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REVIEW

Poplar rust systematics and refinement of *Melampsora* species delineation

Agathe Vialle · Pascal Frey · Sarah Hambleton · Louis Bernier · Richard C. Hamelin

Abstract We present a review of previous taxonomic treatments of the *Melampsora* species occurring on poplar and describe the features associated with each spore stage in a typical poplar rust life cycle. The morphological, biological and ecological characters traditionally used for taxonomy are summarized for all *Melampsora* taxa, including 17 accepted species, 2 *formae speciales* and 2 hybrids, currently listed in the literature as pathogenic on *Populus* spp. We discuss the historical taxonomic decisions that led to nomenclatural and classification complications for this group of rusts, and highlight the lack of type material for three species known only from the original collections: *M. cumminsii*, *M. multa*, and *M. osmaniensis*. Even when all the traditional features are considered, the taxonomy of *Melampsora* poplar rust species remains uncertain and incomplete. An overview of recent molecular studies suggests the need for a comprehensive revision of species concepts, based on phylogenetic relationships. To that end, we propose a polyphasic approach, including the Genealogical Concordance Phylogenetic Species Recognition method, be used to build robust and meaningful systematic framework for the *Melampsora* poplar rusts.

Keywords *Melampsora* · *Populus* · Taxonomy · Systematics · Species definition · Rust

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Introduction

Rust fungi are obligate biotrophic plant parasites, causing disease on a broad range of hosts, from all classes of flowering plants, trees and ferns. The reproductive structures produced during some stages of their life cycles can produce abundant orange- or brownish-colored spores, giving infected plants the appearance of being dusted with iron rust, which led to their common name (Arthur 1903). The rusts are traditionally classified in the order *Uredinales* (current name *Pucciniales*) of the phylum *Basidiomycota*. This group of fungi exhibits three unique features: i) a single species can have up to five or six morphologically and functionally different spore stages during its life cycle (macrocyclic); ii) some species need two unrelated host plants to complete their life cycle (heteroecious) whereas others complete their life cycle on a single host (autoecious); and iii) species usually have narrow and specific host ranges (Cummins and Hiratsuka 2003). Efforts to develop a robust taxonomic framework and classification scheme for the rusts has been challenging due to an incomplete knowledge of the whole life cycle for the many species with multiple spore stages on various hosts, and a historical emphasis on spore morphology for species descriptions.

Rust infections caused by the members of the genus *Melampsora* Cast. are the most widespread and damaging

diseases of willows and poplars. The genus *Melampsora* is estimated to comprise between 80 and 100 species (Hiratsuka and Sato 1982), of which 9 to 32 occur on poplar. Reliable identification is the critical first step in assessing potential impact and disease risk, and for determining management options for poplar and willow cultivation. However, the taxonomy of *Melampsora* has presented notorious difficulties for taxonomists and pathologists (Arthur 1903). Like the other rusts, species were established based mainly on their morphological characters, but overlapping criteria and unclear morphological distinctions between species have led to confusion. A comprehensive review of species concepts and elaboration of a classification based on natural relationships is crucial for these fungi.

In this paper, our objective is to clarify the current taxonomic status of *Melampsora* species affecting poplar. First, we discuss the different morphological characters that have been commonly used for their taxonomy and classification. Second, we review all recognized *Melampsora* species described on poplars. Finally, we identify weaknesses and gaps in the current *Melampsora* taxonomy and propose a polyphasic approach that would ultimately result in a more meaningful systematic framework, by incorporating evolutionary history into an updated sub-generic classification.

The genus *Melampsora* delineation within the rust order

Traditionally, classification of the order *Pucciniales* at the generic and suprageneric levels was based almost exclusively on morphology of teliospores and telia (Dietel 1900; Sydow and Sydow 1915; Arthur and Cummins 1962; Maier et al. 2003). Two families were described using a single criterion: the *Pucciniaceae*, with stalked teliospores, and the *Melampsoraceae*, with unstalked teliospores (Dietel 1928). The latter family included 4 genera: *Melampsora*, *Coleosporium* Lév., *Melampsoridium* Kleb. and *Pucciniastrum* G.H. Otth. However, this general reliance on teliospore characters as the basis for major subdivisions of rusts was questioned, and other characters were later considered for systematic revisions, such as those related to the spermagonial (Arthur 1903; Hiratsuka and Sato 1982; Cummins and Hiratsuka 2003) or uredinial (Kenney 1970) spore stages, spore ontogeny (Hughes 1970), host association (Arthur 1903), complexity of life cycle (Savile 1976, 1978) and DNA sequences (Maier et al. 2003; Aime 2006; Maier et al. 2007). Recently, Cummins and Hiratsuka (2003) proposed a 13-family classification, with *Melampsora* as the only genus in the family *Melampsoraceae*. Morphology of the spermagonial stage was emphasized based on the hypothesis that the resulting classification would better reflect phylogenetic relationships than any previous system. Molecular phylogenies confirmed the genetic separation of the genus

Melampsora from the other genera (*Coleosporium*, *Melampsoridium* and *Pucciniastrum*) previously included in the *Melampsoraceae* (Maier et al. 2003; Pei et al. 2005; Aime 2006). However, the phylogenetic relationship of *Melampsora* to the rest of the *Pucciniales* is still under debate (Maier et al. 2003; Frey et al. 2005; Pei et al. 2005; Pei and Shang 2005; Sharma et al. 2005; Tian and Kakishima 2005; Aime 2006).

Castagne described the genus *Melampsora* in 1843 based on *Melampsora euphorbiae* (Scheb.) Cast., a rust found on *Euphorbia* sp. (Castagne 1843). The main attribute of the genus is the formation of a crust of sessile, laterally adherent single-celled teliospores under the host epidermis (Pei et al. 2005). Morphological characteristics of the spermagonia and teliospores are similar in *Coleosporium*, *Melampsoridium* and *Pucciniastrum* (Dietel 1928), however, aecia with rudimentary peridia or the lack of peridia (Sato and Sato 1985) and uredinia with abundant capitate paraphyses (Maier et al. 2003) are two distinct features of *Melampsora*. Moreover, the genus differs from the three other genera in having a wide variety of host associations and lack of host plant genus specificity. Whereas *Coleosporium*, *Melampsoridium* and *Pucciniastrum* each attack a single genus of *Pinaceae*, *Melampsora* attacks species of *Abies*, *Cedrus*, *Larix*, *Pinus*, *Pseudotsuga* and *Tsuga* (Maier et al. 2003). *Melampsora* species are either heteroecious or autoecious with heteroecious species occurring in alternation between *Salicaceae* and *Pinaceae* or between *Salicaceae* and a variety of flowering plants (monocotyledonous and dicotyledonous). Most of the autoecious species occur on dicotyledonous plants, including *Euphorbiaceae* and *Linaceae* (Sydow and Sydow 1915; Cummins 1950; Cummins and Hiratsuka 2003; Maier et al. 2003; Pei and Shang 2005).

Due to the reticulate nature of traditional taxonomic characters, i.e. the tendency of morphological characters to overlap between species and genera, the taxonomy of rusts is an ongoing challenge (Arthur 1903; Hiratsuka and Sato 1982). The genus *Melampsora* is no exception. Host range variations, the complexity of life cycles and similarities among spore characteristics make differentiation and recognition at the species level difficult. Thus, to date, there is no consensus as to how many species should be recognized in the genus *Melampsora*, including those species on poplar (Arthur 1903; Bagyanarayana 1998; Pei and Shang 2005).

Melampsora species on poplar: taxonomy and classification

Life cycle and morphological characteristics

Typically, the *Melampsora* species known on poplar are macrocyclic, producing five different spore stages during their life cycle: spermagonium (syn. pycnium), aecium,

uredinium, telium and basidium (Fig. 1). None of the described species is clearly defined as microcyclic (i.e. a life cycle with only the telium and basidium spore stages) and autoecious (Tian et al. 1991; Pei and Shang 2005). However, several species are described as hemicyclic (i.e. a life cycle with only the uredinium and telium stages) and/or are suspected to overwinter in poplar buds (Savile 1973). The aecial host range includes conifers, dicotyledonous and monocotyledonous plants. During their life cycle, poplar rusts display different morphological characters, which are useful for identification and classification. The importance and the contribution of each character depends on the taxonomic level considered (Arthur 1903; Cummins and Hiratsuka 2003). Here, we present the specific characteristics for each stage in a typical life cycle of a heteroecious species (Fig. 1) and their application for taxonomic assessments. The definitions used to describe the different stages refer to the ontogenic system described by Hiratsuka (1973).

Spermagonium (pl. Spermagonia, spore stage 0; syn. pycnium/pycnidium) and spermatia Spermagonia are produced on a haploid thallus that results from infection of the aecial host by a basidiospore. Spermagonia are generally associated with visible aecia. They produce spermatia, hyaline monokaryotic spores that have little or no diagnostic value. Nevertheless, morphological types of spermagonia are valuable in generic and suprageneric classification. All *Melampsora* species exhibit spermagonia with flat hymenia, determinate growth and no bounding structure. The position in the host tissue is either subepidermal (spermagonia morphological type 2) or subcuticular (spermagonia morphological type 3) (Cummins and Hiratsuka 2003).

Aecium (pl. aecia, spore stage I) and aeciospores Aecia primordia (receptive hyphae), are produced on the same haploid thallus as spermagonia on the aecial host. Aecia develop as a consequence of fertilization between receptive
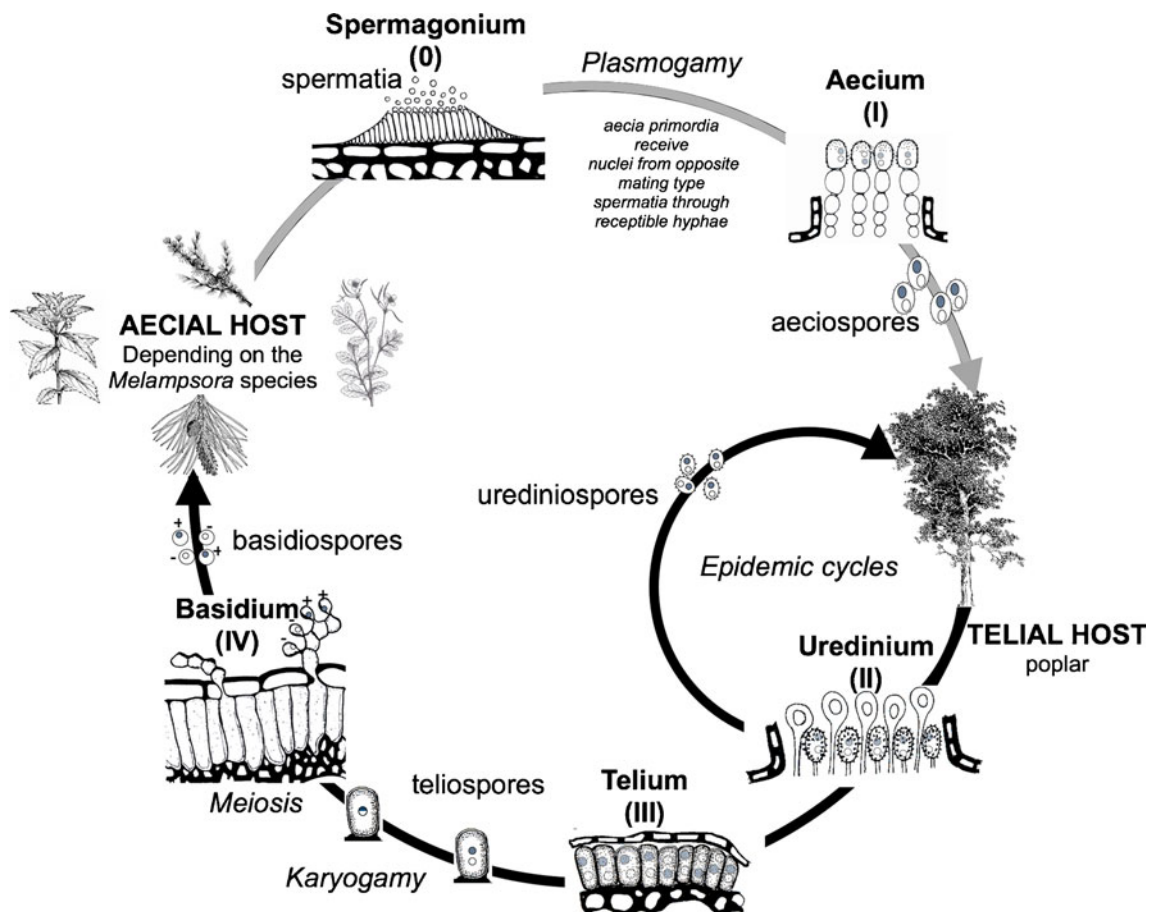

Fig. 1 Typical life cycle of heteroecious *Melampsora* sp. retrieved on poplar. The grey arrow links all stages retrieved on the aecial host (*Pinaceae*, monocotyledonous or dicotyledonous plant depending on the *Melampsora* species); the black arrow links all stages retrieved on the telial host (poplar). Schematic illustrations adapted from (0) spermagonium morphological type 3 (Cummins and Hiratsuka 2003); (I) Aecium *caeoma*-type with catenulate aeciospores, without bound-ing structure (Hiratsuka and Sato 1982); (II) Uredinium with intrasoral paraphyses and pedicellate urediniospores retrieved in many *Melampsora* species (Hiratsuka and Sato 1982); (III) Subepidermal telium with one-celled sessile teliospores of *Melampsora* sp. (Bagyanarayana 1998); (IV) Germinating teliospores producing basidia and basidiospores (www.agricola.es)

hyphae and spermatia with opposite mating types and produce dikaryotic aeciospores, which disperse to the telial (poplar) hosts. Aecia morphological types (generally *caeoma*-type; Cummins and Hiratsuka 2003) and aeciospore morphology are of little value in distinguishing *Melampsora* rusts at the species level, but the identity of the aecial host can be determining (Klebahn 1899; Arthur 1903; Cummins and Hiratsuka 2003).

