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Studies on *Venturiaceae* on Rosaceous Plants

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By

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With 10 Figures

I

General Introduction

A. *Venturiaceae*

The family *Venturiaceae* has been created mainly on the studies of PETRAK (1924, 1925, 1947) by MÜLLER and von ARX in a joint paper (1950). They have considered it in great detail. Later von ARX (1952) and PETRAK (1954) have added to our knowledge of the family still further.

The members of this family are characterised by the production of perithecium like ascostromata with a well differentiated "sphaerical centrum" (LUTTRELL, 1955). VON ARX (1952) has stated "the ascospores are at first hyaline or pale green; later they nearly always become olive-brown or greyish green, rarely dark brown but remain translucent. In many cases the transverse septum is not in the middle of the spore but displaced a little to the bottom or the top, so that the spore is unequally two celled".

"The asci are elongated or oblong or nearly cylindrical, rounded at the top, sometimes a little broader in the lower third part. They have a rather delicate membrane with the same thickness throughout or apically slightly thickened, and contain eight spores, rarely four."

"In the initially fully closed perithecium the asci penetrate between the tissue of hyaline parenchymatous cells or vertically arranged threads (pseudoparaphyses) which are connected above or below. When ripening the perithecia or locules open by an apical pore formed by the histolysis of the usually thin walled cells in the centre of the beak like upper part of the perithecial wall. The pseudoparaphyses then loosen at their top, absorb water, elongate and fill the pore as gelatinous threads. When ripe, the outer membrane of the ascus splits. The inner membrane is elastic and protrudes and in consequence of this the apex of the ascus reaches into the pore. As a result of the pressure inside, the spores break through the membrane, are ejected and the empty ascus collapses."

"In the *Venturiaceae* the stroma may have very different positions in the substratum; its development can take place either subepidermally or subcuticularly. The perithecia can be erumpent or completely superficial, or innate with a foot like hypostroma. This is either strongly developed, crustose and parenchymatous, or — especially in the forms on leaves — reduced to a simple layer of light coloured cells. In some cases this layer is obliterated with the perithecia ripening, and the conidia are then abstricted from the surface of a subcuticular stromatic cushion."

"The formation of hairs or setae on the fruiting bodies or the existence of a superficial dematoid subiculum is characteristic of many *Venturiaceae*. Besides these forms there are also species with glabrous fruiting bodies. However characteristic the setae or hyphae may be for many species, they are still not fitted for the classification of the genera or the species. The reason for this is that in one and the same species may be fruit bodies either glabrous or with appendices; the latter may also be inconspicuous and sometimes disappear at an early stage."

The investigations in this paper are restricted to the *Venturiaceae* occuring on the plants belonging to Rosaceae. This work has been carried out at the Department of special Botany of the Swiss Federal Institute of Technology under the guidance of Prof. Dr. E. GÄUMANN to whom I wish to acknowledge my grateful thanks for advice and constant help. I am deeply indebted to Dr. E. MÜLLER, who supervised the work, for his unfailing help with numerous suggestions and criticisms.

The work has been financed from the Swiss Coordination Commission for Technical help, later from Volkart-Stiftung, Winterthur. Grateful thanks are expressed to the authorities concerned. I am also grateful to Dr. R. FRITZSCHE of the Research Station at Wädenswil and Dr. E. SURBER of the Federal Forest Research Station for the supply of the seedling plants for the inoculation experiments.

B. *Venturiaceae* on *Rosaceae*

Under the family *Venturiaceae* occuring on the different host plants of *Rosaceae* are included the genera *Venturia* de Not., *Coleroa* Rbh., *Gibbera* Fr., *Xenomeris* Syd. and *Apiosporina* v. HÖHN. In spite of the fact that

mention of these genera has been made in previous literature, it is the genus *Venturia* de Not. that has received the greatest attention from early workers. In the genus itself *Venturia inaequalis* (Cke.) Winter has been known from the first part of the nineteenth century, variously referred as "apple scab", "scurf", "black spot", "black spot fungus", "Tasmanian black spot", "black spot scab", and "rust". The scab attacks leaves, blossoms, fruits and sometimes the young twigs.

On the leaves the infections are evident as circular brownish or grey spots in the early stages, turning gradually to olive green and black. The spots are covered by dendritic ramifications of the mycelium, visible under a hand lens.

On the fruits the lesions appear as small, raised, brown or black spots. The cuticle covering the spots is ruptured exposing the mycelia with the conidia as a grey bloom.

Infections also occur on the young twigs but these are rather rare in occurence.

Severe infections on an epidemic scale are common in the apple and pear orchards in many parts of Europe, Australia, New Zealand, South Africa and Northern parts of North America. The incidence of the disease is very much favoured by a cool, humid climate especially in the spring when the temperature goes to 12—16 ^{0} C. In the arid tropical parts there is little evidence of the disease. The dominance of the fungus is therefore mainly dependent on the temperature.

During the last fifty years much work has been done on *Venturia inaequalis* (Cke.) Winter especially with regard to the control of the disease. This in its turn has given impetus to pathological, cytological and genetical studies. Pioneers in the field were ADERHOLD (1896, 1903) and KILLIAN (1917). During the recent years it is the biochemical aspect of the species that has met with great consideration. Monosporic genetical studies have been made by the American School of KEITT and LANGFORD (1940, 1941 a and b), SHAY (1943) and ASHCROFT and FOTHERGILL (1955).

Still at the present day there exist conflicts and doubts as to the taxonomic position and nomenclature of *Venturia* and allied genera. The species under the different genera, occuring on a variety of host plants, show morphological characters distinct from each other. They also exhibit a high degree of host specialization as seen from the inoculation experiments conducted by ADERHOLD (1903), KEITT and LANGFORD (1941) and by us in this paper.

All the genera taken up for our studies (*Venturia* de Not., *Coleroa* Rbh., *Gibbera* Fr.) contain leaf parasites with the exception of *Gibbera rosae* which occurs on the twigs of *Rosa pendulina* L. The conidia, of the *Fusicladium* type, occur on the living leaves. The perfect stages are found on the dead and overwintered leaves in all cases but in some species they may also develop, in addition, on the living green leaves. Morphologically and biologically the fungi under the different genera are distinct. The

species *Venturia inaequalis* (Cke.) Winter has been found to occur on a number of host plants of same group, with scarcely different microscopic characteristics. When grown in artificial media the fungi exhibited a great uniformity. We have conducted these investigations mainly with a view to find out how far the species and the specialised forms were different biologically. Primary consideration was given to *Venturia* de Not. occuring on *Pirus malus* L., *Sorbus aria* Crantz., *Sorbus aucuparia* L., *Cotoneaster integerrima* Med., *Crataegus oxyacantha* L., *Cotoneaster tomentosa* (Ait.) Lindl., *Pirus communis* L., *Prunus padus* L., *Prunus spinosa* L., *Rosa pendulina* L., *Potentilla* species, *Comarum palustre* L. and *Alchemilla* species. Inoculation experiments were made wherever the seedling plants were available. The genera *Gibbera* and *Coleroa* are studied only from the point of view of morphology of the species and their growth in nutrient media.

1. ***Venturia*** de Not. emend. SACCARDO

Atti Sci. Ital. 6, 484 (1844) and Sylloge Fungorum 1, 586 (1882).

Synonyms: *Phaeosphaerella* Karsten — Medd. Soc. Fenn. 16, 28 (1880), teste PETRAK (1940).
Sphaerellopsis Klebahn — Haupt- und Nebenfruchtformen der Ascomyceten, 168 (1918).
Spilosticta Syd. — Ann. Myc. 21, 173 (1923).
Endostigme Syd. — l.c.

Lectotype: *Venturia inaequalis* (Cke.) Winter cf. SHEAR (1948).

The genus comprises a large number of forms including many pathogenic fungi. The nomenclature of the genus has been recently dealt with by MÜLLER and MENON in a joint paper (1955). They have stated that the original type species of *Venturia* de Not. corresponds to the fungi now included under the genus *Gibbera* Fr. By the strict use of nomenclature rules the latter genus should be considered as synonymous with *Venturia* de Not. and for the large number of forms now included in the genus *Venturia*, a new generic name should be suggested. To avoid complications in the existing literature however, the two names *Venturia* de Not. emend. SACCARDO, with the lectotype *Venturia inaequalis* (Cke.) Winter and *Gibbera* Fr. with the type *Gibbera vaccinii* Fr. are retained as such. For the sake of convenience they have renamed *Venturia rosae* de Not. as *Gibbera rosae* (de Not.) MÜLLER et MENON.

2. ***Coleroa*** Rbh.

Herb. Myc. no. 1456 (1850) et Botan. Ztg. 9, 180 (1851).

Type species: *Coleroa chaetomium* (Kze.) Rbh.

There has been a great deal of controversy regarding the systematic position of the genus *Coleroa* Rbh. VON HÖHNEL (1907) has regarded the genus as identical with *Gibbera* Fr. Later (1909) he revised his view and united it with *Antennularia* Reichb. PETRAK (1947) has retained it as a genus coming very near *Gibbera* Fr.

The type species *Coleroa chaetomium* (Kze.) Rbh. occur on the leaves of *Rubus idaeus*, but the fungus has two different forms in the summer and

the winter. The summer forms develop the perithecia on the green living leaves. They have subcuticular hypostroma, small, flat, erumpent perithecia, solitary or in groups. The winter forms occur on the dead leaves, with subepidermal stromata, with the perithecia on the edges of the stromata. VON HÖHNEL (1907) has placed the overwintering forms in the genus *Venturia* de Not. PETRAK (1947) considers the genus *Coleroa* as resembling the genus *Spilosticta* Syd. (= *Venturia* de Not. emend. SACCARDO). Any union between the two genera if considered, can take place only through the overwintering forms of *Coleroa chaetomium*, as in the summer form there are some morphological differences. We are led to believe, by our investigations, that there are indeed close resemblances between the forms under *Venturia* and *Coleroa*. We have not in this connection examined all the different forms under *Venturia*, *Coleroa* and *Gibbera* and as such it is very difficult to form a definite opinion regarding the merging of the genera. We have therefore retained the genus *Coleroa* as such.

3. *Gibbera* Fr.

Summa. Veg. Scand. p. 402 (1849) emend. PETRAK (1947). Synonyms: Refer VON ARX (1952), MÜLLER and MENON (1955).

Type species: *Gibbera vaccinii* Fr.

