

THE BRITISH CAREX RUST FUNGI

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This tentative revision of the rust fungi attacking species of the genus *Carex* in Britain is presented, not in any sense as a complete picture of their taxonomy or as a major contribution to their biology, but rather as a summary of all the collections available for study in the major British herbaria, interpreted in the light of the numerous experiments and observations which have been made on this group in Central Europe and in Scandinavia. No work on the host specialization of these fungi in any way comparable with that of Hasler, Klebahn, Gaumann and Mayor in Central Europe has been carried out in Britain. Similarly, we have nothing comparable to the wealth of observations on the field biology of these fungi on which Jørstad has based his revision of the group in Norway. This situation is all the more regrettable in Britain when it is remembered that some of the most careful early observations and experiments were carried out towards the end of the nineteenth century by C. B. Plowright and a few contemporaries. Moreover, our understanding of these fungi has undoubtedly been retarded by the tendency to label every rust on a *Carex* "*Puccinia caricis*", and leave it at that, except for a few classic "species" recognized in Britain on purely aecidial host relations such as *P. paludosa*, *P. uliginosa* and *P. schoeleriana*, none of whose taxonomic status and relationships were seriously considered. Grove's British Rust Fungi, published in 1913, is certainly most uncritical in its treatment of this group and indeed shows little advance on Plowright's early volume (1889).

As regards the criteria to be used to discriminate taxa and assign ranks to them, there is divergence of opinion between Jørstad's approach and the Swiss-French school exemplified by Gaumann and Guyot whose tendency is to give specific rank to almost every minor morphological variant provided only that it is on a host species distinct from its allies. Nevertheless, this approach has demonstrated that small morphological differences do exist and that often they are correlated with the host specialization pattern of the fungus; it will be apparent in the later part of this paper to what an extent the interpretation of the *Carex* rust fungi in Britain depends upon this type of examination. In contrast to this system is that adopted by Jørstad who insists that specific criteria should be major morphological characters. Nevertheless, his system still faces the major difficulty of how far to spread consideration of the morphology of the fungi, whether to restrict it within host genera or host families. On the whole he comes down in favour of comparisons within host genera although recognizing that the limit is quite arbitrary. For instance, it is quite clear that the *Puccinia confinis-eriophori* group should be considered with the *Carex*-inhabiting *Puccinia* although their dicaryotic stages are on other genera of the Cyperaceae. But the difficulties of this situation become even more apparent if one considers *P. iridis* which is known to alternate between *Iris* and *Urtica*. This species, if one adheres to a classification based on the host family of the dicaryotic stages, should quite obviously

be kept separate from the *Carex* rusts but conversely it cannot be distinguished morphologically from many of the *Carex* rusts and it shares with some of them a common aecidial host, *Urtica*. In this paper I have decided to adopt the specific delimitation used by Jørstad. It is apparent that there are a few clearly defined taxa on Carices principally definable by the number and distribution of the uredospore germ pores. I have not found any morphological character better or more convenient to use than this. As will appear in the later parts of this paper the use of spore measurements is difficult and alone would not produce a classification at specific rank which would bear any relation to the biology of the fungi. The exclusive use of morphology in classifying specialized parasites is fraught with certain difficulties. It is quite obvious that the simpler the structure of the organism one is attempting to classify the fewer the usable morphological characters available. As a result in the classification of the lower and usually morphologically simple organisms recourse is increasingly made to other non-morphological characters—chemical in the bacteria, host relationships in the viruses and many fungi. This recourse is clearly justified for indeed it is fair to suppose that in genetical terms there are more heritable factors involved in determining the close host specificity exhibited, for example by the rust fungi, than are involved in producing small variations in the spore diameters of these fungi. Moreover, host specialization is probably the major evolutionary isolating mechanism permitting differentiation of taxa in specialized parasites. It should be noted, however, that there is no necessity for morphological differentiation to follow a change in host relations. These hypotheses appear to be generally applicable to many specialized parasites and to explain the situation in the *Carex*-rusts. Thus, as Gaumann has quite clearly shown, many of the closely specialized races show small but quite constant morphological differences one from another. The British material certainly supports this finding. Taking the rusts on one *Carex* species it is possible to discriminate the races which Gaumann, Hasler and others have described with some assurance. However, it is equally certain that taking all the *Carex* rusts without regard for the identity of the hosts it is not possible to discriminate all the races which Gaumann has treated at specific rank, but on the contrary only the four major species recognized by Jørstad. I have accordingly recognized Jørstad's specific limits and treated all the races which depend on host identity and minor morphology at varietal rank.

All the descriptions and spore measurements in this work are of British collections. The spore measurements express the range of size of typical spores in all the collections I have seen. They do not include abnormally large or small spores which are best disregarded. So far as possible the identity of the Carices has been checked, usually by comparison of leaf sections, as most mycologists do not seem to have realized that it is of the utmost importance to collect an adequate portion of the host plants for identification.

To the Director of the Royal Botanic Gardens, Kew and to the Keeper of Botany, The British Museum, I am indebted for the loan of collections in their care.

Key to Species

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|---|---------------------|
| 1. Mesospores abundant | <i>P. microsora</i> |
| 1. Mesospores absent or scarce | 2 |
| 2. Uredospores with three or more pores | <i>P. caricina</i> |
| 2. Uredospores with two pores | 3 |
| 3. Pores supra-equatorial | <i>P. dioicae</i> |
| 3. Pores equatorial | <i>P. opizii</i> |

AECIDIAL HOSTS

ASTER. All the collections of aecidia on *Aster tripolium* are from habitats in Southern and Western England where alternation is presumably with *Carex extensa*. This alternation was proved experimentally by Plowright (1889) using infected material from Norfolk. Although the association of *Carex extensa* and *Aster tripolium* extends into Northern Scotland the rust does not appear to be present in the northern part of the range.

CENTAUREA. The only known collections of aecidia on *Centaurea* in Britain are the collections on *Centaurea nigra* of Plowright's *Puccinia arenariicola* (here treated as *P. dioicae* var. *arenariicola*). All the aecidial material in Plowright's herbarium in the British Museum is from inoculation experiments; there is no trace of the material collected in nature from Norfolk (Plowright, 1888).

CIRSIUM. The aecidia on *Cirsium palustre* are quite frequent in Scotland in habitats where the host grows in close association with *Carex dioica*. As Magnus's original description of *P. dioicae* refers to a rust on *Carex dioica* and any infection experiments (Jacky, 1899) have shown only the *Cirsium* race on this sedge it appears reasonable to assume that the *Cirsium* race should in fact be considered the typical variety of *P. dioicae*. In Ireland both *Cirsium palustre* and *C. dissectum* are aecidial hosts.

LACTUCA. Apart from a few recorded cases of infected lettuces being imported, the only records of aecidia are due to Ellis (1950 and 1951) in East Anglia. He showed by experiment that the dicaryon hosts were *Carex paniculata* and *Carex appropinquata* and that *Lactuca virosa* could also serve as a aecidial host for this race, which is undoubtedly *P. opizii*.

PARNASSIA. So far as is known the race on *Parnassia palustris* described by Juel as *Puccinia uliginosa* alternates only with *Carex nigra* and possibly the related species *C. bigelowii* and *C. juncella*. There is field evidence of alternation with only the first-named in Britain. The race is also distinctive in lacking spermogonia and in having relatively short teliospores. From the meagre evidence on these rusts in Britain the distribution of var. *uliginosa* is predominantly northern and montane.

PEDICULARIS. The race forming aecidia on *Pedicularis palustris* was originally described as *Puccinia paludosa*—here treated as *P. caricina* var. *paludosa*—by Plowright (1889). The major host in Britain is undoubtedly *Carex nigra*, a relationship proved by experiments by Plowright himself and by Wilson (1924), although the possibility of other dicaryon hosts cannot be excluded (see Hasler, 1930).

RIBES. Aecidia have been recorded on *Ribes nigrum* L., *R. sanguineum* L., *R. rubrum* agg. and *Ribes uva-crispa* L. (including cultivated forms of

all these species). Only on gooseberries is the rust at all common and with it alternation is probably most frequent with *Carex nigra*, although alternation with several other species of *Carex* has been confirmed experimentally on the continent (Gaumann 1959, for summary). The *Carex nigra*—gooseberry alternation was proved by Soppitt using collections from Lake Windermere (Soppitt, 1898). From examination of the rusted *Carex* material I think it likely that the following races are present in Britain: *P. caricina* var. *caricina*, var. *magnusii*, var. *pringsheimiana*, var. *ribis-nigri-lasiocarpae*, var. *ribis-nigri-paniculatae* and var. *ribesii-pendulae*.

SENECIO. All the collections of aecidia of heteroecious rusts on *Senecio jacobaea* in Britain are from maritime localities and most must belong to *P. dioicae* var. *schoeleriana*, whose dicaryon host is *Carex arenaria*. There is no evidence of the occurrence of a race alternating with *C. acutiformis* as described by Hasler, Mayor and Cruchet (1922). The *P. dioicae* rust on *C. maritima* may well form aecidia on *Senecio jacobaea*, but this race requires investigation.

