ANTIRRHINUM RUST, PUCCINIA ANTIRRHINI D. & H., IN AUSTRALIA.

By J. Walker, Biological Branch, New South Wales Department of Agriculture.

(Plate vii; two Text-figures.)

Sijno2)sis.

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The origin and the spread of the disease in Australia are discussed. An American origin for the disease is proposed and evidence is presented to show the importance of wind-borne uredospores in the spread of this disease.

Introduction.

The rust disease of Antirrhinum spp. caused by the parasitic fungus Puccinia antirrhini Dietel and Holway is the most destructive disease of these plants known. Until October, 1952, it had not been recorded in Australia, but at that time a severe outbreak occurred in New South Wales in the Sydney metropolitan area, and within a short time it had spread throughout eastern New South Wales. Since then it has been recorded from Victoria, Queensland, South Australia and Tasmania. In this paper details of the work carried out on this disease since its first outbreak are given.

History of the Disease.

Antirrhinum rust was first recorded by Blasdale (1903), who, in 1895, had found it doing considerable damage in Californian gardens. Specimens of the rust had been collected in California before this date, however, and a specimen in Professor J. C. Arthur's collection from Santa Cruz is dated 1879 (Peltier, 1919). The fungus was described as Puccinia antirrhini by Dietel and Holway (1899) from specimens submitted by Blasdale.

In 1913 the disease was recorded from the eastern State of Illinois, and by 1919 (Peltier, 1919) had spread throughout the United States. In 1921 it was reported by Dickson (1921) from Canada, and in 1922 Whetzel (1924) found it causing severe damage to snapdragons in Bermuda.

Up to 1931 no new records of rust were made, but Lepik (1941) states that, in that year, Viennot-Bourgin reported it in the north of France. Soon after, the disease was reported in England. Green (1938), reporting the outbreak, stated that the rust appeared at a number of localities simultaneously and that spread was rapid and destructive. Spread to other European countries occurred rapidly, and four years later it had been recorded from as far east as Odessa (Lepik, 1941), Palestine (Rayss, 1937) and Egypt (Fikry, 1937). More recently it has been recorded in South Africa (Bottomley, 1940), Norway (Jorstad, 1946) and Tanganyika (Wallace, 1952).

The first record of the disease in Australia was made during October, 1952, on plants growing in a Sydney (N.S.W.) suburban nursery. It spread rapidly and within eighteen months was common in eastern New South Wales and had been reported from all other States of the Commonwealth with the exception of Western Australia. Details of its spread are given in the "Epidemiology" section below.

More recently, in December, 1953, rust was reported in New Zealand at Auckland. So far, no further spread in that country has been noticed (Brien, 1954, personal communication).
NOTES ON AUSTRALIAN BEETLES IN THE TRIBE BOLBOCERATINI FORMERLY IN THE GENUS BOLBOCERAS.

By Henry F. Howden, Department of Zoology and Entomology, University of Tennessee, Knoxville, Tennessee.

(Communicated by Dr. P. B. Carne.)

[Read 28th July, 1954.]

Synopsis.

The name Bolboceras could not be applied to any Australian species of the subfamily Bolboceratini. Consequently Boucomont's subgeneric names Blackburnium, Bolborhachium, and Bolbapium are elevated to generic rank and a key is given to the Australian genera in the subfamily. Also new names are proposed for two synonyms: Blackburnium quadriarmigerum new name for Bolboceras armigerum MacLeay and Blackburnium bifoveatum new name for Bolboceras cornigerum MacLeay.

In a recent publication Cartwright (1953, Proc. U. S. N. M., 103:95-120) has shown that the name Bolboceras should be applied to a small genus of beetles represented by ten North American and one European species. Cartwright (1953, p. 101) presents the reasons as follows:

"The genus Bolboceras was erected by Kirby in 1818 for the eight species Scarabaeus mobilicornis Linnaeus [should read Fabricius], S. mobilicornis var. testaceus Fabricius, S. quadridens Fabricius, S. farctus Fabricius, S. luzarium Fabricius, S. cyclops Olivier, S. cephus Fabricius, and Bolboceras australasiae Kirby. Technically no genotype was designated although he wrote, 'My details of Bolboceras were taken from B. quadridens'. Nearly all of the species mentioned have since been moved to other genera. Curtis, 1829 (British Ent., vol. 1, pt. 1, p. 74), selected the species Scarabaeus mobilicornis Fabricius [= armiger Scopoli] as the type of Bolboceras. Therefore, since our species of Odontocrus are congeneric with mobilicornis, they now take the generic name Bolboceras and it becomes necessary to find an available name for those species we have formerly placed in Bolboceras."

