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The Aecial Stage of Alsike Clover Rust

W. H. Davis
State Teachers College

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THE AECIAL STAGE OF ALSIKE CLOVER RUST.

W. H. DAVIS.

A rust belonging to the genus *Uromyces* is rather prevalent in this latitude on the common clovers, white (*Trifolium repens* L.), red (*Trifolium pratense* L.) and alsike (*Trifolium hybridum* L.). The rusts on clovers were formerly classified as a single species or one rust until the work of Liro separated them into two species, one on red and one on white clover. The disposition of the rust on alsike clover is not clear. Liro (9), in his inoculations 93-94, tried to inoculate alsike with urediniospores of white clover rust, but the results were negative. According to Sydow (6, p. 133) Alsike clover is a host for the rust on red clover (*T. pratense*) while Arthur (2, p. 225) gives Alsike as a host for the same rust as found on white clover. There seems to be a general belief that the rust of white and of alsike clover are of the same species. This belief is confirmed by the fact that they are morphologically similar in two respects; the sizes of the urediniospores and teliospores are similar and the urediniospores of each have two to three germ-spores equatorially placed. They differ in the number of known spore forms—white clover has all five spore forms, while alsike has no pyenia and aecia. Rostrup (6, p. 134) reported aecia on alsike in Germany (1886) but the correct determination of the host is questioned. It is not generally accepted that alsike rust has a pyenian and an aecial stage.

On April 25, 1916, several out of door clover plats were under careful observation for the aecial stage of rusts when golden swellings were noticed on the midribs of the leaves on an alsike clover plant. The Alsike plants had been left uncut during the summer and fall of 1915, so the old rusted leaves and stems remained intact.

On April 27, 1916, specimens of aecia were picked and used for inoculating purposes. As aecia and pyenia were abundant during the month of May, material was killed, imbedded for sectioning and pressed for herbarium specimens. The aecial stage continued to develop until June 7 when none could be located. The aecial stage of this rust could not be located around

Cedar Falls, Iowa, during the dry summer and fall of 1916.

Pycnia—Occurrence—Mostly in groups, 1 mm. to 10 mm. long, numerous, mostly along the midrib of the leaflet on the under side. Often found on the upper side, on petioles and stipules, near or remote from aecia. Appearance—Noticeable on account of the swollen areas on the leaf and the striking golden color of the aecia with which they are associated; generally on the smaller leaves covered by a canopy of larger and more vigorous leaves. Color—First white water soaked areas, later, a dirty brown. Shape—Flasked with a globose base. Size—

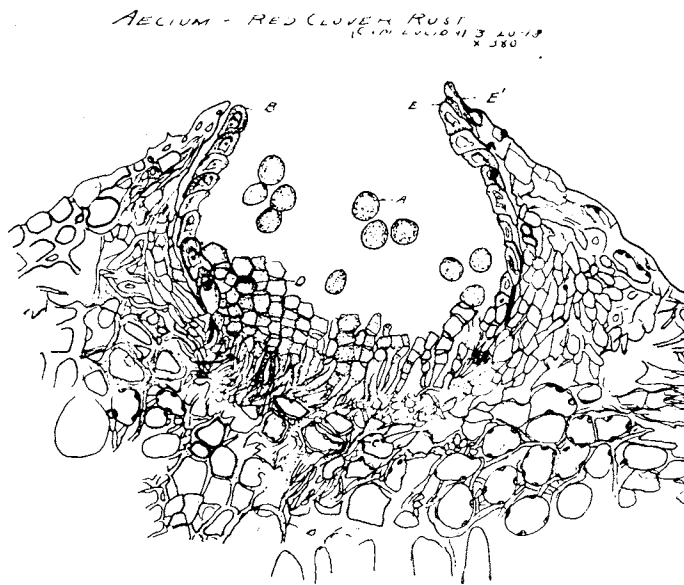


Fig. 89.—An Aecium on Red Clover.

Height 118 Mu. (Aver. of 10); width 118 Mu. (Aver. of 10); osteole 25.4 Mu.; hymenial surface 30 Mu.; paraphyses, length 65 Mu., width 2.4 Mu.; pycnosporos 2.3x4.5 (Standard 3x4). Twenty measured. See figure 94.