TARAXACUM. There have been many records and collections of aecidia on *Taraxacum* which have been referred to "*Puccinia silvatica*". However, I find that only one of the collections I have seen rightly belongs there. All the other collections belong to the autoecious species *P. variabilis* Grev. Unfortunately, there has been continued confusion between these two species in the aecidial stage on dandelion largely because the form of the sori was thought to be sufficient to distinguish them. However a much more reliable method is by the presence or absence of spermogonia. These are present with aecidia of *P. dioicae* and absent in *P. variabilis*. Moreover, as Fischer (1904) pointed out many years ago, the peridial cells of *P. dioicae* have the outer wall thicker than the inner, whereas the converse is true for *P. variabilis* (see fig. 2, a & b).

URTICA. In Britain there are undoubtedly several races alternating with *Urtica*. Unfortunately, it appears impossible to identify these in the aecidial states other than by infection experiments or, failing that, by circumstantial field evidence. From the evidence of the collections on *Carices* the following *Urtica*-races seem to be present: *P. caricina* var. *urticae-acutae*, var. *urticae-acutiformis*, var. *urticae-flacca*, var. *urticae-hirtae*, var. *urticae-inflatae*, var. *urticae-ripariae* and var. *urticae-vesicariae*.

CAREX HOSTS

CAREX ACUTA L.

A rust on this host was shown by Soppitt (1898) to belong to a *Ribes* alternating race. I have not traced Soppitt's collections but it should be assigned to *P. caricina* var. *pringsheimiana*.

CAREX ACUTIFORMIS Ehrh.

Carex acutiformis is one of the most commonly rusted sedges in Britain at least to judge from the evidence of mycological herbaria. Of the twenty-six collections examined nearly one-third have uredinia only, so that in many instances the rust is independent of alternation. A few collections give evidence of obligatory heteroecism in their total lack of uredinia.

All the British collections with uredinia have rather characteristic

uredospores (usually over $30\ \mu$ in their greatest diameter) with three and very often four equatorial pores. There is no collection which could be assigned to the continental race *P. senecionis-acutiformis* which belongs to the *P. dioicae* group with two supra-equatorial pores in the uredospores. The large uredospores with often more than three pores also exclude the *Ribes*-alternating *P. magnusii* from consideration, where uredinia are present; but this race may well be present in Britain as it certainly occurs on *Carex riparia*. In uredospore morphology British collections agree perfectly with the variety *urticae-acutiformis* described by Klebahn and shown to be completely restricted to *C. acutiformis* (Hasler, 1945). The formation of aecidia on *Urtica* by the rust on *Carex acutiformis* was demonstrated in field experiments by Grove (1913), who also demonstrated the reciprocal alternation.

CAREX APPROPINQUATA Schum.

The only collections on this host are those made by Ellis (1950) who showed by infection experiments that the fungus produced aecidia on *Lactuca* species and belonged to *Puccinia opizii*.

CAREX ARENARIA L.

The alternation of a race between *C. arenaria* and *Senecio jacobaea* has been known since Plowright's classic experiments recorded in 1885. The race, here reduced to a variety of *Puccinia dioicae*, is quite frequent on sand-dunes in Britain, most commonly on the east coast, but also recorded from the west (Wilson, 1934, p. 393). The uredospores are obviously of the *P. dioicae* type with two supra-equatorial pores and cannot be distinguished from those on *Carex maritima* and *Carex extensa*, and all three maritime rusts obviously form one close-knit group, for they cannot be distinguished from one another in telial characters either. All the uredospores are pale and almost completely smooth and differ from the darker and more markedly echinulate uredospores of *P. dioicae* var. *dioicae* in this minor respect. On *Carex arenaria* telia predominate and it is doubtful if uredo-perennation takes place. *Senecio* plants are often very heavily infected in the vicinity and, next to those on nettle, are some of the most striking aecidial fructifications occurring in Britain.

Plowright also described *Puccinia arenariicola* on *Carex arenaria* and showed that it alternated with *Centaurea nigra*. There have been no records of this race in Britain since that time. I have seen only one specimen originating from Plowright's experiments, the holotype is not present in his herbarium.

CAREX BIGELOWII Torr.

Of the two collections of rust on this host only one bears telia. The host is a mountain plant of exposed slopes usually above 1500 ft. and it is noteworthy that the telial collection is from the shores of Loch Eunach in the Cairngorms one of the less common habitats where the *Carex* grows in company with suitable aecidial hosts. The uredinal collection which is of the *caricina* rather than the *dioicae* type occurs at higher altitudes where alternation with *Urtica*, *Pedicularis*, *Parnassia* or *Ribes* would be hazardous if not impossible. The teliospores of the Loch Eunach collection measure $50-60 \times 18-20\ \mu$ and probably belong to the var. *paludosa*. I have placed the uredinal collection in the same variety with which it agrees entirely

in uredospore characters. Jørstad (1954) has found a similar race in Norway which he suspects may be associated with aecidia on *Pedicularis palustris*.

CAREX BINERVIS Sm.

An obviously uredo-perennating rust, never producing telia, is quite common on this host from the lowlands to over 3000 ft. on the mountains. A similar rust occurs throughout Europe on this host and Jørstad (1954) and Gaumann (1959) both remark on the lack of telia. The spores of all the British collections are obviously very similar and there seems no doubt that they represent one race which has become completely independent of alternation.

A name based on a perfect stage should presumably not been given to such an "imperfect race" if the rules governing fungal nomenclature were strictly followed, but as the purpose of taxonomy is to clarify the relationships of plants and the relation of this race to *P. caricina* is not in doubt I have placed it in *P. caricina* sens. lat. with other similar rusts.

CAREX CAPILLARIS L.

Only one collection on this host is known in Britain and from the preponderance of telia it may well be obligatorily heteroecious at this site in Sutherland. The scanty uredospores are of the *dioicae* type with two supra-equatorial pores. Four races have been described on *C. capillaris*, one of the *caricina* type, *P. urticae-ferrugineae*, and three of the *dioicae* type, *P. capillaris* (alternating with *Bellidiastrum* in Central Europe) *P. jaceae-capillaris* (alternating with *Centaurea* in Central Europe and north to Scandinavia) whose existence in Britain is unlikely as the aecidial host is an uncommon introduced species, and a *Taraxacum*-alternating race corresponding to *P. silvatica* in the broad sense. The Sutherland collection seems most likely to belong to this latter type as there is evidence that aecidia of this group occur in Britain. One collection (Henderson 2793) of aecidia on *Taraxacum officinale* from Ben Lawers, Perthshire certainly belongs to a heteroecious rust of the *Carex* type. The aecidia are accompanied by spermogonia and the outer wall of the peridial cells is thicker than the inner, in contrast to the corresponding cells of the autoecious species *P. variabilis*, where the relative proportions of the cell walls is reversed. In this locality also *Carex capillaris* is quite frequent although to date no rust has been found on it.

CAREX DEMISSA Hornem.

Only one collection has been found on this host, on herbarium specimens of the sedge gathered from Co. Wicklow, Eire. The collection bears telia only. It is probably a *dioicae* type rust similar to the race on *C. lepidocarpa* but in the absence of uredinia it cannot be assigned to any particular variety.

CAREX DIOICA L.

Only a few collections on this host are known, all corresponding morphologically to typical *P. dioicae*. In two collections only uredospores are present so that it may be inferred that uredo-overwintering takes place, just as Jørstad (1954) suggests occurs in Norway. Aecidia are fairly frequent in Scotland on the mountains of Perthshire but so far they have been found only on *Cirsium palustre* not on *C. heterophyllum* or *C. oleraceum* both of which are recorded as hosts abroad. The latter is an uncommon

introduced species and the former is sparsely distributed and can rarely grow in the vicinity of *Carex dioica* in Britain.

CAREX ELATA All.

Only four collections of rust on this host have been found. Two of them have rather large uredospores with very frequently four pores and in this respect closely resemble *P. caricina* var. *urticae-acutiformis*. However this variety has never been recorded as attacking *Carex elata* and *P. caricina* var. *urticae-acutae* which has been recorded on *C. elata* often has rather large uredospores so the collections have been assigned provisionally to this latter variety. The other two collections which have rather spherical, thick-walled uredospores seem referable to *P. caricina* var. *paludosa*. The evidence regarding this host is so scanty that it is probable that other races are present in Britain such as the *Ribes* alternating race described by Hasler (1945) as *P. ribis-nigri-acutae*.

CAREX EXTENSA Good.

C. B. Plowright described *P. extensicola* from Norfolk and showed by experiments that the aecidial stage on *Aster tripolium* was connected with uredinia and telia on *Carex extensa*. This race undoubtedly belongs to the *P. dioicae* group; the uredospores having two slightly or definitely supra-equatorial pores. However, as mentioned under *Carex arenaria* the maritime races form a well-defined group differing slightly from typical *dioicae* in having paler and smoother uredospores. In Britain this variety seems to be confined to southern England. It is absent from Scandinavia but occurs in France (Viennot-Bourgin, 1956).

CAREX FLACCA Schreb.