Several names formerly placed in synonymy and a number of subgeneric names are available. Most of these names are applicable to European and American forms which are quite distinct from the Australian species. Of these only three seem easily referable to the Australian forms. Blackburnium, Bolborhachium and Bolbapium were proposed as subgenera under Bolboceras by Boucomont (1910, Ann. Soc. ent. Fr., 79:339-340) and are herein slightly modified and raised to generic rank.

With some redenifion of generic characteristics, most of the Australian species can be included in the genus Blackburnium. Boucomont's description, translated from the French, is as follows (1910, p. 339): First joint of the antennal club with a denuded area not clearly delimited; anterior edge of the prothorax bearing behind the eyes two little round and deep foveae; prosternal cavities carinate at the external edge; anterior lobe of the mesosternal plate tectiform or more exactly cariniform, raised in front like the prow of a boat; posterior lobe terminated in an acute angle with an abrupt edge and vertical slant; first stria of elytra, as in most of the Australian species, reaching the base by going around the scutellum from which it is separated by a fine carina; base of elytra carinate.

From the material the writer has examined it seems doubtful if several of the above characters should be given generic weight. Deep foveae can be found behind the eyes in some species, indications of them in other species, and in many cases they are com-
As with other rust fungi, various races of *P. antirrhini* have been found. Up till 1937 only one race of this rust was known, but in that year Yarwood (1937), working with excised leaves of various snapdragon varieties, demonstrated in America the existence of another race. This new race was known as race 2, the original being race 1. Race 2 proved to be more virulent than race 1 and was able to attack all those varieties that were hitherto resistant to the disease and, at the present time, there are no commercial lines of snapdragon resistant to race 2. Apart from these two races, it is quite possible that others also exist. Baker (1953, personal communication) stated that work done in California indicated clearly that other races are present there.

The second of Boucomont's subgenera, *Bolborhachium*, here accorded generic status, has the prothorax with an abrupt, carinate edge parallel to the base, the prothorax before the carina abruptly decollvicious, often excavated; first elytral stria shortened, barely reaching scutellum; elytral base margined; seven striae between suture and humeral umbone; mesosternal plate anteriorly flat between the middle coxae and truncate in front.

**Type of Bolborhachium** as designated by Boucomont (1910, p. 339): *B. recticorne* Guérin. Less than ten species have been placed in this strictly Australian genus.

The third of Boucomont's subgenera accorded generic rank is *Bolbapium*. As defined by Boucomont the genus includes both Australian and South American species. Since none of the Australian species have been examined, a translation of Boucomont's description is given unchanged (1910, p. 349): Elytra with five striae between the humeral umbone and the suture, the first reaching the base; ocular cavities of the prostromum large, with lateral edges at a right angle with a carina at the intersection of the two planes; mesosternal plate large, convex, pear-shaped.

Most species with elytral base unmarginated. However, several Australian species, according to Boucomont, have a small basal carina and their present inclusion in this genus is open to question.

To facilitate the placement of the Australian species in the tribe Bolboceratini a brief key to the genera is included below.