Aecia—Numerous, scattered with pycnia which appear three to five days before aecia open. In mass, color a striking golden; leaf appears swollen and puffed at this point or in some cases the entire length. More striking than the aecial stages of red and of white clover rust. More like the white because the symptoms show better on the upper leaf surface. The first aecia ap-

peared April 26, 1916, and the aeciospores proved viable. When on the petiole, they were located at or below the lower half. Size—the patches vary from 0.1 mm. to 150 mm. in length and tend to the elliptical, near or remote from pycnia; height, 182 Mu. (20 measured), width, 172 Mu.; peridial cells length, outer

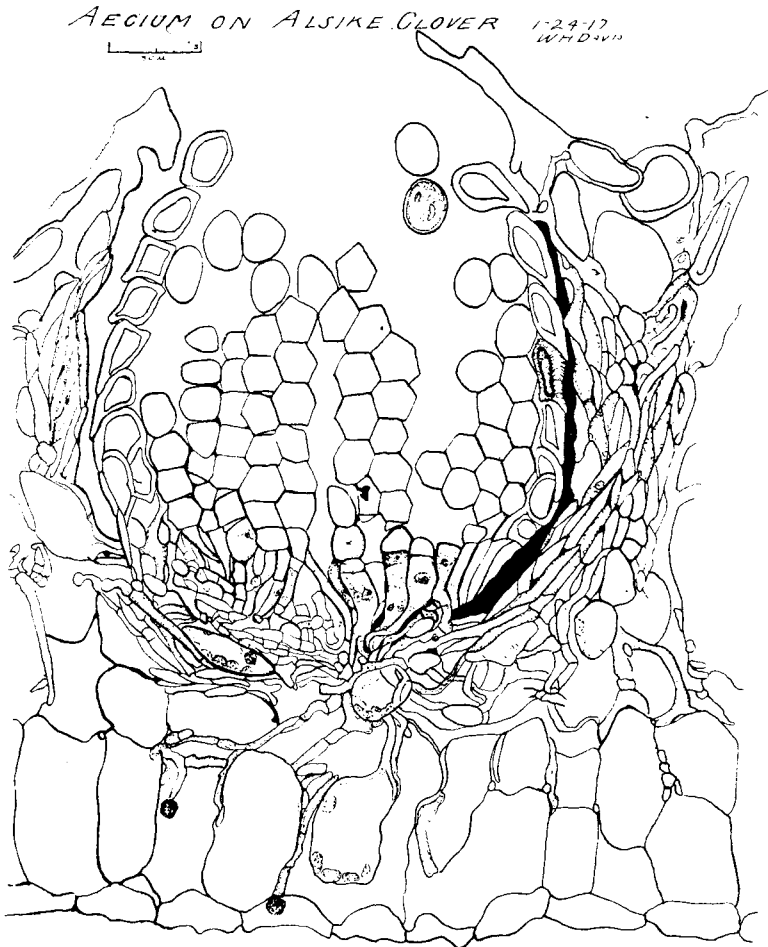


Fig. 90.—An Aecium on Alsike Clover. For measurements see Tables I and II.

22 Mu. (10 averaged), inner 15 Mu. (10 averaged), width, 14 Mu. (10 averaged). Lumen, length 12.5 Mu., width, 10 Mu., outer wall, transversely striated 2.5-3.5 Mu. thick; inner wall minutely verrucose, 0.7-1.5 Mu. thick. The cups present a white

waxy appearance when emptied of aeciospores. The peridial wall is not recurve as in white and red clover rust but more flask shaped. See figure 90; figure 92 (1, 2, 3); Plate XV, A; Plate XVI, A.

