ON THE LIFE-HISTORY OF A FUNGUS PARASITIC ON ANTIRRHINUM MAJUS, WITH SOME REMARKS ON THE GENUS HETEROSPHAERIA.

(With 8 Text-figs.)

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Occurrence and Description of Disease.

In 1917 and 1918 Antirrhinums were received from two different sources showing a leaf disease which appeared to be distinct from anything previously recorded on this host. What was obviously the same disease was noted in 1920 by Miss Cayley and described by her in some detail, though the fungus was not fully identified (1).

Since then the disease has frequently been recorded, and appears to be at present one of the most common and at the same time perhaps the most destructive disease of cultivated Antirrhinums in this country. It does not appear, however, to have been noted outside Great Britain.

A brief recapitulation of the chief characteristics of the disease may be given here.

At suitable temperatures, in about ten days after spraying young and still tender leaves with a spore suspension, there appear the first visible signs of infection in the form of pale green rounded spots, about 5 mm. in diameter. As has been mentioned in a previous note (2), the growth of the mycelium and production of spores of the fungus is active only under somewhat cool conditions, but when once started in a bed the disease spreads very rapidly during spells of cool, moist weather. The leaf spots become more clearly defined owing to the collapse of the affected cells. The subsequent appearance depends to some extent on the variety of Antirrhinum, and also upon weather conditions. The central portion of each spot gradually becomes pale and dries out. Sometimes a definite purplish margin may be developed but in other cases there is no such distinction of colour. Sometimes also the dried areas fall out, leaving holes in the leaf, and the appearance is then like that known as "shot-hole" in plums, etc., or as if the leaves had been eaten by an insect (Fig. 1). Although the leaf phase is always the most conspicuous form of attack, in cases of heavy infestation the green stems also develop lesions which eventually become swollen canker-like areas owing to the production of wound cork beneath the pustules of conidia. When the stems

are infected the flower-stalks may be poor and distorted, and the whole plant has a sickly appearance. Eventually, badly attacked plants are killed outright.

Under suitable moist conditions conidia are produced abundantly on both sides of the leaf, and the numerous acervuli are seen easily with the aid of a pocket lens. Under dry, hot conditions, however, the formation of conidia is temporarily restricted. The acervuli are crowded closely on each spot, are of a very pale pinkish tinge and somewhat waxy or moist in

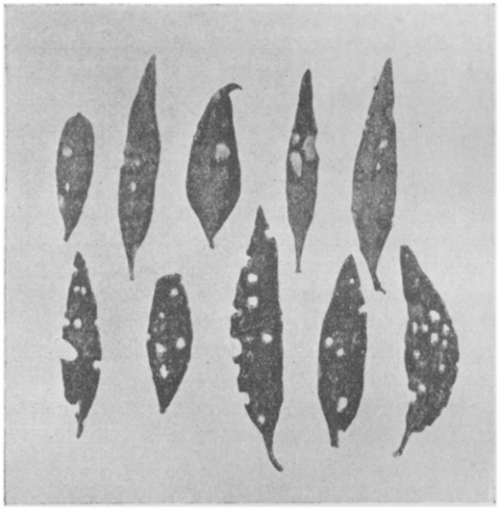

Fig. 1. Leaves of *Antirrhinum majus* showing spots caused by *Cercosporella Antirrhini*.
Upper row—early stages.
Lower row—showing subsequent "shot-hole" effect.

appearance rather than pulverulent. Vertical sections show that each acervulus arises just beneath a stoma as a minute cushion of closely woven hyaline hyphae. This cushion bears on its outer surface numerous erect, branched conidiophores, which burst through the epidermis and produce at the exterior the curious conidia (Fig. 2, *a–c*). These are at first narrowly obclavate, curved, for a long time non-septate but finally one- to three-septate (Fig. 2, *c*). At length, sometimes only after separation from the conidiophore, the apical portion becomes drawn out into a long fine awl-like point, while after the shedding of the conidia a second but shorter appendage may appear at the base of the spore (Fig. 2, *c*).

Presumably the conidia are washed away in drops of rain or

dew or in the splashes made by watering, and in this way infection is spread. In no case has any other form of fructification been observed on the living plants, and an examination of dead plants left standing in the beds revealed no fungus which could conceivably be regarded as being connected with the Hyphomycete under consideration.

At the time the disease was first received a careful search was made in the literature, but no mention could be found of any fungus occurring on *Antirrhinum* or related genera which was at all suggestive of this species. The fungus was accordingly described as a new species of *Cercosporella*, *C. Antirrhini* Wakef. (3).

