of *H. umbellatum;* while on the other hand the two plants examined in 1907 and 1909 are true *H. umbellatum*. In consequence, the one case of apogamy in *H. umbellatum* has to drop.

The other set of *H. umbellatum*, which gave fruit after castration, is from St. Petersburg and was named *H. umbellatum*, var. *linearifolium*, but looks like a typical *H. umbellatum*. Dr. DAHLSTEDT confirms that it is a true *H. umbellatum*. There is then a form of *H. umbellatum* which is capable to fruit apogamically, but which in outer appearance does not differ from the other forms of *H. umbellatum*, which all require fertilization. The differences in percentage of full fruits in the apogamic form between castrated and non-castrated heads seem to indicate that the apogamy is not absolute (79 : 91, 82 : 79, 46 : 78, 56 : 86, 61 : 74, 63 : 52, and 51 : 84). — All the other examined sets of *H. umbellatum*, including all those that proceed from spontaneous forms, and further the nearly allied species *H. lactaris* Bert., have not given any fruit capable of germination after castration and thus agree with the cytological investigations by O. JUEL (1905). We have thus in *H. umbellatum* the peculiarity that most of the forms, "races", are normally sexual, while a single form is apogamic[1]).

Looking through Table II it is curious to see how unlike the races of *H. umbellatum* are in regard to fruiting and how small the percentage of full fruits is in most cases. It seems to be a species whose fruiting at the present time is little stable and in which we might hope to find something to help us to an understanding of the mysterious phenomenon of apogamy. Still, I have as yet no hints of this understanding, but I hope that further investigations on this species will clear up the matter.

3. *Subgenus Pilosella.*

In my paper of 1906 I could record that *H. auricula* L. did not fruit after castration — which ROSENBERG's cytological investigations (1907) also confirmed — while the other five examined species of the subgenus *Pilosella* were able to do so. I have later repeated my experiments with *H. auricula*, also using other sets of this species, and with the same result. Connected with this fact is, no doubt,

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[1]) In *Rosa* something similar seems to be the case. DINGLER (1907), who previously supposed apogamy in some cases, doubts that there is apogamy, and STRASBURGER (1904) has shown that in the species examined, among others in *Rosa canina*, the development of the embryo-sac is quite typical and that fertilization is necessary. On the other hand O. ROSENBERG (1909, p. 155—158) has examined a form, *R. canina*, subsp. *persaticifolia* Almq., in which the development of the embryosac points to apogamy, consequently differing from the "race" of *R. canina* studied by STRASBURGER.

Besides E. LUNDSTRÖM (1909, p. (16)) in a preliminary note has recorded, that he has had fruits developed after castration in *R. virentiformis* Matss. and in *R. glauca* Vill., subsp. *Afzeliana*, var. *dilatans* Almq., which latter according to ROSENBERG (l. c., p. 156) must also be supposed apogamic.

It is remarkable that the number of chromosomes in the apogamic race of *R. canina* is about double what it is in the normally sexual race of the same species.

the pronounced disposition of this species to hybridize, as will be mentioned later.

All the other species of *Pilosella* examined in 1906—1909 have been able to give fruit after castration. My investigations, unfortunately, do not comprehend so many species as is desirable — altogether 23 sets belonging to 14 species. The species of *Pilosella* have comparatively small heads and are therefore, technically, rather difficult to castrate, the heads easily being spoilt during the operation, especially in the very small-headed forms. The small fruits are also difficult to count from their outer appearance, and in several species each head gives few fruits. All these circumstances impede the investigation. The countings tabulated in the Table III are therefore much more incomplete than in the case of *Archieracium*, and the numbers given are admittedly too small. Still, I think they point to the general conclusion that the number of full fruits is somewhat diminished by castration — in other words, that the apogamic species of Pilosella are not absolutely apogamic, but that some of the flowers of each head require fertilization.

There are altogether 7 sets that can be used for comparison, and, of these, five distinctly point in the direction named. Of the two pointing the opposite way, one (*H. florentinum* All.) at least is too insufficiently investigated, as the numbers are small. The other is a set of *H. aurantiacum* and is hardly very convincing. Just about this species MENDEL (CORRENS 1905) has written, that it is absolutely unable to be used for crossing experiments (that is to say as mother plant, but its pollen can very well fertilize other species), and this would agree well with its being absolutely apogamic. Further, another set of *H. aurantiacum* gives the opposite result. The general conclusion from these cases is, therefore, in my opinion, that the countings given are without value, so far as *H. aurantiacum* is concerned.

Although the experiments with species of *Pilosella* are not so comprehensive as they ought to be, we may sum them up in the following general sentences: Within the subgenus Pilosella the species *H. auricula* is absolutely sterile after castration¹), while the other species examined are capable to fruit apogamically, yet apparently in such a way that, at least in most species, a small part of the flowers require fertilization. This result agrees with ROSENBERG's cytological investigations (1907) and with the great number of hybrids known in this subgenus.

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¹) Several experiments seem to indicate that it is even self-sterile.

Table III.

No.	Pilosella	Origin of the Plants	Year of the Experiments	A. Castrated Heads: Number of Heads	A. Castrated Heads: Full Achenes	A. Castrated Heads: Empty Achenes	A. Castrated Heads: Percentage of full Achenes	B. Not castrated Heads: Number of Heads	B. Not castrated Heads: Full Achenes	B. Not castrated Heads: Empty Achenes	B. Not castrated Heads: Percentage of full Achenes	Difference between A and B, Percentage
342	*aurantiacum* L.	Odessa	1909	7	393	23	94					
343	*aurantiacum* L.	Lyon	1909	8	436	37	92	5	262	32	82	+ 10
345	*aurantiacum* L.	Zürich	1909	5	144	265	35	5	196	128	60	÷ 25
348	*aurantiacum* L.	Stockholm	1909	3	116	41	74					
125	*brachiatum* Bess., subsp.	Herculesbad (spont.)	1906		x >	y						
226	*colliniforme* N. & P.	Braunschweig	1906		33	13	72					
270	*colliniforme* N. P.	Bukarest	1906		117	17	87		90	12	88	÷ 1
209	*colliniforme* N. P.	Göttingen	1907		x <	y						
355	*colliniforme* N. P.	Stockholm	1909	1	21	15	58					
211	*cruentum* N. P.	Göttingen	1909	4	136	71	66					
268	*florentinum* All., subsp.	Göttingen	1906		55	8	87		277	97	74	+ 13
201	*macrolepideum* Norrl.	Karlsruhe	1907	1	93	29	76					
214	*magyaricum* N. P., subsp.	Triest	1906		57	33	63		131	22	86	÷ 23
210	*nigriceps* N. P., aff.	Göttingen	1907		25	82	24					
124	*pannonicum* N. P., subsp.	Herculesbad (spont.)	1906		x >	y						
437	*pilosella* L.	St. Petersburg	1909	1	112	27	81					
M 18	*pilosella* L., forma	Danmark (spont).	1906		x >	y						
M 18	,, ,,	,, ,,	1907		x >	y						
367	*praealtum* Vill.	Lyon	1909	1	11	9	55					
204	*substoloniflorum* N. P.	Bonn	1906		25	47	35					
204	,, ,,	,,	1907		315	293	52		217	104	68	÷ 16
427	,, ,,	Offspring of 204	1909		257	173	60		216	26	90	÷ 30
306x	*subpraealtum* Ldbg.	Öland (spont.)	1907	1	x >	y						
205	*auricula* L.	Göttingen	1906		0	∞	0					
205	,, ,,	,	1907	10	0	∞	0					
M 17	*auricula* L.	Danmark (spont.)	1906		0	∞	0					
M 17	,, ,,	,, ,,	1907	20	0	∞	0					
351	*auricula* L., f. pilosa	Tabor	1909		0	∞	0					

II.

Hybridization Experiments.

In my paper of 1906 I reported that I had artificially produced the following hybrids:

H. pilosella × *aurantiacum*
H. excellens × *aurantiacum*
H. excellens × *pilosella*.

My method of crossing was as simple as possible: I isolated under bell-jars before unfolding some heads of the plants I wished to use. When a few days later the heads had opened — at any rate the outer flowers of the heads — I picked off the head whose pollen was to be used and rubbed it cautiously to and fro over the stigmas of the head of the plant to be used as mother parent; this manipulation was sometimes repeated one or two days later with a new head of the father plant, but with the same one of the mother plant in which now the more central flowers of the head had opened. The head thus pollinated was kept continually under the bell-jar, closed below with wadding, until sometime after the flowers had withered. As soon as the withered corollas, on touching, easily dropped off in a clump, the wadding was removed, as it caused the air in the jar to be continually saturated with vapour and thus sometimes furthered an attack of mould on the heads. The head was now permitted to ripen under the bell-jar, but with free access of the air from below. The jar only served to prevent the ripe fruits from being carried away by the wind, if the gathering happened to be a little delayed. — In the sowing of the fruits, the same precautions were taken as have been mentioned under the castration experiments.