Aeciospores—Shape—(Globose, subglobose, to ellipsoid-angular; wall color, starchy white, less than 1 μ . thick; surface minutely verrucose; sizes 10-22x15-26 μ .; standard 17-20x20-24 μ . (54 measured); germination. Minimum, 4° C., Optimum, 14° C., Maximum, 22° C. The first spores emitted from an aecium are more viable, more active and have a quicker pene-

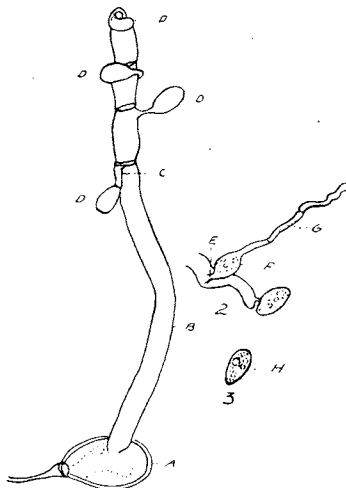


Fig. 91.—Tracing from a camera lucida drawing. 1, Teliospore of Alsike Clover rust germinating: Spore collected October 31, 1916. Set to germinate December 19, 1916. Drawn December 22, 1916. Spore 20.4x27.2 μ . Pro-mycelium 6.8x170 μ . Sterigmata 2x4 μ . (average). Sporidia 14x17 μ . (average). 2, A sporidium of 1 germinating while on the sterigma. Germ tube 3.4x31 μ . long. 3, An average sized sporidium 7x14 μ .

tration than later ones. These aecia differ in that about twenty-four hours after opening, the spores seem mostly lifeless. The most successful time to inoculate with these spores is just as they come from the aecial cup. Viability one to three hours. Period of noted infection nine to fourteen days. See figure 90.

The following tables show the relative measurements of spores and peridial cells from the rusts on three clovers. All measurements are in microns, the width being first indicated.

TABLE I.

Host	Stage I			Aeciospores					
	Arthur	Saccardo	Sydow	Howell		Davis			
				Size	Temp.	Temp.	Size	Stand 'rd	No
T. repens	15-17 x 16-21	14x23	14-18 x 17-21	14x22	15-18 26°C	3 20 27 3	6-24 x 16-30	18-22 x 22-26	50
T. pratense	-----	-----	-----	-----	-----	12 25-35	8-24 x 20-29	18-22 x 22-24	73
T. hybridum	-----	-----	-----	-----	-----	4 14 2	10-22 x 15-26	17-20 x 21-24	54

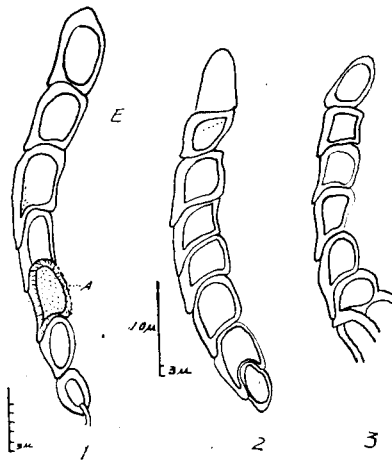


Fig. 92.—Peridial cells of Aecia from Alsike Clover rust. Camera lucida drawings from prepared slides of material collected out of doors May 13, 1916. 1, A shows the inner surface of a peridial cell; C, The striated outer wall; E, The large lumen of the cell. Note the overlapping of the outer walls, also the thickness compared with the inner wall. For measurements see table II. 2 and 3, Other peridial cells of the same rust.

The proper names used as headings signify the authors whose reports are used. The germinating temperatures are given in degrees centigrade, beginning at the top, minimum, optimum and maximum in order. "Number" in the last column refers to the number of spores measured. The measurements given

under *T. pratense* are those of Davis and Johnson, who connected this stage with the life cycle of rust on red clover. See report of the National Association for the Advancement of Science, December, 1916: The Aecial Stage of Red Clover Rust by Davis and Johnson.

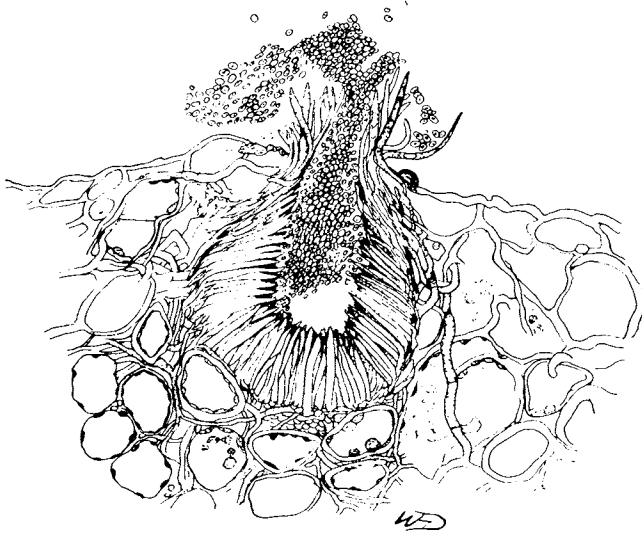


Fig. 93.—A Pycnium on Red Clover. April 20, 1916. X 650.