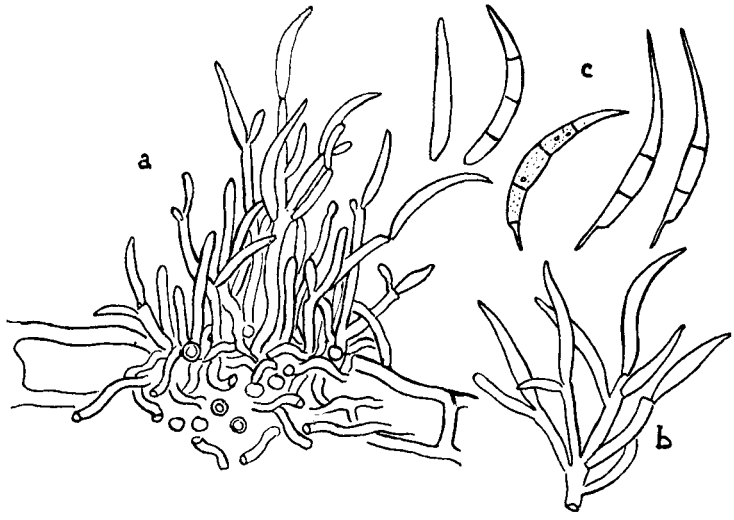

Fig. 2. *Cercosporella Antirrhini*. *a*, Vertical section of acervulus. *b*, Branched conidiophore. *c*, Conidia at various stages. (× 850.)

The reference to *Cercosporella*, as in many cases of Hyphomycetes whose other stages are unknown, was purely a matter of convenience, *Cercosporella* being the nearest "form genus" into which the species would fit. It was recognised at the time, however, that the fungus differed in several respects from a typical *Cercosporella*, and might later have to be removed from the genus.

Temperature Relations of Parasite.

Towards the end of 1923 cultures were started from conidia, and were put on several different media which happened to be available at the time—chiefly Dox's agar, prune agar, and malt extract agar.

At the outset some difficulty was experienced in obtaining abundant growth. Microscopic observations of platings of the conidia on agars revealed the fact that a remarkably high proportion of the conidia failed to germinate, and some rough experiments on the effect of heat on the conidia were therefore carried out.

The conidia germinate slowly and do not lend themselves well to the adoption of the identical technique used by Henderson Smith (4) in his careful study of the effect of heat on the spores of *Botrytis cinerea*. The following method was adopted. Tubes of agar were melted and cooled to the desired temperature in a water bath. After the tubes in each batch had attained the temperature of the bath, equal drops of a heavy suspension of conidia of the fungus were added to each tube, the dilution of conidia in the agar maintained, with shaking, at the particular temperature for one or five minutes, and at the end of the period the contents of the tube were poured quickly into a sterile Petri dish. The dishes were then incubated at 18° C., and after the lapse of an ample period (three weeks) to allow of all viable conidia producing colonies the numbers on the plates were counted.

With malt extract agar as the medium in which the conidia were heated the results shown in Table I were obtained. Very

Table I.

Number of colonies of *Cercosporella Antirrhini* developing on plates of malt extract agar when approximately equal numbers of conidia are heated at the temperatures given, for the times stated, suspended in that medium.

Temperature maintained in water bath	Time of heating	
	1 minute	5 minutes
41° C.	Approx. 10,000	24
43° C.	Approx. 2,500	1
45° C.	5	Nil
47° C.	Nil	Nil

Table II.

Number of colonies of *Cercosporella Antirrhini* developing on plates of prune agar when approximately equal numbers of conidia are heated at the temperatures given, for the times stated, in that medium.

Temperature maintained in water bath	Time of heating		
	Nil (Suspension poured at once)	1 minute	5 minutes
41° C.	Approx. 10,000	—	—
	—	290	Nil
43°, 45° and 47° C.	—	Nil	Nil

similar results were obtained in a duplicate set with malt extract agar, and also with potato gelatine, using different suspensions of conidia. Comparison with the curves of Henderson Smith

indicates that the conidia of *Cercosporella Antirrhini* in malt extract agar and potato gelatine are killed at an appreciably lower temperature (*circa* 5° C.) on the average than those of *Botrytis cinerea* heated in distilled water. The effect of the medium is, however, strikingly shown by the results in Table II, obtained by heating suspensions of the conidia in prune agar (Difco). The conidia were from the same heavy suspension as those used with malt extract agar for the results shown in Table I, and drops of equal size were used for each tube. A duplicate set with prune agar, using a different suspension of conidia, gave very similar results. The figures show that when heated for one minute in the medium the average conidium of *Cercosporella Antirrhini* will withstand a temperature 2–3° C. higher in malt extract agar or potato gelatine than in prune agar. The results also emphasise the advantage of using a gelatine medium when plating out the conidia of an unknown fungus.

The growth of the fungus in pure culture is extremely slow, colonies started from spores not attaining a diameter of 3 cm. until after the lapse of a month at the optimum temperature. This appears to be at approximately 18° C., but growth is almost as good at a low laboratory temperature averaging about 13° C. No growth at all, either from spore inoculations or of colonies of the fungus, takes place at a temperature of 25° C. or higher, although exposure to 25° C. on agar plates for a month does not kill the organism.