1. Scutellum very narrow, almost linear
   - *Stenaspis* dian 

2. Scutellum triangular, not linear
   - *Bolboceras* (formerly *Odontacrus*)

3. Middle coxae subcontiguous, mesosternum linear between coxae
   - *Bolbapium* (formerly *Odontacrus*),

4. Middle coxae separated one from the other by the anterior lobe of the mesosternal plate which is never linear
   - *Bolbapium*

5. Elytra with five dorsal striae between suture and humeral umbone; males with clypeus not greatly elongated
   - *Plecanthus*

6. Elytra with seven dorsal striae between suture and humeral umbone; males with mouth inferior with clypeus greatly elongated
   - *Bolboceras*

7. Mesosternal plate testiform or cariniform, often raised in front like the prow of a boat; sutural striae of elytra curving around scutellum to the base
   - *Blackburnium*

8. Mesosternal plate flat, truncate in front; sutural stria of elytra short, barely reaching scutellum
   - *Bolborhachium*
ANTIRRHINUM RUST IN AUSTRALIA, on the upper side of the leaf and in some cases the uredosori were slightly smaller than those on the "fully susceptible" types.

Of the varieties listed in Table 1, Watkins and Simpson's Pink Freedom, Wisley Bridesmaid, Wisley Cheerful and Wisley Golden Fleece were sent out by Mr. D. Green of Wisley, England, and No. 61 by Dr. K. F. Baker of California. These five varieties were strain-1 resistant types and, as is seen from the table, they were quite susceptible to the local rust race. This indicates that the race of *P. antirrhini* present in Australia is not race 1, but is similar to the virulent race 2.

Two varieties of *Linaria*, Excelsior Hybrid and Fairy Bouquet, were also inoculated with rust. Both showed no sign of infection. In the United States, Blasdale (1903) recorded *P. antirrhini* on two species of *Linaria*.

Table 1.

Results of Antirrhinum Rust Inoculations. List of Varieties Tested and Their Reaction.

<table>
<thead>
<tr>
<th>Variety</th>
<th>Reaction</th>
</tr>
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<tbody>
<tr>
<td>Fully Susceptible</td>
<td></td>
</tr>
<tr>
<td>Uredospore Longevity</td>
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</tbody>
</table>

In the literature on the longevity of uredospores of rust fungi, one of the most important points made is the variation in the life of the uredospores under varying conditions of temperature and humidity. With *Puccinia antirrhini* the life of uredospores has been given from as short as six to eight weeks (Green, 1941) to as long as almost a year (Baker, 1953, personal communication). Because of the importance of the length of life of this spore stage, tests have been carried out to determine the longevity of locally produced spores.

Leaves bearing uredosori were collected from plants growing outside and, after drying at room temperature for 24 hours, were stored in closed jars at three different relative humidities: 25%, 50% and 75%. The humidity was controlled by sulphuric acid/water mixtures. Jars at each humidity were incubated at each of five different temperatures: 5°, 10°, 20°, 25° and 30°C., giving fifteen different treatments in all.

Spore samples were taken at regular intervals and their germination tested by dusting onto the surface of a dilute aqueous extract of antirrhinum leaves in a Syracuse dish and incubating at 10°C. The antirrhinum leaf extract was used in preference to plain water as preliminary tests showed that much better germination was obtained with it.

Results of the germination tests are shown in Table 2. It is readily seen that the temperature and relative humidity under which the spores are kept considerably influence their longevity. Best germination occurred after storage at the lower temperatures and relative humidities, and as each rose a falling off in the life of the spores was observed.
ANTIRRHINUM RUST, *PUCCINIA ANTIRRHINI* D. & H., IN AUSTRALIA.

By J. Walker, Biological Branch, New South Wales Department of Agriculture.

(Plate vii; two Text-figures.)

[Read 25th August, 1954.]

**Synopsis.**

The rust disease of *Antirrhinum* spp. caused by the fungus *Puccinia antirrhini* D. & H. is recorded from Australia. All plant parts except the petals and the roots were attacked and severe damage was caused. A determination of the physiologic race of rust present showed that it is similar to the virulent race known in America as race 2. Studies on uredospore longevity indicated that these spores remained alive longest at low temperatures and relative humidities and their longevity fell off as both temperature and humidity rose.

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**INTRODUCTION.**

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**HISTORY OF THE DISEASE.**

Antirrhinum rust was first recorded by Blasdale (1903), who, in 1895, had found it doing considerable damage in Californian gardens. Specimens of the rust had been collected in California before this date, however, and a specimen in Professor J. C. Arthur’s collection from Santa Cruz is dated 1879 (Peltier, 1919). The fungus was described as *Puccinia antirrhini* by Dietel and Holway (1899) from specimens submitted by Blasdale.