TABLE II.

Hosts	Peridial Cells—Stage 1			Aecia					
	Sydow	S. p. 161 Ivanhoff		Davis		High	Wide	Open- ing	No
	Wall	Wall	Lumen	Wall	Lumen				
<i>T. repens</i> ----	2* 1 5†	1.5 4.5	13.5	1.7-3 5	8-12 X 20-22	308	290	310	10
<i>T. pratense</i> -----	-----	-----	-----	2.3-3.5 5-6.8	8-10 X 12-16	189	178	224	5
<i>T. hybridum</i> -----	-----	-----	-----	1.5 2.5-3.5	8-12 X 10-14	182	172	140	10

*Thickness of the inner wall of the peridial cells.

†Thickness of the outer wall of the peridial cells.

The heading "number" refers to the number of aecial cups measured. The measurements were made from stained slides.

TABLE III.

Stage 0---Pycnia						
Host	Spores	High	Wide	Osteole	Paraphyses	Hymenial Surface
<i>T. repens</i> ----	1.7x2.4	150	120	17	Numerous 2.5 x 40	35
<i>T. pratense</i> ..	2-3.5 x 3.5-5	100	100	25	Numerous to 25 2-5 x 34-40	25
<i>T. hybridum</i> ..	2-3 x 4-5	119	119	26	Numerous 2-4 x 65	30

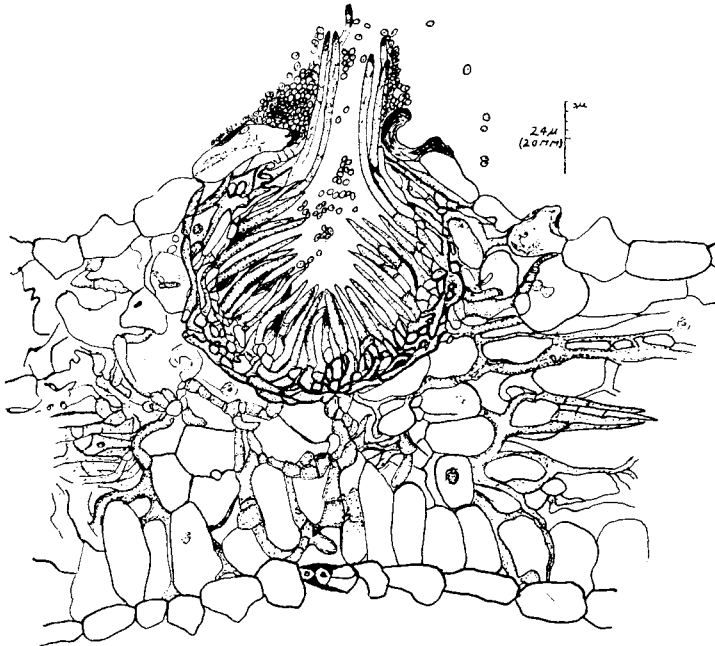


Fig. 94.—A Pycnium on Alsike Clover. For measurements see Table III.

The above numbers are averages of measurements and counts of ten pycnia, killed, sectioned serially and stained.

Summary of the tables comparing the aecia and pycnia of the rust on *T. hybridum* with that on *T. repens* and *T. pratense*.

1. The aeciospores on alsike clover rust are smaller than those of red and of white clover rust.
2. The range of temperature for germination is much narrower than that of the other aeciospores.

3. The inner and the outer walls of the peridial cells are much thinner than the corresponding peridial walls of the other rusts. The outer peridial wall of each clover rust is transversely striated while the inner wall is minutely papillose.

4. The lumen in the cells of the peridium averages smaller.

5. The openings of the aecia are smaller, the edges do not recurve but incurve while those on *T. repens* recurve considerably, on *T. pratense* slightly or are straight.