Uredinium (pl. uredinia; spore stage II) and urediniospores Uredinia are produced on a dikaryotic mycelium on poplar upon germination of aeciospores. This dikaryotic spore stage can lead to repeated cycles of infection during the growing season, often resulting in epidemics. The majority of poplar rusts form uredinia mainly on the lower side of leaves (hypophyllous). Urediniospores are ornamented with surface echinulations and two types are recognized on poplar: i) relatively small urediniospores, with evenly spaced echinulations (Figs. 2a, b, d, e, g, i, l, m and n); and ii) relatively large urediniospores, often with a smooth spot on the surface (Figs. 2c, f, h, j and k). The location of uredinia (epiphyllous, hypophyllous or amphigenous), urediniospore size and wall thickness, and especially urediniospore ornamentation are determining characters in the distinction of poplar rust species (Arthur 1903; Cummins and Hiratsuka 2003; Pei and Shang 2005).

Telium (pl. telia; spore stage III) and teliospores All *Melampsora* species on poplar form grouped telia in subepidermal crusts on leaves with the dikaryotic teliospores overwintering on fallen leaf litter. After karyogamy, the teliospores germinate to produce basidia, and then basidiospores that infect aecial hosts during the growing season. Features of the telia and teliospores are the most important for generic distinction but are useful for differentiating only a few *Melampsora* species. Most poplar rust species, all except 5, produce telia on the lower side of leaves with a teliospore wall of uniform thickness (< 2.5 μm) (Arthur 1903; Sydow and Sydow 1915).

Basidium (pl. basidia; spore stage IV) and basidiospores Following meiosis, each basidium produces four spherical basidiospores that transfer to and infect the aecial host, forming the haploid thallus responsible for the production of spermagonia and aecia. Basidia and basidiospores have received limited attention in general rust classification, even if basidiospores differ in size and shape between genera and species (Cummins and Hiratsuka 2003). Today, specific characteristics of basidia and basidiospores are poorly documented in *Melampsora* rusts, probably because of the difficulty in obtaining them in the field or in the laboratory.

Host specificity and number of poplar rust species

In 1863, Anders Sandøe Ørsted discovered for the first time the phenomenon of heteroecy in the juniper-pear rust fungus *Gymnosporangium sabinae* (Dicks.) G. Winter (Ørsted 1863). Two years later, in 1865, Anton De Bary established for the first time the connection between *Puccinia graminis* subsp. *graminis* Pers. and the anamorph fungus *Aecidium berberidis* Pers. following artificial inoculation on detached leaves (De Bary 1866). The discovery that the same fungus could infect, at different periods of growth, unrelated plants was a turning point for taxonomists and in vitro experiments with rusts modified and broadened the understanding of rust fungus biology and resulted in improved species concepts (Arthur 1903). Following this new taxonomic approach, known as the culturist school, most *Melampsora* species on poplar were described in the late 19th to early 20th centuries based on their morphology, but also on their aecial and telial host ranges.

Originally, most taxonomists recognized the various rusts found on poplar under the single species name *Melampsora populina* Jacq., described in 1796 (Arthur 1903). Later, based mainly on urediniospore morphology, three different morphological *Melampsora* species were recognized on poplar by Schröter (1889). The culturist Klebahn redefined poplar rust taxonomy by considering his inoculation results in the context of a broader range of described species. As the first one to suggest the probable existence of ecologically distinct but morphologically similar species, Kleban recognized seven species (Klebahn 1899, 1902, 1917). In other taxonomic treatments, these morphologically similar rusts with distinct aecial hosts were classified variously (see discussion of the *Melampsora populnea* (Pers.) P. Karst. species complex, next section). Thus, species recognition in *Melampsora* on poplar has since been problematic, with multiple authors describing various numbers of species and *formae speciales* (f. sp.), i.e. a classification not formally recognized in taxonomy but based on the ability of strains to attack specific host genera (Viennot-Bourgin 1937; Peace 1962; Wilson and Henderson 1966; Boerema and Verhoeven 1972; Van Kraayenoord et al. 1974; Shang et al. 1986; Dai 1989; Bagyanarayana 1998; Cellerino 1999; Tian and Kakishima 2005).

Today, the only official monograph available for *Melampsora* dates from 1915, with a reprinting in 1971, comprising just 10 species on *Populus* spp. (Sydow and Sydow 1915). A few illustrated taxonomic keys to recognize and identify *Melampsora* species on poplar have been published but solely at the level of individual countries or specific geographical regions (Sydow and Sydow 1915; Cummins 1943, 1950; Ziller 1955; Kuprevich and Tranzschel 1957; Arthur and Cummins 1962; Pinon 1973; Hiratsuka and Sato 1982; Shang et al. 1986; Shain 1988; Cellerino 1999; Tian et

al. 2004; Frey et al. 2005; Pei and Shang 2005; Sharma 2005; Liang et al. 2006). As no previous study or review has considered all described *Melampsora* poplar rust species together, a summary is presented in the next section.

Uncertainty in poplar *Melampsora* species

We inventoried all poplar *Melampsora* species cited in the literature for a total of 20 different species (17 species considered as accepted taxa, of which one comprises two *formae speciales*, plus 3 considered here as *nomina dubia*), and 2 hybrids. Among the accepted species, we recognized six which were considered by some uredinologists as *formae speciales* and members of the species complex *M. populnea*. *Melampsora populnea* (syn. *Melampsora tremulae* Tul.; Saccardo et al. 1882) was described in 1879, for all *Melampsora* rusts with similar morphology retrieved from *Populus tremula* (Karsten 1879; Saccardo et al. 1882; Schröter 1889; Société Linnéenne de Bordeaux 1889). Later, the concept was expanded to include all morphologically similar *Melampsora* species that develop the uredinial-telial stages on all poplars from section *Populus* (Wilson and Henderson 1966; Boerema and Verhoeven 1972). Traditionally, the *M. populnea* species complex consisted of four *Melampsora* species recognizable by their aecial host specificity: *Melampsora larici-tremulae* Kleb. with alternation on *Larix* spp.; *Melampsora magnusiana* G.H. Wagner with alternation on *Papaveraceae* such as *Chelidonium* spp. and *Corydalis* spp., essentially, and a few records on *Fumaria officinalis* and *Papaver dubium* (Bagyanarayana 1998); *Melampsora pinitorqua* Rostr. with alternation on *Pinus* spp.; and *Melampsora rostrupii* G.H. Wagner with strict alternation on *Mercurialis perennis*. Two other species have sometimes been considered part of the complex: i) *Melampsora aecidioides* (DC.) J. Schröt, which occurs on *Populus alba* and the hybrid *Populus canescens* (*P. alba* x *P. tremula*) with no aecial host recorded; and ii) *Melampsora pulcherrima* Maire, called the white poplar Mediterranean rust (Moriondo et al. 1989; Bagyanarayana 1998; Pei and Shang 2005). Differentiation of species within the complex is cryptic and the similarity in urediniospore morphology has led to conflicting classifications with varying numbers of species or other taxa accepted. On the one hand, some taxonomists recognized a number of 'races' (*formae speciales*) that do not differ essentially in their morphology to be considered as distinct species (Peace 1962; Wilson and Henderson 1966; Boerema and Verhoeven 1972; Bagyanarayana 1998). On the other hand, based on the few morphological differences and aecial host specificity and pathogenicity, other authors suggested that all *formae speciales* be considered as distinct species (Klebahn 1899; Viennot-Bourgin 1956; Pinon 1973; Tian et al. 2004; Frey et

al. 2005; Pei and Shang 2005; Tian and Kakishima 2005; Feau et al. 2009). Recent molecular studies have supported the latter approach (Tian et al. 2004; Tian and Kakishima 2005; Feau et al. 2009). Thus, in this review, we recognized the 6 species listed above as distinct.

This taxonomic section comprises information from multiple sources in the literature, as cited, including the original descriptions. Type material was not examined nor were synonym citations verified for accuracy, rather we complied and organized all relevant information from the literature to provide a sound basis for a future monographic revision. For each species accepted based on a synthesis of this information, the main morphological features are summarized, with synonyms (those referring to other accepted species are listed as rejected), aecial and telial host ranges and geographic distribution, followed by a notes section including: i) notable features useful for delimiting, differentiating and/or identifying each species, and ii) historical taxonomic decisions that help to understand the current taxonomy. Selected herbarium specimens were examined and photographed for illustrative purposes only (Figs. 2 and 3).

Melampsora abietis-canadensis C.A. Ludw., Phytopathol. 5: 279 (1915). (Fig. 2a)

Literature: Ludwig, Phytopathol. 5: 279 (1915); Arthur and Cummins, Manual of the rust in United states and Canada : 53 (1962).

Accepted synonyms: *Caeoma abietis-canadensis* Farl., Proc. Am. Acad. 20: 323 (1885) (fide Arthur and Cummins 1962).

Peridermium fructigenum Arth., Bull. Torrey Club 37: 578 (1910) (fide Arthur and Cummins 1962).

Melampsora populi-tsugae J.J. Davis, Trans. Wisconsin Acad. 19: 676 (1919) (fide Arthur and Cummins 1962).

Rejected synonyms: *Melampsora medusae* Thüm., Bull. Torrey Club 16: 216 (1878) (fide Bagyanarayana 1998; Pei and Shang 2005).

Morphological features: Spermagonia amphigenous, punctiform, noticeable, subcuticular. Aecia amphigenous, on young stems and cones, oblong, subepidermal; aeciospores broadly ellipsoid or obovate, 13–18 × 17–26 μm, wall colorless, 1–2 μm thick, finely verrucose. Uredinia chiefly amphigenous, round, pulverulent; urediniospores broadly ellipsoid or globoid, 13–18 × 16–24 μm, wall colorless, 1–2 μm thick or twice as thick on the flattened sides, sparsely and evenly verrucose, sometimes with a smooth spot on the flattened side; paraphyses intermixed. Telia chiefly amphigenous, roundish, small, sometimes confluent, subepidermal; teliospores prismatic, 9–12 × 30–40 μm, wall cinnamon brown, 1 μm thick or slightly thicker above, smooth.

Aecial host: *Tsuga canadensis*.

Telial hosts: *Populus* section *Populus* (*P. grandidentata*), *Populus* section *Tacamahaca* (*P. balsamifera, P. trichocarpa*), uncertainties for *Populus* section *Aigeiros* (*P.*

deltoides subsp. *monilifera*) and *Populus* section *Leucoides* (*P. heterophylla*).

Geographic range: Canada, USA.

The distinguishing feature of this species is its ability to alternate between *Tsuga canadensis* and poplar (Ludwig 1915). The occasional presence of an equatorial smooth spot on urediniospores and its ability to infect *Larix* spp. in vitro (Fraser 1912) has led to confusion with *Melampsora medusae* Thüm. (Arthur and Cummins 1962) and for a few decades the two species were considered synonymous (Bagyanarayana 1998; Tian and Kakishima 2005). However, recent molecular studies confirmed the status of *M. abietis-canadensis* as a genetically distinct species, chiefly distributed in eastern North America (Tian and Kakishima 2005; Feau et al. 2009). It was also reported in China on *Populus davidiana* (Yuan 1984), but phylogenetic analyses suggest those specimens were probably confused with *M. larici-tremulae* (Tian et al. 2004; Tian and Kakishima 2005). While this species is considered to be restricted to section *Populus* (Newcombe 1997), the telial host range remains unclear due to possible confusion with *M. medusae* in published reports.

Melampsora abietis-populi S. Imai, Trans. Sapporo Nat. Hist. Soc. 17: 164 (1943).

Literature: Imai, Trans. Sapporo Nat. Hist. Soc. 17: 164 (1943); Bagyanarayana, Proc. 1st IUFRO Fore. Trees Working Party Conf.: 39 (1998); Tian et al., Mycoscience 45: 56–66 (2004); Pei & Shang, Rust diseases of willow and poplar: 53–56 (2005); Tian & Kakishima, Rust diseases of willow and poplar: 100–101 (2005).

Accepted synonym: *Caeoma abietis-mayrianae* S. Imai, Ann. Phytopathol. Soc. Jpn 12: 68–69 (1942) (fide Bagyanarayana 1998).

