Two species of rust fungi, *Puccinia arenariae* and *P. behenis*, both of which grow on living leaves of red campion, *Silene dioica*, have been known to occur in Britain since the pioneer days of rust studies in the 19th and early 20th centuries (Wilson & Henderson, 1966 who considered them to be ‘common’ and ‘scarce’ respectively). When recording of rust fungi increased during the second half of the 20th century there was an abundance of records of *P. arenariae* on red campion with very few sporadic records of *P. behenis* at widely scattered locations. In Warwickshire, where detailed recording of fungi began in 1965, only *P. arenariae* was recorded until the first find of *P. behenis* in 2002. Was this an example of the sporadic occurrence of *P. behenis*? However both rust species continued to be recorded in most subsequent years and curiosity about the occurrence of *P. behenis* reached a peak in 2010 when the 1km grid squares of the eight earliest Warwickshire records of *P. arenariae* (1966-1976) were re-visited. *P. arenariae* was re-found in six of these but *P. behenis* was present in a different combination of six. The ‘scarce’ rust appeared to be scarce no longer in Warwickshire and the puzzle was whether this was so elsewhere in Britain. It was time to establish the current status of the two species nationwide and in 2011 the opportunity arose to put an appeal for specimens of these rusts on the Field Mycology section of the British Mycological Society’s website.

The 2011 Appeal

The two species in the survey

Although many rust fungi have complex life cycles with a specific sequence of up to five spore stages on two alternate host plants, these two rust species form only one or two spore stages and are readily distinguished microscopically. *P. arenariae* forms only two-celled teliospores which normally germinate immediately to form basidiospores on the telia (Figs. 1 & 2). Germination of teliospores formed in the autumn may be delayed until the following spring (Wilson & Henderson, 1966). In Britain *P. behenis* forms almost entirely one-celled urediniospores, rarely forming two-celled teliospores (Fig. 3). Although pustules of the two species differ in texture, and circinate (= in rings) clusters of pustules occur more frequently in *P. arenariae*, sometimes infections of the two species can look very similar in the field and can even appear together on the same leaf (Fig. 4). A third campion rust, confusingly with the same specific epithet as *P. behenis*, is *Uromyces behenis*. This was not included since it has only been recorded on bladder and sea campions (*Silene vulgaris* and *S. uniflora*), has a different combination of spore stages, and is readily distinguishable from the two species in the survey.

Method

The essential requirement of the 2011 survey was that the spores of every specimen must be checked microscopically. Contributors were asked to send material, ideally of two or more rusted leaves from two plants at each site, and to continue recording throughout the year. The majority of the 60 contributors sent pressed rusted leaves to me, whilst experienced rust recorders checked spores themselves, and a few people sent photomicrographs of the spores. A monthly news sheet reporting progress was sent to all and contributors were urged to continue recording both at the same and different sites. Over the year two-thirds of contributors sent in records on more than one occasion and also new contributors were added. It was only in August that it was appreciated that although red campion was difficult to find in eastern England, rusted white campion (*Silene latifolia*) was present there. Through the news sheet contributors were asked also to record rust on white campion.

Results on red campion

Seasonal development of the two rust species

Red campion is perennial with basal leaves persisting for all or most of the year (Fig. 8).
There was a preponderance of *P. arenariae* when rust records began to increase early in the plant’s growing season (April to June), with *P. behenis* catching up later (Table 1). During the autumn peak fungus recording season there were similar numbers of records of the two species. Overall the ratio of records of *P. arenariae* to *P. behenis* is 1.2 : 1.

<table>
<thead>
<tr>
<th>Months</th>
<th>P. arenariae</th>
<th>P. behenis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jan</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Feb</td>
<td>-</td>
<td>1</td>
</tr>
<tr>
<td>Mar</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Apr</td>
<td>9</td>
<td>3</td>
</tr>
<tr>
<td>May</td>
<td>30</td>
<td>9</td>
</tr>
<tr>
<td>Jun</td>
<td>56</td>
<td>28</td>
</tr>
<tr>
<td>Jul</td>
<td>78</td>
<td>66</td>
</tr>
<tr>
<td>Aug</td>
<td>38</td>
<td>54</td>
</tr>
<tr>
<td>Sep</td>
<td>57</td>
<td>54</td>
</tr>
<tr>
<td>Oct</td>
<td>44</td>
<td>32</td>
</tr>
<tr>
<td>Nov</td>
<td>47</td>
<td>46</td>
</tr>
<tr>
<td>Dec</td>
<td>21</td>
<td>18</td>
</tr>
<tr>
<td>Total</td>
<td>382</td>
<td>312</td>
</tr>
</tbody>
</table>

