THE MELAMPSORA EPITEA COMPLEX ON MOUNTAIN WILLOWS IN SCOTLAND

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In a previous paper (Henderson, 1953) some account of infection experiments with the saxifrage-willow group of *Melampsora epitea sensu lato* was given, but at that time so few collections were available for study that no general account of the Scottish members of this group could be prepared. Although there are still gaps, particularly in experimental investigation of host specialisation, which must be filled before the group is thoroughly understood, collecting during the last few years and examination of rusted host specimens in the Edinburgh Herbarium have more than doubled the material available. The present paper deals with the rusts attacking *Salix herbacea*, *S. reticulata*, *S. lanata*, *S. lapponum*, *S. myrsinites* and *S. arbuscula*. Of all these the only species which might be described as of moderately frequent occurrence in Scotland is *Salix herbacea*. The remainder are occasionally quite abundant in small areas particularly in the mountains of Perthshire, but certainly the rich arctic willow associations of northern Scandinavia, from which Jørstad has published some comprehensive accounts of the rust flora, are absent from Scotland.

All these rusts develop only uredinia and telia on willow hosts.*

Throughout their world distribution rusts on these willows have been correlated with caeomata on the following genera: *Abies* (*Melampsora abieti-caprearum* on *Salix herbacea* in northern Canada, Fraser, 1912), *Larix* (*Melampsora larici-reticulatae* on *Salix reticulata* in Switzerland, Schneider, 1906), *Saxifraga* (several saxifrage and willow hosts), *Viola* (on *Viola epipsila* and *V. palustris* and *Salix lapponum* in Scandinavia and Iceland, Jørstad, 1951 and 1953) and *Epilobium* (*Caeoma epilobii-alpini* Jørst. in Scandinavia may belong to a rust of the *Melampsora epitea* type). As the alternate hosts of heteroecious rusts can function only if they grow in reasonable proximity it seems unlikely that the genera *Ribes*, *Larix* and *Abies* can act as effective aecidial hosts of mountain rust fungi in this country. There are no records of *Viola* or *Epilobium* bearing caeomata in Britain although both are connected with *Salix* rusts in Scandinavia and *Epilobium anagallidifolium* and *E. alsinifolium* ascend Scottish mountains and *Viola palustris* is locally frequent. *Viola epipsila*, a caeoma host of *Melampsora lapponum* in Scandinavia is absent from Scotland. Thus, in default of information to the contrary, it seems probable whatever experimental studies may be conducted in the future that most, if not all, the Scottish mountain willow rusts will be found to belong to the saxifrage alternating group of the aggregate *Melampsora epitea*.

* In this paper I have used a combination of the earlier "european" terms for spore and soral types and some proposed by Arthur. Arthur's terms telium, uredinium and teliospore seem preferable to the rather clumsy teleuto-sorus, uredo-sorus and teleutospore. On the other hand, uredospore seems preferable to urediospore or urediniospore.

Notes of further experiments

Undoubtedly many of the problems of these rusts can only be solved by inoculation experiments. The connection between caeoma on *Saxifraga hypnoides* and *Salix herbacea* and *Saxifraga aizoides* and *Salix reticulata* in Scotland has been dealt with in a previous paper (Henderson, 1953). Several subsequent experiments using telia on various willows in attempts to infect saxifrages have failed. Caeoma on *Saxifraga oppositifolia* has been collected only once in Scotland (Wilson, 1919) and seems to be genuinely scarce as it has been searched for repeatedly in suitable situations during the last few years.

In July 1952 uredospores on *Salix herbacea* (D.M.H., 100) collected from Ben Heasgarnich, Perthshire, were used to inoculate a series of willows. Only *Salix herbacea* became infected, *S. reticulata*, *S. x Sadleri*, *S. lanata* and *S. repens* remained rust-free. From the same locality uredospores on *Salix reticulata* (D.M.H., 96) were used to inoculate *Salix herbacea*, *S. lanata*, *S. x Sadleri* and *S. repens* and *S. reticulata*. In this case only *S. reticulata* became infected. These two series confirm previous findings that the rusts on *Salix herbacea* and *Salix reticulata* are strictly specialised.

In the Lawers region of Perthshire, *Salix arbuscula* is frequently heavily rusted. In 1952 plants bearing uredinia from Creag an Lochan, Lawers (D.M.H., 97) were used as a source of inoculum. *Salix repens*, *S. x Sadleri*, *S. lanata* and *S. herbacea* were uninfected, *Salix reticulata* bore sparse uredinia within one month and by autumn bore abundant telia. In 1954 this experiment was repeated with the same result. The significance of this last result is discussed below.