This method, which I still use, is thus much simpler than that used by MENDEL (1870) and F. SCHULTZ (1856), and it has the shortcoming that it does not give results which can be used for counting, self-fertilization (when the mother plant is hermaphrodite) not being excluded; but I consider it as the only easily practicable method when working with *Compositae* that have small flowers.

F. SCHULTZ transferred, by means of a fine brush, the pollen on to the stigmas, but did not take special precautions against self-fertilization; his method is thus not more exact than mine, but more difficult to carry out.

On the other hand, MENDEL's method is the most exact; by means of fine pins he removed the anthers before the opening of the flower (most of the flowers of the head were taken away) and fertilized the thus rightly castrated flower with the pollen of the father species. This method, however, is so difficult and gives such small results, as the delicate flowers are often destroyed in the operation, that a patience and dexterity like MENDEL's are required in order to employ it.

In the following I shall give the results of my crossing-experiments, obtained since 1905, especially the results of the study of the later generations of the first produced crosses, together with a report of a new cross.

1. *H. pilosella* × *aurantiacum.*

In 1904 I had obtained a hybrid (No. 55) by crossing *H. pilosella* with *H. aurantiacum.* The single individual of this cross (represented in the plate af the 1906 paper as fig. 7) did not fruit in 1905 after isolation or castration, in contrast to both parents. But when the heads were left to themselves during flowering, a few full fruits were developed, from which plants arose, different from one another and to be considered as the result of new crosses caused by visits of insects. Some of these were apparently pure *H. pilosella* and might be supposed to be segregations, by back-crossing with the mother parent.

The castration was repeated in 1906, 1907 and 1909, but always with negative result. Isolation of some few heads was also tried, but no fruit capable of germination was obtained in that way either. The hybrid may thus be regarded as self-sterile.

An experiment of crossing it with the pollen of the father plant (*H. aurantiacum*) has until now given only a single individual as offspring; this was very much nearer to *H. aurantiacum* than was the primary hybrid, but was still not a pure *H. aurantiacum* and was also quite sterile¹).

2. *H. auricula* × *aurantiacum.*

As before mentioned, *H. auricula* requires fertilization in order to produce fruits capable of germinating, and it was therefore to be

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¹) An experiment with similar result has already been made by MENDEL (CORRENS 1905, p. 245) by crossing the hybrid *H. praealtum* × *aurantiacum* (= *H. magyaricum* × *aurantiacum*) with *H. aurantiacum.* He got as offspring: „zweierlei Pflanzen, solche nämlich, welche mit der Bastard-Mutterpflanze ganz übereinstimmten, und andere, welche dem *H. aurantiacum* um vieles näher standen.“ The former of these categories is evidently apogamic F_2, while the latter corresponds to my experiment.

supposed that this species would be favourable to crossing experiments, as, indeed, MENDEL had already pointed out. He writes in a letter to NÄGELI (CORRENS 1905, p. 230) that: "*H. auricula* ist . . . bei einiger Vorsicht eine vollkommen verläßliche Versuchspflanze". He has crossed more than a hundred heads of this with several other species, and whenever he got fruits capable of germinating, they always gave rise to hybrids ("allein die aus denselben erzogenen Pflanzen sind ohne Ausnahme Bastarde"; CORRENS 1905, p. 230).

In his short paper on *Hieracium* MENDEL (1870, p. 51) already mentions that by crossing *H. auricula* with *H. aurantiacum* he got two specimens of the same cross differing from each other, one red-flowered and quite sterile, and one yellow-flowered in which "ein einziger gut ausgebildeter Same", appeared. In his letters he repeatedly mentions this hybrid combination, a great number of which he has produced. For example, in a letter of 1870 he reports that he has planted 98 specimens out in his garden; of these, 84 flowered in the same year, some died, and others did not reach flowering. About the flowering specimens he says (CORRENS 1905, p. 238): "Die Abweichungen unter denselben sind sehr beträchtlich. Jedes Bastard-Merkmal erscheint in einer gewissen Anzahl von Varianten, welche Übergänge von einem Stamm-Merkmale zu dem anderen darstellen. Es scheint, daß die Varianten der verschiedenen Merkmale miteinander in allen möglichen Verbindungen auftreten können. Das letztere wird dadurch wahrscheinlich, daß an den vorhandenen Bastardpflanzen die Anordnung der Merkmal-Varianten eine außerordentlich mannigfaltige und kaum in zwei Fällen eine völlig gleiche ist." And further (l. c., p. 239) that: "etwa der vierte Theil als vollkommen fruchtbar, die Hälfte als theilweise und ein Viertel als ganz unfruchtbar zu bezeichnen ist. Der Grad der Fruchtbarkeit erscheint als unabhängig von der Form des Bastardes". Once more this hybrid is mentioned in MENDEL's letters (l. c., p. 243), when he says that in 1871 he put down the following remark on it: "Circa 90 Bastarde zum Theile fruchtbar, sehr verschieden". The last words have been written to show the contrast to crosses between *H. auricula* and several races of *H. pilosella*, in which crosses all the specimens of each cross were alike.

My experiments are, strictly speaking, only repetitions of those made by MENDEL; but the fact that *H. aurantiacum* is capable to fruit after castration and consequently is, at least in part, apogamic, throws a new light on the matter.

a. The 7th of July 1906 I pollinated an isolated head of *H. auricula* (the same set which was used for castration experiment; No. M 17) with pollen from an isolated head of *H. aurantiacum* (this too had been used — and with positive result — for castration experiment; No. 58). Only four specimens appeared from the sowing of the seeds gathered, and these were all hybrids, all unlike each other, standing in their characteristics in different degrees between the parents. No correlation seems to exist between the different characters; e. g. a hybrid, in colour of the flowers near to *H. aurantiacum*, does not also in other characters resemble the father.

With regard to the colour character the family showed the following gradation:

1 specimen (No. 286_1) was very near to *H. aurantiacum.*

1 specimen (No. 286_3) was less near than the preceding, but still nearer to the father than to the mother.

1 specimen (No. 286_2) was intermediate or perhaps a little nearer to the mother.

1 specimen (No. 286_4) died before I had noticed its flower colour; it was a decided hybrid.

The first two specimens do not seem to be able to have full fruit; at least, it appears from castration and isolation experiments, that they are self-sterile. The third one (No. 286_2), however, has yielded fruit after castration. Already under the first scanty flowering in autumn 1907 one head was castrated. The small number of fruits gathered from this experiment were sown in May 1908, and the plants (F_2) reached a scanty flowering in September of the same year and have later flowered copiously in 1909 (June). Again the family F_2 consists of only four specimens, but these are all quite alike in all characters and quite similar to the parent plant; they have given a fair number of fruits. Castration of F_1 (No. 286_2) was repeated in 1908 and out of the much more numerous offspring (No. 467) one plant reached flowering in September 1909; it was also quite similar to the parent plant, and the same seems to be the case with the remaining ones, as far as can be judged from the vegetative characters alone.

We are thus allowed to conclude, that while the first generation (F_1) of *H. auricula* × *aurantiacum* is heterogeneous, the second generation (F_2) is quite homogeneous and like the parent individual of F_1, in so far as it can arise at all.

b. As the experiment reported on only gave a few hybrid specimens, the same cross, with the same parent individuals, was repeated in 1907.

One isolated corymb (two heads) of *H. auricula* was pollinated with isolated heads of *H. aurantiacum* (also from only one corymb). The fruits gathered were sown in April 1908 and produced a family of 29 individuals, most of which reached flowering in the autumn of the same year. They presented an astonishing variety or heterogeneity, and there were not two individuals completely alike and all (with perhaps one exception?) were hybrids. They varied with regard to the colour of the flowers, of which the annexed reproduction of coloured drawings on Plate 4 will give a better idea than long descriptions. The specimens in flower in autumn 1908 have been arranged on the plate after flower colour alone, forming a series from *H. auricula* to *H. aurantiacum.* Further, they varied with regard to the size and hairiness of the head; the number of heads; the length and hairiness of the scapes; the form, colour and hairiness of the leaves; the form and vigour of the stolons, e. t. c. No correlation between the variations of the different characters was discovered.

Some heads of the autumnal flowering specimens were isolated. In 12 specimens all the fruits were empty, but in 5 specimens at least some few fruits were apparently full and were sown in the spring of 1909. Four of these gatherings have germinated and produced a few plants of F_2 which, however, owing to the bad summer, did not reach flowering in the same year, and about which I can say nothing more than that the rosettes of each set seem to be homogeneous.

In the winter 1908—09, unfortunately, 7 of the 29 plants of F_1 died. Among the rest, heads of several individuals were isolated in the summer of 1909 and with similar result as in the preceding year, most of them producing only empty fruits. Some experiments of crossing the hybrids with the parents also gave only empty fruits, but these experiments must necessarily be repeated.

The hybridization experiments hitherto carried out with *H. auricula* and *H. aurantiacum*, thus agree fully with the above-mentioned extensive experiments made by MENDEL. My experiments have the advantage that only one single corymb of both father and mother has been employed for the cross, so that is cannot be objected that the heterogeneity in F_1 depends on different father or mother individuals.