PETRAK (1947) has written a monograph on the genus with the addition of many new genera to *Gibbera*. Later again VON ARX (1952, 1954) and PETRAK (1954) have further extended the genus. In our studies in this paper we have considered only *Gibbera rosae* (MÜLLER and MENON, 1955).

4. *Xenomeris* Syd.

Ann. Mycol. **22**, 185 (1924)

Type species: *Xenomeris Nicholsoni* (Cke.) Petr.

SYDOW (1924) has described and illustrated the genus. VON ARX (1954) has united it with *Gibbera* Fr., but PETRAK (1954) again gives it a generic status. *Xenomeris* Syd. differs from *Gibbera* Fr. in having small perithecia without setae. Until now the type species has been collected only once and nothing is known about its life cycle and biology. In our investigations we have not considered the genus in detail.

5. *Apiosporina* v. Höhn.

Sitz.Ber. K. Ak. Wiss. Wien, math.-naturw. Kl. **119**, 439 (1910)

Type species: *Apiosporina collinsii* (Schw.) v. HÖHN.

VON ARX (1954) has placed the genus in *Venturiaceae* considering it as related to *Gibbera* Fr. But in *Apiosporina* the forms have long, pear shaped, hyaline spores, septated at the lower end. Conidia are of the *Hormodendron* type. The type species *Apiosporina collinsii* has been collected on the leaves of *Amelanchier* spec. A second species *Apiosporina morbosa* (Schw.) v. ARX [Synonym: *Dibotryon morbosum* (Schw.) Theiss. et Syd.] occurs on the twigs of *Prunus* species in North America. We have not worked out the life history and morphology of these fungi.

II.
Experimental Part
A. Cultural Studies

The fungi *Venturia inaequalis* (Cke.) Winter, *Venturia pirina* Aderh., *Venturia palustris* Sacc. Bomm. et Rouss., *Venturia Mülleri*, *Coleroa chaetomium* (Kze.) Rbh., *Gibbera rosae* have been isolated on malt agar by the "spore shooting method". A piece of the host leaf containing mature perithecia was wetted for a few minutes and fixed to the cotton plugs of 100 ml Erlenmeyer flasks containing malt agar (2 % malt extract). Abundant spore discharge took place in all cases but the growth of the colonies was very slow. They were visible macroscopically only after two to three weeks. Successive transfers of the cultures were now made on malt agar slants (2 %). In this medium at room temperature (21—24 ° C) mycelial development was extensive, conidia were produced in small numbers. But no perithecia were observed even after one to two months.

Where there was no spore discharge from the perithecia the micromanipulator was used to isolate spores from a crushed perithecium. These were introduced into the malt agar slants with profuse growth of the colonies after two to three weeks. All cultures from this method were polysporous.

Since the fungus did not produce the perithecia in malt agar, attempts were made to grow it in apple and pear decoction with the addition of 2 % malt agar after KEITT and LANGFORD (1941 b). Apple and pear leaves in the dry state were crushed to a fine powder with a pestle in a mortar. Thirty grams of this powder were steamed in distilled water for twelve hours. The solution was filtered and sterilised at 120 ° C for half an hour. Twenty ml of this decoction were added to five grams of malt agar. All the species grew in this medium and perithecial initials were produced after a month. Mature asci with a large number of ascospores were produced after four to five months.

Temperature was found to be a deciding factor in the production of the perithecia and more so in the formation of ascospores. At room temperature vegetative growth was extensive with a large number of chlamydospores. Conidia were few and in some cases scattered, aborted perithecia resembling sclerotia were produced. At 15—18 ° C conidia were produced in all media in plenty but the perithecia matured and produced the ascospores only at 8 ° C (Table 1).

Light was a secondary factor in the production of perithecia. Cultures exposed to constant illumination from the neon lamps produced the perithecia in large numbers and more rapidly than those kept in the dark. But this stimulus was not so vital as temperature.

KEITT and LANGFORD (1941 b) have stated that *Venturia inaequalis* (Cke.) Winter isolated from *Pirus malus* leaves did not grow in pear decoction. In our experiments we found that all species of *Venturia* and all forms of *Venturia inaequalis* grew on pear decoction and apple decoction

Table 1

Influence of temperature on the conidial and perithecial production of *Venturia inaequalis* f. sp. *mali* on different media

Medium	Room temperature	8 °C	16 °C	18 °C	20 °C	22 °C	24 °C
Malt agar Perithecia	A	A	A	A	A	A	A
Conidia	P	P	P	P	A	A	A
Apple decoction							
Perithecia	A	P	A	A	A	A	A
Conidia	P	A	P	P	A	A	A
Pear decoction							
Perithecia	A	P	A	A	A	A	A
Conidia	P	A	P	P	A	A	A

A absent.
P present.

with the production of mature perithecia. A difference was noticed in the relative small size of the fruit bodies in decoctions other than the host leaves (Table 2). It is possible in this connection to theorise that with the decrease in the vegetative growth the sexual organs are stimulated and function more efficiently.

Table 2

Growth of *Venturia inaequalis*, *Venturia pirina*, *Venturia pruni-cerasi*, *Venturia palustris* on malt agar, apple decoction and pear decoction. Temperature 16 °C, with light

Media	*Venturia inaequalis* f. sp. *mali*	f. sp. *aucupariae*	f. sp. *crataegi*	*Venturia pirina*	*Venturia pruni-cerasi*	*Venturia palustris*
Apple decoction	P	P	P	P	P	P
Pear decoction	P	P	P	P	P	P
Malt agar	C	C	C	C	C	—
Straw	—	—	—	—	—	—
Corn agar	—	—	—	—	—	—

P perithecia.
C conidia.
— negative results.

ASHCROFT and FOTHERGILL (1955) have found that the addition of ascorbic acid and thiamin greatly increases the vegetative growth of *Venturia inaequalis* (Cke.) Winter in culture. We have not tried to discover

whether the influence of these growth stimulants extends to the perithecial production also.

The growth of the different fungi in all the different artificial media is described on p. 129—131.

B. Inoculation Experiments

1. Introduction

Existing literature on *Venturia inaequalis* (Cke.) Winter (SCHMIDTT, 1936, 1937), (KEITT and LANGFORD, 1941 a and b), (SHAY, 1943), (ADERHOLD, 1903) has shown that the fungus exhibits a large number of physiological races differing in their pathological reactions and host selection. Much of this work has however been done on the species occuring on different apple varieties. We have considered the species from a wider host range — on *Sorbus aria* Crantz., *Sorbus aucuparia* L., *Crataegus oxyacantha* L., *Cotoneaster integerrima* Med. In all these hosts the fungus shows no specific morphological differences. Only the fungus on *Cotoneaster tomentosa* (Ait.) Lindl. differs in morphology from *Venturia inaequalis.*

The type host is *Sorbus aria* Crantz., as *Sphaerella inaequalis* (= *Venturia inaequalis)* has been collected by COOKE (1866) on the dead leaves of this host plant.

All the fungi,, when cultivated artificially, showed a great uniformity in growth characters. The problem that faced us was how far the forms differ biologically. Recourse was therefore taken to inoculation experiments on seedling plants of the different hosts, from conidial and ascospore suspensions, from the culture and from nature. Inoculation trials were made with *Venturia inaequalis, Venturia pirina* and *Venturia pruni-cerasi.*

2. Inoculation studies

a) Conditions of experiments: One year old seedlings were kept in the open air for three weeks after which they were trimmed and fitted into pots of covenient sizes and later transferred to glass houses where the temperature at the time of these experiments was 19—20 ° C during the day and 10—12 ° C during the night. When a sufficient number of leaves were developed on the seedlings, (8—10), the leaves were sprayed with a suspension of conidia and ascospores. Infected plants were kept at the room temperature (21 ° C) and in a temperature-constant room with the temperature adjusted to 16 ° C, and also in the glass houses. In the temperature constant room the seedlings showed extensive chlorosis and necrosis on the leaves. In the glass house plants only chlorosis developed and at the room temperature the plants remained healthy.

Continuous wetting was necessary to the infected leaves for two days after infection. This was provided artificially in the glass houses. Later the seedlings were transferred to the temperature-constant room where the humidity was adjusted to 50 %. Controls exposed to normal weather changes showed slight chlorosis of the leaves.

Continuous illumination was also provided with neon lamps. Infection was more rapid in these plants than in seedlings kept in normal daylight and night.

b) Inoculation: Pieces of the fungal mycelia obtained from malt agar cultures were fixed to the leaves of the seedlings after bruising the epidermis with the finger nails. Infection in this case did not succeed.

Seedlings at the 10—12 leaf stage, were sprayed with conidia from three week old malt agar and 4 months old decoction cultures. Suspensions of the conidia were made in 50 ml of distilled water. The concentration of the suspension was roughly controlled at fifty to sixty spores in a drop under the low power of the microscope. The upper and lower surfaces of the leaves were sprayed with the fluid using an atomiser. Ascospores were taken from four month old decoction cultures, washed in distilled water, and sprayed as before. Lastly pieces of the host leaf containing the ripe perithecia were wetted for five to six hours, cut into pieces one cm square, and fixed to the seedling plants at suitable positions to ensure ample ascospore discharge.

After the spraying, the seedlings were kept in the glass houses for forty eight hours under a constant spray of water. Later they were tranferred to the temperature- and humidity-constant room. Illumination was provided with neon lamps and the plants were regularly watered.

3. Results

Initially the infection took place from the ascospores alone, both under natural and artificial conditions. Secondary infection succeeded, mostly from conidia. Under favourable conditions of humidity, temperature and light, the symptoms of disease appeared on the infected plants. The period of incubation in the different hosts for *Venturia inaequalis* varied — thirty five days for *Pirus malus*, twenty three days for *Sorbus* species, seventeen days for *Crataegus oxyacantha*. In *Pirus communis* infection with *Venturia pirina* took seventeen days. In all cases irregular chlorotic and necrotic spots appeared on the lamina confined to the edges or at the centre. In a few cases as in *Sorbus* species and *Pirus communis* conidia of the *Fusicladium* type appeared on the diseased areas. Cross inoculations with the different species and forms did not succeed. In *Prunus spinosa* which was infected with suspensions of *Venturia cerasi* isolated from *Prunus padus*, only light brown discoloured areas were evident. Self inoculation was not tried in this instance for lack of material. 18—20 seedlings were self-inoculated, four of each crossed and four were kept as controls. In no case the control showed any disease symptom (Table 3).