Morphological features: Spermagonia hypophyllous, subcuticular. Aecia hypophyllous; aeciospores globose, subglobose, obovate or broadly ellipsoid, 20–33 × 17–27 µm, wall 2–3.5 µm thick, densely verrucose. Uredinia hypophyllous; urediniospores oblong, ellipsoid or pyriform, 21–35 × 15–20 µm, wall 1.5–2 µm thick, evenly echinulate; paraphyses wall up to 10 µm thick at the apex. Telia mostly hypophyllous, subepidermal; teliospores 25–48 × 7–13 µm, wall 1 µm thick.

Aecial host: *Abies* spp.

Telial hosts: *Populus* section *Aigeiros* (*P. nigra, P. × euramericana*), *Populus* section *Tacamahaca* (*P. koreana, P. maximowiczii, P. simonii*).

Geographic range: Japan.

Urediniospore morphology in this species is similar to that of *M. magnusiana* and *M. larici-tremulae* (Ito and Murayama 1943; Tian and Kakishima 2005). Nevertheless, the thinner wall of the urediniospores, the reduced density of echinulations and its alternation on *Abies* spp. provide stable features for distinguishing *M. abietis-populi* (Tian et al. 2004; Tian and Kakishima 2005).

Fig. 2 Urediniospores of *Melampsora* species from dry herbarium specimens. **a**: *M. abietis-canadensis* specimen 1400MEA-POG-USA/PUR 61512: USA, Wisconsin, on *P. grandidentata*, 21 Sept. 1959, H. C. Green, PUR; **b**: *M. aecidioides* specimen 664ME-POA-BC45/QFB 25028: Canada, British Columbia, on *P. alba*, 19 June 2007, B.E. Callan, QFB; **c**: *M. allii-populina* specimen PFH03-33/QFB 25065: Republic of Turkey, on *P. nigra*, 20 Jul. 2003, F. Toplu, QFB; **d**: *M. castellana* specimen 1339MECA-POA-SP/BPI 0022645: Spain, Madrid, on *P. alba*, 1 Sept. 1928, A. Caballero, BPI, holotype; **e**: *M. ciliata* specimen 1413MECL-POCL-IND/PUR F131919: India, Kashmir, on *P. ciliata*, Sept 1908, E.J. Butler, PUR; **f**: *M. larici-populina* specimen 837MLP-POP-VI18/QFB 25043: Canada, Québec, on *P. balsamifera*, 28 Aug. 2007, A. Vialle, QFB; **g**: *M. magnusiana* specimen 1365MEG-POV-CHI/BPI 0023763: China, Kitsurin, on *P. davidiana*, 22 July 1940, N. Hiratsuka, BPI; **h**: *M. medusae* specimen 761MMD-POD-BA2/QFB 25044: Canada, Québec, on *P. deltoides*, 2 Aug. 2007, P. Tanguay, QFB; **i**: *M. microspora* specimen 1407MEMI-PON-IRQ/PUR F17540: Iraq, Sulaimaniya Liwa, on *P. nigra*, 1 Oct. 1950, A.R. Adhami, PUR; **j**: *M. nujiangensis* specimen 1423MEN-POY-CHI/TSH-R20042: China, Yunnan, on *P. yunnanensis*, 29 Sept. 1998, M. Kakishima, TSH, holotype; **k**: *M. occidentalis* specimen 1453MO-POT-USA/QFB 25045: USA, Idaho, on *P. trichocarpa*, 2 Sept. 2002, G. Newcombe, QFB; **l**: *M. pinitorqua*, specimen 1347MPI-PTA-FI/BPI 875451: Finland, Nylandia, on *P. tremula*, 8 Oct. 1935, H. Roivainen, BPI; **m**: *M. pruinosae* specimen 1366MEPR-POPR-UR/BPI 0031207: ex-USSR., Buchara, on *P. pruinosae*, 12 Aug. 1910, M. Androssow, BPI, type; **n**: *M. pulcherrima* specimen 1341MEPU-MEA-LB/BPI 0031212: Republic of Lebanon, Shemlan, on *P. alba* subsp. *Nivea*, 16 Feb. 1958, T.D. Maitland & R. Maire, BPI. Scanning Electron Microscopy (SEM) pictures taken at IBIS Microscopy and Histology Unit (http://www.rsvs.ulaval.ca) with a JEOL JSM 6360LV microscope, 2000x magnification. *Herbarium acronyms*: PUR: Purdue University, Arthur Herbarium, Department of Botany and Plant Pathology, USA; BPI: U.S. National Fungus Collections, USDA - Agricultural Research Service, USA; QFB: Laurentian Forestry Centre, Herbier René Pomerleau, Canadian Forest Service, Canada; TSH: University of Tsukuba, Mycological Herbarium, Japan

Melampsora aecidioides (DC.) J. Schröt., Krypt.-Fl. Schl.: 362 (1889). (Fig. 2b)

Literature: Schröter, Krypt.-Fl. Schl.: 362 (1889); Arthur and Cummins, Manual of the rust in United States and Canada : 54 (1962).

Accepted synonym: *Uredo aecidioides* D.C., Fl. Fr. 2: 236 (1805) (fide Arthur and Cummins 1962).

Melampsora populnea (Pers.) P. Karst., Bid. K. Fin. Nat. Folk 31: 53 (1879) (fide Bagyanarayana 1998).

Rejected synonyms: *Melampsora magnusiana* G.H. Wagner, Tul. Osterr. Bot. Z. 46: 273–274 (1878) (fide Tian et al. 2004).

Melampsora rostrupii G.H. Wagner, Öst. Bot. Z. 46: 273–274 (1896) (fide Klebahn 1899; Tian et al. 2004).

Melampsora abietis-canadensis C.A. Ludw., Phytopathol. 5: 279 (1915) (fide Arthur and Cummins 1962).

Morphological features: Spermagonia and aecia unknown. Uredinia suspected to be produced from overwintered bud-protected urediniospores large and caeomoid; early general infection epiphyllous, small, uniformly round and aecidioid, later infection hypophyllous, very pulverulent; peripheral incurved paraphyses, 40–60 × 15–22 µm; urediniospores obovate or broadly ellipsoid, 15–22 × 20–30 µm, wall
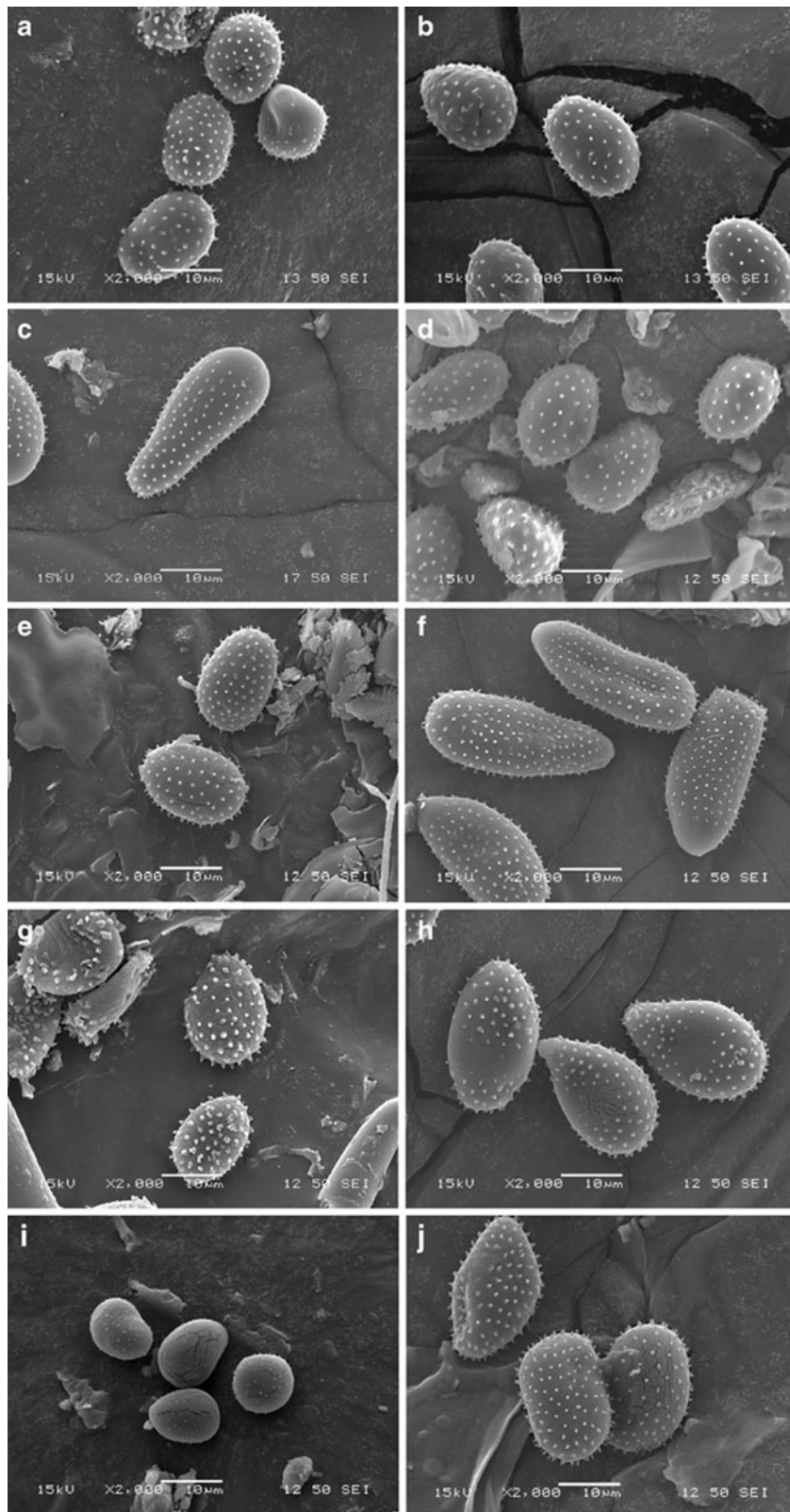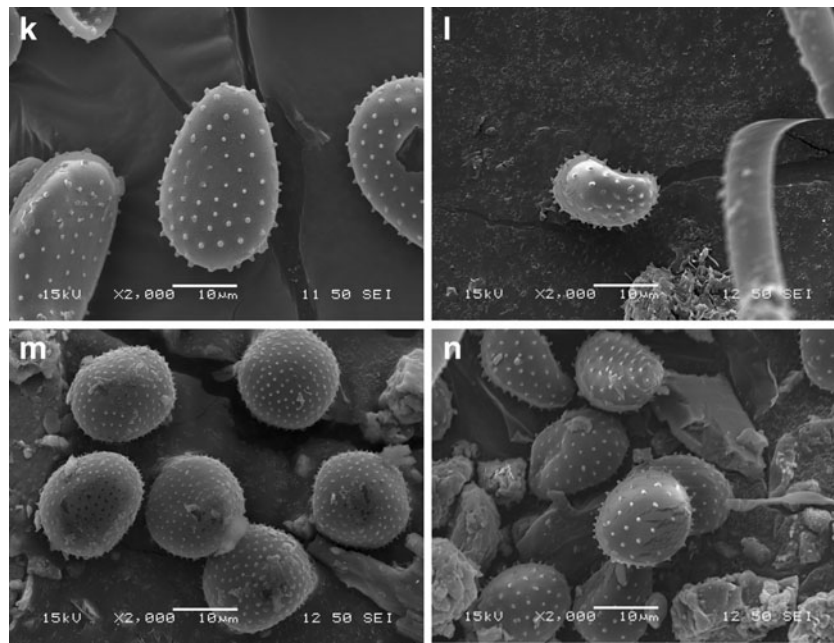
Fig. 2 (continued)

yellowish or colorless, 2–3 μm thick, prominently echinulate-verrucose, without any smooth spot. Telia unknown.

Aecial host: unknown.

Telial hosts: *Populus* section *Populus* (*P. alba*, *P. x canescens*).

Geographic range: Canada, China, Korea, Europe, India, Japan, USA, ex-USSR.

Melampsora aecidioides has a worldwide distribution, with aecial host unknown (Cummins 1943; Arthur and Cummins 1962). Due to its ability to grow on *P. alba* and the hybrid *P. canescens*, and lack of aecial stage, numerous authors included this species in the *M. populnea* complex, as a synonym of either *M. magnusiana* (Tian et al. 2004) (Figs. 2b, g) or *M. rostrupii* (Klebahn 1899; Tian et al. 2004), or as the entire *M. populnea* complex (Bagyanarayana 1998). A recent molecular study revealed that *M. aecidioides* was closely related to, but genetically different from both *M. magnusiana* and *M. rostrupii*, thus supporting the recognition of *M. aecidioides* as a distinct species (Feau et al. 2009). Based on DNA barcode homology, that study also revealed the probable confusion between *M. magnusiana* and *M. aecidioides* in China, and suggested that *M. magnusiana* was erroneously reported in this part of the world (Feau et al. 2009). To date, the aecial host of *M. aecidioides* is unknown and the species is suspected to overwinter in poplar buds (Arthur and Cummins 1962; Savile 1973; Feau et al. 2009). Telia are unknown though some authors have speculated that this stage occurs in small brown crusts (Schröter 1889; Arthur and Cummins 1962).