In 1913 the disease was recorded from the eastern State of Illinois, and by 1919 (Peltier, 1919) had spread throughout the United States. In 1921 it was reported by Dickson (1921) from Canada, and in 1922 Whetzel (1924) found it causing severe damage to snapdragons in Bermuda.

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The first record of the disease in Australia was made during October, 1952, on plants growing in a Sydney (N.S.W.) suburban nursery. It spread rapidly and within eighteen months was common in eastern New South Wales and had been reported from all other States of the Commonwealth with the exception of Western Australia. Details of its spread are given in the “Epidemiology” section below.

More recently, in December, 1953, rust was reported in New Zealand at Auckland. So far, no further spread in that country has been noticed (Brien, 1954, personal communication).
**Symptoms.**

*Puccinia antirrhini* is able to attack all above ground parts of the plant except the petals. On the leaves, the first sign of infection is usually a small yellowish spot seen on the under surface. This gradually enlarges to form a shiny, brown, slightly raised blister, about 1 mm. in diameter, which finally breaks through the leaf epidermis as a reddish-brown uredosorus. Quite often, later uredosori are produced in rings around the initial one, giving a distinctive pattern (Plate vii, 1). Sometimes, corresponding to the masses of uredosori on the underside, a chlorotic area can be seen on the upper side of the leaf (Plate vii, 2). As the season progresses, the leaf pustules darken and the leaves become covered with black teleutosori.

Stems and petioles are also attacked and uredosori have been observed on the sepals of young buds (Plate vii, 3). On the stems the pustules consist largely of teleutosori, which often completely encircle the stems. In later stages of infection plants may be almost completely covered with rust pustules (Plate vii, 5).

Quite commonly on infected leaves necrotic areas are seen to develop, especially where many uredosori are massed together on the underside of the leaf (Plate vii, 4). This effect has been noted in America by Dimock and Baker (1951), who found that, under semi-arid conditions, injury resulted almost entirely from drying out of the rust-invaded tissues. They found, however, that where the humidity was high and rainfall frequent, damage was caused by facultative parasites entering through the rust pustules and advancing into previously healthy tissue. In New South Wales the main cause of these necrotic areas seems to be drying out of the tissues during hot weather.

An interesting observation was made by Fikry (1938) in Egypt, who found teleutosori occurring on the roots of some heavily infected snapdragon plants. No such occurrence has been observed during this work.

**The Causal Fungus.**

The uredospores of the Australian isolate of *P. antirrhini* (Text-fig. 1, A) are roughly spherical to slightly elongated in shape, and measure 19-27 μ × 19-23 μ (mean of 20 measurements: 23 μ × 21 μ). The outer wall is finely echinulate, 1½-3 μ thick, and penetrated by 2-3 germ pores which are sometimes arranged in an equatorial plane around the spore but often appear to occur irregularly. The spore wall is slightly thicker at the point of attachment of the stalk.

The teleutospores are of two main types (Text-fig. 1, B). One type is short and measures 30-42 μ × 21-27 μ (mean of 20 measurements: 36 μ × 23 μ). It has a blunt apical cell, quite thick at the top and dark reddish-brown in colour. The other type is longer, measuring 43-57 μ × 17-21 μ (mean of 20 measurements: 49 μ × 19 μ), and has a more or less acute apical cell. This cell is lighter in colour than the apical cell of the shorter type. Other workers have noticed these two teleutospore types in *P. antirrhini* (Doidge, 1941).

Both types of teleutospore are constricted at the septum, tapering or somewhat rounded towards the base, and with a long pedicel, up to 95 μ long. In both the top cell is darker in colour than the basal cell. The germ pore in the top cell is apical and in the basal cell obscure.

