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SHORT COMMUNICATION

Hidden treasures—historical specimens from the late blight pandemic discovered in the Herbarium of the State Museum of Natural History Karlsruhe

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Abstract
Phytophthora infestans (Peronosporaceae, Oomycota) is the causal agent of late blight of potato (*Solanum tuberosum*) and a native to Central America. When introduced to Europe, it rapidly spread in 1845, triggering the Irish Potato Famine, which claimed millions of lives and led to an exodus of Europeans to North America. The spread of the species was recently traced using historical specimens from various herbaria. However, there are critical spatial and temporal gaps in the documentation of the early spread of the species. Within the framework of a digitalization and restoration project of the mid-nineteenth century fungus collections of the herbarium of the State Museum of Natural History Karlsruhe, several specimens of *Phytophthora infestans* from North-East Germany collected in 1853, 1855 and 1856 were discovered. In addition, we revised already deposited material and identified a specimen of *Ph. infestans* that was collected no later than 1852. These specimens are among the oldest from Central Europe and are now available to the scientific public. Further, we searched for thus far overlooked specimens, using online catalogues. We found specimens from 23 European countries, with the oldest material from western Europe and almost no data from eastern Europe, south-eastern Europe and southern Europe. Our results emphasize the need for archiving and digitizing natural history collections in order to document the historical spread of agricultural and forest pathogens and to better understand current-day epidemic spreads.

Keywords Natural history collections · Epidemic spread · Plant pathogens · DNA · Oomycota · Neomycetes · Exsiccatae

Introduction

Fungal specimens stored in public herbaria are of fundamental value for the scientific community (e.g. Lang et al. 2019; Borsch et al. 2020). They enable taxonomic and systematic studies and are a valuable source for new species discoveries (e.g. Bebber et al. 2010; Wen et al. 2015). They play a critical role in advancing scientific knowledge about biodiversity responses across large spatial and temporal scales (e.g. Lavoie 2013; Lang et al. 2019). They provide important resources for teaching purposes (e.g. Flannery 2013). Further, they offer a historical perspective on distribution patterns of fungi, which is crucial for conservation efforts (e.g. Nualart et al. 2017; James et al. 2018). Moreover, they provide genetic material for molecular analyses, which enables researchers to deeper understand evolutionary relationships and population genetics and provide reference material for molecular species identification (e.g. Geiger et al. 2016; Bieker and Martin 2018; Lang et al. 2019). Therefore, natural history collections offer a wealth of information for various fields of research.

Due to recent advances in the development of molecular tools, the value of public herbaria has even increased. Methods have now been developed to the point where DNA can be extracted and amplified from fungi and other plant pathogens even from the nineteenth century historical specimens (Ristaino et al. 2001; Larsson and Jacobsson 2004; Telle and Thines 2008; Martin et al. 2013; Bradshaw et al. 2023; Saville and Ristaino 2021). An example for this is

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the reconstruction of the spread of *Phytophthora infestans* (Mont.) de Bary (Peronosporaceae, Oomycota) which is the causal agent of potato late blight. After it arrived in Europe, it soon began to spread, triggering the Great Irish Famine from 1845 to 1852 that led to political changes and emigration from Europe, especially from Ireland (Bourke 1964; Grünwald and Flier 2005). By using molecular data obtained from historic herbarium specimens, it was found that it emerged from Mexico, and that the lineage Herb-1 that triggered the famine was replaced in a second wave after potato plants resistant to Herb-1 were grown (Yoshida et al. 2013). Later, Saville and Ristaino (2021) largely confirmed these results by sequencing historical specimens collected between 1845 and 1991. The study of Saville and Ristaino (2021), however, shows that there is still a lack of historical data for many geographical regions. In Central Europe, the earliest record cited by the authors comes from Germany in 1873, while no specimens were obtained from Austria and Switzerland. Furthermore, no specimens were obtained from Czech Republic, Poland and Norway. The oldest sequenced material from Denmark (1876) and Sweden (1882) was also collected a long time after the initial wave.