Taxonomy

The taxonomic treatment of this group poses the usual problem as to what extent the classification of the rust should be influenced by the host genera. If the aggregate species *Melampsora epitea* is used, then it is possible to name haploid and diploid phases of this group of *Melampsora* using the same nomenclature for both. If, however, the group is split into " taxa " on the basis of the haploid host genera, the caeoma collections can be named but most willow collections have to be relegated to an aggregate *M. epitea* in the absence of infection experiments to determine the caeoma host. Indeed, classification based on caeoma may eventually be found to be justified, as from a few published accounts the caeomata on different host genera appear to differ in morphology, but all these studies have been carried out on a very few collections and are not sufficient as a basis for a usable classification.

The characters available for segregating taxa within the *Melampsora epitea* group are few. Jørstad has emphasised that so far as possible classification should be based on morphological characters. The group as a whole is characterised by extremely uniform thin-walled subepidermal teliospores. On most hosts telia are amphigenous although on some there is a greater proportion of epiphyllous or hypophyllous sori, but this seems to depend chiefly on host anatomy. The uredinia similarly vary in their disposition from one host to another, for example, epiphyllous uredinia

are almost absent on *Salix reticulata* in which the cuticle of the upper epidermis is very thick.

TABLE I

(Dimensions of paraphyses heads in microns)

Host	*Coll. No.*	*Diameter of Head* (range & mean)	*Wall thickness* (range & mean)
Salix herbacea	1	19–23 (21)	6–7 (6·5)
	2	12–17 (15)	3–5 (3·5)
	4	10–22 (17)	3–6 (4)
	5	14–24 (19·5)	3–7 (4·5)
	6	12–14	2–4 (sparse collection)
	7	15–21 (17)	3–5 (4)
	8	16–26 (23)	2–4 (3·5)
	9	14–18 (16·5)	3–5 (4·5)
Salix herbacea x myrsinites	10	21–24 (23)	3–6 (4·5)
Salix myrsinites	11	16–22 (19)	3–8 (5)
Salix lapponum	12	19–24 (21·5)	5–8 (6·5)
	13	17·5–23 (20·5)	5–8 (6·5)
Salix arbuscula	14	20–24 (22)	3–7 (4·5)
	15	20–24 (22)	3–7 (4·5)
	16	20–25 (24)	5–8 (6)
	17	17–21 (19)	5–8·5 (7)
	18	19–23 (21)	4–7 (6)
	19	20–30 (26)	5–8 (7)
Salix reticulata	20	23–29 (26)	6–9 (7·5)
	21	22·5–26·5 (24)	6·5–8 (7·5)
	22	20–30 (25)	5–10 (7·5)
	23	20–31 (26·5)	6–10 (7·2)
	24	20–32 (26·5)	7–9 (8)
	25	22–32 (28)	3–9 (6·5)
Salix lanata	26	20–27 (23)	6·3–8 (7·2)
	27	22–32 (26·5)	6–10 (7)

From examination of uredospores of the collections under observation it was evident that they are just as invariable as the teliospores and afforded no characters useful in subdividing the group. There remained the only character of the dicaryon which has been extensively used by previous workers—the dimensions of the capitate uredinial paraphyses.

In Table I are given the dimensions of the paraphyses heads of all the collections available for analysis. The range and arithmetical mean for ten measurements are given in each case. It is clear that on the whole the collections fall into two major groups, those with large heads the maximum usually above 25μ and walls with a mean thickness often over 7μ, the other with smaller heads with thinner walls. This is in agreement with Jørstad's findings for Scandinavian collections. The small-headed type predominates on *Salix herbacea*, *S. herbacea x myrsinites*, *S. myrsinites*

and *S. lapponum* whilst the large-headed type occurs typically on *Salix reticulata* and *S. lanata*.

The small-headed type corresponds to *Melampsora epitea* (K. & S.) Thuem. var. *epitea* whilst the larger type corresponds both in size and host relations to *Melampsora epitea* var. *reticulatae* (Blytt) Jørstad.