6. The paraphyses are longer, hymenial surface of the pycnia deeper than that of *T. repens*.

7. The pycnia are taller and the osteoles wider than those of *T. pratense*, smaller than those of *T. repens*.

8. There are as many morphological differences between the aecial and pycnial stages of the rust on *T. hybridum* and *T. repens* (also *T. pratense*) as between that on *T. repens* and *T. pratense*, which are regarded as two separate rusts.

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Inoculations					Results		
No. of Inoculation	Spores Used	Date of Sowing	Host Plant Inoculated	No. of Leaves	Date	No. Infected	Remarks
31	I of Alsike from out of doors	4-26-16	Alsike A	6	5-24-16	2	4 died
			Alsike B	7		6	
32	I of Alsike-----	4-28-16	Red	6	5-22-16	0	
			White	6		0	
33	I of Alsike-----	5- 4-16	Alsike	7	5-14-16	7	Appeared
					5-23-16	7	Highly infected II
34	I of Alsike-----	5-10-16	Red	Sprayed on the leaflets	5-22-16	0	
			White			0	
			Alsike			0	Highly infected II
			*Crimson			0	
35	III Alsike from out of doors	5-12-16	Alsike	Sprayed on between stipules	5-26-16	2	Showed 0 and I
			White			0	
36	I Alsike-----	5-13-16	Alsike	Spread on	5-27-16		All highly with II
37	II Alsike-----	5-23-16	White	9	6- 5-16	0	
			White	Spread on		0	All highly with II;
			Alsike	Spread on			later III
38	III Alsike-----	5-23-16	White	Between leaflets	6- 5-16	0	
39	I of White out of doors	10-17-16	Red	6	11-13-16	0	
			White	6			All showed infection
			†Mammoth	6		0	
			Alsike	6		0	
			Alfalfa	6		0	
			Seedlings		11-17-16		All clear save
			9-28-16				white; highly infected

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Inoculations					Results		
No. of Inoculation	Spores Used	Date of Sowing	Host Plant Inoculated	No. of Leaves	Date	No. Infected	Remarks
40	I of White-----	10-26-16	White	6	11-17-16	5	11-14-16. All infected
			Alsike	3		0	
41	Alsike II -----	10-26-16	Red	3	11-17-16	0	Abundantly II
			Mammoth	3		0	
			Alsike	3		3	
			White	3		0	
42	Alsike III germinating from out of doors (30 per cent)	11-26-16	Alsike A	7	12-18-16	3	With 0I
			Alsike B	6		2	
			White	6		0	
			Red	5			
			(Seedlings 9-26-16)				
43	III of Alsike-----	12-26-16	Alsike	5	1-10-17	1	5 on 1-15-17
			White	5		0	
			Red	5		0	Highly infected
44	I of Alsike-----	1-27-17	Alsike	3	2-16-17		
			‡Alfalfa	3		0	
			§Melilot	3		0	Good, see Plate XVI, A
45	III of Alsike-----	2-27-17	Alsike	5	2-30-17	5	
			Crimson	5		0	

**Trifolium incarnatum* L.

‡*Trifolium medium* L.

‡*Medicago sativa* L.

§*Melilotus alba* Desr. (Classified according to Gray's Manual--1908 Edit.)

Conclusions from the above spore sowings:

1. The aecial stage of alsike clover will not inoculate red clover, white clover, mammoth clover, crimson clover, alfalfa and white melilot.
2. The aeciospores of alsike clover will inoculate alsike clover and produce the characteristic urediniospores.
3. The urediniospores of alsike clover rust fail to inoculate the same plants that the aeciospores fail to inoculate.
4. The urediniospores will inoculate alsike and produce the characteristic uredinia and telia.
5. The teliospores germinate and produce the characteristic sporidia (which were observed in spore sowings on water) which produce the aecia on alsike clover *only*, following the aeciospores and urediniospores in this respect.
6. The rust on alsike clover is a long cycled, autoecious rust with all spore forms which have not been transferred to the other clovers.

The Synonymy of Clover Rusts.

Host, undetermined species of Trifolium.