It may be noted here that similar temperature relations were found by Vestergren ((5), p. 17) when working with the fungus *Heteropatella cercosperma* (Rostr.) Lind (= *Rhabdospora cercosperma* (Rostr.) Sacc.). In that case temperatures of 25° to 30° C. inhibited conidial formation. The maximum lay between 30° and 35° C. and the optimum at about 20° C. (between 18° and 25° C.). The point will be referred to again in the section on taxonomy.

Growth on Various Media.

Cultures which had been kept for some time were noted during the winter to have produced different growth according to the medium used. On Dox's agar or potato agar the mycelial growth is white and scanty, and closely adpressed to the surface of the medium in a radiating form. Minute pinkish pustules of conidia are developed, on potato agar all over the colony, but on Dox's agar tending to be aggregated towards the centre. No further development was noted on either of these media. On prune agar, however, mycelial growth is rather more vigorous, and in addition to the radially spreading, closely adpressed hyphae tufts of erect filaments consisting of bundles of hyphae

often occur towards the centre of each colony. Conidia are formed abundantly in four days, and at the end of a fortnight there are seen here and there, especially towards the middle of the colony, small black bodies resembling sclerotia.

On malt extract agar the mycelial growth is more compact than on the other media mentioned and conidial pustules develop

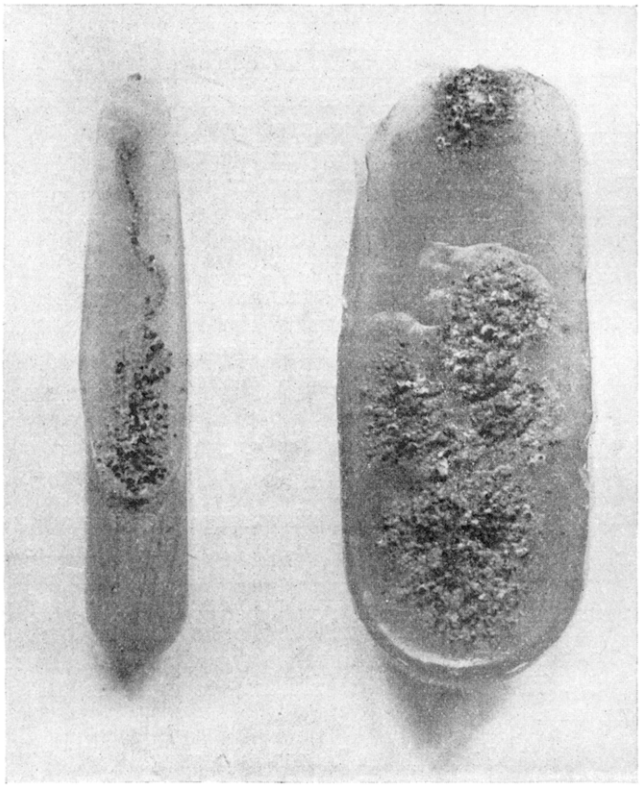

Fig. 3. Two cultures of *Cercosporella Antirrhini* on malt extract agar, showing abundant *Heteropatella* pycnidia (nat. size).

abundantly in the middle of the colony. On this substratum also the sclerotium-like bodies occur, but they are more slowly formed than on prune agar (Fig. 3).

Similar bodies were found later to be produced also on sterilised antirrhinum stems.

As these blackish bodies seemed most likely to throw light on the affinities of the fungus, observations were concentrated

on them. At first they were rounded and compressed in form (more or less "bun"-shaped) and quite solid, black externally but composed within of thick-walled, closely interwoven, colourless hyphae. Later it was noted that some of them had opened out above and become discoid, with a slightly raised, torn margin. The appearance suggested that the bodies represented the perfect form of the fungus and that this was to be sought amongst the Discomycetes. Repeated examination of even the most well-developed discs, however, failed to reveal any trace of asci. Cultures showing them were kept until almost drying up, and were exposed to low temperatures outdoors for 24–48 hours. Further, various media and concentrations of media were tried. If left in the tube in which they were formed, the discoid bodies always remained sterile, the erect filamentous hyphae composing the disc eventually becoming much swollen in parts and obviously abnormal. When transferred to another tube, however, and thus supplied with fresh food material and moisture, the supposed hymenial surface immediately produced an abundant crop of conidia, similar to the original *Cercosporella* conidia.

Over-wintering of Diseased Antirrhinums.

At this point further observation of pure cultures was abandoned, and during the winter of 1924–5 attempts were made to find similar bodies produced in nature. Numerous antirrhinums of several different varieties had been inoculated during the summer and had become badly infected with the disease. Some of these, both at Reading and at Kew, were left standing in the beds; affected leaves and stems of others were placed in empty flower-pots covered with muslin and stood out of doors throughout the winter.