Thus we have substantiated in the cross *H. auricula* × *aurantiacum* an astonishing heterogeneity in F_1, and no correlation as to the characters mutually. Most individuals of F_1 are sterile, but a few of them bear some few fruits and these are even developed apogamically as in the father. With regard to the fertile F_1 individuals, they produce an F_2 which is completely homogeneous and quite like the parent individual of F_1; this must no doubt be attributed to the apogamy. From another point of view, the origin of species by means of hybridization, we may be allowed to say that the cross *H. auricula* × *aurantiacum* can give rise to new forms or species, at once quite constant.

3. *H. excellens* × *aurantiacum.*

a. As mentioned in my paper of 1906 (p. 239), in June 1904 I castrated some heads of the many-headed *H. excellens* (related to *H. magyaricum* N. P.) and isolated others, and at the same time pollinated some heads of another corymb of the same individual with *H. aurantiacum.* The castrated and the isolated heads gave rise to a new, apogamically developed generation, while the result of the crossing was 20 individuals of pure *H. excellens* and 6 hybrids. These 6 were all different to one another, but the differences in characters were almost always within the range of the characters of the two widely different parents. Most prominent was the difference in sexuality; the mother plant, *H. excellens*, is purely female, while the father plant, *H. aurantiacum,* is hermaphrodite, and some of the hybrids followed the mother, others the father. The characters of the 6 hybrids can be described briefly in the following way:

No. 46_1. Vegetative part comparatively weak, and development of stolons much poorer than in either of the parents; hermaphrodite; corolla pure yellow.

No. 46_2. Vegetative part vigorous; very similar to the mother, but more robust; female; corolla yellow as in the mother, but the head a little larger and with dark, more hairy involucre.

No. 46_3. Vegetative part vigorous; similar to the mother, but more robust; female; corolla orange-yellow with a red stripe on the underside and red teeth; head as in 46_2.

No. 46_4. Vegetative part vigorous; rather intermediate; hermaphrodite; corolla yellow-orange-red with red underside and red teeth; head as in 46_2. (Figured in the paper of 1906 as fig. 5.)

No. 46_5. Vegetative part weak; development of stolons rather poor; hermaphrodite; corolla nearly as 46_4, perhaps a little nearer to the father; quite sterile, died after first flowering.

No. 46_6. Vegetative part weak; leaves of the rosette narrower than in the parents. Died in the winter of 1906—07 without any flowering.

These short descriptions will show how different the members of this family were. It is worth noticing that No. 46_1, 46_5 and 46_6 are vegetatively, especially with regard to the development of stolons, weaker than both the parents. Most frequently hybrids are said to be vigorous and often more vigorous, than the parents.

Only the four first enumerated specimens have kept under cultivation, and I have followed them through several generations.

1. *H. excellens* × *aurantiacum*, No. 46_1.

The primary hybrid, F_1, died in 1905, after bearing fruits under isolation. Hence arose an F_2 of 3 individuals, all of which were vegetatively weak, without regular development of stolons and with pure yellow hermaphrodite flowers, thus quite like the F_1. In one of these individuals castration, as well as isolation, was made with respectively 4 and 3 heads, but the development of full fruits was very slight. Thus the F_3, which arose from sowing of these fruits, consisted of only 4 and 8 individuals, all alike und all like F_1. F_4 came out in 1909, but did not reach flowering.

We thus have full constancy in the second and the third hybrid generation, in so far as the small number of developed fruits permits us to judge.

2. *H. excellens* × *H. aurantiacum*, No. 46_2.

The primary hybrid from 1904 is still alive. Without isolation seeds were got, which gave rise to an F_2 of 25 individuals, all alike and like F_1, and female. As this experiment was not exact, a corymb of the primary hybrid was isolated in 1906, and from the gathered seeds there came 85 individuals of F_2, all alike and all like F_1, yet with the exception of one individual which had reddishly tinged leaves and scape. One corymb of this individual was isolated, and an F_3 of 38 individuals was produced, all alike and like F_1, i. e. without any reddish tint; nor was the F_2-individual itself this year reddishly tinged. The reddish colour is consequently not inheritable, but is no doubt a result of bad conditions, most probably of drought, and was here most likely caused by ants, which, by establishing their nest round the base of the plant, let too much fresh air into the soil and perhaps also injured the roots.

In this hybrid also there is full constancy in the second and the third generation.

3. *H. excellens* × *aurantiacum*, No. 46_3.

The primary hybrid is still alive. With the first isolation (in 1905) only one individual of F_2 was obtained; it was quite like F_1. Isolation was therefore repeated in 1906, and now there came out an F_2 of 53 individuals which flowered in 1908. Out of these, 52 were homogeneous and quite like F_1, but one individual differed very considerably. This mutant is vegetatively weak and with slight development of stolons, with yellow corollas and with copious pollen, apparently hermaphrodite, while all the other individuals as well as F_1 are female[1]). It resembles much No. 46_1, but differs with regard to the colour of the corollas, being in the mutant orange-reddish on the underside. Unfortunately it is quite sterile on isolation, which has been tried both in 1908 and 1909.

F_3, sprung from the normal F_2, was planted out in 1909, but did not reach flowering.

We have then here a case where the main part of the second generation of the hybrid behaves as in the two foregoing cases, but where suddenly an individual has come out which is a distinctly and easily recognisable mutant. It is not a retrograde step to any of the parent species, but a new combination of their characters. It is a pity that it is not possible to work further with this mutant, as it seems quite sterile.

4. *H. excellens* × *aurantiacum*, No. 46_4.

From the primary hybrid, which is now dead, was got by isolation an F_2 of 27 individuals and by castration 11 individuals, and all 38 specimens were quite homogeneous and like F_1. By isolation of one of the 27 individuals of F_2 were obtained 107 individuals of F_3, and by castration of one of the 11 individuals of F_2 were obtained 98 individuals; altogether, F_3 consisted of 205 individuals, all alike and like F_1. Still, several of them were reddishly tinged and somewhat weaker than the others, but this must no doubt be explained in the same way as above. F_4 was planted out in 1909, but did not reach flowering.

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[1]) It is not unknown that a mutant differs from its parent with regard to sexuality; e. g. *Oenothera lata*, one of DE VRIES's classical mutants, is purely female while *O. Lamarckiana* is hermaphrodite. See R. R. GATES (1907a, 1907b, 1909a) who has worked out its behaviour thoroughly.

In this hybrid there is thus full constancy with regard to the second and the third generation, just as in the two first hybrids of *H. excellens* × *aurantiacum.*

b. In the summer of 1904 another cross with *H. excellens* and *H. aurantiacum* was made, using another specimen of *H. aurantiacum*. The result was, besides some pure *H. excellens,* one hybrid (No. 48a) which was near to the mother in characters. It differed in having somewhat larger and more dark-hairy heads and, at least, in some of the outer yellow corollas, a distinct, though often small and feeble red stripe on the underside. Like the mother the hybrid was purely female. It is still alive.

By castration was obtained only one individual of F_2 and by several isolations altogether 13 individuals, all alike und like F_1. By means of isolation a third generation, F_3, consisting of 106 individuals came out, all alike, still with individual differences with regard to the intensity of the feeble reddish tint on the underside of the marginal corollas. As in the first reported cross here also constancy in the later hybrid generations rules.

c. A cross between *H. excellens* and *H. aurantiacum*, made in 1907, produced one hybrid, which quite resembled the just mentioned No. 48a, but has not been studied further.

All the experiments here reported on show that the crosses between *H. excellens* and *H. aurantiacum* give a heterogeneous F_1, but that each individual of these primary hybrids is able to produce a quite constant and homogeneous offspring, if it is not quite sterile. The explanation of this constancy is probably that the offspring comes from seeds developed apogamically. The one mutant in F_2 of No. 46_3 is hitherto an isolated fact, which does not allow far reaching conclusions, still it shows that also apogamic plants are able to mutate.

The little table (IV) given here recapitulates the number of hybrid offspring produced during the experiments:

Table IV.

Number of Hybrid-Offspring of *Hieracium excellens* × *H. aurantiacum.*

	F_1	F_2	F_3
46_1	1	3	12
46_2	1	110	38
46_3	1	52(1)	—
46_4	1	38	205
48a	1	14	106

(1) To these is to be added a single mutant.

Several experiments of crossing the hybrids with the parent species have hitherto given no results of interest, the offspring always being like the mother plant, i. e. the offspring have always been produced apogamically, the crossing being quite ineffective. The experiments made may just be enumerated:

a. *H. excellens* × [*excellens* × *aurantiacum*, No. 46_4]. Result: 3 pure *H. excellens*.

b. *H.* [*excellens* × *aurantiacum*, No. 46_3] × *aurantiacum*. Result: 19 individuals, like No. 46_3.

c. *H. excellens* × [*excellens* × *aurantiacum*, F_2 of No. 46_4] Result: 29 pure *H. excellens*.