There was a difference in their patterns of spread, with *P. arenariae* occurring as relatively few individual infections, each soon forming circinate clusters of pustules, whereas *P. behenis* was more ‘explosive’, and often appeared as many scattered single pustule infections especially later in the year (Figs. 5 & 6). These single pustule infections might later develop into circinate clusters.

**Distribution**

Although there were few individual collections containing both rust species, comments were received that the other species was found within a short distance. Accordingly the 1 km National Grid square was used as the unit for comparison of the relative distribution of the two species. The presence of each rust species in the 1 km squares containing rusted red campion was counted giving the red (*P. arenariae*) and blue (*P. behenis*) numbers in each of the 100 km lettered squares (those defined by the letters in the OS grid references) in Britain (Fig. 7). No records were received from the Channel Isles or Ireland. In the rest of Britain rusted red campion was recorded in 376 1 km squares and in these *P. arenariae* was present in 72% and *P. behenis* in 64%, with both species present in 36%.

Most of the blank lettered squares were in the Scottish highlands and islands. Eight lettered squares had only one of the two rust species recorded, all based on very few (1 or 2) collections. In all the other 100 km lettered squares both rusts were recorded, although the sample size (of 1 km squares) varied greatly, from 1 to 90. In most 100 km lettered squares each rust species occurred in a high proportion (50 to 90%) of the sample. Over most of Britain neither species was predominant in a discernible region. The exception is northern Scotland where, of the 19 sampled 1 km squares in NH, NM and NO, 90% contained *P. arenariae* and only 22% *P. behenis*, suggesting that there was less *P. behenis* up there.

This survey shows that *P. behenis* was widespread and only a little less common than *P. arenariae* in most of Britain in 2011. The next puzzle is what evidence is there about the history of occurrence of *P. behenis*?

**Comparison with earlier records**

Major sources of earlier records are the database, *Fungus Records Database of Britain and Ireland* (FRDBI), which includes Herb K, the list of herbarium specimens at the Royal Botanic Garden Edinburgh and the database of Welsh rusts compiled by Nigel Stringer (pers. comm.). Combining all these sources, before 1998 there were between 0 and 7 records of *P. behenis* per decade, in comparison with consistently more, between 2 and 162, records per decade of *P. arenariae*.

One difficulty in interpreting earlier records is that records in national herbaria are based on herbarium specimens, which tend to over-emphasize rarities. A difficulty about FRDBI records without herbarium specimens is not knowing the criteria on which each record is based, potentially varying from a distant field sighting to a microscopic check.

Information supporting the view that *P. behenis* was rare before 1998 can be obtained from records on FRDBI made by individuals.
Fig. 1. *Puccinia arenariae* teliospores (approx 38 x 15 μm).

Fig. 2. *Puccinia arenariae* teliospores with some germinating from the apical cell (arrowed).

Fig. 3. *Puccinia behenis* single-celled urediniospores (approx 24 x 21 μm) and a mature two-celled teliospore (30 x 21 μm).

Fig. 4. Circinate clusters of telia of *Puccinia arenariae* (left) and *P. behenis* (right) on the same leaf of red campion.

Figs 1–6 © A.W. Brand.

Fig. 5. Circinate clusters of telia of *Puccinia arenariae* on red campion, October 2011.

Fig. 6. Many mainly scattered uredinia of *Puccinia behenis* on red campion, October 2011.