Usually both uredinia and telia occur on this host but in one collection only uredinia are present representing presumably a uredo-overwintering race. There is no information on the alternation of this rust in Britain but in Switzerland alternation may take place with *Urtica* (*P. urticae-flaccae* Hasl.) or with *Ribes uva-crispa* (*P. ribesii-diversicoloris* Gaum., see Gaumann, 1959). The morphological differences between these races is small but the means of the spore measurements of the British material favours the view that the rust belongs to *P. caricina* var. *urticae-flaccae*.

CAREX HIRTA L.

Uredinia and telia, as well as telia alone, have been collected. The abundance of telia in all the British collections suggests that the race is habitually alternating. The morphology of the spores is remarkably constant in all the collections and only one race *P. caricina* var. *urticae-hirtae* has been recorded for the sedge host. The presence of this race in Britain was demonstrated by Plowright (1889) by the production of aecidia on *Urtica dioica* after exposure to germinating teliospores on *Carex hirta*.

CAREX JUNCCELLA (E. Fr.) Th.Fr.

Only one collection is known on this host in Britain which in Central Europe houses *P. caricina* var. *uliginosa* (Gaumann, 1959) but which in Scandinavia is also a host for typical *P. caricina* (Jørstad, 1954) and is probably a potential host for all the varieties which attack the closely related *C. nigra*. As only telia are present in the British collection it is not possible to assign it with certainty to any race and I have placed it provisionally in *P. caricina* sens lat.

CAREX LAEVIGATA Sm.

Three uredinial collections are known on this host but there is no information on this rust from Central Europe or Scandinavia. It is certainly uredo-perennating and probably related to a uredo race of *P. caricina* recorded in Scandinavia and Central Europe on the closely related host *C. distans*.

CAREX LASIOCARPA Ehrh.

The only British collection on this host bears uredinia and telia and probably alternates. I have placed it in *P. caricina* var. *ribis-nigri-lasiocarpae*, the only race known on this sedge but I have no evidence of the occurrence of aecidia on *Ribes nigrum* in the vicinity.

CAREX LEPIDOCARPA Tausch

The rust on this host appears to be quite common where the host is abundant. It is undoubtedly of the *P. dioicae* type and the same as Jørstad has found in Scandinavia (Jørstad, 1954, under *C. oederi* s. lat.). As in Scandinavia, some collections lack telia and are presumably independent of host alternation whilst others bear them abundantly. Certainly in Scotland this fungus does not alternate with the only known aecidial host of a *Carex flava* group rust—*Serratula tinctoria* (see Hasler, 1921 p. 38). In the two localities where I have seen it in the field the only possible alternate composite hosts were *Cirsium palustre* and *Taraxacum* spp. and on the former aecidia are present in this locality in spring but *Carex dioica* in also heavily rusted in the vicinity. The single collection on *Carex demissa* from Ireland probably belongs to a similar race but uredinia would have to be examined to check the relation to *P. dioicae*.

CAREX MARITIMA Gunn.

This sedge has been found rusted only as herbarium specimens in the phanerogamic herbarium. Both collections were from Morayshire. The uredospores conform to the *P. dioicae* type but the frequency of telia in one collection suggest that the rust alternates, in which case the most likely hosts are *Aster tripolium* (like var. *extensicola*) or *Senecio jacobaea* (like var. *schoeleriana*). In the morphology of the uredospores this collection matches the other maritime varieties of *P. dioicae* perfectly. As var. *extensicola* appears to be confined to southern England the *C. maritima* rust is probably best placed with var. *schoeleriana*.

CAREX NIGRA (L.) Reichard

On this host there occur both obviously alternating rusts represented by telia only, facultatively alternating ones with uredinia and telia and probably uredo-perennating strains with uredinia only. All collections bearing uredinia are of the *P. caricina* group, with usually three, occasionally two or four, equatorial pores. Viennot-Bourgin (1956) lists *C. nigra* as host of *P. dioicae* var. *silvatica* presumably with the *P. dioicae* type uredospores but there is no evidence of the existence of a race of this type in Britain unless some of the telia-only collections belong there.

The telia-bearing collections fall into two fairly sharply defined groups; the one with teliospores mostly within the length range 40–50 μ corresponding to var. *uliginosa* alternating with *Parnassia* which is often heavily infected in the vicinity; the other with teliospores within the range of 50–60 μ long which may belong to a number of races of *P. caricina* alternating with *Pedicularis*, *Ribes* or *Urtica*. One collection (Henderson 2178)

grew near heavily infected *Pedicularis palustris*, and is certainly *paludosa*. Wilson (1924) has demonstrated this host relation experimentally with Scottish material. The presence of *Ribes* alternating races on *C. nigra* was demonstrated by Soppitt (1898) who produced aecidia on gooseberry with telia on *C. nigra*. On the continent the following have been recognized at specific level on *C. nigra*: *P. urticae-acutae* Kleb., *P. uliginosa* Juel, *P. pringsheimiana* Kleb., *P. paludosa* Plow., *P. circaeae-caricis* Hasl., *P. silvatica* Schroet.

There is no evidence of the occurrence of the *Circaea* alternating race in Britain—it appears to be of Central European distribution and does not reach Scandinavia either. None of the British collections with uredospores, as I have already noted, belong to *P. dioicae* var. *silvatica*. The remaining four varieties of *P. caricina* may be keyed out as follows:

- | | |
|--|----------------------------|
| 1. III spores mostly less than 50 μ long | var. <i>uliginosa</i> |
| 1. III spores mostly more than 50 μ long | 2 |
| 2. II spores mostly more than 25 μ in greatest diameter | 3 |
| 2. II spores spherical less than 25 μ in greatest diameter | var. <i>pringsheimiana</i> |
| 3. II spore wall not exceeding 2 μ in thickness | var. <i>urticae-acutae</i> |
| 3. II spore wall 2.5–3 μ thick | var. <i>paludosa</i> |

This key, however, is in no sense foolproof. It is in many cases impossible, especially when one spore stage only is present and there are no field notes to give a clue as to possible aecidial hosts, to decide with complete certainty to which race a given collection belongs. The present disposal of the British collections on this host, and this key, must therefore be used with these cautions in mind. For example, var. *uliginosa* is fairly well characterized by relatively short teliospores but its almost spherical uredospores cannot be distinguished with complete assurance from those of var. *pringsheimiana*. Similarly, it is not possible to separate the other races entirely on the basis of uredospore morphology. The most distinctive of all the varieties in the uredo-stage is var. *paludosa* with rather small thick-walled spores. As regards teliospores, continental authors give the impression that var. *uliginosa* is easily separable from the others in teliospore length but this criterion cannot be used absolutely, for some of Plowright's type material of var. *paludosa* from Norfolk with small sori has teliospores 44–47 μ long, just as short as typical var. *uliginosa*. Nevertheless, where uredospores are present these two races are distinguishable and it is true that in most collections which are certainly var. *paludosa* from their host relations in the field a high proportion of the teliospores exceed 50 μ , whereas in the collections of var. *uliginosa* I have seen this is not so.

I am far from satisfied that var. *pringsheimiana* and var. *urticae-acutae* are clearly distinct morphologically and there is no information with any of the collections to assist in determining the aecidial hosts. The only course I have been able to follow is to assign the collections with globose spores to var. *pringsheimiana* and those with elliptic-oblong spores to var. *urticae-acutae*. Of course it is quite possible that some races exist largely independent of any host alternation and hence should not be associated with any of the varieties but this can only be learnt by more extensive field observations coupled with infection experiments.

CAREX OVALIS Good.

This host is quite commonly rusted with a uredo-perennating rust of the *P. dioicae* type bearing uredinia only. Jørstad (1954) has recorded a similar rust in Norway with sparse telial production. He suggested a relation to *P. jaceae-leporinae*. In Central Europe two species of this group are recognized; *P. jaceae-leporinae* (*Carex ovalis* and *Centaurea* spp. including *C. cyanus*) and *P. caricis-montanae* (*Carex montana* and *C. ovalis* as chief hosts and *C. alba* and *C. umbrosa* minor hosts and aecidia on *Centaurea* spp. including *C. cyanus*, *jacea*, *nigra* and *scabiosa*) (Gaumann, 1959). According to Gaumann (1959) the races cannot be distinguished in the uredinial stage. The lack of alternating strains in Britain is probably explained by the rarity with which suitable aecidial hosts grow in the vicinity of *Carex ovalis*. The British collections are assigned to *Puccinia dioicae* sens. lat.

CAREX PAIRAEI F. Schultz

Three British collections on this host are known, two from old collections in the Edinburgh phanerogamic collections. They are all typical *P. opizii* with usually two, occasionally three, equatorial pores. The thickness of the apical caps of the teliospores are less than those described by many continental authors (Gaumann (1959) gives 11–18 μ ; Viennot-Bourgin (1956) gives 14–18 μ) but an isotype in herb. BM. (Rabh. Fungi Eur. 4422) agrees completely with the British collections in having apices usually 6–10 μ only rarely up to 14 μ in thickness.

CAREX PALLESCENS L.

The rusts on this host in Britain are all in the uredo state only and from their close morphological homogeneity belong obviously to one race. The uredospores have two or three equatorial pores, most frequently only two, and are therefore somewhat different from the usual *caricina* type as is also noted by Jørstad (1954). In Scandinavia the rust is also predominantly uredosporic but a few telia also occur. This race may well be that described by Tranzschel (1910)—often referred to as *P. urticae-pallescentis* Tranz., a name which has never been validly published—for which the correct name may be *P. urticae-ferrugineae* Gaumann. Provisionally the British collections are referred to *P. caricina* sens. lat., but its possible relationship to *P. opizii* should be borne in mind.