1. *Puccinia trifolii* ("Puccinia des trefles"), Hedw. f., 1805 ("Le trefles rampant, le trefle filiforme et le trefle hybride") (alsike). See Ref. 5, p. 5.
2. *Uredo fabae trifolii*, Alb. and Schw., 1805.
3. *Uredo trifolii* D. C., 1808.
4. *Aecidium trifolii-repentis* Cast., 1842.
5. *Uredo fallens*. Desm. ("in follis trifoliorum"), 1843.
6. *Aecidium trifolii* (Hedw. f.) Liro, 1847.
7. *Trichobasis fallens*, Cooke, 1870.
8. *Uromyces trifolii* (Hedw. f.) Liro (4, p. 534).

On red clover T. pratense L.

On white clover T. repens. L.

9. *Uromyces trifolii* (Hedw. f.) Liro, 1906. (The rust on Alsike clover is placed here by Sydow.)
10. *Uromyces fallens*(Desm.) Nov. Comb. Kern, 1911.
11. *Nigredo fallens* (Desm.) Arthur, 1912.

Uromyces trifolii-repentis. (Cast) Liro, 1906. 6, p. 131-132.

Uromyces trifolii (Hedw. f.) Liro, 1911, p. p. 6.

Nigredo trifolii (Hedw. f.) (2, p. 219.) Arthur, 1912. Res. Sci. Con. Bot. Vien., 344. 1906.

(The rust on alsike clover is assigned to this species by Arthur.)

The causal organism for rust on alsike clover has been given as *Uromyces trifolii* (Hedw. f.) Liro and *Nigredo trifolii* (Hedw. f.) Arthur, thus placing it with the rust on red clover in the former case and with that on white clover in the latter.

The question which naturally arose as to its disposition can now be answered in a more satisfactory manner. As the aecial stage has been definitely located and connected in the life cycle by inoculations, it shows the rust to be long cycled, autoecious, with all spore forms. Inoculations show that none of the spore forms have been transferred to the other clovers. The measurements show many morphological differences, at least as many as exist between the rust on white and on red clover. *Nigredo fallens* (Des.) Arthur, is the rust on red clover; *Nigredo trifolii* (Hedw. f.) Arthur, the rust on white clover.

If the rust is to be named, probably *Nigredo hybridi* Davis would be in best keeping with Arthur's classification, which transfers the rust from the genus *Uromyces* to that of *Nigredo*. Otherwise *Uromyces hybridi* Davis.

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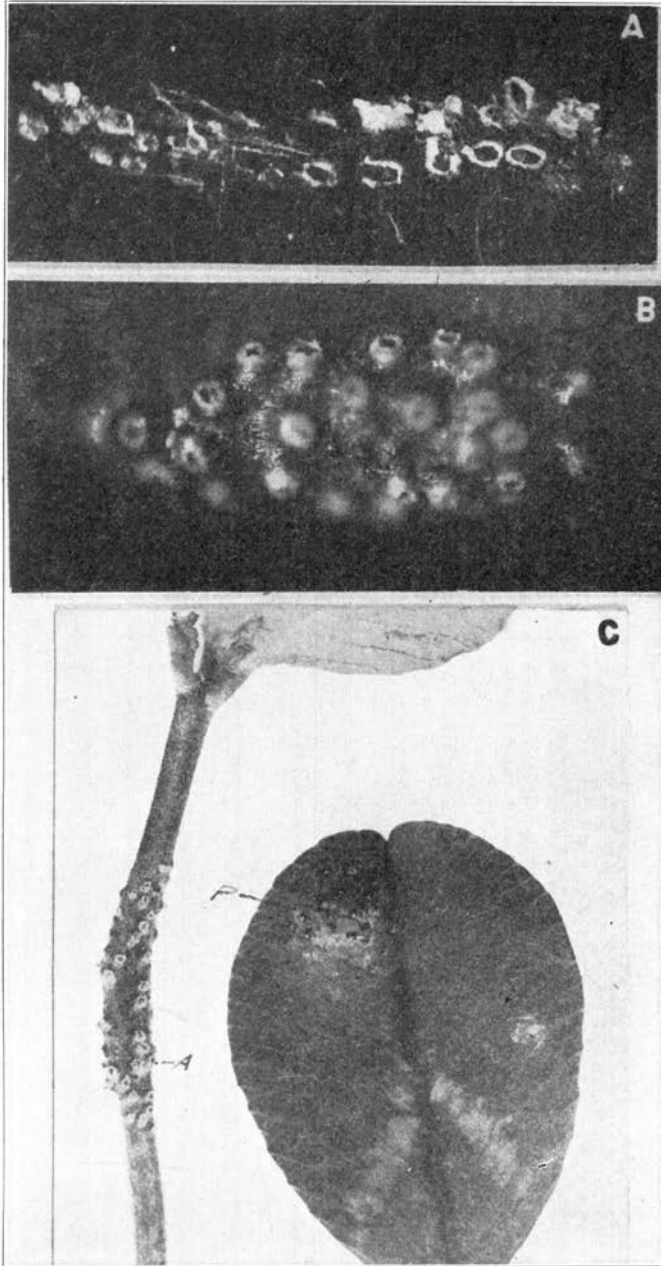
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PLATE XV.