Salix lapponum has not been previously recorded with rust in Britain where it is only sparsely distributed. The uredinia are covered by the rather dense leaf indumentum and are rather inconspicuous. In Glen Clova *Salix lapponum* grows in considerable quantity with *Salix lanata* and, although the latter is abundantly rusted with a fungus I assign to *Melampsora epitea* var. *reticulatae*, I could find no rust on *Salix lapponum*.

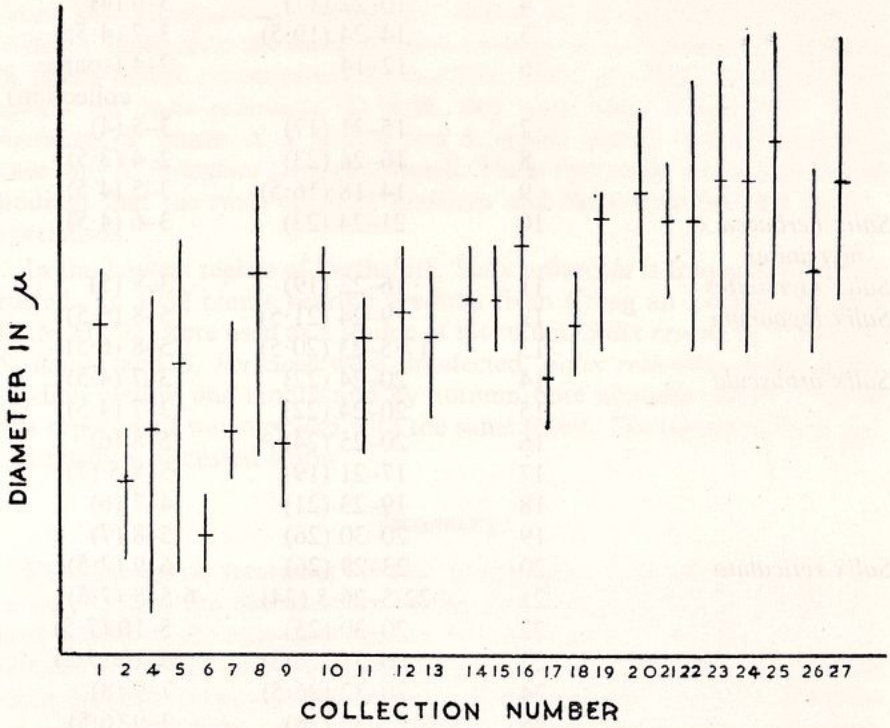

FIG. 1. Range (vertical line) and mean (horizontal line) of diameters of paraphyses heads of *Melampsora epitea*. The collection numbers refer to those used in table 1 and in the enumeration of specimens examined. Numbers 1–9 on *Salix herbacea*, 10 on *S. herbacea* × *myrsinites*, 11 on *S. myrsinites*, 12–13 on *S. lapponum*, 14–19 on *S. arbuscula*, 20–25 on *S. reticulata*, 26–27 on *S. lanata*.

In Scandinavia and Iceland *Salix lapponum* bears two rusts according to Jørstad; typical *Melampsora epitea* and *M. lapponum* Lindfors, the latter alternating with *Viola epipsila* and *V. palustris*. Lindfors (1913) distinguished *M. lapponum* as having large-headed paraphyses, 15–30μ in diameter, with relatively thin walls. Jørstad (1953) states, however, that the two intergrade.

From Table I it is clear that the only two collections on *Salix lapponum* in Britain fall well within the limits of *Melampsora epitea* var. *epitea* on, for example, *Salix herbacea* (specimens 1–9 excluding 8) in respect to the differential character, namely, the dimensions of the paraphyses heads.

The rust on *S. arbuscula* occupies a somewhat intermediate position between var. *reticulatae* and var. *epitea* (see Table I). The diameters of

the paraphyses heads are fairly consistently greater (mean of means of six collections, 22μ) than usual in the small-headed type (mean of means of seven collections on *S. herbacea*, 18μ), but in only two collections do they attain 25μ.

In the infection experiments described above the rust on *S. arbuscula* infected *Salix reticulata* but none of the hosts of var. *epitea*. I therefore provisionally assign the collections of *S. arbuscula* to var. *reticulatae* although fully conscious that further work may show that more taxa are required to deal with the complexities of the fungi involved in this group.