Locally produced uredospores germinate readily in 18 hours when dusted onto water or a dilute aqueous extract of antirrhinum leaves and incubated at 10°C, but so far it has not been found possible to germinate teleutospores. Some workers (Green, 1941; Mains, 1924) have succeeded in germinating them, however, but have been unable to reinfect *Antirrhinum* or infect any other plant with them. It thus appears probable that *P. antirrhini* is a heteroecious rust whose alternate host has not yet been found. Mains (1924) discusses this in some detail. The alternate host is not necessary, however, as the rust is able to persist by means of continual infection of *Antirrhinum* with its uredospore stage.
Physiologic Specialization.

As with other rust fungi, various races of *P. antirrhini* have been found. Up till 1937 only one race of this rust was known, but in that year Yarwood (1937), working with excised leaves of various snapdragon varieties, demonstrated in America the existence of another race. This new race was known as race 2, the original being race 1. Race 2 proved to be more virulent than race 1 and was able to attack all those varieties that were hitherto resistant to the disease and, at the present time, there are no commercial lines of snapdragon resistant to race 2. Apart from these two races, it is quite possible that others also exist. Baker (1953, personal communication) stated that work done in California indicated clearly that other races are present there.

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Table 3.

<table>
<thead>
<tr>
<th>Country</th>
<th>Spores Present</th>
<th>Spores Not Seen</th>
</tr>
</thead>
<tbody>
<tr>
<td>Italy</td>
<td>+</td>
<td>—</td>
</tr>
<tr>
<td>France</td>
<td>+</td>
<td>—</td>
</tr>
<tr>
<td>Germany</td>
<td>+</td>
<td>—</td>
</tr>
<tr>
<td>America</td>
<td>+</td>
<td>—</td>
</tr>
</tbody>
</table>

Note. — The figure of "100% infection" given in the above table for seed samples coming from Italy, France, Germany and America is a misleading one in view of the small number of samples examined from these countries. Examination of further samples would probably reveal the presence of some without rust spores.

2. Spread of the Disease in New South Wales.

After the first outbreak of rust was found in a Sydney suburb it spread rapidly throughout eastern New South Wales. Within four and a half months it had been recorded 100 miles from its source and within a year from its first discovery was widespread in eastern New South Wales.

From a study of the records it has been found that spread in New South Wales occurred in two main ways. These were: (i) primary spread by wind dispersal of uredospores and (ii) secondary spread by the carrying of the diseased seedlings and cuttings from place to place.

(i) Spread by wind-borne uredospores.

Wind is one of the most important agents for the dispersal of plant pathogens. With rust fungi, the uredospore stage is well adapted for wind spread and considerable work has been done in tracing the spread by air currents of many of these organisms, especially the cereal rusts. Lambert (1929) showed that evidence exists that uredospores of wheat stem rust may be carried in air currents several hundred miles from their

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Figure 1.

Text-fig. 1.—(A) uredospores and (B) teleutospores of *P. antirrhini*.

Text-fig. 2.—Map showing initial zones of spread of Antirhinum rust in New South Wales.

As far as can be determined, race 2 of *P. antirrhini* has been reported to date only in America and Southern Rhodesia. In other parts of the world where this rust has been recorded, race 1 appears to be the race present and, in these areas, the resistant varieties are still quite successful.

Tests were conducted to identify the race of rust present in New South Wales and to test the reaction of a number of snapdragon varieties to inoculation with this race.

Method:

All plants to be tested were raised from seed in four-inch pots in a glasshouse, hardened in a frame outside and then inoculated in the frame by dusting with heavily rusted plants. Plants were kept damp, giving optimum conditions for rust infection.

Results:

Inoculation results are summarized in Table 1. All varieties tested were quite susceptible to the local rust isolate and, although some variation in reaction did occur, all were quite heavily rusted. In the table those varieties classed as "fully susceptible" showed profuse uredosorus development, with practically no chlorosis visible on the upper side of the leaf. With those classed as "susceptible" some chlorosis was visible...
on the upper side of the leaf and in some cases the uredosori were slightly smaller than those on the “fully susceptible” types.

Of the varieties listed in Table 1, Watkins and Simpson’s Pink Freedom, Wisley Bridesmaid, Wisley Cheerful and Wisley Golden Fleece were sent out by Mr. D. Green of Wisley, England, and No. 61 by Dr. K. F. Baker of California. These five varieties were strain-1 resistant types and, as is seen from the table, they were quite susceptible to the local rust race. This indicates that the race of P. antirrhini present in Australia is not race 1, but is similar to the virulent race 2.