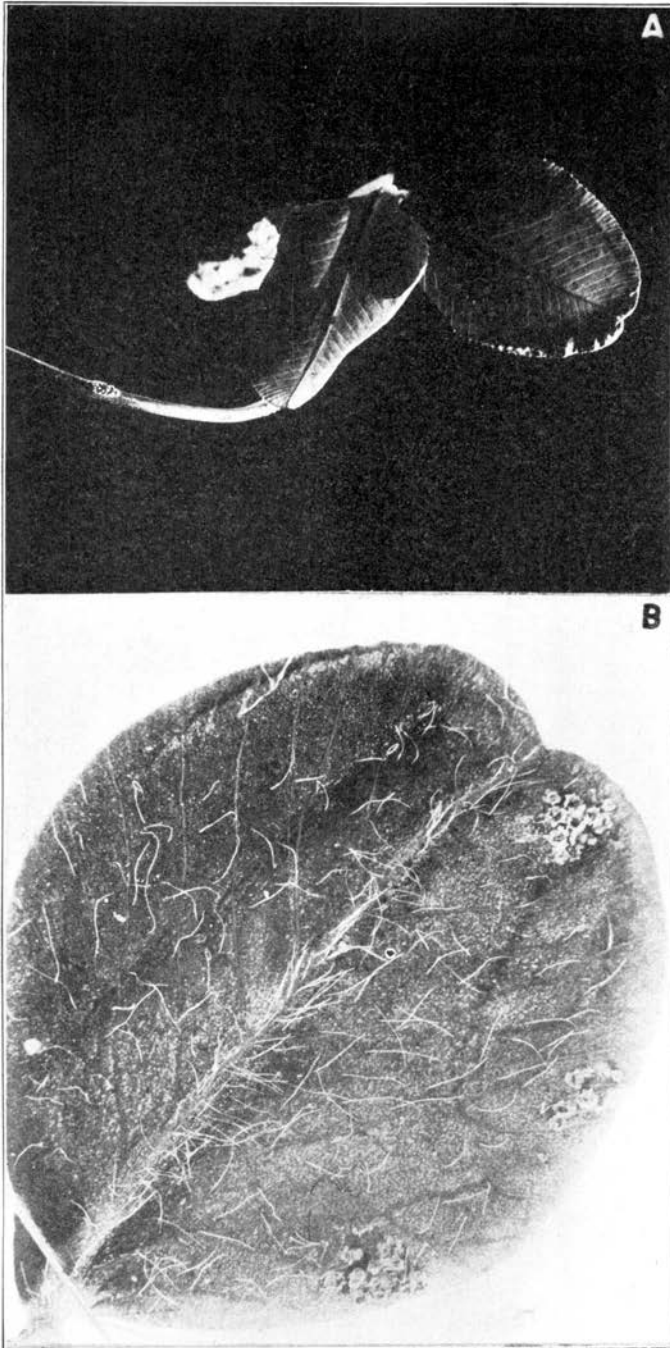


A. Aecia on Red Clover; B, Aecia on Alsike Clover; C, Aecia and Pycnia on White Clover.

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PLATE XVI.



A, Aecia on a leaf of Alsike Clover; B, Aecia on a leaf of Red Clover.