The nineteenth century collections of fungi from North-East Germany at the University of Greifswald, Germany (GWD), were recently transferred to the State Museum of Natural History Karlsruhe (KR). The collections were restored and digitalized (Scholler et al. 2016; Bänsch et al. 2022). We previously checked these collections for *Ph. infestans* specimens, and we initially found three specimens from the old botanical garden in Greifswald from 1877 (Bänsch et al. 2022). Further studies of previously uncatalogued specimens from Greifswald revealed even older material. The aim of this short communication is (i) to showcase the material that underpins the importance of natural history collections for gaining information on the past spread of alien species and (ii) to illustrate critical spatial and temporal gaps in the documentation of the early spread of the species. We argue that closing those gaps is possible and that much can be learnt from historic spreads for current-day and future pandemics.

Material and methods

In order to find *Ph. infestans* specimens from Greifswald, we screened uncatalogued old fascicules in which the collections were arranged in alphabetical order and found specimens deposited under the following names: "*Botrytis infestans* Mont.", "*Peronospora infestans* Caspari", "*P. trifurcata* Unger" and "*P. devastatrix* Casp.". In addition, we revised already deposited material of *Ph. infestans* in the collection of Museum of Natural History in Karlsruhe (KR). Identification of pathogens was done using a light microscope (Olympus BX53) by measuring sporangia at 400× magnification. Microscopic photographs were taken with an Olympus SC50 camera attached to the microscope. We used an internal manuscript catalogue in the Karlsruhe Herbarium to identify the handwriting and thus also the collectors.

Further, we searched for previously overlooked specimens of *Ph. infestans*. We checked the Global Biodiversity Information Facility (gbif.org) and the Mycology Collections Portal (mycoportal.org) and included all data with reliable taxon identification and information on collection year and country in our overview. We compared the result with the compilation recently published by Saville and Ristaino (2021), who made an effort to find the oldest known herbarium specimens.

Results

As a result of our screening of the Greifswald collection, we found four specimens collected in 1853, 1855 and 1856 on potato (*Solanum tuberosum*) (Table 1 and Figs. 1 and 2). All species identifications were confirmed using light microscopy. Only sporangia, but no oospores were observed (Fig. 3). The specimen from 1853 (Fig. 1) was given the name *Botrytis infestans*, the scientific name under which the taxon was originally described in 1845. The original label provides only information on the collection year and host plant, but no exact locality ("Kartoffelkraut" is the German word for the herbaceous, green

Table 1 List of oldest known specimens of *Phytophthora infestans* on potato (*Solanum tuberosum*) from Germany in the herbarium of the Natural History Museum Karlsruhe (KR)

Collection date	Origin	Accession number	Collector	Annotation
1853	Between Greifswald and Wolgast, Germany	KR-M-0009933	Tesch	Figures 1 and 3
16.8.1855	Rügen, Mönchgut, Gager, Groß Zicker, Germany	KR-M-0017862	J. Münter	Figure 2
1856	Neu Boltenhagen ("Boltenhagen"), Germany	KR-M-0057552	Tesch	
14.8.1856	Ribnitz-Damgarten, Germany	KR-M-0012908	H. Zabel	
1852	Berlin, Germany	KR-M-0008738	J.X.R. Caspary	

Fig. 1 *Phytophthora infestans* from North-East Germany, collected in 1853 (KR-M-0009933)

part of the potato plant). We know, however, that the collector, a gardener named Tesch, only collected in the area between Greifswald and Wolgast (Scholler et al. 2016), which is part of the north-eastern German mainland. The specimen from 1855 (Fig. 2) is a record from the nineteenth century from a German Island (Baltic Sea Island of Rügen). The data were uploaded and are now available online (www.naturkundemuseum-karlsruhe.de; www.gbif.org).

Further, we found a specimen of *Ph. infestans* (under *P. infestans* (Mont.) Caspary) published as part of an exsiccate collection (G. L. Rabenhorst, Klotzschii herbarium vivum mycologicum sistens fungorum per totam Germaniam crescentium collectionem perfectam. Cent. 19: no. 1879 (1854), accessed, e.g. in Karlsruhe, Germany, under KR-M-0008738 and in Kew, Great Britain under K 89) collected by J.X.R. Caspary. The label does not provide information on the collection date. However, there is a short, published note as part of a protocol of the general meeting of an association named "Verein zur Förderung des Gartenbaus in den Königlich Preussischen Staaten" (Anonymus 1853) in September 1852 in which Caspary reports of the fungus he found in Berlin on an small island on the river Havel called "Pfaueninsel". We assume that Caspary used material from this location for his exsiccatae material. If so, the material was collected no later than 1852, possibly even earlier.