4. Conclusions

In summing up our results we find that the ascospores of *Venturia inaequalis*, *Venturia pirina*, and *Venturia pruni-cerasi* are able to infect healthy seedlings. But these fungi are highly specific to their hosts. In addi-

Table 3

Results from cross inoculation of *Venturia inaequalis* (Cke.) Winter, *Venturia pirina* Aderh. and *Venturia pruni-cerasi* Sacc. Temperature 16° C and humidity 50 %

Inoculum	*Pirus malus* L.	*Sorbus aria* Crantz.	*Sorbus aucuparia* L.	*Crataegus oxyacantha* L.	*Pirus communis* L.	*Prunus spinosa* L.
Venturia inaequalis f. sp. *mali*	+	—	—	—	—	—
Venturia inaequalis f. sp. *aucupariae*	—	+	+	—	—	—
Venturia inaequalis f. sp. *crataegi*	—	—	—	+	—	—
Venturia pirina	—	—	—	—	+	—
Venturia pruni-cerasi	—	—	—	—	—	±

+ Infected.
± Doubtful.
— Negative.

tion *Venturia inaequalis* has many physiological races, confined to definite host plants. Morphological studies of this species occuring on the different hosts showed little differences. Earlier workers have however described these forms as distinct species, as *Venturia aucupariae* on *Sorbus* species, *Venturia crataegi* on *Crataegus oxyacantha;* but as evident from inoculation we regard these as biotypes, with only biological differences. It is therefore proposed in this paper to unite the different races under the name *Venturia inaequalis* (Cke.) Winter. Since the races are specific to individual host plants we consider them as "formae speciales" (Table 4).

Table 4

Artifical inoculation symptoms with or without sporulation on test plants. Temperature 16° C, humidity 50 %

Symptoms	*Pirus malus* L.	*Sorbus aria* Crantz.	*Sorbus aucuparia* L.	*Crataegus oxyacantha* L.	*Pirus communis* L.	*Prunus spinosa* L.
Chlorosis	+	+	+	—	+	+
Necrosis	+	+	—	+	+	±
Chlorosis & necrosis conidia	—	C	C	—	C	—

+ Chlorosis.
+ Necrosis.
C Chlorosis & necrosis (Conidia).
— negative results.

III.

Morphological and Cultural Studies

Key for the genera under *Venturiaceae* taken up in the paper.

1. Perithecia hypophyllous, solitary, distinct stroma lacking, sometimes a skin like, subcuticular layer formed like the stroma ..... *Venturia* (p. 127)
*1. Perithecia epiphyllous, on a distinct hypostroma 2
2. Hypostroma well developed; perithecia more or less large ..... *Gibbera* (p. 142)
*2. Hypostroma subcuticular, skin like, perithecia small ..... *Coleroa* (p. 140)

A. Genus *Venturia* de Not. emend. Sacc.

(Refer. MÜLLER and MENON, 1955)

The fungi belonging to the genus *Venturia* are characterised by dark brown mycelia forming extensive ramifications inside the tissues of the host leaf. The spongy cells show the hyphal branches between the intracellular spaces and in a later stage of development in the intercellular spaces. The fruit bodies are aggregated on the necrotic spots or scattered indiscriminately all over the lamina. They may be found on the upper or under surface of the leaf, in the dead and overwintered leaves, and in a few species in the green leaves. Perithecia are globose or pyriform, hypophyllous to partially emergent, but always innate in the early stages of development. Ostioles are present, emerging out of the epidermis of the host leaf. In colour the perithecia vary from light to dark brown. At the top of the perithecia, in a large number of species setae occur in clumps. Where these structures are absent, hyphal tangles surround the perithecia.

The asci are saccate to cylindrical, bitunicate, the two walls thickened at the apex alone or along the entire length of the ascus. Paraphysoids are sparse and are in the form of colourless threads. Ascospores are in all shades of olive and brown, eight in number, two celled, often with the upper cell shorter or longer than the lower; but the two cells may also be equal in size. Type species: *Venturia inaequalis* (Cke.) WINTER.

Key for the species of *Venturia* occuring on *Rosaceae*.

1. Ascospores with the upper cell shorter than the lower 2
*1. Ascospores with the upper cell longer than the lower 4
**1. Ascospores with the two cells more or less similar 6
2. Perithecia with fan shaped mycelium on living leaves, very minute, on *Alchemilla* species, 15—16 × 3—4 μ ..... *Venturia alchemillae* (p. 139)
*2. Perithecia on dead leaves alone, on *Pirus, Sorbus, Cotoneaster* and *Crataegus* 3
3. Ascospores 13—16 × 6—8 μ ..... *Venturia inaequalis* (p. 128)
*3. Ascospores 16—20 × 6—8 μ on *Cotoneaster tomentosae* *Venturia tomentosae* (p. 132)
4. Perithecia on dead leaves of *Pirus communis* ..... *Venturia pirina* (p. 133)
*4. Perithecia on living and dead leaves, minute aggregated on small areas 5
5. Ascospores almost hyaline, narrow, 11—14 × 2.5—4 μ on *Comarum* *Venturia palustris* (p. 138)
*5. Ascospores light green, 12—14 × 4—5 μ on *Potentilla* . *Venturia potentillae* (p. 137)
6. Perithecia very minute, ascospores 10—12 × 2—4 μ on *Rosa alpina* leaves *Venturia Mülleri* (p. 136)
*6. Perithecia lager and ascospores 11—14 × 2—3 μ on *Prunus* . *Venturia prunicerasi* (p. 135)

1. *Venturia inaequalis* (Cke) Winter

Synonyms: *Sphaerella inaequalis* Cke. — J. Bot. **4**, 248 (1866).
Venturia inaequalis Wint. — in THUEMEN Myc. Univ. Eur. Nr. 261 (1865).
Didymosphaeria inaequalis Niessl — RABENH. Fungi Eur. Nr. 2663 (1881).
Venturia inaequalis Aderh. — Hedw. **36**, 81 (1897).
Endostigme inaequalis Syd. — Ann. Myc. **21**, 171 (1923).
Spilosticta inaequalis Petr. — Ann. Myc. **38**, 193 (1940).
Sphaeria cinerascens Fuck. — Fungi Rhen. no. 824 (1863) (non *Sphaeria cinerascens* Schwein.).
Sphaerella cinerascens Fuck. — in RABENH. Fungi Eur. no. 845 (1865) (non *Sphaerella cinerascens* Cooke).
Endostigme cinerascens Jørst. — Nytt. Mag. Nat. **84**, 252 (1944).
Spilosticta cinerascens Petr. — Sydowia **1**, 197 (1947).

Perithecia occur on the dead overwintered leaves, on both sides of the lamina, scattered or grouped on the necrotic areas. They are innate, globose, or pyriform, ostiolate, with setae occuring in profusion at the apex and sides of the ostiole. Walls of the perithecia are pseudoparenchymatous 14—16 μ; the individual cells vary in shape from rectangular to polyhedral, 10—12 μ in size. In many forms a hypostroma is developed but this structure may also be lacking. Along the lower epidermis of the leaf the fungal hyphae aggregate to form stromatic cushions.

Asci are numerous, saccate to cylindrical, broader at the base than at the top where they taper, 45—70 $\times$ 10 μ, eight spored. The ascospores are light olive in colour, monostichous, often irregular at the base of the ascus, two celled, the upper cell shorter or longer or even similar to the lower. A well marked constriction is often seen at the point of occurence of the septum. In size the ascospores vary from 13—16 $\times$ 6—8 μ. A few paraphysoids occur intermixed with the asci in the form of hyaline hairs.

The conidial stage has been described as *Fusicladium dendriticum* (Wallr.) Fuck.

Synonyms: *Asteroma mali* Desm. — Pl. crypt. de France no. 1099 (1840).
Spilocea pomi Fr. — Systema **1**, 260 (1846).
Fusicladium dendriticum (Wallr.) Fuck. — Symb. Myc. **357** (1869).
(= *Ascospora mali*).
Cladosporium dendriticum Wallr. — Fl. crypt. **2**, 169 (1883).

Fungal hyphae are effuse, bearing epiphyllous conidiophores. Conidiophores are filiform, erect, fasciculate, 50—60 $\times$ 5 μ, septate, with conidia at the top. The conidia are apical, fusoid, obclavate, 30—40 $\times$ 7—9 μ, two-celled, dark, solitary. The cytoplasm in the conidia is uniformly granular.

Venturia inaequalis (Cke.) WINTER has been first published under the name *Sphaerella inaequalis*, by COOKE (1866). He has collected the perithecia on the dead leaves of *Sorbus aria* Crantz. *Sorbus aria* has therefore to be considered as the type host. Other Rosaceous plants like *Pirus malus* L., *Sorbus aucuparia* L., *Crataegus oxyacantha* L. and *Cotoneaster integerrima* Med. are also infected by the fungus. Morphologically the fungus varies

little in the different host species but as seen from the inoculation experiments (p. 126) they are biologically distinct with a high degree of host specialization. In the following accounts these forms of the fungus *Venturia inaequalis* are treated as "formae speciales".

a) *Venturia inaequalis* f. sp. *mali* f. spec. nov.

The fungus in its conidial and perithecial stages resembles closely *Venturia inaequalis* (Cke.) Winter described above (Fig. 1).

This form occurs on the dead leaves of *Pirus malus* L. found in all temperate regions. The material used for inoculation and isolation was *Pirus malus* L.

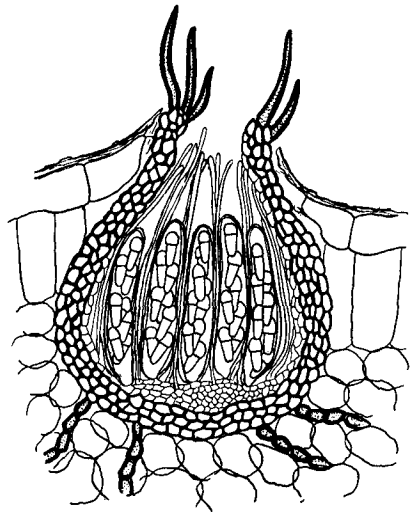

Figure 1. Section through the perithecium of *Venturia inaequalis* f. sp. *mali*. × 500

Cultural studies: On malt agar medium the colonies appear as fluffy white, cottony masses 1—1.5 mm in diameter. Later the mats are appressed to the substratum turning grey green at the centre while the edges remain colourless with small, fibrillar filaments diverging from each other. After a fortnight the colonies become orbicular, brown; at the deeper levels they are colourless. The centre of each colony is cushion shaped (mammelon, after SACCAS, 1944), still fibrillar at the edges. In twenty days the mammelon at the centre is raised above the general surface, the colonies attain a size of 6—8 mm in diameter. Sporulation in the culture is intense at this period. Conidia are found in large numbers with considerable chlamydospores. With further growth the colonies are 0.5—1.0 cm in diameter, and the conidial formation recedes to the edges of the colonies. The surface of the fungal mat is very irregular at this time with more than one mammelon. Areas of thin hyphae plane off all round the mammelons. After three to four months the conidia disappear. No perithecia occur in this medium.