As already mentioned, plants left in the beds gave no result, probably because the stems were not under sufficiently uniform moist conditions. Stems and leaves over-wintered in pots also showed nothing. It was difficult to keep these sufficiently moist and at the same time protected from being eaten by slugs, woodlice, etc., and in London possibly the heavy black fogs of that winter may have had a deleterious effect. At Reading, however, better fortune was met with. In March 1925 numerous decorticated stalks from a large heap of dead Antirrhinums, which during the summer had shown the disease, were found to show an abundance of black Discomycete-like bodies similar in appearance to those formed in pure culture (Fig. 4).

These fructifications proved to be pycnidial only, and although the stems were kept under observation for some months

no ascigerous stage was ever found. From the evidence now obtained, however, it seems certain that the perfect stage, if produced at all, would be a Discomycete. The pycnidial form as found on the over-wintered stems is an undoubted *Heteropatella*, a genus of Excipulaceae, species of which are known

Fig. 4. *Heteropatella* pycnidia developed on over-wintered dead stems of *Antirrhinum* (nat. size).

in other cases to belong to the Discomycete genus *Heterosphaeria*. Apart from the similarity to the bodies seen in cultures, proof of the connection of the *Heteropatella* on the dead stems with the parasitic *Cercosporella* was obtained by inoculation of living Antirrhinums with spore-suspensions from pure cultures of the former, when the characteristic disease spots on the leaves were produced.

Morphology.

(a) *Cercosporella* stage. It has been already stated that the acervuli of the parasitic Hyphomycetous stage develop beneath the epidermis of the leaf or green stem as small hyaline hyphal masses. From these arise erect branched conidiophores which burst through the epidermis in small tufts and produce the conidia externally. The conidiophores are hyaline, branched from near the base, and 2–4 μ in diameter. The conidia arise at the tips of the branches, and are at first non-septate, slightly

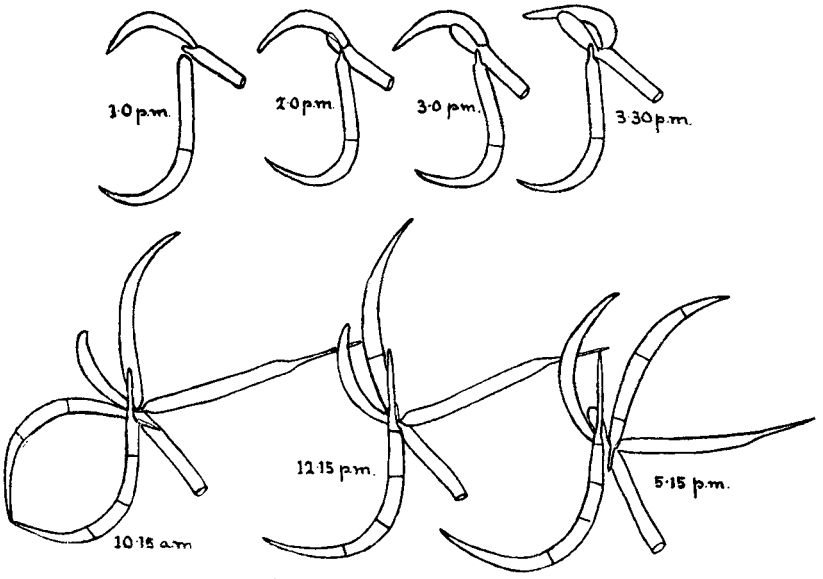

Fig. 5. The production of conidia in a hanging drop. The same conidiophore drawn at intervals on two successive days to show successive development of conidia (× 850).

curved, and narrowed towards the apex but not sharply pointed. The size at this stage is about 25–30 × 2·5–3·5 μ. Gradually the apex becomes more drawn out and at the same time from one to three septa appear, giving the *Cercosporella* appearance which is that usually seen when diseased leaves are examined. After this the conidia fall away from the conidiophores and are no doubt soon washed away. In cultures in hanging drops of sterilised antirrhinum extract the whole development was followed more in detail, and is shown in Fig. 5. The first-formed conidium is pushed to one side by continued growth of the apex of the conidiophore and a second conidium is quickly produced. By the time the primordium of

a third conidium becomes visible between the two previously formed the first conidium has acquired its pointed apex and has begun to show the transverse septa. By continued growth of the third conidium it is gradually pushed more to one side and falls away, remaining (unless disturbed) lying free by the side of the parent conidiophore. Almost immediately after the conidium has become detached it is seen to have a small pedicel-like projection at its base. In the course of a few hours this projection elongates and finally becomes a more or less pointed appendage of about one-third the length of the spore at the time of detachment. Simultaneously the apex of the spore has become drawn out to a long, fine point, with the result that the final form of the spore, prior to germination, is as shown in Figs. 2, *c* and 5. The late development of the basal appendage

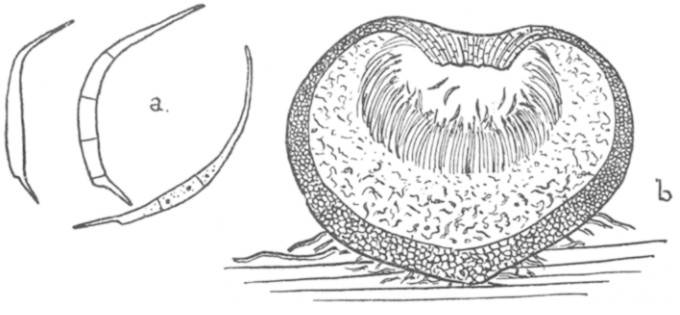

Fig. 6. *Heteropatella* stage. *a*, Conidia (× 850).
b, Vertical section of young pycnidium.

is a point of morphological importance, because the similarly shaped spores of species of *Heteropatella* have by various authors been described as "pedicellate."