Fig. 7. Numbers of 1 km squares reported as containing *Puccinia arenariae* (red numbers at left) and *P. behenis* (blue numbers at right) in 100 km (lettered) OS squares, with the total number of productive 1 km squares in black.
known to have taken an interest in rust fungi. Although Willis Bramley, the noted Yorkshire
mycologist, recorded *P. behenis* on red campion in 1939 all the rest of his 11 records between 1939
and 1972 are of *P. arenariae*. Following Bramley in Yorkshire, Chris Yeates recorded *P. arenariae*
27 times between 1985 and 2002 with only one record of *P. behenis* in 1999. In Warwickshire the
Fungus Survey began in 1965 with strict criteria for identification and confirmation of each speci-
men (Clark, 1980) and before 2002 all 18 Warwickshire records on red campion were of
*P. arenariae*, partially confirmed by a check on the six pre-2002 herbarium specimens. In North
Lincolnshire Jack Houghton, who took close-up photographs of rust pustules, had found
*P. behenis* on white campion in 1987 but all 18 records on red campion between 1982 and 1991
were of *P. arenariae*. At 25 scattered locations Jerry Cooper between 1987 and 2000 recorded
only *P. arenariae* on red campion except for 1 record of *P. behenis* in 1998. In Kenneth Payne’s
specimens and notes (held in Leeds Museums and Galleries Collections) there are 15 records of
*P. arenariae* between 1946 and 2005, with his first and only record of *P. behenis* in 2001,
confirmed from the herbarium specimens.

Records on FRDBI from 1998 and 1999 signal a greater proportion of *P. behenis* but only in
certain areas. At the BMS foray on Arran (NS) in 1998 four localities produced records of both
*P. arenariae* and *P. behenis*. In 1999, in addition to Chris Yeates’s Yorkshire record, Nick Legon
reported several records of both *P. arenariae* and *P. behenis* at four localities in North Somerset
(ST) and Surrey (SU/TQ). However there has been no further recording of these fungi on Arran
and only *P. arenariae* has been recorded subse-
quently in ST, until the 2011 survey.

After 2000 on red campion the detailed and microscopically-confirmed records of rust fungi in
Wales, compiled by Nigel Stringer from his own and other observations, can be combined with
records from those in England and Scotland (FRDBI and Roy Lemmon, personal comm.) who
recorded both *P. arenariae* and *P. behenis* at least once during this period (Table 2).

These point to an increase, at least in these areas, in the proportion of records of *P. behenis*
starting in 2003 which has been maintained over subsequent years. Similarly Chris Yeates in
Yorkshire (mainly but not exclusively in SE) reported that half of his records of *P. behenis* had
been made in the last 4 years (personal comm., 2010). On FRDBI alone over the decade, after
allowing for duplicate entries with the same date, location and recorder, the ratio of *P. arenariae* to
*P. behenis* remained high, at 7.3 : 1. There is an excess of records of *P. arenariae*.

<table>
<thead>
<tr>
<th>Year</th>
<th>Number of records</th>
<th>ratio records</th>
<th>100 km grid squares containing</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>P. arenariae</em></td>
<td><em>P. behenis</em></td>
<td><em>P. arenariae</em> to <em>P. behenis</em></td>
</tr>
<tr>
<td></td>
<td>to <em>P. behenis</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2000</td>
<td>17</td>
<td>3</td>
<td>5.7 : 1</td>
</tr>
<tr>
<td>2001</td>
<td>15</td>
<td>3</td>
<td>5.0 : 1</td>
</tr>
<tr>
<td>2002</td>
<td>55</td>
<td>8</td>
<td>6.9 : 1</td>
</tr>
<tr>
<td>2003</td>
<td>64</td>
<td>25</td>
<td>2.6 : 1</td>
</tr>
<tr>
<td>2004</td>
<td>49</td>
<td>36</td>
<td>1.4 : 1</td>
</tr>
<tr>
<td>2005</td>
<td>63</td>
<td>37</td>
<td>1.7 : 1</td>
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<tr>
<td>2006</td>
<td>18</td>
<td>25</td>
<td>0.7 : 1</td>
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<td>9</td>
<td>1.3 : 1</td>
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<td>2008</td>
<td>31</td>
<td>19</td>
<td>1.6 : 1</td>
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<tr>
<td>2009</td>
<td>10</td>
<td>5</td>
<td>2.0 : 1</td>
</tr>
<tr>
<td>2010</td>
<td>23</td>
<td>20</td>
<td>1.2 : 1</td>
</tr>
</tbody>
</table>
Records on white campion
With little recording on white campion before August there were only 40 records during 2011, giving a P. arenariae to P. behenis ratio of 0.5 : 1. Samples of rusted white campion were obtained from 22 x 1 km grid squares, and 88% of these contained P. behenis in comparison with only 45% containing P. arenariae. There was some evidence of a regional difference, with only P. behenis recorded in all the sampled more easterly 100 km grid squares in England (Table 3, squares SE and those with T Eastings).