Two varieties of Linaria, Excelsior Hybrid and Fairy Bouquet, were also inoculated with rust. Both showed no sign of infection. In the United States, Blasdale (1903) recorded P. antirrhini on two species of Linaria.

| Results of Antirrhinum Rust Inoculations. List of Varieties Tested and Their Reaction. |
|---------------------------------|---------------------------------|
| Fully Susceptible. | Susceptible. |
| Campfire. | Copper King. |
| Defiance. | Giant Ruffled Tetraploid. |
| Grandiflorum Rust-proof de Luxe Mixture. | Giant Skyscraper. |
| Queen Victoria. | Grandiflorum Rust Resistant University of California de Luxe Mixture. |
| Rust Resistant Autumn Glow Shades. | Grandiflorum University of California. |
| Rust Resistant Orange Shades. | Hybrids Mixed. |
| Rust Resistant Tall Mixed. | Luteum. |
| Rust Resistant Yellow. | No. 61. |
| Snowflake. | Rose Marie. |
| Tango. | Ruby. |
| Tetraploid Rust Resistant Selected Superfine Mixed. | Rust Proof de Luxe Mixture. |
| University of California Mixed. | Rust Proof Good Mixed. |
| University of California Rust Resistant Mixed. | Rust Resistant Spotlight. |
| Watkins’ and Simpson’s Pink Freedom. | The Rose. |
| Wisley Bridesmaid. | Yellow King. |
| Wisley Cheerful. | Yellow Wonder. |
| Wisley Golden Fleece. | |
| World Favourite. | |

**Uredospore Longevity.**

In the literature on the longevity of uredospores of rust fungi, one of the most important points made is the variation in the life of the uredospores under varying conditions of temperature and humidity. With *Puccinia antirrhini* the life of uredospores has been given from as short as six to eight weeks (Green, 1941) to as long as almost a year (Baker, 1953, personal communication). Because of the importance of the length of life of this spore stage, tests have been carried out to determine the longevity of locally produced spores.

Leaves bearing uredosori were collected from plants growing outside and, after drying at room temperature for 24 hours, were stored in closed jars at three different relative humidities: 25%, 50% and 75%. The humidity was controlled by sulphuric acid/water mixtures. Jars at each humidity were incubated at each of five different temperatures: 5°, 10°, 20°, 25° and 30°C, giving fifteen different treatments in all. Spore samples were taken at regular intervals and their germination tested by dusting onto the surface of a dilute aqueous extract of antirrhinum leaves in a Syracuse dish and incubating at 10°C. The antirrhinum leaf extract was used in preference to plain water as preliminary tests showed that much better germination was obtained with it.

Results of the germination tests are shown in Table 2. It is readily seen that the temperature and relative humidity under which the spores are kept considerably influence their longevity. Best germination occurred after storage at the lower temperatures and relative humidities, and as each rose a falling off in the life of the
Zone 4, the rust spread over an area approximately 10 times greater than that which it had covered during its first nine weeks. This indicates that an initial build-up of uredospore inoculum occurred on snapdragons in the Sydney suburban area (Zone 1 and part of Zone 2) during the first nine weeks and later spread in epidemic proportions over a much wider area. The rapid spread and widespread destruction had all the marks of a progressive or spreading epidemic, characteristic of the invasion of a new area by a pathogen (Gaumann, 1950). The severity of the epidemic was increased by the fully susceptible nature of all the host varieties being grown.

(ii) Spread on diseased plant material.

Once the disease had become established over a fairly wide area by means of wind-borne uredospores, secondary spread began to occur by the transport of diseased seedlings and cuttings from this area to other parts of the State. Quite often the transported plant material was only very lightly infected and the disease escaped attention, but, when planted out, the disease developed and set up secondary foci of infection from which further wind spread could occur. In this way it was introduced to Cooma in southern New South Wales, about 270 miles from Sydney, and also to other areas. This considerably assisted its spread in Australia. Soon after the Cooma outbreak it was widespread in southern New South Wales.