In our online database search, we found specimens from 23 European countries (Fig. 4). Thus, 24 countries remained without any herbarium material. The oldest material originated from western Europe (Belgium, France, the UK, Ireland and the Netherlands). Specimens were found for most Central European countries (Germany, Switzerland, Austria, Czechia, Poland, Slovakia, Hungary, Latvia and Estonia), but often with a considerable time lag (37 years on average). Similarly, a large time lag (40 years on average) was found for the North European countries (Denmark, Sweden, Norway and Finland). Almost no specimens were found for eastern Europe, south-eastern Europe and southern Europe. Here, specimens were found for only five out of 19 countries (Ukraine, Russia, Romania, Italy and Spain).

Discussion

In the past, several authors evaluated herbaria in order to document the spread of pathogens of wild, agricultural and ornamental plants, as well as the spread of forest pathogens (e.g. Böllmann and Scholler 2006; Scholler 1996; Sydow

Fig. 2 *Phytophthora infestans* specimen from Rügen, Germany, collected in 1855 (KR-M-0017862)

1930; Yoshida et al. 2013; Saville and Ristaino 2021). Besides herbaria focusing on plant pathogens, plant herbaria have proven to be a major source for microfungi, as botanists often collect infected plants unintentionally (Scholler 2016; Scholler et al. 2021). However, there are a large number of fungal and plant herbaria that do not have catalogued inventories, especially historic ones, in which a systematic cataloguing was not always common practice. If data are not

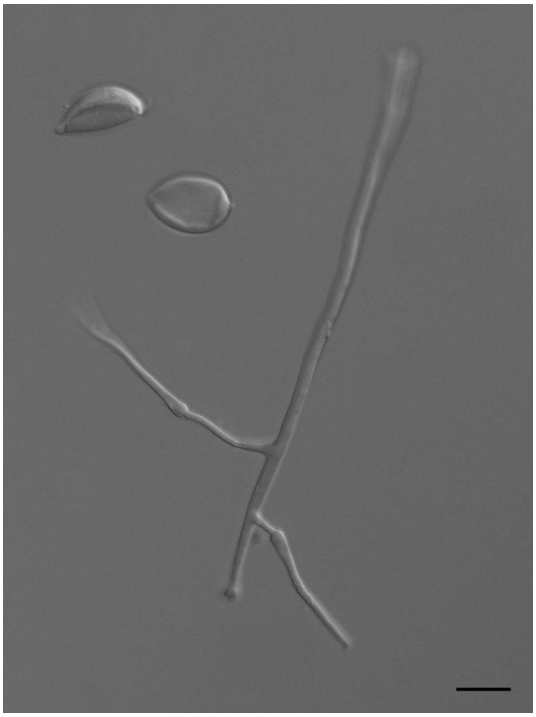

Fig. 3 Micrograph of sporangia and sporangiophore of *Phytophthora infestans* (KR-M-0009933). Bar = 20 µm

easily accessible via online data platforms such as GBIF or the Mycology Collections Portal, they are highly likely to be overlooked in large-scale studies investigating, e.g. global biogeographic patterns or population dynamics across large time scales, which constitutes are a serious source of information bias (cf. Hughes et al. 2021; Schertler et al. 2023).

Due to these circumstances, the specimens of *Ph. infestans* collected in 1853, 1855 and 1856 from the Greifswald collection from North-East Germany and the material collected in 1851–1852 as part of an exsiccate series have previously been overlooked. As the latter material is part of a numbered set of preserved specimens, it was also deposited in other collections. For example, we are now aware of material deposited in the Kew Mycology Collection (K) in Great Britain. Currently, we assume that the material originating from Berlin collected by Caspary in year 1851–1852 (KR-M-0008738; K 89) represents the oldest known specimens for Central Europe. These records were overlooked by Saville and Ristaino (2021) and by Bänsch et al. (2022), who dated the oldest known specimen to 1873 and 1870, respectively. Thus, our discovery pushed the date for the oldest specimen of *Ph. infestans* for Central Europe back by 18–21 years and increased the number of known specimens.

Although the specimens from the 1850s cannot provide information on the earliest appearance in North-East Germany, which was already reported by Bourke (1964), they can provide DNA, which may deliver valuable information on spread of the pathogen and provide further data on the genetic changes that occurred in the pathogen over the years (cf. Saville and Ristaino 2021). However, for population genetic studies, a high spatio-temporal resolution can be critical to reconstruct population dynamics appropriately, especially when the spread is during the 1st years of a new pandemic. Thus, we hope that the specimens, which are now available to the scientific public, will help to add another mosaic stone to the increasing knowledge on the historic spread of plant pathogens, thereby providing information that can be used to model current-day and future outbreaks.