The development of the conidium from its first appearance as a small projection at the tip of a conidiophore until it is ready to be detached appears to occupy about seven hours at ordinary room temperatures. After the conidium is shed the development of the basal appendage and the elongated apex may occupy several hours more, but the times have not been exactly noted. The measurements of mature conidia are: body 25–30(–35) × 3·5–4 μ, apical appendage about 20–25 μ, basal appendage up to 10 μ long.

The successive formation of conidia goes on for some time, and in an undisturbed hanging drop fairly large bunches of conidia may be found at the tips of the conidiophores. The slightest motion in the liquid, however, disperses them, and only the two or three conidia as yet immature remain attached.

(b) *Heteropatella* stage. The pycnidial form of the fungus has not been observed on leaves. On dead stems of antirrhinum it arises from the lignified tissue beneath the cortex, and eventually becomes superficial owing to the weathering away of the latter.

At first the pycnidium is a solid, somewhat flattened sclerotium-like body, consisting of a closely-woven mass of hyaline thick-walled hyphae, covered externally by a blackish pseudoparenchymatous cortex. Soon there appears near the outer surface a small flattened cavity, on the floor of which a dense layer of conidiophores is produced. It is now seen that the upper portion of the wall is thinner and different in structure from the basal part, in that the cells show a characteristic radial arrangement (Fig. 6, *b*). Later this lid-like outer wall is torn into segments from the centre outwards, the segments remaining as minute teeth fringing the margin of the flat conidia-bearing disc.

The conidia (Fig. 6, *a*) produced by this *Heteropatella* form of fructification are similar in shape and size to those of the *Cercosporella*, and behave similarly on germination.

Germination of Conidia.

The germination of the conidia, whether those of the *Cercosporella* or of the *Heteropatella*, and the subsequent early stages of development of the colonies, follow in general the course described by Brefeld (6) for the conidia of *Heterosphaeria Patella* and *H. Linariae* and by Vestergren (5) for *Heteropatella cercosperma*. In the media used by the authors, however (distilled water and sterilised antirrhinum extract), the production of secondary conidia immediately, without the formation of mycelium, has not been observed. Germination is always by means of a germ tube.

The cells of the conidium become much swollen, and at first a single germ tube arises laterally from one of the middle cells (Fig. 7, *b*, *d*). Later a second is formed towards the base of the conidium, and in forty-eight hours others may have been produced (Fig. 7, *a*, *c*, *e*). The basal appendage is often visible for a time (Fig. 7, *e*) but is soon obscured owing to the continued development and branching of the hyphae. Meanwhile the first-formed germ tubes have begun to produce conidia. As observed by Brefeld in the case of *Heterosphaeria Patella*, the first conidia are often different in form from the original sickle-shaped spores: they are smaller, aseptate, oblong-elliptical, and straight or only slightly curved, and blunt at each end. After the second or third day the primary conidia are replaced by others which are drawn out at the apex and more distinctly curved (Fig. 8, *a*),

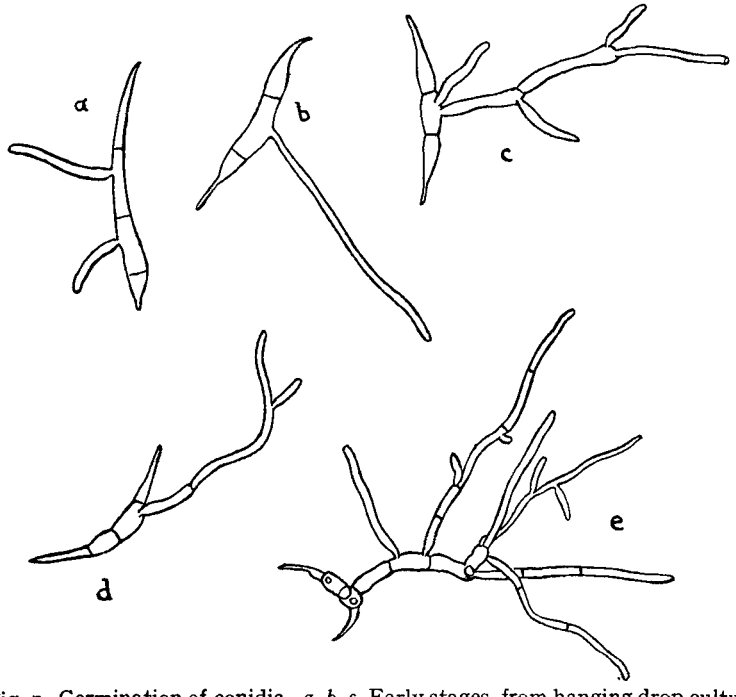

Fig. 7. Germination of conidia. *a*, *b*, *c*, Early stages, from hanging drop culture of *Cercosporella* conidia. *d*, *e*, Later stages, from hanging drop culture of *Heteropatella* conidia.