CAREX PANICEA L.

All but one of the collections on this host bear uredinia only and are presumably independent of host alternation. Two races have been described as occurring on *Carex panicea*, *P. urticae-paniceae* and *P. paludosa*; the latter with subglobose uredospores.

The British collections have uredospores mostly subglobose with a range of 24–27 \times 22–26 μ and thus agree more closely with var. *paludosa* to which I have assigned them. The race *urticae-paniceae* is known so far only from Switzerland where its specialization has been worked out by Mayor (1949). The one telial collection may belong to this *Urtica* alternating race, as Jørstad (1954) has suggested for the few telial collections he found in Norway, but in the absence of uredospores or experimental results the evidence is too slender to assign it there at present.

CAREX PANICULATA L.

At present the rusts on *C. paniculata* and the closely related *Carex appropinquata* present some problems. Ellis (1951) has shown that in

Norfolk both these sedges may house rusts capable of infecting and producingaecidia on cultivated lettuce (*Lactuca sativa*) and on *Lactuca virosa*. He has also demonstrated the alternation from infected *Lactuca* to sedge. Examination of the several collections on these two sedge hosts, however, showed that only a few seemed to belong to *Puccinia opizii* the species to which Ellis quite correctly assigned his experimental material. *Puccinia opizii* has been somewhat confused in the literature and is unusual in having a rather extensive host range, as far as can be judged from accounts of infection experiments which have been conducted with it. However, it stands apart from both major sedge rusts, *P. caricina* and *P. dioicae*, in having only two, very rarely three, equatorial pores in the uredospore. This feature is confirmed by examination of Bubak's isotype material mentioned in the second part of this paper. Much of the confusion of *P. opizii* has been due to the inclusion of descriptions of other rusts in the accounts of this species. Only three collections from Norfolk seem to belong to *P. opizii*. In Norfolk and throughout Britain there also occurs another rust on *P. paniculata* often with uredospores only. This race undoubtedly uredo-perennates and is placed in *P. caricina* var. *ribis-nigri-paniculatae*.

CAREX PENDULA L.

There appears to be only one common rust on *Carex pendula* in Britain with rather uniformly large elliptic-oblong uredospores with three equatorial pores and large teliospores. Fully half of the collections I have seen have only uredospores so the race is often independent of host alternation.

On the continent two races have been demonstrated on *C. pendula*, *P. ribesii-pendulae* and *P. petasites-pendulae*. The latter, in common with other composite alternating rusts, has only two pores in the uredospores whereas the former, to which I have assigned all the British material, has three.

CAREX PSEUDOCYPERUS L.

In Britain there are two varieties of *P. caricina* on this host a position agreeing with the findings of continental investigators. These are var. *urticae-acutiformis* and var. *caricina*. The former, which otherwise occurs only on *Carex acutiformis*, forms only uredospores on *C. pseudocyperus* and these are quite characteristic; relatively large, $30-34 \times 24-28 \mu$, and with three, often four equatorial pores. Four collections belong to the former whilst those with telia I have placed under var. *caricina*. This disposition is strongly supported by the fact that in all the collections with uredospore only the uredospores are large whilst the few telia collections which have uredinia have small uredospores ($26-28 \times 18-20 \mu$) within the range of var. *caricina*.

CAREX RIPARIA Curt.

I have been able to find only five collections on this host, one of them with uredospores only, collected in Ireland. In two of the remainder, those from Cheshire and Edinburgh, the teliospores are larger ($58-70 \times 16-21 \mu$) than the limits given by Gaumann (1959) ($37-56 \times 15-21 \mu$) for the *Ribes* alternating var. *magnusii* and almost certainly belong to var. *urticae-ripariae*. The other two collections both from Gloucestershire appear to belong to the *Ribes* race var. *magnusii* which also infects *C. acutiformis*.

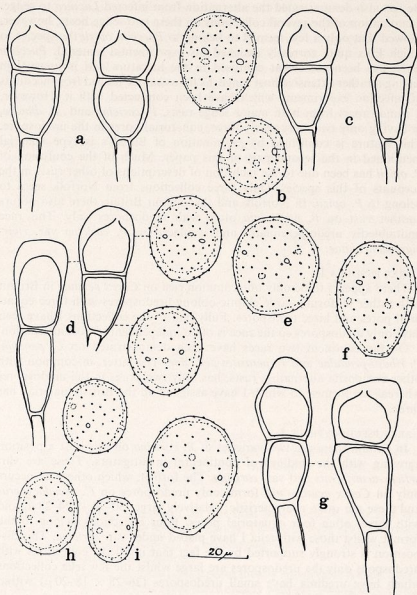


FIG. 1. Uredospores and teliospores of *Puccinia caricina*.
 a, var. *caricina*. b and c, var. *paludosa*. d, var. *uliginosa*. e, var. *urticae-acutae* (II only).
 f and g, var. *urticae-acutiformis*. h, *P. caricina*, sensu lato, on *Carex binervis* (II only).
 i, *P. caricina*, sensu lato, on *Carex pallescens* (II only).

CAREX ROSTRATA Stokes

Rust on this host is relatively common and usually bears abundant telia suggestive of frequent alternation and probably represents the var. *urticae-inflatae* although no infection experiments have been carried out with it in Britain. Certainly, however, if abundant telial production is indicative of obligatory alternation this race must behave so. Infection must spread over considerable distances, however, for *Carex rostrata* bearing heavy telial infection often occurs considerable distances from the nearest *Urtica*.

The telia and uredinia on this host occur almost exclusively on the upper surfaces of the leaves and Gaumann (1959) has pointed out that this is correlated with the stomata being largely restricted to this surface. Hasler's (1925) experiments with this race has demonstrated its complete specialization to *Carex rostrata*.

CAREX VESICARIA L.

Abundant rust was collected on this host at Aviemore, Scotland in 1959. The small hypophyllous sori containing abundant uredospores, a few small teliospores and abundant mesospores agree exactly with *P. microsora*, a distinctive species whose alternation is unknown. *Carex vesicaria* is a somewhat uncommon sedge and scrutiny of the host material of this species in the Edinburgh Herbarium has yielded only two other rusted specimens—from Killin, Perthshire, and Sussex. These collections, however, contain uredospores and teliospores only and probably represent the race *P. caricina* var. *urticae-vesicariae* which has been recorded in continental Europe on this host and whose complete host specialization to *Carex vesicaria* has been demonstrated by Klebahn (1907), Eriksson (1920) and Hasler (1945).

TAXONOMIC TREATMENT

***Puccinia caricina* DC., Fl. Fr. v, 60 (1815).**

var. ***caricina***

Syn.: *P. ribesii-pseudocyperi* Kleb. in Jahrb. Wiss. Bot. xxxiv, 391 (1900).

Type: on *Carex pseudocyperus*; France.

Uredospores $26-28 \times 18-20 \mu$ with three equatorial pores; teliospores $45-52 \times 18-20 \mu$, apex $6-8 \mu$.

On *Carex pseudocyperus* L.

II & III. ENGLAND: Vize, Micro-Fungi Exs. 121 (K); Brooke Mill, Norfolk, April 1954, Dennis (K—Fig. 1a).

III only. ENGLAND: Byfleet, Surrey, June 1947, Burt B113 (E).

***Puccinia caricina* var. *magnusii* (Kleb.) Henderson, comb. nov.**

Basionym: *P. magnusii* Kleb. in Zeitschr. f. Pflanzenkr. v, 79 (1895).

Type: on *Carex riparia*, Germany.

Uredospores $24-30 \times 20-22 \mu$ with three equatorial pores; teliospores $50-60 \times 18-21 \mu$, apex $6-10 \mu$.

On *Carex riparia* Curt.

II and III. ENGLAND: near R. Leadon, Gloucs., Aug. 1944, *Sprague* (K).

II only. IRELAND: Limerick, *Somerville* (E).

III only. ENGLAND: West of Yate Rocks, Gloucs., Dec. 1954, *Garlick* (K).

***Puccinia caricina* var. *paludosa* (Plow.) Henderson, comb. nov.**

Basionym: *Puccinia paludosa* Plow., Brit. Uredineae and Ustilagineae, 174 (1889).

Type: on *Carex nigra*, Irstead, Norfolk, England.

Uredospores broadly elliptic to subglobose $22-26 \times 20-24 \mu$, wall $2-3 \mu$ thick, with three equatorial pores; teliospores $44-62 \times 17-22 \mu$, apex $8-10 \mu$ thick.

On *Carex nigra* (L.) Reich.

II and III. ENGLAND: Irstead, Norfolk, *Plowright*, Sydow Ured. 327 (K). SCOTLAND: Loch Pityoulish, Inverness-shire, Sept. 1959, *Henderson* 4819 (E); Taynuilt, Argyllshire, July 1921, *Wilson* (E).