Melampsora allii-populina Kleb., Z. Pflanzenkr. 12: 25 (1902). (Fig. 2c)

Literature: Klebahn, Z. Pflanzenkr. 12: 25 (1902); Sydow & Sydow, Monographia uredinearum: 348 (1915); Pinon, Eur. J. Forest Pathol. 3: 223–224 (1973); Frey & Pinon, Eur. J. Forest Pathol. 27: 397–407 (1997); Pei & Shang, Rust diseases of willow and poplar: 53–56 (2005).

Accepted synonyms: Caeoma alli-ursini Winter, Plize Deutschl. 1: 255 (1881) (fide Sydow and Sydow 1915).

Caeoma ari-italici (Duby.) Wint., Plize Deutschl.: 256 (1882) (fide Species Fungorum www.speciesfungorum.org).

Uredo alli-populina Arth., Résult. Sc. Congr. Int. Bot. Vienne: 338 (1905–1906) (fide Sydow and Sydow 1915).

Melampsora allii-populina f. sp. *muscaridis-populina* Viennot-Bourgin, Rev. Pathol. Veg. Entomol. Agric. Fr. 24: 78–85 (1937) (fide Frey and Pinon 1997).

Melampsora allii-populina f. sp. *allii-populina* Kleb., Rev. Pathol. Veg. Entomol. Agric. Fr. 24: 78–85 (1937) (fide Frey and Pinon 1997).

Melampsora allii-populina f. sp. *typica* Dupias, Bull. Soc. Mycol. Fr. 81: 188–196 (1965) (fide Frey and Pinon 1997).

Rejected synonym: Melampsora populnea f. sp. *allii-populina* (Kleb.) Bagyanarayana, Proc. 1st IUFRO Fore. Trees Working Party Conf.: 47 (1998) (fide Bagyanarayana 1998).

Morphological features: Spermagonia subepidermal, yellow, 100 × 140 μm. Aecia group in pale yellow spots, 1 mm diam., subepidermal, surrounding by red-orange detached epidermal cells; aeciospores globoid, obovate or pyriform, 17–23 × 14–19 μm, wall 2 μm thick, finely verrucose. Uredinia mostly hypophyllous, usually less than 1 mm diam.; urediniospores broadly ellipsoid or oblong, rarely obovate, 24–38 × 11–18 μm, wall evenly thick, 1–2 μm,

smooth at the apex; paraphyses capitate, 50–60 × 14–22 μm, 2–3 μm thick. Telia minute, hypophyllous, subepidermal, 0.25–1 mm diam.; teliospores irregular, prismatic, 35–60 × 6–10 μm, wall light brown, 1–1.5 μm thick.

Aecial hosts: *Allium* spp., *Arum* spp., *Muscari* spp.

Telial hosts: *Populus* section *Aigeiros* (*P. nigra, P. deltoides, P. x euramericana*), *Populus* section *Tacamahaca* (*P. balsamifera, P. trichocarpa*).

Geographic range: North and South Africa, China, Europe, Russia.

Urediniospores of *M. allii-populina* possess a recognizable smooth spot at the apex (Fig. 2c). The existence of two *formae speciales* was suggested according to the specificity on the aecial host (Viennot-Bourgin 1937): f. sp. *allii-populina*, which alternates on *Arum* spp. and *Allium* spp., and f. sp. *muscaridis-populina*, which alternates only on *Muscari comosum* and *Allium sphaerocephalum* and has thin spinules at the apex of the urediniospores. A third *forma specialis* (f. sp. *typica*), alternating on *Allium* spp., *Arum* spp. and *Muscari comosum*, was also described (Dupias 1965). However, a pathogenicity study of *M. allii-populina*, combined with scanning electron microscopy examination, revealed that neither the morphological features of urediniospores nor pathogenicity on poplar could be used to distinguish the three *formae speciales* (Frey and Pinon 1997). The separation of this species into *formae speciales* is no longer used. and *M. allii-populina* is recognized as distinct.

Melampsora castellana Caball., Bol. R. Soc. Esp. Hist. Nat. 28: 425 (1928). (Fig. 2d)

Literature: Caballero, Bol. R. Soc. Esp. Hist. Nat. 28: 425 (1928) (Caballero 1928).

Morphological features: Spermagonia and aecia unknown. Uredinia early infection hypophyllous, then amphigenous, 0.25–1.5 mm diam., surrounded by paraphyses forming a white circle, clavate, rarely capitate, 40–120 × 6–30 μm; urediniospores globoid, ellipsoid or obovate, rarely angular, 16–25 × 13–19 μm with intermixed paraphyses, wall colorless, 2–4 μm thick, verrucose. Telia hypophyllous, 0.75 mm diam.; teliospores prismatic, round at the apex, 30–49 × 9–16 μm.

Aecial host: unknown.

Telial host: *Populus* section *Populus* (*Populus alba*).

Geographic range: Spain.

Little is known about this species. The amphigenous position of the uredinia, and especially the presence of a white ring of paraphyses around the uredinia, led the author to describe the specimen as a new species (Caballero 1928). The only known specimen recorded is the type specimen preserved by Caballero.

Melampsora ciliata Barclay, J. Asiat. Soc. Bengal 60: 223 (1891). (Fig. 2e)

Literature: Barclay, J. Asiat. Soc. Bengal 60: 223 (1891); Sydow & Sydow, Mongraphia uredinearum: 345 (1915); Bagyanarayana, Proc. 1st IUFRO Fore. Trees Working

Party Conf.: 39 (1998); Pei & Shang, Rust diseases of willow and poplar: 53–56 (2005); Sharma, Challenging problems in horticultural and forest pathology : 337–344 (2005); Sharma et al., Rust diseases of willow and poplar: 113–117 (2005).

Morphological features: Spermagonia and aecia unknown. Uredinia minute, hypophyllous, scattered, subepidermal, erumpent, pulverulent; urediniospores ovate to ellipsoid, 18–30 × 13–22 μm, wall 1.5–2 μm thick, echinulate; paraphyses capitate, 30–50 × 12–18 μm, apically 3–6 μm thick. Telia minute, hypophyllous, scattered, subepidermal, not-erumpent, orange-brown to dark-brown; teliospores 30–34 × 8–9 μm, wall 1–2 μm thick.

Aecial host: unknown.

Telial hosts: *Populus* section *Aigeiros* (*P. deltoides, P. nigra, P. x euramericana*), *Populus* section *Populus* (*P. alba, P. ciliata, P. tremula*), *Populus* section *Tacamahaca* (*P. trichocarpa, P. yunnanensis*); hybrids *P. maximowiczii* x *P. berolinensis* and *P. nigra* x *P. trichocarpa*.

Geographic range: India.

This species occurs in the Indian Himalayas between 700 and 3130 m above sea level (Barclay 1891). *Melampsora ciliata* was described as microcyclic and autoecious (Sharma 2005; Sharma et al. 2005). However, by definition a microcyclic rust exhibits stage III (telium/teliospore) and stage IV (basidium/basidiospore) during its life cycle (Cummins and Hiratsuka 2003). In this case, only the uredinial and telial stages (stages II and III) of *M. ciliata* are known, and we suggest that this Indian rust should be considered as hemicyclic, with no alternate host or sexual cycle identified.

Melampsora larici-populina Kleb., Z. Pflanzenkr. 12: 32 (1902). (Fig. 2f)

Literature: Klebahn, Z. Pflanzenkr. 12: 32 (1902); Sydow & Sydow, Monographia uredinearum: 346 (1915); Pinon, Eur. J. Forest Pathol. 3: 223–224 (1973); Bagyanarayana, Proc. 1st IUFRO Fore. Trees Working Party Conf.: 39 (1998); Pei & Shang, Rust diseases of willow and poplar: 53–56 (2005).

Accepted synonyms: *Sphaeria populi* Sowerby, Coloured Figures Engl. Fung. Mushr. 3: 157 (1803) (fide Species Fungorum www.speciesfungorum.org).

Phoma populi (Sowerby) Fr., Syst. Mycol. (Lundae) 2: 547 (1823) (fide Species Fungorum www.speciesfungorum.org).

Caeoma laricis Hart., Wichtige Krankh. Wäldbaume: 93 (1847) (fide Sydow and Sydow 1915).

Melampsora populina (Jacq.) Lev., Ann. Sci. Nat.: 375 (1847) (fide Sydow and Sydow 1915).

Melampsora cylindrica Arth., Résult. Scient. Congr. Intern. Bot. Vienne: 338 (1905, 1906) (fide Bagyanarayana 1998).

Uredo larici-populina Arth., Résult. Scient. Congr. Intern. Bot. Vienne: 338 (1905, 1906) (fide Bagyanarayana 1998).

Melampsora laricis-populina Kleb., Saccardo's Syll. Fung., 17: 463 (1905) (fide Species Fungorum www.speciesfungorum.org).

Uredo cylindrica Str., Ann. Wetter. Ges. 2: 92 (1910) (fide Bagyanarayana 1998).

Melampsora populi (Sowerby) M. Morelet, Cryptogam. Mycol. 6: 107 (1985) (fide Species Fungorum www.speciesfungorum.org).

Morphological features: Spermagonia amphigenous, subepidermal, 150 μm diam., 100 μm high. Aecia caeomoid, 1 mm diam., orange; aeciospores globoid to ovoid, 17–22 × 14–19 μm, wall colorless, finely verrucose, 1.5 μm thick. Uredinia subepidermal, erumpent, mainly hypophyllous, 200–400 μm diam.; urediniospores clavate to broadly ellipsoid, some oval to ovate, a few obovate to irregular, apex rounded, truncated base, 30–50 × 14–22 μm, wall colorless, 2 μm thick, thickened equatorially on two sides to 7 μm, acute-echinulate, smooth at the apex; paraphyses abundant, scattered, capitate, 45–85 × 12–18 μm, wall up to 10 μm thick at the apex. Telia abundant, epiphyllous, subepidermal; teliospores cylindrical to angular, 25–45 × 10–17 μm, wall hyaline to pale yellowish brown, 1 μm thick, slightly thickened at the apex, 2.5–3 μm.

Aecial hosts: *Larix* spp.

Telial hosts: *Populus* section *Aigeiros* (*P. nigra, P. deltoides, P. fremontii, P. x euramericana*), *Populus* section *Tacahamaca* (*P. angustifolia, P. balsamifera, P. ciliata, P. koreana, P. laurifolia, P. maximowiczii, P. suaveolens, P. simonii, P. ussuriensis, P. trichocarpa*), *Populus* section *Leucoides* (*P. lasiocarpa, P. wilsonii*).

Geographic range: Africa, Australia, South America, Central America, Canada, China, Korea, Europe, India, Japan, New Zealand, Russia, USA.

Differentiated by the culturist Klebahn for its aecial stage on *Larix* spp. (Klebahn 1902), *M. larici-populina* possesses a recognizable smooth spot at the round apex of its urediniospores. This species is economically important since it is the most widespread poplar rust and the first tree rust to have its genome sequenced (Tian et al. 2004; Tuskan et al. 2006; Joint Genome Institute 2007). The spelling of the name as *Melampsora laricis-populina* Kleb. (Saccardo et al. 1905) is an orthographic error. Although the genitive case of *Larix* is *Laricis*, in a Latin compound epithet the case ending of the genitive singular (−*is*) is removed and replaced by the connecting vowel (−*i*) according to the recommendation 60 G of the International Code of Botanical Nomenclature (McNeill et al. 2006). The incorrect spelling has been adopted in some databases (Species Fungorum: www.speciesfungorum.org; NCBI: www.ncbi.nlm.nih.gov), but a large majority of authors have used the original spelling of Klebahn (1902). According to the literature, *P. alba* should be included in the telial host range of *M. larici-populina* (Bagyanarayana 1998).

However, this record is considered doubtful by mycologists (Pei and Shang 2005). And similarly, although *Populus euphratica* was slightly infected in inoculation experiments with *M. larici-populina*, such infection has never been observed under natural conditions (Tian and Kakishima 2005).

Melampsora larici-tremulae Kleb., Forst. Naturw. Zeitschr. 6: 470 (1897).

Literature: Klebahn, Forst. Naturw. Zeitschr. 6: 470 (1897); Sydow & Sydow, Monographia uredinearum: 339 (1915); Pei & Shang, Rust diseases of willow and poplar: 53–56 (2005); Tian & Kakishima, Rust diseases of willow and poplar: 103–104 (2005).

Accepted synonyms: Uredo laricis West., Bull. Sc. Congr. Int. Bot. Vienne: 338 (1861) (fide Sydow and Sydow 1915).

Melampsora populnea (Pers.) P. Karst., Bidr. Känn. Finl. Nat. Folk 31: 53 (1879) (fide Wilson and Henderson 1966).

Caeoma laricis Wint., Pilze Deutschl.: 256 (1881) (fide Sydow and Sydow 1915).

Melampsora laricis Hartig, Allg. Forst-U. Jagdztg., Frankfurt: 326 (1885) (fide Tian and Kakishima 2005).

Melampsora tremulae f. sp. *laricis* Hartig, Lehrb. Baumkrankh.: 14 (1889) (fide Tian and Kakishima 2005).