4. *H. excellens* × *pilosella*.

By crossing, in 1904, *H. excellens* with *H. pilosella* there came out, besides some pure *H. excellens*, 8 hybrid specimens, which did not behave quite as the hitherto mentioned hybrids, being indeed somewhat heterogeneous, but not in the same degree as these.

Here follows a list over this family of hybrids with characteristics:

No. 50_1. Vegetative part vigorous; well developed stolons; the corymb with long scape and many subumbellate heads of which some indeed on long stalks issuing from the lower part of the scape; on the whole rather near *H. excellens*, but a little coarser and lower and the heads a little larger; female.

No. 50_2. Much as the preceding and also female, but perhaps still a little nearer *H. excellens*.

No. 50_3. Much as the preceding, also female. (A not typical, slender and few-headed corymb from an autumnal flowering has been figured in 1906 as fig. 6.)

No. 50_4. Low and nearer to *H. pilosella*; the corymbs with few, distant and long-stalked, large heads; hermaphrodite; yet the rosette leaves resemble those of *H. excellens*.

No. 50_5. Much as the foregoing; hermaphrodite.

No. 50_6. Died without flowering, but was an evident hybrid.

No. 50_7. Also died without flowering.

No. 50_8. Tall and vegetatively vigorous with subumbellate rich corymb on a long scape; resembles 50_2 and 50_3, and female.

If we do not consider the two hybrids that died before flowering, we have six individuals left, and of these the four were fairly, but not absolutely, alike, and near *H. excellens* from which they differed in being coarser and somewhat lower in the corymb-scape and with slightly larger heads, all characters from *H. pilosella*. The two others (No. 50_4 and 50_5) were also much alike and near *H. pilosella*, but still greatly differing by the corymb-scapes having several (not solitary), long-stalked heads, whose size was a great deal under that of the heads of *H. pilosella*. They were hermaphrodite, while the four other individuals (*sub-excellens*) were female.

All 6 individuals have in common that their power of fruiting is very slight. Notwithstanding repeated experiments in different ways I have not yet succeeded in getting more than a few apparently full fruits in any experiment and in most of them no full fruits at all. Thus, after isolation I have got only a single F_1-individual of 50_2, of 50_3 and of 50_8 each, — that is of three individuals of the *sub-excellens*-group; these F_2 individuals have all been like their F_1.

An experiment of crossing 50_5 with the mother parent (*H. pilosella*) gave rise to only three individuals which were different from one another and all three different from their F_1-parent. One (No. 406_1) was, at least apparently, pure *H. pilosella*, and consequently a complete segregation must have taken place. The other two showed hybrid characters; one of them (No. 406_3) was rather near the mother (the primary hybrid), still somewhat nearer *H. pilosella*, and the third (No. 406_2) was very peculiar; it had leaves narrower than those of both parents, long thin stolons, mostly approaching the *excellens*-type; the corymb bore long branches with few flower-heads, much as the inflorescences on the stolons of *H. excellens*. Unfortunately both the last named plants were weak and died in the winter after the first flowering; they seemed to be quite sterile.

The cross between *H. excellens* and *H. pilosella* has thus given only the following result: the primary hybrid is heterogeneous, but less than in the other crosses, being nearly dimorphous[1]). All the individuals of F_1 are nearly sterile, the few individuals of F_2 point to constancy, while the poor experiment of back-crossing may be said to show segregation.

On the whole, this hybrid combination seems to be unfavourable as a subject of experiment. It has therefore not been used so much for experiments, as interest in its peculiar behaviour would merit.

If we sum up the result of all the hybridization experiments hitherto made, we get the following conclusions:

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[1]) Such cases H. DE VRIES (1907, 1908) has named Twin-hybrids.

1. It seems natural to place in one group *H. pilosella* × *aurantiacum* and *H. excellens* × *pilosella*, consequently both combinations, with *H. pilosella* as the one parent plant¹). In this group the F_1-generation is (under isolation) wholly or nearly without power of forming fruits capable of germination, — consequently self-sterile. By crossing the F_1 with one of the parents, an F_2 of few individuals has been produced which seems to segregate.

2. Opposed to this stands the other group where F_1 is rather fertile by isolation and where F_2 and F_3 show full constancy. The type of this group is *H. excellens* × *aurantiacum*; still perhaps No. 46_1 and the mutant of No. 46_3 belong to the first group.

The hybrid *H. auricula* × *aurantiacum* must probably be divided so that most individuals of F_1 belong to the first group, while some few belong to the second.

The second group is of more interest, for here an experimental proof is given that by hybridization between far distant species within the subgenus Pilosella new forms can arise which are fully constant and which behave as new species.

III.

Apogamy and its Relation to Polymorphism.

From the researches of MURBECK (1904), KIRCHNER (1905) and especially from the cytological investigations of ROSENBERG (1906, 1907) on the apogamy of *Hieracium*, it has been shown that the development of the non-fertilized embryo goes on in different ways, partly by true apogamy, partly by the curious apospory discovered by ROSENBERG. We shall not enter into the cytology at great length, but only mention that the embryo is always developed from an "egg-cell" which has the vegetative (unreduced) number of chromosomes; this form of apomixis is by H. WINKLER (1908, p. 11) called somatic parthenogenesis. Still, I prefer to maintain the terminology of STRASBURGER (1904, p. 113 and p. 118), according to which our case falls under apogamy, as we speak of parthenogenesis only in the case where the egg-cell has the reduced number of chromosomes and yet develops into an embryo without fertilization (H. WINKLER's

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[1] As regards the dimorphism of *H. excellens* × *pilosella*, it is worth recalling that MENDEL has produced a great number of hybrids between *H. auricula* (as mother) and different races of *H. pilosella*, and that these hybrids of F_1 have been like one another (CORRENS 1905, p. 243). It seems thus that *H. pilosella* hybrids behave in a different way from those in which *H. aurantiacum* is father parent.

generative parthenogenesis); this has hitherto not been found in the phanerogams.

The definition I gave for apogamy in my paper of 1906 was perhaps rather indistinct; it runs: "that it comprehends all cases where a plant gives seeds, developed from the ovules, without fertilization, whether the egg-cell or other cells of the embryo-sac or a cell from the nucellus are the starting point" (l. c., p. 233, footnote). The last-named case was intended to correspond to the apospory which ROSENBERG had then found. Now, I shold prefer to use the following short definition, employing the terminology given by H. WINKLER. Apogamy is the apomictic development of a sporophyte from one or several cells of the gametophyte, assuming that the number of chromosomes is unreduced. Thus I include in apogamy both WINKLER's apogamy and his somatic parthenogenesis, making no sharp distinction between the apomictic development of the "vegetative egg-cell" and that of the other gametophyte cells, but considering the former case only as a special case of apogamy.

H. WINKLER in his excellent account of parthenogenesis and apogamy in plants (1908) has put together all the then known cases of apogamy in its different forms. Since then, several new cases have been found, especially with regard to the phanerogams. In the following I restrict myself to the phanerogams and the considerations expressed apply only to these and among them especially to the dicotyledons, with the apogamy of *Hieracium* as main point of view.

A list of the hitherto known cases of apogamy (in my sense) among phanerogams will have the following appearance:

Monocotyledones.

Triuridaceae: *Sciaphila nana* Bl. (V. A. POULSEN, 1905).
Burmanniaceae: *Burmannia coelestis* Don. (A. ERNST, 1909).
Thismia clandestina Miq. (K. MEYER, 1909).
Thismia javanica J. J. Sm. (A. ERNST and Ch. BERNARD, 1909).

Dicotyledones.

Saururaceae: *Houttuynia javanica* Thbg. (SHIBATA and MIYAKE, 1908).
Moraceae:[?] *Ficus hirta* Vahl, and perhaps other species (TREUB, 1902),

Urticaceae: [?] *Elatostema acuminatum* Brogn. (Treub, 1905).
Elatostema sessile Forst. (Modilewsky, 1908).
Menispermaceae: [?] *Disciphania Ernstii* Eichl. (Ernst, 1886).
Ranunculaceae: [?] *Thalictrum Fendleri* Englm. (Day, 1896).
Thalictrum purpurascens L. (Overton, 1902).
Rosaceae: *Alchimilla*, sect. *Eualchimilla* (Murbeck, 1897, 1901)
Rosa glauca Vill., subsp.
Rosa virentiformis Matss. } (E. Lundström, 1907).
Thymelaeaceae: *Wikstroemia indica* L., Buitenzorg (H. Winkler, 1904).
Balanophoraceae: *Balanophora elongata* Bl. (Treub, 1898).
Balanophora globosa Jungh. (Lotsy, 1899).
Helosis guyanensis Rich. (Chodat and Bernard, 1900).
Compositae: *Antennaria alpina* (L.) Gärtn. (O. Juel, 1898, 1900).
Antennaria fallax Greene
Antennaria neodioica Greene } (Leavitt and Spalding, 1905).
Taraxacum, all species examined (Raunkiaer, 1903).
Hieracium, subgen. *Pilosella*
Hieracium, subgen. *Archieracium* } nearly all species, (Ostenfeld and Raunkiaer, 1904; Ostenfeld, 1906).