III only. ENGLAND: Irstead, Norfolk, June 1934, *Ellis & Rhodes* (K, BM). Irstead, Norfolk, *Vize* Micro-Fungi Brit. 557 (K, BM, holo., Fig. 1c). WALES: Barmouth, Merioneth, April 1933, *Grove* (BM). SCOTLAND: Lumphanan, Aberdeenshire, Oct. 1922, *Wilson* (E).

II only. ENGLAND: Irstead, Norfolk, *Plowright*, *Vize* Micro-Fungi Brit. 570 (BM). SCOTLAND: Glen Uig, Inverness-shire, I on *Urtica* associated on beach shingle. July 1957, *Dennis* (K—fig. 1b).

On *Carex panicea* L.

III only. ENGLAND: Hyde Green, Essex, Dec. 1955, *Garlick* (K).

II only. ENGLAND: Highgate, Middlesex. *Herb. Cooke* (E, on "*C. flacca*"); Durdham Downs, Bristol, July 1955, *Garlick* (K); Bookham Common, Surrey, July 1947, *Sandwith* (K). SCOTLAND: West Kilbride, Ayrshire, July 1921, *Boyd* (BM); Inchadamph, Sutherland, July 1955, *Davis* (E); Ben Lui, Argyll, 1300 ft., Sept. 1959, *Henderson* 4725 (E); Creag an Lochan, Loch Tay, Perthshire, Aug. 1953, *Henderson* 921 (E).

On *Carex elata* All.

II only. ENGLAND: Ruston Fen, Norfolk, July 1933, *Dennis & Ellis* (K).

On *Carex bigelowii* Torr.

III only. SCOTLAND: East shores of Loch Eunach, Aviemore, Inverness-shire, July 1892, *Somerville* (E).

II only. SCOTLAND: West Corrie, Cairngorm, Aviemore, Inverness-shire, July 1893, *Somerville* (E).

On *Pedicularis palustris* L.

O, I. ENGLAND: Irstead, Norfolk, 20 June 1888, *Plowright* (BM); *ibid.*, *Vize* Micro-Fungi Brit. 555 (BM); Dilham, Norfolk, May 1866, *Cooke*, Brit. Fungi Exs. 105 (BM); Irstead, Norfolk, June 1934, *Ellis* (BM); *ibid.*, June 1934, *Ellis & Rhodes* (K). SCOTLAND: North-East Scotland, June 1874, *Ferguson*, *Vize* Fungi Brit. 168 (BM); Rothiemurchus, Inverness-shire, July 1907, *Herb. Grove* (BM); Kincardineshire, 1876, *Ferguson*

(BM); Kinloch, Isle of Rhum, July 1951, *Dennis* (K); Glen Lyon, Perthshire, 400 ft., in *Carex nigra* marsh, June 1956, *Henderson* 2778 (E); Lumphanan, Aberdeenshire, July 1922, *Wilson* (E); Taynult, Argyllshire, July 1921, *Wilson* (E); Ballindalloch, Banffshire, July 1936, *Mackenzie* (E).

***Puccinia caricina* var. *pringsheimiana* (Kleb.) Henderson, comb. nov.**

Basionym: *P. pringsheimiana* Kleb. in Zeitschr. f. Pflanzenkr. v, 79 (1895).

Type: on *Carex nigra*, Germany.

Uredospores subglobose $20-25\ \mu$ diameter, wall $2\ \mu$ thick; teliospores $50-75 \times 15-20\ \mu$, apex $5-8\ \mu$ thick.

On *Carex nigra* (L.) Reichard

II & III. SCOTLAND: Strathnaver, Sutherland, Sept. 1954, *Dennis* (K).

II only. SCOTLAND: Kintail, W. Ross, Aug. 1933, *Wilson* (E).

On *Carex acuta* L.

Recorded by Soppitt (1898), who demonstrated the alternation experimentally with material from Windermere.

***Puccinia caricina* var. *ribis-nigri-lasiocarpae* (Hasler) Henderson, comb. nov.**

Basionym: *P. ribis-nigri-lasiocarpae* Hasler in Ann. Mycol. xxviii, 350 (1930).

Type: on *Carex lasiocarpa* between Muri and Bünzen, Switzerland. Uredospores $28-30 \times 22-24\ \mu$ with 2-3 equatorial pores; teliospores $40-50 \times 20-22\ \mu$, apex $4-5\ \mu$.

On *Carex lasiocarpa* Ehrh.

II & III. SCOTLAND: Loch Pityoulish, Inverness-shire, Sept. 1959, *Henderson* 4820 (E).

***Puccinia caricina* var. *ribis-nigri-paniculatae* (Kleb.) Henderson, comb. nov.**

Basionym: *P. ribis-nigri-paniculatae* Kleb. in Jahrb. Wiss. Bot. xxxiv, 393 (1900).

Type: on *Carex paniculata*, Triglitz, Germany, *Jaap*.

Uredospores $26-30 \times 17-20\ \mu$ with three equatorial pores; teliospores $45-60 \times 18-20\ \mu$.

On *Carex paniculata* L.

II & III. ENGLAND: Wheatfen, Norfolk, *Wilson* (E); Wheatfen, Norfolk, June 1957, *Dennis* (K). SCOTLAND: Resteneth Bog, Angus, Oct. 1944, *Duncan* (E); Crichton, Midlothian, Oct. 1959, *Henderson* 4857 (E); Luffness Marsh, W. Lothian, July 1902, *Evans* (E).

II only. ENGLAND: Wheatfen, Norfolk, Aug. 1959, *Dennis* (K); Amberley, Sussex, June 1951, *Burt* (E).

***Puccinia caricina* var. *ribesii-pendulae* (Hasler) Henderson, comb. nov.**

Basionym: *P. ribesii-pendulae* Hasler in Ber. Schweiz. Bot. Ges. lv, 15, (1945).

Type: on *Carex pendula* L., "auf dem Bruggerberg", Switzerland.

Uredospores $26-32 \times 20-26 \mu$ with three equatorial pores; teliospores $42-54 \times 18-21 \mu$, apex $6-10 \mu$.

On *Carex pendula* L.

II & III. ENGLAND: Cumnor Hill, Berks., April 1944, *Burns* (E); Rodford, Gloucs., no collector (K). Monkswood, Hunts., Sept. 1954, *Dennis & Gilbert* (K); Studley, Warwickshire, Oct. 1910, *Grove* (BM); Barton Green, Aug. 1883, *Grove* (BM). SCOTLAND: Cadzow, Hamilton, Lanarkshire, Sept. 1959, *Henderson* 4686 (E).

II only. ENGLAND: Wyre Forest, Aug. 1939, *Wilson* (E); near Taunton, Somerset, Sept. 1911, *J. Ellis* (K); Shrawley Woods, Worcs., Aug. 1957, *Sandwith* (K); Bishops Wood, May 1864, *Cooke* (BM, K); Highgate, *Cooke*, Fungi Brit. Exs. II, 317 (K, BM); Chislehurst, Kent, 1855 (K); Malham, Yorks., 1901, *Crossland* (K); Isle of Wight (K); Bewdley, Worcs., Aug. 1907, *Grove* (BM); Taunton, Somerset (BM); Hampstead, June 1864, *Cooke*, Fungi Brit. Exs. 67 (BM); Blaise Castle, Bristol, Gloucs., Sept. 1955, *Henderson* 2262 (E). SCOTLAND: Roslin, Midlothian, June 1946, *Wallace* (E). IRELAND: Cahir River, Co. Clare, July 1958, *Henderson* 4035 (E).

III only. ENGLAND: no loc., *Herb. Cooke* (K); Bishops Wood, May 1864, *Cooke* (K, BM); Barford, Nov. 1927, *Grove* (BM).

Puccinia caricina* var. *uliginosa (Juel) Jørst. Skr. Vidensk.-Akad. Oslo, i, 1951, 30 (1952).

Basionym: *P. uliginosa* Juel in Ofvers. Vet.-Akad. Förh. 410 (1894).

Type: on *Carex nigra*, 'im Gudbrandsdal und Baeverdal in Norwegen'.

Uredospores $20-24 \times 21-23 \mu$, wall 2μ thick, with three equatorial pores; teliospores $34-50 \times 15-22 \mu$, apex $4-8 \mu$ thick.

On *Carex nigra* (L.) Reichard.

II & III. SCOTLAND: Taynult, Argyllshire, Sept. 1942, *Wilson* (E—Fig. 1d).

III only. SCOTLAND: Ben Lui, Perthshire, 1200 ft., with *Parnassia*, Aug. 1953, *Henderson* 913 (E); Thornhill, Dumfriesshire, *Wilson* (E); Cyradale, Orkney, Aug. 1888, *Trail* (BM).

On *Parnassia palustris* L.

I only. SCOTLAND: New Pitsligo, Aberdeenshire, June 1874, *Ferguson* (BM); Berwickshire, *Johnston* (K); Glen Sloy, Dunbartonshire, June 1915, (E); Taynult, Argyllshire, July 1921, *Wilson* (E); Lumphanan, Aberdeenshire, July 1922, *Wilson* (E); Ben Nevis range, Inverness-shire, Aug. 1922, *Pealling* (E); Ben Lui, Argyllshire, 1200 ft., growing with rusted *Carex nigra* Aug. 1953, *Henderson* 912 (E); about Glasgow, 1823, *Greville* (E).