This vegetative transmission of snapdragon rust hastened its spread by carrying it long distances and allowing it to become established in widely scattered places in a comparatively short time.


By the methods outlined above, snapdragon rust became widespread in eastern New South Wales. Very soon after, spread to other States in Australia occurred and the disease was reported from the southern State of Victoria. Later, in the spring of 1953, it was recorded from Queensland and, in January, 1954, from South Australia. By March it had reached Tasmania, leaving Western Australia as the only State still free of the disease at the time of writing.

The exact method of introduction of the disease to other States is not known but most probably both wind and vegetative spread were concerned. It is known that diseased seedlings were sold in some States and quite possibly they provided foci from which further spread by wind occurred.

4. Outbreak of the Disease in New Zealand.

Towards the end of December, 1953, rusted snapdragons were observed in a private garden at Auckland, New Zealand. Brien (1954, private communication) states that no further spread from this area appears to have occurred.

Possible sources of infection include seed and wind-borne uredospores. The question of seed transmission has been discussed in the case of the New South Wales outbreak and similar conclusions were reached in New Zealand. It is possible, however, that uredospores have been carried by wind from Australia to New Zealand and resulted in the outbreak of the disease in that country. Quite often, dust from Australia is deposited in New Zealand, having been carried across by north-west winds, and it would seem quite possible that with the large bulk of uredospore inoculum available in eastern Australia some uredospores would reach New Zealand in air currents. The distance from Sydney to Auckland is about 1,400 miles, but it is not improbable that spores could be carried this distance in air currents.
uredospores was noted. The longest period for which uredospores remained viable during these tests was 116 days at 5° and 10°C at relative humidities of 25% and 50%. The shortest period was 21 days at 30°C at all humidities.

The longevity of uredospores is of great importance in the epidemiology of rust diseases. These spores are specially suited to transport by air currents, but they must be able to remain viable under the conditions existing in the atmosphere if this is to be an effective method of spreading the disease. Many factors are concerned but here only temperature and humidity have been considered. The results show that, at low temperatures and relative humidities up to 50%, uredospores of *P. antirrhini* produced under local conditions are able to remain viable for about four months. Their transport in cool air currents, probably at high altitudes (Gäumann, 1950), would thus constitute a definite hazard to plants quite long distances away.

It is also apparent that uredospores could remain viable for some time under cool conditions in dust in seed samples. Such samples are dry and, unless conditions of very low humidity adversely affected uredospore longevity, as has been found with some rusts (Gäumann, 1950), they would seem to provide an excellent means for rust dispersal. Air transport of seed samples would make this even more effective.

Further discussion of wind and seed transport of uredospores is given under "Epidemiology".

**Epidemiology.**

In this section will be considered first the possible means by which the fungus was introduced to Australia, and second its spread within the country.

1. **Entry of the Disease.**

   The way in which *Antirrhinum* rust was introduced to Australia is not definitely known. In seasons when locally grown snapdragon seed is in short supply, bulk lots of seed are imported from Europe and America, and small quantities of new varieties are constantly being introduced from both countries. The crop on which the first infection was recorded was grown from European seed. Before the identity of the race present was established, it was therefore thought that the Australian outbreak had a European origin. As race 2, however, has been recorded only in America and Southern Rhodesia, it now seems that the original entry must have been from America. A European origin for the Australian outbreak would seem to be disproved unless race 2 has become established fairly recently in some countries there. No record of snapdragon seed being imported from Africa has been seen.

   Examination of many seed samples showed that the majority of overseas seed coming into New South Wales contained rust uredospores and sometimes teluutospores as well. Of 185 seed samples examined, 139 (75%) were found to contain rust spores. The results of these examinations, with the country of origin of the seed, are given in Table 3. A rough estimate of the number of uredospores present in the seed samples, made using a Bausch and Lomb mould counter, showed that, in most samples, there were from $1 \times 10^5$ uredospores present per ounce of seed. However, it was not found possible to germinate these spores or to obtain infection on susceptible seedlings with them. Moreover, plants grown from this seed, and from seed dusted with fresh local uredospores, always produced disease-free plants.