It will be seen that the apogamy appears here and there in the families of the phanerogams without relation to their systematic position or affinities; still it is noteworthy that it is so common in the young family of *Compositae*, which must be supposed to be in its full vigour. There is therefore no reason for setting apogamy in any communication with degeneration.

The quoted cases of apogamy are not all certain, at least the cytological evidence is still wanting for several of them. Among the uncertain ones is *Ficus*, and among the imperfectly examined are *Sciaphila*, *Thismia* and the North-American *Antennaria*'s. Quite unexamined in cytological regard are *Disciphania* and *Thalictrum Fendleri*. These two and *Ficus* are omitted in the following considerations.

Now, if we look at the list, bearing this in mind, we find the peculiarity that not all the species within a genus are apogamic; some are normally sexual. This applies to all the genera named of *Compositae*, as Rosenberg has lately (1909, p. 151) shown that a species of *Taraxacum* (*T. confertum* Dahlst.) must be supposed to be sexual. *Taraxacum* was hitherto taken to be the only example of a wholly apogamic genus. Further, it applies to *Elatostema*, *Thalictrum*, *Wikstroemia*, *Alchimilla*, *Rosa* and *Balanophora*. We do not know the condition in *Thismia*, *Burmannia*, *Sciaphila* and *Helosis* — all saprophytic or parasitic plants — as cytological investigations have not yet embraced other species of the genera named than the apogamic ones here enumerated. Lastly, it has to be added that *Houttuynia* is a monotypic genus.

Another noteworthy fact with regard to apogamic plants is that comparatively many apogamic plants are pale, chlorophyll-wanting saprophytes or parasites, viz.: *Sciaphila*, *Thismia*, *Burmannia coelestis*, *Balanophora* and *Helosis*. Whether this fact may be of some importance or is casual, is difficult to decide at present. A. ERNST and ED. SCHMID are no doubt right in saying in their paper on the normally sexual *Rafflesia patma* Bl. (1909, p. 184): "so wird man auch bei anderen Parasiten in der Annahme von Beziehungen zwischen Reduktion der vegetativen Organe und Anomalien in der Embryosackentwicklung mit oder ohne Apogamie vorsichtig sein müssen."

The list shows, however, a third fact worthy of interest and which has already called forth many considerations, that is, the evident relation of apogamy to polymorphism. We must here except the pale saprophytes and parasites, and further *Houttuynia*, in which we know nothing about polymorphism. But with these exceptions all the hitherto thoroughly examined cases of apogamy (in the dicotyledons) fall within polymorphic genera, that is, genera in which at the present time an intense evolution of species is supposed to be taking place. The polymorphism in *Alchimilla*, *Rosa*, *Taraxacum* and *Hieracium* is well known. In *Antennaria* we find polymorphism in North America (not in Europe), in *Thalictrum* both in North America and in Northern Europe; *Elatostema* is a "critical" genus. Finally, H. WINKLER (1908, p. 147) and STRASBURGER (1909, p. 85—87) have shown that *Wikstroemia indica* is a polymorphic species, of which for the present only the examined "race" from the Buitenzorg Gardens has been proved to be apogamic, while others seem to be normally sexual. Thus it cannot longer be used as an instance of "Apogamie ohne Polymorphismus" (TISCHLER, 1908, p. 139)[1].

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[1] It would also agree very well with the relation of apogamy to polymorphism, if R. R. GATES (1909b) is right in his new supposition, that *Oenothera lata*, one of

The first who touched upon this apparent relation of apogamy to polymorphism, was SV. MURBECK, who as early as 1897 (p. 277) — he accentuates it a little too strongly later (1904, p. 295) — has intimated that for the *Alchimilla*'s there must be a certain relation between the constancy shown by the apogamy and the polymorphism. His words, however, are very vague. Having mentioned that the reason for the great constancy of the *Alchimilla* species has to be sought in the apogamic development of the seeds, which is really to be considered as a kind of layer-formation, he says that in a later detailed cytological investigation he will perhaps also have occasion to express himself "on a question at present obscure, how the polymorphism now ruling within the genus has come about. For that, however, is required an exact knowledge of the geographical distribution of the forms"[1]).

Somewhat more fully and decisively RAUNKIAER expresses himself (1903, p. 136—138) about the *Taraxacum* species. From the fact that all the species examined by him, which have widely different geographical distributions, are apogamic, he concludes "that the power of forming seeds without fertilization has originated in *Taraxacum* before this genus was split into many species and that the existing species have originated without any fertilization or crossing"[2]). If this conclusion is right, he thinks that in *Taraxacum* we have a genus which may be of importance for the study of the origin of species, and that future investigations on the species and their geographical distribution will contribute to the solving of the question, whether the origin of species has been occasioned in the Lamarckian way or in the Darwinian way (incl. that of mutation).

In his paper on apogamy in *Taraxacum* and *Hieracium* MURBECK (1904) — as already mentioned — comes back to this problem,

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the mutants of *Lamarckiana*, is partly apogamic, "though only in a small percentage of cases". But "this indication of apogamy in *O. lata* of course requires to be substantiated by a more detailed study".

Mrs. R. HAIG THOMAS has recently (1909) published a short paper on „Parthenogenesis in Nicotiana", and probably we have here a new case of apogamy, which agrees well with the relation-theory, as *Nicotiana* is a critical genus.

[1]) "om ett annat för närvarande dunkelt spörsmål, huru den nu rådande polymorfismen inom släktet en gång kommit til stånd. Härför erfordras emellertid en noggran kännedom om formernas geografiska utbredning".

[2]) "at Evnen til at danne Kim uden Befrugtning er opstaaet hos Taraxacum, för denne Slaegt er blevet spaltet i flere Arter, og at de existerende Arter er opstaaet, uden at Befrugtning og Krydsning har spillet nogen Rolle".

and says, that the geographical distribution of the Scandinavian *Alchimilla* species has not been able to contribute to the solving of the problem, as they have proved to be widely distributed in Europe[1]). He then says: "Ganz anders verhält sich *Hieracium*. Betreffs dieser Gattung weiß man gewiß — besonders infolge der sorgfältigen und eifrigen Forschungen DAHLSTEDT's und seiner Schüler —, daß Hunderte von kleinen Arten auf die Skandinavische Halbinsel beschränkt sind und daß eine Menge von ihnen nur kleinere Teile derselben bewohnen. Da unter den übrigen Phanerogamen Skandinaviens Endemismen äußerst selten sind, weil ja die ganze Flora der Halbinsel nach der Eiszeit eingewandert ist, so muß man annehmen, daß eine große Menge Hieracien in einer verhältnismäßig sehr späten Zeit daselbst entstanden sind und daß eine lebhafte Artbildung sozusagen vor unseren Augen stattfindet. Dagegen ist man geneigt, die Apogamie bei dieser Gattung als eine Erscheinung von verhältnismäßig hohem Alter zu betrachten, da sie innerhalb verschiedener Gruppen und auch bei der Untergattung *Pilosella* aufgewiesen ist. Ist diese Auffassung die richtige, so würde daraus folgen, daß eine Menge Hieracien aus Formen, die selbst apogam waren, entstanden sind und noch immer entstehen. Da aber so beschaffene Formen nicht individuell variierend sind[2]), so muß man annehmen, daß die jetzt lebenden apogamen Hieracien aus inneren und unbekannten Ursachen und sozusagen sprungweise entstanden sind." To these interesting suppositions, which I have quoted *in extenso*, he adds, however, the following weakening words: "Von der Richtigkeit dieser Folgerung bin ich doch selbst keineswegs recht überzeugt, da die wichtigste Prämisse, nämlich die Annahme des hohen Alters der Apogamie, wie wahrscheinlich sie auch sein mag, doch nicht auf hinlänglich sicherem Grunde ruht. Um zu einem solchen zu gelangen, sind jedenfalls mehr umfassende Untersuchungen vonnöten als die bisherigen". I think that the investigations made since then are all in favour of MURBECK's suppositions and go against the reservation so strongly accentuated by himself.

In the meantime, both MURBECK'S and RAUNKIAER'S reflections touch more upon the question of the origin of species and its relation to apogamy, and not so much upon the question if there is a causality

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[1]) The just published monograph of the northern *Alchimillae* by HARALD LINDBERG (1909) shows that there are considerable and very interesting differences in the distribution of the species, pointing to quite different ways of immigration.

[2]) This is scarcely correct, see later. C. H. O.

between apogamy and polymorphism, and the question probably connected herewith, the origin of the apogamy.