Puccinia caricina* var. *urticae-acutae (Kleb.) Henderson, **comb. nov.**

Basionym: *P. urticae-acutae* Kleb. in Zeitschr. f. Pflanzenkr. ix, 152 (1899).

Type: on *Carex acuta*, "on experimental plants", Germany, *Klebahn*.

Uredospores $25-34 \times 25-30 \mu$ with three equatorial pores, wall $1-2 \mu$ thick; teliospores $48-60 \times 20-22 \mu$, apex $8-12 \mu$ thick.

On *Carex nigra* (L.) Reichard

II & III. SCOTLAND: Loch Lundie, Inverness-shire, Sept. 1942, *Duncan* (E—Fig. 1e); Glenshee, Perthshire, 1000 ft., Aug. 1955, *Henderson* 2178 (E).

III only. ENGLAND: Lowe Woods, Gloucs., *Garlick* (K). SCOTLAND: Inshriach, Aviemore, Inverness-shire, Sept. 1959, *Henderson* 4812 (E); Thriepmuir, Midlothian, Nov. 1959, *Henderson* 4798 (E); Achnasheen, Ross-shire, Oct. 1946, *Dennis* (K). IRELAND: Clare Is., Co. Mayo, 1910 (BM).

II only. SCOTLAND: Avelochan, Inverness-shire, Aug. 1955, *Milne* (E).

On *Carex elata* All.

II & III. ENGLAND: Wheatfen, Norfolk, Aug. 1959, *Dennis* (K).

II only. ENGLAND: Oswestry, Salop, *Salwey* (K).

***Puccinia caricina* var. *urticae-acutiformis* (Kleb.) Henderson, comb. nov.**

Basionym: *P. (urticae-) caricis* f. *urticae-acutiformis* Kleb. in Zeitschr. f. Pflanzenkr. xv, 70 (1905).

Type: on *Carex acutiformis*, Triglitz, Germany, *Jaap*.

Uredospores $30-38 \times 24-30 \mu$ with three or four equatorial pores; teliospores $50-60 \times 18-22 \mu$, apex $8-10 \mu$.

On *Carex acutiformis* Ehrh.

II & III. ENGLAND: nr. Birmingham, 1911, *Grove* (BM); Solihull, 1906, *Grove* (BM); Pickering, Yorks., Aug. 1959, *Bramley* (E); Wheatfen, Norfolk, Aug. 1949, *Wilson* (E); Lincs., *Woodruffe-Peacock*, Herb. Crossland (K); Barnton-on-Humber, Yorks., June 1911, *Herb. Crossland* (K); Colney Hatch, July 1864, *Cooke* (K). SCOTLAND: Crichton, Midlothian, Aug. 1930, *Wilson* (E); *ibid.*, Oct. 1959, *Henderson* 4858 (E—fig. 1g).

III only. ENGLAND: Solihull, Birmingham, May 1911, *Grove* (BM); *ibid.*, Aug. 1906 (BM); Studley Castle, Warwickshire, Oct. 1905, *Grove* (BM); *ibid.*, Sept. 1906 (BM); Halifax, Yorks., Feb. 1911, *Grove* (BM); Istead, Norfolk, 1864, *Cooke*, Brit. Fungi Exs. 634 pro parte (K, E.)

II only. ENGLAND: Flatford Mill, Suffolk, June 1956, *Fletcher* (E); Lower Hilcot, Gloucs., June 1944, *Sprague* (K); Wheatfen, Norfolk, June 1957, *Dennis* (K); (near infected *Urtica*), Kings Langley, Herts., *Reid* (K); Tottenham, Middlesex, 1864 (K); Shirley Park, Yorks., *Crossland* (K); Walton Moor, Somerset, Sept. 1953, *Sandwith* (K—fig. 1f); Solihull, 1908, *Grove* (BM); Hampstead, London, *Cooke*, Fungi Brit. 67 (K).

On *Carex pseudocyperus* L.

II only. England: Fulbourne, Cambs., (E); Plym Bridge, Devon, 1886, *Nore* (E); near Snaith, Yorks., *Cooke* (K); Eastham Rake, Ches., Aug. 1911, *Ellis* (K).

***Puccinia caricina* var. *urticae-flacca* (Hasl.) Henderson, comb. nov.**

Basionym: *P. urticae-flacca* Hasl. in Ber. Schweiz. Bot. Ges. Iv, 6 (1945).

Type: on *Carex flacca* "in der Nahe des Oschinensees in Berner Oberland", Switzerland.

Uredospores $24-30 \times 20-24 \mu$, wall 2μ thick with three equatorial pores; teliospores $40-50 \times 17-21 \mu$, apex $5-8 \mu$.

On *Carex flacca* Schreb.

II & III. ENGLAND: Pickering, Yorks., Aug. 1952, *Bramley* (E). SCOTLAND: Ben Lui, Perthshire, 2500 ft., Aug. 1953, *Henderson* 919 (E); *ibid.*, 1300 ft. Sept. 1959, *Henderson* 4734 (E); Creag an Lochan, Lawers, Perthshire, 2200 ft., Sept. 1959, *Henderson* 4775 (E); Kishorn, Ross-shire, Oct. 1959, *Henderson* 4914 (E).

III only. SCOTLAND: Strome, Ross-shire, Oct. 1959, *Henderson* 4882 (E).

II only. ENGLAND: Randan Woods, Sept. 1904, *Herb. Grove* (BM). SCOTLAND: Taynuilt, Argyllshire, July 1921, *Wilson* (E); Ben Lui, Argyllshire, Sept. 1959, *Henderson* 4725 (E). IRELAND: Lucan, Dublin, Oct. 1911, *Herb. Grove* (BM).

***Puccinia caricina* var. *urticae-hirtae* (Kleb.) Henderson, comb. nov.**

Basionym: *P. urticae-hirtae* Kleb. in Zeitschr. f. Pflanzenkr. ix, 152 (1899).

Type: on *Carex hirta*, Niendorf near Hamburg, Germany.

Uredospores $26-28 \times 18-20 \mu$ with three equatorial pores; teliospores $45-67 \times 18-24 \mu$, apex $8-11 \mu$.

On *Carex hirta* L.

II & III. ENGLAND: Spar Pools, Yate, Gloucs., Aug. 1955, *Garlick* (K); Epsom, Surrey, May 1916, *Wilson* (E). SCOTLAND: Arbroath, Angus, *Duncan* (E); Gullane, E. Lothian (close to infected *Urtica dioica*), Aug. 1929, *Wilson* (E).

III only. ENGLAND: Bookham Common, Surrey, Oct. 1949, *Castell* (BM); Hadzow, Nov. 1929, *Herb. Grove* (BM). SCOTLAND: Peasedean, Berwickshire, May 1929, *Wilson* (E). IRELAND: Cashel, Tipperary, Sept. 1911, *Herb. Grove* (BM).

***Puccinia caricina* var. *urticae-inflatae* (Hasl.) Henderson, comb. nov.**

Basionym: *P. urticae-inflatae* Hasler in Mitt. Aarg. Naturf. Ges. xvii, 64 (1925).

Type: on *Carex rostrata*, Muri, Switzerland.

Uredospores subspherical $26-28 \times 23-26 \mu$, wall 2μ thick, with three equatorial pores; teliospores $50-65 \times 18-21 \mu$, apex $7-9 \mu$.

On *Carex rostrata* Stokes

II & III. SCOTLAND: Stormont Loch, Perthshire, Sept. 1959, *Henderson* 4753 (E); Douglaston, Dunbartonshire, Sept. 1959, *Henderson* 4629 (E).

III only. ENGLAND: Buxton Heath, Norfolk, (as *P. dioicae*, aecidia abundant on *Cirsium palustre* in vicinity), June 1934, *Rhodes* 5495 (BM). SCOTLAND: Thriepmuir, Balerno, Midlothian, Oct. 1955, *Henderson* 239 (E); Stormont Loch, Perthshire, July 1953, *Henderson* 805 (E); Reseneth Bog, Angus, Oct. 1944, *Duncan* (E); Loch Insh, Inverness-shire, Oct. 1959, *Henderson* 4873 (E).

II only. SCOTLAND: Inschriach, Aviemore, Inverness-shire, Sept. 1959, *Henderson* 4813 (E).

***Puccinia caricina* var. *urticae-ripariae* (Hasl.) Henderson, comb. nov.**

Basionym: *P. urticae-ripariae* Hasler in Ber. Schweiz. Bot. Ges. lv, 8 (1945).

Type: on *Carex riparia*, "between St. Louis and Neudorf on the Rhine below Basle", Germany.

Teliospores only in British collections, $58-70 \times 16-21 \mu$, apex $8-12 \mu$.

On *Carex riparia* Curt.

III only. ENGLAND: Meols, Cheshire, Feb. 1914, *J. Ellis* (K). SCOTLAND: Duddingston, Edinburgh, no collector (K).

***Puccinia caricina* var. *urticae-vesicariae* (Kleb.) Henderson, comb. nov.**

Basionym: *P. (urticae-) caricis* f. sp. *urticae-vesicariae* Kleb. in Zeitschr. f. Pflanzenkr. xv, 70 (1905).

Type: on *Carex vesicaria*, Triglitz, Germany, *Jaap*.