   In favour of seed transmission are the facts that under dry and cool conditions rust uredospores can remain viable for a considerable time and that air transport of seed could allow seed to be introduced within a couple of months of harvesting. Under these conditions there seems to be little reason against the production of the disease, for example in a nursery, by the accidental dusting of spores on to snapdragon seedlings when seed was being sown in adjacent beds.

   The entry of the rust into other countries has sometimes been attributed to seed transmission, e.g., Sweden (Palm, 1937), South Africa (Bottomley, 1940) and Italy (Preti, 1935), but other workers, after various investigations, have rejected seed transmission (Green, 1941; Hassebrauk, 1937). These latter workers, however, did not seem
to consider the possibility of viable spores, carried in seed, being dusted onto established plants in a nursery area. Baker (1963, personal communication) considered this a distinct possibility and definitely favoured seed transmission.

In the case of the Australian outbreak, evidence against seed introduction are the facts that it was not found possible to germinate the uredospores found in seed samples or obtain infection with them and that, if seed transmission were effective, one would have expected the disease to have been introduced some time ago, considering the large number of uredospores in introduced seed.

Other methods by which this disease could be spread are on cuttings and seedlings, by wind and by spores adhering to clothing. In view of the strict plant quarantine regulations in force in New South Wales it is most unlikely that seedlings or cuttings could have been imported. Wind entry of the disease is unlikely as, at this time, the nearest known source of inoculum was in the Hawaiian Islands, more than 4,000 miles from Sydney. The entry of the disease by spores adhering to clothing is doubtful.

It can thus be seen that the most likely method of entry of this disease was by means of viable uredospores adhering to seed.

### Table 3.

**Results of *Antirrhinum Seed Examinations***

<table>
<thead>
<tr>
<th>Country of Origin</th>
<th>Number of Samples</th>
<th>Total Number Examined</th>
<th>Percentage Containing Spores</th>
</tr>
</thead>
<tbody>
<tr>
<td>Holland</td>
<td>125</td>
<td>144</td>
<td>87</td>
</tr>
<tr>
<td>New Zealand</td>
<td>4</td>
<td>28</td>
<td>14</td>
</tr>
<tr>
<td>United Kingdom</td>
<td>4</td>
<td>6</td>
<td>67</td>
</tr>
<tr>
<td>Italy</td>
<td>2</td>
<td>2</td>
<td>100</td>
</tr>
<tr>
<td>France</td>
<td>1</td>
<td>1</td>
<td>100</td>
</tr>
<tr>
<td>Germany</td>
<td>1</td>
<td>1</td>
<td>100</td>
</tr>
<tr>
<td>America</td>
<td>1</td>
<td></td>
<td>100</td>
</tr>
<tr>
<td>Tasmania</td>
<td></td>
<td>1</td>
<td>0</td>
</tr>
</tbody>
</table>

| Total             | 139               | 185                  | 75                           |

+ = spores present.

− = spores not seen.

Note.—The figure of "100% infection" given in the above table for seed samples coming from Italy, France, Germany and America is misleading as in view of the small number of samples examined from these countries. Examination of further samples would probably reveal the presence of some without rust spores.

2. **Spread of the Disease in New South Wales.**

After the first outbreak of rust was found in a Sydney suburb it spread rapidly throughout eastern New South Wales. Within four and a half months it had been recorded 100 miles from its source and within a year from its first discovery was widespread in eastern New South Wales.

From a study of the records it has been found that spread in New South Wales occurred in two main ways. These were: (i) primary spread by wind dispersal of uredospores and (ii) secondary spread by the carrying of the diseased seedlings and cuttings from place to place.

(i) **Spread by wind-borne uredospores.**

Wind is one of the most important agents for the dispersal of plant pathogens. With rust fungi, the uredospore stage is well adapted for wind spread and considerable work has been done in tracing the spread by air currents of many of these organisms, especially the cereal rusts. Lambert (1929) showed that evidence exists that uredospores of wheat stem rust may be carried in air currents several hundred miles from their

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