In apple decoction the mammelons at the centre are very prominent, deep grey green to brown in colour. Towards the edges the hyphae are darker, deep brown to tawny green. The upper surface of the mat is from the start irregular. On the reverse of the flasks the colonies are green and there are no mammelons. Conidia arise in large numbers in the culture after three to four weeks, two-celled, or rarely one-celled, truncate, thickened at the top. They have short pedicels, pale green in colour. In size the conidia vary from 14—24 × 7—10 μ. The germ tubes arising from the conidia are mostly from the upper cell. Perithecia arise in this medium after two to

three months, producing the asci and ascospores still later. The fungal hyphae forming the perithecia are thick walled, densely granular and deep brown colour. Perithecia are setose, 60—100 × 40—80 μ. Asci are saccate colourless, with a few paraphysoids in the form of threads. Ascospores are two-celled, olive green, 10—14 × 6—8 μ.

b) *Venturia inaequalis* f. sp. *aucupariae* (Lasch) comb. nov.

Synonyms: *Sphaerella aucupariae* Lasch — in Plowright: Sphaer. Brit. 3, no. 65 (1878).
Didymosphaeria aucupariae Oud. — Rév. Champ. 2, 466 (1897).
Venturia aucupariae Rostr. — in Lind, Danish Fungi, 213 (1913).
Venturia chlorospora var. *sorbi aucupariae* Sacc. — Michelia 1, 386 (1879).
Septoria sorbi Lasch — in Klotzsch: Herb. Myc. No. 459 (1842).
Phyllachora sorbi Rostr. — Tids. Skofbrug 4, 144 (1880).

Perithecia occur on the dead leaves with a feeble hypostroma developed in some cases. Setae are found but more often they are absent. In the latter instances hyphal tangles surround the perithecia. The fruit bodies are deep brown, 60—170 × 56—120 μ.

The asci are saccate, 68—80 × 8 μ. Ascospores are uniform in size to some extent 12—14 × 4—5 μ (mean of 200 spores).

The perithecia occur on the dead leaves of *Sorbus aria* Crantz. and *Sorbus aucuparia* L.

On *Sorbus aria:* § Kt. Solothurn, Egerkingen, Sandthal, 9/5/54. leg. P. STUDER.
Kt. Wallis, Savièse, 2/7/54. leg. E. MÜLLER.
§ Kt. Graubünden, Filisur, Solis, 11/6/55. leg. E. MÜLLER.

On *Sorbus aucuparia:* Champex du Haut, 15/5/54. leg. R. KUOCH.
§ Kt. Wallis, Stalden, 23/5/53. leg. E. MÜLLER.
Kt. Graubünden, Filisur, Solis, 11/6/55. leg. E. MÜLLER.

Cultural studies: Appearance and growth of the colonies on malt agar medium are similar to those in f. sp. *mali.* As distinguished from f. sp. *mali,* in f. sp. *aucupariae,* however many aborted perithecia resembling sclerotia arise even in malt agar. In the apple and pear decoctions a large number of mammelons are formed with flecks of cottony white mycelium covering them. Chlamydospores are profuse in malt agar but conidia arise in larger numbers in the decoctions.

c) *Venturia inaequalis* f. sp. *crataegi* (Aderh.) comb. nov.

Synonyms: *Venturia crataegi* Aderh. — Ber. Dtsch. Bot. Ges. 200 (1902).
Ann. Myc. 1, 520 (1903).

Perithecia occur on the dead leaves with incipient ostioles. In other respects they resemble perithecia in f. sp. *mali* and f. sp. *aucupariae.* Asci are 40—70 × 9—11 μ. Ascospores range in size from 13—15 × 4.5—6 μ.

§ Isolation has been done from this material.

On *Crataegus oxyacantha:* § Kt. St. Gallen, Amden, 15/5/54. leg. E. MÜLLER and R. MENON. Kt. Graubünden, Filisur, Solis, 11/6/55. leg. E. MÜLLER.

Cultural studies: In malt agar medium the growth of the colonies is very slow, seen only as hyaline structures against the light, after three to four weeks, elapsing from the time of spore discharge from the mature perithecia. Hyphae are fibrillar, adpressed to the substratum. They are brown at the centre where the mammelons are present, but colourless at the edges. Conidia arise in small numbers after two months, when the colonies are 2 cm in diameter. They are 20—30 × 4 μ in size. Chlamydospores are very typical for this fungus. They are large, double walled, terminal in position when solitary, or in chains one above the other. The contents of the spores are granular and filled with prominent oil drops.

Perithecia arise in the apple decoction after three months and are 60—80 × 60—80 μ. In the pear decoction the colonies increase rapidly in size, with a tendency in the individual colonies to fuse. In other respects the culture is similar to the forms described before.

d) *Venturia inaequalis* f. sp. *cotoneasteris* nov. f. sp.

Perithecia occur on the dead leaves and are confined to the under surface. They have subepidermal hypostromas. The fruit bodies are globose and deep brown. The perithecial walls are pseudoparenchymatous, four to five layers in thickness, ostiolate. The ostioles are incipient, setose. Setae occur in clumps at the apex of the ostiole and are deep seated. In size the perithecia are 86—110 × 84—100 μ.

Asci are saccate, clavate, bitunicate, 72—80 × 8—10 μ. Paraphysoids are sparse. Ascospores are olive brown, two-celled, upper cell shorter than the lower, 10—14 × 5—6 μ. They are massed irregularly at the base of the ascus but are monostichous at the top.

The form occurs on the dead leaves of *Cotoneaster integerrima* Med. and has been found at Kt. Wallis, Gabi, Simplon, 10/6/53. leg. E. MÜLLER.

Cultural studies: In malt agar medium the colonies are visible after six days as white tufts turning gradually brown. Chlamydospores occur in profusion. They are intensely thick walled, intercalary or terminal in position, 8—10 μ. A very prominent oil drop is found in the centre of the chlamydospore.

In apple decoction the colonies are dark olive in colour with the mammelon at the centre. The entire mat is covered over with short, white to dark fluffy, cottony hyphae. Conidia and perithecia are as in the other formae speciales.

In the pear decoction mycelia form diffuse patches, deep orange in colour. Conidia and chlamydospore are found but the perithecia did not appear in this medium.

§ Isolations have been made from these materials.

2. *Venturia tomentosae* nov. spec.

In this species the perithecia occur on the dead leaves, but are gregarious, on the upper or lower surfaces of the leaf (Fig. 2). They are black, shiny, hypophyllous, innate, ostiolate. Setae are mostly lacking; when present, appear as short stubs. Perithecial walls are pseudoparenchymatous, four to five layers in thickness, thin along the lower side. On the under surface of the leaf the fruit bodies are small and comparatively erumpent. Perithecia are much larger than in the case of *Venturia inaequalis* (Cke.) Winter, 110—130 × 100—110 μ in size.

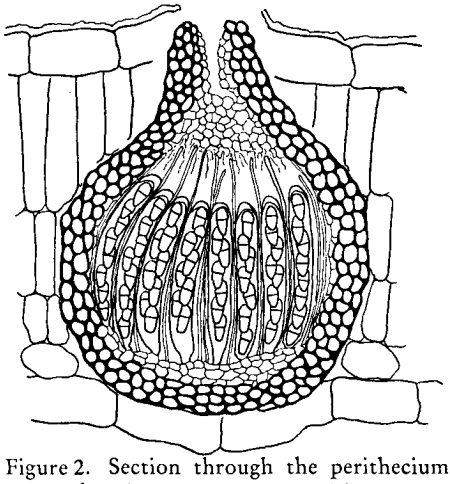

Figure 2. Section through the perithecium of *Venturia tomentosae*. ×500.

Asci are saccate, often cylindrical, bitunicate, walls thickened along the entire ascus. The asci fill up the space inside the perithecium. Paraphysoids are few in number tending to be cellular in their arrangement, especially at the top, 70—100 μ in length. Ascospores are monostichous, two-celled, upper cell longer than the lower, dark brown in colour, larger than in *Venturia inaequalis*, 16—20 × 6—8 μ, thick walled.

On *Cotoneaster tomentosa* (Ait.) Lindl. Kt. Tessin, Airolo, Val Nante, 1300 m. s. m. 28/9/1937. leg. A. VOLKART (type, deposited in the Herbarium E.T.H.).

Perithecia gregaria, nigra, hypophylla, globosa, base applanata, 110—130 μ diam; ostiolum breve, 30 × 40 μ, setis rigidis ornato; asci clavati, breviter stipitati, 70—100 × 8—10 μ, octospori; sporae superiores monostichae, inferiores distichae, oblonge-ellipsoideae, 16—20 × 6—8 μ, bicellulares, parte superiore septatae, fusco-viridae. Paraphysoides singulae, fibrosae, sero mucosae. Hab. in foliis emortuis Cotoneasteris tomentosi.

Venturia tomentosae has been given a specific status because this fungus differs from *Venturia inaequalis* (Cke.) Winter in having very large, entirely innate, ostiolate perithecia. The ostiole emerges out of the host epidermis when the fungus is fully developed. Setae are often lacking, but when present are seen as short stubs. Hypostroma is absent and in the mesophyll of the leaf there are a few hyphal anastomoses. Asci are cylindrical, large, with a few paraphysoids showing a tendency for cellular arrangement. Ascospores are very characteristic with various shapes, and a wide range in the size, always larger than in *Venturia inaequalis*. They are also deep brown and thick walled.

As in the fresh material the mature perithecia were not available, cultural studies in this fungus did not succeed.

The other species of *Venturia*, *Venturia pirina* Aderh., *Venturia pruni-cerasi* Sacc. along with the new species *Venturia Mülleri* are different from *Venturia inaequalis* and *Venturia tomentosae*. In *Venturia inaequalis*, *Venturia pirina* and *Venturia pruni-cerasi* the conidia represent a parasitic phase on the living green leaves. The perithecia in all species of *Venturia* occur on the dead and overwinterd leaves. The species on *Alchemilla* species, *Comarum palustre* L., and *Potentilla* species develop the perithecia on the dead and the living leaves.