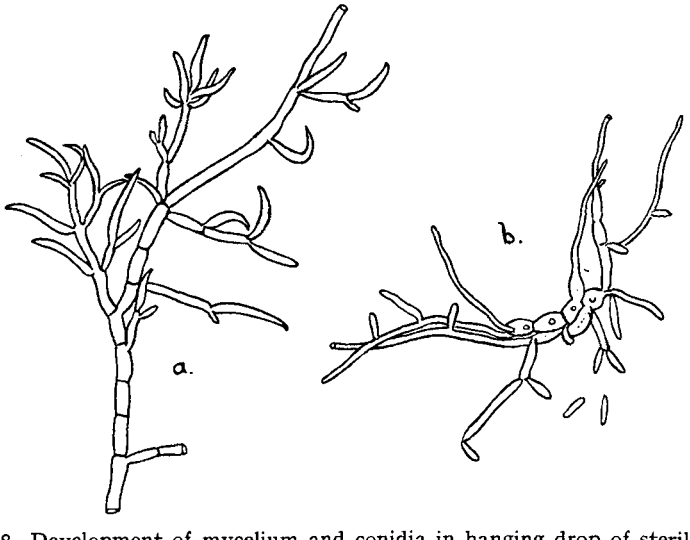

Fig. 8. Development of mycelium and conidia in hanging drop of sterilised antirrhinum extract. *a*, Normal conidia (early stage). (Culture from a *Cercosporella* spore.) *b*, Showing development of simple cylindrical conidia in a medium which is drying out. (Culture from a *Heteropatella* spore.)

while on the fourth day the normal, septate, sickle-shaped conidia are present in great abundance, and when undisturbed remain hanging together in radiating clusters as already described. There appears to be a tendency for the primary form of conidium to be produced especially when the medium is drying out (Fig. 8, *b*).

Taxonomy.

The discovery of a second "imperfect" fructification in the form of pycnidia belonging to the group Excipulaceae raises some interesting questions with regard to this fungus.

The first obvious comparison is with the so-called "winter conidial stage" which was described by Klebahn (7) in the case of *Entomopeziza Soraueri* and *Pseudopeziza Ribis*. In these two species the summer conidial form, in which the conidia are produced as in the Melanconiales, gives place on over-wintered leaves to a pycnidial fructification. Exactly the same type of conidium is produced, but the conidiophores are enclosed in a wall several layers of cells in thickness, at first closed but later widely open and more or less cup-shaped as in the Excipulaceae.

Klebahn later described a similar state of affairs in *Fabraea Fragariae* (8), where actually the winter conidia occur sometimes side by side with asci in an apothecium-like fruit body, and he compared this with the similar development which had been described by Tulasne (9) for *Heterosphaeria Patella*.

A further interesting point is to be noted in connection with *Pseudopeziza Ribis*. In the form of this species occurring on *Ribes Grossularia*, while the winter pycnidia are very freely produced, Klebahn was unable ever to induce the development of the ascigerous stage.

As already mentioned, the winter pycnidia of the antirrhinum fungus agree in character with the genus *Heteropatella*, species of which are known to be conidial stages of the Discomycete *Heterosphaeria*. Consequently an effort was made to find a perfect stage in this also. Up to the present, however, the search has been without success. Neither in culture nor on the old over-wintered Antirrhinum stems and leaves, even though kept under observation for some months, has there been any indication of the formation of asci.

It is, of course, possible that an ascigerous fructification does occur, and that the right conditions for its production have not been found. The various recorded observations on species of *Heterosphaeria* tend to show that the mature ascophore is formed only under specially favourable conditions. Thus Tulasne mentions that the perfect fruit bodies of *Heterosphaeria Patella* occur on the parts of stems nearest the soil, where the moisture

tends to be more constant. Fries held the view that the ascophore (his form *α alpestre* of *Phacidium Patella*) occurs chiefly in subalpine regions because it requires a constantly damp atmosphere*.

On the other hand, it is not unlikely that we have here a species which, in addition to developing the parasitic habit, has lost or is losing the power of developing asci. Klebahn discusses such a possibility in the case of *Fabraea Fragariae*, of which he says: "Nach den vorliegenden Beobachtungen macht *Fabraea Fragariae* den Eindruck eines Pilzes, der im Begriff steht, die Schlauchfruchtbildung zugunsten der Konidienbildung aufzugeben." Still more to the point is the case of *Gloeosporium Ribis* on *Ribes Grossularia* mentioned above, in which the *Pseudopeziza* stage has not been found, although it is known on other species of *Ribes*.