The two host species hybridise and one pair of recorders distinguished hybrids (S. x hampeana) and showed that both rust species occur on them in NT.

On FRDBI there are only 22 earlier records on white campion, including 14 records of P. arenariae and 8 of P. behenis, a higher proportion of the latter (1.8 : 1) than on red campion.

Discussion
The maps on the website of the Botanical Society of the British Isles show that red campion occurs commonly and widely in Britain, less so in northern Scotland. White campion is widespread but has a more easterly distribution with fewer records in the west, in Devon, Wales, north-west England and especially Scotland. The two host species hybridise and some pink flowered hybrids may have been included with red campion.

In this 2011 survey, using microscopic characters to distinguish the two rust species, both rusts were widespread on red campion, with P. behenis little less common than P. arenariae. Regional differences were not detected, although the sparse information from northern Scotland suggests a preponderance of P. arenariae there.

There is good evidence from the records of past and present rust specialists that although P. arenariae was consistently widespread, P. behenis occurred infrequently on red campion before 1998. The proportion of P. behenis increased around the turn of the 21st century and since 2003 has continued at a high level despite yearly fluctuations in the total number of records. During the last decade the continued excess of records of P. arenariae on FRDBI cannot be due to this species being more common in the autumn. It could be because of scarcity of P. behenis in some regions or possibly this species was sometimes mistaken for the similar-looking P. arenariae, as suggested in the Checklist of the British and Irish Basidiomycota (Legon & Henrici, 2005).

The few records of both rust species on white campion indicate a similar trend of a greater proportion of P. behenis in 2011 than in previous records, but with an overall bias towards P. behenis.

This leads to the ultimate puzzle: why has P. behenis increased? What change occurred around the turn of the century that has persisted over years and regions? This is inevitably speculation and possibilities include changes in the abundance of other host plants, man-made environmental changes in habitats and climate change.

P. arenariae occurs on other host species in the Caryophyllaceae (Henderson, 2000) and infection studies by early mycologists indicate that cross infection can occur. P. behenis also occurs on sea campion (Silene uniflora) and bladder campion (S. vulgaris) but there are few records on FRDBI.

Habitats were not specifically asked for in this survey. The majority of my records of both species (square SP) were from road and pathsides and showed a preponderance of P. behenis. The best specimens that were sent in of P. arenariae alone were from within woodland, especially at infrequently visited locations. White campion is characteristically a plant of roadside verges. The basidiospores of P. arenariae are discharged actively with a drop of liquid as in Hymenomycetes (Buller, 1924). The dry wind-borne urediniospores of P. behenis could be dispersed by the greater air movement along the sides of roads and paths.
\textit{P. behenis} is now widespread. In comparison with larger fungi the rust fungi are poorly recorded. These survey records will be placed on FRDBI and will provide a benchmark for comparison with future records.

Acknowledgements
This survey would not have been possible without the sharp eyes and persistence of all the recorders:-

My thanks go to Paul Kirk for access to a sortable version of the relevant sections of FRDBI, and special thanks to Nigel Stringer, Roy Lemmon and Chris Yeates for access to their records. I am indebted to the management of Leeds Museums and Galleries Collections for access to Kenneth Payne’s material. I thank Debbie Evans for help and encouragement and for illustrated articles on related rusts and hosts for the survey’s news sheet. I thank Bert Brand for the photos (Figs 1–6) and his continued patience and encouragement.

Stop Press!
During 2012 records have been received from an additional 100km grid square: both \textit{P. arenariae} and \textit{P. behenis} in SW (West Cornwall, Pauline Penna).

References and websites
Books

Internet Links
Fungal Records Database of Britain and Ireland (FRDBI, managed by the British Mycological Society) http://www.fieldmycology.net/FRDBI/FRDBI.asp
Mycologia Scotica. https://sites.google.com/site/scottishfungi/mycologia-scotica