All the species described in the following pages have been mentioned in existing literature except *Venturia Mülleri*.

3. *Venturia pirina* (Bref.) Aderh.

Synonyms: *Venturia ditricha* f. *piri* Bref. — Unters. a. d. Ges.-Geb. d. Myc. 10, 221 (1891).
Venturia pirina Aderh. — Ldw. Jhrb. **25**, 875 (1896).

The perithecia occur on the dead leaves confined to the under surface, in small groups. They are hypophyllous, globose to pyriform, ostiolate; ostiole is incipient or long. Setae are lacking in the early stages of development, when the perithecia are surrounded by hyphal tangles. Setae appear in clusters round the ostiole at a later stage. In size the perithecia vary from 120—160 × 100—110 μ.

Asci are saccate, bitunicate, 40—70 × 8—12 μ eight-spored, with few paraphysoids gelatinising at an early stage.

Ascospores are light olive green, two-celled, the upper cell longer than the lower, guttulate, 14—20 × 4—8 μ (mean of 100 spores). The spores are monostichous at the top, distichous at the base.

On *Pirus communis* L.: § Kt. Zurich, Affoltern, 1/4/55. leg. E. Müller.
Dielsdorf, 28/5/42. leg. H. Zogg.

The conidial stage of the fungus has been described as *Fusicladium pirinum* (Lib.) Fuck. — Symb. Myc. 357, (1869).

Synonyms: *Helminthosporium pirinum* Li. — Exs. no. 188 (1832).
Fusicladium virescens — Bon. Handb. 80 (1851).

The hyphae are effuse, light olive in colour. Conidiophores are erect, rarely two-celled, corrugated 20—60 μ long, and abstrict the conidia at the top. Conidia are ovate to fusoid, 28—30 × 6—7 μ, continuous, rarely one-celled, guttulate. A layer of stromatic cells is found beneath the cuticle of the host leaf.

Cultural studies: On malt agar medium the colonies are orbicular to begin with. After eight days the colonies are macroscopic, 1 mm in diameter, brown at the centre and green at the edges. At the outer fringe of the colonies the hyphae are fibrillar, colourless, closely adhering to the substratum. After eighteen days the colonies are round, 2 mm in diameter, with a well developed mammelon at the centre. The hyphae taking part in the formation of the mammelon are greenish violet, more olive brown

§ Isolation has been done from this material.

at the outer edges; at this time there is maximum sporulation in the colonies. The vegetative development attains a maximum density and the mycelia are articulate. After a month the size of the colonies increase to 5—8 mm. The olive green hyphae penetrate deeper into the substratum; at the same time the conidial production wanes off. When the colonies are 1.0—1.5 cm, the large number of mammelons present make the surface of the mat irregular. Hyphal branches from these structures reach almost to the base of the tube. The older portions of the mycelia are deep brown, coriaceous, even though the hyphae at the edges of the colonies may still produce the conidia.

In apple decoction the mycelium is olive green, with the septa occuring at long intervals. Colonies are round, cushion shaped, copper green in colour. Walls of the hyphae are corrugated, thick, with a profusion of chlamydospores. These chlamydospores are intensely thick walled, terminal or intercalary in position with granular contents. In size they measure 50×30 μ. Perithecia are produced in large numbers made up of thick walled, brown hyphae. Setose ostioles are common features of the perithecia. Asci and ascospores appear after four to five months and these structures closely resemble the ones formed in nature.

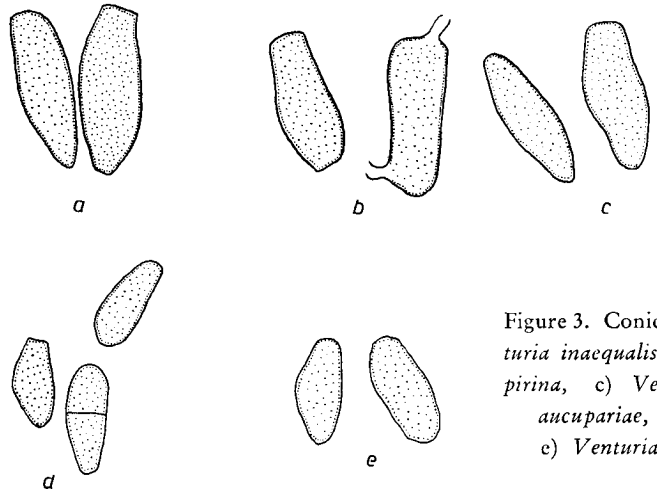

Figure 3. Conidia from culture: a) *Venturia inaequalis* f. sp. *mali*, b) *Venturia pirina*, c) *Venturia inaequalis* f. sp. *aucupariae*, d) *Venturia palustris*, e) *Venturia pruni-cerasi*. ×500.

In the pear decoction the colonies are russet brown and orbicular. Many of them fuse together making the surface of the hyphal mat irregular. Mammelons arise in the centre grading off at the sides in the form of light coloured fibrils, closely adpressed to the substratum. Conidia are formed in the colonies after nine to twelve days. After three weeks these conidia completely disappear. Unlike in the apple decoction, in this medium the colonies are purely superficial, remaining on the surface layers of the substratum. Perithecia develop after three to four months. Size and shape of the asci and the ascospores are similar to those in nature. In many perithecia hyphal tangles are found instead of setae.

4. *Venturia pruni-cerasi* Sacc.

Michelia 1, 382 (1878).

Synonyms: *Venturia cerasi* Aderh. — Landw. Jahrb. 541 (1900).

The perithecia occur on both sides of the leaf, showing a tendency for aggregation on the necrotic spots. Mostly they are solitary but in rare cases they also show a tendency to fuse along the lateral walls. They are hypophyllous, globose, ostiolate with setae occuring in clusters at the top of the ostiole. Walls of the perithecia are two to three layers in thickness, the cells on the inner side being lighter in colour than the cells on the outer. The individual perithecia may come up to a diameter of 150 μ.

The asci are saccate to cylindrical, subsessile, bitunicate, 60—70 $\times$ 10—12 μ. Paraphysoids occur in the form of hairs.

Ascospores are clavate, light olive green, two-celled, septum occuring in the middle of the spore or at the top or the base, 11—14 $\times$ 2—4 μ. They are irregulary arranged at the base but monostichous at the top.

On the dead leaves of *Prunus padus* L.:

Kt. Graubünden, Filisur, Solis, 11/6/55. leg. E. MÜLLER.
Alpes Maritimes, Tende, Rio Freddo, 23/5/55. leg. R. MENON.

The conidial stage occurs as *Fusicladium cerasi* (Rbh.) Sacc.

Synonyms: *Acrosporium cerasi* Rabenh. — Braun Krankh. Pflanz. 16, f. B. (1854).
Fusicladium cerasi Sacc. — Syll. 4, 346 (1886).
Fusicladium pruni Dueomet — Thèse Fac. Sc. Paris 137 (1907).

The hyphae are effuse, light brown in colour, velvety, short, simple, uniseptate at the base, subdenticulate, with granular cytoplasm. 16—18 $\times$ 3—4 μ. Conidia are oblong, fusoid, truncate, subapiculate, varying in size from 20—25 $\times$ 4—4.5 μ.

Cultural studies: On malt agar medium the growth of the fungus is very slow. The colonies become macroscopic after a fortnight and turn light blue in colour. The hyphae at the edges of the colonies thin out, are colourless and fibrillar. Progressively the colonies become round and after two months the mat is entirely adpressed to the substratum. Mammelons may occur in more than one group, making the surface of the colonies irregular. After a month the conidial production is at its maximum. Chlamydospores also occur in considerable numbers either intercalary or terminal in position. The contents of these structures are granular with prominent oil drops in the middle. No perithecia were observed in this medium.

In apple decoction the colonies are visible, when held against the light, after six days from spore discharge. These turn orbicular in another week. Mammelons arise in the centre as dark olive brown structures. Towards the edges of the colonies the hyphae are fibrillar, radiating and colourless, the colour deepening again at the fringes to deep bluish green and black. In the submerged parts of the hyphae the growth is sparse.

The whole fungal mat is very tough and coriaceous. Conidia arise in large numbers, 10—18 × 4—6 μ. Perithecia are also plentiful, thick walled, ostiolate. Setae are few arising at the top of the ostiolar region. In this medium the asci and the ascospores are not as large as those in nature. We however feel that in the decoction of *Prunus* leaves this difference will not be apparent. Due to lack of material we did not attempt this.

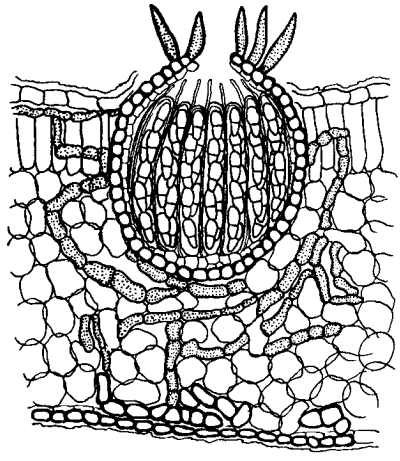

Figure 4. Section through the perithecium of *Venturia Mülleri*. ×500.

In pear decoction the colonies are grey brown and orbicular. Mammelons develop at the centre of the individual colonies. Towards the edges of the colonies the hyphae thin out with widely spaced filaments. Small sclerotia appear on the surface layers of the medium showing a tendency to disappear in the deeper layers. Chlamydospores occur, are deep golden brown, three to four form chains.

The species *Venturia pruni-cerasi* has been described by SACCARDO as early as 1878. The description agrees with that of *Venturia cerasi* Aderh. (1900), described as a new species. As *Venturia pruni-cerasi* is undoubtedly the older name we propose that this should be accepted as the valid name instead of *Venturia cerasi.*

5. *Venturia Mülleri* nov. spec.

Perithecia occur on the dead leaves confined entirely to the upper surface (Fig. 4). They are usually aggregated on the necrotic spots, are very minute, black, shiny, subepidermal, ostiolate. Setae arise in large numbers along the apex or the sides of the perithecia. Walls of the fruit bodies are two layers in thickness, light yellow in colour. In size the perithecia are 50—60 μ.