Melampsora laricis-tremulae Kleb. Saccardo's Syll. Fung. 17: 463 (1905) (fide Species Fungorum: www.speciesfungorum.org).

Caeoma laricis Hart., Wichtige Krankheiten der Waldbäume: 93 (1906) (fide Sydow and Sydow 1915).

Uredo laricis Arth., Résult. Scient. Congr. Intern. Bot. Vienne: 338 (1905, 1906) (fide Sydow and Sydow 1915).

Melampsora populnea f. sp. *laricis* (Hart.) Boerema & Verh., Neth. J. Plant Pathol. 78: 25 (1972) (fide Bagyanarayana 1998; Tian and Kakishima 2005).

Morphological features: Spermagonia subepidermal, scattered, 70–80 μm diam. Aecia minute, round or oblong, yellow, 0.75 mm diam., pulverulent; aeciospores globoid, oblong or angular, 14–17 × 12–16 μm (European strains), 14–27 × 13–22 μm (Far Eastern strains), wall 1 μm thick, finely verrucose. Uredinia hypophyllous, scattered, minute, 0.5 mm diam., pale yellow; urediniospores oblong or ellipsoid, rarely subgloboid, 15–22 × 10–15 μm (European strains), 16–29 × 12–19 μm (Far Eastern strains), wall 1.5–2 μm thick, evenly echinulate; paraphyses 40–45 × 8–17 μm (European strains), 34–65 × 7–15 μm (Far Eastern strains), capitate, wall 3–5 μm thick. Telia hypophyllous, subepidermal, minute; teliospores prismatic, rounded on both sides, 40–60 × 7–12 μm (European strains), 23–51 × 3–11 μm (Far Eastern strains), wall 1–2 μm thick.

Aecial hosts: *Larix* spp.

Telial hosts: *Populus* section *Populus* (*P. alba, P. tremula, P. x canescens*)

Geographic range: Africa, China, Europe, Japan, Russia.

Melampsora larici-tremulae is one of the species included in the *M. populnea* complex. The synonymy of *M. larici-tremulae* with *M. pinitorqua* was suggested by Naldini Longo et al. (Naldini Longo et al. 1985), and while the two species are morphologically similar, they differ in aecial host. *Melampsora larici-tremulae* occurs on *Larix* spp. whereas *M. pinitorqua*, known as the pine twisting rust, occurs on *Pinus* spp. (Rostrup 1889, 1890; Klebahn 1899). However, these two species have a partial overlap in their aecial host range, based on laboratory experiments showing that both can infect either *Larix* spp. or *Pinus* spp. However, only *M. pinitorqua* will infect *Pinus sylvestris* (Naldini Longo et al. 1985; Desprez-Loustau 1986; Naldini Longo et al. 1988). Some morphological characteristics, such as the difference in teliospore length and the presence or absence of bilateral wall thickenings in urediniospores, were originally noticed between the two species (Sydow and Sydow 1915; Viennot-Bourgin 1956; Kuprevich and Tranzschel 1957; Wilson and Henderson 1966; Pinon 1973). Nevertheless, morphological studies later showed the weakness of such characteristics for reliable identification and differentiation between these two species (Desprez-Loustau 1986). The natural variability of the morphological characters seems to be under-estimated for *M. larici-tremulae* (Naldini Longo et al. 1985; Desprez-Loustau 1986). The size ranges observed for *M. larici-tremulae* urediniospores and aeciospores between Asian strains (syn. *Melampsora laricis* Hartig.) and European ones are larger than expected based on the original description (Pei and Shang 2005; Tian and Kakishima 2005). The difference in pathogenicity, particularly the ability to infect or not *Pinus sylvestris*, appears sufficient to consider *M. pinitorqua* and *M. larici-tremulae* as two distinct taxonomic entities (Naldini Longo et al. 1985; Desprez-Loustau 1986; Naldini Longo et al. 1988). As with *M. larici-populina,* a similar orthographic error was made in the spelling of *M. laricis-tremulae* Kleb. in 1905 (Saccardo et al. 1905).

Melampsora magnusiana G.H. Wagner, Öst. Bot. Z., 46: 274 (1896). (Fig. 2g)

Literature: Wagner, Öst. Bot. Z., 46: 274 (1896); Sydow & Sydow, Monographia uredinearum: 339 (1915); Pei & Shang, Rust diseases of willow and poplar: 53–56 (2005); Tian & Kakishima, Rust diseases of willow and poplar: 106–108 (2005).

Accepted synonyms: Caeoma fumaria Lk., Spec. Plant. 2: 24 (1825) (fide Sydow and Sydow 1915).

Uredo fumariae Rabh., Krypt. Flora Deutschl. 1: 7 (1844) (fide Sydow and Sydow 1915).

Melampsora tremulae Tul., Ann. Sci. Nat. 4 sér. 2: 95 (1854) (fide Sydow and Sydow 1915).

Caeoma chelidonii Magn., Hedwigia 14: 20 (1875) (fide Sydow and Sydow 1915).

Melampsora populnea (Pers.) P. Karst., Bidr. Känn. Finl. Nat. Folk 31: 53 (1879) (fide Bagyanarayana 1998; Tian and Kakishima 2005).

Melampsora klebahni Bubak., Z. Pflanzenkr. 9: 26 (1899) (fide Sydow and Sydow 1915).

Melampsora chelidonii-tremulae Kleb., Jahrb. F. wissensch. Botanik 35: 690 (1901) (fide Sydow and Sydow 1915).

Uredo magnusiana Arth., Résult. Scient. Congr. Intern. Bot. Vienne: 338 (1905, 1906) (fide Sydow and Sydow 1915).

Melampsora populnea f. sp. *magnusiana* (Wagn.) Bagyanarayana comb. Nov., Proc. 1st IUFRO Fore. Trees Working Party Conf.: 48–49 (1998) (fide Bagyanarayana 1998).

Rejected synonyms: *Melampsora aecidioides* (DC.) J. Schröt., Krypt.-Fl. Schl.: 362 (1889) (fide Tian and Kakishima 2005).

Melampsora pulcherrima Maire, Bull. Soc. Bot. Fr. 21: 159 (1921) (fide Tian and Kakishima 2005).

Melampsora rostrupii G.H. Wagner, Öst. Bot. Z. 46: 274 (1896) (fide Tian and Kakishima 2005).

Morphological features: Spermagonia amphigenous, subepidermal, yellow, 140–150 × 80–100 μm. Aecia hypophyllous, up to 4 mm diam.; aeciospores globoid, ellipsoid or angular, 14–23 × 12–20 μm, wall 1–1.5 μm thick, finely and densely verrucose. Uredinia hypophyllous, minute, 0.3–0.5 mm diam.; urediniospores obovate, ellipsoid or oblong, rarely subgloboid or angular, 17–28 × 12–21 μm, wall 2.5–3 μm thick, verrucose-acute; paraphyses 40–54 × 13–23 μm, capitate, rarely clavate, wall 3–5 μm thick. Telia hypophyllous, subepidermal, minute, 1 mm long; teliospores prismatic, 40–55 × 7–10 μm, wall 1–2 μm thick.

Aecial hosts: *Chelidonium majus*, *Corydalis* spp., *Fumaria officinalis*, *Papaver dubium*.

Telial hosts: *Populus* section *Populus* (*P. alba*, *P. tremula*, *P. x canescens*)

Geographic range: Europe and Russia, doubtful report in China.

Melampsora magnusiana is one of the species included in the *M. populnea* complex. Due to similar urediniospore morphology, *M. magnusiana* has probably been confused with *M. aecidioides* and erroneously reported in China. Tian and Kakishima (2005) suggested a probable synonymy between *M. magnusiana*, *M. rostrupii,* and *M. aecidioides.* Molecular analyses revealed the genetic distinction of *M. aecidioides* (see notes under *M. aecidioides* for details; Feau et al. 2009). Although DNA barcode sequences did not differentiate *M. magnusiana* from *M. rostrupii* but the two are accepted as distinct based on their markedly different aecial host associations, *Papaveraceae* and *Mercurialis perennis* respectively (Pinon 1973; Naldini Longo et al. 1985; Desprez-Loustau 1986; Wagner 1896).

Melampsora medusae Thüm., Bull. Torrey Club 6: 216 (1878). (Fig. 2h)

Literature: Thümen, Bull. Torrey Club 6: 216 (1878); Sydow & Sydow, Monographia uredinearum: 349 (1915); Arthur and Cummins, Manual of the rust in United states and Canada : 51 (1962).

Accepted synonyms: Uredo medusae Arth., Résult. Scient. Congr. Intern. Bot. Vienne: 338 (1905, 1906) (fide Sydow and Sydow 1915).

Melampsora albertensis Arth., Bull. Torrey Bot. Club 6: 216 (1878) (fide Hennen and McCain 1993).

Caeoma pseudotsugae-douglasii Tub., Nat. Z. Forst. Landw. 12: 91 (1914) (fide Arthur and Cummins 1962)

Caeoma faulliana Hunter, J. Arnold Arb. 17: 118 (1936) (fide Ziller 1960).

Rejected synonyms: Caeoma abietis-canadensis Farl., Bull. Torrey Bot. Club 6: 216 (1885) (fide Bagyanarayana 1998).

Melampsora abietis-canadensis C.A. Ludwig ex Arth, N. Am. Flora 7: 664 (1924) (fide Bagyanarayana 1998; Tian and Kakishima 2005).

Melampsora populi-tsugae J.J. Davis, Trans. Wisconsin Acad. 19: 676 (1919) (fide Bagyanarayana 1998).

Peridermium fructigenum Arth., N. Am. Flora 37: 578 (1910) (fide Bagyanarayana 1998).

Morphological features: Spermagonia chiefly epiphyllous, subcuticular, minute, inconspicuous. Aecia hypophyllous, round or oblong, small, yellow when fresh, pulverulent, 0.5–1 mm diam.; aeciospores globoid, 19–26 × 16–21 μm, wall colorless, 2.5–3 μm thick, thickened at the equator. Uredinia hypophyllous, roundish, orange-yellow, 0.3–0.5 mm diam.; urediniospores ellipsoid or obovate-elipsoid, usually flattened laterally, 23–35 × 15–23 μm, wall colorless, smooth, 5–10 μm thick on the flattened sides, 2.5–3 μm thick and sparsely verrucose on the other sides; paraphyses up to 60 × 13–15 μm, wall 3–6 μm thick. Telia hypophyllous, round on both sides, pale reddish brown, subepidermal; teliospores prismatic, 20–45 × 10–15 μm, wall cinnamon brown, 1–1.5 μm thick.

Aecial hosts: *Abies* spp., *Larix* spp., *Picea* spp., *Pinus* spp., *Pseudotsuga* spp.

Telial hosts of *M. medusae* f. sp. *deltoidae*: *Populus* section *Aigeiros* (*P. nigra, P. deltoides, P. x euramericana*), *Populus* section *Tacamahaca* (*P. maximowiczii, P. simonii, P. trichocarpa*).

Telial hosts of *M. medusae* f. sp. *tremuloidae*: *Populus* section *Populus* (*P. tremuloides*).

Geographic range: South Africa, Argentina, Australia, Canada, France, India, Japan, USA.

The urediniospores of this native North American species frequently possess a smooth equatorial spot (Thümen 1878). *Melampsora medusae* was split into two *formae speciales* differing in telial host specialization (Shain 1988).

Melampsora medusae f. sp. *deltoidae* is pathogenic primarily on *Populus deltoides* (section *Aigeiros*), whereas *Melampsora medusae* f. sp. *tremuloidae* is pathogenic primarily on *Populus tremuloides* (section *Populus*) and produces slightly larger urediniospores (Shain 1988; Newcombe 1997). Since the telial hosts of these *formae speciales* belong to two different and intersterile sections of the genus *Populus*, Shain (1988) suggested they might in fact represent two distinct species.

Melampsora microspora Tranzschel & Erem., Conspectus Uredinalium URSS: 155 (1939). (Fig. 2i)

Literature: Tranzschel Conspectus Uredinalium URSS: 155 (1939); Bagyanarayana, Proc. 1st IUFRO Fore. Trees Working Party Conf.: 44 (1998); Pei & Shang, Rust diseases of willow and poplar: 53–56 (2005).

Morphological features: Spermagonia and aecia unknown. Uredinia minute, mostly hypophyllous, occasionally epiphyllous, scattered, often fusing; urediniospores globoid or broadly ellipsoid, 11–17 × 11–13 μm, wall up to 4 μm thick, faintly verrucose, almost smooth; paraphyses clavate to capitate, 60 × up to 15 μm, wall 5 μm thick. Telia mostly hypohyllous, scattered, often fusing, subepidermal, not erumpent, chestnut brown; teliospores 30–68 × 10–13 μm, not thickened apically.

Aecial host: unknown.

Telial hosts: *Populus* section *Aigeiros* (*P. nigra, P. usbekistanica*).

Geographic range: Ex-USSR, Iran, Tajikistan.

This species differs from the others essentially by having small and faintly verrucose urediniospores (Tranzschel 1939; Kuprevich and Tranzschel 1957) (Fig. 2i). The species is apparently rare, recorded only a few times in the former USSR, Iran and Tajikistan (Bagyanarayana 1998; Pei and Shang 2005). *Melampsora microspora* Sawada, described on *Euphorbia tarokaensis* in Taiwan, is an unrelated homonym (Sawada 1943; Commonwealth Mycological Institute 1951–1960).