Our online database search revealed large spatial and temporal gaps in the records of *Ph. infestans* specimens. Especially from eastern Europe, south-eastern Europe and southern Europe, we largely lack specimens of *Ph. infestans*. This finding points towards a general problem: It is a worldwide dilemma of natural history collections that most specimens are not digitalized and, therefore, are not accessible to the scientific public. We speculate that there are many additional historical specimens of *Ph. infestans* in European herbaria. In Germany, a recent survey in 2019 revealed that 87% of the specimens (plants and fungi) of public herbaria are still not digitalized (Borsch et al. 2020). In most other countries, the situation may be comparable (or worse). Therefore, most data from herbaria are not accessible via an internal or online databases and require a complex, time-consuming search by the collection managers and curators. In order to get access to these important data scientific collections, funding to support digitalization is urgently needed.

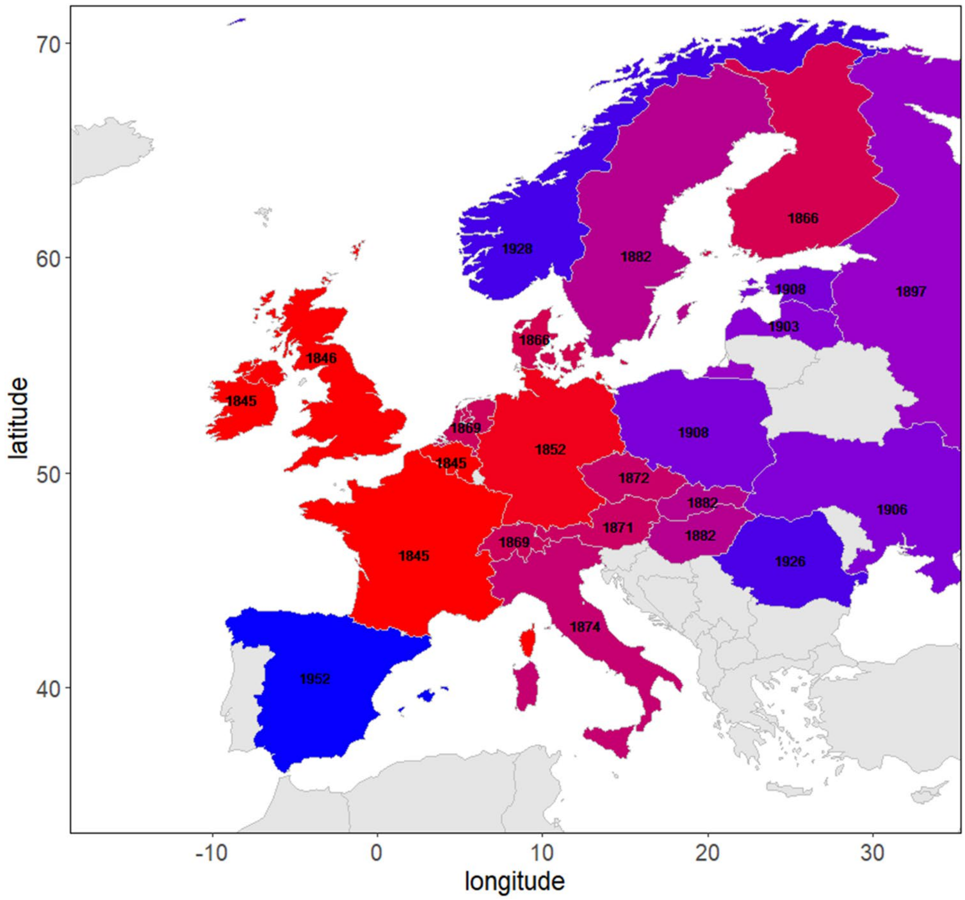

Fig. 4 Map of the oldest known specimens of *Phytophthora infestans* in Europe

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Author contributions MS made the concept, carried out the herbarium studies and wrote a first draft of the manuscript. MS and MW carried out the microscopic studies. MW and MT delivered major contributions to the manuscript. All authors have read and agreed to the published version of the manuscript.

Declarations

Conflict of interests The authors declare no competing interests.

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