Uredospores $28-30 \times 18-20 \mu$ with three equatorial pores; teliospores $40-46 \times 18-20 \mu$, apex $4-6 \mu$ thick.

On *Carex vesicaria* L.

III only. ENGLAND: Sussex, Nov. 1934, *Herb. Grove* (BM); Goosehill Woods, Yorks., *Herb. Grove* (E).

II only. SCOTLAND: Finlarig Woods, Killin, Perthshire, *Somerville*, (E).

***Puccinia caricina* DC. sens. lat.**

On *Carex binervis* Sm.

Uredospores $26-34 \times 20-23 \mu$, wall 2.5μ thick, with three equatorial pores.

II only. ENGLAND: Otley, Yorkshire, Aug. 1885, *Soppitt* (BM). SCOTLAND: Hermaness, Unst, Aug. 1952, *Dennis* (K); Loch Rannoch, Perthshire, July 1957, *Dennis* (K); Cairngorm, near summit, Inverness-shire, Sept. 1957, *Reid* (K); Lumphanan, Aberdeenshire, July 1922, *Wilson* (E); Ballindalloch, Banffshire, Apr. 1937, *Wilson* (E); Taynuilt, Argyllshire, July 1921, *Wilson* (E); Glen Clova, Angus, Nov. 1944, *Duncan* (E); Creag an Lochan, Loch Tay, Perthshire, 2200 ft., Sept. 1959, *Henderson* 4766 (E); *ibid.*, Aug. 1953, *Henderson* 900 (E); Benmore Garden, Argyllshire, Sept. 1959, *Henderson* 4711 (E—fig. 1h); Plockton, W. Ross, June 1955, *Henderson* 2042 (E); Kishorn, W. Ross, 2500 ft., Oct. 1959, *Henderson* 4901 (E).

On *Carex laevigata* Sm.

Uredospores $24-26 \times 20-22 \mu$, wall $2-2.5 \mu$ thick, with three equatorial pores.

II only. ENGLAND: Newton Ferrers, Cornwall, June 1931, *Hurst* (BM); La Salina, Jersey, June 1934, *Hall* (E). SCOTLAND: Blackwaterfoot, Arran, July 1904, *Somerville* (E).

On *Carex juncella* (E.Fr.) Th.Fr.

III only. ENGLAND: Basingstoke Canal, Surrey, 1898, *Marshall* (E).

On *Carex pallescens* L.

Uredospores $26-30 \times 22-24 \mu$, wall 2μ thick with two rarely three, equatorial pores.

II only. ENGLAND: Lady Wood, Besford, Worcs., Aug. 1931, *Grove* (BM); Keswick, Cumberland, June 1933, *Wilson* (E). SCOTLAND:

Rowardennan, Stirlingshire, Aug. 1831, *Campbell* (E); Lawers burn, Loch Tay, Perthshire, June 1931, *Hall* (E—Fig. 1i).

The following collections of aecidia on various hosts in the genera *Urtica* and *Ribes* are enumerated here as they cannot be placed in any of the varieties of *P. caricina* with certainty.

On *Ribes nigrum* L.

O, I. ENGLAND: on cultivar 'Seabrook's Black', Lingwood, Norfolk, May 1918, *Herb. Grove* (BM); Ely, Cambs., June 1932, *Herb. Grove* (BM); Wheatfen, Norfolk, June 1954, growing in contact with *Carex acutiformis* with teliospores, *Dennis* (K).

On *Ribes rubrum* agg.

ENGLAND: recorded from Surlingham, Norfolk (Ellis, 1933, p. 496). SCOTLAND: "Clyde", recorded by Dennis & Foister (1941).

On *Ribes sanguineum* L.

ENGLAND: recorded from Earlham Park, Norfolk (Ellis, 1933, p. 496). SCOTLAND: Mull and Skye, recorded by Wilson (1934).

On *Ribes uva-crispa* L. (often as "gooseberry" and it does not seem possible to discriminate between any truly wild collections and cultivated gooseberries from the scrappy materials of the hosts). Between thirty and forty specimens have been seen from localities scattered throughout Britain, these are not enumerated in detail.

On *Urtica dioica* L. and *U. urens* L.

Aecidia and spermogonia on the common nettle *U. dioica* are very common throughout the mainland of Britain, although detailed information on their occurrence in the more isolated islands would be of interest. The only record of aecidia on *Urtica urens* was made by Ellis (1943) from Hellington, Norfolk, where he showed that the race on *Carex hirta* could produce spermogonia and aecidia on this nettle.

Puccinia dioicae Magn. in Amtl. Ber. 50. Versamml. Deut. Naturf. Arzte, München, 199 (1877), n.v.

var. **dioicae**

Type: on *Carex dioica* in Germany (fide Hylander, Jørstad & Nannfeldt, 1953).

Uredospores $24-27 \times 20-22 \mu$, wall 2μ thick with two supra-equatorial pores; teliospores $36-48 \times 16-19 \mu$, apex $6-8 \mu$ thick.

On *Carex dioica* L.

III only. SCOTLAND: Creag an Lochan, L. Tay, Perthshire, Sept. 1959, with *Cirsium palustre*, *Henderson* 4783 (E—fig. 3a).

II only. SCOTLAND: Ben Lui, Perthshire, Sept. 1959, *Henderson* 4718 (E—fig. 3b); Orkney, 1928, *Johnston* 3867 (E).

On *Cirsium dissectum* (L.) Hill

O, I. IRELAND: Oldhead, Co. Mayo, *Adams*, June 1910 (BM).

It is hardly surprising that this species should be a host for *P. dioicae* for

it is an inhabitant of wet peat bogs where it comes in contact with several *Carex* species. Dicaryont stages have not been discovered in Ireland but the aecidia have been collected also on *Cirsium palustre* (O'Connor, 1936), so the sedge stages have probably been overlooked.

On *Cirsium palustre* (L.) Scop.

O, I. ENGLAND: Saxlingham, Norfolk, June 1934, *Ellis* (BM); Buxton Heath, Norfolk, June 1933, *Ellis* (BM, K); *ibid.*, *Carex dioica* near it, June 1934 (BM). SCOTLAND: Lumphanan, Aberdeenshire, July 1922, *Ramsbottom & Wilson* (BM, E); Ben Lawers, Perthshire, 1500 ft., June 1950, *Henderson* (E).

***Puccinia dioicae* Magn. var. *arenariicola* (Plow.) Henderson, comb. nov.**

Basionym: *P. arenariicola* Plow. in Journ. Linn. Soc. Bot. xxiv, 90 (1888).

Type: on *Carex arenaria*, Hemsby, Norfolk.

Uredospores $22-26 \times 20-22 \mu$, wall faintly echinulate with two supra-equatorial pores. (Teliospores $40-50 \times 20 \mu$, *fide* Plowright.)

On *Carex arenaria* L.

II only. Plowright experiment 529 from artificial inoculation from *Aec. centaureae*, May 1885, *C. B. Plowright* (BM—fig. 3c).

There appears to be no telia material of this rust in Plowright's herbarium and I have been unable to trace the collection from Hemsby which he quotes in his original description.

On *Centaurea nigra* L.

O, I. "Produced by artificial culture on *Centaurea nigra*" by Plowright, Exp. 732, June 1888 (BM); *ibid.*, no exp. number, Vize Micro-Fungi Brit. 452 & 549 (BM).

***Puccinia dioicae* var. *extensicola* (Plow.) Henderson, comb. nov.**

Basionym: *P. extensicola* Plow., British Uredineae and Ustilaginae, 181 (1889).

Type: on *Carex extensa*, Wells-next-the-Sea, Norfolk.

Uredospores broadly elliptic $22-28 \times 19-20 \mu$, wall pale, very faintly echinulate with two supra-equatorial pores; teliospores $42-60 \times 16-22 \mu$, apex $6-10 \mu$ thick.

On *Carex extensa* Good.

II & III. ENGLAND: Wells-next-the-Sea, Norfolk, *Dr. Long*, Vize Micro-Fungi Brit. 552 (holo. BM (fig. 3d), iso. K).

III only. ENGLAND: Berrow, Somerset, Aug. 1956, *Garlick* (K); Norfolk, *Dr. Long*, Sydow Ured. 318 (K); 1887, *Plowright*, Roum. Fungi Sel. Exs. 5407 (K).

II only. ENGLAND: Polperro, Cornwall, July 1929, *Rhodes* (BM).

On *Aster tripolium* L.

O, I. ENGLAND: Looe, Cornwall, June 1929, *Rilstone* (BM, K); Wells-next-the-Sea, Norfolk, 1890, *Long*, Syd. Ured. 424 (K); Berrow, Somerset, Aug. 1956, *Garlick* (K); by culture, June 1888, *Plowright* (BM); *ibid.*, Vize Micro-Fungi Brit. 544 (BM).

Puccinia dioicae Magn. var. *schoeleriana* (Plow. & Magn.) Henderson, comb. nov.

Basionym: *P. schoeleriana* Plow. & Magnus in Quart. Jour. Micr. Sci. N.S. xxv, 170 (1885).

Type: on *Carex arenaria*, North Wootton, King's Lynn, Norfolk, England, Vize Fungi Brit. 434.