Asci are saccate, bitunicate, walls of the asci thickened along their entire length, shortly pedicillate, 24—50 × 6—10 μ. Paraphysoids are very few, hair like.

Ascospores are eight in number, light olive, two-celled, clavate, upper cell is longer or shorter than the lower, irregularly arranged at the base of the ascus but distichous at the top, 10—13 × 2—3 μ (mean of 200 spores).

On *Rosa pendulina* L. (*Rosa alpina* L.): Kt. Graubünden, Bivio, 12/6/55. leg. E. MÜLLER. France, Névache, 7/5/54. leg. E. MÜLLER.

Type species is the above material and has been deposited in the Herbarium of the Department of special Botany, E. T. H.

Perithecia singula vel gregaria, nigra, epidermide tecta, immersa, globosa, 50—60 μ, pariete fulvo; setae rigidae, 3—5 congregatae flavae; asci brevissime stipitati, bitunicati, saccati, ventricosi, 20—50 × 6—10 μ, octospori, hyalini; sporae uniseptatae, clavatae, fulvae, 10—13 × 2—3 μ in parte inferiore distichae, in parte superiore irregulariter dispersae; paraphysoides filiformes.

In foliis emortuis *Rosae pendulinae* L.

Cultural studies: In malt agar medium the colonies are orbicular after three to four weeks, attain a diameter of 1—2 mm. The mammelon at the centre of the colonies is olive green, the fungal hyphae planing off at the edge. At the edge of the colonies the hyphae are fibrillar, cottony. In many cases the colonies fuse together making the surface of the entire mat irregular. Chlamydospores occur on the aerial hyphae. In the submerged portions of the fungus the hyphae are lighter in colour and thin walled. Septae in these occur at very long intervals. Conidia were not produced in this medium. The fungus was not grown in apple and pear decoctions.

Venturia Mülleri is regarded as a new species for the following reasons: The perithecia are minute, thin walled, with numerous setae at the apex or sides. Ascospores have a very characteristic form with the upper cell shorter and broader than the lower one.

6. ***Venturia potentillae*** (Fries) Cooke

Synonyms: *Dothidea potentillae* Fr. — Systema **2**, 563 (1822).
Chaetomium potentillae Wallr. — Fl. crypt. **2**, 266 (1833).
Stigmatea potentillae Fr. — Summa. Veg. Scand. 422 (1846).
Venturia potentillae Cooke — Grevillea **6**, 76 (1877).

The perithecia in this species occur on the upper sides of the leaf showing a tendency to be grouped in rows along the veins and the veinlets. Necrotic spots are not formed by the invading fungus. Perithecia are epiphyllous, rarely hypophyllous, minute, globose, brown in colour, setose, ostiolate.

Asci are oblong, cylindrical, clavate, subsessile, 50—60 × 10 μ, paraphysoids few thread like, colourless. Ascospores are oblong, egg shaped, subpyriform, two-celled, 12—14 × 4—5 μ, light coloured.

Occurs on the dead and living leaves of *Potentilla* species.

On *Potentilla anserina* L.:

leg. F. Petrak, Herbarium E. T. H.
leg. Martianoff, Herbarium E. T. H.

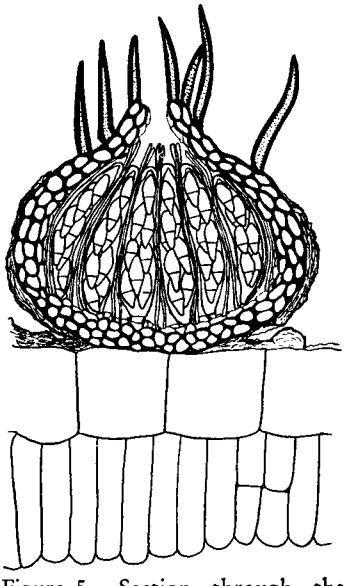

Figure 5. Section through the perithecium of *Venturia palustris* on living leaves. ×500.

7. *Venturia palustris* Sacc. Bomm. et Rouss.

Soc. R. Bot. Belg. 172 (1886).
Synonyms: *Stigmatea comari* Schröt. — Die Pilze Schlesiens 331 (1908).
Spilosticta comari Petr. — Ann. Myc. **23**, 232 (1925).

The fruit bodies appear on the dead and the living leaves. In the living leaves (Fig. 5) the perithecia are on the upper surface of the lamina, hypophyllous, subcuticular, globose to pyriform, dark brown, loosely aggregated on the necrotic spots. Walls of the perithecia are one to two layers in thickness, formed of light brown cells with living cytoplasmic contents.

In the dead leaves the perithecia (Fig. 6) occur on the lower surface, subepidermal in position. The perithecial walls are three to four layers in thickness of dark brown cells, thick walled, with no cytoplasmic contents.

Ostioles in both perithecia are incipient, setae arise in profusion at the apex or along the sides. In size there is not much difference between the living and the dead forms 70—100 μ.

Asci are saccate, bitunicate, 30—50 $\times$ 10—12 μ. Paraphysoids are sparse in forms on living leaves, but many in the forms on dead leaves.

Ascospores are light olive in colour, two-celled, upper cell longer than the lower, monostichous at the top distichous at the base. In size they are 11—14 $\times$ 2.5—4 μ.

Cultural studies: In malt agar medium the colonies are very characteristically diffuse, orbicular, light green to copper olive, velvety, closely adherent to the substratum. At the edges the hyphae turn dark grey to black, fibrillar and diverge from each other. Chlamydospores occur in profusion either intercalary or terminal in occurence. They are deep olive brown to golden brown in colour, thin walled as compared to the ones in the other species. The aerial hyphae are slender, 3—4 μ in diameter, septate at irregular intervals. The interior of the cells is filled with dense cytoplasm and oil drops. Perithecia and conidia did not form in this medium.

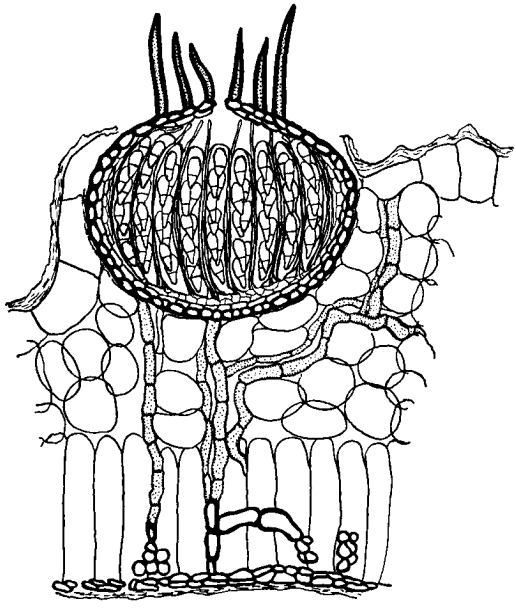

Figure 6. Section through the perithecium of *Venturia palustris* on dead leaves. $\times$500.

In the apple decoction the hyphae are light grey closely adpressed to the substratum, wooly cottony. The mycelium forms a superficial cover on the substratum. Chlamydospores are plentiful, and resemble the ones in malt agar. After a fortnight the colonies

attain a diameter of 5—8 mm but the mammelons are very feebly developed. Conidia are small, truncate 12—18 × 2—4 μ. Perithecia occour but are smaller than the ones found in nature. Asci and spores arise after three to four months.

In the pear decoction the colonies are dark grey brown, orbicular, with mammelons at the centre. Towards the edges of the colonies the filaments are thin, fibrillar and divergent. Small sclerotia appear on the superficial layers of the substratum but these also disappear deeper down. Chlamydospores occur in large numbers, and are deep gold brown in colour; three to four form chains but they may also be terminal in position. Oil drops and granules occupy the interior of these structures.

On *Comarum palustre* L.: Hochmoor, Linden, Keesenthal, 9/6/33. leg. A. VOLKART.
Kt. Zurich, Katzensee, 3/9/53 and 20/4/54. leg. E. MÜLLER.

8. ***Venturia alchemillae*** (Grev.) Berk. & Br.

Synonyms: *Asteroma alchemillae* Grev. — Flor. Edin. 369 (1824).
Chaetomium alchemillae Wallr. — Comp. no. 1810 and (Addit.) 1833.
Stigmatea alchemillae Fr. — Summa. veg. Scand. 423 (1846).
Venturia alchemillae Berk. et Br. — Notic. of Brit. Fungi no. 1493 (1876).
Dothidea ceramioides Duby — Bot. Gall. **2**, 715 (1830).

Perithecia occur on the living leaves confined to the upper surface of the lamina. The mycelium is extramatrical, form black patches, forming fan shaped structures when mature. Very rarely the perithecia form small groups, on the pale yellow necrotic spots. The perithecia are globose, hypophyllous, setose, ostiolate.

Asci are clavate, 60—66 × 6—8 μ. Paraphysoids are thin and gelatinise at an early stage.

Ascospores are light olive in colour, two-celled, constricted at the septum, 15—16 × 3—4 μ. They are irregularly arranged at the base of the ascus, but are monostichous at the top.

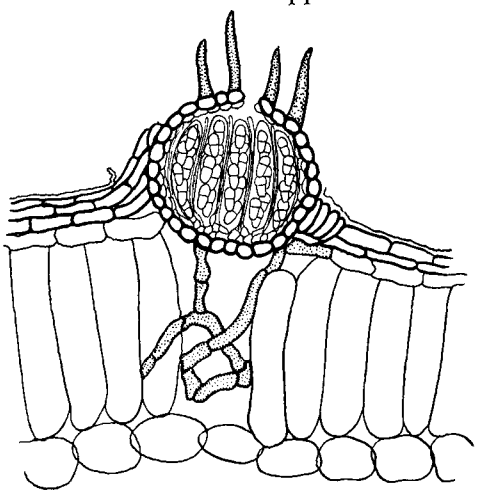

Figure 7. Section through the perithecium of *Venturia alchemillae*. ×500.

On *Alchemilla* species: France, Hautes Alpes, Val Queyras, Echalpe, 5/8/55. leg. E. MÜLLER.
Alchemilla glaberrima L.: Tessin, Airolo, Lago de Ravina, Capanna Busen, 12/9/43. leg. A. VOLKART.
Safier-Berg, 20/8/1901. leg. A. VOLKART.

Appendix: ***Fusicladium eriobotryae*** Cav.