One collection on *Salix herbacea* (Table I, No. 8) is quite clearly different from the others on this host, approaching var. *reticulatae* in the diameter of the paraphyses heads. However, in wall thickness of the heads 2–4μ (Table I) it resembles var. *epitea*. Jørstad has also noticed that the two varieties are not sharply delimited and that intermediates occur. In his latest papers on this group in Norway (Jørstad, 1953) he records a number of collections of var. *reticulatae* on hosts other than *Salix reticulata* and *S. lanata*. In the case of this Scottish collection it is interesting that the field data suggest that the alternate host may be *Saxifraga hypnoides* which is known by experiment to house var. *epitea*. It should be noted that in paraphyses characters this collection agrees with *Melampsora lapponum*. However, there is no other evidence that this species, which typically alternates between *Salix lapponum* and *Viola* spp., occurs in Britain. I prefer to assign the collection to *Melampsora epitea* var. *reticulatae*. This example once again emphasises the need for cross infection experiments to investigate the relation between rust morphology and host specificity.

The following enumeration of specimens examined summarises the disposition of collections to the two taxa involved. All the specimens are deposited in the Herbarium of the Royal Botanic Garden, Edinburgh, except for a few in the private collection of Dr. Malcolm Wilson, to whom I am indebted for permission to examine them. Citations followed by (E.) denote that the record is based on rusted specimens in the Edinburgh phanerogamic herbarium; in these cases only a small token specimen bearing rust is deposited in the fungal collections. My own collections are indicated by a personal collecting number.

Specimens examined:—

Melampsora epitea (K. & S.) Thuem. var. **epitea.**

On Salix herbacea. (1) Ben Heasgarnich, Perthshire, 2500 ft., with *Saxifraga oppositifolia*, July 1952, D.M.H. 100. (2) Ben Laoigh, Aug. 1953 (fruit bearing uredinia) D.M.H. 917. (3) Caenlochan Glen, Angus, May 1953, D.M.H. 283. (4) Artificial infection from *Saxifraga hypnoides*, Aug. 1951. (5) Beinn Eighe, West Ross, Oct. 1955, Coll. D. McVean, D.M.H. 2424. (6) Shetland, Coll. D.H.N. Spence, Aug. 1952, D.M.H. 13. (7) Creag an Lochan, Lawers, Perthshire, 2300 ft., near *Saxifraga oppositifolia*, Aug. 1953, D.M.H. 904. (9) Ghlas Maol, Angus, Sept. 1945, Coll. U.K. Duncan.

On Salix herbacea x myrsinites. (10) Artificial infection from *Saxifraga hypnoides*, Aug. 1951,

On Salix myrsinites. (11) Little Craigindal, Angus, Aug. 1847 (E).
On Salix lapponum. (12) Glen Clova, Angus, Wm. Gardiner (E). (13) Choire Chairn, near Dalwhinnie, Inverness, July 1911, E. S. Marshall (E).

Melampsora epitea (K. & S.) Thuem. var. **reticulatae** (Blytt) Jørstad.
On Salix arbuscula. (14) Ben Laoigh, Perthshire, 2000 ft., Aug. 1954, D.M.H. 1570. (15) Creag an Lochan, Lawers, Perthshire, 1200 ft., July 1954, D.M.H. 1514. (16) *ibid.* 2000 ft., July 1952, D.M.H. 95. (17) *ibid.* near *Saxifraga aizoides*, 1700 ft., July 1952, D.M.H. 97. (18) *ibid.* 2000 ft., Aug. 1953, D.M.H. 903. (19) *ibid.* 2000 ft., July 1952, D.M.H. 99.
On Salix reticulata. (20) Ben Heasgarnich, Perthshire, 2500 ft., growing with *Saxifraga hypnoides*, *S. aizoides* and *S. oppositifolia*, July 1952, D.M.H. 96. (21) Creag an Lochan, Lawers, Perthshire, 2500 ft., July 1952, D.M.H. 98. (22) Glen Dole, Angus, July 1831, W. Brand (E). (23) Ben Lawers, Perthshire, Aug. 1900, no collector (E). (24) Meall an Soane, Glen Lochay, Perthshire, Wm. Evans 1909 (E). (25) Artificial infection from *Saxifraga aizoides*, Aug. 1951.
On Salix lanata. (26) Glen Fee, Angus, 2500 ft., D.M.H. 62. (2) Glen Callater, Aberdeenshire, no other data (E).
On Salix herbacea. (8) Glen Isla, Angus, 2800 ft., growing with infected *Saxifraga hypnoides*, July 1953, D.M.H. 573.

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