STRASBURGER is the first who has raised this problem particularly. In his interesting paper on the apogamy in *Alchimilla* (1904), he has rather extensively treated the question of the relation of apogamy to polymorphism. By examination of some *Rubi* and *Rosae* he has shown that they were normally sexual, so that we dare not speak of an absolute connection between the two phenomena. Still, he supposes that in the polymorphic *Eualchimillae* "übermässige Mutation" has caused the sexual abnormality which here also becomes apparent by the degeneration of the pollen. His opinion is the following (l. c., p. 152): "Wenn aber übermäßige Mutation die Sterilität fördern sollte, so würde sie das Fortbestehen der betroffenen Art gefährden. Apogame Fortpflanzung stellt sich als Aushilfe in bestimmten Fällen ein, doch auch sie dürfte Rettung wohl nur für eine phylogenetisch begrenzte Zeitdauer bringen, da die apogame Art aller der Vorteile verlustig geht, welche die geschlechtliche Fortpflanzung mit sich bringt". In his summary (p. 160) he repeats the same opinion. It seems then that he thinks the commencement of the period of mutation to be prior to the apogamy and the latter called forth by excess of the mutation. In *Eualchimilla* he supposes that the mutation period is over, while about *Hieracium* he says (p. 157): "An sich erscheint die Möglichkeit der Fortdauer der Mutation bei Hieracien nicht ausgeschlossen. Denn es ist durchaus nicht bewiesen, daß diese mit Eintritt des Geschlechtsverlustes ihr Ende nehmen müsse", and here he refers to the polymorphic alga genus *Caulerpa*, in which no sexual propogation has been found, and to the inheritable bud-mutation found by R. v. WETTSTEIN (1904) in *Sedum reflexum*. In my opinion the investigations on the *Hieracia* are rather to be interpreted in the following way. The presence of apogamy fixes the new mutants, which in a normally sexual genus would perhaps disappear by crossing with the parent species; but mutation (polymorphism) and apogamy cannot be considered as cause and effect.

After STRASBURGER another German botanist G. TISCHLER has taken up the question in his cytological studies on hybrids (1908), taking a special interest in the slight production of pollen, so frequent in many polymorphic genera, a fact which he connects with the apogamy. He says (l. c., p.138): "Es erscheint wohl dabei sicher, daß nicht die Apogamie das Primäre, die Pollenreduktion das Sekundäre ist, sondern daß gerade umgekehrt erstere sich einfand, nachdem eine normale Befruchtung nicht mehr möglich war,“ and further (p. 146): „Apogamie hat sich als “Aushilfe” auf die Mutation und Sterilität des Pollens eingestellt und ist nicht das Primäre und die Pollenobliteration das Sekundäre.” He thus expresses himself much more explicitly than STRASBURGER. I think that these considerations are untenable, as e. g. *Hieracium aurantiacum* is a typical apogamic species, which must be admitted already from MENDEL's experiments (CORRENS 1905, p. 240), at least compared with mine, but it has good pollen able to fertilize other species, as shown by the hybridization experiments. This has been pointed out by CORRENS (1905, p. 249), and both O. ROSENBERG (1909, p. 160) and H. WINKLER (1908, p. 136) have used this fact as an objection against STRASBURGER and TISCHLER.

H. WINKLER again, as a further objection, points to *Thalictrum purpurascens* and *Taraxacum* — both apogamic and with apparently good pollen —, in which, without proof certainly, he supposes that the pollen must be able “eine wirksame Befruchtung auszuführen”. WINKLER himself is very cautious and weighs all possibilities for an explanation of the origin of apogamy, as appears clearly from his summarizing words, viz.: “Nach dem gegenwärtigen Stande unserer Kenntnisse können wir also über die Faktoren, die phylogenetisch die Einführung der habituellen Parthenogenesis oder Apogamie bewirkt haben, ebensowenig etwas Sicheres aussagen als über die Natur der Reizvorgänge, die jeweils im Verlauf der Ontogenese sie auslösen” (p. 138). In his last chapter he advances the possibility, that in strongly mutating forms there is greater probability for the arising of a mutant, which is apogamic or has apogamic tendencies, sooner than in not-mutating forms, and as in such cases the “ausgleichende Moment” of the fertilization is absent, the mutant can keep constant. Here he refers to MURBECK's explanation of the remarkable constancy of the *Eualchimillae*. Still, this view implies, in his opinion, the following supposition, “daß parthenogenetisch oder apogam gewordene Pflanzen nicht mehr mutieren oder variieren können” (l. c., p. 148). I do not see that this supposition is necessary or even correct, and here my opinion agrees with that of STRASBURGER quoted above.

Quite recently O. ROSENBERG (1909) has put together the hitherto known “Tatsachen” about apogamy. He points out the correlation between apogamy and a great number of chromosomes, in contrast to, most frequently, half the number in the non-apogamic species within the same genus. He discusses the possible causes of apogamy and, as mentioned above, refers among other things to the fact that apogamy does not originate as a reaction against sterility of the pollen (the case of *H. aurantiacum*).

Taking all the quoted opinions together I regard the above given sentences of H. WINKLER as a good expression for the present position of the question with regard to the origin of apogamy.

I may sum up my views on these matters in the following way, bringing together what the investigations, in my opinion, have proved: — There is, at least with regard to the dicotyledons, an evident relation of apogamy to polymorphism, but it is not allowable to draw any conclusion as to causality between them or as to the age of the apogamy.

The supposition of STRASBURGER and TISCHLER, that apogamy is a secondary thing while degeneration of pollen is primary, is not tenable.

WINKLER's supposition, too, that apogamic plants do not vary or mutate, is scarcely correct.

As to *Hieracium* it must even be considered unlikely that the species now existing have originated before apogamy arose. Nothing hinders the supposition that new species can originate from apogamic parents, and we may compare this case with the inheritable bud-mutations which have been studied, e. g. by WETTSTEIN (1904) and W. JOHANNSEN (1908). The results of my hybridization experiments, mentioned in the earlier part of this paper, point in that direction. It has there been proved that a mutant has arisen in F_2 of an apogamic hybrid; — certainly only one specimen.

The hybridization experiments show further that hybrids are able to propagate apogamically and then are constant. This makes it allowable to conclude, 1° that within *Hieracium* the evolution of new species goes on coincidently with the existence of apogamy; 2° that the new species reach constancy at once just because of the apogamy[1]); 3° that the polymorphism is correlated to the apogamy in such a manner only that apogamy, through the constancy of the species, apparently furthers the polymorphism.

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[1]) Almost the same conclusion has been drawn by R. v. WETTSTEIN (1904, p. 517), who says, "Es ist leicht verständlich, daß bei solchen Pflanzen [*Alchimilla* and *Hieracium*], bei welchen die Rückführung in den ursprünglichen Typus durch Kreuzbefruchtung ausgeschlossen ist, jede auftretende Mutation sofort fixiert werden und — insofern die so entstehende Pflanze nicht unzweckmässig ist — zur Neubildung einer Art führen kann. Der Polymorphismus solcher Gattungen ist dann — zum Teile wenigstens — direct der Ausdruck der Mutationsfähigkeit derselben."

IV.

The Importance of Hybridization for the Origin of New Species, with special regard to Hieracium.

It would far exceed the scope of the present paper to give a full account of the question about the importance of hybridization for the origin of species. Much has been said *pro et contra* in this matter, which in the last decennium has entered upon a quite new phase by the general acknowledgment of the fundamental importance of the Mendelian segregation, both in the animal and the vegetable kingdom.

In the following pages I restrict myself to some remarks — with the *Hieracia* as starting point — on the question what views are now applicable to this interesting and important matter.

We find the only detailed remarks on the importance of the Hieracium hybrids for the origin af new forms in the monumental work by C. VON NÄGELI and A. PETER on the *Piloselloideae* of Central Europa (1885) and in the detailed paper by A. PETER on the hybrids of the *Piloselloideae* (1884). A most remarkable thing, regarding our question, in these papers is to see how little these authors have understood the value of MENDEL's experimental researches, and this seems still more extraordinary when we think of the letters from MENDEL to NÄGELI, published posthumously by CORRENS (1905), letters which have so often been quoted in the preceding pages and which contain much more copious information on Hieracium hybrids than MENDEL's own short account of 1870. The importance of MENDEL's researches has evidently not become clear to the eminent botanist NÄGELI; nor to W. O. FOCKE, who in his meritorious book "Die Pflanzenmischlinge" (1881) only briefly enumerates the hybrids published by MENDEL (1870), and, later on, incidentally mentions *Hieracium* as an exception from one of his rules ("Sätze"), viz.: that all individuals of the first hybrid generation are "einander in der Regel völlig gleich" (l. c., p. 469).