Melampsora nujiangensis Y.M. Liang, C.M. Tian & Kakish., Mycoscience 47: 200–202 (2006). (Fig. 2j)

Literature: Liang et al., Mycoscience 47: 200–202 (2006);

Morphological features: Spermagonia and aecia unknown. Uredinia hypophyllous, subepidermal, scattered or rarely aggregated in small groups, round or ellipsoid, 0.2–0.8 mm diam., orange-yellow or pale yellow, initially covered by epidermis, later becoming erumpent, pulverulent; urediniospores mostly globoid or, rarely, ovoid, 17–27 × 18–23 μm, wall 1–2 μm thick, echinulate, distance between spines 1–2 μm; paraphyses capitate, 33–56 × 12–15 μm, wall colorless, smooth, 2–6 μm thick. Telia hypophyllous, subepidermal, scattered, minute, yellow to reddish brown when fresh, 0.4–0.8 mm; teliospores prismatic, clavate or cylindrical, 23–44 × 5–12 μm, wall 1 μm thick.

Aecial host: unknown.

Telial hosts: *Populus* section *Tahacamaca* (*Populus yunnanensis*).

Geographic range: China.

Although specimens of this species were initially identified as *M. abietis-populi*, they were later considered to represent a new species (Tian et al. 2004). Based on a molecular phylogenetic analysis of ribosomal DNA sequences, this rust is genetically separated from the other *Melampsora* species. Moreover, the urediniospores are globoid with a thinner cell wall compared to all other species (Liang et al. 2006). *Melampsora nujiangensis* is the most recently described *Melampsora* on poplar and constitutes the first one defined with the aid of molecular phylogeny.

Melampsora occidentalis H.S. Jacks., Phytopathol. 7: 354 (1917). (Fig. 2k)

Literature: Jackson, Phytopathol. 7: 354 (1917); Bagyanarayana, Proc. 1st IUFRO Fore. Trees Working Party Conf.: 44 (1998); Arthur and Cummins, Manual of the rust in United states and Canada : 52 (1962).

Accepted synonyms: *Caeoma occidentalis* Arth., Bull. Torrey Bot. Club 34: 591 (1907) (fide Arthur and Cummins 1962; Bagyanarayana 1998).

Morphological features: Spermagonia subcuticular, on current year's needles on young shoots. Aecia 0.3–1 mm diam., on current year's needles on young shoots; aeciospores globose, subglobose or broadly ellipsoid, 26–35 × 22–27 μm, wall thickened at the equator, verrucose. Uredinia chiefly hypophyllous, round, pulverulent, yellow when fresh; urediniospores broadly ellipsoid, oblong or pyriform, usually flattened laterally, 30–50 × 17–30 μm, wall colorless, 1.5–3 μm thick, thickened up to 8 μm at the equator, prominently echinulate; paraphyses numerous, capitate to clavate, up to 75 × 15–25 μm, up to 6.5 μm thick apically. Telia hypophyllous, subepidermal, minute, orange-brown when fresh; teliospores prismatic, 40–66 × 10–20 μm, wall 1–2 μm thick, apically thickened up to 6 μm, yellow-brown when fresh.

Aecial hosts: *Abies concolor*, *Larix* spp., *Picea sitchensis*, *Pinus* spp.

Telial hosts: *Populus* section *Aigeiros* (*P. nigra*, *P. fremontii*), *Populus* section *Tacamahaca* (*P. trichocarpa*, *P. angustifolia*, *P. balsamifera)*.

Geographic range: Canada, USA.

This species is known only from western North America (Jackson 1917; Ziller 1974). The morphology of its urediniospores is similar to that of *M. larici-populina* but with echinulations at the apex, although similar spinules are observed in rare cases in *M. larici-populina* (Tian and Kakishima 2005). This overlap in morphological features led to a misdetermination and incorrect report of *M. occidentalis* in China (Tian and Kakishima 2005).

Melampsora pinitorqua Rostr., De Farligste Snyltesvampe i Danmarks Skove (Copenhagen): 10 (1889). (Fig. 2l)

Literature: Rostrup, De Farligste Snyltesvampe i Danmarks Skove (Copenhagen): 10 (1889); Sydow & Sydow, Monographia uredinearum: 340 (1915); Pei & Shang, Rust diseases of willow and poplar: 53–56 (2005).

Accepted synonyms: *Caeoma pinitorqum* de Bary, Monatsber. K. Akad. Wiss. Berlin: 264 (1863) (fide Sydow and Sydow 1915).

Melampsora pinitorqum (Rostr.) Hartig, Allg. Forst u. Jadz. 61: 326 (1885) (fide Bagyanarayana 1998).

Melampsora tremulae f. sp. *pinitorqum* Hartig, Lehrb. D. Baumkrankh.: 140 (1889) (fide Bagyanarayana 1998).

Uredo pinitorqua Arth., Résult. Scient. Congr. Intern. Bot. Vienne: 338 (1905, 1906) (fide Sydow and Sydow 1915).

Melampsora populnea (Pers.) P. Karst., Bidr. Känn. Finl. Nat. Folk 31: 53 (1879) (fide Bagyanarayana 1998).

M. populnea f. sp. *pinitorqua* (Hart.) Boerema & Verh., J. Plant Pathol. 78: 82–201 (1972) (fide Bagyanarayana 1998).

Rejected synonym: *Melampsora pruinosae* Tranz., Mycoth. Ross. No 265 (1912) (fide Bagyanarayana 1998).

Morphological features: Spermagonia yellow, 130 × 45 μm. Aecia 20 × 4 mm, pulverulent; aeciospores globoid, subgloboid or ovoid, rarely oblong, 15–22 × 11–17 μm, wall 1.5–2 μm thick, subtly verrucose. Uredinia hypophyllous, 0.3–0.5 mm diam., pulverulent; urediniospores ovoid, rarely subgloboid, 14–23 × 12–16 μm, wall 2 μm thick, thickened up to 6 μm at the equator, acute-verrucose; paraphyses numerous, colorless, clavate-capitate or capitate, 40–60 × 20–25 μm, wall 3–7 μm thick. Telia hypophyllous, subepidermal, minute, 0.5 mm diam., brown; teliospores prismatic irregular, 22–45 × 7–12 μm, wall 1 μm thick.

Aecial hosts: *Pinus* spp.

Telial hosts: *Populus* section *Populus* (*P. alba*, *P. tremula*, *P. x canescens*).

Geographic range: Europe.

Melampsora pinitorqua is one of the species included in the *M. populnea* complex. *Melampsora pinitorqua* is responsible for the pine twisting rust, an important forest disease in Europe causing stem infection on its aecial host (*Pinus* spp.) (Desprez-Loustau 1986; Rostrup 1889). The species was reported in North America on *Pinus ponderosa* seedlings in a British Columbia nursery in the early 1960s (Ziller 1962). Based inoculation experiments, this report was later judged questionable by Molnar and Sivak (Molnar and Sivak 1964), with Ziller himself concurring a few years later (Ziller 1974), and confirmed by a recent DNA barcode study (Feau et al. 2009).

Melampsora pruinosae Tranzschel, Mycoth. Ross. No 265 (1912). (Fig. 2m)

Literature: Tranzschel, Mycoth. Ross. No 265 (1912); Sydow & Sydow, Monographia uredinearum: 345 (1915); Pei & Shang, Rust diseases of willow and poplar: 53–56

(2005); Tian & Kakishima, Rust diseases of willow and poplar: 109–110 (2005).

Rejected synonym: *Melampsora pinitorqua* Rostr., De Farligste Snyltesvampe i Danmarks Skove (Copenhagen): 10 (1889) (fide Bagyanarayana 1998).

Morphological features: Spermagonia and aecia unknown. Uredinia amphigenous; urediniospores subgloboid, ovoid or ellipsoid, 20–28 × 16–18 μm, wall 3–4 μm thick, densely verrucose-echinulate; paraphyses capitate or clavate-capitate, 45–60 × 6–20 μm, wall colorless, 1.5–4 μm thick. Telia amphigenous, subepidermal, minute or moderate, orange-brown; teliospores prismatic, yellow, 40–50 × 10–18 μm.

Aecial host: unknown.

Telial hosts: *Populus* section *Turanga* (*P. euphratica*).

Geographic range: China, Russia.

Urediniospores of this Asian rust are morphologically similar to those of *M. magnusiana* but with smaller and more densely echinulate. Moreover, unlike *M. magnusiana*, under natural conditions, *M. pruinosae* is specific to poplars from section *Turanga* and non-pathogenic on poplars from section *Populus* (Tian and Kakishima 2005).

Melampsora pulcherrima Maire, Bull. Soc. Bot. Fr. 21: 159 (1921). (Fig. 2n)

Literature: Maire, Bull. Soc. Bot. Fr. 21: 159 (1921); Magnani, Pub Ente Naz Cel Carta 5:221–236 (1961); Moriondo et al. Phytopathol Mediterr 28:46–52 (1989); et al., Phytopathol Mediterr 32:129–134 (1993).

Accepted synonyms: *Caoema pulcherrimun* Bub., Saccardo's Syll. Fung. 17: 459 (1905) (fide Saccardo et al. 1905).

Rejected synonyms: *Melampsora rostrupii* G.H. Wagner, öst. Bot. Z. 46: 274 (1896) (fide Bagyanarayana 1998).

Melampsora populnea f. sp. *rostropii* Boerema & Verh., Neth. J. Plant Pathol. 78: 802–201 (1972) (fide Bagyanarayana 1998).

Melampsora magnusiana G.H. Wagner, Öst. Bot. Z., 46: 274 (1896) (fide Tian and Kakishima 2005).

Morphological features: Aecia on stems, rarely on leaves, usually coalescing in linear groups, 2–10 cm long; aeciospores globoid to ellipsoid, 15–28 × 14–23 μm, wall yellowish when mature, densely verrucose. Uredinia minute, 0.8–1 mm, hypophyllous; urediniospores ovoid or subgloboid, rarely oblong, 17–28 × 12–21 μm, wall colorless, 2.5 μm thick, evenly echinulate; paraphyses numerous, clavate-capitate, 35–50 × 18–25 μm, colorless. Telia minute, 0.1–0.8 mm diam., hypophyllous, subepidermal; teliospores sub-prismatic, 25–50 × 6–11 μm.

Aecial host: *Mercurialis annua*.

Telial hosts: *Populus* section *Populus* (*P. alba, P. x canescens*).

Geographic range: Southern Europe (France, Spain, Italy), North Africa (Morocco, Tunisia), West Asia (Lebanon, Palestine).

Melampsora pulcherrima is one of the species included in the *M. populnea* complex. Most authors do not consider *M. pulcherrima* as distinct from *M. rostrupii* due to their similar urediniospore morphology and the close relationship existing between their two aecial hosts, *Mercurialis annua* and *Mercurialis perennis*, respectively (Bagyanarayana 1998; Tian et al. 2004; Pei and Shang 2005; Feau et al. 2009). *Melampsora pulcherrima* was described at the beginning of the 20th century based on its host specificity (alternation between *P. alba* and *M. annua* exclusively) and its geographic distribution restricted to the Mediterranean basin (Maire 1915; Magnani 1961; Moriondo et al. 1989; Naldini et al. 1993). Moreover, this species shows a different pathogenic behavior than the other species included in the *M. populnea* complex, supporting the differentiation of this Mediterranean poplar rust as a species. In fact, *M. pulcherrima* is highly infectious on *P. alba* and its hybrid *P. canescens*, but only light uredinial infection has been observed on *P. tremula* (Moriondo et al. 1989).

Melampsora rostrupii G.H. Wagner, Öst. Bot. Z. 46: 274 (1896).

Literature: Wagner, Öst. Bot. Z. 46: 274 (1896); Sydow & Sydow, Monographia uredinearum: 343 (1915); Pei & Shang, Rust diseases of willow and poplar: 53–56 (2005).

Acepted synonyms: *Uredo confluens* Schum., Enum. Plant. Saell. 2: 227 (1803) (fide Sydow and Sydow 1915).

Uredo circinalis Straus var. *mercurialis* Strauss, Annal. Wetter. 2: 88 (1810) (fide Sydow and Sydow 1915).

Uredo mercurialis Mart., Prodr. Fl. Mosq.: 229 (1812) (fide Sydow and Sydow 1915).

Uredo confluens var. *mercurialis-perennis* DC., Flore Fr. 6:86 (1815) (fide Sydow and Sydow 1915).

Caeoma mercurialis Link., Spec. Plant. 2: 35 (1825) (fide Sydow and Sydow 1915).

Caoema confluens Schlecht., Flo. Berol. 2: 123 (1824) (fide Sydow and Sydow 1915).

Erysibe confluens Wallr., Fl. Crypt. Germ. 2: 201 (1833) (fide Sydow and Sydow 1915).

Melampsora populnea (Pers.) P. Karst., Bidr. Känn. Finl. Nat. Folk 31: 53 (1879) (fide Bagyanarayana 1998).