Synonyms: *Basiascum eriobotryae* Cav. — Atti Ist. Bot. Pavia II. ser. **1**, 433 (188).
Fusicladium eriobotryae Cav. — in BRIOSI e CAVARA: Funghi parass. delle piante .. N. 186 (Pavia, 1892).

Fusicladium pirina var. *eriobotryae* Peglion — Riv. d. Pat. Veg. 3, 13 (1894).
Fusicladium dendriticum var. *eriobotryae* Scalia — Boll. Acc. dei Sc. Nat., Catania 101, p. 5.

Acervuli are epiphyllous, black in colour. Conidiophores are short, swollen, one to two septate, 12—18 μ long. They are large at the base and bear only one conidium. Conidia are ovate, lanceolate, truncate, constricted, continuous, acuminate at the top, 6—20 × 6—7 μ.

On *Eriobotrya japonica* L.: The material has been sent to E. MÜLLER, from Kt. Tessin, Lugano, with only the conidial stages. On the leaves brown to deep black spots are seen with the conidia. We have not come across the perfect stage in nature or in culture. Literature does not mention of any perithecia also. Attempts to grow the fungus in malt agar, apple and pear decoctions failed.

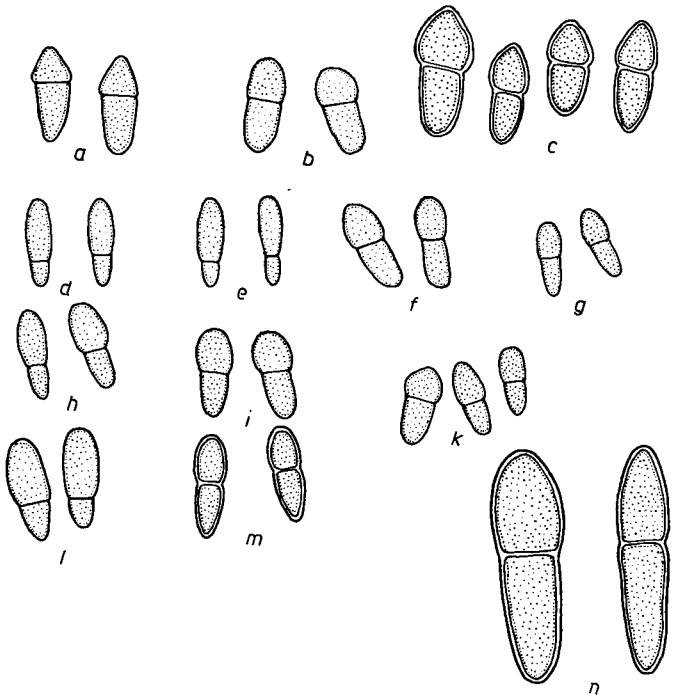

Figure 8. Ascospores from nature:
a) *Venturia inaequalis* f. sp. *mali*,
b) *Venturia inaequalis* f. sp. *aucupariae*,
c) *Venturia tomentosae*,
d) *Venturia potentillae*,
e) *Venturia palustris*,
f) *Venturia inaequalis* f. sp. *crataegi*,
g) *Venturia Mülleri*,
h) *Coleroa chaetomium*,
i) *Venturia alchemillae*,
k) *Venturia inaequalis* f. sp. *cotoneasteris*,
l) *Venturia pirina*,
m) *Venturia pruni-cerasi*,
n) *Gibbera rosae*.
× 1000.

B. Genus *Coleroa* Rbh.

The genus *Coleroa* is characterised by erumpent, thin walled perithecia. Asci have not the apical thickenings developed to the same extent as in the genus *Venturia*. Paraphysoids are numerous as compared to the latter genus. Spores are two-celled, green or light yellow brown.

1. *Coleroa chaetomium* (Kze) Rbh.

Synonyms: *Dothidea chaetomium* Kunze — Systema 2, 563 (1822).
Stigmatea chaetomium Fr. — Summa. Veg. Scand. 422 (1849).
Coleroa chaetomium Rabh. — Klotzsch-Rbh. Herb. Myc. no. 1455 (1850).

Chaetomium circinans Wallr. — Flor. crypt. **2**, 266 (1833).
Venturia Kunzei Sacc. — Syll. **1**, 588 (1822).

The type species *Coleroa chaetomium* occurs on the living and the dead leaves of *Rubus idaeus* (Fig. 9). The differences between the summer and the winter forms are considerable. In the summer forms the mycelia are subcuticular and fan shaped with a tendency for forming patches. Perithecia occur on the pale green or yellow necrotic spots, round or irregular, solitary or rarely fused along their lateral walls. They are globose, applanate subcuticular, ostiolate, ca. 100 μ in diameter. Perithecial walls are light to deep brown, two to three layers in thickness. Often the cells show cytoplasmic contents. Asci are saccate, few in number, bitunicate, with slightly thickened apical portions, eight spored. Paraphysoids are thread like, numerous, reaching to the top of the asci. Asci measure 50—52 $\times$ 7—8 μ. Ascospores are light yellow, fusoid, irregularly distichous, two-celled, upper cell longer than the lower, 10—14 $\times$ 4,5—7 μ.

In the summer of 1955, we were able to obtain the overwintering leaves of *Rubus idaeus* L. with mature perithecia of *Coleroa chaetomium*. These perithecia appear on the lower surfaces of the leaves, with a stroma on the upper surface varying from 8—10 μ. In the spongy cells of the host mesophyll, fungal hyphae build up a dark thick walled stroma. Perithecia are found on the edges of this stromatic plate and are globose, ovoid, ostiolate. The ostiole is lined with papillate cells. Setae arise in profusion at the top or the sides. Asci are saccate, few, bitunicate, with few to many paraphysoids. Ascospores are eight in number, light yellow, two celled, upper cell longer than the lower. They are irregularly arranged, 14—15 $\times$ 4.5—7 μ.

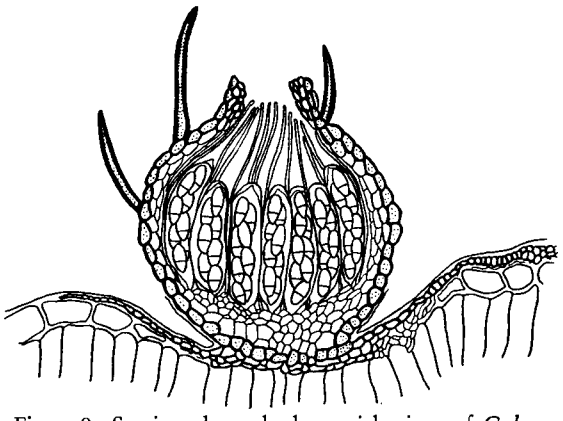

Figure 9. Section through the perithecium of *Coleroa chaetomium* on living leaves. $\times$500.

On *Rubus idaeus* L.: Alpes Maritimes, Tende, north side of Rocca maima, 24/6/55. leg. E. MÜLLER.
15/7/55. leg. E. MÜLLER and H. SCHÜEPP. 24/6/55. leg. R. MENON.
Kt. Graubünden, Filisur, Solis, 12/6/55. leg. E. MÜLLER.
Kt. Tessin, Nante, Airolo, 17/10/39. leg. A. VOLKART.

FUCKEL has described the conidial stage as *Exosporium rubi* Nees (WINTER, 2, 200 [1887]). We did not find any conidia in the culture and therefore regard these conidia as doubtful.

Cultural studies: In malt agar medium the growth of the fungus is very slow. The colonies become orbicular, fluffy and cottony after three to four weeks. Soon these turn into crusty, sooty black, cushion shaped structures, closely adpressed to the substratum. Mammelons are conspicuously absent in this fungus. The hyphae at the edges of the colonies are divergent and fibrillar. On the reverse the mat is black. Aerial hyphae are thick walled dark, septate, 0.5—1.0 μ in diameter, corrugated. The submerged mycelium is thin, 1.0—1.5 μ. Deep brown, thick walled hyphae are seen in addition to these two. Chlamydospores are profuse, occuring in chains mostly, strangulate, with granules and oil drops in them. Conidia and perithecia were not observed in this medium even after four months.

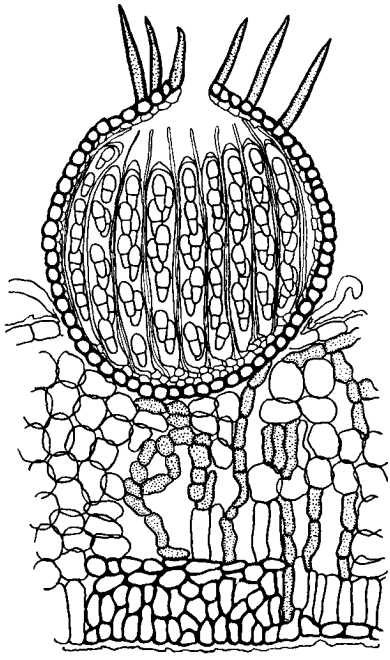

Figure 10. Section through the perithecium of *Coleroa chaetomium* on dead leaves. ×500.

The genus *Coleroa,* as seen from *Coleroa chaetomium,* does not differ that of *Venturia* especially in the winter forms. Morphologically the variations between the two genera are the smaller number of asci, profusion of paraphysoids and the formation of an extensive hypostroma in *Coleroa.* But in the asci and the ascospores the two genera do not show any differences. Even though the cultures in the two genera showed variations we cannot definitely conclude much, due to the lack of conidia and perithecia. Inoculation experiments were not performed to give further evidence. Therefore we cannot say at the present stage of our investigations whether *Coleroa* can be merged with *Venturia* or not. In this paper we retain the genus.

C. Genus *Gibbera* Fr.

The genus *Gibbera* has a free mycelium in many cases but this may also be lacking. Perithecia are surrounded by interlocking hyphal branches and sharp, stiff setae are present at the top of the fruit bodies. Perithecial walls are pseudoparenchymatous, dark brown, with the outer layers of cells darker than the inner ones. Hypostroma is superficial. Ascospores are dark olive grey to brown. *Gibbera* species occur mostly on Ericaceous plants. Although the necessity for a new name for the genus is felt, (MÜLLER and MENON, 1955) the genus is retained, as we feel that any change in the present nomenclature would be causing too great confusion in the forms included in the genus *Gibbera.*

1. ***Gibbera rosae*** (de Not.) MÜLLER et MENON

The species is of significance in nomenclature since the genus *Venturia* was based on the species occuring on *Rosa pendulina* L. In the studies of MÜLLER and MENON (1955) this fungus has been identified as *Gibbera*. A new name could be suggested for the fungi occuring under the genus *Gibbera*. For the new combination *Gibbera rosae* the following synonyms have been retained.