The papers of NÄGELI and PETER, mentioned above treat only of the subgenus *Pilosella*. The authors point out that by hybridization is "im allgemeinen keine neue Erscheinung hervorgebracht, weil die Bastarde lediglich eine Mischung der elterlichen Merkmale repräsentieren" (1885, p. 63). The heterogeneity of the first hybrid generation (F_1) is well known to them, and they even give an explanation of it, viz.:

"Diese Thatsache wird erklärlich, wenn man bedenkt, daß die Merkmale der beiden Eltern mit ihrem ganzen Formenkreise aus den Bastard vererbt werden, und daß demnach unter günstigen Umständen der Formenkreis des Bastardes ein beträchtlich weiterer sein kann, als der jeder Elternsippe eigene" (l. c., p. 63), — an explanation which, in my opinion, does not say anything. Besides, they attribute to the hybrids remarkably small importance for the evolution of the genus: "Bastarde sind vorübergehende Erscheinungen, ihre Befestigung ist nur ausnahmsweise möglich, fast nur dann, wenn ein Bastard zufällig isolirt wird und im Laufe der Generationen vermöge der allgemein geltenden [1]) Eigenschaft der Bastarde, nach und nach fruchtbarer zu werden, sich dauernd fortpflanzen kann" (l. c., p. 64). These considerations are, however, as hypothetical as those which the authors make on the slight chances of the hybrids for maintaining their existence when growing in company with the parents. As a proof of how difficult it is for hybrids to arise and of how little worth they are for the genus, the authors refer to the fact that in the Botanic Gardens of Munich, "unter den denkbar günstigsten Bedingungen" [1]), when more than 2000 sets of *Piloselloideae* have been cultivated, during 17 years only about 70 hybrid combinations have arisen. In the opinion of the authors the hybrids are of value only when the relationship of the species (forms) among one another is to be decided on, — a rather theoretical value, if I may say so.

The hieraciologists of the present time have, on the whole, more confidence in the importance of the hybrids for the origin of species within this genus, at any rate with regard to the subgenus *Pilosella* [2]). But we find no investigations to prove the considerations about the matter, merely casual remarks here and there.

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[1]) ? C. H. O.

[2]) Recently F. VOLLMANN (1909) has made some considerations on the matter. He is of the opinion that NÄGELI and PETER have greatly underrated this species-forming factor. After a short remark on MURBECK's discovery of apogamy in Hieracium and "die auf demselben Gebiete sich bewegenden Versuche von OSTENFELD und RAUNKIAER" [sic!], he enumerates a whole series of cases, where he thinks it necessary to suppose, that the forms in question have arisen by hybridization, but he has made no experiments to prove these suppositions. Instead of these speculations, which may be correct enough, I should have preferred to see some experiments from him. Purely theoretical assertions have not much more worth than his introductory considerations, where among other things he says about "die direkte Bewirkung" [i. e. Lamarckismus], "daß dieser Art von Variation so manche Hieracium-Form ihre Entstehung verdankt, ist so gut wie sicher."

In order to get better information, we must touch the great problem of the importance of hybridization for the origin of species in general and not restrict ourselves to a study of the papers on *Hieracia*, but we will not lose sight of the fact that our principal object is to answer the question with regard to the *Hieracia*. Generally taken, the question runs: Is hybridization of any importance as a species-producing factor in the Flowering Plants?

But before we can try to answer this question, we must briefly make clear what inheritance in hybrids means; in other words, we must learn what, at the present time, the workers in the problem of heredity say about the matter.

In his "Mutationstheorie" (vol. II, 1902—03) and later in his lectures (1906), HUGO DE VRIES has copiously treated the problem. He distinguishes sharply between variety hybrids and species hybrids, just by reason of the supposed difference in inheritance ("balanced and unbalanced crosses"). In variety hybrids we find Mendelian segregation in force, while "es eine nicht unerhebliche Reihe von constanten Rassen giebt, welche durch künstliche Verbindung von zwei verschiedenen Arten entstanden sind, und sich im Laufe der Generationen in jeder Beziehung, höchstens mit Ausnahme der verminderten Fruchtbarkeit, wie gewöhnliche Arten verhalten" (Mutationstheorie, II, p. 73). He has himself produced a constant hybrid, *Oenothera muricata* × *biennis*, which indeed has only a very limited fertility; moreover, he mentions as examples the hybrid *Aegilops speltiformis*, famous in the last century, and a hybrid *Anemone silvestris* × *magellanica* produced by JANCZEWSKI, and calls attention to A. KERNER's merits for having emphasized the hybridization as an important factor in the origin of species in nature.

To be sure, the examples of natural hybrids, put forth by KERNER, cannot be said to be unassailable proofs, as we do not know the origin of these hybrids exactly, nor do we know whether the hybrids now existing are several generations old (consequently constant) or only the first generation which in course of time has propagated vegetatively; then all the examples are perennial plants. Nevertheless DE VRIES seems to agree with KERNER's supposition and to be inclined to consider species hybrids as important and as constant. It must not be forgotten, however, that by segregation through several generations new constant forms can also be produced, and that in the long run it is of no consequence whether the hybrid is constant at once as F_1, or only later becomes so[1]). But here we only speak about species hybrids which become constant in the first generation and in which no segregation takes place. DE VRIES has called this type the Hieracium type, as, referring to MENDEL's experiments, he took the Hieracium hybrids as the best known case of this form of inheritance in hybrids.

It appears, from what I have quoted here as well as from many other remarks of DE VRIES, that he considers this non-segregating type as rather widely spread, though only very few exact experiments have been carried out to prove its existence. A concurrent cause hereof is that species hybrids are so often quite sterile. A well known example is the *Verbascum* hybrids, which very easily arise both in nature and in Botanic Gardens, but which, as far as I know, are always quite sterile.

In contrast to DE VRIES, W. BATESON goes so far that he considers the non-segregating hybrids as rare exceptions. In his recent publication "Mendel's Principles of Heredity" (1909) he deals with these exceptions in the first part of a particular chapter (XIV), which he begins with the following words "Of the various cases alleged to be exceptional, or declared to be incompatible with Mendelian principles, few have any authenticity. Several rest on errors of observation or of interpretation and some have even been created by a mistranslation or a misprint." The part of the chapter interesting to us here is "Crosses breeding true without segregation" (pp. 246—251); it comprehends two sections, viz. A. Parthenogenetic cases, and B. Sexual Types.

The first section consists even of *Hieracium*, and BATESON here briefly reports what has been known hitherto about the hybridization

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[1]) Of this case we have an example in *Rubus*. B. LIDFORSS (1905. 1907) has by experiments shown that new species in this genus can arise both by mutation and by hybridization. As to the hybridization he has discovered the peculiarity that, while F_1 most frequently is homogeneous and oftenest intermediate, there arises after self-fertilization a very polymorphous F_2 the heterogeneity of which, at any rate in part, must be supposed to be called forth by a mutation released by the hybridization. Also F_2 is inconstant, but in a less degree, and it seems as if constancy increases with the number of generations, so that constant new forms finally can be produced in this way.

As to the well known polymorphy in *Rubus*, it must be remembered that each individual has, practically seen, an indefinite lifetime and is able to form whole stocks by propagating only vegetatively. Thus both F_1 as well as the multifarious forms of F_2, etc. can respectively keep to the spot where they have risen, even if they do not give constant offspring sexually.

of the *Hieracia* and the pure-breeding of the hybrids. Together with this case he puts forward the remarkable fact that in certain Orchids a species, when fertilized with the pollen of different other species, still gives rise to an offspring which is completley like itself and shows no trace of the father parent. He considers this phenomenon, which he calls monolepsis, as "tantamount — as regards heredity — to parthenogenesis" (l. c., p. 249).

With regard to the sexual types (B) almost all the known cases are, in BATESON's opinion, "open to the criticism made in the last section, that either actual parthenogenesis or monolepsis may be occurring" (p. 249), as far as the question is about plants. He quotes as the most trustworthy cases DE VRIES's above mentioned *Oenothera muricata* × *biennis* and JANCZEWSKI's *Anemone silvestris* × *magellanica;* but both these cases have in common that the fertility in the hybrid is very limited, which fact BATESON expressly mentions as weakening the convincing power of the cases. The same objection is made more emphatically by R. H. LOCK (1909) who says that such cases do not prove anything, for perhaps the segregating factor is hidden in such a way that those germ-cells which should give the segregating individuals. are not functional. This objection is, in my opinion, valid. If then the vegetable kingdom does not show any incontestable case of true-breeding hybrids[1]), still some, though few, are found within the animal kingdom (mulatto, rabbits, butterflies), so that the existence of true cross-breeding cannot be denied, but we must clearly understand that it is the exception, and segregation the rule.

Even if BATESON's position is rather extreme, I think that this reaction is useful, especially as it makes clear to us what we know with certainty in this matter, — and that is very little, at least with regard to species hybrids.

In W. JOHANNSEN's "Elemente der exakten Erblichkeitslehre" (1909), published a few weeks before BATESON's book, similar points of view are held out. JOHANNSEN defines clearly and appropriately constant hybrids thus: "darunter versteht man ein Kreuzungsprodukt, F_1, das nicht spaltet" (p. 424), and also for him they are the exception, segregation the rule. In contradiction to DE VRIES, he — as

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[1]) BATESON does not seem to know a paper (written in Swedish) by T. HEDLUND (1907), according to which a *Malva* hybrid (*M. parviflora* × *oxyloba*) seems to be quite fertile and constant in its offspring and still to have full fertility, but the experimental method of HEDLUND is perhaps not quite indisputable.

also BATESON (1909, p. 285) — means, that there is no settled difference between segregating variety hybrids and non-segregating species hybrids, and here I quite agree with these authors.