Comparison of the pycnidial stage of the antirrhinum fungus with described species of *Heteropatella* has shown that morphologically there is little or no distinction. All have conidia which average about 18–25 × 3–4 μ without the appendages, and are from one- to three-septate. There are probably greater differences in the characters of the ascophores, but in the absence of the perfect stage it is difficult to say whether the species in question is new or can be referred to one of the others.

It is interesting to note, however, that there is a species, *Heterosphaeria Linariae* (Rabh.) Rehm, with its conidial stage *Heteropatella lacera* Fuck., which grows on the very closely allied host plant *Linaria vulgaris*. A careful comparison of the Antirrhinum *Heteropatella* with dried material of *H. lacera* has shown that morphologically they are very similar. Unfortunately fresh material of *H. lacera* has not been available, but fresh specimens of *Heterosphaeria Patella* on *Heracleum* were obtained at Tintern in April, 1925, and opportunity was taken to make pure cultures of this species. The growth in culture of *H. Patella* is quite different from that of the antirrhinum fungus, and the latter must therefore be regarded as distinct at least from the common species on Umbelliferous stems.

As there has been some confusion with regard to the taxonomy and nomenclature of the species of *Heterosphaeria*, it may be useful to summarise the facts as far as known.

The genus *Heterosphaeria* was proposed by Greville (10) in 1824, for a plant growing on dead herbaceous stems, chiefly of Umbelliferae, which had been called by Persoon *Sphaeria Patella*. Greville recognised that it was an Ascomycete, though

* This may, however, be due merely to the fact that the species of *Heterosphaeria* in general grow best at low temperatures. See notes on temperature relations above.

not a *Sphaeria*, and described the "thecae," but was unable to find spores. Fries(11) in 1828 had apparently observed, but without understanding, the two stages of the fungus. In his *Elenchus Fungorum*, p. 133, he described two forms of what he called *Phacidium Patella*: the first, *α alpestre*, was described as having an apothecium with asci, while the second *β campestre*, was said to differ in remaining closed, and in never forming mature asci. He described the contents of the supposed closed fruit bodies of his *β campestre* as consisting of "sterile filiform asci."

It was left for Tulasne(12) to interpret the life history correctly, and to show that Fries's form *β campestre* was in reality the pycnidial stage, while his *Phacidium Patella, α alpestre* was the perfect stage of the fungus now known as *Heterosphaeria Patella* Grev.

Previous to Tulasne, Bonorden(13) in 1864 had given a full description of the pycnidial stage, referring it to Greville's *Heterosphaeria Patella*, and suggesting that Greville had been in error in thinking his plant an Ascomycete. Subsequently Hazslinzsky(14) proposed the name *Excipula Bonordeni* for Bonorden's fungus, and this has been recently changed by Lind(15) to *Heteropatella Bonordeni*.

Meanwhile the genus *Heteropatella* had been proposed by Fuckel(16) in 1873, with the one species *H. lacera*, said to grow "on dead stems, chiefly of *Linaria vulgaris*." Fuckel supposed it to be "a Discomycete producing only conidia." The following year Winter(17) discovered asci in the *Linaria* fungus, and gave a description of this ascigerous stage under the name *Heteropatella lacera* (Fuck.) Wint. Rabenhorst later gave the name *Peziza Linariae* (changed by Rehm to *Heterosphaeria Linariae*) to this ascigerous stage, rightly reserving the generic name *Heteropatella* for the Excipulaceous conidial stage to which Fuckel's original description applied.

There seems to be little doubt that the species on *Linaria* and on Umbelliferae are distinct from one another. As indicated by Winter, both apothecia and ascospores are slightly smaller in *Heterosphaeria Linariae* than in *H. Patella*. It is obvious from Fuckel's description and from the specimens on *Linaria* distributed by him in his *Fungi Rhenani* no. 2565, that in the event of the two species being regarded as distinct, as they usually are, the name *Heteropatella lacera* should be applied only to the conidial stage of *Heterosphaeria Linariae* (Rabh.) Rehm. In spite of this however the name seems to have been used loosely even quite recently. Thus von Höhnel (*Ann. Myc.* III (1905), p. 552 and *ibid.* XVI (1918), p. 35) speaks of *Heteropatella lacera* as the "young form of *Heterosphaeria Patella*," and Petrak (*Ann. Myc.* XIX (1921), p. 285) has fallen into the same error.

The best and clearest presentation of the common European species is that given by Lind in his *Danish Fungi* (15), where he has the following pairs of forms:

Ascigerous	Conidial
Heterosphaeria Patella Grev.	*Heteropatella Bonordeni* (Hazsl.) Lind.
Heterosphaeria Linariae (Rabh.) Rehm.	*Heteropatella lacera* Fuck.
Heterosphaeria Patella v. *alpestris* Fr.	*Heteropatella cercosperma* (Rostr.) Lind.