Synonyms: *Venturia rosae* de Not. — Atti. Sci. Ital. 6, 484 (1844).
Pyrenophora rosae Sacc. — Syll. 2, 285 (1883).
Protoventuria rosae Berl. et Sacc. — Atti. Soc. Veneto-Trent (1886).
Gibbera rosae MÜLLER et MENON — Phytopath. Z. 25, 190 (1955).

The perithecia occur on the twigs of the host plant, solitary or in small groups, with a subcuticular hypostroma. The stroma very often rises deeper down. Perithecia lack ostioles, but a pore is formed by the hystolysis of the cells at the top of the perithecium. Deep, dark setae occur in clusters at the apex and sides of the perithecia. The fruit bodies vary from 120—200 × 150—250 μ. (cf. MÜLLER et MENON for description and figures.)

Cultural studies: In malt agar medium the growth of the fungus is very slow. Colonies are orbicular, cottony white, fluffy, turning to olive green and black. Mammelons are more than one in number, and the edges of the colonies are light coloured and thin. The hyphae at the outer fringe are fibrillar, closely adpressed to the substratum. On the reverse the mat is dark green. Aerial hyphae are light olive green, 1.0—2.5 μ in diameter, septate, with oil drops inside. The submerged mycelium is colourless, 0.5 μ in diameter, sparsely septate. Perithecia and conidia were not observed.

Summary

1. In this paper the family *Venturiaceae* occuring on *Rosaceous* hosts is discussed; the genera *Venturia* de Not. (emend. SACCARDO), *Coleroa* Rbh. and *Gibbera* Fr. are investigated in detail and are found to show morphological similarities.

2. Most of the species have been isolated and maintained in pure culture. Conidia of the *Fusicladium* type have been found to occur in the species *Venturia inaequalis, Venturia pirina* and *Venturia pruni-cerasi.* Ripe perithecia are formed in the above species and in addition in *Venturia palustris.*

3. Infection experiments were conducted with *Venturia inaequalis, Venturia pirina* and to some extent with *Venturia pruni-cerasi.* Further studies on *Venturia inaequalis* show that this species exhibit morphologically similar biotypes; these biotypes are described as "formae speciales" and we have distinguished f. sp. *mali* on *Pirus malus,* f. sp. *aucupariae*

on *Sorbus* species, f. sp. *crataegi* on *Crataegus* species and f. sp. *cotoneasteris* on *Cotoneaster integerrima.*

4. Two new species are described, *Venturia tomentosae* on *Cotoneaster tomentosa* (Ait.) Lindl. and *Venturia Mülleri* on *Rosa pendulina* L.

Zusammenfassung

1. In der vorliegenden Arbeit wurden die auf *Rosaceae* parasitierenden *Venturiaceae* aus den Gattungen *Venturia* de Not. (emend. SACCARDO), *Coleroa* Rbh. und *Gibbera* Fr. morphologisch untersucht und miteinander verglichen.

2. Die meisten Arten wurden auch isoliert und in Reinkultur verfolgt. Konidien vom Typus *Fusicladium* bilden folgende Arten: *Venturia inaequalis, Venturia pirina* und *Venturia pruni-cerasi.* Reife Perithecien bildeten in Reinkultur: *Venturia inaequalis, Venturia pirina, Venturia pruni-cerasi* und *Venturia palustris.*

3. Infektionsversuche wurden mit *Venturia inaequalis, Venturia pirina* und zum Teil auch mit *Venturia pruni-cerasi* durchgeführt. Aus den Versuchen mit *Venturia inaequalis* geht hervor, daß diese Art in einige morphologisch nicht unterscheidbare Biotypen zerfällt, welche als "formae speciales" beschrieben und entsprechend benannt werden. Wir unterscheiden demnach: f. sp. *mali* auf *Pirus malus,* f. sp. *aucupariae* auf *Sorbus*-Arten, f. sp. *crataegi* auf *Crataegus*-Arten und f. sp. *cotoneasteris* auf *Cotoneaster integerrima.*

4. Als neue Arten werden beschrieben *Venturia tomentosae* auf *Cotoneaster tomentosa* (Ait.) Lindl. und *Venturia Mülleri* auf *Rosa pendulina* L.

Literature cited

ADERHOLD, R., 1896: *Venturia pirina.* Ldw. Jb. **25**, 875.

— —, 1903: Kann das *Fusicladium* von *Crataegus* und von *Sorbus*-Arten auf den Apfelbaum übergehen? Abh. Biol. Abt. Land- u. Forstwirtsch. Kais. Gesundheitsamt **3**, 436—439.

ARX, J. A. VON, 1952: Studies on *Venturia* and Related Genera. Tijdschrift over Plantenziekten **58**, 260—266.

— —, 1954: Revision einiger Gattungen der Ascomyceten. Acta Botanica Neerlandica **3**, 83—84.

ASHCROFT, R., and FOTHERGILL, P. G., 1955: The Nutritional studies of *Venturia inaequalis* (Cke.) Winter. J. gen. Microbiol. **12**, 387.

COOKE, M. C., 1871: The Handbook of British Fungi **2**, 916.

FOTHERGILL, P. G., and ASHCROFT, R., 1955: Further Nutritional studies of *Venturia inaequalis* (Cke.) Winter. J. gen. Microbiol. **13**, 399—407.

FREY, C. N., 1924: The Cytology and Pathology of *Venturia inaequalis* (Cke.) Winter. Trans. Wisc. Acad. Sci. **21**, 303—343.

GÄUMANN, E., 1949: Die Pilze. Basel, 159—161.

HÖHNEL, F. VON, 1907: Fragmente zur Mykologie no. 115.

— —, 1909: Ibid. no. 379.

— —, 1918: Mykologische Fragmente. no. 290. Ann. Myc. **16**, 172—174.

— —, 1929: *Asteroma mali* Desm. Mitt. a. d. bot. Institut d. Techn. Hochsch. Wien **6**, 2.

KEITT, G. W., 1926: Some relations of the environment to the epidemiology and control of the apple scab. Proc. Nat. Acad. Sci. **12**, 68—74.

— —, LEON, K., and JONES, L. K., 1926: Studies on the epidemiology and control of apple scab. Wisc. Agric. Exper. Sta. Res. Bull. **73**, 1—104.

— —, and PALMITER, D. H., 1926: Heterothallism and variability in *Venturia inaequalis*. Amer. J. Bot. **29**, 338—345.

— —, and LANGFORD, M. H., 1938: Heterothallism and segregation for pathogenicity in *Venturia inaequalis*. Phytopathology **28**, 12, Abstr.

— —, — —, 1940: A preliminary report on the variability and inheritance of *Venturia inaequalis*. Phytopathology **30**, 452—453.

— —, — —, 1941 a: *Venturia inaequalis* (Cke.) Winter, I. A ground work for genetic studies. Amer. J. Bot. **28**, 805—820.

— —, — —, 1941 b: A preliminary report on genetic studies in the pathogenicity and nature of saltation in *Venturia inaequalis*. Phytopathology **31**, 1142.

— —, and SHAY, J. R., 1943: *Venturia inaequalis* (Cke.) Winter. Genetic studies in the pathogenicity and certain mutant characters. Amer. J. Bot. **30**, 491—500.

KILLIAN, K., 1917: Über die Sexualität von *Venturia inaequalis* (Cke.) Aderh. Z. Bot. **9**, 353—398.

LANGFORD, M. H., and KEITT, G. W., 1942: Heterothallism and Variability in *Venturia pirina*. Phytopathology **32**, 357—369.

LUTTRELL, E. S., 1955: The ascostromatic Ascomycetes. Mycologia **47**, 511—530.

MÜLLER, E., und ARX, J. A. VON, 1950: Einige Aspekte zur Systematik pseudosphärialer Ascomyceten. Ber. Schweiz. Bot. Ges. **60**, 329—397.

— —, 1951: Beiträge zur Kenntnis der Gattung *Gibbera* Fr. emend. Petr. Sydowia **8**, 60—73.

— —, und MENON, R., 1955: Über *Venturia rosae* de Not. und die Nomenklatur der Gattung *Venturia* de Not. Phytopath. Z. **25**, 190—195.

PALMITER, D. H., 1934: Variability in monoconidial culture of *Venturia inaequalis*. Phytopathology **24**, 22—47.

PETRAK, F., 1924: Mykologische Notizen. VII. Ann. Myc. **22**, 1—82.

— —, 1927: Mykologische Notizen. IX. Ibid. **25**, 181—260.

— —, 1938: Beiträge zur Systematik und Phylogenie der Gattung *Phaeocryptopus* Naoumov. Ann. Myc. **36**, 9—26.

— —, 1940: Mykologische Notizen. XII. Ann. Myc. **38**, 181—267.

— —, 1947: Über *Gibbera* Fr. und verwandte Gattungen. Sydowia **1**, 169.

— —, 1954: Beiträge zur Pilzflora von British Nord-Borneo. Sydowia **8**, 71—73.

— —, und SYDOW, H., 1925: Kritisch-systematische Originaluntersuchungen usw. Ann. Myc. **23**, 230—232.

SACCAS, A., 1944: Étude morphologique et biologique des *Fusicladium* des Rosacées. Paris.

SCHMIDT, M. 1936: *Venturia inaequalis* (Cke.) Aderh. VI. Zur Frage nach dem Vorkommen physiologisch spezialisierter Rassen beim Erreger des Apfelschorfes. Erste Mitteilung. Gartenbauwissenschaften **10**, 478—499.

— —, 1937: *Venturia inaequalis* (Cke.) Aderh. VII. Zur Morphologie und Physiologie der Widerstandsfähigkeit gegen den Erreger des Apfelschorfes. Gartenbauwissenschaften **11**, 221—230.

SHAY, J. R., 1943: Genetic studies of certain mutant characters in *Venturia inaequalis*. Abstr. Phytopathology **33**, 1—2.

SHEAR, C. L., 1948: Mycological Notes. LX. Mycologia **40**, 748—759.

SYDOW, H., und WEDERMANN, E., 1924: Über einige neue oder interessante Pilze der Kanarischen Inseln. Ann. Myc. **22**, 186.

WINTER, G., 1887: Die Pilze Deutschlands, Österreichs und der Schweiz. Rabenhorst's Kryptogamen-Flora **2**, 199—436.

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