JOHANNSEN reports briefly the main points of my investigations on the Hieracia which I had placed at his disposal for this purpose, and points out, that: "diese Sache eine große Bedeutung haben kann für das Entstehen neuer Biotypen" (p. 425), but that we are still only at the beginning of the investigations. A little later he comes back to the constant Hieracium hybrids and says: "Es sind eben gleich als F_1, neue Rassen oder Species gebildet. Denn diese Biotypen verhalten sich ja wie homozygotische Organismen — ja sie sind es wohl eigentlich" (p. 437), — sentences with which I fully agree. Moreover, the investigations have now confirmed JOHANNSEN's supposition in the following sentence, viz.: "Inwieweit das Nichtspalten, wie es bei den S. 425 erwähnten Ostenfeld'schen Hieracium-Bastarden wohl der Fall ist, oft mit Apogamie zusammenhängt, läßt sich noch nicht entscheiden". This supposition is now proved, as far as the Hieracia are concerned.

In my opinion, BATESON is therefore right in saying that no indisputable examples of non-segregating crosses have been found among plants, as the Hieracium hybrids, which apparently were a proof of non-segregation, have by my investigations been unravelled to be constant only on account of apogamy, and probably would segregate when crossed back with the parents. —

The results of our going through the literature do not seem to indicate that hybridization is of great importance for the origin of species. However, it would be too precipitate to deny its value absolutely. There are many facts to indicate that it is still of some consequence. Firstly, as already stated above, new constant forms can arise also in segregating hybrids through segregation during several generations. And secondly, we have our special case, *Hieracium*, where the artificially produced hybrids immediately act as new species which breed true from seed (on account of apogamy). In nature the same thing must happen; the hybrids act quite as normally sexual species and have consequently the same worth as these. However, this method of the origin of species has, as already pointed out by NÄGELI and PETER, the restriction, that the hybridogenous new species do not bring new characters, but only new combinations of already existing characters, or as DE VRIES says (1903, p. 492): "Wenn auch durch Bastardierung keine neue Artmerkmale entstehen können, so können doch andererseits, zweifelsohne aus Bastarden neue Arten hervorgehen".

New species certainly arise through hybridization, but this method of the origin of species is limited to certain cases, e. g. Hieracium, and is checked in many ways.

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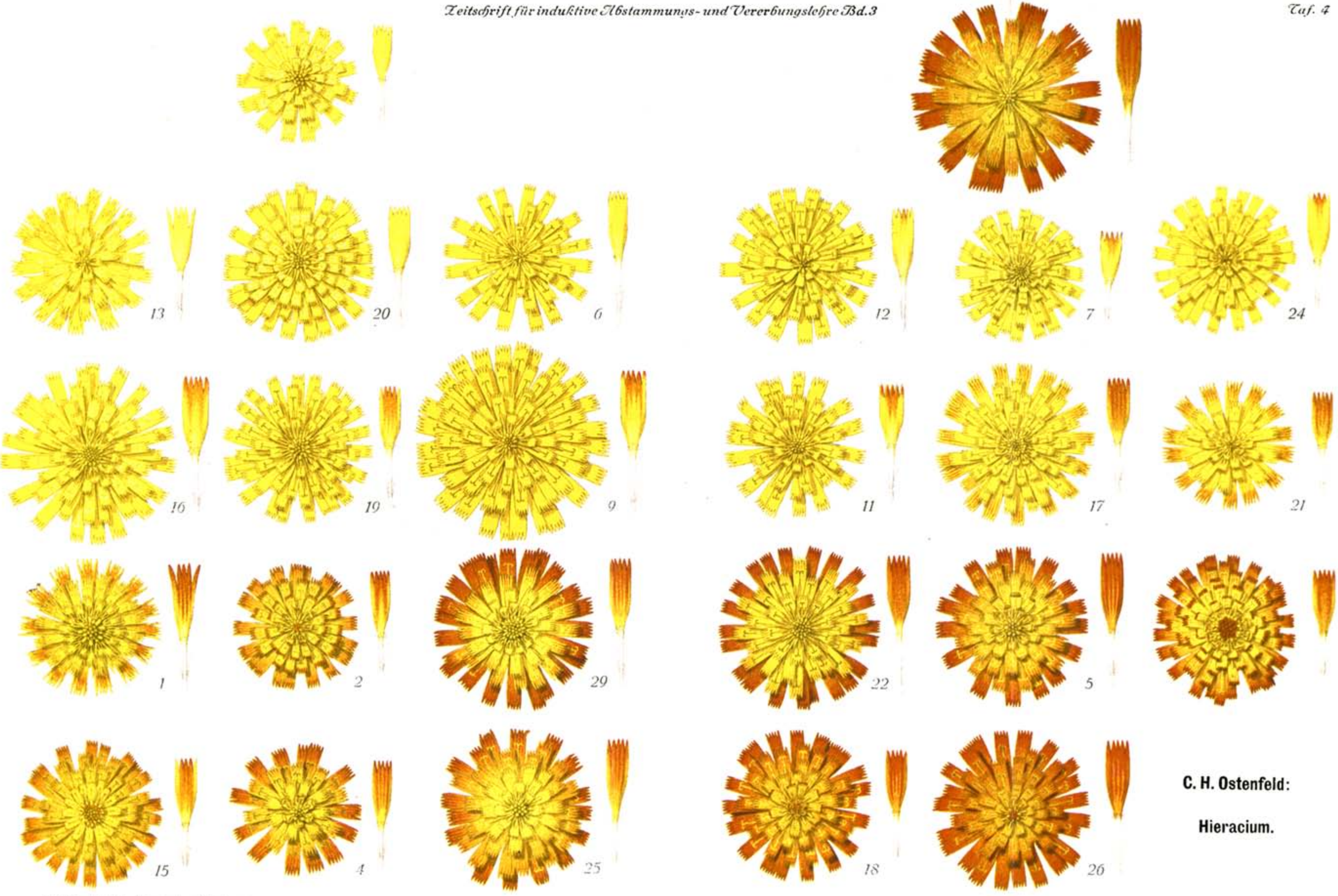

C. H. Ostenfeld:

Hieracium.

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Explanation of Plate 4.

Reproduction of coloured drawings of flowering heads, seen from above and of the outer flowers, seen from below ($^3/_2$ and $^3/_1$ nat. size). Uppermost: *Hieracium auricula* and *H. aurantiacum*. Beneath: 23 specimens of one and the same family of hybrids between these two species. The figures have protocol numbers; but the arrangement here used should show the gradation in flower colour, reaching from the yellow mother to the orange-red father. This gradation is not correlated to the vegetative characters.

The drawings have been made by Mr. N. HALKJAER.

Referate.

Lang, A. Über Vererbungsversuche. 3. Fig. i. T. und 2 Taf. Verhandl. Deutsch. Zoologischen Gesellschaft 1909. S. 17—84.

In experimentellen Untersuchungen über Vererbung, Bastardierung und Artbildung haben während der letzten Jahre unstreitig die Botaniker die Führung gehabt. Die Zoologen haben sich sehr zurückgehalten und ganz besonders gilt dies für die deutschen Zoologen. Das scheint jetzt anders zu werden. Auf der letzten Tagung der Deutschen Zoologischen Gesellschaft haben gerade Vererbungsfragen die wichtigste Rolle gespielt. Ref. erinnert hier nur an die ausgezeichneten Untersuchungen an Daphniden, über die Woltereck berichtet hat. Die erweiterte Wiedergabe eines andern, auf der gleichen Tagung gehaltenen Vortrages von A. Lang liegt in der hier zu referierenden Abhandlung vor. Die Arbeit gibt in klarer, gedrängter Form eine speziell für Zoologen bestimmte erste Einführung in die wichtigsten Ergebnisse und die neuen Fragestellungen der „exakten Erblichkeitslehre“, um mit Johannsen zu reden. Daß diese Einführung inhaltlich vollkommen auf der Höhe ist, braucht wohl nicht erst hervorgehoben zu werden, und es ist auch wohl nicht nötig, auf Einzelheiten hier einzugehen. In allen prinzipiellen Fragen vertritt Lang Anschauungen, die denjenigen Johannsens und wohl der Mehrzahl der übrigen experimentell arbeitenden Botaniker ungefähr entsprechen.

Möge die anregend geschriebene Abhandlung Propaganda machen! Es gibt doch sehr zahlreiche Tiere, deren Kultur, auch bei sehr großen Individuenzahlen nicht mehr Mühe macht als die Kultur der Pflanzen. Besonders für die Frage der experimentellen Auslösung von Mutationen nach dem Beispiel der wichtigen Untersuchungen Towers dürften sicher auch viele andere Tiere gute Versuchsobjekte abgeben, bessere als im allgemeinen die