With regard to the third species, the conidial stage is that described by Vestergren in detail under the name *Rhabdospora cercosperma* (Rostr.) Sacc. It is obvious from the description and figures that the species is a *Heteropatella*. Vestergren recorded it as growing on numerous plants belonging to very different Natural Orders, in alpine and arctic regions, and for this geographical reason Lind has referred it to Fries's var. *alpestre* of *Heterosphaeria Patella*. It seems probable, however, that the name includes several species, and in view of the fact that Vestergren found temperature relations which agree with those of our Antirrhinum parasite, and may therefore be common to the whole group, it does not appear to be wise to take up the name *alpestris* with no further distinction. Obviously more exact work, with modern methods, is required as to the host relations and cultural characters of the Heterosphaerias.

In conclusion, reference must be made to the parasitic Hyphomycetous stage, *Cercosporella Antirrhini* Wakef., which was the starting point of the present investigation. In none of the known species of *Heterosphaeria* has such a stage been recorded. There is however a fungus which from the published descriptions is suggestively similar. This is a species on *Bupleurum* which was referred to *Heteropatella hendersonioides* Fautr. et Lamb. by Diedicke (18). Fautrey and Lambotte described their fungus on *Bupleurum falcatum* as having a pycnidium, and the spores as having three basal setae, Diedicke found his species on *Bupleurum longifolium*, and rightly or wrongly referred it to the same name. According to Diedicke, however, the structure of his plant is that of the Melanconiales, and not of a *Heteropatella*; that is, it has no pycnidial wall, but produces conidia in a layer covered only by the epidermis. Further, he was never able to see more than one basal appendage.

As every systematist knows, the distinction between the Melanconiales and the Hyphomycetes in certain species is difficult to draw, being a question of degree of development of the sporiferous layer. Diedicke's fungus, which he referred tentatively to *Pestalozzina* (19), is distinctly reminiscent of *Cercosporella Antirrhini*; it may possibly also have been para-

sitic, as it is said to occur "on extensive dry patches on leaves and stems."

It seems possible that the loss of a definite limiting pycnidial wall may be a new development in the life history of *Heterosphaeria* correlated with the adoption of a parasitic mode of life. One may perhaps go further and suggest that the antirrhinum parasite has arisen as an adaptation—a mutation even—from the species *Heterosphaeria Linariae* which occurs on the very closely allied host plant *Linaria vulgaris*, and that with the adoption of the parasitic mode of life it has lost the power to form asci and survives from season to season by means of the winter pycnidia.

Such a supposition would explain why an organism causing such conspicuous injury should yet apparently not have been described until so recently as 1918. It may be mentioned that one attempt has been made to inoculate *Linaria* with the antirrhinum fungus, but without result. It is hoped to do some further work in this direction.

Summary.

The paper records observations on the life history of *Cercosporella Antirrhini* Wakef., described for the first time in 1918 as a parasite of cultivated Antirrhinums.

In pure culture on certain media blackish apothecium-like bodies are produced, which however remain sterile unless transferred to fresh tubes, when they produce conidia.

Similar bodies were found on over-wintered dead stems of Antirrhinums which had shown the disease in the previous summer. These bodies were definitely pycnidial fructifications and were recognised as belonging to the genus *Heteropatella* Fuck.

The connection with the *Cercosporella* was proved by inoculation of living Antirrhinum leaves with conidia from pure culture of the *Heteropatella*, when the characteristic leaf-spots were produced.

No ascigerous stage has as yet been found.

Relationship with *Heteropatella* is further confirmed by the temperature relations of the fungus, which agree with those found by Vestergren for a species identified as *Rhabdospora cercosperma* (Rostr.) Sacc. (= *Heteropatella cercosperma* (Rostr.) Lind).

The optimum temperature lies at approximately 18° C., and no growth takes place at temperatures of 25° C. or higher. The conidia are killed by heating at 41° C. for five minutes in malt extract agar, and after one minute in prune agar.

A discussion of the taxonomy of the genera *Heteropatella* and

its ascigerous stage *Heterosphaeria* is appended, and it is suggested that the *Cercosporella* may be a new development in the life history of *Heterosphaeria* correlated with the adoption of the parasitic habit. The antirrhinum fungus may have arisen as a saltation from *Heterosphaeria Linariae*, which occurs on dead stems of the closely related host plant *Linaria vulgaris*.

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SUPPLEMENTARY NOTE.

By W. Buddin and E. M. Wakefield.

SINCE the foregoing paper was submitted for publication the authors have obtained living material of *Heteropatella lacera* Fuck. through the kindness of Mr A. S. Thomas, B.Sc., who collected it on old stems of *Linaria vulgaris* near Odiham, Hants, in the early spring of this year. Pure cultures of this species have been made, and compared as to growth characters and pathogenicity with those of the Antirrhinum parasite.

Morphologically there is very little distinction between the pycnidia of the two fungi. Those of *H. lacera* are larger ($\frac{1}{2}$ to