Uredospores $27-30 \times 18-24 \mu$, wall almost smooth with two supra-equatorial pores; teliospores $50-60 \times 18-24 \mu$, apex $8-12 \mu$ thick.

On *Carex arenaria* L.

II & III. ENGLAND: N. Wootton, Norfolk, *Plowright*, Vize 434 (K, II only, BM. holo.—fig. 3e & f).

III only. ENGLAND: Winterton Dunes, Norfolk, Jan. 1935, *Ellis* (K). WALES: Oxwich, Glamorgan, Sept. 1915, *Wakefield* (K). SCOTLAND: Gullane, E. Lothian, Apr. 1915, *Wilson* (E); Aberlady, E. Lothian, with *Senecio jacobaea*, Sept. 1953, *Henderson* 957 (E).

On *Carex maritima* Gunn.

II & III. SCOTLAND: "Elginshire", *Gordon* 1802 (E).

II only. SCOTLAND: Findhorn, Morayshire, *Walker Arnott* (E).

On *Senecio jacobaea* L.

O, I. ENGLAND: Bawsey, Norfolk, May 1872, *Plowright* (BM); King's Lynn, Norfolk, June 1950, *Ramsbottom* (BM); Scolt Head, Norfolk, June 1933, *Ellis* (BM, K); Holm-by-the-sea, Norfolk, April 1922, *Bloom* (BM). Experiment 260, aecidia on *Senecio jacobaea* produced by inoculation from *Carex arenaria*, 17 Feb. 1884, perfect aecidia developed by 11 Apr. *Plowright* (BM); similar collections, experiments 285, 291, 293, 294 (BM); Holy Is., Northumberland, July 1957, *Ellis & Dennis* (K); North Wootton, Norfolk, *Plowright*, Vize Micro-Fungi Brit. 434 (K); *ibid.*, 1874, Fungi Brit. 156 (K, BM); Braunton, Devon, growing with infected *Carex arenaria*, May 1954, *Henderson* 1373 (E). SCOTLAND: Montrose, Angus, June 1946, *Wallace* (E); Sandhead, Galloway, June 1930, *Wilson* (E); Gullane, E. Lothian, June 1928, *Wilson* (E); Carnoustie, Angus, May 1845, *Gardiner* (E); Burntisland, Fife, June 1821, *Greville* (holo. of *Aecidium jacobaeae* Grev.—E, BM).

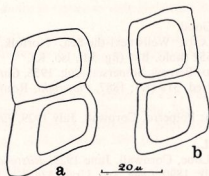


FIG. 2. Peridial cells of aecidia on *Taraxacum* in longitudinal section; outer surface to the left. a, *P. dioicae*. b, *P. variabilis*.

***Puccinia dioicae* var. *silvatica* (Schroet.) Henderson, comb. nov.**

Basionym: *P. silvatica* Schroet. in Cohn, Beitr. Biol. iii, 68 (1879).

Type: on *Carex brizoides*, near Freiburg, Germany.

Uredospores sparse, about $24 \times 16 \mu$, wall 2μ with two supra-equatorial pores; teliospores $38-44 \times 16-18 \mu$, apex $4-5 \mu$.

On *Carex capillaris* L.

II & III. SCOTLAND: Clach toll, Sutherland, July 1955, Flannigan (E).

On *Taraxacum officinale* agg.

O, I. SCOTLAND: Ben Lawers, Perthshire, 2500 ft., June 1950, Henderson 2792 (E—fig. 2a peridial cells).

***Puccinia dioicae* Magnus sens. lat.**

On *Carex lepidocarpa* Tausch

Uredospores $22-25 \times 18-20 \mu$, wall 2μ thick, with two supra-equatorial pores, teliospores $45-60 \times 20-23 \mu$, apex $7-8 \mu$.

II & III. SCOTLAND: Creag an Lochan, L. Tay, Perthshire, 2000 ft., Aug. 1953, Henderson 920 (E—fig. 3g); *ibid.*, Sept. 1959, Henderson 4776 (E); Gairloch, W. Ross, Aug. 1934, Wilson (E).

II only. SCOTLAND: Creag an Lochan, L. Tay, Perthshire, Sept. 1959, Henderson 4781 (E); *ibid.*, 4784 & 4785 (E); Orkney, Johnston (E); Strome, Ross-shire, Oct. 1959, Henderson 4884 (E).

On *Carex ovalis* Good.

Uredospores broadly elliptic $25-28 \times 19-21 \mu$ with two supra-equatorial pores.

II only. ENGLAND: Monkswood, Hunts., Townsend (E). SCOTLAND: Pitcundrum, Angus, 1832, Kirk (E); Hopes Reservoir, Gifford, E. Lothian, Aug. 1946, Wilson (E); *ibid.*, 1881, Terras (E); Wick River, Caithness, 1902 (E); Northbay, Barra, 1936, Edinburgh University Biological Society (E—fig. 3h).

On *Carex demissa* Hornem.

III only. IRELAND: Enniskerry, Wicklow, Ball (E)—(in absence of uredospores placed here with some doubt).

***Puccinia microsora* Koern. in Fuckel, Symb. Myc. Nacht. iii, 14 (1875).**

Type: on *Carex vesicaria*, Casselsruhe nr. Bonn, Germany, Nov. 1873.

Sori small, hypophyllous; uredospores $28-32 \times 20-22 \mu$, hyaline, thin-walled; mesospores $34-43 \times 23-28 \mu$, unicellular, brown, with rough wall; teliospores $55-60 \times 16-18 \mu$, hyaline, thin-walled.

On *Carex vesicaria* L.

II & III. SCOTLAND: Inshriach marsh, Aviemore, Inverness-shire, Sept. 1959, Henderson 4817 (E—fig. 3i, j & k).

***Puccinia opizii* Bubak in Centralbl. Bakt. 2 Abt., ix, 925 (1902).**

Type: on *Carex muricata*, in Bohemia "St. Joannes (by Unter-Berkovic Jedomelic) near Schlan" (iso. BM—fig. 3, l).

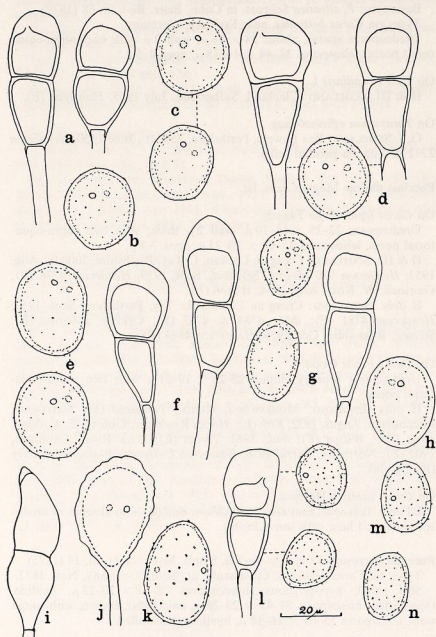


FIG. 3. a-h, Uredospores and teliospores of *Puccinia dioicae*.

a and b, var. *dioicae*. c, var. *arenariicola* (II only). d, var. *extensicola*. e and f, var. *schoel-eriana*. g, *P. dioicae*, sensu lato, on *Carex lepidocarpa*. h, *P. dioicae*, sensu lato, on *Carex ovalis* (II only). i-k, *Puccinia microsora*: i, teliospore. j, mesospore. k, uredospore. l-n, *Puccinia opizii*: l, type material on *Carex "muricata"*. m, uredospore only on *Carex pairaei*. n, uredospore only on *Carex paniculata*.

On *Carex paniculata* L.

Uredospores $18-22 \times 16-17 \mu$ with two rarely three, more or less equatorial pores; teliospores $44-48 \times 14-16 \mu$, apex $8-10 \mu$.

II only. ENGLAND: Wheatfen, Norfolk, July 1951, *Ellis* (E—fig. 3n).

III only. ENGLAND: Wheatfen, Norfolk, June 1951, *Ellis* (BM).

On *Carex appropinquata* Schum.

Teliospores $40-46 \times 16-20 \mu$, apex $8-10 \mu$ thick.

III only. ENGLAND: Wheatfen, Norfolk, May 1951, *Ellis* (E, K, BM).

(O, I. followed on lettuce and *Lactuca virosa* after inoculation from this rust on *C. appropinquata*.)

On *Carex pairaei* Schultz

II & III. ENGLAND: Belford, Northumberland, 1882, *Terras* (E).
SCOTLAND: Arthur's Seat, Edinburgh, July 1875, *McNab* (E).

II only. SCOTLAND: Pitcandly Hill, Forfar, Angus, Oct. 1944, *Duncan* (E—fig. 3 m.).

On *Lactuca sativa* L.

O, I. ENGLAND: Rockland St. Mary, Norfolk, June 1951, *Ellis* (E); Surlingham, Norfolk, June 1950, *Ellis* (K); Claxton, Norfolk, June 1950, *Ellis* (K); Wheatfen, Norfolk, June 1951, following inoculation from *Carex appropinquata*, *Ellis* (BM, K, E); "On lettuce imported from Holland", June 1932, *Pethybridge* (K).

On *Lactuca virosa* L.

Produced on this host by inoculation (*Ellis*, 1951).

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