Caeoma mercurialis-perennis Wint., Pilze Deutschl.: 257 (1881) (fide Sydow and Sydow 1915).

Melampsora mercurialis-tremulae Kleb., Jahrb. F. wissenschaft. Bot. 35: 690 (1901) (fide Sydow and Sydow 1915).

Melampsora populnea f. sp. *rostropii* Boerema & Verh., Neth. J. Plant Pathol. 78: 802–201 (1972) (fide Bagyanarayana 1998).

Rejected synonyms: *Melampsora aecidioides* (DC.) J. Schröt., Krypt.-Fl. Schl.: 362 (1889) (fide Tian and Kakishima 2005).

Melampsora pulcherrima Maire, Bull. Soc. Bot. Fr. 21: 159 (1921) (fide Bagyanarayana 1998).

Morphological features: Spermagonia 200 × 90 μm, yellow or yellow-brown. Aecia hypophyllous, 1–1.5 mm diam., pulverulent; aeciospores globoid, angular-globoid, ellipsoid or ovate, subtly verrucose, 13–24 × 11–17 μm. Uredinia hypophyllous, round, subpulverulent, 1 mm diam.; urediniospores subgloboid, ovate or ellipsoid, 18–25 × 14–18 μm acute-verrucose, wall 2.5–3 μm thick, acute-verrucose; paraphyses capitate, 46–55 × 15–23 μm, wall 3–6 μm thick. Telia hypophyllous, minute, 0.5–1 mm diam., dark brown; teliospores prismatic, round at the apex, 40–52 × 7–11 μm, wall 1–1.5 μm thick.

Aecial host: *Mercurialis perennis*.

Telial hosts: *Populus* section *Populus* (*P. alba*, *P. tremula*, *P.* x *canescens*).

Geographic range: Europe, Russia.

Melampsora rostrupii is one of the species included in the *M. populnea* complex. Tian and Kakishima (2005) considered this species as *nomen nudum* of *M. aecidioides* and suggested synonymies with *M. aecidioides* and *M. magnusiana*. However, *M. aecidioides*, *M. magnusiana* and *M. rostrupii* remain distinct because their aecial-host specificities (see notes under *M. aecidioides* and *M. magnusiana* for details).

Melampsora hybrids described on poplar

Melampsora × medusae-populina Spiers, Mycol. Res. 98: 889–903 (1994). (Fig. 3a)

Literature: Spiers & Hopcroft, Mycol. Res. 98: 889–903 (1994).

Morphological features: Spermagonia and aecia unknown. Uredinia mainly hypophyllous, subepidermal, 150–500 μm diam., golden yellow, pale orange to orange; urediniospores clavate to broadly ellipsoid, some oval to ovate, a few obovate to irregular, apex rounded, base truncated, 25–35 × 12–25 μm, wall 2–10 μm thick, thickened equatorially, uniformly echinulate with both apical and equatorial smooth patches; paraphyses abundant, capitate, pyriform oval to clavate, 18–40 × 12–22 μm, wall 2–12 μm thick. Telia mainly epiphyllous with some hypophyllous, subepidermal, 0-5–2.5 mm; teliospores cylindrical to triangular in side view, circular to angular in cross section, 24–50 × 8–16 μm, wall 1–2.5 μm thick, occasionally slightly thickened at the apex.

Aecial host: unknown.

Telial hosts: *Populus* section *Aigeiros* (*P. deltoides*, *P.* x *euramericana*) and hybrids *Populus* section *Aigeiros* x *Populus* section *Tacamahaca* (*P. deltoides* x *P. yunnanensis*, *P. deltoides* x *P. trichocarpa*, *P. deltoides* x *P. maximowiczii*).

Geographic range: New Zealand and South Africa.

Melampsora × *medusae-populina* shares the morphological and physiological features of both parental species *M. medusae* f. sp. *deltoidae* and *M. larici-populina* (Spiers and Hopcroft 1994; Pei and Shang 2005) (Figs. 2f, h and 3a). Nevertheless, its host range is more typical of *M. medusae* f. sp. *deltoidae* (Spiers and Hopcroft 1994; Spiers 1998). The spermagonial and aecial stages of *M.* × *medusae-populina* are still unknown (Spiers and Hopcroft 1994). Molecular studies (Internal Transcribed Spacer (ITS) of the nuclear ribosomal cistron sequences, RAPD profiles) revealed that *M.* × *medusae-populina* shared alleles from both parental species, supporting the probable homoploid hybrid nature of this taxon (Frey et al. 2005; Pei and Shang 2005). The hybridization between *M. medusae* f. sp. *deltoidae* and *M. larici-populina* is recurrent and the natural hybrid appears occasionally, dying out without producing the next generation (Spiers and Hopcroft 1994; Spiers 1998). Reappearance of the hybrid was reported in South Africa in 1997 (Frey et al. 2005) and again in New Zealand in 1998, in its first reported location (Spiers 1998).

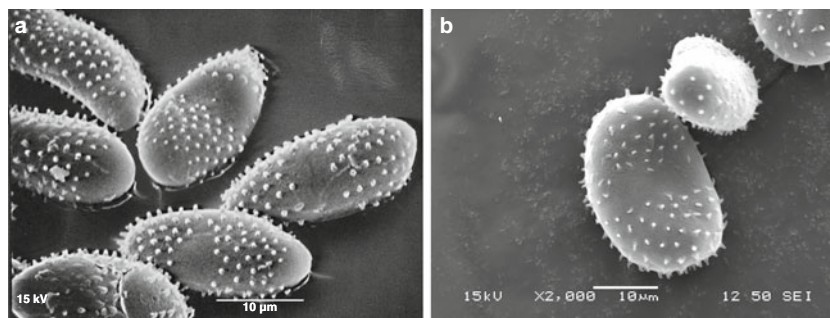**Melampsora × columbiana** G. Newc., Mycol. Res. 104: 271 (2000). (Fig. 3b)

Fig. 3 Urediniospores of *Melampsora* hybrids from dry herbarium specimens. **a**: *M.* x *medusae-populina* specimen 97G13: South Africa, on *Populus* x *euramericana* '65-29', May 1997, Mark Laing, P. Frey, personal collection. Scanning Electron Microscopy (SEM) pictures taken at the Forest Ecology and Ecophysiology Microscopy platform (http://www4.nancy.inra.fr/eef_eng/), INRA Nancy, France, with a Stereoscan 90B scanning electron microscope (Cambridge Instrument, Cambridge, UK); **b**: *M.* x *columbiana* specimen MxC06UBC03: Canada, British Columbia, on *Populus* sp., summer 2006, culture collection of R. Hamelin. Scanning Electron Microscopy (SEM) pictures taken at IBIS Microscopy and Histology Unit (http://www.rsvs.ulaval.ca), QC, Canada, with a JEOL JSM 6360LV microscope, 2000x magnification

Literature: Newcombe et al., Mycol. Res. 104: 271 (2000); Newcombe et al., Ecol. Pop. Biol. 91: 981–985 (2001).

Morphological features: Spermagonia and aecia unknown. Uredinia mainly hypophyllous, occasionally epiphyllous; urediniospores 29–38 μm long, wall echinulate with spine density 0.11–0.20 spines/μm², equatorial smooth spot on 1–84 in a single plane of focus. Teliospores 40–53 μm long.

Aecial host: unknown.

Telial hosts: *Populus* section *Aigeiros* (*P. deltoides*), *Populus* section *Tacahamaca* (*P. trichocarpa*) and hybrid *P. trichocarpa* x *P. deltoides*.

Geographic range: Northwestern America.

This hybrid presents intermediate morphological characteristics between *M. medusae* f. sp. *deltoidae* and *M. occidentalis* in uredinial and telial morphology (Newcombe et al. 2000; 2001) (Figs. 2h, k and 3b). The hybrid's host range combines both parental species (*M. medusae* f. sp. *deltoidae* and *M. occidentalis*) host ranges with a particular adaptation in pathogenicity to the hybrid poplars *Populus trichocarpa* × *P. deltoides* (Newcombe et al. 2000; 2001; Frey et al. 2005). Examination of old herbarium specimens from the early 20th century suggests the earlier appearance and wide distribution of this hybrid in North America (Newcombe et al. 2000). Newcombe et al. (2000) noticed either the presence of ITS DNA sequence copies from both parental species or from only one of them. Based on these results, Newcombe et al. (2000) proposed that this hybrid could have produced further generations through sexual cycling such as an F2 or backcrosses. However, since the ITS amplicons of *M. × columbiana* were not cloned in order to quantify the proportion of each parental ITS copy, this hypothesis seems very speculative (Newcombe 2000, pers. comm. to P. Frey). In order to properly assess introgression in these hybrids, additional markers should be characterized in the parental species and the putative hybrids.

Melampsora poplar rust species considered as *nomina dubia*

During this study conducted to review *Melampsora* poplar rust species, we were unable to find specimens identified as *Melampsora cumminsii* Bagyan. & Ramachar, *Melampsora multa* Y.Z. Shang, M.H. Pei & Z.W. Yuan, and *Melampsora osmaniensis* Bagyan. & Ramachar. These three species were each reported once and, to date, only herbarium type (holotype and/or isotype) specimens have been recorded under these species names, which cannot now be found. According to the different herbarium curators and/or the authors of the species description, specimens may have been lost, misplaced or never returned after loan (D. Pfister

& G. Lewis from Harvard University Herbarium, 2009, pers. comm. to A. Vialle; G. Thijsse from Herbarium of NHM Leiden, 2009, pers. comm. to A. Vialle; and M. Pei, 2009, pers. comm. to A. Vialle). Due to the lack of other recorded specimens under these species names and the disappearance of the nomenclatural types, they must be considered as *nomina dubia* (doubtful names). This designation, allowed under the International Commission on Zoological Nomenclature, is applied when the original type series (i.e. holotype and paratype) are lost or destroyed. A *nomen dubium* is not invalid, in the way a *nomen nudum* is, and is still available for consideration in terms of synonymy and/or homonymy (International Commission on Zoological Nomenclature 1999). However, in the case of a *nomen dubium*, it may be impossible to determine whether a new specimen belongs to that species or not due to the lack of original type material for comparison. Thus, unless the types are located, they should be replaced by neotypes (i.e. new type specimens; McNeill et al. 2006) before these species are considered in further studies.

Melampsora cumminsii Bagyan. & Ramacha, Curr. Sci. 53: 863 (1984). *Nomen dubium*.

Literature: Bagyanarayana & Ramachar, Curr. Sc. 53: 863 (1984); Bagyanarayana, Proc. 1st IUFRO Fore. Trees Working Party Conf.: 40 (1998).

Morphological features: Spermagonia and aecia unknown. Uredinia minute, hypophyllous, scattered, subepidermal, erumpent, pulverulent, up to 0.2 mm, orange-yellow; urediniospores globose, subglobose, ovate to ellipsoid, 21–32 × 12.5–21 μm, wall 1.5–2 μm, echinulate; paraphyse clavate to spatulate, up to 45 × 10–20 μm. Telia minute, hypophyllous, dense, very closely aggregated, subepidermal, not erumpent, 0.3 mm diam., dark cinnamon-brown; teliospores 24–40 × 8–16 μm, cylindraceo-prismatic, wall 1.5–2 μm thick, the corners are prominently thickened apically up to 3–5 μm, brown.

Aecial host: unknown.

Telial hosts: *Populus* sp. (not specified).

Geographic range: USA.

Described in 1984 and included in a taxonomic study reviewed by Bagyanarayana in 1998, the specimen originally found in the United States of America exhibited conspicuously thickened apical corners of the teliospore wall (Bagyanarayana and Ramachar 1984; Bagyanarayana 1998). This feature was reported as species-specific by the authors, but since the original description of the type specimen, this species has never been reported again.

Melampsora multa Y.Z. Shang, M.H. Pei & Z.W. Yuan, Acta Mycol. Sinica, supp. 1: 180 (1986). *Nomen dubium*.

Literature: Shang, Pei & Yuan, Acta Mycol. Sinica, supp. 1: 180 (1986); Pei & Shang, Rust diseases of willow and poplar: 53–56 (2005); Tian & Kakishima, Rust diseases of willow and poplar: 108–109 (2005).

Morphological features: Spermagonia and aecia unknown. Uredinia hypophyllous, subepidermal, scattered, round or ellipsoid, golden yellow, 0.2–0.4 mm diam.; urediniospores mainly ellipsoid, oblong or obovate, 26–44 × 16–25 μm, wall echinulate, smooth at the apex; paraphyse clavate or capitate, 42–62 × 16–25 μm, wall 8–16 μm thick. Telia amphigenous, subepidermal, scattered or aggregated, 0.3–0.8 mm diam., yellow-brown; teliospores prismatic, round at both ends, 30–45 × 6.5–13 μm, wall pale brown, 1 μm thick.

Aecial host: unknown.

Telial hosts: *Populus* section *Aigeiros* (*P.* x *euramericana*).

Geographic range: China.

This species from China is similar to *M. larici-populina*, but with hypophylous telia and larger teliospores. As several attempts to inoculate *Larix* spp., *Picea* spp., *Pinus* spp. and *Sabina* spp. failed (Shang et al. 1986), the aecial host of this species is still unknown. Apart from type and isotype herbarium specimens retrieved in 1985, Chinese mycologists have failed to find other specimens (M. Pei, 2009, pers. comm.). Recent examination of the isotype of *M. multa* suggests synonymy with *M. larici-populina* due to their similarity in telium morphology (Tian and Kakishima 2005).

Melampsora osmaniensis Bagyan. & Ramachar, Curr. Sci. 53: 863 (1984). *Nomen dubium*.

Literature: Bagyanarayana & Ramachar, Curr. Sc. 53: 863–864 (1984); Bagyanarayana, Proc. 1st IUFRO Fore. Trees Working Party Conf.: 45 (1998).

Morphological features: Spermagonia and aecia unknown. Uredinia hypophyllous, dense, scattered over the entire leaf, subepidermal, erumpent, pulverulent, but sometimes the epidermis is intact, 0.5–1 mm diam., pale orange; urediniospores ellipsoid, obovate to pyriform, 28–48 × 11–21 μm, wall 1–1.6 μm thick, thickened on both sides, echinulate; paraphyses numerous, clavate to capitate, up to 60 × 15–25 μm. Telia minute, epiphyllous, scattered, subepidermal. Not erumpent, up to 0.3 mm diam., orange-brown to cinnamon-brown; teliospores cylindrical, round at both ends, 17.5–31.5 × 8–13 μm, wall 1 μm thick, pale brown.

Aecial host: unknown.

Telial hosts: *Populus* section *Populus* (*P. sieboldii*).

Geographic range: Germany.

Described at the same time as *M. cumminsii*, this species is similar in urediniospore morphology to *M. larici-populina*, but produces smaller teliospores (Bagyanarayana and Ramachar 1984; Bagyanarayana 1998). Like *M. cumminsii*, this species has never been reported again since its original description.

Incomplete life cycles and arguable synonyms: contributions to an obscure taxonomy

In this review, we present a list of accepted poplar rust species from across the world that we judge exhaustive.

Three of them (*M. cumminsii*, *M. multa* and *M. osmaniensis*) are considered as *nomina dubia*. Moreover, several species, such as *M. castellana*, *M. ciliata*, *M. microspora*, *M. nujiangensis* and *M. pruinosae*, were recorded very few times and described only on the basis of morphological differences in the uredinial and telial stages. Little is known about their occurrence, their life cycles or their phylogenetic relationships with other poplar rusts. Thus, they may be occasional natural variants, which have complicated poplar rust taxonomy.

Confusion in species morphology has led to the reduction of some species names to arguable synonyms or to erroneous reports of *Melampsora* species on poplar throughout the world. The classification of morphologically similar, but ecologically dissimilar, poplar rust taxa has been debated for more than a century (Klebahn 1899; Klebahn 1902; Arthur 1903; Fraser 1912; Arthur and Cummins 1962; Dupias 1965; Wilson and Henderson 1966; Ziller 1974; Naldini Longo et al. 1985; Desprez-Loustau 1986; Shain 1988; Dai 1989; Frey and Pinon 1997; Bagyanarayana 1998; Pei and Shang 2005; Tian and Kakishima 2005; Feau et al. 2009). However, the host specificity of *Melampsora* poplar rust species (telial and aecial host ranges) remains an undeniable attribute of the *Melampsora* life cycle (and rust fungi in general), and should be an essential component of their recognition and classification. Laboratory experiments and/or overlapping host ranges have led to some misidentifications and incorrect synonymies. For example, similar morphology and successful infection obtained from *M. abietis-canadensis* on *Larix* spp. suggested this rust species might be considered a form of *M. medusae* (Arthur and Cummins 1962). A few decades later, *M. abietis-canadensis* was reduced in synonymy with *M. medusae* (Bagyanarayana 1998; Pei and Shang 2005; Tian and Kakishima 2005). However, a molecular study based on ITS barcode sequences reestablished the status of *M. abietis-canadensis* as distinct from *M. medusae* due to its unique barcode sequence (Feau et al. 2009).

Even when considering morphological characteristics in conjunction with host ranges, the taxonomy of *Melampsora* poplar rust species remains unclear. The classification history of these species follows a succession of new names and descriptions with little consideration of previously described taxa. Any reflection of evolutionary relationships among species was undeniably absent. However, recent analyses integrating molecular data have laid out the foundations for a more meaningful classification (Tian et al. 2004; Tian and Kakishima 2005; Feau et al. 2009). Unfortunately, none of these studies considered all described *Melampsora* poplar rust species. In our opinion, taking into account their evolutionary and genetic relationships is essential for defining natural groups, to revise and clarify poplar rust taxonomy in a systematics context. Today, recent advances in molecular methods and the growing availability

of genetic data for a broad range of rusts make this type of comprehensive revision possible.

Recent developments in *Melampsora* systematics: the contribution of molecular taxonomy

Phylogenetic relationships and molecular taxonomy in fungi

The molecular revolution in fungal taxonomy began in the early 1990s with analyses of PCR-amplified ribosomal RNA genes (Bruns et al. 1991). The evaluation of phylogenetic relationships among taxa may be affected by the taxonomic level considered, the molecular methods and the genetic regions targeted (White et al. 1990; Bruns et al. 1991). Today, fungal molecular systematics is a mature discipline in which multi-locus datasets, extensive taxon sampling, and rigorous analytical approaches are standard. Global kingdom-level phylogenies have been initiated to understand the early evolution of fungi resulting in an important reorganization at the highest level of fungal classification (Lutzoni et al. 2004; James et al. 2006; Hibbett et al. 2007; Matheny et al. 2007). *Ascomycota* and *Basidiomycota* are now classified in a sub-kingdom called *Dikarya*, and major changes have occurred in the classification of the fungi formerly known as *Zygomycota* and *Chrytridiomycota*, now recognized as polyphyletic phyla (Lutzoni et al. 2004; James et al. 2006; Hibbett et al. 2007; Shenoy et al. 2007).

Molecular phylogenetic studies have also focused on rust fungi. At the higher levels (class, order and genus), phylogenetic relationships have been inferred using the nuclear small subunit of ribosomal DNA (SSU) and the nuclear large subunit of ribosomal DNA (LSU) (Maier et al. 2003; Wingfield et al. 2004; Aime 2006; Aime et al. 2006). Phylogenetic analyses indicated a strong correlation between clades and host specificities, underlining the importance of this feature in the natural classification of rust fungi (Aime 2006; Kolmer et al. 2009). All these studies considered *Melampsora* as the only genus in a monophyletic *Melampsoraceae*. This classification concurs with the 13-family system proposed by Cummins and Hiratsuka (2003) based on morphological and biological features.

At the species level, studies of the ITS sequences provided clarification of relationships among closely related species in different rust groups such as the *Phakospora*, *Puccinia*, *Uromyces* and *Cronartium* genera (Zambino and Szabo 1993; Kropp et al. 1997; Roy et al. 1998; Vogler and Bruns 1998; Pfunder et al. 2001; Chatasiri and Ono 2008; Alaei et al. 2009; Liu and Hambleton 2010). Unfortunately, few molecular studies have focused exclusively on *Melampsora* spp. (Nakamura et al. 1998; Frey et al. 1999; Tian et al. 2004; Frey et al. 2005; Pei et al. 2005), and thus little is known about phylogenetic relationships among *Melampsora* species. A global effort to morphologically and molecularly characterize *Melampsora* rusts occurring on poplars in China was attempted (Tian et al. 2004). Based on the ITS regions, Tian et al. (2004) compared morphological/taxonomic groups with the molecular phylogenetic clades and suggested the following taxonomic changes: i) recognition of a new species *M. nujiangensis*, based on its phylogenetically distinct profile (Tian et al. 2004; Liang et al. 2006); and ii) the probable synonymy between *M. aecidioides*, *M. magnusiana* and *M. rostrupii* (Tian et al. 2004). However, that study only included specimens from *Populus* spp. and did not include any from the recorded aecial hosts, an essential criterion for species identification among members of the *M. populnea* complex. A recent ITS and LSU DNA barcode study emphasized the probability of misidentifications of specimens of *M. magnusiana* and *M. rostrupii* from China, highlighting a general problem regarding herbarium specimen misdeterminations (Feau et al. 2009). Although DNA barcoding aims to complement existing taxonomies and is not appropriate for delimiting new species or assessing synonymy (Hebert et al. 2003; Hebert and Gregory 2005), these two recent molecular studies underscored the unclear boundaries of described *Melampsora* species found on poplar and the need for a revision of the genus.

Species concepts, species criteria and *Melampsora* species definition

A number of species concepts have been defined, the Morphological Species Concept, Biological Species Concept, Ecological Species Concept, and Phylogenetic Species Concept. This review does not aim to launch a debate about these concepts, but in general there seems to be some convergence toward a useful species definition: species correspond to a sub-group within an evolutionary lineage that has evolved independently from other sub-groups (De Queiroz 2007; Giraud et al. 2008). Other concepts, the so-called secondary species criteria, emphasized different events that occur during the separation and divergence of these lineages: morphological divergence, reproductive isolation, adaptation to a particular ecological niche, and nucleotide divergence (Taylor et al. 2000; De Queiroz 2007; Giraud et al. 2008). In general, the phylogenetic species criterion performs best to identify independent evolutionary lineages because changes in gene sequences can be recognized before resulting changes in mating and ecological behaviors or in morphology (Taylor et al. 2000). Thus, during the last decade, many cryptic species have been defined within fungal morphological species using this secondary species criterion. Today, the most widely used method for molecular taxonomic revision is the Genealogical Concor-

dance Phylogenetic Species Recognition (GCPSR) developed by Taylor et al. (2000) and derived from the Phylogenetic Species Concept. GCPSR uses the concordance of several unlinked gene genealogies to identify evolutionary independent lineages (Taylor et al. 2000). This method applied to understanding relationships among fungal taxa has proven to be immensely useful due to its discriminating power and the convenience with which it can be applied (Dettman et al. 2003; Sites and Marshall 2004; Le Gac et al. 2007; Shenoy et al. 2007; Giraud et al. 2008; Peterson 2008).

Except for the recent study of the Asian grapevine leaf rust (*Phakopsora euvitis* Y. Ono) and its allies (Chatasiri and Ono 2008), investigations of cryptic rust taxa at the species level have yet to be conducted using multiple gene genealogies concordance. A few studies on heteroecious rust fungi, based generally on ITS phylogenetic trees, have shown correspondence between molecular clades and species circumscribed by morphology (Ono 2000; Pfunder M, Schürch S, Roy BA 2001), by life cycle and/or host specificity (Chatasiri et al. 2006; Szabo 2006; Alaei et al. 2009; Liu and Hambleton 2010), or by none of the previously emphasized taxonomic characters (Roy et al. 1998). However, probably due to the difficulty in obtaining reliably identified specimens of these unculturable fungi and because genetic data were not available in the past, GCPSR has not been applied to *Melampsora* species. Implementation of the Phylogenetic Species Concept through the GCPSR method for species described on poplar will result in a clarification and consensus of *Melampsora* species concepts. Besides providing robust phylogenetic frameworks for understanding their evolution, GCPSR will help identify evolutionary independent lineages within this group. Thus, species boundaries could be determined in spite of a lack of other taxonomic features (Taylor et al. 2000). Such work will undoubtedly help to clarify recurrent taxonomic questions such as host-specific species within the *M. populnea* and *M. medusae* complexes, dispel the synonymy conflicts and affirm (or not) the distinction of species described with incomplete life cycles such as *M. castellana*, *M. ciliata*, *M. microspora*, *M. nujiangensis* and *M. pruinosae*.

Obviously, applying GCPSR to *Melampsora* will bring significant clarification compared with the current situation. However, even if molecular characters provide the greatest number of variable features for fungal taxonomy and are unquestionably an indispensable part of fungal systematics, there is no sole criterion (morphological, ecological or phylogenetic) that works flawlessly to recognize and delimit species. A consensual species definition must be proposed and applied to *Melampsora* species. To avoid the continuing proliferation of potential synonyms and further complication of the current taxonomy, revisions should be undertaken with a polyphasic approach (Vandamme et al.

1996), including morphological, ecological (host specificity) and phylogenetic data. Such an approach would make possible the construction of a meaningful classification. The consensual classification should result in a synthesis with a minimum of contradictions (Samson and Varga 2009) between all available characters. This approach has already been applied to diverse fungal groups and has resulted in extremely robust species definitions for *Aspergillus* spp., *Cryptococcus* spp., and *Fusarium* spp. (Nirenberg and O'Donnell 1998; Montes et al. 1999; Yli-Mattila et al. 2002; Zeller et al. 2003; Samson and Varga 2009). To conclude, the description of new species of *Melampsora* with incomplete life cycles or based solely on minor morphological differences has probably resulted in more than one name for individual taxa and must be avoided in the future. In contrast, the reticulate nature of traditional taxonomic characters used for the delineation of *Melampsora* species may also have led to the underestimation of the real diversity of *Melampsora* species on poplar all over the world. Thus, we recommend that in addition to morphological descriptions, host range and life cycle features, any new *Melampsora* species proposed must show evidence of evolutionary divergence based on analyses of multilocus sequence data.

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